Pollination of 'Sundrop' Apricot

An Analysis of the effect of Self Incompatibility and Bloom Phenology on Fruit Set in Hawkes Bay

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To Mum who got me started,
Rosalind who kept me going,
and Charlotte who saw me finish.

For everything there is a season and a time for every purpose under heaven...
Ecclesiastes 3:1

Abstract

A range of observational, experimental and simulated data are analysed to discover how self incompatibility, relative bloom phenology and dormancy alleviation affect fruit set on 'Sundrop' apricot in Hawkes Bay. The derivation of two mathematical models, one of cross pollination, the other of bud development, provides a unifying theme to the study.

Controlled pollination experiments demonstrated that 'Sundrop' displays gametophytic self incompatibility. Pollen tubes from 'Sundrop' pollen generally fail to penetrate styles of 'Sundrop' flowers and this prevents fruit set under Hawkes Bay conditions. Study of apricot pollen tube growth at five constant temperatures between 5° and 25°C suggested that the penetration failure was not due to adverse temperature conditions since self pollen tube penetration was strongest at 10° and 15°C, temperatures typical of Hawkes Bay during apricot bloom. Field observations of honey bee foragers illustrated the strong influence that weather conditions have on honey bee foraging activity, but showed that activity on 'Sundrop' flowers is normally sufficient to achieve satisfactory cross pollination.

Analysis of bloom records indicated that relative times of bloom of apricots in Hawkes Bay and other North Island sites vary considerably from year to year. A simple model of pollenizer pollen transfer was therefore derived to estimate the optimum pollenizer bloom divergence for 'Sundrop'. It indicated 'Sundrop' should bloom slightly before (1-2 days) a pollenizer. Optimum divergence was most sensitive to the durations of pollen release and floral receptivity. Delayed pollination experiments showed that the duration of receptivity of 'Sundrop' flowers was the same as petal lifespan. Significant opportunity for cross pollination was still predicted when the pollenizer bloomed as late as six days after 'Sundrop'. By this criteria, 'Trevatt' (the most commonly-used pollenizer) appeared satisfactory under most, though not all, conditions.

The pollen transfer model indicated that relative bloom phenology needed consideration for selection of pollenizers for 'Sundrop'. However, the 'Utah' chill unit index was a poor predictor of dormancy alleviation and bloom for apricots under Hawkes Bay conditions. Hence, a model of low temperature-mediated alleviation of dormancy incorporating a progressive shift in bud temperature response was established based on an analysis of dormancy as the depression of a 'thermal response window' and chilling as a twofold seasonal signal controlling window size. Initial evaluation confirmed that the resulting PHYSHIFT model was highly flexible and could reproduce many of the responses that dormant buds of *Prunus* species display to constant and cyclic temperature regimes. Hence, the results suggest that the PHYSHIFT model may offer more reliable prediction of relative bloom timing for the purpose of pollenizer selection than chill unit models.

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1.1   Project Background

1.1.1   Significance of the Hawkes Bay Apricot Industry

New Zealand's established apricot industry lies in the South Island, centred in an area of Central Otago surrounding Alexandra, Roxburgh and Cromwell. Detailed recent statistics describing the apricot industry are lacking but in 1983 the area held almost 75% of New Zealand's total apricot orchard area of 630 ha which together produced over 7400 tonnes of apricots (Wilton, 1984). The total area had risen to 854 ha in 1990 and is predicted to rise to 950 ha by 2000 (Foundation for Research, Science and Technology, 1993). This is still very small on a world scale. Though the New Zealand industry represents about 10% of Southern Hemisphere production, almost two-thirds of the world's apricots are produced in the Mediterranean area. Turkey, Italy, Spain, Greece and France together accounted for nearly half the 1.86 million tonnes of apricots produced in 1986 (de Stefano and Rotundo, 1991). New Zealand's annual harvest of about 10,000 tonnes therefore represented only 0.5% of the world total at that time. However, the short storage life of fresh apricots means there is no seasonal overlap with the Northern Hemisphere. The out-of-season market in areas such as the Middle East, Asia and western North America therefore represents a major potential export market.

The volume of apricots exported increased sharply in the late 1980's. In 1987/88, exports were under 200 tonnes, reached 849 t in 1990/91 and peaked at 1137 t in 1993/94 (New Zealand Summerfruit Export Council, 1994). This represented about five percent of the total crop in that year. Volume to March 1995 was 958 t, down slightly on 1991/92 and 1993/94. The value of exports reached $4.3M in 1991/92 and is expected to reach $4.0M for 1994/95. The proportion of summerfruit exports represented by apricots has also risen. In 1988/89 apricots made up 20% of exports whereas they accounted for 49% in 1993/94, partly because of lower exports of cherries and nectarines due to adverse weather conditions (New Zealand Summerfruit Export Council, 1994). Apricots are exported fresh mainly to Australia, reflecting the time difference in production in the two

countries, but increasing competition is directing attention to other markets. In 1990/91, Australia received 760 tonnes of fruit, 90% of exports and in 1994/95 641 tonnes or 67% of exports (New Zealand Summerfruit Export Council, 1994). The west coast of North America received most of the remainder , the volume rising from 50 t in 1990/91 to 249 t in 1994/95. Asia and the Middle East remain largely untapped as export markets.

In 1983, the Hawkes Bay region in the North Island contributed only 7% of total apricot area in New Zealand (Wilton, 1984). This proportion has probably increased slightly since then but the real significance of the Hawkes Bay apricot industry lies in its location. Proximity to Auckland (New Zealand's main market) constitutes a major domestic commercial advantage. Two thirds of apricots in New Zealand are consumed fresh as are about one half of the worlds' production (de Stefano and Rotundo, 1991). Rapid access to markets is therefore vital. Hawkes Bay's advantage is aided by relatively early fruit maturation which allows shipment of significant quantities of apricots prior to Christmas and before the arrival of South Island apricots. Hawkes Bay orchards are also directly adjacent to an international seaport (Napier) and within hours of Auckland airport, the main New Zealand gateway for international air-freight. Hawkes Bay therefore appears well positioned to produce fresh apricots for domestic consumption and for export.

1.1.2   Unreliable Fruit Set on 'Sundrop' Apricot

The promise of Hawkes Bay apricot production is marred by reports of unreliable cropping due to poor fruit set on 'Sundrop', a relatively new cultivar which dominated commercial plantings in Hawkes Bay made in the 1980's. Before this time, the New Zealand apricot industry was based on long-established cultivars. In 1958, 'Moorpark' represented 55% of all trees while 'Newcastle' and 'Roxburgh Red' made up another 27% (Coombe and Watts, 1962). Over 50 other cultivars were grown, including 'Trevatt', 'Oullins Early Peach', 'Dundonald' and 'Bolton', but no variety except 'Moorpark' was of outstanding quality. A report in 1974 suggested that 'Roxburgh Red' was actually responsible for depressing demand for apricots (Ministry of Agriculture and Fisheries, 1974). This has now changed due to the arrival of North American cultivars such as 'Sundrop', 'Royal Rosa' and 'Goldrich' in the 1970's (Glucina and Logan, 1983), the continued introduction of overseas selections and the recent release of New Zealand-bred cultivars. 'Sundrop' and 'CluthaGold' both produce clean, attractive fruit with average to good flavour, size and texture. 'Sundrop' fruit have a moderate storage life but those of

'CluthaGold' and 'Goldrich' store well (Glucina et al., 1988; 1990). These cultivars, which are now grown in Hawkes Bay, therefore produce fruit suitable for export.

The problem of poor yields on 'Sundrop' is not restricted to Hawkes Bay but is also observed in Marlborough (Gilchrist, 1990) and Central Otago (McLaren, Fraser and Grant, 1992). Nor are unreliable yields and limited profitability of apricots unusual. Apricots bloom very early in spring and are therefore susceptible to damage by spring frosts and to climate-related diseases such as blast (*Pseudomonas syringae*). Together these factors cause dramatic fluctuations in annual production and volatile financial returns. In Central Europe, large-scale crop loss due to frost is common (Djuric, 1982; Tamássy and Zayan, 1982). In the Mediterranean region, poor yields from certain cultivars are observed in coastal areas similar to Hawkes Bay which, again, have been blamed on climate (Guerriero and Bartolini, 1991; Legave, 1978). In North America, apricot production has declined substantially in recent decades, particularly in marginal regions. In British Columbia, the area declined from 810 ha in 1954-55 to 200 ha in 1980. Production in Washington State dropped over the same period from a peak of 21,150 t in the 1940's to only 2,600 t in 1979 (Ramming, 1980). By comparison, orchard area in California (the major North American production region which produced 141,000 t of apricots in 1977), only declined from 14,600 ha in 1965 to 11,100 ha in 1980.

However, the production risk due to climatic conditions before, during and after bloom is probably exacerbated by the need for cross pollination on 'Sundrop' (Lane, 1978; Wood, 1983). 'Sundrop' is an open-pollinated seedling of 'Perfection', a cultivar known to require cross pollination (Schultz, 1948). Pollen transfer from suitable pollenizers is therefore needed and this issue has been under study in Central Otago (McLaren, Fraser and Grant, 1992). However, apricots are distinctive in that most cultivars have limited ecological adaptation and often can be grown successfully in only one region (Mehlenbacher et al., 1991). Research based in Hawkes Bay therefore complements investigations in other locations. Cross pollination is also needed by 'Goldrich' (Fogle and Toyama, 1972), by 'CluthaGold' (Glucina et al., 1988), and by other New Zealand-bred cultivars (McLaren, Lewis and Glucina, 1992). Hence, measures identified to minimise the risk to fruit set and crop yields on 'Sundrop' may prove relevant for other newly-introduced cultivars in Hawkes Bay and in other apricot growing regions.

1.2   Apricot Pollination and Fruit Set

1.2.1   Reproductive Development of *Prunus* Species

1.2.1.1   Flower bud initiation and development

Apricots (*Prunus armeniaca* L.) belong to the large genus *Prunus* (Rosaceae) together with other stonefruit such as plums, peaches, almonds and cherries. In this genus, bloom occurs once each year in spring and fruit typically mature from early to mid summer. Most flower buds are borne laterally on spurs or short shoots intermixed with vegetative buds (Gur, 1985). Flower buds are also borne on vigorous shoots, particularly in peach, but also apricot. Histological differentiation associated with flower initiation occurs after bud break and continues in the newly formed axil as shoots elongate (Dorsey, 1936). Differentiation of floral parts begins after cessation of bud scale formation in early summer and extends beyond harvest, particularly on more vigorous shoots. Differences in timing between cultivars may be more marked than differences between species (Gur, 1985). In apricots temperatures of up to 30.5°C benefit initiation (Jackson, 1970) but in other *Prunus* species high temperatures may cause floral abnormalities. Differentiation is acropetal and culminates in the formation of sporogenous tissue in ovules and anthers by early autumn (Brooks, 1940). Over-wintering flower buds therefore contain all floral parts except mature gametophytes.

Under very low temperature winter conditions, floral development ceases completely (Gur, 1985). Where winter conditions are mild, differentiation of sporogenous tissues continues slowly until dormancy is lifted (Chandler and Tufts, 1934; Erez and Lavee, 1971; Viti and Monteleone, 1991). Formation of apricot pollen mother cells occurs in early winter but can vary between cultivars and years by up to one month (Nyútjó et al., 1982). Tetrads appear about the time of first bud movement and formation of first single then binucleate grains occurs as the flower bud expands (Nyútjó et al., 1982; Viti and Monteleone, 1991). Ripened apricot pollen is ovate, with three apertures (Szujkó-Lacza, 1985) and is binucleate when released, containing the vegetative nucleus and generative cell only (Brewbaker, 1967). Megagametophyte development coincides with that of pollen. The megasporocyte appears in the nucellus epidermal layer and produces an

embryo sac of *Polygonum* type (Szujkó-Lacza, 1985). At anthesis, some apricot flowers contain functional egg cells (Eaton and Jamont, 1965). However, in almond, the presence of compatible pollen tubes in the ovary promotes final maturation (Pimienta et al., 1983). Various disorders of floral development are observed: apistilly and twin pistils (Socías i Company, 1983), stylar malformation (Guerriero et al., 1985c) and complete bud necrosis or abscision. These appear to be related, at least in part, to warm winter temperatures which inhibit normal flower bud development (Brown, 1952; Legave, et al., 1982).

1.2.1.2   Floral morphology

Apricot flowers are bisexual, pentamerous, actinomorphic and are borne on a short pedicel. The bottom two-thirds of the calyx is fused with the petals and with the filament bases to form a green to deep red cup-shaped structure, the interior of which is the site of an orange-red nectiferous area (Szujkó-Lacza, 1985). Calyx 'teeth' initially cover the petals within the bud, but on opening they recurve fully. Petals are compressed tightly in the bud and are typically light pink on opening, gradually bleaching to white as the petals age. In this respect 'Sundrop' is distinctive for the strong pink coloration of its petals. Each apricot flower usually contains about 30 stamens arranged spirally around the corolla cup. However, the number of stamens can vary greatly (Szujkó-Lacza, 1985) and is commonly higher in self incompatible cultivars (Surányi, 1976). Stamens comprise a filament 10-15 mm long and anthers with two separate locules. Dehiscence begins with the smaller, inner stamens and proceeds to the larger, outer anthers.

Stigmas of *Prunus* flowers are of the 'wet' type (Heslop-Harrison and Shivanna, 1977), the interstitial spaces between papillae filling with a secreted fluid immediately prior to anthesis (Cresti et al., 1985; Uwate and Lin, 1981). The volume increases as flowers open and as papillae cells degenerate with the result that secretions flood interstices in receptive flowers. Styles are enclosed, solid and traversed by a core of transmitting tissue through which pollen tubes penetrate intercellularly. Transmitting tissue cells have thin transverse walls with abundant plasmodesmata and provide nutrients for heterotrophic growth of pollen tubes (Shivanna, 1982). The cells are separated from one another and surrounded with fluid-like intercellular substance within which pollen tubes grow. The end of the transmitting tissue in marked by the obdurator, a papillate mound of tissue on the ovary wall, facing the micropyle (Sterling, 1964). In peach, secretion by the

obdurator appears coordinated with ovule development and therefore possibly controls access of pollen tubes to the ovule (Arbeloa and Herrero, 1987). Two fused integuments that separate only at the micropyle surround a large multicellular nucellus within each of the two ovules. These are attached, one to each carpellary margin, high on the ovary wall with the micropyle directed toward the style (Sterling, 1964). In most flowers, one ovule predominates at the expense of the smaller ovule which may have aborted by anthesis. Fertilization occurs after a pollen tube penetrates the micropyle and results in a zygote and triploid primary endosperm cell. Early embryo growth is spherical, supported by several suspensor cells, in association with free endosperm nuclei and a large central vacuole (Szujkó-Lacza, 1985). Subsequent cell wall formation and cell division results in formation of secondary endosperm tissue which initially grows with the embryo and nucellus. However, from pit-hardening the embryo expands at the expense of endosperm, nucellus and integuments and at maturity fills the entire seed.

1.2.1.3   Pollen germination and tube growth

In *Prunus*, pollen grains are shed dehydrated and rapidly rehydrate when deposited on the stigma. Germination occurs within hours (Becker, 1933) and the microgametophyte emerges through one of three apertures to penetrate intercellularly into the stylar transmitting tissue. Optimal temperatures for germination of *Prunus* pollen vary widely and range from 10° to 32°C depending on species and location (Becker, 1933; Cerović and Ružić, 1992; Randhawa and Ramakrishnan Nair, 1960). This may relate to the time of bloom and maximal temperatures normally experienced during flowering (Weinbaum et al., 1984). For apricots, 9° to 15°C was optimal for several cultivars (Vachun, 1981), a temperature range that is commonly experienced during bloom in New Zealand apricot growing regions, including Hawkes Bay. Stigmatic deterioration reduces pollen germination in apricots (Burgos et al., 1991; Egea et al., 1991) though in sweet cherry, pollen can still germinate and penetrate even after styles turn brown and shrivel (Stösser and Anvari, 1983). It was the principal determinant of floral receptivity and fruit set in Spanish apricots (Egea and Burgos, 1992), especially at temperatures of 20°C and above.

Pollen tube growth is apical and longitudinal differentiation within the tube is quickly established as pollen tubes penetrate the style. Extension growth is associated with the regular occlusion of the lengthening tubes by callose plugs (Cresti et al., 1979; Uwate

and Lin, 1980). Deposition of the callosic inner cell wall is progressive, initially very thin near the apex but thicker towards the nuclear region and very thick in the final region near the plug. Initial growth of pollen tubes is autotrophic and dependent upon reserves (Herrero and Dickinson, 1981) but accelerates once within the style (Herrero and Dickinson, 1980) as the microgametophyte draws on starch and other nutrients sequestered in the transmitting tissue (Herrero and Dickinson, 1979). Tube extension rates can range from 1.0 to 5.0 mm/day depending on temperature and cultivar (Guerrero-Prieto et al., 1985; Keulemans and van Laer, 1989; Socias i Company et al., 1976) and also position in the style (Jefferies et al., 1982). Growth rates increase from near zero at 5°C to a maximum between 20° and 25°C (Becker, 1933; Jefferies et al., 1982; Keulemans, 1984; Keulemans and van Laer, 1989; Vachun, 1981) though the optimum for tube growth may differ from the optimum for germination (Becker, 1933; Jefferies et al., 1984; Vachun, 1981). *In vitro* growth rate can also differ markedly between cultivars (Keulemans and van Laer, 1989; Vachun, 1981) but differences are not necessarily observed *in vivo*, presumably due to the overriding influence of stylar genotype (Keulemans and van Laer, 1989; Guerrero-Prieto, et al., 1985). Penetration to the base of the style in *Prunus* flowers typically occurs within about 48 h at 20°-25°C (Burgos et al., 1993; Cerović and Ružić, 1992; Cresti et al., 1979; Socias i Company and Felipe, 1992; Socias i Company et al., 1976; Stott et al., 1974) and 5-6 days at 10°C (Cerović and Ružić, 1992; Guerrero-Prieto et al., 1985; Stott et al., 1974). Pollen tube extension slows on entry to the ovary (Arbeloa and Herrero, 1987; Pimienta et al., 1983) and consequently, based on observations from sour cherry and almond (Cerović and Ružić, 1992; Pimienta et al., 1983) the time to ovule penetration can be about twice that for stylar penetration.

1.2.2 Self-Incompatibility, Self-Sterility and Fruit Set

1.2.2.1 *Self sterility and self incompatibility in apricots*

Many almond, apple, pear and sweet cherry cultivars are self sterile and require cross pollination. The biological basis for this is now well understood and the identification of suitable pollenizer cultivars is a common practice (Horticultural Education Association, 1961; Jackson, 1986; Westwood, 1993). In contrast, most apricot cultivars grown in Europe, North America, South Africa, Australia and New Zealand (i.e. 'European'-type cultivars: Mehlenbacher et al., 1991) have been classed as self fertile and

special provision of pollenizers was not needed (Bradt et al., 1978; Coombe and Watts, 1962; Mehlenbacher et al., 1991). In this respect, 'European' apricot cultivars are distinguished from other eco-geographical groupings such as the Central Asian and Irano-Caucasian in which self sterility is common (Mehlenbacher et al., 1991).

Self sterility can be caused by the production of pollen of low viability (male sterility). Male sterility has been shown to result in one Portuguese apricot cultivar from abnormal cytokinesis during meiosis (Medeira and Guedes, 1991). Two Spanish apricot cultivars, 'Arrogante' and Colorao', are male sterile as shown by failure of pollen to germinate or penetrate the style (Garcia et al., 1988). Pollen from the cultivar 'Pacorro', though viable, was found to be slow to germinate, preventing 'Pacorro' acting as a pollenizer. Other cultivars tested showed satisfactory pollen viability (acetocarmine staining) and germination. In another study 22% to 49% viability was estimated by staining (Parfitt and Almehdi, 1984) whereas most French cultivars tested showed higher (46% to 99%) levels of staining (Vachun, 1981). However, pollen viability data needs to be interpreted carefully. In vitro germination of apricot pollen is very dependent on temperature and osmotic potential (Vachun, 1981) while most staining techniques used to measure viability are not reliable on *Prunus* pollen (Parfitt and Ganeshan, 1989). Apricot pollen viability data based on acetocarmine staining (Lagutova, 1987; Vachun, 1981) are therefore indicative only.

Self sterility may also be caused by pollen tube self incompatibility (SI). Self incompatibility systems that encourage out-breeding are present in over half the angiosperm plant families (de Nettancourt, 1977). They take a variety of forms which may affect pollen germination, pollen tube growth in the style, ovary or ovule, fertilization or post-fertilization embryo development. In *Prunus*, self incompatibility is determined by inter-action of the genotypes of pistil and microgametophyte (gametophytic SI) and usually appears as blockage of pollen tubes in the style. Ultrastructural studies of self incompatibility in *Prunus avium* and in Solanaceous species (which also display gametophytic SI) show that the rejection response is not immediate. Self and cross pollen tubes in sweet cherry styles appeared the same for the first six hours post-pollination at 25°C (Uwate and Lin, 1980). Inhibition was typically expressed after self tubes had grown about a third down the style. At this point in *Lycopersicon peruvianum* the callosic inner wall

of self tubes became thinner and many small (0.2 µm) particles accumulated in the cyto-plasm (de Nettancourt et al., 1973). The inner wall then disappeared and the outer wall became thicker, giving tubes a swollen appearance. Eventually, incompatible tubes burst open, spilling cytoplasm into the intercellular space. In *Petunia hybrida*, incompatible tubes may burst or they may simply stop growing and die (Herrero and Dickinson, 1980). This may reflect the fact that, in *Petunia*, transfer of stylar reserves to support pollen tube growth is only triggered by compatible pollination (Herrero and Dickinson, 1979).

In *Prunus avium*, recognition of self tubes occurs through the matching of identical alleles of a single gene (the '*S*' gene), which displays multiple alleles (Crane and Brown, 1937; Way, 1968). In classical genetic studies, the genotype of a self incompatible plant was only revealed by its breeding behaviour or by pollen tube penetration. However, molecular biology has significantly advanced understanding of the physiology of gameto-phytic self incompatibility in recent years. Molecular techniques have linked genetically-identified '*S*' alleles to polymorphic glycoproteins present at high levels in styles in several systems, including *Prunus* (Ebert et al., 1989). In *Nicotiana alata*, glycoproteins of this type have been identified as ribonucleases (McClure et al., 1990). Hence, it is possible that degradation of pollen tube RNA is the means by which self pollen tubes are inhibited in *Prunus* species, including apricots.

Despite the past history of self fertility in apricots, the frequency of self incompatibility as a cause of partial or complete self sterility now appears sufficiently common to warrant direct attention in relation to fruit set (Table 1.1). Provision for cross pollination therefore appears destined to be an increasingly important dimension to the selection of apricot cultivars and to apricot orchard design. Self incompatibility as a cause of self sterility has an additional implication that groups of cultivars may be reciprocally cross incompatible. This is found with almonds, sweet cherries and plums (Jackson, 1986; Kester et al., 1994; Way, 1968). Cross incompatibility still remains rare between apricot cultivars and has been observed only between closely-related cultivars such as 'Riland' and 'Earliril' and between some Spanish and Hungarian cultivars (Brooks and Olmo, 1972; Egea et al., 1991; Szabó and Nyéki, 1991).

Table 1.1   Reported self sterility of 'European'-type apricots and recently-introduced cultivars arising from apricot breeding programmes.

Cultivar	Cause [z]	Parentage [y]	Site + year of introduction		Reference
'Ceglédi óriás' [x]	1-4 1, SI	No data	Hungary		Nyujtó et al., 1982; 1985 Szabó and Nyéki, 1991
Clutha 12/113	SI?	'Moorpark' × 'Sundrop'	Clyde, N.Z.		Glucina et al., 1988
Clutha 13/177	SI	'Moorpark' × 'Sundrop'	Clyde, N.Z.		McLaren et al., 1992b
Clutha 14/32	SI?	'Moorpark' × 'Sundrop'	Clyde, N.Z.		McLaren et al., 1992b
'CluthaGold'	SI	'Moorpark' × 'Sundrop'	Clyde, N.Z.	1988	McLaren et al., 1992b
'CluthaGem'	SI	'Moorpark' × 'Sundrop'	Clyde, N.Z.	1990	McLaren et al., 1992b
'Earliril' [v]	SI?	'Riland' × open poll.	Prosser, U.S.A.	1957	Lamb and Stiles, 1983
'Early Divinity'	1, ??	Unknown	Adelaide, Australia	1962	Szabó and Nyéki, 1991
'Goldbar'	SI?	'Goldrich' × 'Blenril'	Prosser, U.S.A.		Not confirmed
'Goldrich'	SI?	'Sun Glo' × 'Perfection'	Prosser, U.S.A.	1972	Fogle & Toyama, 1972
'Goldstrike'	SI?	'Goldrich' × open poll. ??	Prosser, U.S.A.		Not confirmed
'King'	SI?	? 'Perfection' × open poll.	Merced, California	1964	Brooks and Olmo, 1972
'Ligeti óriás'	1, SI	No data	Hungary		Szabó and Nyéki, 1991
'Moniquí Fino'	1, SI	No data	Spain		Egea et al., 1991; Burgos et al., 1993
'Moongold'	??	'Superb' × 'Manchu'	Minnesota, U.S.A.	1961	Anon, 1961
'Nagykőrösi óriás'	1,3 1, SI	No data	Hungary		Nyujtó et al., 1982; 1985 Szabó and Nyéki, 1991
'Orange Red'	??	Iranian cv. × (M604 × open poll.)	New Jersey, U.S.A.		Hough et al., 1982; Audergon et al., 1991
'Paviot'	??	Prob. 'Luizet' × open poll	France	1885	Audergon, 1988
'Perfection'	2, SI 2	Unknown	Washington, U.S.A.	1937	Schultz, 1948; Szabó and Nyéki, 1991
'Riland'	1, SI	Unknown	Washington, U.S.A.	1932	Schultz, 1948
'Rival'	??	No data	Prosser, U.S.A.		Fogle & Toyama, 1972
'Skaha'	SI?	'Perfection' × open poll.	Summerland, B.C.	1975	Lapins, 1975
'Stella'	3, ??	No data			Szabó and Nyéki, 1991
'Sundrop'	2, SI? 2 3	'Perfection' × open poll.	Summerland, B.C.		Lane, 1978; McLaren et al., 1992b; Wood, 1983
'Sun Glo'	2, ??	Unknown	Washington, U.S.A.	1946	Szabó and Nyéki, 1991
'Sungold'	??	'Superb' × 'Manchu'	Minnesota, U.S.A.	1961	Anon, 1961; Lamb and Stiles, 1983
'Szegedi Mammut'	1, 1, SI	No data	Hungary		Nyujtó et al., 1982 Nyujtó et al., 1985
'Tomcot'	??	'Rival' × PA63265	Prosser, U.S.A.		Not confirmed
'Valleygold'	SI	Reliable, Geneva, Naramata	Vineland, Ontario		Glucina et al., 1990
'Velázquez Tardío'	1, SI	No data	Spain		Egea et al., 1991 Burgos et al., 1993
'Viceroy'	2, ??	'Geneva' × 'Naramata'	Vineland, Ontario	1964	Szabó and Nyéki, 1991
'Wilson Delicious'	??	No data			Sharma & Sharma, 1991

[z] Self fertility: 1 = Fully self sterile (0% set); 2 = Self sterile (0.1-1% set); 3= Marginally self fertile (1.1-10% set); 4 = Self fertile (10.1-20% set). Categories from Szabó and Nyéki, 1991. Cause: SI= Self incompatible, demonstrated by pollen tube penetration or by reciprocal cross pollination; SI?= Inferred from parentage; ??= Unknown.
[y] Cultivar information: Brooks and Olmo, 1972; Audergon, 1988; Audergon et al., 1991
[x] Cross incompatibility found between 'Ceglédi óriás', 'Nagykőrösi óriás' and 'Szegedi Mammut' (Nyujtó et al., 1985).
[v] Cross incompatible with 'Riland' (Brooks and Olmo, 1972)

1.2.2.2   Manipulation of self-incompatibility

Many techniques can modify the expression of self-incompatibility (van Marrewijk, 1989). Most have application only as experimental tools or breeding techniques but the effects of temperature and the dynamics of stigmatic receptivity do provide insights into potential causes of variable fruit set under field conditions. In other taxa, high temperatures during pollen tube growth can reduce self-incompatibility (Ascher and Peloquin, 1970; Leffel and Muntjan, 1970) but in the Rosaceae, self pollen tube growth is generally least inhibited between 10° and 20°C. Examples include almonds (Socías i Company et al., 1976; Vasilakakis and Porlingis, 1984), apples (Modlibowska, 1945; Williams and Maier, 1977), pears (Modlibowska, 1945) and sweet cherries (Lewis, 1942). Relative promotion of self tubes by optimum temperature may be limited in species that are strongly self incompatible, for instance, pears (Modlibowska, 1945; Vasilakakis and Porlingis, 1985), but appears greater where inhibition of self tubes is weaker. Two exceptions to reduced self incompatibility at low temperature stand out. Laboratory study showed self incompatibility was most pronounced in sour cherry at 5°C in one of three years (Cerović and Ružić, 1992). These tubes may have been under stress since the lower limit of *Prunus* pollen tube growth is about 5°C (Jefferies et al., 1982; Keulemans, 1984). More importantly, a recent laboratory study suggested that inhibition of selfed 'Sundrop' apricot tubes did not occur in 'Sundrop' flowers at constant 20°C whereas growth of self tubes was inhibited in the field (McLaren, Fraser and Grant, 1992). This observation is surprising given the pattern for other Rosaceae that higher temperatures generally increase self incompatibility. However, this could provide insight into the variation of cropping on 'Sundrop' since temperatures during bloom are frequently low.

Manipulation of pollen composition on the stigma using inviable 'mentor' pollen (irradiated, methanol-treated or freeze-thaw killed) can reduce pollen-stigma incompatibility. The method was initially used for interspecific hybridization (Knox et al., 1972) but can promote self fertilization and fruit set in gametophytic systems (Dayton, 1974; Lane, 1984). It is not always successful (Visser, 1981; Visser and Marcucci, 1986; Williams and Church, 1978) and its importance to fruit set is probably limited since stigmas in experiments were thoroughly saturated with pollen. This is less

likely to occur in orchards under natural levels of pollen transfer. Application of inviable compatible pollen 1-2 days ahead of self pollen ('pioneer' pollination) can also increase self fertility (Visser, 1983). Temperature and timing of the second pollination are crucial to effectiveness (Visser and Marcucci, 1983) and the method seems less successful where self-incompatibility is stronger (Visser and Marcucci, 1986; Visser and Oost, 1982). The 'pioneer' effect has been observed on peaches (El-Agamy and Sherman, 1987) but its significance for fruit set of self incompatible *Prunus* species is unclear. Changes in stigmatic receptivity alone appear insufficient to explain the effect (Visser and Verhaegh, 1980b) and pollination twice with self pollen is ineffective (Visser and Marcucci, 1984). Instead, 'pioneer' pollen may promote tube growth by accelerating maturation of transmitting tissue since reports of its effectiveness all involve pollination of emasculated (immature and depetalled) flower buds. Heavy early-deposits of self pollen could therefore enhance fruit set by promoting the development of later self pollen tubes of partially self-compatible cultivars.

1.2.3 Fruit Set and Pollen Transfer Dynamics

1.2.3.1 Pollen transfer in apricot orchards

Pollen of the Rosaceae is not well suited to wind transfer as grains are relatively large, tend to be sticky and are generally poorly disseminated by wind. In addition, the stigmas of flowers present a relatively small surface area for pollen deposition. Consequently, despite significant levels of air-borne pollen in apple and pear orchards (Burchill, 1963; Langridge and Jenkins, 1969), insect visitation greatly increases fruit set on apples, pears and *Prunus* species such as peaches, almonds and apricots (Bulatovic and Konstantinovic, 1962; Free, 1970; Godini et al., 1992; Langridge and Goodman, 1981; Langridge and Jenkins, 1969; Langridge and Jenkins, 1975). Modelling of factors influencing the probability a flower will set as a fruit also shows that the number of forager visits to a flower is the major determinant of fruit set (Brain and Landsberg, 1981).

Insect-mediated pollen transfer is therefore the major mechanism of cross pollination for deciduous fruit crops such as apricots (Free, 1970). Wild insects can contribute to cross-pollination in Europe and North America under some conditions (Boyle and Philogène, 1983; Klug and Bünemann, 1983) but, in New Zealand, apricots bloom before the rise in activity of native bees (*Leioproctus* spp.) in early summer (Donovan and MacFarlane,

1984). Bumblebees, if present in number, are highly effective pollinators due to their size, large pollen load (Kendall and Solomon, 1973) and activity at low temperatures (Wratt, 1968). Again, however, apricots bloom before the establishment of new colonies in spring by over-wintered queens and are therefore not visited by significant numbers of bumblebees. As a consequence, only honeybees, which predominate as foragers on apricots in Australia (Langridge and Goodman, 1981) and in New Zealand apple and plum orchards (Palmer-Jones and Clinch, 1967; Palmer-Jones and Clinch, 1968; Roberts, 1956), are likely to be significant insect pollen vectors in Hawkes Bay apricot orchards. Restricted honeybee activity in apricot orchards is therefore likely to be an important factor reducing intervarietal pollen transfer and reliability of fruit set.

The factors determining honeybee activity level and honeybee-mediated pollen transfer can be categorised into five broad groupings to facilitate discussion. These include: environmental factors, forager, orchard and floral characteristics and factors related to pollenizer bloom phenology (Table 1.2). Each grouping represents a different conceptual subsystem within the overall pollination system, grossly simplified since in reality the different subsystems and factors interact at a variety of levels and in a manner not represented within such a simple schema.

1.2.3.2   Environmental factors

Light and temperature together with wind speed are the primary environmental influences on the level of honeybee foraging activity (Free, 1970; McCall and Primack, 1992). Foraging is restricted entirely to daylight hours and is strongest in full sun. Light

Table 1.2   Factors influencing potential for honeybee-mediated cross-pollination.

1. Environmental factors	3. Floral characteristics	4. Orchard characteristics
Light intensity	Pollen viability	Competitor crops
Air temperature	Pollen production	Planting layout
Wind speed	Nectar attractiveness	Varietal ratio
2. Forager characteristics		5. Bloom phenology
Forager ratio		Stigmatic receptivity
Pollen load composition		Ovule lifespan
Foraging area & trip length		Bloom divergence

intensity also modulates the relationship of temperature to foraging activity. Under low light intensities foraging activity ceases at about 16°C but at high light intensity continues at a low level down to about 12°C (Szabó, 1980). Below 9-10°C honeybee flight activity ceases entirely and at around 7°C bees soon become motionless (DeGrandi-Hoffman, 1987; Gary, 1975). Colony strength can influence activity as foraging from weak colonies was negligible below 16°C whereas foragers from strong colonies were still active at 13°C (Martin, 1975). Relative humidity has little effect on flight or foraging activity apart from its negative association with temperature (Szabó, 1980). Wind, however, is very important and a windspeed of 25 km hr^{-1} greatly slows bee activity while winds above 35-40 km h^{-1} prevent it entirely (Horticultural Education Association, 1961). The environmental conditions which typify early spring in Hawkes Bay therefore restrict most honeybee foraging activity to the period from late morning to early afternoon. They also mean that poor weather can entirely prevent foraging activity for days at a time (cf. Visscher and Seeley, 1982; Williams and Sims, 1977).

1.2.3.3   Forager characteristics

Most foragers in *Prunus* and other fruit orchards work within a few hundred metres of colonies (Free, 1960b; Gary et al.,1976) but honeybee scouts travel many kilometres in search of nectar and pollen (Visscher and Seeley, 1982). If forager density is high, many foragers will disperse to other, more distant, orchards where honeybee numbers are lower (Gary et al.,1976). There is therefore considerable scope for foragers to be attracted away from a crop by other richer pollen or nectar sources. The potential for competition is illustrated by the fact that bees flying only 2 km in any direction have access to over 1200 ha. A 2 ha apricot block is therefore competing for forager visits against all other plants in that area. Furthermore, while the overall distribution of foragers is subject to almost daily change (Visscher and Seeley, 1982) the phenomenon of flower constancy exhibited by honeybees (Free, 1963) means patterns of foraging, once established, tend to be maintained. For instance, forager constancy to dandelion has been blamed for low forager numbers on apple and plum (Free, 1968). For this reason, hive introduction to orchards is typically delayed until sufficient flowers are open to prevent diversion of foragers to alternative sources. On less attractive crops such as pears this may require 25% or more flowers open (Free, 1970).

The relative numbers of bees foraging for pollen or nectar might influence apricot fruit set but the importance of this factor is not clear. Each honeybee is capable of collecting pollen or nectar (Free 1960a), and priority given to either resource depends on circumstances in the hive at any given time, especially presence of brood (Free, 1967; Todd and Reed, 1970). Pollen foragers are generally considered of greatest value as pollinators (Free, 1960b; Free, 1966a; Thorp et al., 1974). This is because pollen foragers deliberately contact anthers and therefore probably also the stigma, because they typically work flowers faster than nectar foragers (Free, 1960a) and because they tend to visit younger rather than older flowers (Langridge and Goodman, 1981). The tendency of nectar gatherers to 'side-work' flowers through the base of the stamens, particularly on apple (Free, 1966a; Roberts, 1945; Robinson, 1979) but also on plum (Roberts, 1956), may reduce contact with anthers and stigma and so reduce fruit set (Robinson and Fell, 1981). However, 'side-working' is possibly of limited importance on apricot since not only do foragers collecting apricot nectar usually contact anthers (Free, 1960b) but its significance on apple is now questioned (DeGrandi-Hoffman et al., 1985). Furthermore, honeybees from colonies predominantly collecting nectar were as effective pollinators of almond as bees from colonies with a much higher proportion of pollen foragers (Erickson et al., 1977).

The factors that do reduce cross-pollination efficiency are the tendency of individual bees to forage in restricted areas (Ribbands, 1949) and the very limited carryover of pollen beyond the first few flowers visited (Richards, 1986). Both are especially important where self incompatible cultivars are arranged within orchards as blocks and their attract-iveness to bees differs due to either relative bloom stage or other factors (Free, 1966b). To collect pollen honeybees use their tongues and mandibles to dislodge pollen from anthers and then moisten it with regurgitated nectar (Hodges, 1974). After a few visits foragers begin to brush adhering pollen grains from their heads and bodies and, mixing it with moistened pollen, pack the combined pollen into their pollen baskets (corbiculae). The effectiveness of foragers as pollinators *per se* is probably not reduced by cleaning since, while intensive, it is never completely successful. From 4000 to 5000 pollen grains commonly remain spread over the body of honeybee foragers (Kendall and Solomon, 1973). However, cross pollination is dependent on pollenizer pollen grains accumulated on body hairs of foragers during visits to pollenizer flowers remaining

available for deposition. Repeated visitation of one cultivar rapidly dilutes the proportion of foreign pollen and therefore limited visit frequency to pollenizer flowers lowers the overall probability of cross pollination (Kendall, 1973; Vithanage and Douglas, 1987).

An ideal visitation sequence for maximal cross-pollination involves revisitation of pollenizer flowers at a frequency which compensates for the rate at which pollenizer pollen is diluted by self-pollen. However, there is a lack of data describing pollen carryover on fruit trees. Simulations (Lertzman and Gass, 1983) and experimental studies on other species (summarised in Richards, 1986) suggest a carryover of pollenizer pollen of 5-6 flowers, possibly higher in some circumstances. There is also little information on number of flowers or trees visited per foraging trip, due primarily to the difficulty of following individual foragers within an orchard throughout their entire trip. Bees visited very few standard apple trees (mean 1.1-2.7 trees per trip) relative to the number of flowers visited (Free, 1960a; Roberts, 1956) and the data imply only 5% to 10% of flowers are cross-pollinated per trip. Re-capture studies using marked bees also suggest that "satisfied" foragers on attractive cultivars appear to maintain relatively small foraging areas over several days further reducing pollination efficiency (Free, 1966b). Grouping of hives in orchards is suggested as a counter to this since greater interaction between bees as they set up flight patterns can lead to more frequent change of foraging location (Martin, 1975).

1.2.3.4   Floral characteristics

Nectar and pollen resources are major determinants of honeybee foraging activity within an orchard and a deficiencies in either may reduce pollination of apricots. Pollenizer pollen quantity is probably the most important pollen-related variable affecting the probability of cross pollination. Pollen production by flowers of *Prunus* species ranges from 0.3 to 1.2 mg per flower (Hill et al., 1985; Percival, 1955) which compares with 1.2 to 1.7 mg produced by apple and pear flowers (Percival, 1955). However, the large numbers of blossoms per tree means *Prunus* orchards are still significant pollen sources. Anther dehiscence usually begins as soon as petals open and proceeds at a rate controlled by both temperature and humidity. The entire duration is highly variable especially as a single stamen often lags behind the others in dehiscence for one to several days (Percival, 1955). However, if these are excluded, 82% of pear flowers complete anther

dehiscence in 2-4 days and apple and peach anthers dehisce over a period of 2-5 days. Under controlled conditions, full dehiscence of apricot anthers occurred within 72 h at 15°C and 80% relative humidity and proceeded faster at higher temperature or lower humidity (Langridge and Goodman, 1981). Dehiscence of anthers can, however, occur at 100% RH, or sometimes even in rain (Percival, 1955). The limiting temperature for dehiscence was linked to light intensity. For pear, it was as low as 5°C in bright sun but 9-10°C when conditions were dull (Percival, 1955). Honeybees will show a preference for one pollen type over another under controlled conditions (Campana and Moeller, 1977) but the practical significance of this in orchards is uncertain (Estes et al., 1983).

Pollenizer pollen quality (germinability and capacity to grow vigorously to the ovule) is also important to the reliability of apricot fruit set on self-incompatible cultivars because of the highly restricted movement of pollenizer pollen (Richards, 1986). Normal pollination involves deposition of tens or hundreds of pollen grains on the stigma for fertilization of only a single ovule. In theory, fruit set on apricot therefore requires transfer of only a very few compatible grains to each flower. However, if viability is very low (or if transfer of pollen to the stigma was very limited) the probability that those pollenizer pollen grains deposited are capable of achieving fertilisation is diminished. The importance of pollen viability is increased if few pollenizer trees are present since this too reduces the average number of compatible grains reaching the stigma.

Nectar in *Prunus* flowers consists predominantly of equal quantities of glucose and fructose and a much lower amount of sucrose (Percival, 1961; Wykes, 1952). Secretion is an active process (Bieleski & Redgewell, 1980) and is therefore sensitive to temperature; the minimum temperature was 8°C in *Prunus avium* but was as high as 18° to 20°C in *Prunus laurocerasus* (Beutler, 1953). Nectar volume and concentration for *Prunus* species range widely: from 1.1 μl to 30 μl (Brown, 1951; DeGrandi-Hoffman et al., 1991; Erickson et al., 1979) and 5% to 60% sugar (Meheriuk et al., 1987; Vansell, 1934; Vansell, 1952). Preference of honeybees for nectar *per se* is determined principally by sugar concentration and 5-10% sugar is an effective minimum threshold (Meeuse, 1961; Kevan and Baker, 1983). Honeybees prefer sucrose-dominant nectar to glucose or fructose, (Bachman and Waller, 1977; Wykes, 1952) but any effect of composition is probably overridden by that of concentration (Langridge et al., 1976; Southwick, et al.,

1981).   Flowers of all deciduous fruit tree species are visited for pollen and nectar (Robinson and Oertel, 1975). Their nectar concentrations (Butler 1945; Mommers, 1966; Meheriuk et al., 1987; Vansell, 1934; Vansell, 1952) generally lie above the minimum and are therefore attractive to honeybees (Martin, 1975).   Those species with lower nectar concentrations (pears and plums) are commonly less attractive than those with higher sugar levels (Langridge and Jenkins, 1972; Martin, 1975; Roberts, 1956).

The importance of nectar production as an influence on apricot pollination in Hawkes Bay therefore lies in the potential for low nectar attractiveness to lower overall floral attractiveness (Percival, 1955).   Overall preference for a floral resource, measured by actual visitation, does not always match relative nectar concentration (Mommers, 1966) and other factors such as floral density which determine total resource availability (DeGrandi-Hoffman et al., 1991; Free, 1966b) are also important. But the nectar of fruit trees such as apricots has been dismissed as "next to useless" for honeybees under early spring conditions in New Zealand (Walsh, 1967) and honeybees will desert other *Prunus* such as plum in favour of manuka (*Leptospermum scoparium*), kowhai (*Sophora microphylla*), *Hakea saligna* and various forms of brassica (Roberts, 1956).   Apricot nectar is 5-25% sugar (Meheriuk et al., 1987; Vansell, 1934; Vansell, 1952) and is therefore marginally acceptable to honeybees. Honeybees will abandon apricots if other crops are more attractive (Vansell, 1952) making a more attractive non-apricot nectar source also their chief pollen source (Percival, 1947). Apricot nectar is also subject to marked variation in concentration due to environmental factors since it is held in open flowers (Corbet et al., 1979). Low sugar concentration probably occurs at times because of dilution by high humidity, rain or dew (Shuel, 1975). In addition, some cultivars may be affected more than others since varietal differences in nectar secretion rates and concentration have been found in plums, almonds, apricots and sweet cherries (Brown, 1951; Erickson et al., 1979; Meheriuk et al., 1987; Vansell, 1952).   Limited nectar attractiveness in early spring could therefore reduce forager activity and thereby reduce potential pollen transfer to some cultivars in particular.

1.2.3.5   Orchard characteristics

The assumption that bees cross-pollinate 5% or 5.5-6.5% respectively of almond and apple flowers they visit was used to model fruit set (DeGrandi-Hoffman et al., 1987;

DeGrandi-Hoffman et al., 1989) but it is difficult to assess whether this accurately represents transfer on apricots. Several factors may influence actual pollenizer pollen transfer. Redistribution of pollen from cross-pollinated stigmas has been suggested but appears unlikely to be important (Free, 1970). Reduced tree size in modern orchards might be expected to increase intervarietal flight frequency but this is offset by the tendency for honeybees to work along rows. Measurements of foraging areas in a dwarf apple orchard showed bees worked within small areas on the one row and only 10% of foragers moved to another row (Free and Spencer-Booth, 1964b). Many flower visits to flowers on self-incompatible cultivars are therefore unlikely to cause fruit set and consequently the presence of pollenizers within rows has been recommended (Free, 1970). Foraging areas may be increased by unfavourable weather, limited nectar and pollen resources (Free, 1960b) or high forager competition especially at the beginning or end of bloom (Gary, 1975) but effects are probably small relative to the negative effect of adverse conditions on total forager numbers.

Under some conditions, the placement of pollenizers clearly influences pollen transfer as trees closer to pollenizers have higher fruit set (Briggs et al., 1983; Free, 1962; Free and Spencer-Booth, 1964a; McLaren, Fraser and Grant, 1992; Wertheim, 1991). However, this is not always true (DeGrandi-Hoffman et al., 1984; Williams, 1966) and transfer of pollenizer pollen between foragers within the hive may be as important to cross-pollination. Though so far demonstrated only for apple (DeGrandi-Hoffman et al., 1986; Free and Durrant, 1966; Kraai, 1962) and not for *Prunus*, in-hive transfer has the consequence that foragers potentially effect cross-pollination from the start of their trip before visiting a pollenizer. It also means that the overall proportion of pollenizer to main cultivar trees within an orchard becomes important (DeGrandi-Hoffman et al., 1987) and emphasizes the significance of the relative timing of pollenizer and main cultivar bloom as the main determinant of the ratio of pollen types in the mobile pollen pool.

1.2.3.6   Bloom phenology and timing of floral receptivity

Synchronisation of anthesis, pollen tube growth and megagametophyte development is important to fruit set since embryo sac lifespan is finite and the time required for pollen tubes to reach the egg cell is significant (Herrero, 1992). Coordination of pollen tube growth and embryo sac maturation is probably particularly important in *Prunus*, the fruit

of which contain a single large seed and show no natural parthenocarpic or apomictic tendency (Badr and Crane, 1965; Rebeiz and Crane, 1961). Some evidence for coordination exists since pollen tubes in both peach and almond flowers are delayed at the base of the style before renewed growth to the ovule occurs (Arbeloa and Herrero, 1987; Pimienta et al., 1983) while in almond, final embryo sac maturation is stimulated by the presence of compatible pollen tubes in the style (Pimienta and Polito, 1983). By contrast, embryo sac maturation in advance or independent of pollen tube penetration appears to account for poor fruit set in sweet cherry (Eaton, 1959) and loss of floral receptivity in almond (Griggs and Iwakiri, 1964; Pimienta and Polito, 1982). Ovule senescence involves blockage of translocation to the nucellus (Pimienta and Polito, 1982), depletion of carbohydrates (Pimienta and Polito, 1983) and (in apple) a decline in cell division (Williams, 1965). The order of cause and effect is unclear as is the role of plant growth regulators. All applied growth substances accelerated ovule senescence in sweet cherry (Stösser and Anvari, 1982).

Flowers of *Prunus* species do have a limited lifespan but how conditions in Hawkes Bay might interact with this to affect fruit set is difficult to predict. The duration for which pollination of a flower will effect fruit set (i.e. the effective pollination period, EPP = duration of ovule viability minus time required for pollen tubes to enter ovary (Williams, 1966)) has been subject to frequent attention in *Prunus* (Burgos et al., 1991; Dys, 1984; Eaton, 1959; Griggs and Iwakiri, 1964; Keulemans and van Laer, 1989; Lech and Tylus, 1983; Postweiler et al., 1985; Thompson and Liu, 1973; Vitanov, 1983). These studies have shown that EPP varies substantially ranging from one to two days in an early study on sweet cherry (Eaton, 1959) to at least 10 days on some plum cultivars (Keulemans and van Laer, 1989). In cherries and almonds EPP is principally determined by ovule receptivity. In sour cherries, pollen tubes progressively fail to penetrate the micropyle as ovules age (Cerović and Ružić, 1992). High temperatures accelerate ovule senescence (Cerović and Ružić, 1992; Moreno et al., 1992; Postweiler et al., 1985) and may therefore reduce EPP whereas low temperatures tend to extend it. However, if the inhibitory effect of low temperature on pollen tube growth is greater than that on ovule senescence then low temperatures may prevent fruit set (Keulemans, 1984; Thompson and Liu, 1973). The effect of temperature on the expression of partial self incompatibility adds to the complexity of the situation. Thus, it is very difficult to predict the potential effect of, for

instance, periods of cool (<10°C) and mild (18°-20°C) conditions during bloom on the duration of floral receptivity or overall self fertility of apricots in general, and of Hawkes Bay 'Sundrop' in particular. Warm conditions might increase fruit set by reducing the time to fertilization relative to ovule senescence, or they may reduce it by accelerating senescence of ovules and increasing the expression of self incompatibility.

Optimizing cross pollination of self incompatible cultivars is further complicated by the interaction of weather conditions with factors connected to the phenology of flower development. These include anther dehiscence (Randhawa and Ramakrishnan Nair, 1960) stigmatic receptivity (Burgos et al., 1991) and the variable coincidence of flowering of different cultivars (Crane, 1924; Hill et al., 1985). This is illustrated by the well studied problem of unreliable fruit set on 'Cox's Orange Pippin' in Britain which has been related to flower sterility, limited EPP and insufficient cross-pollination (Williams and Smith, 1967). Adverse weather during bloom is associated with lower pollen germination and limited pollen transfer to 'Cox' (Williams et al., 1984) but weather conditions can show no simple correlation with fruit set (Beattie and Folley, 1977). Study of pollen tube growth in relation to timing of pollen transfer to flowers has shown that stigmatic receptivity varies over the life of a blossom and peaks sharply two to three days after opening (Williams et al., 1984). However, periods of weather conducive to substantial honeybee activity on 'Cox' are frequently as short as one day and occur at any time during bloom (Williams and Sims, 1977). Year to year variability of pollenizer bloom period relative to 'Cox' means no single pollenizer produces pollen throughout the 'Cox' bloom period (Church and Williams, 1983) so that at least two pollenizer cultivars are required to maximize opportunities for cross-pollination throughout the 'Cox' bloom period. Other aspects of flower development also potentially influence pollen transfer on 'Cox'. Flower bud position affects both bloom date and pollen production, pollen from earlier spur-borne flowers displaying greater viability than that from later axillary flowers (Church et al., 1983). In addition, observations indicate that petals and anthers develop independently and react differently to weather conditions (Williams et al., 1984). The duration of anther dehiscence and the delay of its start from the opening of the petals differs between cultivars (Church et al., 1983). Data collected to describe anthesis and petal-fall may therefore give only a general indication of pollen availability.

1.2.4   Apricot Pollination and Fruit Set: Conclusions

This summary of the biology of pollination of *Prunus* and related orchard fruit species provides an important background to the problems of fruit set on 'Sundrop'. It suggests that inadequate cross pollination is the most probable cause unreliable fruit set. This reflects the situation of 'Sundrop' apricot as a self incompatible cultivar blooming in very early spring in Hawkes Bay. This hypothesis then requires that the relative contributions of several factors need to be determined:

1). The physiological basis of the need to cross pollinate 'Sundrop';

2). The availability of pollenizer pollen for cross pollination;

3). The influence of low temperature on pollen tube growth;

4). The effectiveness of honey bees and other foragers as pollen transfer agents within Hawkes Bay 'Sundrop' blocks; and

5). The effect of stigmatic receptivity and ovule lifespan on fruit set.

Quantitative information on each of these issues should allow the formulation of practical recommendations that may resolve difficulties experienced by 'Sundrop' apricot growers.

However, the many interactions between the various factors mean that prediction of the effects of environment, forager behaviour, orchard layout and flower development on pollen transfer and fruit set is still in its infancy. Analysis of the risk of fruit set failure on 'Sundrop' under Hawkes Bay by means of pollination system models is not yet possible. Most quantitative treatment of the orchard pollination environment remains at the level of individual system components. Honeybee activity in relation to environment has been described quantitatively (Szabó, 1980) and a simple model of the relationship of activity to weather conditions has been used to analyse the risk weather poses to pollination (Williams and Sims, 1977). Models of pollen transfer have been developed to study gene flow (Lertzman and Gass, 1983; Waser, 1983) and pollen tube growth has been modelled in relation to time and temperature (Jefferies and Brain, 1984; Jefferies et al., 1982). Heat unit models have also been used for some time to describe flower bud development in response to temperature (Anstey, 1966; Buys and Kotze, 1963) and, combined with a distributed delay model, to describe the temporal progression of bud populations (Severini et al., 1986; Severini et al., 1990).

Several more complex models attempt to integrate all four aspects of flowering, forager activity, pollen transfer and fruit set (Brain and Landsberg, 1981; DeGrandi-Hoffman et al., 1987; DeGrandi-Hoffman et al., 1989). The value of these models lies in their ability to synthesize existing knowledge within a coherent framework, to assist decision-making and to direct research into areas where better understanding is still needed. Results from these indicate that temperature, pollenizer : main cultivar ratio and colony number are principal determinants of fruit set but there remain significant areas where assumptions are needed to cover lack of knowledge. Those with particular relevance to apricots in Hawkes Bay are the size of the foraging population in an orchard block, the extent of pollen transfer and effects of floral ageing on bee visitation and potential fruit set. These models therefore provide a second context for the investigation of the fruit set problems of 'Sundrop'. By establishing the basis for application of models of the type described above, investigation of pollination and fruit set on 'Sundrop' may also contribute to the building of systems which allow comprehensive analysis and management of pollination and fruit set risk.

1.3   Modelling Apricot Bloom Phenology

1.3.1   Cross Pollination and Phenological Modelling

1.3.1.1   Introduction

Accurate assessment of the opportunity for cross-pollination requires reliable data on the relative bloom synchrony of main and pollenizer cultivars. Analysis of historical bloom records can provide this information when cultivars have been grown in a region for many years. However, this option is not available where new cultivars or expansion of plantings into new areas are considered. This is the case for apricots in Hawkes Bay and therefore a method of predicting the phenology of bud break and flower development under Hawkes Bay conditions would significantly assist pollenizer assessment.

In this regard, a phenological model able to accurately simulate flower development on the basis of known environmental data is needed. Such a model might encompass the effects of air, plant and soil temperatures, light intensity, daylength, rainfall, soil-type as well as orchard management practices such as provision of shelter and irrigation, pruning regimes and chemical application. The relative flowering behaviour of pears and almond cultivars has been described in relation to pollination by temperature-based models (Rattigan and Hill, 1986; Seeley et al., 1987). Other models of the relationship between these factors and plant growth already exist, those models with a horticultural context commonly using the 'heat unit' concept to describe the relationship between temperature and active growth. However the behaviour of dormant flower buds on different cultivars is also of direct significance to relative bloom phenology since bloom of *Prunus* species directly follows spring bud break. An accurate method of predicting the relative patterns of dormancy alleviation and bud development is therefore needed.

1.3.1.2   The 'heat unit' concept

The era of quantitative phenological modelling dates from the recognition by de Réaumur in the early eighteenth century that the rate of plant growth is dependent upon prevailing temperature (Wang, 1960). de Réaumur introduced the concept of daily temperature summation above a base temperature to study the harvest dates of wheat and grapes and

in doing so made the important assumption that the rate of plant development is linear with temperature within the range of normal growing conditions. He also postulated that one developmental stage of a plant succeeded another once the required 'quantity of heat' had accumulated, the so-called 'Heat Unit Law'.

The 'Law' is essentially a special application of the Arrhenius temperature function which describes the relationship of the rate constant of a chemical reaction to temperature by

$$\ln(k) = a_0 + a_1/T \tag{1.1}$$

where k is the rate constant, a_0 and a_1 are constants and T is the absolute temperature. By adopting a reference temperature T_R the relationship of k to T can be re-expressed as

$$k = k_R.e^{[a_1.(T-T_R)/T.T_R]} \tag{1.2}$$

When the temperature range under consideration is limited (eg $0°$-$30°C$; i.e. 273K-303K) and the reference temperature is within that range, then a simplification is possible since the value of the product $T.T_R$ is relatively constant (Charles-Edwards et al., 1986). This being the case then Equation 1.2 is approximated to within 1% by

$$k = k_R.[1 + b.(T-T_R)] \tag{1.3}$$

where $b = a_1 / T.T_R$ and $b.(T-T_R)$ is less than 0.14. If the rate of transition, v, from one developmental stage S_i to another S_j, expressed by the ratio $(S_j-S_i)/(t_j-t_i)$, is temperature-dependent then Equation 1.3 becomes

$$(S_j-S_i)/(t_j-t_i) = v_R.[1 + b.(T-T_R)] \tag{1.4}$$

where v_R is the rate at the reference temperature. The time needed to move from state S_i to S_j is then the integral of v from t_i to t_j obtained by summing over the time interval: i.e.

$$\sum_{t=i}^{j} (S_j-S_i)/(t_j-t_i) = \sum_{t=i}^{j} v_R.[1+b.(T-T_R)] \tag{1.5}$$

Rearrangement of Equation 1.5 yields

$$t_{ij} = (S_j-S_i)/v_R - b.\sum_{t=i}^{j} (T-T_R) \tag{1.6}$$

which is the formula on which heat unit accumulation is based (Charles-Edwards et al., 1986). Hence, while the reference temperature T_R (or base temperature as it is more commonly known) is such that approximation of Equation 1.3 holds, the time period t_{ij} required for the plant to change from its initial state S_i to the new stage S_j is linearly

related to the sum of the differences between the mean temperature experienced (hourly or daily) by the plant T, and reference (or base) temperature T_R.

Selection of an appropriate base temperature for heat unit accumulation for the species and climatic region is important (Arnold, 1959). Use of a standard 4.5°C (40°F) base temperature for heat accumulation in relation to the 'Utah' chill unit model calculations is common. However, this figure was based originally on the response of annual field crops in western United States and the observation that peach buds did not grow visibly when kept at 4.5°C (Richardson et al., 1975). By comparison, appropriate base temperatures in Norway were as low as -3°C for 'Victoria' plum, -1°C for lilac (*Syringa vulgaris*) and -0.5°C for apple (Weilgolaski, 1974). A base temperature of -0.6°C (31°F) was used for lilac in northwest U.S.A. (Caprio, 1974). Weilgolaski also notes that base temperatures up to 6°C have been used for apple in other regions. Appropriate base temperatures may vary between cultivars if one is more responsive to low temperatures than another (Carlson and Hancock, 1991; Muñoz et al., 1986).

This conversion of chronological time into temperature-weighted 'thermal' time is fundamental to a wide variety of phenological models. It is important for scheduling optimum planting dates of field vegetables (Arnold, 1959) and for predicting the development of wheat and other temperate cereals (Porter and Delecole, 1988). It has been used to predict winter cold hardiness (Winter, 1986) and summer harvest dates (Muñoz et al., 1986; Perry et al., 1987). It is also the basis for models which integrate other environmental data such as photoperiod (Caprio, 1974) rainfall and water stress (Idso et al., 1978) and site effects (Lass et al., 1993). However, in the context of bloom phenology, its most important use has been to simulate spring flower bud development. Early attempts used heat accumulation from fixed reference dates (Anstey, 1966; Buys and Kotze, 1963). Its standard application is now in combination with the chilling requirement concept to form the 'chill unit phenology model' (Gilreath and Buchanan, 1981b; Richardson et al., 1974; Shaltout and Unrath, 1983).

1.3.2   Predicting Dormancy Alleviation and Bud Break

1.3.2.1   *Dormancy alleviation and 'chilling'*

The concept of a 'chilling requirement' for dormancy alleviation plays a fundamental role in modelling the floral bud break of deciduous fruit crops. Dormancy is a temporary suspension of visible growth of any plant structure containing a meristem (Lang et al., 1987). The physiological basis of this in flower buds remains largely unknown (Dennis, 1994) but it is characterised by low respiration rates (Cole, et al., 1982; Young, 1990), reduced free-radical scavenging capacity (Wang and Faust, 1994) as well as altered nucleic acid and respiratory metabolism (Thomas et al., 1985; Wang et al., 1991). In apricots, defoliation studies indicate that its initial induction occurs in mid-summer (Ramsay et al., 1970) and dormancy can be avoided by appropriately-timed manual or chemical defoliation (Saure, 1973; Edwards, 1987). Short days induce dormancy in most northern hemisphere tree species (Noodén and Weber, 1978) but this appears less important in *Prunus* (Nitsch, 1957). Other factors such as low light intensity, low night temperature, heat stress, and also nutrient and water stress may also play a role (Noodén and Weber, 1978; Vegis, 1964).

The range of agents found to promote renewed growth of previously dormant buds is equally diverse (Vegis, 1964). Numerous manipulative treatments accelerate, enhance or delay its release (Crisosto et al., 1989; Erez and Lavi, 1985) but, in *Prunus* and other deciduous tree fruit species, the main natural agent which alleviates dormancy is exposure to low, non-freezing, temperatures during autumn and winter (Chandler and Tufts, 1934; Weinberger, 1950a; 1967a). This is commonly called 'chilling'. Photoperiod does not appear to play a major role in dormancy alleviation in peach. Low light levels during the winter rest period promoted both leaf and floral bud break (Erez et al., 1966,1968; Freeman & Martin, 1981) and while light intensity or quality during forcing can modify the extent of bud break, its effect depends on bud type. Increased illumination of buds increased vegetative bud break, especially of lateral leaf buds but reduced floral bud break (Erez et al., 1966). Other environmental factors such as rainfall and fog can promote bud development (Chandler et al., 1937; Freeman and Martin, 1981; Gilreath and Buchanan, 1981a; Westwood and Bjornstad, 1978) but whether water acts independently or by modifying bud temperature is not clear.

Bell-shaped 'chilling' responses to low temperature have been proposed for dormant buds of apples and peaches. Early studies of bud break on peach showed that exposure to 0.5°-4.5°C broke dormancy more effectively than either 0°C or 9°C (Chandler and Tufts, 1934; Chandler et al., 1937). Under exceptional circumstances, temperatures as low as -15° to -16°C may promote bud break (Tinklin and Schwabe, 1970) and exposure to -3°C also accelerated break of raspberry buds (Lamb, 1948). However, bud break is generally increased and accelerated by temperatures between 0°C and 12°C (Carraut, 1968; Coville, 1920; Erez and Lavee, 1971; Erez and Couvillon, 1987; Gilreath and Buchanan, 1981a; Lionakis and Schwabe, 1984; Norvell and Moore, 1982; Plancher, 1983; Thompson et al., 1975). The temperature range from 3° to 8°C is usually reported as the most effective while the precise limits depend on the plant studied and its situation (Gilreath and Buchanan, 1981b; Norvell and Moore, 1982; Richardson et al., 1974; Shaltout and Unrath, 1983). For peaches and apricots, temperatures of 6° to 10°C have the greatest promotive effect (Brown, 1960; Erez and Lavee, 1971; Erez and Couvillon, 1987; Tabuenca, 1976). Maintaining temperatures above 7°C was the only temperature treatment that increased flower bud abortion in one study of peach bud drop (Weinberger, 1967a). The overall response is very similar to the stratification response of dormant seeds. 7°C promoted peach and apricot seed germination most effectively in one study (Chao and Walker, 1966) while in another, 4° or 6°C were most effective. (Seeley and Damavandy, 1985).

Methodological, genetic, physiological and environmental factors may alter the apparent relative effectiveness of chilling exposure. Different measurement methods (percent bud break versus time to bud break) may modify apparent effectiveness since estimates based on development rates are probably biased by incorporation of the subsequent heat response (Batten, 1983). Chilling temperature optima for some species appear to be lower than that generally accepted for peaches. Chilling at 2°C was more effective for 'Jonathan' apple trees than 6°C (Thompson et al., 1975) while the optimum for black currant cultivars that required long durations of chilling was 0°C (Plancher, 1983). The optimum for cultivars that required a shorter duration for bud break was higher, 3° or 6°C. Similarly, 'Tifblue' blueberries displayed a narrower and lower effective temperature range than some other rabbiteye blueberry cultivars (Gilreath and Buchanan, 1981a). In others, the temperature optimum for 'chilling' may be higher. Buds on low

chill nectarines recovered the capacity for development in warm conditions as quickly at 13 °C (55 °F) as they did at 7°C whereas 13 °C was less effective for 'Nemaguard' rootstocks, regarded as a 'high chill' cultivar (Gurdian and Biggs, 1964). Similarly, while 6° and 10°C had the same effect on flower buds of 'Paviot' apricot (late blooming), buds of 'Búlida' (earlier blooming) required fewer days at 10°C than at 6°C (29 versus 40 days) to begin development when incubated at 20°C (Tabuenca, 1976). Earlier initiation of development by 'Búlida' at 10°C was also observed in a subsequent study (Tabuenca, 1979), whereas buds of 'Paviot' and 'Luizet' apricots began rapid development earliest when incubated at 8°C. Two almond cultivars ('Texas' and 'Desmayo') also studied had relatively high chilling optima of 10° and 12°C respectively.

Response to chilling may be affected by bud type and position. Various other correlative, positional and shoot type factors (crop load, shoot diameter, shoot angle, height in tree, terminal bud condition) can also alter the time buds take to reach a given developmental stage (Latimer and Robitaille, 1981). Terminal vegetative buds initiate growth much more readily than buds in lateral positions (Erez and Lavee, 1971; Erez et al., 1979a) and display little sensitivity to 'chilling' temperature level (Scalabrelli and Couvillon, 1986). For 'Redhaven' peach, lateral vegetative bud response is closer to that of floral buds although floral buds are not so rapidly stimulated by temperatures in the middle of the 'chilling' range (Erez and Couvillon, 1987; Scalabrelli and Couvillon, 1986). Buds on vigorous extension shoots typically bloom later than those on terminating shoots or spurs (Austin et al., 1992; Brown, 1952; Chandler and Tufts, 1934; Guerriero et al., 1985a; Legave, 1978) suggesting that deeper or longer dormancy may be associated with higher shoot vigour. Rootstock vigour and compatibility can also influence bud dormancy (Couvillon et al., 1984; Tabuenca, 1976; Westwood and Chestnut, 1964) though scion response appears unrelated to the chilling requirement of compatible rootstocks (Nee and Fuchigami, 1990; Young and Werner, 1985). However, whether these effect are caused by changes to the physiology of the bud's temperature response is not clear since in many cases, only phenological data is reported. Such measurements only indicate relative dormancy if the starting point of buds is the same and therefore it is not clear whether relative bud development was the same at the point of dormancy induction or the start of forcing. The way correlative effects such as apical dominance influence the winter dormancy and its release is an area that needs further study.

The major environmental influence on bud response to chilling is the effect of intermittent exposure to temperatures above the effective chilling range. This was shown from early field studies of delayed bloom and foliation of peaches (Horne et al., 1926; Weinberger, 1954). It also affects apricots (Bordieanu et al., 1961). Subsequent controlled temperature experiments showed that the inhibition depends on temperature level, cycle duration and on the timing of high temperature exposure during the period of chilling. Peach vegetative bud break declined as the maximum temperature rose above 18°C (Erez and Lavee, 1971; Couvillon and Erez, 1985; Gilreath and Buchanan, 1981b; Overcash and Campbell, 1955). Bud break also fell as the duration of high temperature was increased from two hours to eight hours (Couvillon and Erez, 1985). It was lowest when high temperatures were experienced in a diurnal (24 h) cycle and no effect on vegetative bud break was observed when cycle duration was three days or more (Erez et al., 1979b). Extended periods of high temperature either had no effect on previously-experienced chilling (Erez and Lavee, 1971) or reduced bud break only when imposed early in the chilling treatment (Couvillon and Erez, 1985; Gilreath and Buchanan, 1981b). An apparent enhancement of the effectiveness of 'chilling' was also observed when normally less effective 'chilling' temperatures (9° to 15°C), or even moderately high temperatures (15° to 20°C) were cycled with 'chilling' temperatures. Break of floral and vegetative buds after equivalent total durations of chilling was greater when it had been experienced as part of a diurnal cycle with a higher temperature (Erez and Couvillon, 1987; Guerriero et al., 1985b). Enhanced bud break (or, at least, the absence of any inhibitory effect) was also observed after exposure of peach vegetative buds to diurnal cycles incorporating very short durations of 20°C, normally inhibitory of bud break (Couvillon and Erez, 1985). The highest bud break for the same number of hours at low temperature occurred when the moderate temperatures were experienced towards the end of the period of chilling (Erez and Couvillon, 1987).

Enhanced bud break when moderate temperatures were cycled with low temperatures has been explained by proposing that 15°C has a weak 'chilling' effect for leaf buds under a 5°/15°C cyclic temperature regime (Guerriero et al., 1985b). However, the dominant interpretation has been expressed in terms of the modification the promotive effect of low temperatures by 'chilling negation' and 'chilling enhancement' processes (Erez et al., 1979a,b; Erez and Couvillon, 1987). Periods of high temperature of sufficient duration

and warmth depress bud break by reversing the promotive effect of 'chilling'. Complete reversal of the chilling effect by extended high temperature periods is prevented by 'chilling fixation' within a few days of exposure (Erez and Lavee, 1971). In contrast, brief periods at moderate temperature increase the effectiveness of 'chilling' temperatures (Erez and Couvillon, 1987). This response, in particular, is explained by a cooperative interaction between the low and high temperature periods. This is the basis for the "Dynamic model" of peach bud dormancy release which assumes that completion of dormancy depends on the level of a 'dormancy-breaking factor', accumulated by a two-step process. The first step is reversible, forming and destroying a thermally-labile precursor while the second, irreversible step converts the precursor into a stable 'dormancy-breaking factor', but only once a critical amount of precursor has accumulated (Fishman et al., 1987a,b).

1.3.2.2   The 'chilling requirement' concept

In the United States, study of dormancy alleviation by low temperature was encouraged early this century by the practical problems faced by growers and breeders of deciduous fruit crops in southern regions with mild winters (Horne et al., 1926). Peach flowers which opened after warmer-than-normal winters were small and deformed, leaf development was irregular and in severe situations buds failed to break and abscised without any sign of growth. Importantly, however, leaf and flower buds were also greatly delayed in starting development in spring, despite apparently favourable growing conditions (Weinberger, 1950b). Observations as to the importance of low temperature exposure had been made by Howard (1910) and by Coville (1920). These authors concluded that normal bud development depended on plants experiencing a minimum duration of low temperature which broke dormancy. Thus, selection of climatically-adapted peaches was guided by the understanding that time of bloom was determined two distinct characteristics, a cold (or 'chilling') requirement for bud break and a heat requirement for blooming (Yarnell, 1944).

Initially, the relative chilling requirements of different varieties were expressed as grades based on severity of abnormal bud break symptoms (Lesley, 1944; Yarnell, 1944) or by comparison of the date of leafing with that of a standard cultivar (Lammerts, 1941). Explicit expression of the requirement in terms of duration arose by adopting the practice

of summing hours at or below a given temperature (eg 40° or 45°F, 4.4° and 7.2°C) which was used as an index of relative winter coldness (Lammerts, 1941; Yarnell, 1939). The estimated minimum duration at low temperature needed for normal budbreak and development then provided a numerical index of the 'chilling requirement' (Weinberger, 1950a). The concept of low temperature duration is now the standard means of interpreting dormant bud behaviour: "[Buds] ... accumulate or sum the periods of exposure to cold. Thus, they measure the length of the winter and anticipate spring when it is safe to resume growth" (Salisbury and Ross, 1969).

Weinberger used the concept of a cultivar-specific chill requirement, expressed in chilling hours (i.e. hours below 45°F) to assess the suitability of peach cultivars for areas in Georgia and to describe flower bud abscision. Calculated chill requirements expressed in chill hours are frequently rather broad but this did not reduce the index's value for cultivar description. For breeders and orchardists it offered a simple numerical method of describing climatic and genotypic differences in leafing and floral budbreak, especially when related to the mean temperature of the coldest winter month (Weinberger, 1956), when calculated from average monthly temperatures (Costello, 1984) or when estimated from blooming sequence (Sherman and Rouse, 1988). The concept has been used widely for a range of climates and species (George et al., 1988; Ruck, 1975) and selection for short 'chilling requirement' (expressed in chilling hours) has successfully guided breeding of peaches and nectarines for warm climates (Bowen, 1971; Sherman and Rouse, 1988) as well as that of other crops such as blueberries (Sharpe and Sherman, 1971).

The weighted chilling hour or Chill Unit (CU) was proposed to reduce differences between chilling requirements estimated in different climates (Erez and Lavee, 1971; Richardson et al., 1974) or between extreme years at one site (Lombard and Richardson, 1979). The 45°F base temperature used for calculation of 'chilling' hours initially represented a correlation with the climate of south-eastern U.S.A. and therefore the suitability of the index in other regions is dependent upon similarity of weather patterns (Weinberger, 1967b). Extended periods of sub-zero conditions or high daily maximum temperatures clearly led to erroneous estimates by the chilling hour index. Richardson et al. (1974) therefore drew on their own plus other experimental evidence to modify the chilling hour index so that hours at a given temperature were weighted in proportion

to their effect on the promotion of bud break. No chill units were accumulated below 1.4°C (34°F) and accumulation became negative above 12.5°C (55°F). Hours at 2.5°-9.1°C (37°-48°F) each contributed one unit and each hour at 1.5°-2.4°C or 9.2°-12.4°C (35°-36°F and 49°-54°F) contributed a half unit (Richardson et al., 1974). Calculations were based on 'effective bud temperatures', a derived value intermediate to actual bud temperatures and temperatures measured in an instrument shelter (Lombard and Richardson, 1979) though this is not mentioned in the original paper. Accumulation of chill units was begun just after the day in the fall when the largest negative accumulation (due to high daytime temperatures) was recorded. Inception of chill unit accumulation coincident with 50% leaf fall (used as an arbitrary index of physiological maturity) was subsequently found to be more accurate (Walser et al., 1981). Prediction of full bloom dates for 'Elberta' and 'Redhaven' peaches in Utah, Washington and Georgia then used chilling requirement fulfilment as the starting point for heat accumulation to describe bud development (Richardson et al., 1974). The concept of a minimum duration of 'chilling', a chilling requirement measured not in chill hours but in chill units, is therefore the key to the 'Utah' model.

This concept is consistent with the intended application of the 'Utah' model to determine chilling requirement fulfilment as an estimate of the start of spring flower bud development and loss of resistance to freezing temperatures. The horticultural significance of this estimate lies in the potential then to delay flower bud development using evaporative cooling and thereby reduce the risk of crop-loss due to frost damage (Anderson et al., 1975; Robertson and Stang, 1978). Initial chilling requirements for 'Redhaven' and 'Gleason Early Elberta' were determined by using vegetative bud response to gibberellin (Hatch and Walker, 1969) as an index of flower bud dormancy intensity. Appropriate heat unit (growing degree hour, GDH) sums from chilling requirement fulfilment to each phenological stage were calculated from using observations of flower bud development on 'Redhaven' under controlled temperature conditions or on 'Elberta' in the field (Richardson et al., 1974, 1975). Subsequently, chilling requirement duration was estimated statistically as the chill unit accumulation which minimised the variance of GDH sums to a phenological stage calculated from historical bloom data (Ashcroft et al., 1977). The heat unit curve by which temperatures were related to GDH accumulation has also been refined from the original linear approximation (Anderson et al., 1986).

Fundamental to the Utah chill unit model is the simulation of flower bud development on different cultivars as a temperature-dependent movement through two sequential phases. The durations of each phase are cultivar-specific but within which identical temperature accumulation functions were assumed to hold. It is assumed that growth during dormancy, prior to fulfilment of the chilling requirement, is insignificant and therefore the principle effect of low temperature is release of dormancy. A similar bipartite sequential scheme also underlies the method used to describe the effect of temperature on bloom of apples and apricots in France (Bidabé, 1967; Legave et al., 1984) although calculation of the temperature effect differs. By this method the phenological differences between cultivars may be explained in terms of differing chilling and heat requirements. Later bloom in areas with mild winter climates is attributed to delayed fulfilment of chilling requirements (Sherman and Rodriquez-Alcazar, 1987). The overall bloom period is extended by the delay being greater for cultivars with longer than average chilling requirements. This sequential arrangement of generalised temperature functions quantifying physiologically-distinct 'chilling' and heat accumulation responses has subsequently provided the basis for several other bloom phenology models which modify the original 'Utah' chill unit weightings (Andersen, 1992; del Real Laborde et al., 1990; Gilreath and Buchanan, 1981b; Norvell and Moore, 1982; Shaltout and Unrath, 1983; Tabuenca, 1979), or else propose an alternative method of calculating chilling accumulation (Fishman et al. 1987a).

1.3.2.3   Limitations of chill unit phenology models

The various modifications to the original 'Utah' chill unit model have improved the performance of this type of bloom phenology model in specific circumstances. However, it is possible that their potential accuracy is limited by the simplification represented by their biphasic nature. For instance, inaccurate simulation appears likely when the change in plant response is more gradual than that represented by the change from CU accumulation to GDH summation. If there is a progressive transition in temperature response, then CU accumulation underestimates the promotive effect of moderate temperatures (i.e. $>10°C$) towards the end of the winter period. There is also potential for error if the seasonal movement in temperature range during the modelled period is insufficient to shift the bulk of time spent from out the CU accumulation range ($\sim10°C$ and less) and into that of GDH summation ($\sim5°C$ and higher). The abrupt transition from

CU to GDH accumulation appears most reasonable in climates with a similarly abrupt temperature transition between winter and spring. This is because the model can not represent the possible effect of heat accumulation after the partial fulfilment of the chilling requirement. This may explain why the 'Utah' model did not accurately predict the start of bud development in New Jersey when spring and winter temperatures fluctuated widely (Bailey et al., 1982). Fulfilment chilling requirements calculated using the 'Utah' model also did not correlate with the occurrence of flower bud anomalies observed on late-blooming cultivars grown in coastal or tropical regions (Balandier et al., 1993; Lombard and Richardson, 1979; Guerriero and Bartolini, 1991).

'Utah' chill unit-type models therefore do not appear well suited to mild maritime regions such as Hawkes Bay where the temperature distinction between winter and spring is limited. If the transition between bud development phases is progressive then average winter temperatures are warm enough for significant development to occur before the predicted end of dormancy (calculated by completion of chill unit accumulation) and the start of heat unit accumulation. Consequently, bud development before the calculated fulfilment of the chilling requirement is under-estimated and predicted bloom is late. Over-estimation of development stimulated by warm temperatures early after the calculated release of dormancy is also possible if temperature response during this period does not immediately match the GDH model. Therefore, where the chilling requirement of two cultivars differ, relatively warm periods occurring between fulfilment of the respective chilling requirements will affect simulated development of the two cultivars differently. Development may be over-estimated for cultivars with short chilling requirements and underestimated in the case of those with long requirements.

1.3.3 Modelling Apricot Bloom Phenology: Conclusions

Two forms of temperature-weighted time- heat units and chill units- therefore provide the principal existing methods for modelling apricot bloom phenology as the basis for assessing the opportunity for cross pollination. Both are essentially practical methods developed for pragmatic purposes although, as shown, the summation of temperature data as performed in heat unit accumulation does have a basis in thermodynamic. This is not the case for the chill unit which is an entirely empirical device whose accuracy appears

to depend on suitable climatic conditions given the many modifications needed to extend application of chill unit models to regions with other climates.

The empiricism of the chill unit does not deny its validity as a tool for the task it was designed to perform. The chill hour and chill unit are both eminently suitable modelling solutions where significant computational capacity is not available. Nor does it rule out *a priori* the possibility that chill unit models could adequately describe apricot bloom phenology in Hawkes Bay. However, the suitability of sequential developmental indices (chill units and GDH) may also reflect the specific seasonal temperature range of climates such as that of Utah more than the actual physiology of dormancy induction and release. In particular, the assumptions of a uniform response to chilling and insignificant growth during dormancy appear most appropriate in a climate where temperatures are low enough to prevent significant growth until dormancy is completely alleviated. Since this is not the case in Hawkes Bay the sequential combination of such empirical indices may prove an inadequate method for modelling dormancy alleviation and flower bud development. Instead, more robust and accurate phenology modelling may require an alternative modelling framework that allows more detailed consideration of dormancy duration and depth and intervarietal variation. The establishment of such a framework is therefore a key objective in this investigation of the pollination of 'Sundrop' apricot.

1.4   References

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Chapter 2
Self Incompatibility of 'Sundrop' Apricot

2.1   Introduction

Self sterility in the genus *Prunus* is commonly caused by pollen tube self incompatibility, a gametophytically-determined trait normally expressed by the inhibition of pollen tubes in the upper half of the style (de Nettancourt, 1977). Almost all sweet cherry cultivars and most almonds and plums need cross pollination because of self incompatibility (Gur, 1985) but apricot cultivars have been regarded as self fertile, at least in countries where 'European'-type apricots predominate (Mehlenbacher et al., 1991). Some apricot cultivars recently introduced to New Zealand are exceptions to this rule. Those requiring cross-pollination include 'Goldrich' and 'Rival' (Fogle and Toyama, 1972), 'Earliril' (Lamb and Stiles, 1983), 'Skaha' (Lapins, 1975) and also 'Valleygold'. 'Sundrop' also appears to require cross pollination for commercial levels of set. The cultivar has acquired a reputation for unreliable fruit set in the South Island regions of New Zealand and in Hawkes Bay, 'Sundrop' blocks which crop satisfactorily in some years, produce little or no fruit in others (Gilchrist, 1990; Noiton, *pers. comm.*). Hand self pollination gave only two percent fruit set compared with 19% and 38% after cross pollination with 'Moorpark' and 'Trevatt' pollen respectively (Wood, 1983).

Poor fruit set after self pollination is probably due to pollen tube self incompatibility, a genetic trait inherited from 'Perfection', a parent of 'Sundrop' which also requires cross pollination (Schultz, 1948) and thus passed on to 'CluthaGold' and 'CluthaGem', offspring of 'Sundrop'×'Moorpark crosses (Glucina et al., 1988, McLaren, Lewis and Glucina, 1992). However, mono-varietal blocks of 'Sundrop' in Central Otago can sometimes set adequate crops and under some conditions pollen tubes from 'Sundrop' pollen penetrate the style of 'Sundrop' flowers (McLaren Fraser and Grant, 1992). It may therefore also reflect the influence of low temperature on pollen tube development which is suggested as the principal reason for low set of fruit and nuts during cool spring seasons (Westwood, 1978). Development of apricot and other *Prunus* microgametophytes is strongly temperature-dependent (Cerović and Ruzič, 1992; Keulemans, 1984; Stott et al.,

1974; Vachun, 1981) but in Hawkes Bay apricots bloom in late winter when mean air temperatures are 10°-12°C. Sensitivity to low temperature of tubes from 'Sundrop' pollen or of tubes in 'Sundrop' styles might prevent fruit set by retarding pollen tube penetration so that fertilization could not occur before ovules senesced (Thompson and Liu, 1973). Male sterility in 'Sundrop' would also necessitate cross pollination.

The extent and time course of pollen tube growth after self and cross pollination of 'Sundrop' was therefore investigated to identify the cause of the cross pollination requirement and establish potential fruit set levels under Hawkes Bay conditions. In addition, modification of pollen tube development in 'Sundrop' styles by temperature and interaction between pollen applications was also investigated. Early-deposited pollen has been reported to enhance the penetration of subsequently-developing pollen tubes (Visser and Verhaegh, 1980). Since under natural conditions pollen is transfered to 'Sundrop' pistils over several days it is possible that early 'pioneer pollen' might also reduce self incompatibility or stimulate penetration by tubes from later-deposited self pollen. Low temperature also reduces the expression of self incompatibility in cherries and almonds (Lewis, 1942; Socias i Company *et al.*, 1976) and in other gametophytic systems (de Nettancourt, 1977) but possibly not in 'Sundrop' (McLaren, Fraser and Grant, 1992). Development of self pollen tubes after repeated self pollination was therefore measured to test whether heavy self pollination permitted self fertilization and overcame the need for cross pollination. The growth of pollen tubes in 'Sundrop' styles after self and cross pollination at a range of controlled temperatures was also investigated to measure the response of pollen tube growth rate to incubation temperature and investigate the potential effect of temperature on self incompatibility.

Finally, the cross compatibility of 'CluthaGold' and 'Sundrop' was investigated. 'CluthaGold' shows promise as a cultivar for Hawkes Bay (Glucina et al., 1990) but both cultivars require cross pollination (Glucina et al., 1988; Wood, 1983). The two cultivars overlap in their flowering period (Glucina et al., 1990) and the close relationship between them suggests they may respond similarly to climate and therefore could be reliable reciprocal pollenizers. However, genetic similarity also introduces the risk of cross incompatibility and this possibility was therefore investigated by controlled reciprocal cross pollination.

2.2   Methods and Materials

2.2.1   General Techniques

2.2.1.1   Emasculation and hand-pollination

Pollen for pollination experiments in 1990 was prepared from flowers forced on cuttings. Budwood was collected in late July from orchards at Havelock North Research Centre (HNRC) and Massey University Fruit Crops Unit (FCU), recut under water and forced at 20°C in a glasshouse for one week. Anthers were removed manually from flower buds at 'balloon' stage, shaken to ensure homogeneity and dried at 25°C for 12 h. The dehiscent anthers were used immediately or were sealed in 1.5 ml plastic centrifuge vials and stored at -20°C for later use. In 1991 and 1992, 'Sundrop' and 'Trevatt' pollen for field experiments at Fernhill Farm and FCU was prepared from 'popcorn' stage buds collected at Fernhill on the first day of emasculation. Anthers were spread on petri dishes and dried in the open air until dehiscence was complete (3-4 h). Anthers were either used immediately or divided into sealed vials and stored at 4°C if used at Fernhill or -20°C for later use at FCU. 'Goldrich' and 'Trevatt' pollen samples used to investigate the influence of temperature on pollen tube growth were collected from Fernhill Farm: 'Goldrich' on 31 July 1992 and 'Trevatt' on 15 August 1992. 'CluthaGold' pollen was collected on 9 August 1992 from Campbell's Orchard at Bridge Pa in Hawkes Bay. 'Sundrop' pollen was prepared from the same flowers collected from FCU for the experiment.

Flowers were emasculated at the 'balloon' stage 1-2 days before natural anthesis (Bailey and Hough, 1975) by removing petals and anthers at the corolla cup with forceps or fingers. Emasculated flowers were pollinated later the same day by applying pollen directly to the stigma with the tip of a finger. Hands were swabbed with 70% alcohol between pollen types to prevent cross contamination. Under field conditions anthers of 'Sundrop' flowers did not dehisce within flower buds before emasculation.

2.2.1.2   Pistil preparation and dissection

Pollen tube development in stylar transmitting tissue and the ovarian cavity was observed using fluorescence microscopy and aniline blue to stain callose in pollen tubes (Kho and

Baer, 1968). Pistils were fixed immediately after harvesting without dissection. In 1990 and 1991 entire flower buds were fixed in 1:3 glacial acetic acid:ethanol and transferred to 70% ethanol 24 h later. Since this method appeared to cause shrinkage of the pollen tubes it was replaced in 1992 by FAA (5:5:90 formalin : glacial acetic acid : 70% ethanol) as fixative and preservative. In addition, only pistils were fixed since tannin from bud scales diminished fluorescence of pollen tubes.

For dissection, fixed pistils were placed in 10% Na_2SO_3 (w/v) and softened in a pressure cooker. After 5 min at 120°C, samples were quickly removed and washed with distilled water once cool enough to handle. Excessive maceration caused the epidermis and transmitting tissue to lose structural integrity. Pistils were immersed overnight at 4°C in 0.1% w/v water-soluble aniline blue (BDH Gurr, C.I 42755) decolorised in 0.1 M $K_3PO_4.H_2O$. Dissection involved removing the stylar epidermis and epidermal hairs (which both fluoresced brightly) and ovary tissue surrounding the ovules. Dissected styles were mounted in 1:1 glycerol:aniline blue dye solution, squashed gently, and observed immediately. At 100% relative humidity and 4°C prepared slides stored for several weeks without marked deterioration.

Initial dissections in 1990 demonstrated that pollen tubes and transmitting tissue were clearly distinguished by callose fluorescence after pistils were stained with aniline blue but that the fluorochrome was not entirely specific to callose. The stylar epidermis and epidermal hairs also fluoresced strongly and therefore were removed in dissections along with parenchyma tissue surrounding the ovarian cavity. Stylar transmitting tissue also fluoresced weakly. This sometimes obscured the weak fluorescence of pollen tube tips but Normarski differential interference microscopy usually distinguished the thicker-walled tubes from the thinner-walled transmitting tissue.

Pollen tube numbers were counted in the first quarter of the style below the stigma, at the entrance to the ovary and at the ovule micropyle. Maximum pollen tube length was measured in conjunction with style length (distance from start of transmitting tissue to stylar abscission zone) using a stage-mounted vernier scale. In senescent styles, a band of fluorescent sclerified tissue marked the abscission zone. Younger presenescent styles lacked this feature and constriction of transmitting tissue and frequent overlap (in dissected

material) of xylem strands in this region were used as markers. Pollen grains retained by stigmas were also counted but were too variable to reliably estimate pollen germinability.

Measurement of individual tube length was not attempted since squashes frequently contained many tubes and because some tubes usually broke during squashing. Maximum tube length was calculated as the distance from the top of the transmitting tissue to the tip of the most penetrative pollen tube. Where pollen tubes in the ovular cavity had curled or bent during squashing the original length was estimated by adding the length of the displaced tube. Pistils were also scored for the length of pollen tube plugs relative to pollen tube diameter in the top 25% of the style using a 5-point scale: 0=no plugs; 1=width equivalent to 1-2 pollen tube diameters; 2=2-5 diameters; 3=5-10 diameters; 4=10-20 diameters. Irregular callose deposition in abortive tubes was recorded separately by counting any brightly fluorescent tubes over the entire style.

2.2.1.3   Microscopy and photomicrography

Pollen tube fluorescence was observed using a Reichert Diapan or an Olympus BH2 binocular microscope fitted with Sylvania FCR quartz-halogen bulbs. A Kodak Wratten No 12 gelatin filter and a 10% solution of copper(II) ammonium complex in a flat-sided tissue-culture bottle were used as barrier and exciter filters. The solution had a transmission maximum of 340 nm when freshly prepared and was replaced when precipitation of $Cu(OH)_2$ occurred. In cases where fluoresence was too weak (eg high power observation of thin-walled tips of tubes) Normarski differential interference microscopy was used to aid observation.

Colour slides were made on Kodak Ektachrome 160T transparency film. Colour prints were prepared from transparencies and monochrome prints from negatives taken on Kodak T-Max 100. Daylight colour transparencies were taken on Kodak Ektachrome 100 or 100 Plus film using an Olympus OM1 camera and a standard 50 mm Olympus f 1.4 lens. Diopter lenses (+2 and +4) and a Olympus 80 mm lens/bellows combination were used to give a range of magnifications. A quartz-halogen flood lamp or a Schott-Mainz KL150B quartz-halogen light source provided additional lighting when needed and colour rendition was corrected with a Hoya 80B blue filter.

2.2.2   **Pollen Viability and Self Incompatibility of 'Sundrop'**

In 1990, an experiment to measure pollen tube growth in 'Sundrop' pistils and the viability of 'Sundrop' pollen was performed on a single 5-year-old 'Sundrop' tree at Massey University Fruit Crops Unit (FCU). This preliminary study was performed in association with an investigation of interspecific pollination of 'Sundrop' (Appendix 1). To compare pollen tube growth in 'Sundrop' styles, four sets of 50 flowers on labeled branch sections were emasculated on 22 August and pollinated with 'Sundrop', 'CluthaGold', 'Royal Rosa', or 'Valleygold' pollen which had been prepared earlier from flowers on forced cuttings (Section 2.2.1.1). Spurs carrying the pistils were enclosed in waterproof, double-walled paper bags to prevent accidental pollination after hand pollination. Pistils were collected 72 h and one week after pollination and fixed in 1:3 acetic ethanol. Later, to check the viability of 'Sundrop' pollen, two sets of 100 flowers spread over three three-year-old 'CluthaGold' trees at FCU were emasculated on 1 September and hand-pollinated with either 'Sundrop' or 'CluthaGold' pollen. Flowers were bagged and collected after one week and fixed in 1:3 acetic acid/ethanol. Data analysis was performed using PROC GLM (SAS Institute, 1989).

A second pollination trial to confirm the viability of 'Sundrop' pollen and establish the cross-compatibility of 'Sundrop' and 'CluthaGold' as reciprocal pollenizers was conducted at FCU in 1993. On 3 September 1993 over 200 flowers were emasculated on each of three 'Sundrop' and 'CluthaGold' trees. Half the flowers on each tree were hand-pollinated with 'Trevatt' pollen. On 'CluthaGold', the remainder were pollinated using 'Sundrop' pollen while those on 'Sundrop' were pollinated using 'CluthaGold' pollen. Pollen was prepared from anthers collected from FCU on the day of emasculation. Pollination was delayed three days after emasculation due to frequent rain in the period following emasculation. Twelve days after pollination a subsample of five pistils was collected from each treatment replicate for examination of pollen tube penetration. Counts of fruit set were made at pit-hardening (late October) and at harvest (late December).

Self incompatibility of 'Sundrop' was tested in 1991 and 1992 using mature trees at FCU and at Fernhill Farm orchard (Rex Graham Associates Ltd) in Hawkes Bay. Five well-

formed trees were selected at both sites in 1991 and again in 1992. 'Sundrop' and 'Trevatt' pollen was prepared as described (Section 2.2.1.1). Self and cross pollination treatments using 'Trevatt' pollen (Table 2.1) were randomly allocated to labelled branch segments carrying sufficient flowers to leave at least 20 pistils for fruit set measurements after removal of histology samples. Pistils were collected 4, 8 and 12 days after emasculation (and pollination), fixed immediately and then dissected for measurement of pollen tube penetration (Section 2.2.1.2). The experiment was replicated on each tree by applying each treament to two blossom cohorts, one emasculated and pollinated at 5% Bloom, the other at 50% Bloom. At Fernhill Farm Orchard, two days separated the cohorts while at FCU the separation was four days. The trees also carried treatments belonging to experiments investigating ovule senescence and the effect of delayed pollen application (Chapter 4). Several treatments were shared in common between experiments to minimise total flowers required per tree. Blossom quality at Fernhill Farm Orchard was poor in 1992 and up to 50% of flowers lacked functional pistils. Shortage of flowers at the ideal stage for emasculation therefore made it necessary to distribute treatments over two or three adjacent trees. Allocation of treatments to branch sections was randomised anew for each group of trees. Trees at FCU were each enclosed in white 30% shade-cloth netting to exclude honeybee foragers and other insects but close tree spacing at Fernhill Farm Orchard made this impossible. Fruit set was measured at 'pit-hardening' and immediately before harvest (Table 2.1) and was calculated as the fraction of fruit remaining from fruitlets present three weeks after emasculation. This initial count coincided with the conclusion of abscission of pistils damaged during emasculation.

Air temperature within the tree canopy 1.5 m above ground level (height of the lowest emasculated pistils) was monitored during bloom (Table 2.2). In 1991 shielded max-min

Table 2.1   Recording dates for measurement of fruit set after hand-pollination of 'Sundrop' trees at Fernhill Farm and FCU, 1991 and 1992.

Site and Year		Initial pistil count	Pit-hardening	Pre-harvest
Fernhill Farm	1991	5 September	15 October	17 December
	1992	15 September	28 October	16 December
FCU	1991	20 September	25 October	9 January 1992
	1992	1 October	30 October	5 January 1993

Table 2.2 Maximum and minimum air temperatures at 1.5 metres during apricot bloom periods at FCU and Fernhill Farm Orchard, 1991 and 1992.

Site and Date	Date of first emasculation	Mean Maximum	Mean Minimum	Lowest Minimum
Fernhill Farm				
12-30 August 1991	12 Aug	15.7°±0.6	2.5°±1.2	-1.0° (19 Aug)
5-19 August 1992	5 Aug	15.3°±0.6	5.5°±1.2	-0.8° (6 Aug)
FCU				
26 Aug-13 Sept 1991	26 Aug	15.9°±0.3	8.2°±0.6	1.5° (7 Sept)
20 Aug-5 Sept 1992	18 Aug	12.1°±0.5	4.3°±0.9	-1.0° (30 Aug)

thermometers were used while in 1992 a data-logger recorded hourly temperatures from temperature sensors housed in a Stephenson screen. Temperatures during the pollination period at FCU in 1992 were significantly cooler than in 1991 and cooler than Fernhill Farm Orchard in 1991 and 1992. The experiments used a split-block design nested in year and site in which trees served as experimental blocks, bloom cohorts as splits blocks and the branch sections to which treatments were applied as the experimental units. Data describing microgametophyte development and fruit set were analyzed using PROC GLM (SAS Institute Inc., 1989). Data for pollen tube counts and fruit set were transformed by square-root and probit transformations respectively.

2.2.3 Temperature and Pollen Tube Development

Germination of apricot pollen, growth of pollen tubes and the expression of self incompatibility was investigated in 'Sundrop' pistils incubated at 5°, 10°, 15°, 20° and 25°C. Fifty centimetre shoots bearing flower buds at 'popcorn' stage were collected on 27 August 1992 from mature 'Sundrop' trees at FCU, recut under water, and stood in Chrysal preservative solution (Pokon & Chrysal, 30 ml l^{-1}) at 15°C until flowers reached 50% anthesis (two days). The most advanced flowers (completely open: about 5% of total buds) and the least developed (tightly closed at the time of pollination: about 10%) were discarded to increase flower uniformity. Shoots were then cut into 10 cm bud-sticks, each carrying 2-5 flowers, placed in fresh Chrysal in 30 ml disposable plastic vials and randomly allocated to trays in incubators controlled to within 0.2°C. Preservative solution was replaced after four and eight days.

Pollen of the cultivars 'CluthaGold', 'Goldrich', 'Sundrop' and 'Trevatt' was applied with a needle to coat the stigmas of equal numbers of flowers at each incubation temperature. Flowers were not emasculated and were therefore covered to limit accidental self pollination.   Five randomly-selected flowers were removed from each cultivar/ temperature combination 1, 2, 4, 5 and 12 days after pollination.   Pistils were fixed in FAA, stored at 4°C until dissected and ovary, ovule and pollen tube development measured (Section 2.2.1.2).   The distribution of pollen tube count data was adjusted by the square-root transformation (Snedecor and Cockrane, 1980) and analysed as a factorial/split-plot-in-time design using PROC GLM (SAS Institute, 1989).

2.3   Results

2.3.1   Viability of 'Sundrop' Pollen and Pistils

Initial development of 'Sundrop' pollen tubes in 'Sundrop' pistils was similar to that of other apricot cultivars at FCU in 1990 (Table 2.3; Methods section 2.2.2) and numbers of tubes from 'Sundrop' pollen lay in the middle of the range observed at the top of styles. Only pistils pollinated with 'CluthaGold' pollen held significantly more tubes. By contrast, penetration by tubes from 'Sundrop' pollen grains was much weaker than that of other cultivars and one week after pollination their length was only half that of tubes from 'CluthaGold', 'Royal Rosa' and 'Valleygold' pollen grains. No 'Sundrop' tubes had reached the ovary whereas in several pistils pollinated with 'CluthaGold' and 'Royal Rosa' pollen the ovary had been penetrated. Substantial loss of pistils (due to damage to pistils as wind shook the bags enclosing spurs) meant fruit set results were inconclusive.

Viability of 'Sundrop' pollen was confirmed by crosses with 'CluthaGold' which also tested cross compatibility and self incompatibility of 'CluthaGold'. At FCU in 1990, similar numbers of pollen tubes were present below the stigma of 'CluthaGold' pistils pollinated with 'Sundrop' and 'CluthaGold' pollen and the penetration of 'Sundrop' and 'CluthaGold' tubes 72 h post-pollination was the same (Table 2.4). However, one week after pollination, 'Sundrop' tubes had reached the ovary of 'CluthaGold' pistils whereas the tips of 'CluthaGold' tubes had penetrated less than halfway down the style. Extension

Table 2.3   Number of pollen grains retained on stigma, pollen tube growth one week after cross and self pollination of 'Sundrop' pistils and resulting fruit set: FCU, 1990.

Pollen cultivar	No. grains on stigma	No. tubes in style	Tube length (mm)	Number of	
				Pistils	Fruit
'CluthaGold'	48 a	37 a	13.9 a	44	5
'Royal Rosa'	20 bc	14 b	15.4 a	22	1
'Valleygold'	7 c	8 b	12.3 a	31	0
'Sundrop'	29 ab	15 b	6.7 b	30	0
Contrast					
'Sundrop' vs Others	ns	ns	***		

ns, *** Contrasts non-significant or significant at $P \leq 0.001$. Means separated within columns by Tukey's multiple range test, $P = 0.05$.

Table 2.4   Pollen tube growth and final fruit set after pollination of 'CluthaGold' pistils with 'Sundrop' and 'CluthaGold' pollen: FCU, 1990.

Pollen cultivar	No. grains on stigma	No. tubes in style	Tube penetration (mm) 72 h	Tube penetration (mm) 1 week
'Sundrop'	57 ± 11	8 ± 2	5.5 ± 0.8	15.0 ± 0.8
'CluthaGold'	30 ± 3	8 ± 2	3.6 ± 0.6	5.8 ± 1.2
Significance	ns	ns	ns	**

[ns, **] Difference between means non-significant or significant at $P \le 0.01$.

by 'Sundrop' tubes in 'CluthaGold' styles was therefore similar to that of tubes from 'Royal Rosa', 'CluthaGold' and 'Valleygold' pollen in 'Sundrop' styles (Table 2.3). All 'CluthaGold' tubes failed to reach the ovary. Some fruit set after pollination with 'Sundrop' pollen but none set after self pollination of 'CluthaGold'. Wind damage, however, again severely reduced pistil numbers.

The ability of 'Sundrop' pollen to set fruit and the cross compatibility of 'Sundrop' and 'CluthaGold' were confirmed at FCU in 1993 (Table 2.5). Fruit set on 'Sundrop' and 'CluthaGold' after both reciprocal crosses was similar to that induced with 'Trevatt' pollen. Set was lower than that expected on the basis of previous experiments at FCU. This was probably due to the poor conditions (persistent light showers) in which pollen was applied.

Table 2.5   Fruit set at FCU in 1993 after reciprocal cross pollination of 'Sundrop' and 'CluthaGold' compared to pollination with 'Trevatt'.

Pistil cultivar	Pollen cultivar	Original pistils	Fruit set At pit-hardening	Fruit set At harvest
'Sundrop'	'Trevatt'	287	65 (23%)	53 (18%)
	'CluthaGold'	300	45 (15%)	40 (13%)
'CluthaGold'	'Trevatt'	221	61 (28%)	57 (26%)
	'Sundrop'	202	66 (33%)	50 (25%)

2.3.2   Self Incompatibility of 'Sundrop'

2.3.2.1   Pollen tube development

Pollen grains germinated on the stigmas of all six treatments (including non-pollinated controls) as indicated by the presence of pollen tubes beneath the stigma in the top 25% of the style (Fig. 2.1a; Methods 2.2.2). The number of tubes varied significantly between treatments (Table 2.6) and was highest in styles of non-emasculated flowers (open

Table 2.6   Analysis of variance for pollen tube development after self, cross and open pollination of 'Sundrop' pistils at Fernhill Farm Orchard, August 1991.

Source	df	Variance components (Type III MS)			
		Stylar tubes	Ovary tubes	Style penetration	Ovule penetration
Model	158				
Tree	4	2005 ns	2.48 ns	0.176 ns	0.0053 ns
Cohort	1	1998 ns	0.53 ns	0.037 ns	0.0005 ns
Residual 1: Cohort×Tree	4	750	2.33	0.080	0.0064
Treatment	5	117230 ***	32.02 *	8.041 ***	0.0699 ns
Residual 2: Treatment×Tree	20	1198	2.39	0.185	0.0108
Cohort×Treatment	5	1996 ns	2.97 ns	0.270 ns	0.0120 ns
Residual 3: Cohort×Trt×Tree	20	959	1.27	0.098	0.0100 *
Time	2	43850 ns	28.71 ns	1.191 ns	0.2927
Time×Cohort	2	4381 ns	1.93 ns	0.311 ns	0.0005 ns
Time×Treatment	10	7278 *	6.38 **	0.276 ns	0.0545 ***
Time×Cohort×Treatment	10	1863 **	1.01 ns	0.200 ns	0.0045 ns
Residual 4: Trt×Co(Time×Tree)	75	567	1.24	0.099	0.0122
Error	717	320	0.64	0.053	-
R^2		0.80	0.53	0.71	0.64
Contrasts					
'Sundrop', Day 0 vs 'Trevatt'	1	493 ns	85.0 ***	15.028 ***	0.4421 ***
'Sundrop', Day 0&2 vs 'Trevatt'	1	42843 ***	89.3 ***	8.552 ***	0.4421 ***
'Sundrop' vs None	1	43182 ***	3.2 *	non-est.	0.0141 ns
'Sundrop' Day 0 vs Day 0&2	1	52463 ***	0.1 ns	1.270 ***	0.0000 ns
'Trevatt' vs Unemasculated	1	111022 ***	3.0 *	0.491 **	0.0075 ns
Open vs Unemasculated	1	28 ns	8.0 ***	0.352 **	0.0432 ns
4 Days vs 8 Days, 'Sundrop'	1	**	ns	ns	ns
4 Days vs 12 Days, 'Sundrop'	1	***	ns	ns	ns

ns, *, **, *** Model effects and contrasts non-significant or significant at $P \le 0.05$, $P \le 0.01$ or $P \le 0.001$ respectively.

pollinated and non-emasculated 'Trevatt'-pollinated controls) and in pistils twice pollinated with 'Sundrop' pollen. In some pistils from non-emasculated flowers there were over 100 pollen tubes in the transmitting tissue immediately beneath the stigma. Fewer pollen tubes were found in pistils hand-pollinated only once. Similar numbers were observed whether the pistil was pollinated with 'Sundrop' or 'Trevatt' pollen and therefore germinability of 'Sundrop' pollen was comparable to that of 'Trevatt' pollen. Pollen tube numbers fell sharply with time from pollination in four of the treatments suggesting that tube fluoresence (and hence visibility) declined in the measurement area as they aged. A small but significant number of tubes was also found in styles of the non-pollinated control treatment, indicating that accidental pollination of emasculated pistils did occur, either by wind or, possibly, by the visit of bees since trees at Fernhill were not enclosed by netting. However, the number of tubes in self pollinated pistils exceeded the number of tubes in non-pollinated pistils.

In all treatments the number of pollen tubes also fell sharply between the top of the style and the entrance to ovary, and especially in open and self pollinated pistils (Fig. 2.1b). Treatment effects were again significant but in this case, the highest tube counts were made in emasculated pistils hand-pollinated with 'Trevatt' pollen. By 12 days after pollination on average two tubes had entered the ovary, significantly more than after self pollination and also more than after open pollination or cross pollination of non-emasculated flowers. Additional self pollen application did not enhance self pollen tube penetration. Very few pollen tubes in self pollinated pistils penetrated to the ovary and the number was significantly fewer than in non-pollinated pistils.

Depth of pollen tube penetration down the style was also strongly influenced by the interaction of pollen and pistil genotype (Fig. 2.1c). Most pollen tube extension by the longest pollen tube occurred in the first four days after pollination and therefore time of sampling had little effect on maximum tube length (Table 2.6). In particular, tubes from 'Sundrop' pollen grains had ceased growth within 4 days of pollination after penetrating one third to one half of the style, much less than the penetration by tubes from 'Trevatt' pollen grains. Repeated application of self pollen (self pollination, Day 0 and Day 2) increased average maximum tube penetration, but penetration to the ovary still did not occur (Fig. 2.1c). Pollen tubes from 'Trevatt' pollen grains first penetrated ovules 12 days
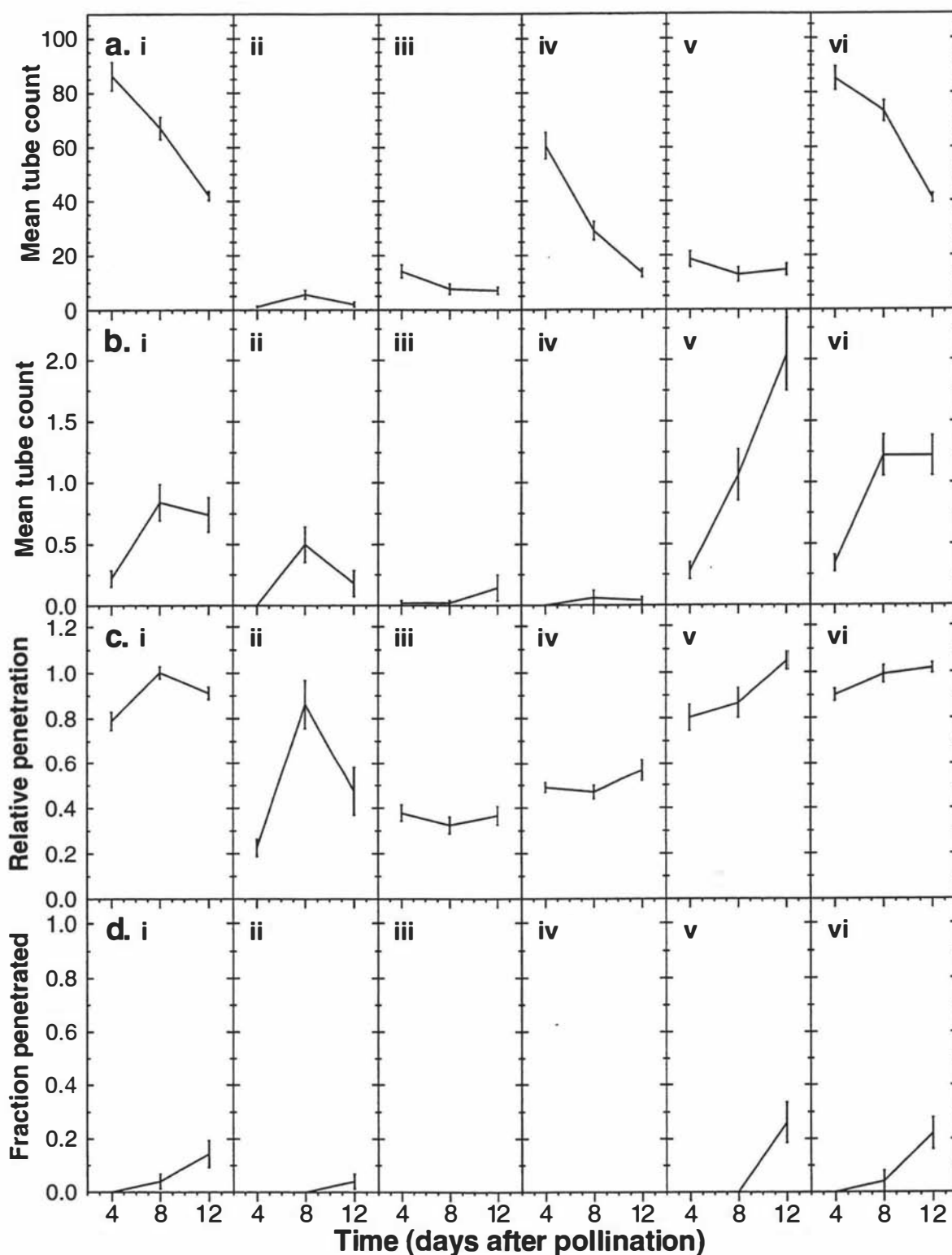
Figure 2.1   Pollen tube count below stigma and at ovary entrance, depth of style traversed by longest tube and fraction of ovules penetrated 4, 8 and 12 days after controlled self and cross pollination of 'Sundrop' flowers at Fernhill Farm Orchard, 1991. a). Pollen tube count per flower in transmitting tissue below stigma; b). Pollen tube count per flower at entrance to ovary; c). Maximum pollen tube penetration as a proportion of style length; d). Fraction of ovules penetrated by pollen tubes.
Pollination treatments: i). Open pollinated; ii). Nonpollinated; iii). Self pollinated, Day 0 only; iv). Self pollinated, Day 0 & 2; v). Cross pollinated with 'Trevatt'; vi). Cross pollinated with 'Trevatt', non-emasculated. (Means±SE of pooled 'Early' and 'Mid' bloom cohorts.)

after pollination in emasculated flowers (Fig. 2.1d) but after only eight days where petals remained on the flowers (open pollinated flowers and unemasculated flowers pollinated with 'Trevatt' pollen). No ovules were penetrated after single or repeated self pollination with 'Sundrop' pollen. Several penetrated ovules were found in pistils from the non-pollinated, emasculated control, possibly due to accidental cross pollination.

Pollen tubes in the style of 'Sundrop' flowers after self pollination and cross pollination with 'Trevatt' pollen differed morphologically in addition to their difference in length. Pollen tubes from 'Trevatt' pollen grains were relatively homogeneous and were punctuated by regular, discrete plugs (Fig. 2.2a). Plugs were longest (0.1 to 0.2 mm) near the top of the style and became shorter (0.02 to 0.05 mm) towards the base. Tube number declined down the style so that only one to five pollen tubes normally lay between the lobes of placental tissue at the entry to the ovarian chamber (flattened during squashing). Occasional abortive tubes with brightly fluorescent tips or irregular callose deposition were observed throughout the style in association with tubes which penetrated most or all of the way to the ovary (Fig. 2.3a). Viewed under Normarski differential contrast, such tubes displayed thicken walls and tips (Fig. 2.3b) similar to those observed in tubes from self pollination. By contrast, pollen tubes from 'Sundrop' pollen grains were characterised by highly fluorescent, thick-walled tubes which typically terminated a short distance down the style (Fig. 2.2b). Pollen tube tips in this area of the style frequently appeared to be occluded with callose (Fig. 2.3c) or, less commonly, had burst (Fig. 2.3d).

Tube appearance was more variable in styles of self pollinated 'Sundrop' flowers than in cross pollinated flowers. In some styles, pollen tubes lacked plugs and fluoresced intensely near the top of the style but displayed a regular pattern of plug formation nearer the ovary. Alternatively, tubes contained regular plugs near the top of the style but became highly fluorescent in the middle or lower regions of the transmitting tissue. Such tubes frequently terminated with swollen or thickened tips suggesting that pollen tube abortion had occurred at that point. Weakly fluorescent, thin-walled pollen tubes with bright regular callose plugs and which penetrated to the ovary were also occasionally observed. Overall, however, the lack of tube extension after 4 days and histological differentiation between tubes from self and cross pollinations indicated that limited tube

Figure 2.2   Photomontages of pollen tube penetration in 'Sundrop' styles eight days after pollination under field and controlled-temperature conditions.   a). Cross pollination 'Trevatt' pollen, Fernhill Farm Orchard 1991; b). Self pollination, Fernhill Farm Orchard, 1991; c). Self pollination, 5°C incubation temperature.   (Bar = 1 mm.   Abbreviations: st = stigma, pt = pollen tubes, tt = transmitting tissue, et = end of pollen tube, es = end of style, po = position of ovules.)
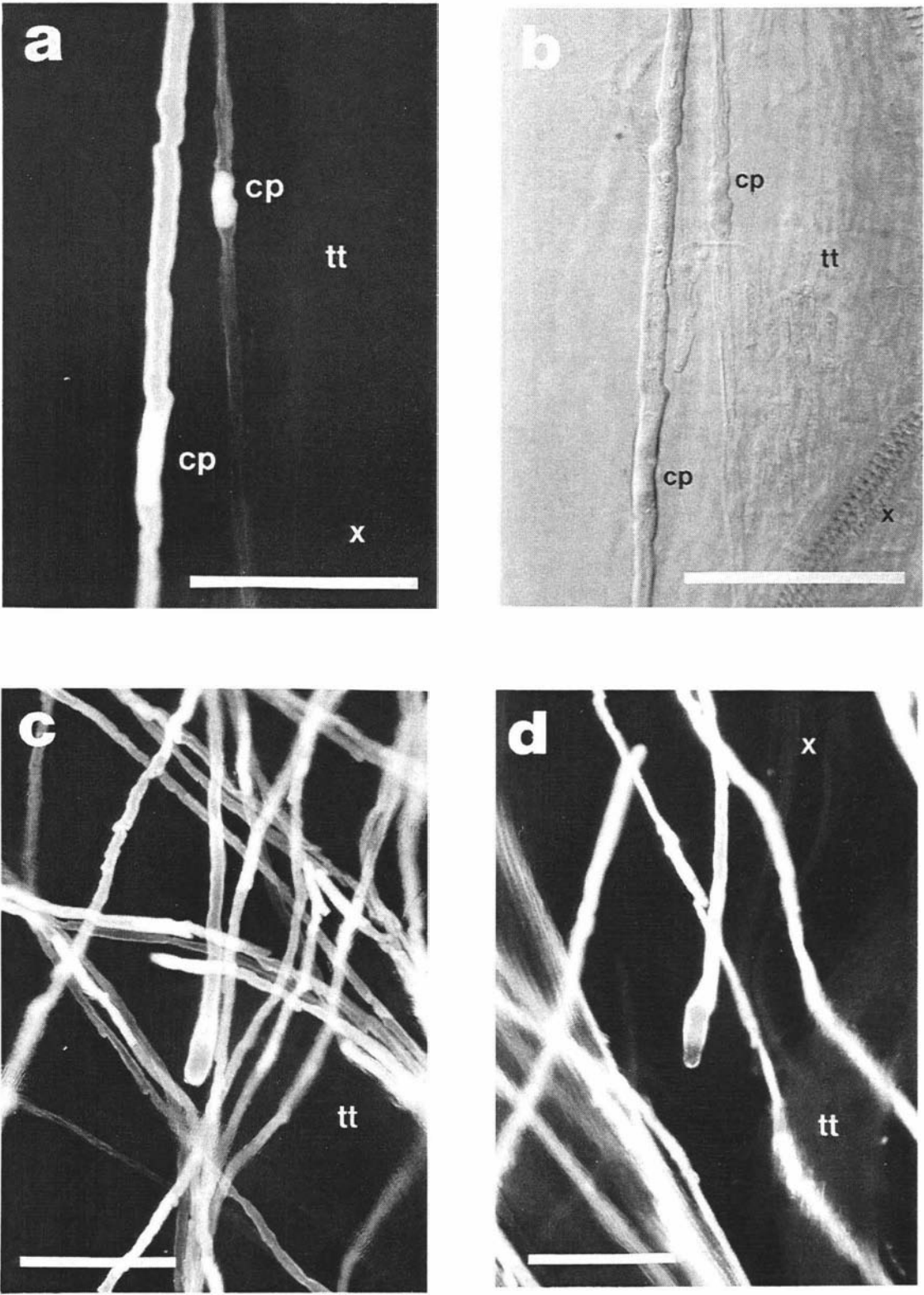
Figure 2.3   Detail of pollen tube development after pollination of 'Sundrop' pistils with 'Sundrop' and 'Trevatt' pollen.   a) & b). Fluorescent and non-fluorescent tubes after cross pollination, fluorescent and Normarski differential interference microscopy (Tubes shrivelled due to dehydration during fixation.); c) & d). Abortive tube tips after self pollination. (Bar = 100 μm. Abbreviations: cp = callose plug; tt = transmitting tissue; x = xylem vessels.)
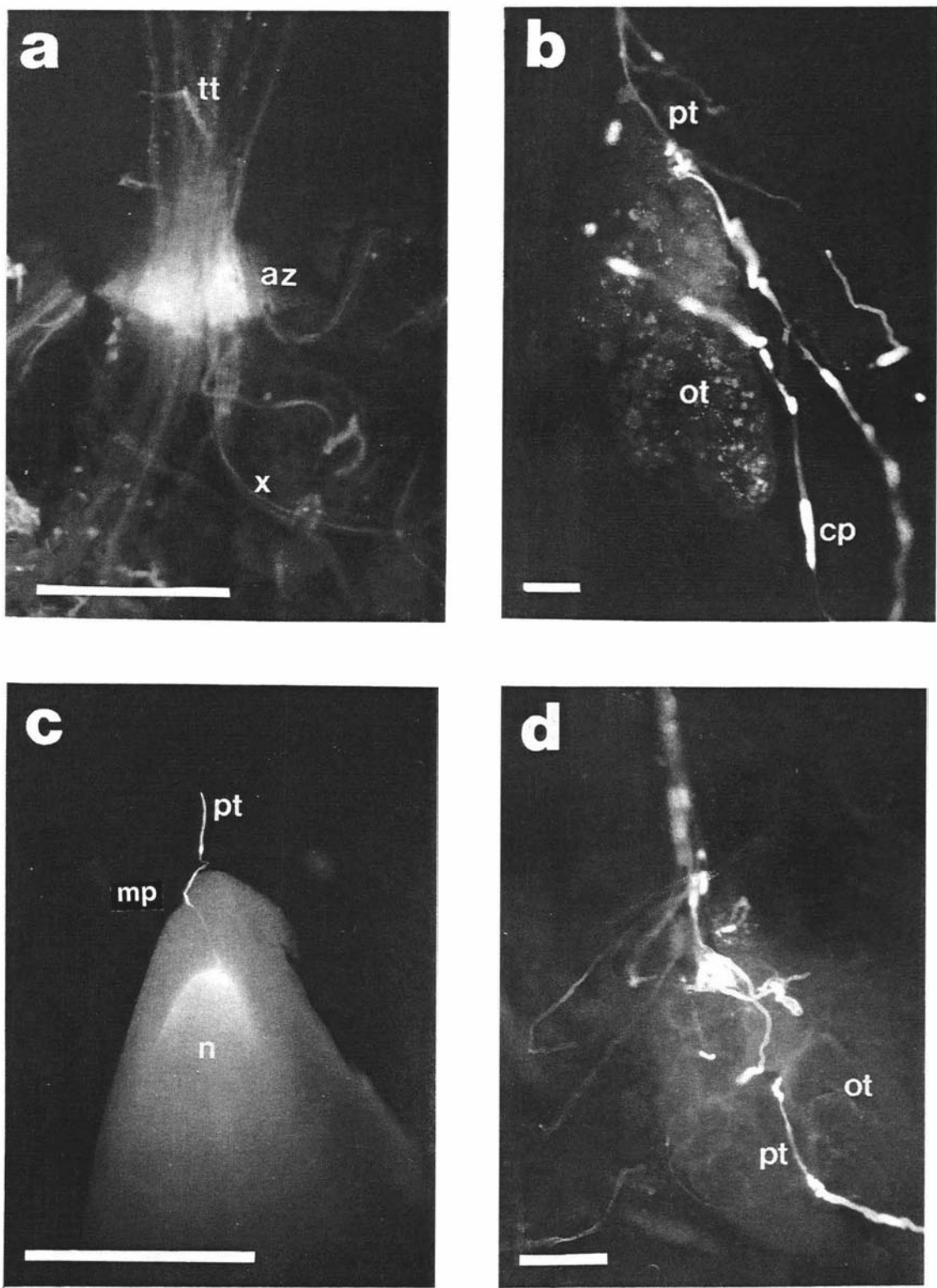
Figure 2.4   Detail of tissue morphology and pollen tube development at entry to ovary and ovules after pollination of 'Sundrop' pistils with 'Trevatt' pollen.   a). Fluorescence of stylar abscission zone (Bar = 1 mm); b). Pollen tube growth over lobed obdurator tissue at entrance to ovary (Bar = 100 μm); c). Penetration of ovule by pollen tube (Bar = 1 mm); d). Coiling of abortive pollen tubes on obdurator tissue at entry to ovary (Bar = 100 μm). Abbreviations: az = abscission zone; cp = callose plug; mp = micropyle; n = nucellus; ot = obdurator tissue; pt = pollen tube; tt = transmitting tissue; x = xylem vessels.)

extension in 'Sundrop' styles after self pollination was due to self incompatibility rather than merely slow growth by tubes from 'Sundrop' pollen grains.

Up to ten pollen tubes from 'Trevatt' pollen grains penetrated past the abscission zone at the base of the style (Fig. 2.4a), over the lobed placental tissue at the entry to the ovary into the ovarian cavity (Fig. 2.4b). Pollen tubes were occasionally observed coiled at the entrance to the ovary (Fig. 2.4c). They were usually brightly fluorescent due to heavy callose plug formation and appeared therefore to have aborted. No immediate cause of abortion was apparent. Precise identification of tube position in relation to ovules after entry to the ovary was not possible due to disruption during removal of ovules and during squashing of dissected ovaries. Inspection of ovules showed that tubes from 'Trevatt' pollen entered the micropyle of primary ovules and penetrated into the nucellus which typically fluoresced brightly (Fig 2.4d). Most penetrated ovules contained a single pollen tube but ovules with two tubes at the micropyle did occur and a few ovules were penetrated by three tubes. No ovule penetration by tubes from 'Sundrop' pollen was observed. Cross pollination with 'Trevatt' pollen therefore resulted in fertilization whereas self pollination did not.

2.3.2.2   Fruit set

Measurement of fruit set after controlled hand-pollination confirmed that 'Sundrop' was self incompatible under Hawkes Bay and Manawatu field conditions in 1991 and 1992.

Table 2.7   Fruit set at pit-hardening and harvest after self, cross and open pollination of 'Sundrop' apricot flowers at FCU and Fernhill Farm Orchard in 1991 and 1992.

| | Fruit set at pit-hardening (%)^z | | | | | Fruit set at harvest (%) | | | | |
| | FCU | | Fernhill | | Mean | FCU | | Fernhill | | Mean |
Treatment	1991	1992	1991	1992		1991	1992	1991	1992	
Non-emasculated flowers										
Open pollinated	40.8	1.3	32.7	13.0	22.0	24.6	1.3	25.2	11.5	15.7
'Trevatt'	30.9	9.7	39.7	26.5	26.7	11.4	6.1	34.7	22.3	18.6
Emasculated flowers										
'Trevatt'	59.7	12.6	50.0	42.1	41.1	18.8	9.6	48.5	35.8	28.2
'Sundrop', Day 0	3.0	1.5	4.0	1.9	2.6	1.6	1.5	2.7	1.8	1.9
'Sundrop', Day 0&2	1.4	1.3	1.8	1.3	1.5	1.5	1.3	1.7	1.8	1.6
None	2.9	0.1	1.2	1.3	1.4	1.5	0.1	1.7	1.4	1.2

^{z} Means of 5% and 50% Bloom cohorts.

Table 2.8   Analysis of variance for normit-transformed proportions of fruit set at pit-hardening and harvest after self, cross and open pollination of 'Sundrop' flowers at FCU and Fernhill Farm Orchard, 1991 and 1992.

Source	df	Variance components (Type III MS)	
		Set at pit-hardening ^{z}	Set at harvest
Model	119		
Site	1	50.67 ns	172.98 ns
Year	1	245.97 ns	98.69 ns
Site×Year	1	109.65 ns	16.83 ns
Residual 1: Tree(Site×Year)	16	9.92	10.73
Treatment	5	481.12 *	331.89 *
Treatment×Site	5	12.00 ns	23.33 ns
Treatment×Year	5	94.07 ns	64.74 ns
Treatment×Site×Year	5	22.69 **	18.52 **
Residual 2: Trt×Tree(Site×Yr)	80	10.18 ns	6.68 ns
Error (within tree)	113	7.73	7.44
R^2		0.89	0.86
Contrasts			
'Sundrop', Day 0 vs 'Trevatt'	1	1330.66 ***	953.04 ***
'Sundrop', Day 0&2 vs 'Trevatt'	1	1249.76 ***	800.93 ***
'Sundrop' vs None	1	1.55 ns	0.20 ns
'Sundrop' Day 0 vs Day 0&2	1	5.79 ns	0.21 ns
'Trevatt' vs Unemasculated	1	38.17 *	21.59 ns
Open vs Unemasculated	1	50.74 *	28.88 ns

ns, *, **, *** Model effects and contrasts non-significant or significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ respectively.
^{z} Proportions transformed using normit transformation for analysis of variance.

Most fruit abscission occurred within two months of pollination, prior to pit-hardening, and only a small proportion of fruit were lost in the second phase of fruit development. Developmental abortion due to lack of fertilization was therefore the most probable cause of fruitlet abscission.   Bloom cohort ('Early'-bloom and 'Mid'-bloom emasculation and pollination) had no consistent effect on fruit set and therefore the two cohorts were pooled to increase the precision of analysis of treatment effects.

Fruit set after self pollination was very low, at pit-hardening and at harvest less than two percent on average and set due to neither self pollination treatment differed significantly to that due to accidental pollination of non-pollinated flowers (Table 2.8). Repeated self pollination to induce a possible 'pioneer pollen' effect (Visser and Verhaegh, 1980) therefore did not increase set from that achieved from a single self pollination. By contrast, fruit set at pit-hardening was as high as sixty percent after pollination of 'Sundrop' pistils with 'Trevatt' pollen and, on average, set at harvest in both years and sites was twenty eight percent (Table 2.7). At pit-hardening, set from hand-pollination of emasculated flowers was higher than that of non-emasculated flowers (Table 2.8) indicating that emasculation did not reduce the potential of 'Sundrop' pistils to set fruit. In turn, the set of hand-pollinated, non-emasculated flowers was greater than that of open pollinated flowers, particularly in 1992 at FCU, suggesting that insufficient natural cross pollination limited fruit set in this year.

2.3.3   Temperature and Expression of Self Incompatibility

Incubation of self and cross pollinated 'Sundrop' pistils at 5°, 10°, 15°, 20°, and 25°C showed that pollen germination and tube growth from self pollen grains had optima below 20°C. Counts of self and cross pollen tubes below the stigma showed that temperature significantly affected pollen germination (Table. 2.9). Stylar transmitting tissue below the stigma contained between 10 and 60 pollen tubes on average (Fig. 2.5a) and an estimated maximum of 80 tubes was observed in one 'Sundrop'-pollinated style incubated at 5°C for 12 days. Styles incubated at 10°, 15° and 20°C contained the most tubes suggesting this was the optimum range for germination. Counts were lower at 5°

Table 2.9   Analysis of variance for counts of pollen tubes below stigma and in ovary, depth of stylar penetration and fraction of ovules penetrated after self and cross pollination of 'Sundrop' pistils incubated at 5°, 10°, 15°, 20° and 25°C.

Source	df	Variance components (Type III MS) No. tubes in style	No. tubes in ovary	df	No. ovules penetrated
Model	79			43	
Cultivar	3	26.78 ^{ns}	22.65 **	3	0.274 ^{ns}
Temperature	4	111.35 **	14.00 ^{ns}	4	0.259 ^{ns}
Residual 1: Cultivar×Temp	12	6.64 *	1.85 **	12	0.062 ^{ns}
Time	3	16.06 ^{ns}	26.86 ***	3	1.058 *
Time×Cultivar	9	5.23 ^{ns}	2.12 **	9	0.130 ^{ns}
Time×Temperature	12	13.98 ***	4.92 ***	12	0.174 **
Residual 2: Time×Cultivar×Temp	36	3.07 *	0.52 ***	36	0.062
Error (within samples)	314	1.88	0.24		-
R^2		0.62	0.80		0.81
Contrasts					
'CluthaGold' vs others	1	7.58 *	7.74 ***	1	0.021 ^{ns}
'Goldrich' vs others	1	55.09 ***	1.21 *	1	0.090 ^{ns}
'Trevatt' vs others	1	41.49 ***	12.69 ***	1	0.195 ^{ns}
'Sundrop' vs others					
within 5°	1	1.75 ^{ns}	0.02 ^{ns}	1	0.000 ^{ns}
within 10°	1	0.02 ^{ns}	8.27 ***	1	0.067 ^{ns}
within 15°	1	0.7 ^{ns}	11.23 ***	1	0.135 ^{ns}
within 20°	1	12.28 *	25.99 ***	1	0.367 *
within 25°	1	7.18 ^{ns}	27.24 ***	1	0.563 **

$^{ns,\ *,\ **,\ ***}$ Effects and contrasts non-significant or significant at $P \leq 0.05$, $P \leq 0.01$ or $P \leq 0.001$ respectively.
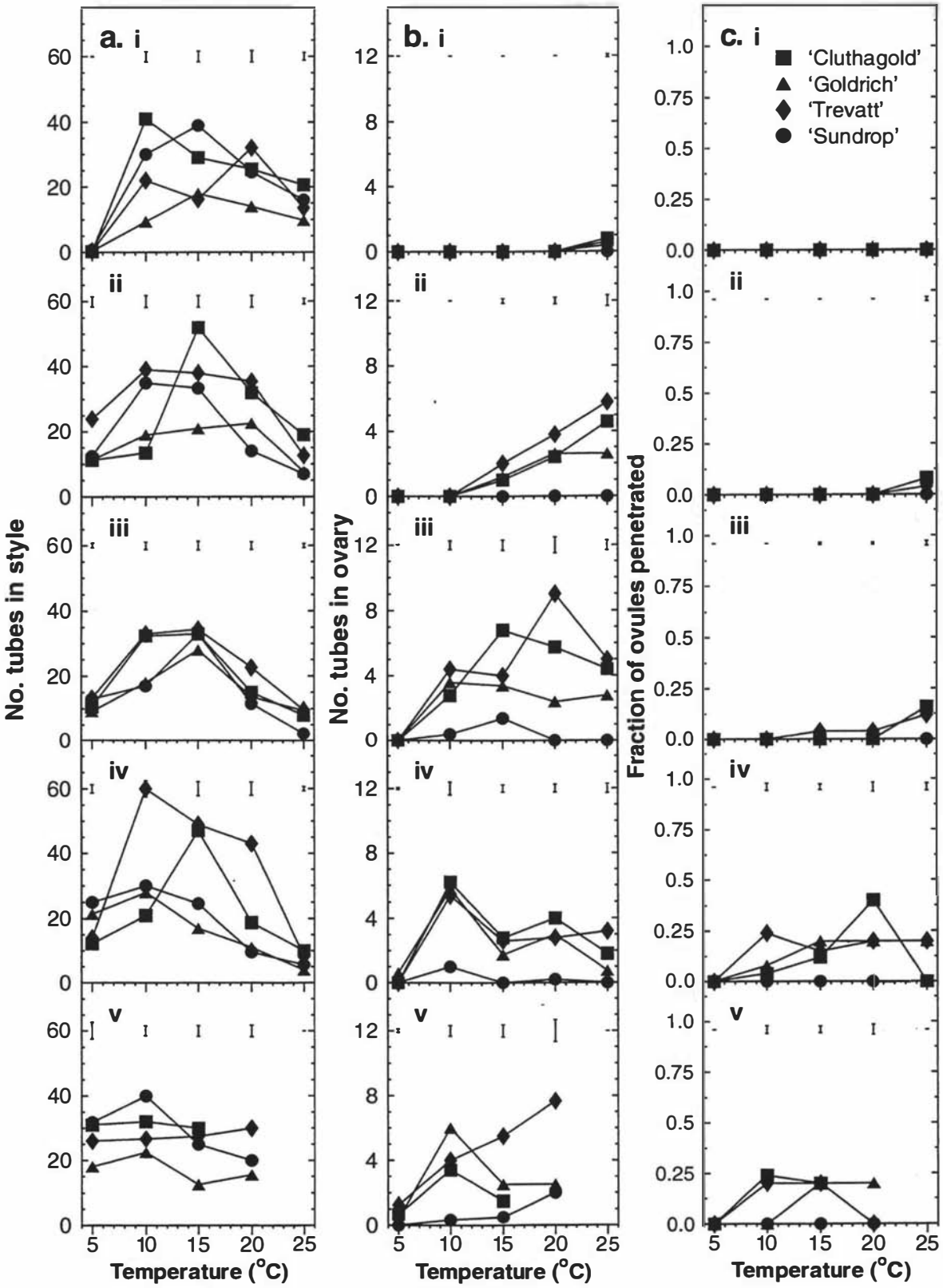
Figure 2.5   Pollen tube count below stigma and at ovary entrance and fraction of ovules penetrated 1, 2, 4, 8 and 12 days after incubation of self and cross pollinated 'Sundrop' pistils at 5°, 10°, 15°, 20° and 25°C. a). Pollen tube count in transmitting tissue below stigma; b). Pollen tube count at entrance to ovary; c). Fraction of ovules penetrated by pollen tubes. Delay after pollination: i). 1 day; ii). 2 days; iii). 4 days; iv). 8 days; v). 12 days; (Bars represent pooled standard errors. Data missing at 25°C on Day 12.)

and 25°C at all times between 1 and 8 days (style abscission had occurred by 12 days at 25°C) indicating that the effect of temperature on germination was not an artifact of delayed tube growth at 5°C or accelerated loss of fluorescence at 25°C. Temperature also greatly affected the time till pollen tubes were first found in the ovary. At 25°C, the tips of a few pollen tubes had already reached the ovary 24 h after pollination whereas at 15° and 20°C, tubes were first observed in the ovary 48 h after pollination (Fig. 2.5b). At 10°C, tubes took 96 h to reach the ovary and at 5°C, tubes were only found in the ovary 12 days after pollination. The effect of temperature on the time until the first observation of ovules penetrated by pollen tubes was very similar (Fig. 2.5c). At 25°C, it took 48 h for pollen tubes to first penetrate into the micropyle of the ovule, 96 h at 15° and 20°C and eight days at 10°C. At 5°C, no ovules penetrated by pollen tubes were found up to 12 days after pollination.

Comparison of the growth of callose plugs in tubes from 'Trevatt' pollen at 10° and 20°C illustrates the acceleration of pollen tube development by higher temperatures. At 10°C, thin-walled tubes (maximum length 2.4±0.3 mm) were actively growing into the top of styles 24 h after pollination and callose plugs were not visible (Fig. 2.6a). After 48 h, the longest tubes had penetrated 7.7±0.7 mm and brightly fluorescent plugs 0.02-0.03 mm long were plainly visible against dimly fluorescing transmitting tissue (Fig. 2.6b). By 96 h, plugs were 0.06-0.09 mm long (Fig. 2.6c) and tube tips had penetrated the ovary, on average 14.0±0.3 mm from the stigma. However, at 20°C, plugs 0.03-0.06 mm long were present in the style below the stigma 24 h after pollination (Fig. 2.6d, maximum tube length 10.5±0.2). After 48 h tubes had penetrated to the ovary (Fig. 2.6e, tube length 13.8±1.0) and plugs were 0.09-0.12 mm long, while by 96 h, some plugs were up to 0.2 mm long (Fig. 2.6f). After both 48 and 96 h at 20°C tube plugs were overall twice the length of those at 10°C due to more rapid development at higher temperature. Tube growth as a result of cross pollination with pollen from 'CluthaGold' and 'Goldrich' was very similar.   In both cases regular callose plugs punctuated thin-walled weakly-fluorescent tubes and plug size increased with age of tube and incubation temperature.

Pollen genotype also significantly affected germination and, in particular, the number of pollen tubes reaching the ovary and ovules (Table 2.9). Pollination with 'Trevatt' pollen resulted in more tubes in the upper style than pollination with other cultivars whereas
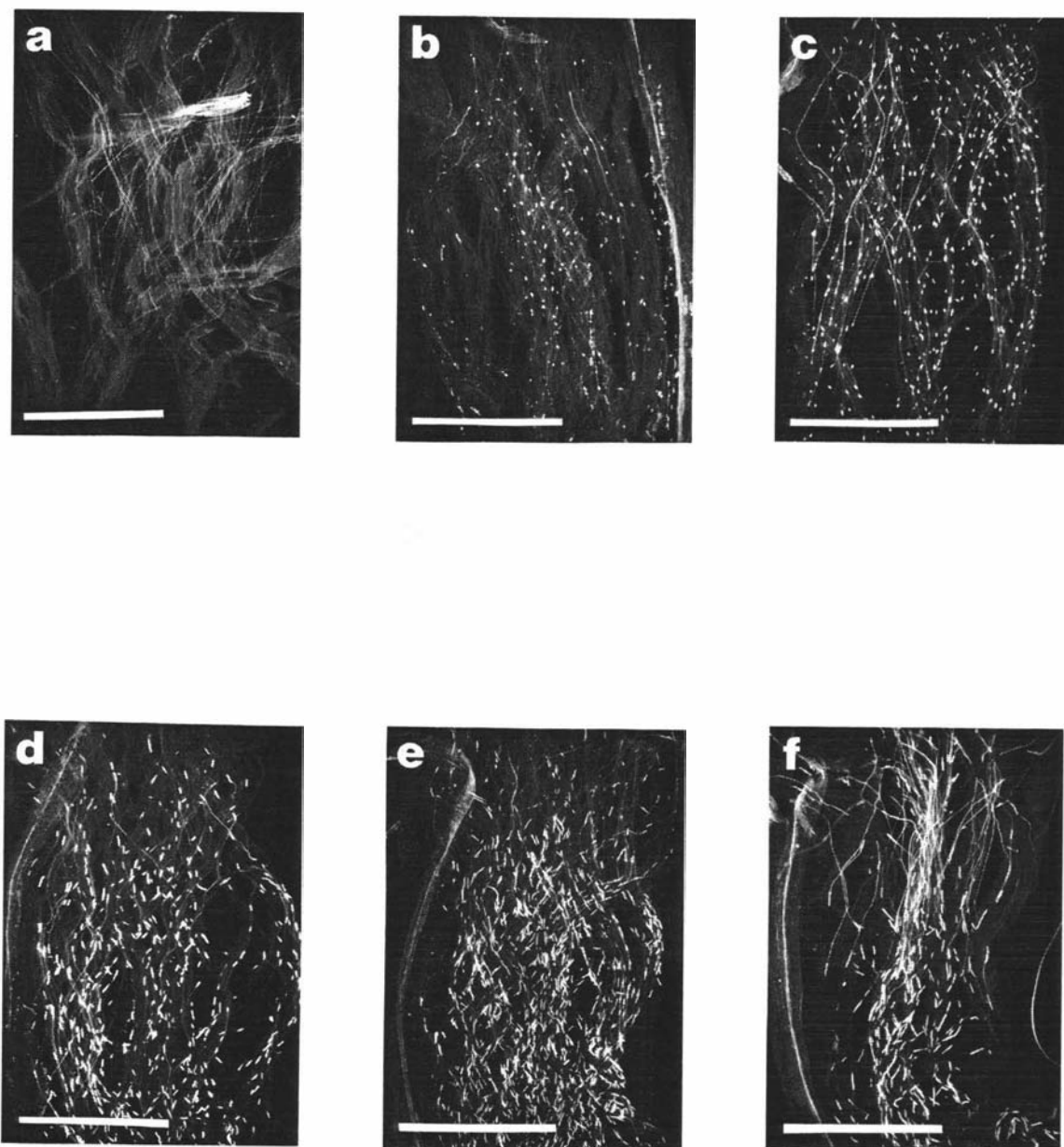
Figure 2.6   Callose plug formation in pollen tubes 24, 48 and 96 h after pollination of 'Sundrop' styles incubated at 10° and 20°C with 'Trevatt' pollen. a-c). 24, 48 and 96 h at 10°C (Bright area in a). is a fragment of epidermal tissue); d-f). 24, 48 and 96 h at 20°C. (Bar = 1 mm).

relatively few were found after pollination with 'Goldrich' pollen. Tube numbers in self pollinated 'Sundrop' styles were similar to those in cross pollinated pistils and therefore germinability of 'Sundrop' pollen at 5°C was comparable to that of other cultivars tested. Consistently fewer 'Sundrop' pollen tubes, however, reached the ovary, especially at 20° and 25°C (Table 2.9). At these temperatures tubes from 'Sundrop' pollen lacked regular callose plugs and instead fluoresced brightly over the length of the tube. By comparison, at 10°C, and at 5°C, the appearance of tubes from 'Sundrop' pollen more closely resembled that of compatible tubes from 'Trevatt', 'CluthaGold' and 'Goldrich' pollen. Tubes with regular callose plugs penetrated deeply into the style (Fig. 2.2c) and few abortive brightly fluorescent tubes were present.

The rate of general flower development after both self and cross pollination increased from 5° to 25°C. At 5°C, development was greatly slowed though it was not stopped completely. Nectar, present initially in all flowers, dried rapidly at higher temperatures which also greatly accelerated floral senescence (Table 2.10) and caused shrivelling of petals before abscission. This did not occur at 15°C or lower. At 20°C and 25°C anthesis was complete within 24 h and petal abscission began within 48 h of incubation. At these two higher temperatures pistil abscission was beginning to occur 8 days after pollination whereas, by contrast, flowers at 5° and 10°C still appeared fresh at this time.

Table 2.10   Estmated floral nectar content and progress of anthesis and petal fall for pollinated 'Sundrop' flowers incubated at 5°, 10°, 15°, 20°, and 25°C.

	Time from pollination				
Temp	1 day	2 days	4 days	8 days	12 days
5°C	Nectar [z] 50% anthesis -	Nectar 80% anthesis -	Nectar 90% anthesis -	Some nectar 100% anthesis 5% petal fall	Slight nectar - 90% petal fall
10°C	Nectar 80% anthesis -	Nectar 90% anthesis -	Nectar 100% anthesis 5% petal fall	Some nectar - 100% petal fall	Slight nectar - 100% petal fall
15°C	Nectar 90% anthesis -	Some nectar 100% anthesis 1% petal fall	Slight nectar - 50% petal fall	Slight nectar - 100% petal fall	No nectar - 100% petal fall
20°C	Some nectar 100% anthesis -	Slight nectar 100% anthesis 5% petal fall	No nectar Shrivelling 90% petal fall	No nectar - 100% petal fall	No nectar - 100% petal fall
25°C	Slight nectar 100% anthesis 5% petal fall	No nectar Shrivelling 90% petal fall	No nectar - 100% petal fall	No nectar - 100% petal fall	No nectar - 100% petal fall

[z] Estimated nectar volume: Nectar = 10-20 µl; Some nectar = 5-10 µl; Slight nectar = < 5 µl.
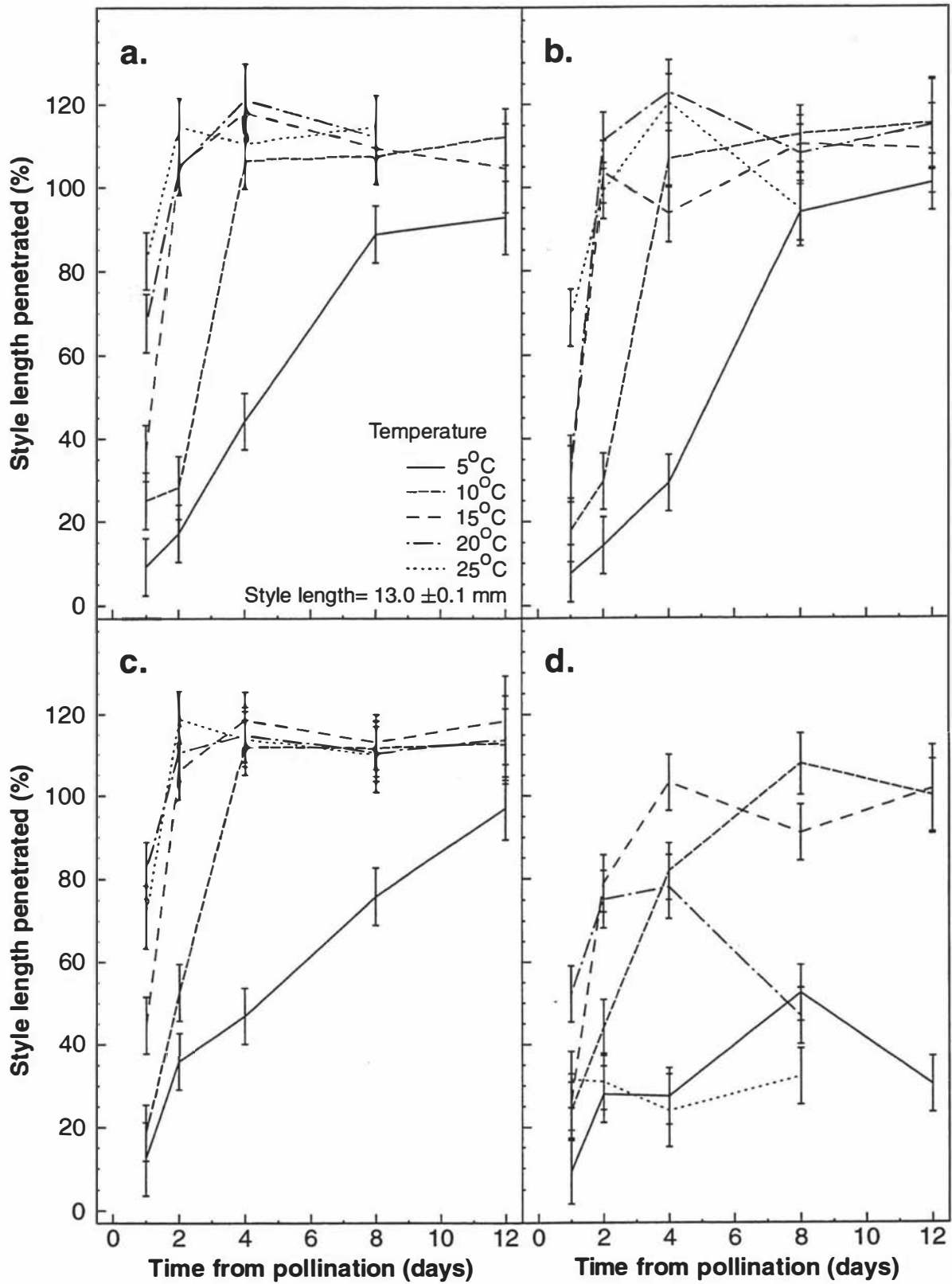
Figure 2.7 Fraction of 'Sundrop' flower style length penetrated by pollen tubes after cross and self pollination of 'Sundrop' pistils at 5°, 10°, 15°, 20° and 25°C. a). 'Cluthagold' pollen; b). Goldrich' pollen; c). 'Trevatt' pollen; d). 'Sundrop' pollen. (100% penetration = tube penetration to stylar abscission zone)

Temperature strongly influenced the rate at which the longest pollen tubes grew from the stigma to the ovary (Fig. 2.7). At 15°, 20° and 25°C the longest tubes from 'CluthaGold', 'Goldrich' and 'Trevatt' pollen all took less than 48 h to penetrate beyond the stylar abscission zone (defined as style end), on average 13.0 ± 0.1 mm from the stigma (Fig. 2.7a,b,c). At 10°C, penetration was slower and tubes took 96 h (4 days) to reach the ovary. At 5°C pollen tube extension was very slow but, despite this, tips were approaching the base of the style 12 days after pollination. At no temperature was there evidence of incompatibility between 'Sundrop' and 'CluthaGold', 'Goldrich' or 'Trevatt', the three cross pollen cultivars. By contrast, at 25°C tubes from 'Sundrop' pollen were strongly inhibited and penetrated little more than a third of the style (Fig. 2.7d). Penetration at 20°C was also less than that displayed by tubes from cross pollen whereas maximum penetration at 15°C and below was not as strongly affected.

Regression analysis of the relationship between temperature and growth rate also indicated a significant effect of cultivar which reflected the relative inhibition of tubes from 'Sundrop' pollen at 20° and 25°C (Table 2.11). Significant growth by tubes from each pollen occurred at all temperatures from 5°C to 25°C and extension rates ranged from 1 mm day^{-1} at 5°C to 10 mm day^{-1} at 25°C (Fig. 2.8a). However, at 15°C and below,the intial growth rate of tubes from 'Sundrop' pollen was not significantly different to that of tubes resulting from cross pollination ($P\leq0.05$). Temperature therefore modified the intensity with which inhibition of self pollen tubes was expressed. However, ovule penetration did not increase as the incubation temperature fell. Even at 10°C few tubes reached the ovary of self pollinated 'Sundrop' pistils and no ovules were penetrated in self pollinated pistils at any temperature (Fig. 2.5b&c). Varying the incubation temperature, therefore, did not reduce the inhibition of 'Sundrop' pollen tube development sufficiently to allow self fertilization.

Linear regression using an exponential model satisfactorily described the relationship between ovary growth rate and temperature for cross pollinated pistils and also suggested a significant pollen cultivar effect on pistil growth (Table 2.11). At 25°C, the width of the largest 'Trevatt'-pollinated ovaries had increased from 2.1 ± 0.1 mm at pollination to almost 10 mm 12 days later and primary ovule length increased linearly from 0.88 ± 0.03 mm to more than 5 mm. The acceleration of ovary and ovule growth by higher
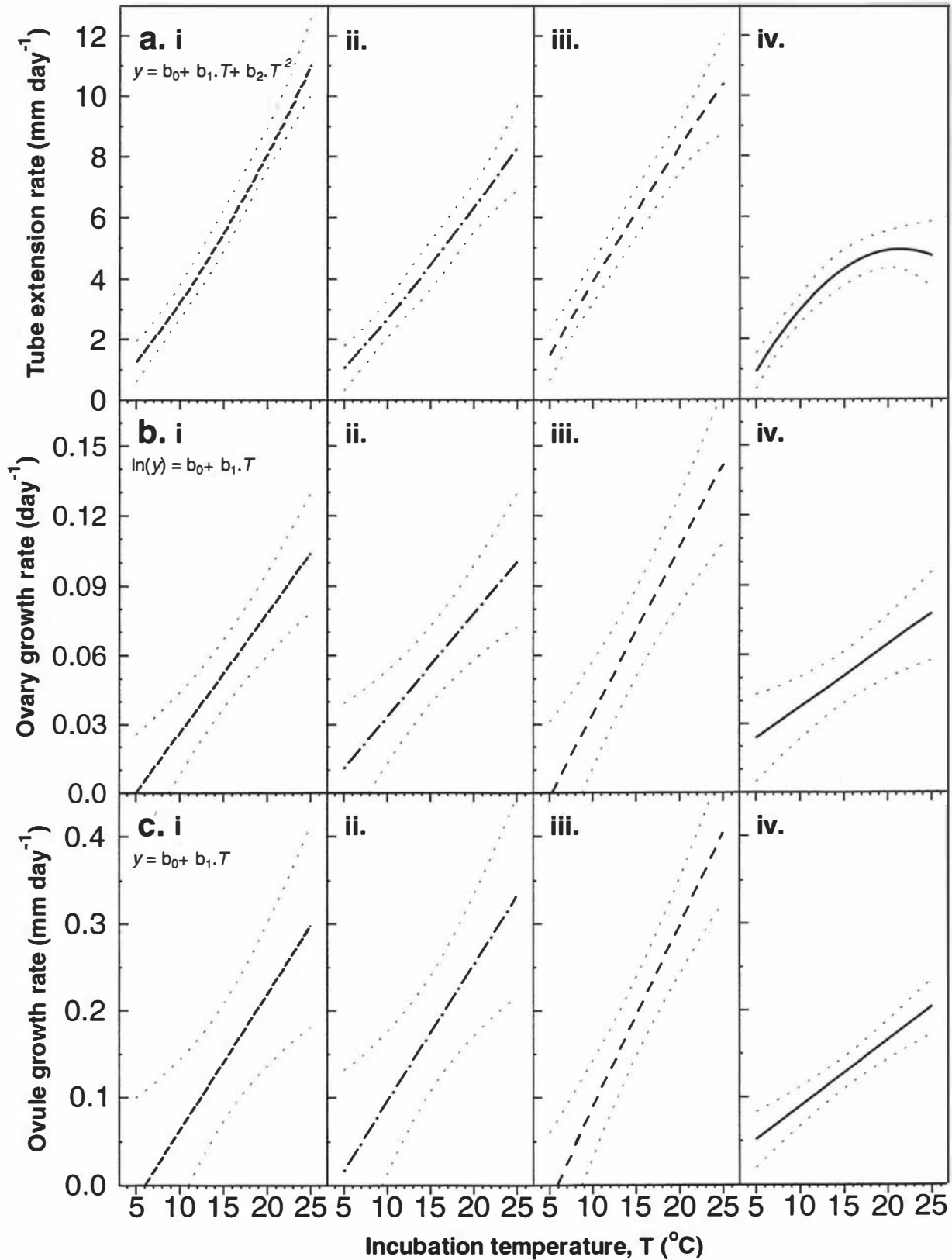
Figure 2.8   Dependence of pollen tube growth rate after cross and self pollination of 'Sundrop' flowers and corresponding ovary and ovule growth rates on incubation temperature. (Pollen cultivars: i). 'Cluthagold'; ii). 'Goldrich'; iii). 'Trevatt'; iv). 'Sundrop'. Regression equations in Table 2.12)

a). Pollen tube extension rate in stylar transmitting tissue (y=pollen tube length, t=days after pollination); b). Growth rate of ovary (y=ovary width); c). Growth rate of primary ovule (y=ovule length).

temperature was greater for cross pollinated pistils than for self pollinated pistils (Fig. 2.8b&c). However, the difference was only significant at 20° and 25°C since at these temperatures development was sufficiently fast for fertilization of cross pollinated pistils to affect their growth relative to non-fertilized, self pollinated pistils.

Table 2.11   Analysis of variance for regressions of ovary and ovule growth rates and pollen tube extension rate on temperature after cross and self pollination of 'Sundrop' flowers incubated at 5°, 10°, 15°, 20°, 25°C.

Source		df	Variance components (Type III MS) Tube extension	df	Ovary width	Ovule length
Model		11		7		
Cultivar		3	1.49 ns	3	0.00116 ns	0.0032 ns
Temperature	(linear)	1	78.93 ***	1	0.02389 *	0.2262 *
Residual 1: Cult×Temp	(linear)	3	3.04 ns	3	0.00086 **	0.0076
Temperature	(quadratic)	1	1.38 ns	-	-	-
Residual 2: Cult×Temp	(quadratic)	3	7.56 *	-	-	-
Error		200	2.53	12	0.00012	0.0014
R^2			0.74		0.95	0.94

Variable	Cultivar	Regression equations	(T=Temperature)
Pollen tube extension	'CluthaGold'	$y = 0.30.T + 0.007.T^2 - 0.39$	$R^2 = 0.81$, ***
	'Goldrich'	$y = 0.30.T + 0.002.T^2 - 0.49$	$R^2 = 0.66$, ***
	'Trevatt'	$y = 0.51.T - 0.002.T^2 - 1.03$	$R^2 = 0.71$, ***
	'Sundrop'	$y = 0.64.T - 0.015.T^2 - 1.90$	$R^2 = 0.59$, ***
Ovary width	'CluthaGold'	$\ln(y) = 0.0052.T - 0.026$	$R^2 = 0.94$, **
	'Goldrich'	$\ln(y) = 0.0045.T - 0.012$	$R^2 = 0.90$, **
	'Trevatt'	$\ln(y) = 0.0072.T - 0.038$	$R^2 = 0.95$, **
	'Sundrop'	$\ln(y) = 0.0026.T + 0.010$	$R^2 = 0.88$, *
Ovule length	'CluthaGold'	$y = 0.0157.T - 0.094$	$R^2 = 0.87$, *
	'Goldrich'	$y = 0.0158.T - 0.063$	$R^2 = 0.87$, *
	'Trevatt'	$y = 0.0211.T - 0.124$	$R^2 = 0.96$, **
	'Sundrop'	$y = 0.0076.T - 0.013$	$R^2 = 0.96$, **

ns, *, **, *** Model effects and regression functions non-significant or significant at $P \leq 0.05$, $P \leq 0.01$ or $P \leq 0.001$ respectively.

2.4   Discussion

The viability of 'Sundrop' flowers at FCU and Fernhill Farm was confirmed by levels of fruit set after controlled cross pollination (Section 2.3.2.2) similar to those previously reported for 'Sundrop' (McLaren et al, 1992; Wood, 1983) and comparable to that reported for other apricot cultivars (Lane, 1984; Pugliano and Forlani, 1985; Schultz, 1948). Fruit set from open pollinated 'Sundrop' flowers at Fernhill Farm (average 21%) was as good or better than that reported for other open pollinated apricots (Crane, 1956; Garcia et al., 1988; Langridge and Goodman, 1979). Set after open pollination at FCU (average 9%) was relatively low, reflecting the unfavourable conditions during bloom at this site, notably frequent wet weather during and following bloom and high average wind-speed (New Zealand Meteorological Service, 1982). Emasculation of flowers for experimental purposes had no detrimental effect on fruit set, but rather increased set over that of non-emasculated flowers. This pattern was observed at both pit-hardening and harvest at both sites and possibly was related to the difficulty of ensuring uniform deposition of pollen by hand on stigmas in non-emasculated flowers.

Histological results from experiments at FCU in 1990 verified the viability of 'Sundrop' pollen and the satisfactory development of 'Sundrop' pollen tubes after cross pollination. These findings were confirmed by the more extensive results from experiments conducted in at Fernhill Farm Hawkes Bay and again at FCU in 1991 and 1992 (Section 2.3.2.1). Microgametophyte morphology was normal and viability (as estimated by stylar and ovary tube counts) was similar to that of Spanish apricots (Egea et al., 1991). Pollen tube development was slow, ovule penetration first occurring eight days after pollination and typically taking 12 to 14 days. This is comparable to the growth rate of pollen tubes in flowers of other *Prunus* species (Cerović and Ruzič, 1992; Keulemans, 1984; Quarta et al., 1990; Stott et al., 1974; Vachun, 1981), especially given prevailing temperatures during bloom (daily mean of $10°$-$12°C$). Analysis of pollen tube development, however, underestimated actual fertilization of ovules since less than 25% of primary (developing) ovules were penetrated 12 days after cross pollination at Fernhill in 1991 whereas fruit set for the corresponding flowers averaged 50% (Table 2.7). This suggests either that ovule penetration and fertilization were incomplete 12 days after

pollination or that dissection dislodged a proportion of tubes from the micropyle. In no instance did fruit set exceed 70% even though the processes of emasculation and removal of pistils for dissection substantially thinned flowers to around two or three fruit per spur. The appearance of pollen tube abortion at the obdurator (Fig. 2.3d) suggests that some fruit loss may be due to the failure of otherwise compatible pollen tubes to grow from the obdurator of 'Sundrop' flowers to the micropyle.

Very low fruit set after self pollination, however, confirmed that the principal cause of unreliable fruit set on 'Sundrop' is inadequate cross pollination as previously reported (Gilchrist, 1990; Wilton, 1983; Wood, 1983). In addition, the failure by otherwise viable pollen tubes from 'Sundrop' pollen to penetrate styles of 'Sundrop' flowers indicates that 'Sundrop' displays a gametophytic self incompatibility syndrome like other *Prunus* species (de Nettancourt, 1977) and other apricots (Burgos et al., 1993). Concentration of fruitlet drop in the two months immediately following bloom is consistent with failure of fertilization as the principal cause of abscission. Fruit loss due to embryo and seed abortion which typically occurs later in the season following pit-hardening (Crane, 1956). That the self incompatibility is genetically determined is also suggested by the similar inhibition of 'CluthaGold' pollen tubes in their own styles, implying that 'CluthaGold' (a 'Sundrop'×'Moorpark' hybrid) has inherited the trait from 'Sundrop'. However, neither histological nor fruit set results indicate any cross incompatibility between 'Sundrop' and 'CluthaGold' despite their close genetic relationship.

The presence of tubes in non-pollinated pistils (Fig. 2.1) implies that pollen transfer to emasculated pistils did occur at a low level. This accounts for the non-parthenocarpic fruit set observed (all fruit collected from treatments were seeded) despite the lack of hand pollination. Insect proof nets excluded all insects from trees at FCU but did not prevent air flow. Wind therefore may have contributed to cross pollination. Nets could not be applied to trees at Fernhill Farm Orchard due to the close spacing of trees in this commercial orchard. The level of accidental bee-pollination was, however, unlikely to have been significant. When bees did visit emasculated pistils, their foraging activity concentrated on the remnants of nectiferous tissue at the pistil base. Furthermore, fruit set on the non-pollinated control at Fernhill Farm Orchard was no greater than at FCU where insect-proof tents excluded bees from all flowers except those deliberately left

outside the netting. Its effect on self pollinated flowers is even less likely. While tubes from later-deposited pollen develop may more strongly than earlier pollen hand-applied to emasculated flowers (Visser and Verhaegh, 1980), in this experiment, earlier hand self pollination reduced pollen tube numbers in the ovary (Table 2.6) and entirely prevented ovule penetration (Fig. 2.1).

The results indicate that it is unlikely a 'pioneer' pollen effect can overcome self incompatibility and increase fruit set on 'Sundrop'. It has been suggested that stimulation of pollen tube growth by earlier deposited 'pioneer' pollen might enhance seed set from self pollination on apples (Visser, 1983). If this were true for 'Sundrop', then early deposition of self pollen might sometimes allow later-developing self pollen tubes to overcome self incompatibility and induce fruit set where cross pollination was insufficient. However, while repeated pollination of 'Sundrop' pistils with self pollen did promote slightly deeper penetration by self tubes, it did not increase the number of self pollen tubes entering the ovary. Hence, the 'pioneer' effect of the earlier pollination was insufficient to overcome self incompatibility and did not increase fruit set. This is a similar result to that observed after repeated self pollination of pear and apple which also failed to overcome self incompatibility (Visser and Marucci, 1984). Effects on pollen tube penetration attributed to a 'pioneer' effect may instead be simply due to stigmatic maturation between the two pollinations (El-Agamy and Sherman, 1987).

Measurements of pollen tube growth at controlled temperature, however, do suggest that expression of self incompatibility in 'Sundrop' flowers is modified by the environment. Self compatibility and self incompatibility are not absolutes but rather the well-defined extremes of a continuum (Estes et al., 1983). This is illustrated by the range of self fertility displayed by apricot cultivars (Szabó and Nyéki, 1991). Pollen tube growth in the style after self pollination was severely inhibited when flowers were incubated at 20° and 25°C but was similar to that after cross pollination at 10° and 15°C. Hence, it may be possible that the self incompatibility of 'Sundrop' is reduced sufficiently at 'normal' field temperatures (i.e 10° to 15°C) for pollen tubes from self pollen to sometimes reach the ovary and effect fertilization. This result is consistent with reduced self incompatibility at lower temperature in *Prunus avium* (Lewis, 1942), *Prunus dulcis* (Socias i Company et al., 1976), apples (Modlibowska, 1945; Williams and Maier, 1977) and pear

(Vasilakakis and Porlingis, 1985). However, as in apple (Williams and Maier, 1977) and pear (Vasilakakis and Porlingis, 1985), the reduction of inhibition was insufficient to significantly increase the numbers of ovules penetrated after self pollination. Self fertilisation under field conditions, even in the optimum temperature range for self tube penetration, is therefore unlikely to be frequent.

Apart from the effect of temperature on expression of self incompatibility it appears unlikely that temperatures from 5° to 25°C act after the deposition of pollen to cause poor fruit set specifically on 'Sundrop'. The observed optimum temperature range for pollen germination, 10° to 15°C, was similar to that of French apricots (Vachun, 1981), almond (Weinbaum et al., 1984), plum (Keulemans, 1984) and sour cherry (Cerovič and Ruzič, 1992) and corresponds to temperatures commonly experienced during bloom in Hawkes Bay orchards. Germination was depressed more by high (25°C) than low (5°C) temperature and therefore initial microgametophyte development should be satisfactory under field conditions despite periods during which temperatures can fall below 10°C. This is confirmed by the numbers of pollen tubes in the styles of pistils from field experiments (Fig 2.1a&b). Pollen tube growth rate in 'Sundrop' styles also appears normal. Poor fruit set on 'Italian' prune was attributed to retardation of pollen tube growth by low temperatures causing embryo-sac abortion before fertilization (Thompson and Liu, 1973). However, calculated tube growth rates (Table 2.12) were faster than those for plum (Jefferies et al., 1982; Keulemans and van Laer, 1989) and closer to apple (Child, 1967; Jefferies and Brain, 1984). Thus, unless ovule lifespan is very short or pollination delayed greatly, pollen tube growth appears unlikely to be limiting fruit set.

Furthermore, the relative sensitivity of ovary and ovule growth rates to low temperature in comparison to that of pollen tube extension suggests low temperature during bloom does not seriously reduce the probability of fertilization. Like apples and plums the extension rate of compatible tubes in 'Sundrop' styles was linearly and positively dependent on temperature so that the optimal temperature for compatible pollen tube extension was higher than for germination. Again, this is similar to the results of other studies of *Prunus* cultivars (Vachun, 1981; Weinbaum et al., 1984). However, significant pollen tube extension occurred at 5°C whereas ovary and ovule growth was almost completely stopped (Fig. 2.8). Ovule senescence is accelerated by higher temperature

(Moreno et al., 1992; Postweiler et al., 1985) but if ovule senescence has the same temperature response as ovary and ovule growth then low temperatures might be expected to increase speed of pollen tube penetration relative to that of ovule senescence. In addition, the fraction of ovules penetrated by pollen tubes was unaffected by temperature (Table 2.9) again suggesting that speed of pollen tube arrival in the ovary was not the sole determinant of fertilization and that higher post-pollination temperatures would not necessarily increase fruit set. Chalazal fluorescence in ovules, an indicator of ovule senescence (Stösser and Anvari, 1982), was not observed during the experiment. The effectiveness of the staining method was, however, indicated by the commonly observed fluorescence of small secondary ovules.

In conclusion, the results of this study demonstrate that 'Sundrop' flowers and pollen were viable and that pollen germination in 'Sundrop' flowers was normal. Pollen tube development after cross pollination led to ovule penetration by pollen tubes and fruit set but pollen tube self incompatibility, exhibited as inhibition of development in the style, prevented significant fruit set on 'Sundrop' after self pollination. The results also indicated that temperatures during bloom in Hawkes Bay are close to optimal for pollen germination and are unlikely to restrict pollen tube growth in 'Sundrop' flowers. Neither modifying temperature nor manipulating the degree of self pollination by repeated pollen application was able to overcome self incompatibility of 'Sundrop'. The principal factor leading to unreliable fruit set appears therefore to be an unfulfilled requirement for cross pollination. In addition, all cultivars used to pollinate 'Sundrop' were compatible, including 'CluthaGold', and cross incompatibility (as indicated by pollen tube inhibition) was not stimulated by incubation of pollinated flowers at higher than normal temperatures. Any of the five cultivars used for cross pollination in this study ('Cluthagold', 'Goldrich', 'Royal Rosa', 'Trevatt' and 'Valleygold') therefore appear to have the capacity to act as a pollenizer for 'Sundrop'. Conversely, low fruit set can be expected when transfer of pollenizer pollen to 'Sundrop' flowers is inadequate, either because the pollenizer pollen supply is insufficient or because adverse weather prevents pollinator foraging activity.

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Chapter 3
Honeybee Foraging on 'Sundrop' Apricot Flowers

3.1   Introduction

Foraging activity by honeybees (*Apis mellifera* L.) is an important contributor to fruit set
on most deciduous crops (Free, 1960b). It significantly increased fruit set on 'Trevatt',
a self fertile apricot cultivar (Langridge and Goodman, 1981). However, the results of
the previous chapter show that self pollination of 'Sundrop' flower will not give adequate
fruit set. Limited or ineffectual honeybee activity on 'Sundrop' would therefore reduce
fruit set by preventing sufficient transfer of pollenizer pollen to 'Sundrop flowers.

Honeybees might be ineffective pollinators for 'Sundrop' in Hawkes Bay for three
reasons. First, honeybee foraging activity is strongly influenced by weather (Szabó,
1980; Williams and Sims, 1977) and therefore frequent poor weather in early spring in
Hawkes Bay during bloom could restrict honeybee activity. Second, honeybees can
display preferences for flowers of one cultivar or species against those of others available
(Brown, 1951, Free, 1966b,1968; Overley and Bullock, 1947). In this respect, nectar
volume and sugar concentration are important determinants of honeybee activity
(Percival, 1947) but apricot nectar concentrations lie near or below the minimum
acceptable to honeybees (Kevan and Baker, 1983; Meheriuk et al., 1987; Vansell, 1934;
Vansell, 1952). Honeybees have been seen to desert apricots for other species with a
higher nectar sugar content (Vansell, 1952) and a New Zealand survey of nectar sources
goes so far as to dismiss all early-blooming fruit trees as "next to useless" for
maintenance of honeybee colonies (Walsh, 1967). Honeybees might therefore avoid
'Sundrop' flowers because of unattractive nectar. Third, the cross pollinating efficiency
of honeybees is reduced if they move infrequently between trees during foraging (Free,
1960a) or fail to contact stigmas on visits to 'Sundrop' flowers and so do not transfer
pollenizer pollen to 'Sundrop' stigmas. In this respect the relative proportions of
honeybees foraging for nectar and pollen may be important (Brown, 1951; Roberts,
1956; Robinson, 1979).

The potential significance of these factors was evaluated in conjunction with study of self incompatibility in 'Sundrop'. Nectar volume and concentration in 'Sundrop' flowers was measured to determine whether 'Sundrop' flowers might be unattractive to honeybees. Honeybee foraging activity on 'Sundrop' trees was measured on several days with different weather conditions to observe the degree to which foraging on 'Sundrop' was affected by weather. Finally, honeybee behaviour on 'Sundrop' flowers was observed to see whether or not honeybee foraging activity appeared likely to contribute to cross pollination.

3.2   Methods and Materials

3.2.1   Analysis of 'Sundrop' Nectar

Field measurement of volume and concentration of nectar utilised nectar drawn from flowers just about to reach anthesis ('balloon' stage) to lessen the impact of environmental variability (Corbet *et al.*, 1979). Nectar was sampled at HortResearch Havelock North Research Orchard, Campbell's Orchard, Bridge Pa, Fernhill Farm Orchard, Fernhill, Sterling Orchard, Bayview, and Massey University Fruit Crops Unit. Volume was estimated by measuring the proportion of a microcapillary tube filled by nectar. Nectar concentration was estimated with a hand-held refractometer after nectar was extracted with a plastic-tipped pipettor from flowers. Where nectar volume was limited (open flowers and 'balloon' stage of some cultivars) a combined sample of 10 µl was drawn from several flowers into a pre-weighed glass micropipette. Nectar concentration was calculated from the weight of dry matter remaining after evaporation in a drying oven (105°C, 24 h).

Composition of 'Sundrop' apricot nectar was determined at HortResearch Mount Albert Research Centre, Auckland in July 1992 using nectar extracted from newly opened 'Sundrop' flowers borne on 15-20 cm cuttings. Budwood for cuttings had been collected from Fernhill Farm Orchard on 17 June 1992 and stored at 7°C for three weeks. Cuttings were forced for one week at 20°C, half the cuttings in water and the rest in 30 ml l^{-1} 'Chrysal' flower preservative (Pokon and Chrysal) to test whether sugar translocation altered nectar composition. Trays carrying forcing vials were each enclosed in plastic bags to reduce transpiration. Initial analysis of apricot nectar was performed using thin layer chromatography on cellulose plates. Nectar (5 µl and 10 µl samples containing about 200 and 400 µg sugar) was applied to plates as 2 cm bands with two external standards: 5 µl containing 50 µg each of raffinose, sucrose, glucose and fructose and 5 µl containing 50 µg of glutamine and glutamic acid. Plates were run with propyl acetate : formic acid : water (11:5:3) for 3 h, dried overnight then sprayed with either anisidine-HCl reagent and heated at 105°C for 10 min to visualise sugars, or with ninhydrin reagent and heated for 15 min to visualise amino acids.

For gas-liquid chromatography, two nectar samples were prepared from flowers forced in water and in Chrysal. Initial nectar concentrations were determined by hand refractometer. 240 µg adonitol was added as an internal standard to three subsamples containing an estimated 100, 250, and 500 µg nectar sugar which were then desiccated for 24 h under vacuum over P_2O_5 and derivatized in 80 µl of Trisyl Z at 75°C. Vials were shaken periodically for 20 min then allowed to cool for over 1 h to complete derivatization. Gas-liquid chromatography was performed on a Varian 3700 attached to a Hewlett Packard 3390A integrator. The column (2 m × 2 mm ID stainless steel) was packed with methyl silicone on diatomaceous earth (OV 101). Injection temperature was 220°C. 1.0 µl aliquots from each subsample containing up to 6 µg nectar sugar plus 3 µg adonitol internal standard were run in conjunction with two sets of external standards (a: adonitol, glucose, inositol, sucrose; and b: adonitol, fructose, inositol, sucrose) with a temperature protocol of: 0-5 min, 160°C; 5-23 min, increasing at 5°C min^{-1}; 23-34 min, 250°C. Nitrogen was used as the carrier gas (flow rate ≈ 22 ml min^{-1}) and detection was by flame ionization at 260°C. The presence of compounds which might interfere with the detector was tested by first passing two 160 µl nectar samples (one each for flowers forced in water and Chrysal) through tandem 1 ml SP Sephadex C-25 and QAE Sephadex A-25 mini-columns. Eluate was dried down, made up to 0.5 ml in 10% isopropanol and 16 µl of each sample derivatized and chromatographed.

3.2.2   Honeybee Foraging

Pollen and nectar foraging of honeybees on apricot trees were observed at Fernhill Farm Orchard on 5-9 August 1992, between 10:00 am and 4:30 pm each day. This commercial orchard comprised two adjacent stands of apricot trees, a smaller eastern stand of 400 'Sundrop' trees with a few scattered 'Goldrich' pollenizers and a larger western stand of 1000 'Sundrop', 600 'Royal Rosa' and 70 'Goldrich' trees (Fig. 3.1). Twenty five 'Goldrich' and fifty 'Trevatt' trees had been planted as pollenizers within rows of the main 'Sundrop' block yielding a 'Sundrop':pollenizer ratio of over 10:1. Distribution of pollenizers was even throughout the 'Sundrop' block but did not follow a specific pattern. Trees were mature, 5-6 m high, planted at 4 m x 3 m spacings and pruned to an open vase form. Soil became very gravelly to the south-west and tree vigour reduced progressively. Observations of foraging activity were concentrated at the eastern end of the northern block of 'Sundrop' which comprised over 800 trees in nine rows.
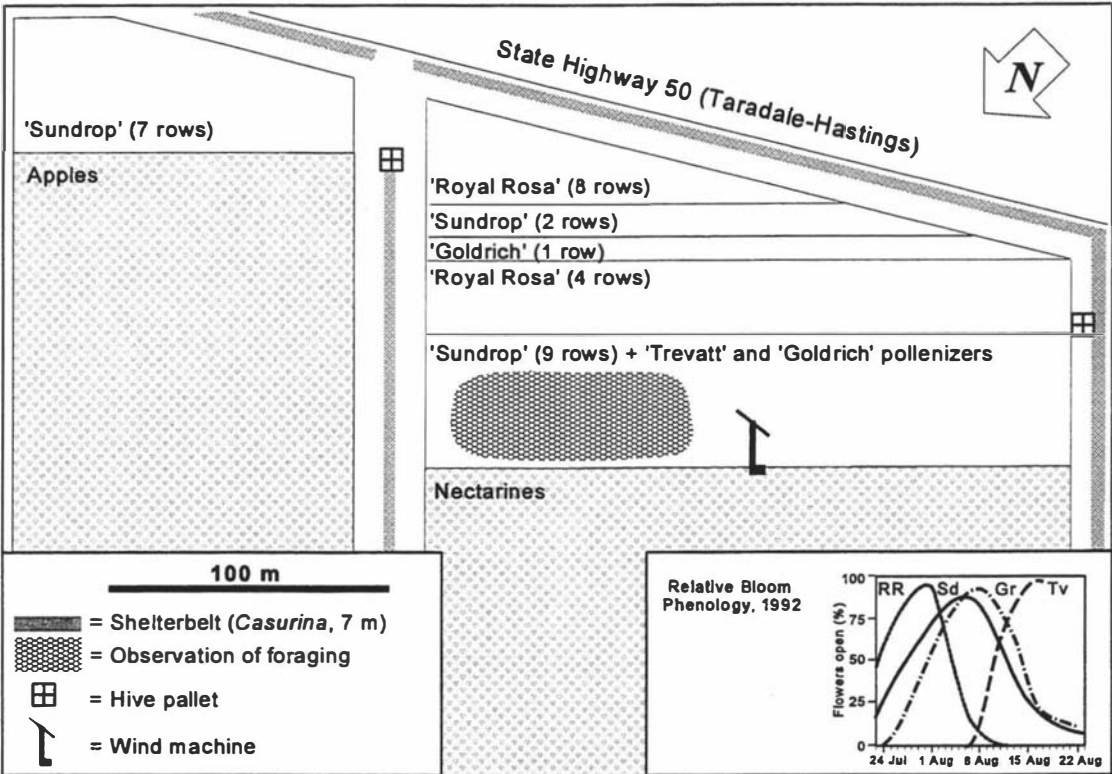
Figure 3.1   Map of Fernhill Farm Orchard, Hawkes Bay indicating position of apricot blocks, location of honeybee hive pallets and foraging observations and relative bloom phenology for July-August 1992. Cultivar abbreviations: RR = 'Royal Rosa'; Gr = 'Goldrich'; Sd = 'Sundrop'; Tv = 'Trevatt'.

At the time of observation, two four-hive pallets of honeybees were positioned in the orchard, one pallet 30 m east of the observation area and one pallet 100 m to the west. Both lay on areas of grass beside access roads and received sun from early in the morning. Honeybee foraging activity was measured in two ways. For the first, overall activity level was estimated at half-hourly intervals by counting the number of honeybees foraging on three randomly-selected 'Sundrop' trees (Choi, 1987). Each set of counts was made on different trees.

For the second, the behaviour of foraging honeybees on 'Sundrop' flowers was observed by following individual bees from three 'Goldrich' pollenizer trees within the 'Sundrop' block which served as contact points to identify foragers. Foraging behaviour (Table 3.1) exhibited at each flower was categorised and the cultivar of flowers visited was recorded until visual contact was lost. Time of first sighting and final loss of contact were recorded for each forager observation as was the number of 'Sundrop' trees visited by foragers during the observation period. Flower 'visits' in which bees merely walked

Table 3.1   Categories used to describe honeybee foraging behaviour on apricot flowers.

Code	Description of foraging behaviour
Ns	Collects nectar, 'side-working' Bee inserts proboscis through stamens from side, without stigma contact
Nt	Collects nectar, approach from top Bee inserts proboscis through stamens from top, with stigma contact.
P	Collects pollen Bee scrabbles for pollen using forelegs on top of anthers
B	Collects both pollen and nectar.
X	Collects neither pollen or nectar. Bee alights but does not forage. May clean itself or leave immediately.

Foraging categories from Free (1960a) and Robinson (1979).

across flowers, or alighted briefly and did not forage, were not counted and only forager visitation sequences involving visits to at least five flowers were recorded. Bees whose predominant foraging behaviour (i.e. that exhibited on >75% of visits observed) was nectar collection were categorised as 'nectar-foragers' and, similarly, bees predominantly collecting pollen were categorised as 'pollen-foragers'. Data analysis considered the proportion of forager trips which visited a 'Sundrop' tree, the number of 'Sundrop' trees visited before loss of contact, the proportion of pollen-foraging flower visits made by each bee, the ratio of pollen-foragers to nectar-foragers, visitation rate of predominantly pollen-foraging and nectar-foraging bees, and proportion of nectar collecting bees which foraged from the top of the flower versus those that 'side-worked' through the anthers. Analysis of data describing forager behaviour was performed using PROC GLM (SAS Institute, 1989) after square-root transformation of original counts to equalise variances (Snedecor and Cochran, 1980).

Similar, though more limited, foraging data were collected at Sterling Orchards, Bayview on 15 August, 1992 from 13:30 to 15:00. Weather was fine and mild with a moderate (force 4) breeze. Counts were made of honeybee forager numbers per tree and relative numbers foraging for pollen and nectar on mature 'Sundrop' and 'Trevatt' trees 50 m to 100 m downwind from two hives. 'Sundrop' had reached 50% Bloom and 'Trevatt' 90% Bloom. Other cultivars in the orchard had either lost all petals ('Royal Rosa'), were in the process of doing so ('Newcastle', 20% Petal Fall), or were still in bloom ('CluthaGold', 90% Bloom).

3.3   Results

3.3.1   Nectar availability in 'Sundrop' flowers

Nectar concentrations of up to 20% sugar (estimated by refractometer or by dry weight) were measured in 'Sundrop' flowers in the field. Data were highly variable, especially for open flowers. Nectar samples from pre-anthesis flower buds ('balloon'-stage) averaged five percent sugar. Initial nectar volume in 'Sundrop' buds was about 20 μl, similar to 'CluthaGold' and greater than other cultivars investigated (Table 3.2). Nectar volume in open flowers appeared to decline as flowers aged and nectar was generally absent from flowers of 'Sundrop' and other cultivars beginning to lose petals. In the laboratory, nectar volume in open flowers on cuttings reduced rapidly when flowers were left open to the air.

Table 3.2   Volume of nectar contained by apricot flower buds at 'balloon' stage in four Hawkes Bay orchards and Massey University Fruit Crops Unit, August 1992.

Nectar volume	Cultivars
0 - 2 μl	'Trevatt', 'Valleygold'
2 - 10 μl	'Castleton', 'Goldrich', 'Royal Rosa'
> 10 μl	'CluthaGold', 'Newcastle', 'Sundrop'

Fructose and glucose were the major sugars present in nectar from 'Sundrop' flowers on forced cuttings. Peaks with retention times corresponding to those of fructose, glucose and sucrose were observed in GLC chromatograms (Table 3.3). Glucose and fructose were present in equal amounts while sucrose was present at a much lower level.

Table 3.3   Sugar composition of nectar from forced 'Sundrop' flowers as determined by gas-liquid chromatography of derivatized samples. (Means of water and Chrysal samples ± SE.)

Nectar sugar	Concentration ($\mu g\ ml^{-1}$)	
	Forced in water	Forced in 'Chrysal'
Fructose	17.9 ± 1.9	18.6 ± 0.3
Glucose	18.4 ± 1.7	19.5 ± 0.4
Inositol	nil	nil
Sucrose	1.8 ± 0.6	1.8 ± 0.6

Total sugar concentration was just under five percent. Thin layer chromatography of nectar samples indicated traces of amino acids but additional Sephadex purification of nectar prior to derivatization did not alter the appearance of chromatograms. Forcing in Chrysal solution did not significantly affect nectar sugar composition.

3.3.2   Honeybee Foraging

Honeybees were the only foragers present in significant numbers on apricot trees at Fernhill Farm Orchard in August 1992 although a few bumblebees (*Bombus*) and a single hoverfly (Syrphidae) were observed to visit flowers. Day-to-day variation in numbers of foragers on 'Sundrop' was pronounced and bees were actively working flowers on only one of the four days on which foraging was observed (Fig. 3.2). Highest activity occurred on 6 August with an average of six bees already foraging on each tree at 10:00 am when first observations were made. Activity peaked at nine bees per tree at 11:30, again at around eight per tree in the afternoon then declined after 4:00 pm (Fig. 3.2b). By contrast, average activity on the other three days rarely exceeded one bee per tree.

Weather conditions appeared more important as the determinant of foraging activity than stage of bloom. Little foraging activity was observed on 5, 7 and 9 August. Twenty percent of 'Sundrop' flowers were open on 5 August and the proportion had reached ninety percent on 9 August. Large numbers of newly opened flowers were therefore present throughout the observation period. However, weather changed from calm, clear and frosty to warm, cloudy and windy over this period (Table 3.4) reflecting a transition from high to low pressure atmospheric conditions. Maximum air temperature increased from 11°C on 5 August to 21.6°C on 9 August but comparison of meteorological and

Table 3.4   Weather conditions at Fernhill Farm Orchard during observations of honeybee foraging, 5-9 August 1992.

Date	Cloud	Max. temp. (°C)	Wind	Windrun (km)[z]
5 Aug	Clear	11.0	Light to moderate SW	92
6 Aug	Clear	Frost, 15.3	Calm. Slight breeze from 12:15	26
7 Aug	O/cast	Frost, 15.3	Moderate W, falling from 13:00	265
8 Aug[y]	Cloud	18.5	Light to moderate W	135
9 Aug	Cloud	21.6	Strong to moderate NW, falling after 14:00	210

[z] Windrun for Havelock North Meteorological Station
[y] No measurements of honeybee foraging activity.
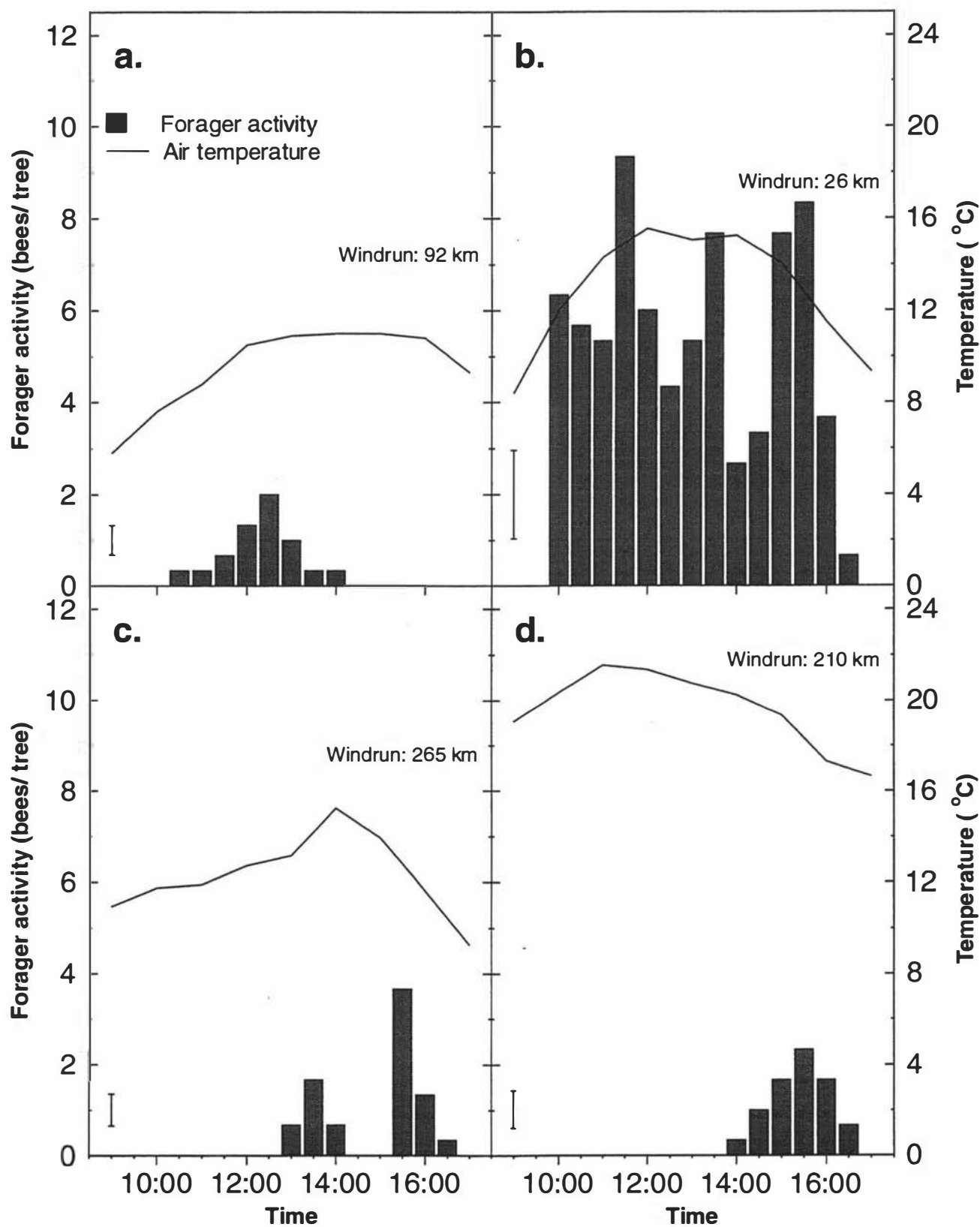
Figure 3.2   Honeybee foraging activity and corresponding air temperature and windrun data during 'Sundrop' bloom at Fernhill Farm Orchard, August 1992. a). 20% Bloom, 5 August; b). 50% Bloom, 6 August; c). 80% Bloom, 7 August; d). 90% Bloom, 9 August. (Bars represent $LSD_{0.05}$ for count means. Windrun measured at Havelock North Meteorological Station)

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forager activity data suggests that high levels of forager activity were only observed on 6 August when clear skies and lack of wind created mild conditions in the orchard (Fig. 3.2b) The effect of wind is illustrated by the contrast between August 6 and 7 on which days temperatures were similar. However, foragers were entirely absent during the morning of 7 August when windforce reached 5 on the Beaufort scale and only appeared in limited numbers when the wind dropped in the afternoon (Fig. 3.2c). It is also illustrated by data for 9 August, the warmest day observed, during which strong gusty conditions appear to have prevented bee flight for most of the day (Fig. 3.2d).

Seventy-two honey bee foragers were followed for more than five visits to flowers over the period 5-9 August 1992. The most common observation period was 2 min (median 3 min, maximum 10 min) and the most common number of visits followed was 6 (median 12 visits, maximum 70 visits). Partially-filled corbiculae (pollen sacs) indicated that most foragers were already well into a foraging trip. Eighty percent of foragers moved from the initial 'Goldrich' pollenizer to a 'Sundrop' tree while being observed. Of those foragers that did move between cultivars, most visited flowers on only one tree before contact was lost (Table 3.5) but up to four 'Sundrop' trees were visited on several occasions.   Initial searching on reaching a branch seemed random but, having settled, foraging was frequently systematic up or down a branch. Pollen collection could involve semi-hovering above the anthers or walking over them with wings at rest and, in both cases, legs were used to brush anthers and stigma. All pollen foragers periodically collected nectar before continuing to forage for pollen. Conversely, nectar foragers often cleaned pollen into their corbiculae after visits which brought them into contact with dehiscent anthers. Nectar collection involved inserting the bees head and proboscis into the base of the flower from the top or side while the legs grasped either the stamens or petals. Where the manner of nectar collection could be classified, three quarters of

Table 3.5   Foraging characteristics of honeybees visiting 'Sundrop' apricot flowers at Fernhill Farm Orchard, 5-9 August 1992.

Forager type	n	'Sundrop' trees visited / observation	'Sundrop' flowers visited / observation	Visitation rate (flowers/min)
Predominantly pollen	33	1.7	13.0	5.3
Predominantly nectar	11	1.4	4.0	2.7
Significance		ns	***	***

ns,*** Comparison of means non-significant (ns) or significant at $P \leq 0.001$ (***).

flowers visited were 'side-worked' and were therefore less likely to have been cross pollinated. Bees foraging for nectar did not show a consistent preference for foraging from the top of the flower over the anthers and style as opposed to from the side through the anthers.

Bees mainly collecting pollen visited significantly more flowers during the period of observation than did those collecting nectar (Table 3.5).   Bees foraging for pollen visited flowers at a rate almost twice that of bees foraging for nectar.   Probably as a consequence, pollen foragers visited more 'Sundrop' flowers before contact was lost than did nectar foragers although there was no difference between the number of 'Sundrop' trees visited in that time.   Of the 44 bees which were followed to 'Sundrop' trees and which mainly collected either nectar or pollen, 33 foraged for pollen on at least three quarters of the visits they made while 11 foraged predominantly for nectar.   The ratio increased to 44 pollen foragers to 22 nectar foragers if bees which did not visit a 'Sundrop' tree before contact was lost were considered.   The remaining six bees foraged mainly for pollen but with more frequent nectar-collecting visits.

Similar data collected at Stirling Orchard in Bayview on 15 August 1992 showed a reverse preponderance of nectar foragers on 'Sundrop' and 'Trevatt'.   Total foraging activity was low, on average between one and three bees per tree and no bees were observed on some trees. Of ninety one bees identified and followed, sixty three appeared to collect nectar predominantly. Visitation sequences followed were short as bees drifted rapidly in the wind.   Pollen dehiscence on each cultivar on this occasion was well advanced but nectar concentrations (17% and 10% sugar in open 'Trevatt' and 'Sundrop' flowers respectively) were relatively high.

3.4   Discussion

The surveys reported were conducted to investigate the possibility that limited honeybee foraging on 'Sundrop' was restricting pollen flow from pollenizer trees and therefore cross pollination. Low nectar concentration is believed to reduce the attractiveness to honeybees of early flowering fruit crops such as plum and apricot relative to other species (Roberts, 1956; Vansell, 1952; Walsh, 1967). Limited nectar volume or otherwise unattractive nectar could also influence honeybee behaviour within an orchard and so determine preference for foraging on one or another cultivar. Despite this the results suggest that honeybee foraging behaviour on 'Sundrop' flowers is unlikely to be a specific cause of unreliable fruit set. Under suitable weather conditions, forager densities at Fernhill Farm were in the same range as those observed on other apricots (Free, 1960a) and in New Zealand apple orchards (Palmer-Jones and Clinch, 1967,1968). Honeybee behaviour on 'Sundrop' was similar to that observed on other apricot cultivars and fruit tree species as was the number of trees visited during each observation (Free, 1960a). In both cases, a large majority of foragers collected pollen and pollen foragers also worked flowers more rapidly than did nectar foragers. Visitation rates calculated by Free (1960a) were higher than at Fernhill Farm as were the number of flowers visited per tree. How these differences might affect pollen transfer between cultivars is unclear but it is probable they reflect the hive and orchard conditions, the temperature when observations were made, the size of trees or the stage of bloom, factors which were not experimentally controlled in either survey.

Nectar production by 'Sundrop' flowers, in particular, appears unimportant as a factor contributing to unreliable fruit set on this specific cultivar. 'Sundrop' flowers produced more nectar than any apricot cultivar examined and volumes observed were as high or higher than those reported for other *Prunus* species (Abrol and Bhat, 1989; Brown, 1951; Erickson, et al., 1979; Meheriuk et al., 1987). The quantity of sugar present in 'Sundrop' flowers (20 µl @ 5% sugar = 1 mg sugar/flower) was therefore equivalent to or greater than that in flowers of other apricot cultivars and represents a nectar resource in the upper range of those presented in spring by flowers of species commonly found in a temperate environment (Southwick et al., 1981). The quantity of sugar present in

'Sundrop' flowers should therefore make them attractive to honeybees whenever weather conditions allow evaporation to the raise the concentration above about 10% sugar (Kevan and Baker, 1983). Nectar composition also appears unlikely to pose a problem. Honeybees can display preferences for different sugars (Wykes, 1952) but analysis of 'Sundrop' nectar showed that glucose and fructose were the main components, similar to previous reports for apricot (Meheriuk et al., 1987) and other *Prunus* species (Bieleski and Redgewell, 1980; Percival, 1955). These two results mean that nectar (as a contributor to the overall attractiveness of 'Sundrop' flowers) does not limit honeybee activity on 'Sundrop'. Rather, the attractiveness of 'Sundrop' flowers may be higher than average for apricots. Nectar attractiveness only appears likely to affect pollenizer pollen flow   if honeybee preference for 'Sundrop' prevents them visiting pollenizer trees.

However, despite the potential attractiveness of 'Sundrop' flowers, only a minority of potential foragers from the eight hives present were active in the orchard when observations were made. Hive quality requirements (Hawkes Bay Pollination Group, 1988) stipulate that colonies supplied for stonefruit pollination consist of at least 22,500 bees (9 frames per hive, 2500 bees per frame). If one quarter of these are foragers then the potential foraging population in Fernhill Farm orchard was approximately 45,000 bees. Forager counts during fine weather averaged six bees per tree, which, over the 1200 'Sundrop' trees in bloom, is equivalent to an actual foraging population of 7,200 bees. Only about 16% of potential foragers therefore appeared to be visiting flowers in the block observed. This is half the number which were estimated to forage locally on apples in Britain (Free, 1966a) but it is not clear whether this indicates significant competition by flowers of other species. Apricot orchards represent a very small proportion of the land area in Hawkes Bay so there is probably considerable dilution of foraging effort over a wide area without compensation from hives in other orchards.

The importance of nectar as a factor in determining cross pollination is also reduced by the relative ineffectiveness of nectar foragers as potential pollinators. At Fernhill Farm there were fewer nectar foragers than pollen foragers, they visited flowers more slowly, and were less likely to contact stigmas due to the tendency to alight on petals and insert the proboscis into flowers through the base of the stamens. The same behaviour has been observed on plums (Brown, 1951; Roberts, 1956). By contrast, more rapid visitation

rates and higher probability of stigmatic contact suggest pollen foragers effect greater pollen transfer, as suggested for other *Prunus* crops (Free, 1960b; Thorp et al., 1974). Feeding honeybee colonies with sugar syrup, as is done frequently in early spring in New Zealand, will also enhance pollen collection (Free, 1965). Pollen collecting bees therefore appear likely to have contributed most to cross pollination at Fernhill Farm in 1992 and therefore the pollen resource presented by an apricot orchard may be the principal determinant of foraging activity. If, however, nectar foragers moved more frequently between trees than did pollen foragers, they might contribute to cross pollination out of proportion to their number. Nectar foragers visited fewer flowers per tree on 'Sundrop' at Fernhill Farm Orchard than pollen foragers but it could not be determined whether they returned to the hive or moved to another tree when contact was lost. Quantitative studies to compare actual pollen transfer due to both types of foraging under conditions with controlled temperature, humidity and wind speed would help to clarify the significance of nectar as a factor influencing the cross pollination of early blooming crops such as apricot. The importance of nectar foragers may increase during warm, dry weather when low relative humidity raises nectar concentration and its attractiveness to bees (Corbett et al., 1979; Shuel, 1975). Either of these instances may have been responsible for the higher proportion of nectar foragers at Stirling Orchards, Bayview. Such weather, however, is not typical during late winter-early spring in Hawkes Bay. Rather, low temperatures reduce active transport processes such as nectar secretion, reducing nectar production. The use of overhead sprinklers for frost protection would also dilute nectar or may wash it out of flowers entirely.

Regardless of the relative importance of pollen and nectar as influences on pollen transfer the forager count data clearly demonstrate the effect on honeybee foraging activity of adverse weather during bloom of apricots in Hawkes Bay. The potential for disruption of cross pollination by adverse weather can be shown quantitatively by calculating the honeybee activity required to set a crop of 15 t ha $^{-1}$ using flower visitation rates observed at Fernhill Farm Orchard and making certain assumptions about the pollination of flowers in the orchard that year which resulted in a 13% set due to open pollination (see Table 2.7). This requires calculation of likely numbers of visits made to each flower and of the probability of cross-pollination occuring at each visit which may be estimated from the foraging data collected at Fernhill Farm Orchard.

For instance, during one day of suitable weather for honeybee foraging such as August 6, (Table 3.4, Fig. 3.2) the total number of floral visits made per tree is given by

$$\text{Total visits per tree} \;=\; t \times b \times r$$

where t = total foraging duration = 6×60 min = 360 min,
    b = average honeybee activity level per tree = 6 bees / tree (Fig. 3.2b),
    r = honeybee foraging rate = 5 flowers / min.

Thus, total visits per tree on a single fine day = $6 \times 60 \times 6 \times 5 = 10800$ visits. If there are 5000 flowers per tree and half are open and likely to be visited at any one time, then the expected number of visits per flower is $10800 / 2500 = 4.32$ visits / flower. This is less than, though near, the 5-13 visits / flower observed on apples (Benedek and Nyéki, 1990). The probability of cross pollination on any one visit may then be calculated as

$$\text{Prob. of cross pollination after } n \text{ visits} \;=\; 1 - \text{prob. of no cross pollination}$$
$$=\; 1 - (1 - x)^{n}$$

where n = the number of visits per flower and
    x = the probability of cross pollination on each visit.

If observed fruit set at pit-hardening is taken as an index of the probability of cross pollination after all n visits to a flower, then the average probability of cross at *each* visit may be calculated by using fruit set data from Fernhill Farm Orchard for 1992 and solving for x. Thus, since observed fruit set after open pollination was 13%, then

$$\begin{aligned}
0.13 \;&=\; 1 - (1 - x)^{4.32} \\
\Rightarrow \quad x \;&=\; 1 - 0.87^{1/4.32} \\
&=\; 0.03 \qquad (i.e.\ 3\%)
\end{aligned}$$

This implies that, on average, each forager cross pollinated 3% of flowers it visited. This cross pollination may have resulted from prior visits to pollenizer flowers or to in-hive pollenizer pollen transfer from other foragers (DeGrandi-Hoffman et al., 1986. The fraction represents a maximum proportion since it is assumed that all visits occurred on a single day. It is slightly less than the estimate of 5% used to model pollen transfer in almond orchards (DeGrandi-Hoffman et al., 1989).

Using these estimates as a basis, the foraging activity required to set a 'typical' apricot crop may be calculated as 9.3 forager-days per tree (Table 3.6). This is equivalent either to a single bee working a tree, six hours a day, for slightly over 9 days, or nine bees working per tree for one day. Only on one day at Fernhill Farm Orchard in 1992 did honeybee activity approach this level, that being August 6 when the weather was fine,

mild and calm. On this occasion activity averaged five bees per tree over seven hours (i.e. about 6 forager-days, assuming a six hour foraging period), theoretically two thirds the foraging activity needed to set 10% of flowers. Since activity for much of the other three days surveyed was either nil or very low due mainly to wind, foraging on August 8 (not observed) on which weather conditions were suitable for honeybee activity (Table 3.4), probably contributed to the 13% set observed at Fernhill Farm Orchard.

These calculations may then be used to estimate theoretically the number of hives required to achieve this level of set. Hives used for stonefruit pollination purposes in Hawkes Bay are required to contain at least 22,500 bees (Hawkes Bay Pollination Group,

Table 3.6   Calculation of honey bee foraging activity needed to set a 'typical' apricot crop.

Item	Value	Comments
Assumed conditions		
Crop size [†]	15,000 kg / ha	*= 15 t ha⁻¹*
Tree density	500 trees / ha	*4m × 5m spacing*
Average fruit size	0.06 kg	*= 60 g*
Foraging period	6 hours / day	*9:30am to 3:30pm*
Visitation rate	5 flowers / min	*Assumes all bees are pollen foragers*
Proportion of flowers set by each forager trip	0.03	*i.e. 3% of flowers visited*
Expected number of fine days during bloom	1.0	*A not uncommon situation*
Colony size [‡]	22,500 bees / hive	*9 frames per hive, 2500 bees per frame*
Effective foragers per hive	900	*Assumes ¼ bees in hive are foragers and that 16% are foraging in orchard*
Calculations		
Fruit number (per tree)	= Crop size / (Tree density × Average fruit size) = 15,000 / (500 × 0.06) = 500	*i.e. 30 kg / tree @ 60 g / fruit, or 10% fruit set @ 5000 flowers / tree*
Forager-days required (per tree)	= Fruit number / (Foraging period × Visitation rate × Proportion of flowers set) = 500 / (6×60×5×0.03) = 9.3	*i.e. 1 bee foraging for 9 days or 9 bees foraging for 1 day*
Hives required (per hectare trees)	= Tree density × (Forager-days required / No. of fine days) / Bees foraging on trees from each hive = 500 × (9.3 / 1.0) / 900 = 5.2	*i.e. 5 hives per hectare of tree canopy*

[†] Crops on N.Z. trees five-years-old and over average 11.8 t ha⁻¹ and can exceed 30 t ha⁻¹ (Wilton, 1984).
[‡] Minimum requirements for hives supplied by Hawkes Bay Pollination Group members.

1988). If one quarter of these are foragers and if the distribution of bees is similar to that estimated above (16% of these actively foraging within the orchard) then about 900 bees are available for pollination from each hive. The required number of hives is then about five per hectare or two per acre (Table 3.6). This estimate compares closely with recommendations of 2-7 colonies / ha made for the pollination of other similar crops (Jackson, 1986; Stanger and Thorp, 1972; Traynor, 1960). Provision of hives at this level should therefore ensure an adequate level of foraging activity on 'Sundrop' trees whenever weather conditions permit. Higher population levels may also have the added benefit of causing greater competition for foraging resources as well as interaction between bees which together may raise the frequency of inter-varietal flights and thus cross pollination.

Cross pollination of self incompatible apricots is clearly highly sensitive to poor weather conditions. Because apricots bloom for a relatively short time, an extended period of adverse weather (low temperature, high wind, cloud and or rain) can greatly reduce opportunites for foraging activity. However, the required number of hives is within the range recommended for other similar crops even when weather conditions permit only one and a half days (nine hours) of honey bee activity during the bloom period. This may not be possible in years with very extended poor weather, but as a general rule, inadequate foraging activity alone should not therefore prevent fruit set on 'Sundrop'. Instead, fruit set is at risk when the frequency with which flowers are cross pollinated is low- probably if it is less than 3%. When it is above 5%, a single fine day with intensive honeybee foraging may be all that is necessary to produce a satisfactory crop. This requires that movements between 'Sundrop' and pollenizer flowers are indeed frequent. The calculations therefore point to the critical importance of adequate numbers of pollenizer trees and of sufficient pollenizer bloom overlap with 'Sundrop' to allow cross pollination. The risk of poor weather cannot be avoided and therefore reliable fruit set depends on maximizing the opportunity for intervarietal pollen transfer over the entire period of 'Sundrop' bloom. Intensive interplanting of pollenizer trees plus the selection of adapted pollenizer cultivars which consistently bloom in synchrony with 'Sundrop' is also essential to capitalize on forager activity whenever it occurs. A better understanding of the degree to which cross pollination is influenced by bloom divergence would contribute greatly to the selection of pollenizer cultivars which would achieve this objective.

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Chapter 4
Bloom Phenology and Pollination of 'Sundrop'

4.1   Introduction

Apricots bloom in Hawkes Bay during a period in late winter from the beginning of August to the start of September. Cold, wet weather unsuitable for honeybee activity is not uncommon during this period. Weather conditions therefore directly affect the success of fruit set on 'Sundrop' apricot as the number of bee visits to a flower strongly influences the probability of it setting a fruit (Brain and Landsberg, 1981). However, apricots in Hawkes Bay also vary considerably in their times of bloom relative to one another. The optimum relative times of bloom for apricots are not known but, for apples, it is recommended that pollenizers bloom slightly in advance of the main cultivar (Wauchope, 1968; Williams and Sims, 1977). Pronounced variation from the optimum bloom divergence could therefore reduce cross-pollination of 'Sundrop' flowers by restricting pollenizer pollen supply when they are receptive. Modelling of apple cross-pollination (Brain and Landsberg, 1981) shows that the effect of cross-pollination probability rises as the number of visits to a flower falls. Reduced synchrony between cultivars therefore may amplify the effect of adverse weather by reducing the probability of cross-pollination on those few visits that do occur.

Cross-pollination also must occur while the flower remains receptive and fertilization can take place (Williams, 1970). Modelling of pollination suggests that the duration of receptivity is less important than the number of bee visits (Brain and Landsberg, 1981). Despite this, the short floral receptivity of *Prunus* species has been widely studied, particularly in relation to ovule senescence (Eaton, 1959; Griggs and Iwakiri, 1964; Keulemans and van Laer, 1989; Lech and Tylus, 1983; Postweiler et al., 1985; Thompson and Liu, 1973). The duration of floral receptivity of some Spanish apricots is also limited by rapid loss of stigmatic receptivity, particularly in warm conditions (Burgos et al., 1991). Petal lifespan is a further aspect of floral receptivity since while bees will visit flowers without petals (Williams et al., 1984), presence of petals clearly plays a crucial role as a visual attractant for individual flowers. Consequently, rapid loss of petals, due

either to genetic tendency or adverse weather (wind or rain), could also reduce the period during which a flower is likely to be visited and cross-pollinated.

Floral receptivity could also be reduced indirectly by the self incompatibility of 'Sundrop'. Energy allocation to female floral function is typically lower in outcrossing species due to the advantage gained from directing greater resources into pollen production (Evenson, 1983). This could mean that self incompatibility is also be linked to lower ovule viability in *Prunus*. Self incompatible *Prunus* species commonly do have smaller pistils and larger stamens (Surányi, 1976). The traits of rapid ovule senescence or abnormal embryo sac development and self incompatibility also occur together in almond (Pimienta and Polito, 1982), sour cherry (Dys, 1984b; Lech and Tylus, 1983), and sweet cherry (Eaton, 1959; Stösser and Anvari, 1982) whereas there are no reports of rapid ovule deterioration in peaches or nectarines which are self compatible. Instead, the reverse association of extended ovule viability with male sterility occurred in *Prunus cerasifera*, *P. mahaleb* and *P. persica* (Martinez-Tellez and Crossa-Reynaud, 1982).

These factors clearly may all affect the pollination of 'Sundrop' given the substantial risk of cold or windy weather in Hawkes Bay in late winter and early spring. However, the petal lifespan and the receptive periods for apricot cultivars under New Zealand conditions have not been determined and bloom data published in association with pollenizer recommendations for New Zealand apricot cultivars (Glucina et al., 1990; MacLaren et al., 1992) do not consider the degree of variation in pollenizer bloom synchrony. Therefore, this study was designed to assess whether bloom divergence could be contributing to unreliable fruit set on 'Sundrop', and in particular, whether 'Trevatt', commonly planted with 'Sundrop', was a reliable pollenizer cultivar. Three aspects of the pollination of 'Sundrop' were investigated: i). the variation in time of bloom of 'Sundrop' relative to other cultivars as shown by historical records of flowering phenology; ii). the duration for which 'Sundrop' flowers remained receptive to pollen and capable of setting fruit; and iii). the manner in which bloom divergence affected the probability of cross-pollination. The investigation prompted the development of a simple model of the effect of bloom phenology on pollenizer pollen transfer since insufficient data was available to permit application of more complex models (eg Brain and Landsberg, 1981; DeGrandi-Hoffman et al., 1987; DeGrandi-Hoffman et al., 1989).

4.2   Methods and Materials

4.2.1   Analysis of North Island Apricot Bloom Records

4.2.1.1   Collection of bloom data

The twin concepts of 'bloom' and 'bloom divergence' were central to quantitatively describing the flowering of apricots in this study: 'bloom' represented the collective anthesis of flowers of a single cultivar, and 'bloom divergence', the time difference between equivalent bloom phases of two cultivars. Three key bloom phases, 5% Bloom, 90% Bloom and 90% Petal Fall were recognised (Table 4.1).   On a cultivar basis 5% Bloom was regarded as the start of bloom, 90% Bloom the effective end to pollen release and 90% Petal Fall the end of the period in which pollination was possible.

Bloom phenology data was collected with three objectives: i). to measure bloom duration in 'Sundrop', 'Trevatt' and 'Royal Rosa'; ii). to determine degree and variability of bloom divergence between cultivars and iii). to estimate individual apricot flower lifespan. Attention focused on the relative flowering of 'Sundrop' with 'Royal Rosa' and 'Trevatt' since the latter were the two cultivars most widely planted as pollenizers for 'Sundrop' in Hawkes Bay and other North Island areas. Continuous representation of all cultivars at each orchard was not always possible due to inadequate tree size, changes in orchard ownership and management (eg application of growth regulators) and loss of trees due to disease. Phenology observations also ended at HNRC in 1990 as all 'Sundrop' trees were felled in autumn 1991. PROC GLM (SAS Institute, 1989) was used to analyze data as a randomised complete-block design in which individual orchard/year combinations served as independent blocks.   Means were separated by orthogonal contrasts.   Time of bloom on different branch types was also compared at Massey University Fruit Crops Unit (FCU), Cox's Orchard and The Downs in 1991 (see Table 4.2) and then again at

Table 4.1   Cardinal bloom phases used to describe flowering of apricot cultivars.

Cardinal phase	Description
5% Bloom	First 5% of flowers open and displaying anthers (anthesis)
90% Bloom	90% of flower buds at anthesis or petal fall stages
90% Petal Fall	Final 10% of flowers still retaining petals

The Downs in 1992. Five replicate trees of 'Royal Rosa', 'Sundrop' and 'Trevatt', spaced evenly within orchard blocks, were each monitored at regular (two day) intervals and progress of bloom recorded for short (10-15 cm) shoots ('Royal Rosa' and 'Trevatt') or spurs ('Sundrop') as well as long extension shoots. For analysis, individual orchard/year combinations were again treated as independent blocks in a two-way randomised complete-block design.

4.2.1.2 Sites for collection of apricot bloom data

Records describing flowering phenology of 'Sundrop', 'Royal Rosa' 'Trevatt' and other apricot cultivars grown at Havelock North Research Centre (HNRC) from 1984 to 1991 were kindly provided by staff at HortResearch. Records covered first bud movement, 5% Bloom, 90% Bloom and 90% Petal Fall. The orchard is located at the southern fringe of the Heretaunga Plains (lat. 39.7°, long. 176.9°) 9 m above sea level on a deep, fertile alluvial soil. Mean annual rainfall is 798 mm with a range of 535 to 1132 mm per annum. Daily mean temperatures are 7.6° to 8.7°C in winter (June, July August) and 16.5° to 18.0°C in summer (December, January, February) with a typical daily range of 11.8°C (New Zealand Meteorological Service, 1983).

For analysis of bloom duration and divergence, bloom records from HNRC (1985 to 1992) and FCU (1990 to 1993) were supplemented by historical bloom data from three Hawkes Bay orchards (Campbell's, Fernhill Farm and Stirling orchards, 1992 only) and several other commercial apricot orchards in Hawkes Bay, Wairarapa and Manawatu (Table 4.2). Records of flowering were also made on trees at FCU which is located on heavy alluvial soil adjacent to the Manawatu River (lat. 40.17° long. 175.35°). Mean annual rainfall is 995 mm with a range of 713 to 1298 mm. Daily mean temperatures are 8.0° to 9.0°C in winter (June, July, August) and 16.1° to 17.6°C in summer (December, January, February) with a typical daily range of 8.6°C. Six cultivars were observed from 1990 to 1993 using trees planted in 1987 ('Royal Rosa', 'Sundrop', 'Trevatt', 'Valleygold') or 1988 ('Cluthagold', 'Earliril'). Five cultivars ('Cluthagold', 'Earliril', 'Sundrop', 'Trevatt' and 'Valleygold') were grafted on peach rootstocks while 'Royal Rosa' was grafted on myrobalan plum (*Prunus cerasifera*). Tree health was variable. Many 'Royal Rosa' trees showed signs of stock-scion incompatibility and were removed in 1993. Symptoms of bacterial blast (*Pseudomonas syringae*) including petal discoloration, leaf and shoot-tip

Table 4.2   Commercial orchards used for observation of apricot flowering phenology.

Orchard & Location	Planted	Cultivars [z]	Rootstock
Cox's Orchard Greytown	mid 1980's	RR, Sd, Tv	plum
The Downs Ponotahi	mid 1980's	RR, Sd, Tv	plum
Stirling Orchard Bayview	1970's - 80's	RR, Sd, Tv, Gr, Cg	plum/peach
Fernhill Farm Orchard Fernhill	mid 1980's	Gr, RR, Sd, Tv	peach
N.T. Hope Trust Twyford	mid 1980's	RR	plum
Campbell's Orchard, Bridge Pa.	mid 1980's	Cg, RR, Sd, Tv Cg	peach plum
Fairview Orchard Kawhatau Valley	mid 1980's	RR, Sd, Tv	plum

[z] Abbreviations: Cg = 'Cluthagold'; Gr = 'Goldrich'; RR = 'Royal Rosa'; Sd = 'Sundrop'; Tv = 'Trevatt'.

necrosis were common on 'Royal Rosa', 'Trevatt' and 'Valleygold', particularly in spring 1992. Although many 'Sundrop' trees were vigorous and apparently healthy, silverleaf disease (*Chondrostereum purpureum*) was a major problem and almost 50% of 'Sundrop' trees were showing varying levels of infection when removed in 1993. Observations were not made on trees with disease symptoms.

4.2.2   Duration of Receptivity of 'Sundrop' Flowers

4.2.2.1   Petal lifespan

Average petal lifespan and distribution of flower bud development were estimated from detailed records of bloom at FCU (1990, 1992 and 1993) and at Campbell's, Fernhill Farm and Stirling Orchards (1992 only). Quantitative records of bloom progress (percent anthesis and percent petal fall) were based on bud development on tagged branches of each cultivar. At FCU in 1990, branch sections bearing short shoots ('Royal Rosa' & 'Trevatt') or spurs ('Sundrop') were tagged on fifteen randomly-selected trees of each cultivar. Each section carried approximately 50 flower buds. Unopen and open flowers as well as those which had lost their petals were counted every two or three days over the four week bloom period. Subsequent bloom surveys in 1992 and 1993 monitored development of 100 buds on tagged branches of five healthy representative trees distributed evenly throughout the apricot blocks. Cumulative bloom on each branch

section was estimated using a ten-point percentage scale (0, 1, 5, 10, 20, 50, 80, 90, 95 & 99%) for both anthesis (presentation of anthers) and petal fall (abscission of petals).

Petal lifespan was calculated as the mean of the delay between 5% Bloom and 5% Petal Fall and between 90% Bloom and 90% Petal Fall. Dates of the bloom phases used to calculate the two delay periods were estimated by regression of cumulative bloom data (cumulative frequency) against time. Cumulative frequency distributions for anthesis and petal fall were asymmetric due to tailing of later opening flowers but were satisfactorily described by Gompertz functions fitted using PROC GLM (SAS Institute, 1989). Consistent allocation of trees to experimental blocks was not always possible due to orchard layout and data were therefore analyzed as a completely randomised design.

4.2.2.2   *Post-pollination development of 'Sundrop' pistils*

Ovary development in 'Sundrop' flowers after cross-pollination was surveyed at Fernhill Farm and FCU in 1991 and 1992 to compare normal development of ovaries, ovules and pollen tubes with that in emasculated flowers. Pistils were sampled from trees used to investigate self-incompatibility (Chapter 2) and duration of floral receptivity (this chapter) and emasculated pistils were sampled from the same labelled branch sections used for these experiments. Each branch section carried sufficient flowers to leave at least 20 flowers for fruit set measurement after removal of histological samples. The non-emasculated control consisted of blossoms reaching anthesis the same day other flowers were emasculated. All flowers were hand-pollinated with 'Trevatt' pollen (Section 2.2.1.1) on the day of emasculation (Day 0). Samples of five pistils were collected 0, 4, 8, 10, 12, 14 and 16 days after pollination, fixed in acetic-ethanol or FAA and prepared for dissection as previously described (Section 2.2.1.2). Pistils were sampled by randomly identifying a pistil within each branch section and removing every fifth subsequent pistil up to the required number (five). The survey was duplicated on each tree for 'Early' and 'Mid-bloom' cohorts corresponding to 5% Bloom and 50% Bloom. Fruit set was recorded at pit-hardening in October and immediately prior to harvest in December or early January.

Ovary width was measured prior to dissection using a calibrated eye-piece graticule fitted to a binocular dissecting microscope. Ovules were removed from ovaries before styles

were squashed, transferred to numbered cells of polycarbonate ELISA trays and covered with aniline-blue dye solution to prevent desiccation. Ovule length (distance from base of integuments to micropylar tip) was measured with an eyepiece graticule and ovules (primary and secondary) scored for senescence using chalazal fluorescence of the nucellus as an indicator (Pimienta and Polito, 1982). Ovules were observed within 4 h of dissection since fluorescence of abortive ovules faded rapidly.

The survey was analysed using PROC GLM (SAS Institute, 1989) as a split-block design nested in year and site in which trees (or groups of trees in 1992 at Fernhill) served as experimental blocks, cohorts as split-blocks and labelled branch sections as experimental units. Year, site and tree were all treated as random effects while cohort was considered a fixed effect. Ovary width and ovule length were analyzed as the natural logarithm of original values while pollen tube counts and fraction of ovules penetrated by pollen tubes were transformed by square-root and arcsine transformations respectively (Snedecor and Cochran, 1980). Fruit set proportions were transformed to probits (since the arcsine transformation insufficiently reduced kurtosis) and analyzed in association with data from the investigation of self-incompatibility (Chapter 2). Means were compared by orthogonal contrasts and back-transformed for presentation in results.

4.2.2.3   Delayed pollination of 'Sundrop' flowers

The consequences of delayed cross-pollination of 'Sundrop' flowers on pollen tube development and fruit set were measured at FCU and Fernhill Farm in 1991 and 1992 to estimate the duration of floral receptivity of 'Sundrop' flowers. Trees involved were those used to investigate self-incompatibility (Chapter 2). Flowers on labelled branch sections were emasculated and pollinated with 'Trevatt' pollen (Section 2.2.1.1) either at emasculation (Day 0), or after progressive delay (Day 2, 4, 6 and 8). Application delay was allocated at random to branch sections on each of the five trees and delay treatments were applied to 'Early' and 'Mid' cohorts, as in previous experiments. Samples of non-pollinated, emasculated pistils were collected on Day 0 for each cohort/tree combination to record relative developmental stage of flowers at emasculation for each site and year.

Five pistils were randomly sampled from each branch section eight days after pollen application to measure pollen tube development after delayed pollen application, fixed

immediately then dissected later (Section 2.2.1.2). Ovary and ovule size, pollen tube development and ovule penetration were measured for each pistil. Ovary widths were transformed to natural logarithms for analysis of variance using PROC GLM (SAS Institute, 1989). Fruit set was recorded at pit-hardening and before harvest. Fruit set proportions were transformed to probits (normits) and analyzed in association with data from the investigation of self-incompatibility (Chapter 2).

4.2.3 Modelling Bloom Divergence and Pollen Transfer

The interaction of bloom divergence with the durations of bloom, floral receptivity and pollen release and its effect on 'Sundrop' fruit set was investigated using a model of intervarietal pollen transfer. The model presupposes that expected cross-pollination (and hence also fruit set) on any given day is proportional to vector activity, pollenizer pollen supply and numbers of receptive 'Sundrop' flowers. However, it is probable that the likelihood of cross-pollination is also inversely related to the supply of 'Sundrop' pollen since both the capacity of individual pollen vectors (honeybees) to transfer pollenizer pollen and the capacity of the stigmatic surface to receive that pollen are finite. Replacement of pollenizer pollen on the vector by 'Sundrop' pollen grains (self pollen) lowers the expected rate with which pollenizer pollen will be deposited on the stigma (Lertzman and Gass, 1983). The expected level of cross-pollination is therefore a function of the number of receptive 'Sundrop' flowers, combined with the genotypic composition of the mobile pollen pool likely to be deposited on 'Sundrop' stigmas.

Since no data was available on the genotypes of pollen grains deposited on 'Sundrop' stigmas in Hawkes Bay orchards, it was assumed as an initial hypothesis that its composition is directly proportional to the ratio of flowers of the two cultivars releasing pollen at any given time. The simulated probability of cross-pollination on any given day is therefore a function of the ratio of pollenizer to 'Sundrop' flowers releasing pollen and of the number of 'Sundrop' flowers receptive to pollination. Higher numbers of pollenizer flowers releasing pollen or of 'Sundrop' flowers receptive to pollination both increase the expected level of cross-pollination on a given day and, consequently, also expected fruit set due to pollen transfered on that day. Conversely, lower numbers of pollenizer flowers releasing pollen and also of receptive 'Sundrop' flowers (due to a shortened average receptive period) or higher numbers of 'Sundrop' flowers releasing

pollen all reduce expected fruit set. Numbers of 'Sundrop' and pollenizer flowers in the categories of interest (i.e. releasing pollen, receptive to pollination) for each day of the total bloom period therefore provide the principal inputs for the pollen transfer model.

In this respect, investigation of cumulative bloom data indicated that cumulative bloom was satisfactorily described by the Gompertz function. Since available data recorded only the beginning and end of bloom (5% Bloom and 90% Bloom) cumulative anthesis, pollen release and floral receptivity was simulated empirically by fitting a generalised Gompertz function to 5% Bloom and 90% Bloom dates. The cumulative frequency of open flowers, f_{open} at time t was therefore simulated by

$$f_{open} = e^{-3e^{-3.3(t-t_{5\%})/(t_{90\%}-t_{5\%})}} \tag{4.1}$$

where $t_{5\%}$ = time of 5% Bloom (relative to an arbitrary start date, July 31), $t_{90\%}$ = time of 90% Bloom, and the constants (3.0 and 3.3) are those needed to fit the line through 0.05 (5% Bloom) and 0.90 (90% Bloom) at times $t_{5\%}$ (Day 0) and $t_{90\%}$ (Fig. 4.1a).

This function, relating cumulative bloom to time (relative to 5% Bloom), is then used to simulate the overall pollen release by both the pollenizer and main cultivars and the duration of floral receptivity of the main cultivar. To do this, the function is shifted with respect to 5% Bloom by t_{σ} (duration of pollen release by a flower[1]) and by t_{φ} (average duration of floral receptivity) to simulate, respectively, cumulative frequencies of flowers no longer shedding pollen and of those no longer likely to set fruit. Hence, the cumulative frequency of flowers no longer shedding pollen, f_{σ}, is defined by

$$f_{\sigma} = e^{-3e^{-3.3(t+[t_{5\%}-t_{\sigma}])/(t_{90\%}-t_{5\%})}} \tag{4.2}$$

where t_{σ} = the average number of days for which flowers release pollen (Fig. 4.1b). Similarly, if there is for each flower a constant non-zero probability of fruit set for a duration t_{φ} and a zero likelihood thereafter, then the cumulative frequency of flowers no longer receptive (able to set fruit), f_{φ}, is:

$$f_{\varphi} = e^{-3e^{-3.3(t-[t_{5\%}+t_{\varphi}])/(t_{5\%}-t_{90\%})}} \tag{4.3}$$

---

[1]   Dates of phenological stages (i.e. population parameters) are italicised while average durations of pollen release and of floral receptivity (i.e. individual flower parameters) are not.

a). Cumulative anthesis (f_{open}), $t_{Bloom} = t_{90\%} - t_{5\%} = 7$ days; b). Cumulative end to pollen release (f_{σ}), $t_{\sigma} = 3$ days; c). Proportion of flowers releasing pollen (p_{σ}), $t_{\sigma} = 3$ days; d). Proportion of receptive flowers with potential to set fruit (p_{φ}), $t_{\varphi} = 5$ days.
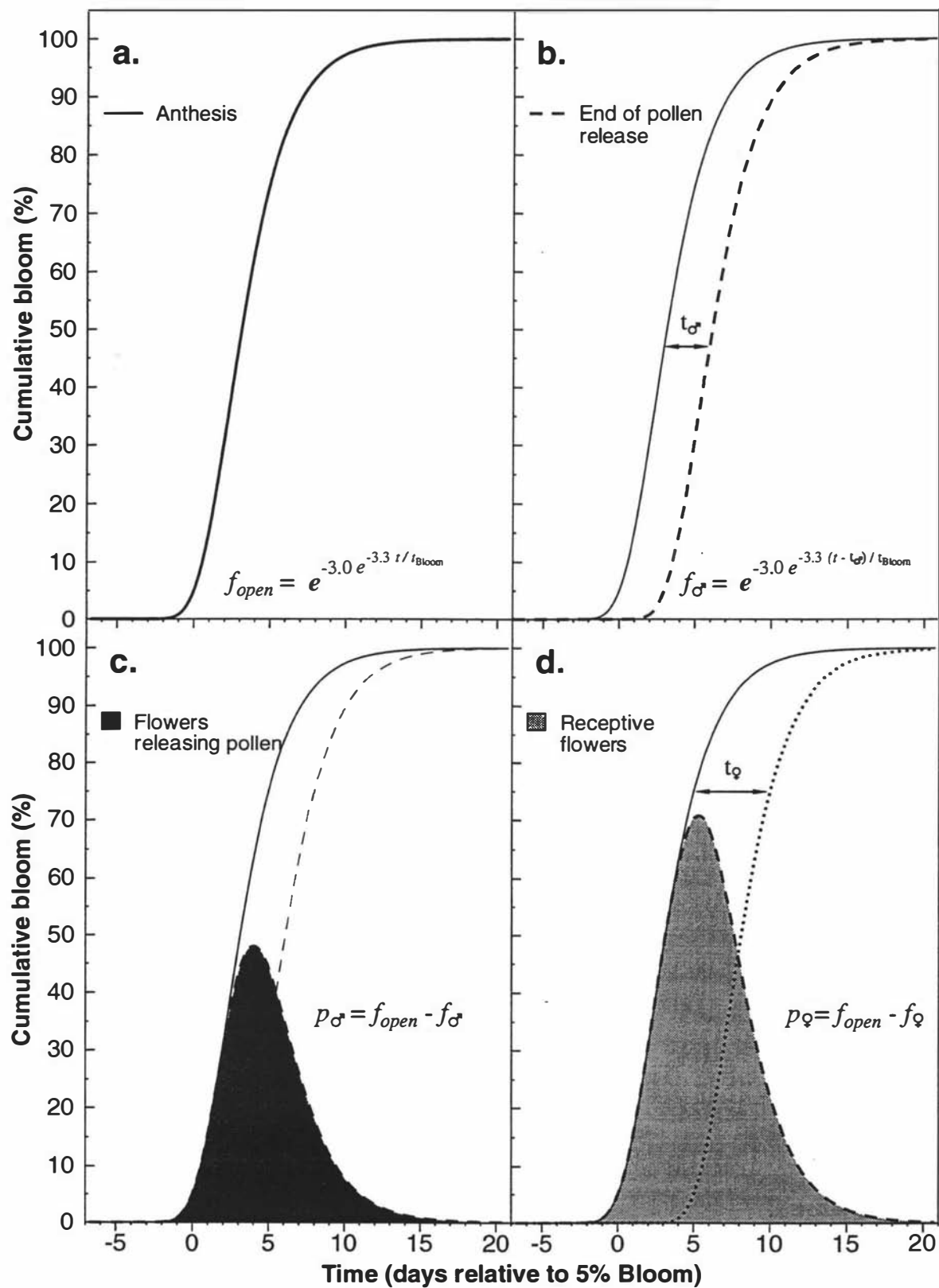
Figure 4.1   Simulation of cumulative bloom distributions (relative to 5% Bloom) for North Island apricots and proportions of receptive flowers and of flowers releasing pollen.

where $t_\circ$ = the average number of days of floral receptivity. The proportions of flowers releasing pollen (p_σ) and of those potentially able to set fruit ($p_\circ$) are therefore described, for any time t, by:

$$p_\sigma = f_{open} - f_\sigma \qquad (4.4)$$

and

$$p_\circ = f_{open} - f_\circ \qquad (4.5)$$

where f_{open}, f_σ and $f_\circ$ are described by equations 4.1 to 4.3 and the proportions for 'Sundrop' and the pollenizer cultivar are denoted by p_σ^{Sd}, p_σ^{poll} and $p_\circ^{Sd}$ respectively (Fig. 4.1c&d). The asymmetry of the functions means the simulated distributions of male and female phase flowers are skewed with an extended tail towards the end of bloom.

Given these relationships between time and cumulative bloom, then the product of p_σ^{poll} and $p_\circ^{Sd}$, weighted by the number of 'Sundrop' flowers releasing pollen (the weighted floral product), provides a daily index of expected effective pollen transfer from pollenizer flowers to main cultivar flowers. Correspondingly, the sum of daily products provides an overall index of expected cross-pollination and fruit set for any combination of floral parameters and bloom divergence denoted by the difference in dates for 5% Bloom, $\Delta t_{5\%}$ (or for simplicity, Δt, assuming divergence remains the same over the entire bloom period). Hence, $I_{\Delta t}$, the index of cross-pollination for the combination of pollenizer and main cultivar ('Sundrop') at a given bloom divergence Δt, is:

$$I_{\Delta t} = r^{poll} \cdot \sum_{t=t_{start}}^{t_{end}} q_t \cdot v_t \cdot \frac{p_{\sigma_t}^{poll} \cdot p_{\circ_t}^{Sd}}{(1 + p_{\sigma_t}^{Sd})} \qquad (4.6)$$

where r^{poll} is the ratio of pollenizer trees in the orchard, evenly distributed throughout the main cultivar block (here assumed that $r^{poll}=1/9$),

t_{start} and t_{end} are start and end dates for summation over the entire bloom period,

q_t is a proportion describing the average relative 'quality' of flowers open on a particular day (here assumed that $q_t=1$ throughout the entire bloom period),

v_t is the fraction of potential forager activity occurring on each day as a result of daily weather conditions (here assumed that $v_t=1$ throughout bloom), and

p_σ^{poll}, p_σ^{Sd} and $p_\circ^{Sd}$ are the predicted proportions of pollenizer and 'Sundrop' male and female phase flowers for each day of the entire bloom period.

The effect of bloom divergence, (as indicated by Δt), between 'Sundrop' and a simulated pollenizer was investigated for values of $\Delta t =$ -10 days to $\Delta t =$ +10 days in association with a range of potential values for the duration of pollen release (t_{σ}) and floral receptivity (t_{φ}) and also for the delay between $t_{5\%}$ and $t_{90\%}$ for either cultivar. The model was then subsequently used to assess the possible impact on cross-pollination of observed bloom divergence of 'Royal Rosa' and 'Trevatt' from 'Sundrop'. Simulated bloom profiles were produced for pairs of 'Sundrop' and 'Royal Rosa' or 'Trevatt' flowering observations by substituting recorded dates into model equations. $I_{\Delta t}$ was then calculated (assuming $t_{\sigma} = 3$ days and $t_{\varphi} = $ 5 or 7 days) by summing the weighted floral products from $t_{start} =$ -10 days to $t_{end} = $ +20 days where Day 0 = the date of 5% Bloom ($t_{5\%}$) for 'Sundrop'. Confidence intervals were calculated for regressions of $I_{\Delta t}$ on bloom divergence for both cultivars and values of t_{φ} using PROC REG (SAS Institute, 1989).

4.3   Results

4.3.1   Analysis of North Island Apricot Bloom Records

Records of bloom phenology for 'Royal Rosa', 'Sundrop' and 'Trevatt' at eight sites in up
to eight years indicate the early and extended bloom that characterises flowering of
apricots in the North Island. Analyses of variance for bloom date records indicated that
both cultivar genotype and the combined differences between years and sites strongly
affected the date of 5% Bloom, 90% Bloom and 90% Petal Fall (Table 4.3). 'Sundrop'
differed significantly from 'Royal Rosa' and 'Trevatt' for each of these bloom parameters.
The overall effect of cultivar therefore was large in comparison with the interaction
between cultivar and year/site record indicating that variation in bloom divergence
between cultivars was generally small. Representation of sites and years was unbalanced
and prevented precise analysis of the relative size of year-to-year versus site-to-site
variation. However, comparison of dates from six orchards observed in 1991 indicated
10-12 days delay between 5% Bloom at the two earliest sites, Fernhill Farm and Cox's
Orchard, and the two latest sites, Fairview Orchard and FCU, Massey University.
Similar year-to-year variability was observed at HNRC, the site with the most extensive
records (1984-1991).

Table 4.3   Analysis of variance of bloom phenology data for 'Royal Rosa', 'Sundrop' and
'Trevatt' apricots in North Island orchards.

| | | Variance components (Type III MS) | | | | |
| | | Bloom dates ^{z} | | | Bloom durations | |
Source	df	5% Bloom	90% Bloom	90% Petal Fall	Anthesis	Petal Fall
Model	25	260.8 ***	279.0 ***	265.9 ***	18.00 *	10.25 ns
Record	23	226.6 ***	258.5 ***	232.0 ***	19.52 **	11.10 ns
Cultivar	2	674.2 ***	557.1 ***	362.6 ***	1.90 ns	5.41 ns
Residual: Cult.×Record	44	10.9	14.6	16.5	8.30	7.36
R^2		0.93	0.92	0.93	0.56	0.52
Contrasts						
'Sundrop' vs 'Royal Rosa'	1	566.0 ***	406.1 ***	250.6 ***	1.81 ns	8.42 ns
'Sundrop' vs 'Trevatt'	1	144.0 ***	152.6 **	111.7 *	0.28 ns	7.96 ns

ns,*,**,***   Variance components and orthogonal contrasts non-significant or significant at $P \leq 0.05$, $P \leq 0.01$
and $P \leq 0.001$ respectively.
^{z} Dates analysed as days from July 31.

Table 4.4   Bloom dates for 'Royal Rosa', 'Sundrop' and 'Trevatt' apricots in North Island orchards.

Cultivar	Date of bloom stage [z]			Duration (days) [y]	
	5% Bloom	90% Bloom	90% Petal Fall	Anthesis	Petal Fall
'Royal Rosa'	12 August	19 August	26 August	7.0	7.5
'Sundrop'	18 August	25 August	31 August	7.0	8.7
'Trevatt'	22 August	28 August	5 September	6.8	8.0
LSD$_{0.05}$	±1.6 days	±1.8 days	±3.0 days	±1.4 days	±1.6 days

[z] Means of 23, 22 and 14 site/year combinations respectively.
[y] Duration of anthesis = 5% Bloom to 90% Bloom, duration of petal fall = 90% Bloom to 90% Petal Fall.

Bloom typically started with 'Royal Rosa' in early-to-mid August and concluded with 'Trevatt' in early September (Table 4.4). On average, 'Sundrop' reached 5% Bloom six days after 'Royal Rosa' and four days ahead of 'Trevatt' and this time difference between cultivars was maintained at 90% Bloom and 90% Petal Fall. Duration of anthesis (5% Bloom to 90% Bloom) did not differ between cultivars nor did the petal fall period (90% Bloom to 90% Petal Fall) and consequently, the entire bloom duration of each cultivar (5% Bloom to 90% Petal Fall) was, on average, two weeks. Overall, the principal effect of genotype was to determine when bloom began and there was no evidence that bloom progressed differently for any cultivar.

While overall variation of bloom divergence from the general pattern was small (as indicated by the small interaction of cultivar and year/site record: Table 4.3), comparison of individual records indicated that some cases there were marked departures from the general pattern. For instance, 5% Bloom of 'Royal Rosa' was 21 days ahead of 'Sundrop' at Stirling Orchards in 1993 while at HNRC in 1989 'Sundrop led 'Trevatt' by 8 days (c.f. means of 6 and 4 days respectively). Reversal of sequence is also possible. 5% Bloom for 'Royal Rosa' varied 17 days from 1988 (overall, an 'early' year at HNRC) to 1989

Table 4.5   Variation in dates of 5% Bloom for 'Royal Rosa', 'Sundrop' and 'Trevatt' apricots at Havelock North Research Centre, 1988-1989.

Cultivar	Date of 5% Bloom		Divergence from 'Sundrop'		Difference, 1989-1988
	1988	1989	1988	1989	
'Royal Rosa'	9 August	26 August	-11	+1	17 days
'Sundrop'	20 August	25 August			5 days
'Trevatt'	23 August	2 September	+3	+8	10 days

Table 4.6   Shoot type and mean time of bloom and petal fall on 'Royal Rosa', 'Sundrop' and 'Trevatt': FCU, Cox's and Ashby's Orchards in 1991 and Ashby's Orchard in 1992.

Cultivar & shoot type	5% Bloom		90% Bloom		90% Petal Fall	
	Date	Δ	Date	Δ	Date	Δ
'Royal Rosa'						
Short/spur	7 August		13 August		20 August	
Extension	11 August	4 days	18 August	5 days	25 August	5 days
'Sundrop'						
Short/spur	12 August		18 August		25 August	
Extension	16 August	4 days	25 August	7 days	30 August	5 days
'Trevatt'						
Short/spur	16 August		23 August		31 August	
Extension	24 August	8 days	31 August	6 days	4 September	4 days
Significance						
Cultivar		•••		•••		•••
Shoot type		•••		•••		•••
Cultivar×Shoot type		••		ns		ns
$LSD_{0.05}$		1 day		2 days		2 days

ns,••,••• Effects non-significant or significant at $P \le 0.01$ or $P \le 0.001$ respectively.

(overall, a 'late' year) whereas 5% Bloom of 'Sundrop' was relatively stable, varying only 5 days (Table 4.5). As a consequence, 'Royal Rosa' reached 5% Bloom one day later than did 'Sundrop' in 1989, in contrast to the normal sequence. A similar situation was observed in 1992 at Stirling Orchards, Bayview where 'Trevatt', normally the latest of the three cultivars, bloomed 1-2 days in advance of 'Sundrop'.

The type of shoot on which buds are borne can also affect time of bloom. Analysis of within-tree variation on 'Royal Rosa', 'Sundrop' and 'Trevatt' indicated that buds on spurs or short shoots opened four to five days in advance of axillary buds on extension shoots (Table 4.6). Consequently, overlap between bloom on 'Royal Rosa' extension shoots and 'Sundrop' spurs was observed despite marked divergence between the dominant periods of bloom of the two cultivars. The buds on long extension shoots on 'Sundrop' also overlapped with the bloom of buds on short shoots on 'Trevatt'. Some variation between cultivars in the effect of shoot type on bud development was also suggested by a significant cultivar/shoot-type interaction for date of 5% Bloom but the interaction was not significant later in bloom.

4.3.2   Duration of Receptivity of 'Sundrop' Flowers

4.3.2.1   Petal lifespan and regressions of cumulative bloom

Using Gompertz functions to describe bloom accounted for 90% and 89% respectively of variation in cumulative anthesis and petal fall of 'Royal Rosa', 'Sundrop' and 'Trevatt' observed at FCU in 1990, 1992 and 1993 and at Campbell and Fernhill Farm orchards in 1992 (Table 4.7). Within-orchard variation of date and rate of bloom among trees was greater than prediction errors for both the anthesis and petal-fall curves. The functions thus provided a simple and effective method for describing apricot bloom. The mean rate at which bloom progressed varied significantly between the site/year records but not between the three cultivars. Adjusting rates of development for temperature by using growing degree hour accumulation (GDH°C, base temperature 5°C) did not improve accuracy over the unadjusted regression against time, possibly because daily mean and maximum air temperatures during bloom did not vary substantially.

The profiles for cumulative anthesis and cumulative petal fall data (Fig. 4.2) illustrate well the differences in date and duration of apricot bloom that occur between years and sites. Bloom at Campbell Orchard and Fernhill Farm orchard (both in Hawkes Bay)

Table 4.7   Analyses of variance for Gompertz regression equations fitted to cumulative anthesis and petal fall data describing bloom on 'Royal Rosa, 'Sundrop' and 'Trevatt' apricots at FCU in 1990,1992 and 1993 and Campbell and Fernhill Farm orchards in 1992.

Source	df	Anthesis	df	Petal-Fall
Model	217	***	185	***
Record	4	120.42 **	4	40.98 *
Cultivar	2	16.09 ns	2	3.07 ns
Residual1: Record×Cultivar	8	5.55	8	2.32
Date	1	1007.43 ***	1	757.28 ***
Date×Record	4	11.62 *	4	17.67 *
Date×Cultivar	2	6.39 ns	2	15.56 ns
Residual 2: Date×Record×Cultivar	8	2.57	8	5.78
Tree(Record×Cultivar)	86	1.47 *	78	1.36 *
Tree×Date(Record×Cultivar)	102	1.54 *	78	1.39 *
Residual 3: Error	616	0.55	530	0.44
R^2		0.90		0.89

ns,*,**,***   Variance components non-significant or significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ respectively.
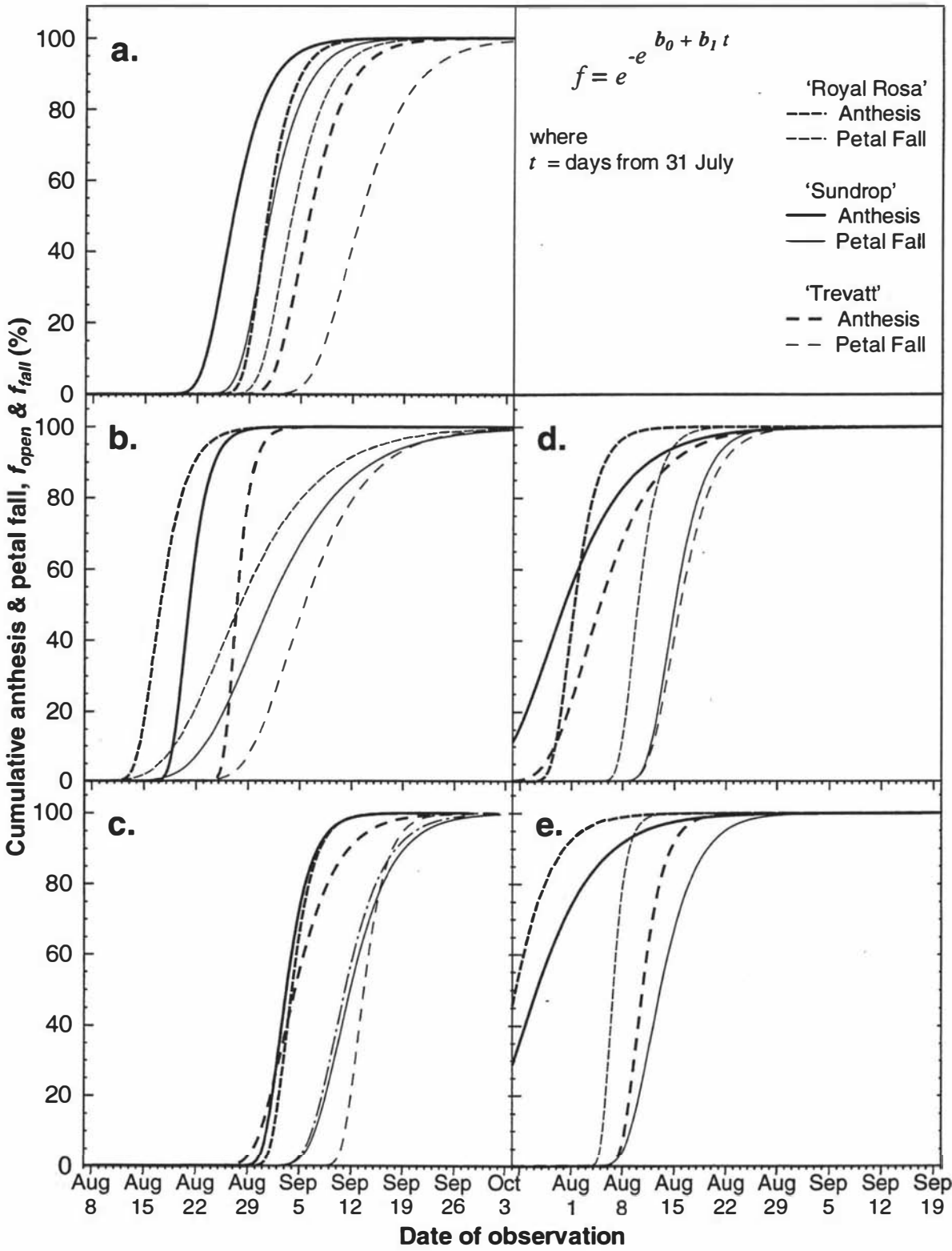
Figure 4.2　　Gompertz functions describing cumulative anthesis and petal fall of 'Royal Rosa', 'Sundrop' and 'Trevatt' for five year/site records.
a). FCU, 1990;　b). FCU, 1992;　c). FCU, 1993;　d). Campbell Orchard, 1992;　e). Fernhill Farm orchard, 1992. (Insufficient petal fall data to fit regression for 'Trevatt' at Fernhill Farm orchard in 1992.)

occurred almost simultaneously in 1992, two to three weeks earlier than bloom at FCU (Fig. 4.2d,e vs Fig.4.2b). On average, bloom also varied by two weeks between 1992 and 1993 at FCU (Fig. 4.2b,c). Cumulative petal fall data showed similar patterns in most cases except in 1992 at FCU when prolonged petal-fall was associated with an extended period of cold, wet weather following initially rapid anthesis. In addition, comparison of years within the one site, FCU (Fig. 4.2a-c), illustrates the potential for marked year-to-year variation in the course of bloom.

The similarities and differences between years and sites are equally clear when the proportion of open flowers holding petals was calculated as the difference between the regressions for anthesis and petal fall (Fig. 4.3). The maximum proportion of flowers open at any one time varied from around 40% ('Royal Rosa' at FCU, 1990) to over 80% at FCU in 1993 (Fig. 4.3c) and at Campbell and Fernhill Farm orchards in 1992 (Fig. 4.3d,e). Bloom peaks of the three cultivars were almost completely synchronous at FCU in 1993 (Fig. 4.3c) whereas, in 1990, bloom divergence between 'Sundrop' and 'Trevatt' within the same block was pronounced when 'Sundrop' preceded 'Royal Rosa' (Fig. 4.3a). Bloom of 'Trevatt' also diverged from that of 'Sundrop' at Fernhill in 1992 (Fig. 4.3e) and to a lesser extent at FCU in 1992 (Fig. 4.3b). In addition, bloom at FCU in 1992 illustrates the effect of extended petal fall which resulted in extended tails to the cumulative frequency plots for each cultivar. Average floral lifespans (i.e. anthesis to loss of all petals estimated at 5% Bloom and 90% Bloom) averaged six to seven days on all three cultivars with no significant differences. However, differences between year/ site records were marked and individual estimates ranged from two to eight days (both 'Royal Rosa' at FCU, in 1990 and 1992 respectively). Petal lifespan is therefore probably not a major factor determining the success of fruit set on 'Sundrop' flowers in particular.

Duration of pollen release from apricot flowers as a factor influencing fruit set was not investigated systematically since 'Trevatt', the principal cultivar planted as a pollenizer for 'Sundrop' usually blooms later than 'Sundrop' and pollen supply is probably therefore of less consequence than floral receptivity. General observations indicated dehiscence began with the smallest anthers at the centre of the stamen whorl and progressed outwards. At Fernhill Farm in 1992 foraging activity by bees meant only two to three dehiscent anthers (about 1 in 10) were heavily laden with pollen at any time. Rates of
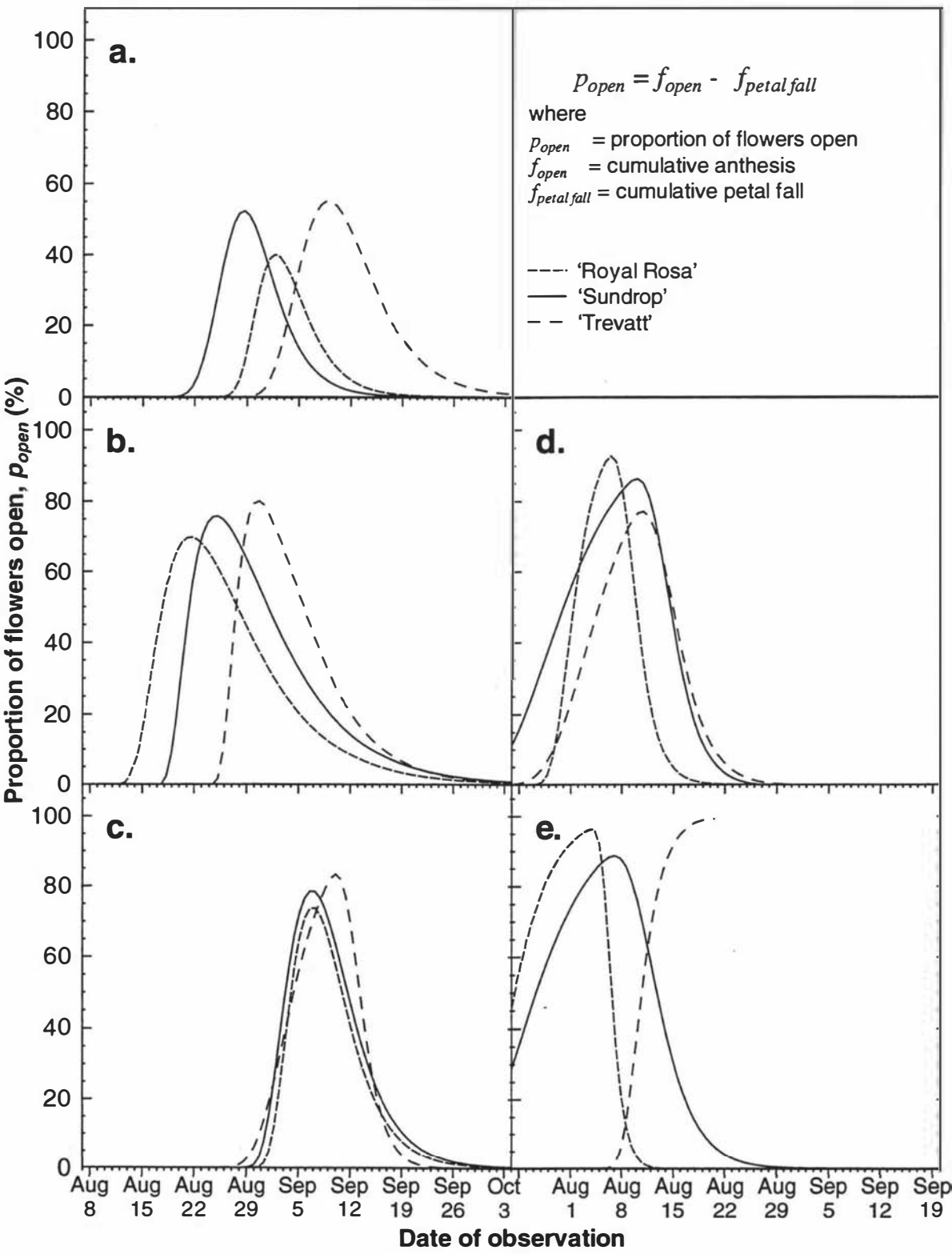
Figure 4.3   Proportions of open flowers of 'Royal Rosa', 'Sundrop' and 'Trevatt' calculated as difference of Gompertz regression functions describing cumulative anthesis and petal fall for five year/site records.
a). FCU, 1990;   b). FCU, 1992;   c). FCU, 1993;   d). Campbell Orchard, 1992;   e). Fernhill Farm orchard, 1992. (Insufficient petal fall data to fit regression for 'Trevatt' at Fernhill Farm orchard in 1992.)

anther dehiscence appeared very weather-dependent and, depending on conditions, could start soon after petal separation and be complete within two days, or could take three to four days with no immediately apparent differences between cultivars.

4.3.2.2   Post-pollination development of `Sundrop' pistils

The survey of post-pollination pistil development at Fernhill Farm in 1991 indicated that rapid senescence of 'Sundrop' pistils was unlikely to be reducing fruit set (methods in Section 4.2.2.1). Styles of emasculated and non-emasculated 'Sundrop' flowers both grew significantly over the sampling period, though styles were shorter in 'Early-bloom' flowers than in 'Mid-bloom' flowers (Table 4.8). Almost all style extension occurred between Day 0 and Day 4 when average length increased from 12.1 ± 0.2 mm on the day of emasculation to 14 ± 0.2 mm to 16 ± 0.2 mm four days later, depending on cohort and treatment (Fig. 4.4a). Little growth occurred after this time and most styles had darkened noticeably six to eight days after emasculation and a small proportion had abscised before the end of sampling. Ovaries of 'Sundrop' flowers grew rapidly during the sampling period and had begun to protrude above the shrivelling corolla cup by the end of sampling, 16 days after pollination. Ovary width more than doubled from under 2.0 mm to over 4.0 mm (Fig. 4.4b). Ovaries and styles of flowers in the 'Early-bloom' cohort were also smaller than those in the 'Mid-bloom' cohort but this and the effect on style length was the only significant effect of bloom cohort on pistil development. Emasculation reduced final style length by about 1.0 mm and retarded ovary growth directly after removal of petals and stamens but the measurements suggest it did not affect pistil development after this time.

Ovary dissections also gave no indication that early ovule senescence in the 16 days after pollination prevented fertilization and fruit set. Two ovules were present in the ovaries of all 'Sundrop' flowers dissected although only one normally appeared to develop much beyond the stage it had reached by anthesis (or emasculation). Developing (primary) ovules were typically twice the length of the smaller (secondary) ovules at emasculation and this difference increased in successive samples. Primary ovule length quadrupled from less than 0.7 mm to over 2.5 mm in the two weeks following anthesis and was slightly less in 'Early-bloom' cohort flowers than in the 'Mid-bloom' cohort (Fig. 4.4c). Average length of smaller secondary ovules increased only slightly (Fig. 4.4d), mainly
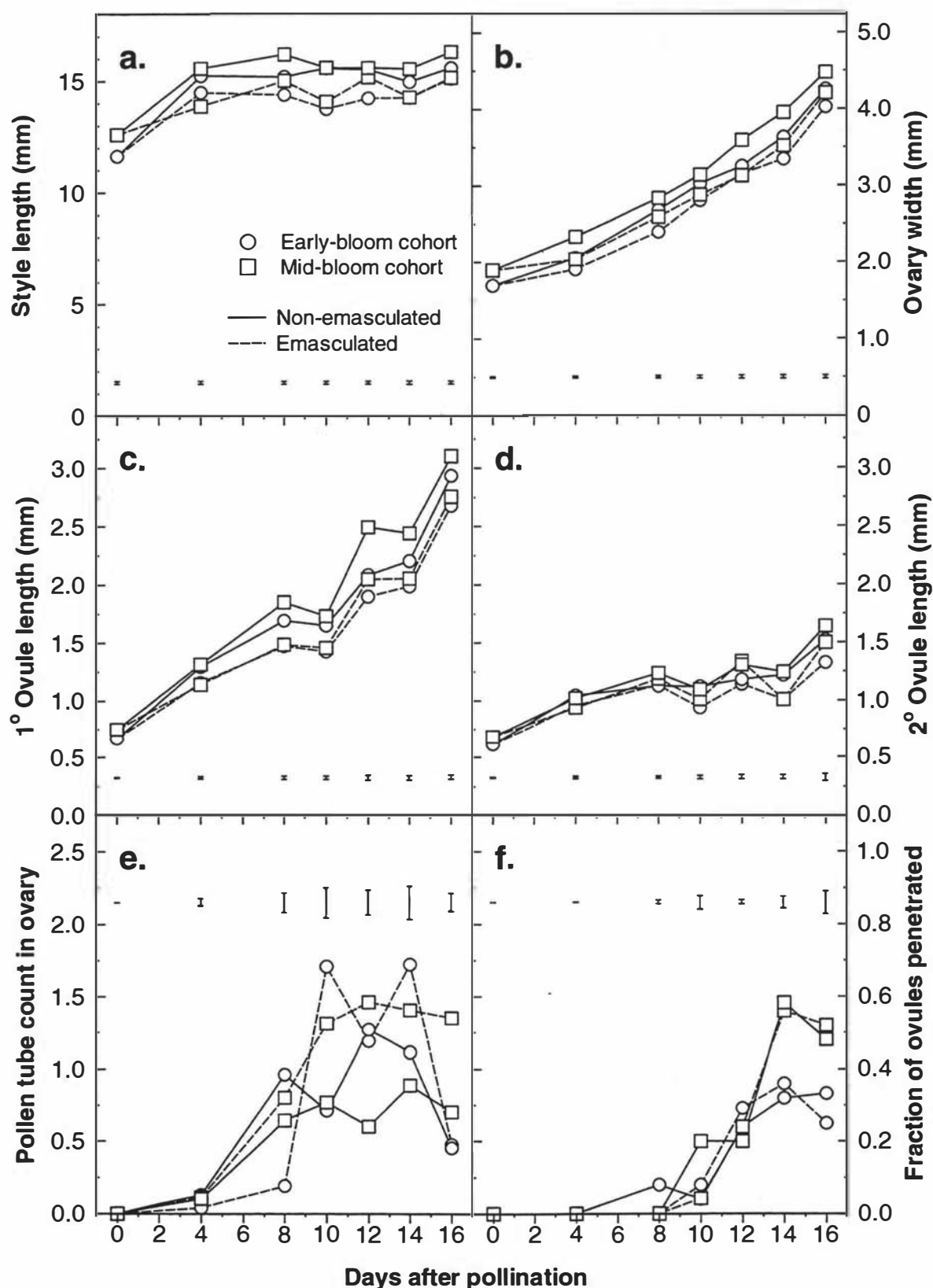
Figure 4.4   Development of emasculated and non-emasculated 'Sundrop' flowers after pollination with 'Trevatt' pollen at Fernhill Farm, 1991. (Bars = pooled SE)
a). Style length (stigma to stylar abscission zone);   b). Ovary width at widest point;
c). Primary (developing) ovule length;   d). Secondary (abortive) ovule length;   e). Pollen tube count within ovarian cavity;   f). Fraction of primary ovules penetrated by pollen tubes.

Table 4.8   Analysis of variance for ovary width, primary and secondary ovule length, style length, pollen tube number in ovary and ovule penetration fraction for emasculated and non-emasculated 'Sundrop' flowers, Fernhill Farm 1991.

Source	df	Ovary Width	1° Ovule length	2° Ovule length	df	Style Length	Ovary Tubes	Ovule Penetration
		Variance components (Type III MS)						
Model	39				43			
Tree	4	0.11 ns	0.03 ns	0.62 ns	4	12.69 ns	1.81 ns	0.095 ns
Cohort	1	0.31 *	0.02 ns	0.00 ns	1	20.89 *	0.14 ns	0.784 ns
Resid. 1: Cohort×Tree	4	0.01	0.06	0.02	4	3.06	2.11	0.110
Emasculation	1	0.02 ns	0.00 ns	0.00 ns	1	113.90 *	1.74 ns	0.450 ns
Resid. 2: Emas×Tree	4	0.02	0.05	0.39	4	5.76	2.28	0.205
Cohort×Emasculation	1	0.08 ns	0.03 ns	0.04 ns	1	6.61 ns	1.71 ns	0.001 ns
Resid. 3: Emas×Co×Tree	4	0.01	0.02	0.19	4	3.98	1.00	0.021
Time	1	60.10 ***	307.74 ***	33.03 ***	6	119.33 ***	20.77 ***	7.301 ***
Time×Cohort	1	0.02 ns	0.53 *	0.21 ns	6	2.19 ns	0.60 ns	0.296 ns
Time×Emas	1	0.16 ***	2.76 ***	0.41 *	6	19.51 ***	1.06 *	0.060 ns
Time×Emas×Cohort	1	0.02 ns	0.09 ns	0.08 ns	6	3.69 **	0.54 ns	0.170 ns
Resid. 4: Ti×Em×Co×Tr	16	0.02	0.13	0.09	96	1.71	0.61	0.183
Residual: Error	672	0.01	0.09	0.09	572	1.30	0.353	0.182
R^2		0.89	0.84	0.41		0.61	0.53	0.74

ns,*,**,*** Variance components non-significant or significant at $P<0.05$, $P<0.01$, $P<0.001$ respectively.

due to a small minority of 'Sundrop' flowers having similarly-sized ovules which developed in parallel. In rare cases, a small third 'ovule', consisting only of an abortive nucellus and the rudiments of integuments, was found on the basal side of a funiculus. However, successive samples gave no sign this structure was still growing. Emasculation significantly reduced growth rate of both primary and secondary ovules (Table 4.8). Chalazal fluorescence of the nucellus (indicating ovule degeneration) was common only in smaller secondary ovules. Some secondary ovules were fluorescent as early as four days after emasculation and almost two thirds (64%) were fluorescent 16 days after emasculation. In contrast, only one primary ovule of 600 collected up to 16 days after pollination displayed chalazal fluorescence when dissected. Neither cohort nor emasculation affected incidence of ovule fluorescence.

Pollen tubes were present at the top of styles below the stigma in almost all dissected pistils and pollen germination (inferred from pollen tube number) was unaffected by either cohort or emasculation. Maximum tube length was also unaffected by cohort although average tube numbers towards the end of the sampling period were higher in

emasculated flowers (Fig.4.4e), possibily as a consequence of more consistent hand-pollination of these pistils. Pollen tubes first reached ovaries four days after pollination and ovules eight to ten days after pollination (Fig. 4.4f). The proportion of ovules penetrated 14 and 16 days after pollination were significantly higher in flowers emasculated at 50% Bloom ('Mid-bloom') than earlier at 5% Bloom ('Early-bloom') despite similar numbers of pollen tubes in the ovary. Ovules of flowers in the later cohort were therefore as receptive to pollen tubes (or possibly more so) than flowers of the earlier cohort. Emasculation had no effect on the proportion of ovules penetrated by pollen tubes. Therefore, although emasculation affected the relative size and growth rate of the ovary and ovules, it did not influence pollen tube development in 'Sundrop' styles in a way likely to be detrimental to fruit set.

4.3.2.3   Delayed pollination of 'Sundrop' flowers

Pollen tube development displayed a significant quadratic trend with respect to the delay between emaculation and pollen application (Table 4.9). The greatest number of pollen tubes were found at the top of the style when pollen was applied to pistils two and four days after emasculation whereas relatively few pollen tubes were present when pollen

Table 4.9   Analysis of variance for pollen tube development after progressively delayed pollination of emasculated 'Sundrop' flowers with 'Trevatt' pollen at Fernhill Farm orchard, 1991.

Source	Stylar tubes		Ovary tubes		Stylar penetration	
	df	Type III MS	df	Type III MS	df	Type III MS
Model	58	16.67 ***	58	4.12 ***	58	0.439 ***
Tree	4	5.30 ^{ns}	4	1.32 ^{ns}	4	0.018 ^{ns}
Cohort	1	3.41 ^{ns}	1	0.28 ^{ns}	1	0.300 ^{ns}
Residual 1: Cohort×Tree	4	2.06	4	1.36	4	0.153
Delay	5	109.08 ***	5	34.38 ***	5	2.659 ***
Resual 2: Delay×Tree	20	8.75	20	1.48	20	0.167
Delay×Cohort	5	13.41 ^{ns}	5	2.23 ^{ns}	5	0.427 **
Residual 3: Delay×Tree×Cohort	20	7.75	20	0.85	20	0.085
Residual: Error	338	2.64	334	0.42	188	0.084
R^2		0.52		0.63		0.62
Contrasts						
Linear	1	23.81 **	1	0.42 ^{ns}	1	0.890 ***
Quadratic	1	100.32 ***	1	43.52 ***	1	2.58 ***

^{ns,*,**,***} Variance components and contrasts non-significant or significant at $P<0.05$, $P<0.01$ and $P<0.001$ respectively.

was applied on the day of emasculation or, six and eight days afterwards (Fig. 4.5a). The number of pollen tubes at the entrance to the ovarian cavity was affected by pollination delay in much the same way (Fig. 4.5b) as was the proportion of the style penetrated by the longest pollen tube in each pistil (Table 4.9). However, this measure of pollen tube development was less sensitive as an index of pollen tube development than pollen tube number as pollen tubes had reached most ovaries when pistils were collected. Measurement of tube and style lengths also became increasingly difficult as styles began to shrivel and abscise towards the end of sampling. Penetrated ovules were only found in flowers pollinated 2, 4 and 6 days after emasculation but numbers of were too low for statistical analysis. Pollen tube count was unaffected by the floral cohort ('Early-' or 'Mid-bloom') to which flowers belonged (Table 4.9). All pollinated treatments contained significantly more pollen tubes than did the non-pollinated control indicating accidental pollination of the unprotected emasculated pistils was infrequent.
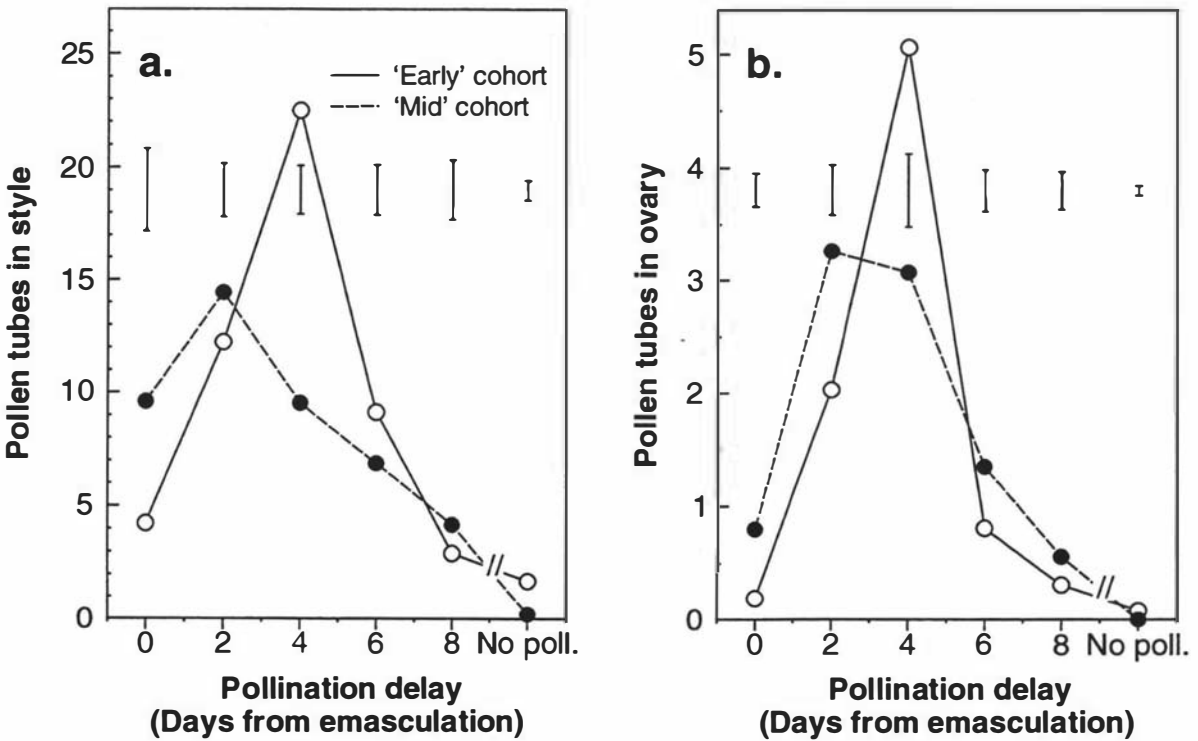
Figure 4.5   Pollen tube development in 'Sundrop' flowers eight days after application of 'Trevatt' pollen, Fernhill Farm orchard 1991. (Bars = pooled SE)
a). Pollen tube count at top of style below stigma; b). Pollen tube count in ovary.

Progressively delaying hand pollination of emasculated 'Sundrop' pistils had a similar effect on fruit set at pit hardening and at harvest. Both showed linear and quadratic trends with respect to the delay between emasculation and pollen application when the relationship between delay periods was analysed by orthogonal contrasts. (Table 4.10). Maximum set occurred when pistils were pollinated four days after emasculation (Fig. 4.6a). However, the nature of the relationship between pollination delay and fruit set varied between sites and years. Fruit set was extremely poor at FCU in 1992 due to adverse weather (rain) during bloom. The quadratic trend in fruit set was also weaker at FCU in comparison with the declining linear trend than it was at Fernhill Farm orchard. In all cases, hand pollination significantly increased fruit set over the non-pollinated control except when pollination was delayed 8 days at FCU in which case fruit set was very low. Emasculation therefore satisfactorily prevented accidental pollination by bees or wind whether trees were covered by screens (FCU) or not (Fernhill Farm) and hence

Table 4.10   Analyses of variance for fruit set at pit-hardening and at harvest on 'Sundrop' apricot after progressively delayed hand-application of 'Trevatt' pollen: Fernhill Farm orchard and FCU, 1991 and 1992.

Source	df	Fruit set at pit-hardening Type III MS	Fruit set at harvest Type III MS
Model	39		
Site	1	461.5 ns	791.8 ns
Year	1	420.3 ns	120.6 ns
Year×Site	1	63.2 ns	0.2 ns
Residual 1: Tree(Year×Site)	16	31.9	29.2
Delay	5	513.4 *	356.1 *
Delay×Site	5	38.7 ns	29.3 ns
Delay×Year	5	27.7 ns	18.2 ns
Delay×Year×Site	16	26.5 *	14.2 ns
Residual: Error	197	10.6	8.3
R^2		0.73	0.73
Contrasts			
Fernhill: Linear	1	110.6 **	127.9 ***
Quadratic	1	257.5 ***	189.6 ***
Combined	2	178.6 ***	153.7 ***
FCU: Linear	1	290.3 ***	70.3 **
Quadratic	1	85.1 **	68.0 **
Combined	2	173.8 ***	62.9 ***

ns,*,**,*** Variance components and contrasts non-significant or significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ respectively for random-effects model analysis of variance: random effects = Site, Year, Tree and Delay.
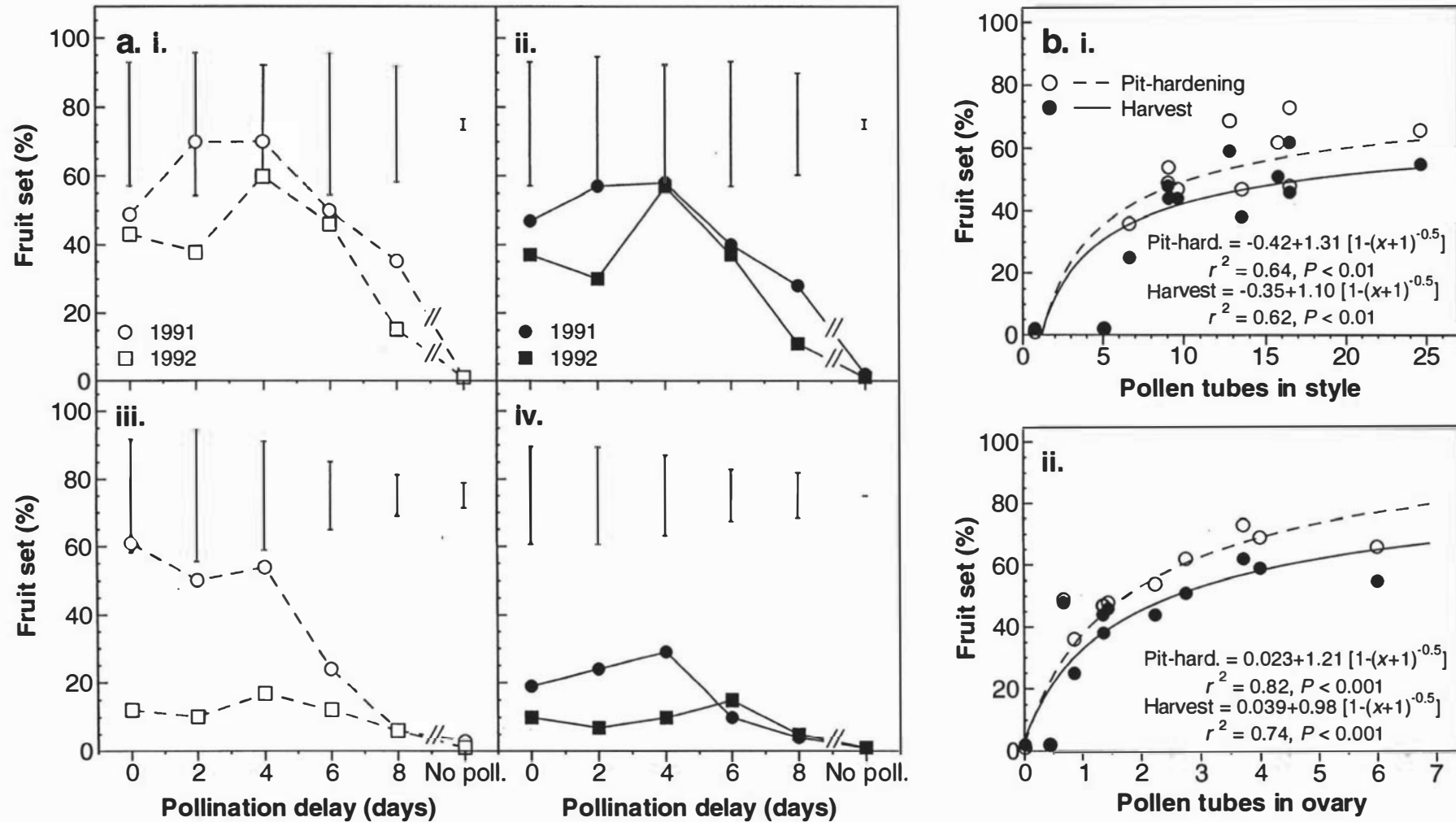
Figure 4.6 Fruit set on 'Sundrop' apricot following delayed application of 'Trevatt' pollen and relationship of fruit set to pollen tube number in the style and in the ovary.

a). Fruit set and pollination delay: i). Pit-hardening, Fernhill Farm; ii). Harvest, Fernhill Farm; iii). Pit-hardening, FCU; iv). Harvest, FCU. (Means of pooled 'Early' and 'Mid' bloom cohorts. Bars = pooled SE)

b). Regressions of fruit set on pollen tube count eight days after pollination including both the delayed pollination and no pollination treatments, Fernhill Farm, 1991: i). Pollen tubes in top of style below stigma; ii). Pollen tubes at entry to ovary.

treatment differences do represent the effect of pollination delay. Floral cohort had no effect on fruit set and, since set varied greatly between trees and branches (the experimental units), data for the two cohorts were pooled to increase precision.

The close correspondence between the pattern of fruit set and pollen tube numbers suggested that the overall receptivity was determined by initial pollen tube development rather than ovule senescence. Least squares regression (using a rectangular hyperbola as the model) of fruit set at pit-hardening and harvest against pollen tube number indicated a significant asymtotic relationship between set and tube number at Fernhill Farm in 1991 (Fig. 4.6b i,ii). Fruit set initially rose rapidly from zero as the number of pollen tubes in the style eight days after pollination increased. The relation-ship between fruit set and the number of pollen tubes in the ovary eight days after pollination displayed a similar pattern. Set then leveled off once the average count exceeded ten tubes below the stigma and two-three tubes in the ovary. The regressions lines did not closely approach the y=100% set asymtote within the range of tube numbers observed which suggests that pollen tube number alone did not limit fruit set. However, fruit set higher than the maximum observed was unlikely without considerable preliminary reduction of flower density to prevent fruit competition. Stigmatic ageing and a consequent decline in pollen tube development are therefore probably primarily responsible for lower fruit set as a result of delaying application of compatible pollen to 'Sundrop' flowers.

Differences in average pistil development at emasculation were not a factor in the differences between years and sites. Subjective assessment suggested flower quality (numbers of malformed or abortive pistils) was generally lower in FCU than at Fernhill Farm orchard but was particularly poor at Fernhill Farm in 1992. Selection of suitable flowers for emasculation might have biased the sample of flowers retained in these instances. Measurements of pistils collected at emasculation showed that style length, which is changing rapidly at anthesis, varied significantly between sites and years (Table 4.11) and was particularly high at Fernhill Farm in 1992 (Table 4.12). However average ovary width and primary ovule size did not differ between sites or years, though individual cohorts may have departed from the general trend. Sample bias introduced by the selection of flowers for emasculation was probably less important to floral receptivity than physiological or environmental differences between sites and years.

Table 4.11   Analyses of variance for site, year and cohort effects on pistil development in 'Sundrop' apricot flowers emasculated at 'balloon' stage: Fernhill Farm and FCU, 1991 and 1992.

Source	df	Variance components (Type III MS)			
		Style length	Ovary width	1° ovule length	2° ovule length
Model	39				
Site	1	52.05 ***	0.056 ns	0.128 ns	0.0645 *
Year	1	14.62 ***	0.000 ns	0.013 ns	0.0303 ns
Site×Year	1	72.69 ***	0.022 ns	0.130 ns	0.0497 *
Residual 1: Tree(Site×Year)	16	1.76	0.018 *	0.048 ***	0.0321 *
Cohort	1	0.43 ns	0.094	0.278 ***	0.0473 **
Cohort×Site	1	8.33 **	0.016 ns	0.194 ***	0.0913 ***
Cohort×Year	1	55.04 ***	0.319 ***	0.323 ***	0.2526 ***
Cohort×Site×Year	1	2.76 ns	0.002 ns	0.005 ns	0.0051 ns
Tree×Cohort(Year×Site)	16	0.77 ns	0.015 ns	0.015 ns	0.0137 ns
Residual: Error	159	1.083	0.009	0.013	0.0114
R^2		0.59	0.42	0.49	0.42
Contrasts					
Year in Fernhill Farm		76.74 ***	0.011 ns	0.114 ns	0.0792 ns
Year in FCU		10.98 *	0.010 ns	0.030 ns	0.0012 ns
Cohort in Fernhill Farm		2.50 ns	0.016 ns	0.004 ns	0.0036 ns
Cohort in FCU		6.25 *	0.093 **	0.465 ***	0.1345 ***

ns,*,**,*** Variance components and contrasts non-significant or significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ respectively for mixed model analysis of variance: random effect = Tree.

Table 4.12   Dimensions of pistils in 'Sundrop' flowers at the time of emasculation at Fernhill Farm orchard and FCU in 1991 and 1992.

Site & Year	Cohort	Pistil dimensions (mm)			
		Style length	Ovary width	1° ovule length	2° ovule length
Fernhill 1991	Early	11.7	1.7	0.67	0.62
	Mid	12.5	1.9	0.75	0.68
Fernhill 1992	Early	14.7	1.9	0.80	0.75
	Mid	13.1	1.8	0.75	0.65
FCU 1991	Early	11.5	1.8	0.70	0.65
	Mid	13.0	2.0	0.92	0.78
FCU 1992	Early	11.8	1.8	0.75	0.70
	Mid	11.5	1.8	0.80	0.71
$LSD_{0.05}$		1.3	0.4	0.15	0.14

4.3.3   Modelling Bloom Divergence and Pollen Transfer

Four simulated bloom scenarios were used to investigate the potential effect of varying several bloom parameters on the overall periods of pollen release by a simulated cultivar and of floral receptivity (Fig. 4.7). These parameters were:

i). t_{Bloom}, the time from 5% to 90% Bloom for main and pollenizer cultivars;

ii). t_{Bloom} for the pollenizer cultivar alone;

iii). t_σ, the average duration of pollen release (floral male phase); and

iv). t_φ, the average duration of floral receptivity (floral female phase).

Periods of pollen release (male phase) and floral receptivity (female phase) were assumed to begin simultaneously but end independently. A 'standard' bloom simulation described by these parameters indicated that the highest proportion of flowers releasing pollen (about 50% of total) occurred 4 days after 5% Bloom and the highest proportion of receptive flowers (70%) occurred 5 days after 5% Bloom (Fig. 4.7a). This was the result of setting t_{Bloom} to 7 days (the observed average) and setting values for t_σ and t_φ to 3 days and 5 days respectively, each near the centre of the probable natural range. By 90% Bloom only one quarter of flowers were still releasing pollen (i.e. male phase) and just over half were still receptive (female phase).

Altering t_{Bloom}, t_σ and t_φ changed the frequency distributions of male and female phase flowers in a predictable manner which compared well with field observations. Increasing t_{Bloom} from 7 days to 13 days, reduced the maximum proportions of male and female phase flowers by about 10% but extended the overall period for which the simulated cultivar released pollen and bore receptive flowers (Fig. 4.7b). Holding t_{Bloom} constant at 7 days while decreasing t_σ to 2 days reduced the maximum proportion of male phase flowers on any given day to one third and the proportion of flowers releasing pollen at 90% Bloom to under 20% (Fig. 4.7c). Increasing t_φ to 7 days (Fig 4.7d) increased the maximum proportion of receptive flowers and meant almost all flowers open at 90% Bloom were still recepetive (female phase) and therefore, theoretically, able to set fruit.

The 'weighted floral product', a daily measure of potential cross-pollination, was calculated as: *proportion of male phase pollenizer flowers* × *proportion of receptive main cultivar flowers* / (1+ *proportion of male phase main cultivar flowers*). The form
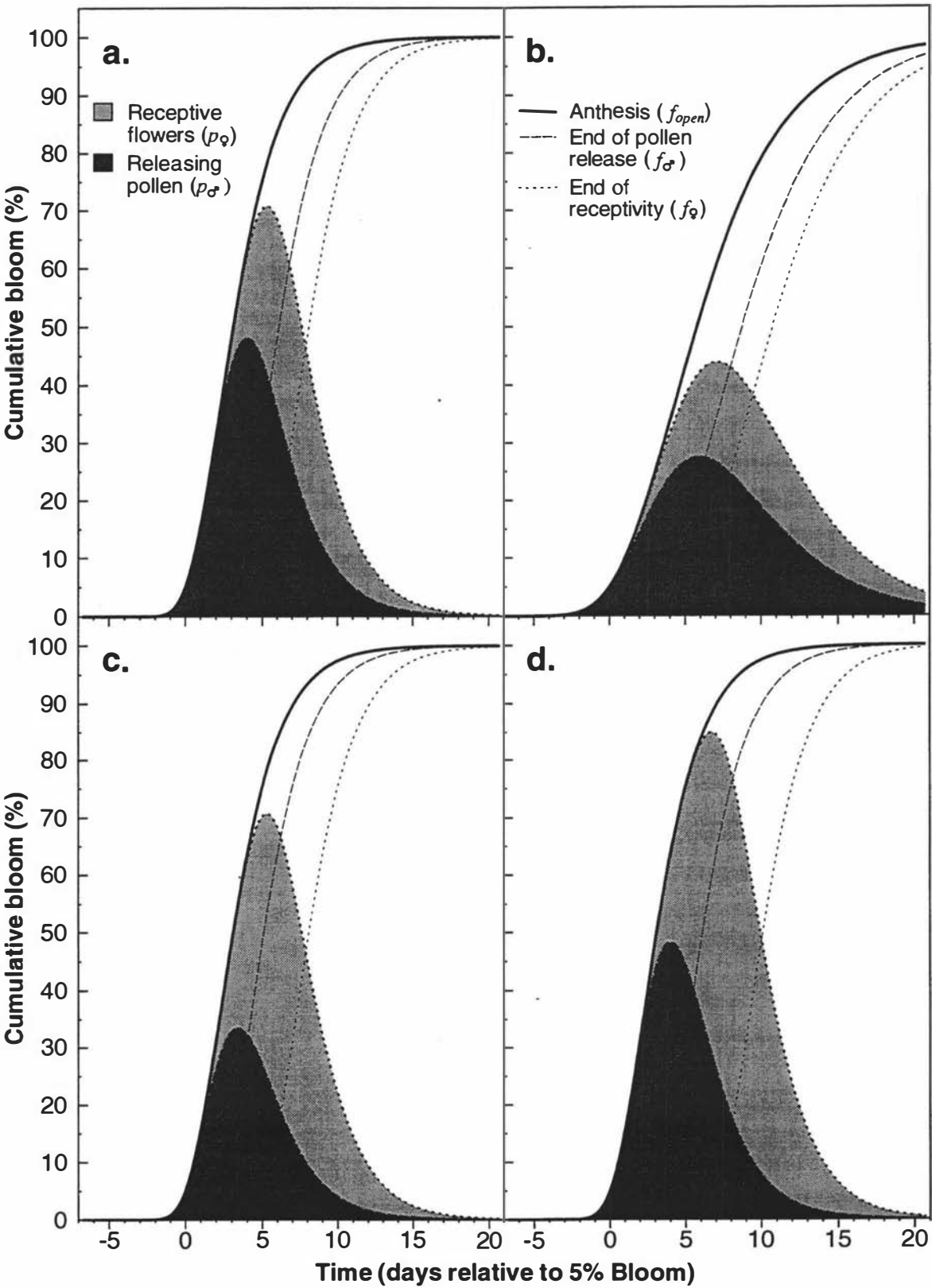
Figure 4.7   Simulated cumulative bloom for North Island apricots showing distributions (relative to 5% Bloom) of receptive flowers and flowers releasing pollen. a). Base simulation ($t_{Bloom} = 7$ d, $t_{\male} = 3$ d, $t_{\female} = 5$ d; b). Delayed flower development ($t_{Bloom} = 13$ d; c). Reduced duration of pollen release $t_{\male} = 2$ d; d). Increased duration of floral receptivity (potential fruit set) $t_{\female} = 7$ d.

of this function causes the highest product values when divergence between pollenizer and main cultivar bloom is such that the potential for transfer of pollenizer pollen to main cultivar flowers is maximal and dilution of pollenizer pollen by self pollen is minimal. Product values calculated for three different degrees of bloom divergence between pollenizer and main cultivar illustrate the relationship between bloom divergence and the floral product (Fig. 4.8a-c). When pollenizer bloom leads that of the main cultivar by 4 days (and for t_{Bloom} = 7 days, t_σ = 3 days and $t_\female$ = 5 days) then the daily 'weighted floral product' peaks two to three days after 5% Bloom of the main cultivar at about 0.01 (Fig. 4.8a). When the pollenizer trails the main cultivar by one day, floral product values peak at 0.027 six days after 5% Bloom of the main cultivar (Fig. 4.8b). As pollenizer bloom is further delayed the maximum daily product value then declines and is delayed. When the pollenizer lags behind the bloom of the main cultivar by six days it reaches a maximum of 0.014 nine days after main cultivar 5% Bloom (Fig. 4.8c).

Calculation of the cross-pollination index, $I_{\Delta t}$, by summation of daily weighted floral products for the entire bloom period, indicated a bell-shaped relationship between overall potential cross-pollination and bloom divergence (Fig. 4.9a). $I_{\Delta t}$ displayed a broad maximum between -2 days to +4 days bloom divergence when calculated using bloom parameters corresponding to the 'standard' bloom simulation (t_{Bloom} = 7 days, t_σ = 3 days and $t_\female$ = 5 days, Fig. 4.7a) and pollenizer bloom divergences of 10 days ahead of main cultivar bloom to 10 days behind (Fig. 4.9a i, solid line). This implies that, for the given bloom parameters, maximum opportunity for cross-pollination can be expected when the pollenizer 5% Bloom is synchronous with or slightly behind 5% Bloom of the main cultivar. Simultaneously varying the durations of pollenizer and main cultivar bloom did not alter the position of the maximum $I_{\Delta t}$ which is predicted when pollenizer 5% Bloom occurs one day after 5% Bloom of the main cultivar regardless of duration of bloom (Fig. 4.9a i, dashed and dotted lines). However, increasing t_{Bloom} lowered and broadened the peak $I_{\Delta t}$ so that it was increased slightly when pollenizer bloom either leads or lags the main cultivar by a large period ($\Delta t_{5\%}$ < -3 days and $\Delta t_{5\%}$ > 5 days respectively).

Varying t_σ (the mean duration of pollen release by individual flowers) and $t_\female$ (the mean duration of floral receptivity) simultaneously for both cultivars indicated that these parameters had a greater effect on the relationship between $I_{\Delta t}$ and bloom divergence
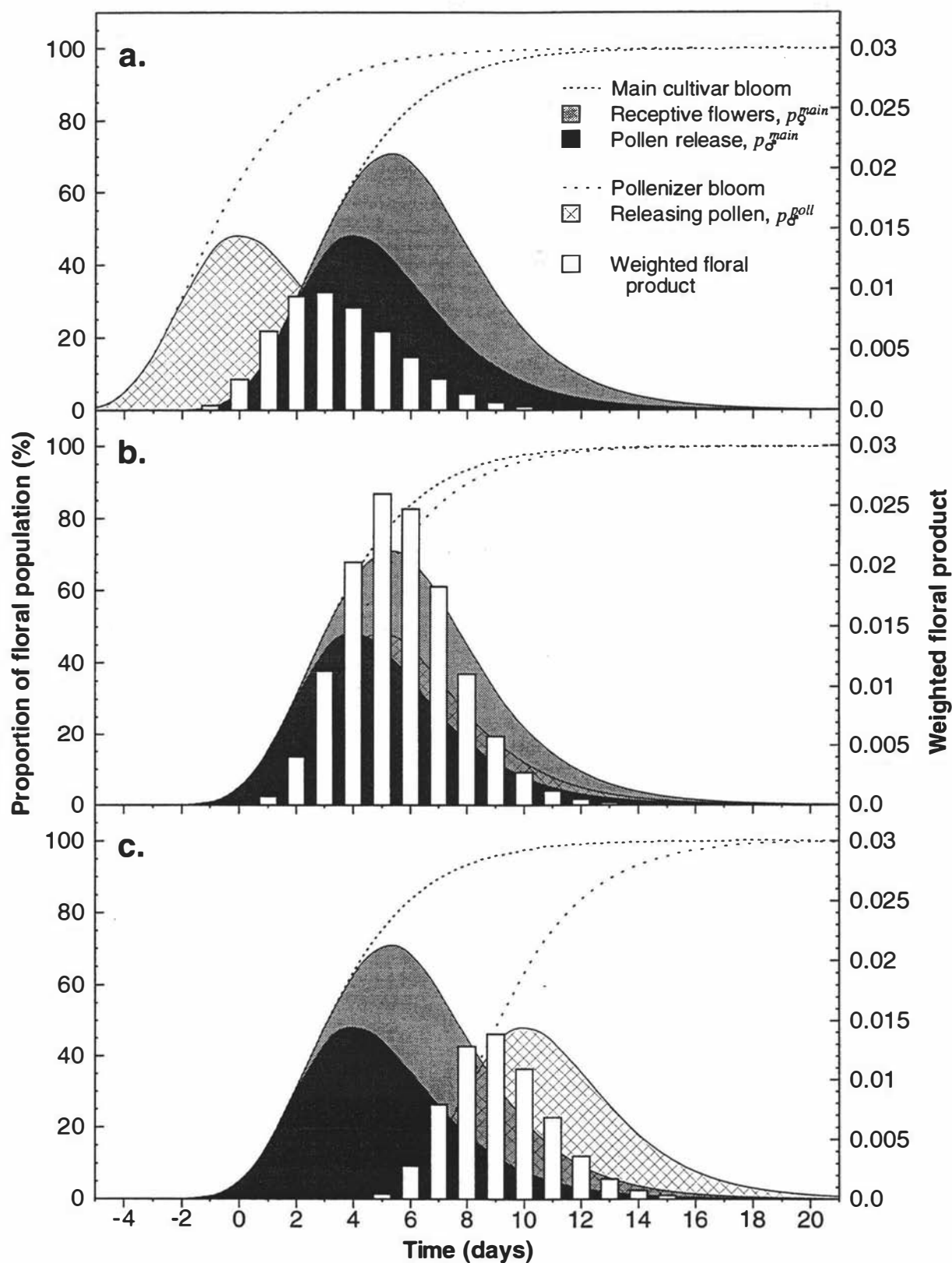
Figure 4.8   Daily floral products calculated at three pollenizer bloom divergence values and weighted for proportion of main cultivar flowers releasing pollen. (Day 0 = 5% Bloom of main cultivar; t_{Bloom} = 7 days; t_{σ} = 3 days; t_{φ} = 5 days; r^{poll} = 1 / 9 .)
a). Pollenizer bloom leading main cultivar by 4 days; b). Pollenizer bloom trailing by 1 day; c). Pollenizer bloom trailing by 6 days.
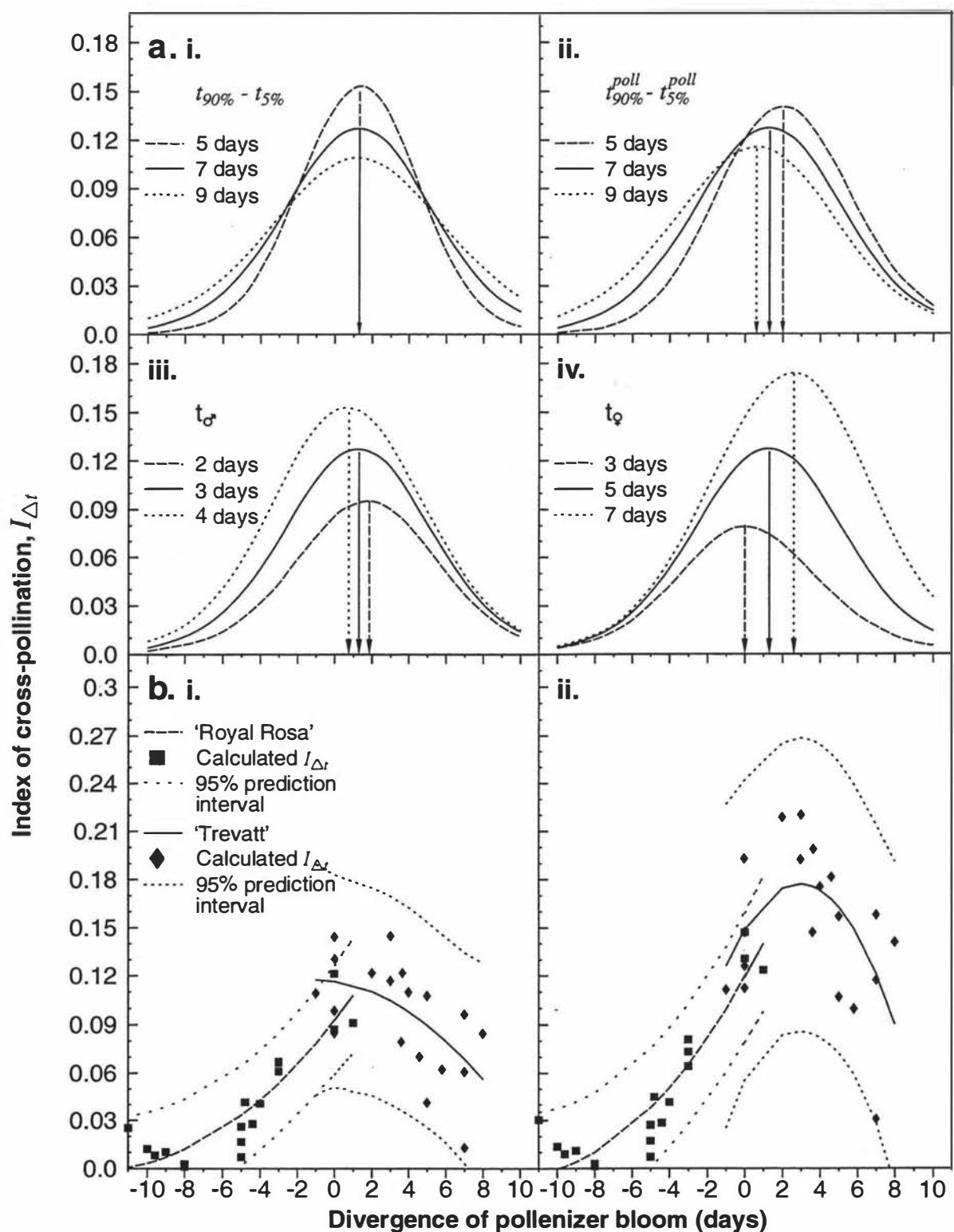
Figure 4.9   Effects of varying simulated pollenizer bloom divergence and bloom parameter values and of the observed bloom divergence for 22 North Island 'Royal Rosa'-'Sundrop' and 'Trevatt'-Sundrop' bloom records on the calculated index of cross-pollination, $I_{\Delta t}$. (Day 0 = 5% Bloom of main cultivar. Arrows indicate optimum pollenizer bloom divergence. $r^{poll} = 1/9$) a). Simulation: i). Bloom duration of main cultivar and pollenizer varied simultaneously; ii). Bloom duration of pollenizer varied independently; iii). Varying duration of pollen release (t_{σ}); iv). Varying duration of floral receptivity (t_{ϱ}).
b. Observed data: i). Duration of receptivity, $t_{\varrho} = 5$ days; ii). Duration of receptivity, $t_{\varrho} = 7$ days.

than did changes to pollenizer bloom duration.   Varying pollenizer bloom duration independently of main cultivar bloom duration did not markedly alter the overall relationship of $I_{\Delta t}$ to bloom divergence (Fig 4.9a ii).   Increasing bloom duration from 5 days to 9 days advanced maximum $I_{\Delta t}$ by almost two days but had little effect on maximum $I_{\Delta t}$.   By comparison, doubling t_{σ} from two to four days (the probable natural range of pollen release periods) increased maximum $I_{\Delta t}$ by 50% although it advanced the optimum divergence of 5% Bloom by only one day, or half the change in t_{σ} (Fig 4.9a iii). The greatest sensitivity of $I_{\Delta t}$ was shown to variation of the duration for which flowers are receptive and retain the potential to set fruit.   When the duration of floral receptivity was 7 days, optimum pollenizer bloom divergence was almost three days behind the bloom of the main cultivar.   Reducing t_{φ} from seven to three days (roughly the range of observed petal lifespan) reduced maximum $I_{\Delta t}$ by over 50% and advanced it by almost three days (Fig. 4.9a iv).   All three sets of simulations run indicated optimum pollenizer bloom divergence of one to three days after main cultivar bloom.   Bloom of the pollenizer in advance of the main cultivar would only increase $I_{\Delta t}$ if t_{σ} (the mean duration of pollen release) exceeded t_{φ} (the mean duration of receptivity).

Calculations of $I_{\Delta t}$ based on bloom data records for 'Sundrop', 'Royal Rosa' and 'Trevatt' apricots in North Island orchards suggested 'Trevatt' had provided adequate cross-pollination in most cases.   Average bloom divergence of 'Trevatt' from 'Sundrop' was +4 days, close to the ideal predicted by the model for cultivars with floral characteristics (t_{Bloom}, t_{σ} and t_{φ}) of 'Sundrop' and 'Trevatt'.   Values of $I_{\Delta t}$ showed that the response of the index to divergence of 'Royal Rosa' and 'Trevatt' from 'Sundrop' (Fig. 4.9b) matched that predicted for the generalised situation (Fig. 4.9a).   Two sets of simulations were run, one assuming a shorter average duration of floral receptivity (t_{φ} = 5 days, Fig 4.9b i) and the other, a longer duration (t_{φ} = 7 days, Fig. 4.9b ii).   Average $I_{\Delta t}$ was greater when t_{φ} was 7 days compared with 5 days.   Maxima for $I_{\Delta t}$ were Day 0 and Day +3 respectively, in both cases for the combination of 'Sundrop' and 'Trevatt'.   However, despite the increase in $I_{\Delta t}$, there was no change in the intersection of lower 95% prediction intervals with the x-axis since greater t_{φ} (i.e. longer floral receptivity) was also associated with greater variability of simulated $I_{\Delta t}$ given similar bloom divergence.   Consequently, the maximum bloom divergence before risk of total cross-pollination failure became significant ($P>0.05$) was -5 days for 'Royal Rosa' and +7 days for 'Trevatt' for both values of t_{φ}.

4.4   Discussion

The results of this study indicate that the receptivity of 'Sundrop' flowers is comparable to those of other deciduous fruit crop species, that petal retention is unexceptional and that the flowers open over a sufficiently long period to allow cross-pollination, so long as weather during that period is suitable for honey bee activity. Petal lifespan by itself does not appear to be a particular problem on 'Sundrop'. Lifespan estimates from regressions of cumulative anthesis and petal fall, and the delay between 90% Bloom and 90% Petal Fall (Table 4.4) indicated that development from anthesis to complete loss of petals on 'Sundrop' took about one week. This was similar to that of 'Royal Rosa' and 'Trevatt' and also of apples (Church et al., 1983). The actual period for which forager visits to an individual 'Sundrop' flower occur is, however, probably less than the petal lifespan. This was observed on 'Cox's Orange Pippin' apples (Williams et al., 1984) and may be because bees may associate senescence of petals or other floral parts (Nakanishi, 1982) with depletion of foraging resources. On plums, honey bees were observed to desert trees once petal fall reached 10-15% (Roberts, 1956) and similar behaviour on 'Sundrop' would reduce the effectiveness of a late-blooming pollenizer though this was not investigated. Anthesis also occurs over a period similar to other deciduous fruit crops. The total duration of bloom (5% Bloom to 90% Petal Fall) is comparable to that of almonds (Hill et al., 1985) and apples (Church et al., 1983; Irwin, 1931), while slightly less than for sweet cherries (Duggan, 1948). The distributions of cumulative anthesis on 'Sundrop' and the other cultivars (initially rising sharply with extensive tailing towards the end of bloom) are also similar to those of apples (Irwin, 1931). The tailing probably reflects the contribution of later-opening buds on extension shoots. Hence, the difference between 5% and 90% cumulative bloom stages does not allow comparison of bud development rates since the relative numbers of different bud types differs between trees and cultivars. Trees predominantly bearing buds on spurs will display more rapid apparent development than trees with a variety of bud types.

Lack of visible ovule fluorescence in dissected flowers from Fernhill Farm and FCU in 1991 also appears to rule out premature ovule senescence as an important factor contributing to unreliable fruit set. Rapid ovule senescence (exhibited by chalazal

fluorescence of the nucellus) has frequently been associated with shortened floral receptivity in *Prunus* species (Dys, 1984; Eaton, 1959; Lech and Tylus, 1983; Martinez-Tellez and Crossa-Reynaud, 1982; Pimienta and Polito, 1982; Stösser and Anvari, 1983; Thompson and Liu, 1973). However, ovule lifespan appears unlikely to be limiting fruit set in 'Sundrop'. In the 16 days following emasculation fluorescence was common only in abortive secondary ovules (rarely penetrated by pollen tubes) and almost entirely absent in the primary ovule of pollinated pistils. Lack of pollination can increase rates of ovule senescence (Herrero and Gascón, 1987; Pimienta and Polito, 1983) but no primary ovule fluorescence was seen in non-pollinated pistils fixed 12 days after emasculation. Nor was fluoresence observed in dissected pistils from the pollination delay experiment, even when pollination was delayed by eight days and pistils were fixed 16 days after emasculation. The satisfactory lifespan of 'Sundrop' ovules also suggests that, in apricots at least, any link between self incompatibilty and lower energy allocation to female reproductive function is not rigid at the level of individual cultivars.

Ovule senescence in cherries was enhanced by exposure to ethylene (Stösser and Anvari, 1982) and hence production of wound-induced ethylene after emasculation could reduce ovule lifespan or inhibit pollen tube growth. Removal of petals and anthers from flowers did reduce pistil growth, as it did for flowers of 'Riland' apricot (Badr and Crane, 1965), but the results suggest that the inhibition was short-term, possibly only four days. Growth rates for the ovary and ovules from four days after emasculation were similar and there was no evidence that pollen tube penetration of the style and ovules or fruit set were negatively affected (Chapter 2). And importantly, the incidence of ovule fluorescence was not increased by emasculation. Consequently, the results indicate that development of emasculated flowers was sufficiently similar to normal flowers that data gained by their use may reasonably be extrapolated to intact flowers.

The absence of ovule senescence and the close association of fruit set with pollen tube numbers (after delayed pollination) therefore suggest that stigmatic and stylar receptivity are the main factors determining the receptive period of 'Sundrop' flowers. Peak pollen tube numbers resulted when pollination was delayed until two or four days after emasculation (Fig. 4.5). This was equivalent to pollination at anthesis or two days later, a result very similar to the association of declining pollen tube penetration and fruit set

observed when pollination of other apricot cultivars was delayed (Burgos et al., 1991; Egea et al., 1991). The duration of receptivity is similar to those found for 'Goldrich' and 'Rival' apricot (Toyama, 1980). It is also similar to that of blueberries (Young and Sherman, 1978) and is longer than the effective pollination period reported for some apple cultivars (Williams, 1966). However, it indicates that the capacity of the stigma and stylar transmitting tissue to support pollen tube growth (Herrero and Arbeloa, 1989) begins to fall before the complete loss of petals 6-7 days after anthesis. Visits by foragers to flowers losing petals are therefore less likely to result in fruit set and desertion of trees as petal fall begins (Roberts, 1956) may be of little consequence to potential fruit set. The pattern of rise and fall of pollen tube numbers also suggests that the stigmatic surface may not have been fully mature at emasculation (Uwate and Lin, 1981). Hence, emasculating flowers as close as possible to anthesis, or delaying pollination until stigmatic maturity, is probably necessary to maximise fruit set under experimental conditions.

The study also produced interesting information on the likely effect of pollenizer bloom divergence on the cross-pollination of 'Sundrop'. Analysis of apricot bloom records confirmed experience that anthesis is normally almost complete on 'Royal Rosa' before flowers open on 'Sundrop' and that 'Royal Rosa' is therefore not suitable as a pollenizer for 'Sundrop'. Variation in relative time of bloom is such that limited pollen transfer from 'Royal Rosa' to 'Sundrop' may occur in some years or sites, particularly from flowers borne on vigorous extension shoots which, on average, bloom one week after those on short terminating shoots and spurs (Table 4.5). However, as also shown by the pollination model, the observed bloom divergences were sufficient to prevent substantial pollination of 'Sundrop' by 'Royal Rosa' under the North Island conditions surveyed.

Instead, the pollination model indicates that maximum opportunity for cross pollination occurs when the main cultivar ('Sundrop') blooms synchronously or slightly ahead of the pollenizer (Fig. 4.9). In this respect the average bloom divergence of four days for the combination of 'Sundrop' from 'Trevatt' (which is commonly planted as a pollenizer of 'Sundrop') was near that required to maximise the index of cross-pollination (I_{At}). This suggests bloom synchrony of 'Sundrop' and 'Trevatt' was sufficient to have allowed cross-pollination in most, though not all, of the site/year combinations observed. Fitting the simulated bloom distributions (Fig. 4.7) to the average bloom parameters of 'Sundrop'

and 'Trevatt' (bloom duration = 7 days, bloom divergence = 4 days) indicated that about half of 'Sundrop' flowers were still to open as anthesis commenced on 'Trevatt'. Measured petal lifespan and floral receptivity (both around 3 to 7 days) suggest that this should not have prevented cross-pollination and fertilisation of a large number of those flowers already open. However, the bloom records also included 'Sundrop'-'Trevatt' pairs for which 5% Bloom of 'Trevatt' occurred six days or more after 5% Bloom of 'Sundrop'. On these occasions the simulation results suggest that the overlap of cumulative pollen release with the cumulative period floral receptivity for 'Sundrop' (measured by the weighted floral product) declined to such an extent that the opportunity for cross-pollination was greatly reduced, even under ideal weather conditions. This may have affected fruit set, especially if the period of overlap coincided with a period of adverse weather which prevented honey bee foraging activity. Variation in bloom divergence of 'Trevatt' from 'Sundrop' therefore appears sufficient that adequate cross-pollination may not always occur where 'Trevatt' is planted as a sole pollenizer for 'Sundrop'. Shortened average floral receptivity, limited forager activity due to adverse weather towards the end of 'Sundrop' bloom and localised pollen transfer within an orchard could then further reduce the adequacy of 'Trevatt' at high bloom divergence.

The conclusion that the optimum time for pollenizer bloom is slightly after that of the main cultivar is the reverse of recommendations previously made for apples and pears. These suggest pollenizers should bloom two or three days ahead of the main cultivar to give the best coincidence of pollen release and the opening of main cultivar flowers (Wauchope, 1968; Williams and Sims, 1977). An early blooming cultivar is clearly of limited benefit if pollenizer numbers are low and introduction of hives is delayed until bloom on the main cultivar is well under way as has been recommended (Free, 1959). Rather, the suitability of earlier blooming polleinzers for pipfruit probably reflects the relationship between time of anthesis and flower quality (flower 'strength' or potential to set superior quality fruit) on apples. The recommendation maximizes pollenizer pollen flow to the earlier and more valuable ('stronger') flowers in terminal buds of spurs (Buban and Faust, 1982) at the expense of later flowers on lateral shoots. For 'Sundrop', there was no evidence for differentiation of 'Early' and 'Mid' bloom flowers and therefore the simulation model makes no assumptions as to the relative quality of flower buds. Consequently, pollen flow to earlier blooming flowers on spurs and short shoots and to

later blooming flowers on extension shoots are treated similarly in regard to potential fruit set. Quantifying the proportions of shoot types and flower quality on 'Sundrop', particularly in relation to tree age and management, would give a better understanding of the relationship between the composition of the floral population and optimum pollenizer bloom divergence.

The balance of advantage is also a reflection of whether or not it is considered that dilution of pollenizer pollen by self-incompatible main cultivar pollen reduces potential for cross-pollination and fruit set. A theoretical floral visitation sequence in which a forager visits pollenizer flowers then a series of main cultivar flowers before visiting a particular main cultivar flower illustrates the conceptual pollen flow system underlying the bloom divergence and pollen transfer model (Fig. 4.10). Principal features of the system are i). Unidirectional flow of pollen from sources (anthers on pollenizer and main cultivar flowers) to pollen sinks, i.e. honeybee forager pollen sacs and body surface plus the main cultivar stigma for which cross-pollination is considered (Pollenizer stigmas are disregarded as significant sinks since pollen flow to them is small relative to the flow to the foragers body surface.); ii). Mixing of pollen of both genotypes during pollen entrainment on the foragers body and during subsequent cleaning; iii). Substantial
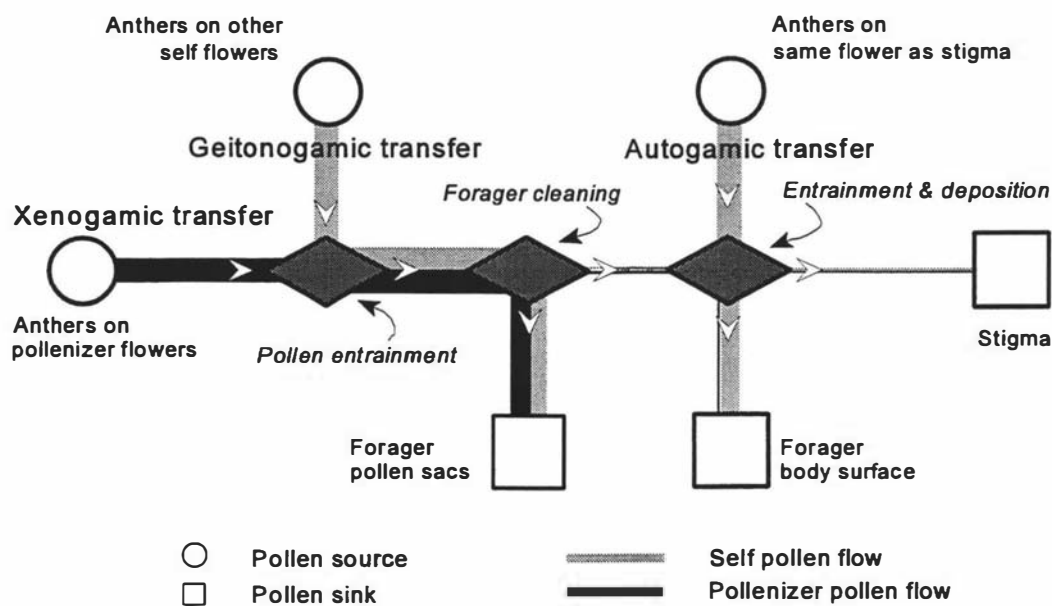
Figure 4.10   Pollen flow system diagram for pollen transfer model illustrating the dilution of pollenizer pollen by geitonogamic and autogamic transfer of self pollen. (Transfer terminology after Estes et al., 1983. Relative flow volumes indicated by line widths are illustrative only.)

removal of pollen by the forager during cleaning and packing of pollen into pollen sacs, and iv). Additional dilution of residual pollenizer pollen by entrainment of main cultivar pollen during foraging on the cross-pollinated flower.

Dilution of pollenizer pollen by main cultivar ('self') pollen is important as it affects the probability that any one of the pollen grains ultimately deposited on a main cultivar stigma is capable of fertilizing the ovule. This, in turn, affects the relative effectiveness of pollenizers blooming at different times relative to 5% Bloom of the main cultivar and hence affects the optimum pollenizer bloom divergence. In practice, the actual flow of pollen is difficult to measure. Flower numbers therefore provide a convenient 'proxy' under the assumption that pollen flow in a orchard is directly proportional to the number of flowers open and able to release pollen to a forager. Weighting the floral product for main cultivar flower numbers in this way is supported by evidence that pollen is carried only a limited number of flowers from its source (Richards, 1986) and that pollen flow in orchards is highly localised (Jackson and Clarke, 1991; Wertheim, 1991). The frequency of intervarietal movements in orchards is probably limited since bees tend to forage in restricted areas (Free, 1966) and the number of open flowers on a tree is often greater than the number needed for a full load of pollen or nectar. Foragers may therefore receive pollenizer pollen only infrequently and the proportion of pollenizer grains in pollen deposited on main cultivar stigmas is therefore likely to be strongly influenced by the supply of main cultivar pollen.

The effect of main cultivar pollen release is to delay the optimum time of pollenizer bloom. Heavy release of main cultivar pollen towards the end of pollenizer bloom, for instance, will lower the proportion of pollenizer pollen grains of the foragers body surface and hence lessen the chance that a particular main cultivar stigma will receive a pollenizer pollen grain. For instance, in the simulations reported in this study the beginning of main cultivar pollen release and receptivity coincide and the average duration of pollen release by a flower (t_σ) is shorter than the average duration of receptivity (t_φ). Thus, under this simplified situation the effectiveness of a pollenizer blooming early in the bloom of the main cultivar is reduced as main cultivar pollen is released. By comparison, the effectiveness of a later pollenizer (blooming after most main cultivar pollen has been released) is relatively greater and consequently the

optimum time of pollenizer bloom is delayed. Altering the duration of main cultivar dehiscence relative to receptivity has a similar effect to changing the duration of receptivity. A longer duration of receptivity and shorter pollen release both increase the apparent advantage gained from a later pollenizer and vice versa, flowers with shorter receptive periods and longer pollen release benefit more from an earlier pollenizer.

By contrast, using a simple non-weighted floral product (*number of pollenizer flowers releasing pollen* × *number of receptive main cultivar flowers*) as an index of orchard cross-pollination implies that the total flow of pollenizer pollen to main cultivar stigmas is a function only of the numbers of pollenizer flowers releasing pollen and of receptive main cultivar flowers receiving it. Dilution of pollenizer pollen by main cultivar pollen therefore does not affect the simulated frequency with which flowers foraged by honeybees receive sufficient pollenizer pollen grains to achieve fertilization. A model using such an index will predict an earlier optimum time for pollenizer bloom. In support of this option is the fact that only a single ovule is normally fertilized in *Prunus* flowers. One compatible pollen grain among the hundreds deposited may be all that is necessary to set a fruit. This species-specific situation, plus evidence that pollen may be transferred further than simple mechanistic pollen transfer models predict (Lertzman and Gass, 1983) and the possibility that in-hive transfer can redistribute pollenizer pollen on foragers (DeGrandi-Hoffman *et al.*, 1986), suggests that the present model may over-emphasize the effect of pollen dilution. However, insufficient is presently known of pollen transfer volumes between flowers in fruit orchards and how they are affected by weather, flower density and factors such as pollen grain size and 'stickiness', to accurately assess the importance of dilution. In this respect, further research to quantify rates of pollen carryover between flowers using scanning electron microscopy to distinguish morphologically dissimilar pollen could be very informative.

Several refinements could be readily included in model if the information was available. Incorporation of weather data and its effect on foraging activity would be important for testing of model predictions against recorded fruit set. As used for this study the model presupposes that interpolation between known start and end dates for anthesis and petal-fall implicitly accounts for the effect of temperature on flower development. However, explicit consideration of the relationship between climate and bloom (DeGrandi-Hoffman

et al., 1989; NeSmith and Bridges, 1992) might improve simulated bloom progression especially if used in association with a model of population development (Severini *et al.*, 1990). Variation in anther dehiscence rate, its duration or the total quantity of pollen released (Church and Williams, 1983; Hill *et al.*, 1985) were also not considered by the model nor was the delay between petal opening and start of dehiscence (Church *et al.*, 1983). Explicit modelling of anther dehiscence or inclusion of dehiscence data (Redalen, 1990) could therefore be beneficial if subsequent research shows that the relative proportions of mobile pollenizer and main cultivar pollen are important.

More detailed simulation of floral receptivity is also possible particularly regarding changes in stigmatic receptivity or ovule viability (Brain and Landsberg, 1981). The present model uses a generalised concept of receptivity such that receptive flowers are those that are attractive to bees and able to set fruit. This categorization therefore combines the effects of: i). Petal lifespan and nectar secretion, determining probability of forager visitation and pollen deposition; ii). Duration of stigmatic receptivity, determining success of pollen tube growth; and iii). The duration of ovule viability, determining success of fertilization (effective pollination period). In addition, it is assumed that receptivity continues at a constant level for a finite period and does not vary between flowers. This simple approximation appears sufficient for the purposes of the model given the complexity with which factors determining overall receptivity may interact. However, explicit simulation of each of these factors and evaluation of the resulting models for self-incompatible cultivars such as 'Sundrop' would add significantly to a quantitative understanding of the factors influencing apricot cross-pollination.

In conclusion, this investigation has provided a better picture of the floral and bloom characteristics of 'Sundrop' while drawing attention to the large areas of the apricot pollination system for which adequate quantitative information is still lacking. The results illustrate the relatively short time-frame within which pollination of apricots occurs and the importance of appropriate pollenizers if the probability of cross-pollination during that period is to be maximized. They demonstrate that the flowering of 'Sundrop' is similar to other deciduous fruit crops in terms of bloom duration and petal lifespan. They also show that floral receptivity, though declining towards the end of the floral lifespan, is not likely to be a major factor limiting fruit set. 'Trevatt' (the

predominant pollenizer used for 'Sundrop' in Hawkes Bay) usually blooms near the predicted ideal pollenizer bloom divergence so it appears unlikely that an unsuitable pollenizer choice is the cause of low yields on 'Sundrop'. However, analysis of bloom data did show considerable variation in the relative times of bloom of the three cultivars investigated which simulation of pollen transfer showed was likely to have reduced the opportunity for cross-pollination. Generous provision of pollenizer trees of at least two cultivars therefore appears essential to minimise the risk of insufficient pollen transfer due to excessive divergence especially since adverse weather conditions will further reduce pollen transfer below that predicted by the model.

4.5   References

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Chapter 5
Winter Development of Apricot Flower Buds

5.1   Introduction

The analysis of apricot bloom data from orchards in Hawkes Bay and in the Wairarapa and Manawatu regions presented in the previous chapter shows that the relative bloom synchrony of apricot cultivars can vary by a week or more between years and sites. This level of variation is large relative to the average difference between cultivars (about 10 days for 'Royal Rosa' and 'Trevatt') and the average duration of bloom (about one week from 5% Bloom to 90% Bloom). Hence, there appeared a significant risk that cross pollination between some apricot cultivars would be reduced on some occasions. This possibility was confirmed by the results from a model of the effect of bloom divergence on pollen transfer which showed that divergence between 'Sundrop' and 'Trevatt' was sufficient to greatly reduce cross-pollination on some cases.

Identification of cultivars with consistent bloom synchrony would increase opportunities for cross-pollination and hence the reliability of fruit set on self incompatible cultivars such as 'Sundrop'. Bloom date variation, particularly site-to-site, can reflect differences in tree vigour, health and management or to rootstock differences (Brown, 1952; Chandler and Tufts, 1934; Latimer and Robertaille, 1981; Tabuenca, 1976) but year-to-year variation in the relative bloom of the same trees at Havelock North Research Centre (HNRC) indicates climate is also important. Exposure to a period of low temperatures (chilling) is necessary for normal flowering on apricots (Brown, 1952; Guerriero et al., 1985) and therefore the variation suggests that the cultivars' responses to the Hawkes Bay climate differ. This appears particularly likely since cultivated apricots display a wide range of chilling requirements (Ruck, 1975) and since all cultivars planted in Hawkes Bay have been imported into the region, mostly from overseas. For instance, 'Sundrop' was selected in British Columbia, 'Royal Rosa' in California and 'Trevatt' in South Australia. The climates of the latter two regions differ considerably from the first. Thus,

the variable flowering phenology of these three cultivars may reflect the enduring effect of physiological adaptation of the cultivars to the region in which they were selected.

A bloom phenology model which accounted for this variability and indicated cultivars with similar responses to climate would greatly assist assessment of the likely suitability of cultivar combinations under Hawkes Bay conditions. In this respect, description of the low temperature response of apricot cultivars could follow one of several established patterns: the chill hour (Weinberger, 1950), the 'Utah' chill unit (Richardson et al., 1974) or one of its modified forms or Bidabé's exponential model (Bidabé, 1967). Of these, the chill hour and 'Utah' chill unit models have been the most widely used to characterise the relative phenology of bud break and bloom of apricots (Bailey et al., 1982; Ruck, 1975; Tabuenca, 1979). Statistical estimation of chill requirements (Ashcroft et al., 1977) also provides a simple method of deriving chill unit models using historical phenological data where it is available.

This study of apricot bud development was therefore conducted with three objectives. The first was to derive 'Utah' chill unit type models for several Hawkes Bay apricot cultivars from historical bloom phenology data and analyse the performance of these models. The cultivars 'Royal Rosa', 'Sundrop' and 'Trevatt' were selected as representative Hawkes Bay cultivars. The second objective was to independently test the predictive accuracy of these models under Hawkes Bay conditions since the perfomance of 'Utah' chill unit-type models is, in some cases, unsatisfactory (Bailey et al., 1982; Balandier et al., 1993a; Gilreath and Buchanan, 1981; Pitacco et al., 1992). The third objective was to independently estimate the relative chilling requirements of the three cultivars by forcing successively-collected samples of floral budwood since the physiological validity of the statistically-derived chill requirement estimates was unknown.

5.2   Methods and Materials

5.2.1   General Techniques

5.2.1.1   Estimation of hourly temperatures

Hourly records of air temperature were generally not available for accumulation of chill units (CU) and heat units (GDH°C). Therefore, hourly data sets were estimated from daily records of maximum and minimum temperatures using a sine-exponential model of diurnal temperature variation (Parton and Logan, 1981). At the Havelock North Meteorological Station (D96689) these data sets covered the period 1 March to 30 September, 1984 to 1991. Model coefficients used for Havelock North were those that minimised residual error between observed and predicted temperatures for the period March 1 to August 31, 1992. (Delay of daily maximum temperature after mid-day=2 h, night-time temperature decline coefficient = -3.20). Daily minimum temperature was assumed to occur at sunrise. Comparison of predicted and actual chill and heat unit accumulations for May 1 to August 31 1989 and March 1 to August 31 1992 indicated an error standard deviation of 2.15°C but that cumulative error in CU and GDH°C sums stabilised at around 3%. This was equivalent to a two-three day error by the end of accumulation. The direction of error bias was reversed in the two years tested.

5.2.1.2   Chill hour and 'Utah' chill unit model calculations

Chill hour estimates were calculated for four Hawkes Bay meteorological sites (Havelock North, Waipukurau D06051, Hastings D96681 and Napier Airport D96481), four other New Zealand sites (Palmerston North E05363, Greytown D15041, Appleby G13211, and Cromwell I59021) and four international sites: Bendigo (Victoria, Australia), Fresno (California, USA), Penticton (British Columbia, Canada) and Naples (southern Italy). Sites were chosen to represent regions for which flowering data was available or from which significant New Zealand apricot cultivars were sourced. ('Trevatt' is an Australian cultivar, 'Royal Rosa' originated in California and 'Sundrop' was bred at Summerlands Research Station, near Penticton). Mean monthly temperatures for each site were compiled from several sources: New Zealand sites- New Zealand Meteorological Service (1983); Bendigo- Commonwealth Bureau of Meteorology (1958); Fresno and Penticton-

Meteorological Office (1958); Naples- Rudloff (1981). Estimated chill hour accumulations were calculated using a regression relationship which predicts chill hour sums in California from average daily maximum and minimum temperatures (Costello, 1984). Estimates for sites with climates markedly different from that of coastal California (Cromwell, Penticton and Naples) are approximations only.

'Utah' CU/GDH models to predict 5% Bloom of 'Royal Rosa', 'Sundrop' and 'Trevatt' apricots were derived from flowering data for HNRC orchard for 1984 to 1991. 'Utah' chill unit sums were calculated from hourly temperature data (Section 5.2.1.1) using MAGICCU, a 'Utah' chill unit calculation programme (Atkins and Morgan, 1990). Calculations incorporated a 20 h chill fixation period during which high temperatures could 'negate' previous chilling. Accumulation was started on March 1, April 1 and May 1 to study the effect of starting date on model precision. GDH°C accumulation used a base temperature of 4°C. CU requirements were estimated statistically (Ashcroft et al., 1977) except that the coefficient of variation of the GDH°C estimates was minimized rather than the standard error. Use of the error C.V. was selected to avoid bias induced by the correlation of the sample variance with the GDH°C estimate mean.

5.2.1.3   Forcing of apricot budwood cuttings

In 1991 and 1992 budwood cuttings of 'Royal Rosa', 'Sundrop' and 'Trevatt' apricots, 15-20 cm long and bearing at least 4 flower buds, were prepared from one-year-old budwood samples collected from commercial orchards in Hawkes Bay (details in Section 5.2.2.2). All cuttings were removed from branches under water to prevent air entry, uniquely labelled, disinfected for 1 h in 0.5% Chinosol (Hoesch AG, a.i. 670 g kg^{-1} 8-hydroxy-quinoline sulphate) and then placed individually in 30 ml vials of tap water arranged on horticultural plug trays. Each tray of 60 vials was placed in a clear polyethylene bag to minimise evaporation. Cuttings were forced at 20°C at Massey University Plant Growth Unit under fluorescent lighting (60-80 μmol m^{-2} s^{-1}) and 12 h photoperiod. Water in vials was replaced twice weekly. Twice weekly measurements of bud development were made to determine the temporal profile of bud break, the maximum stage of flower bud development reached, number of buds which abscised, and the fraction of buds which reached anthesis. Buds were normally observed for 4 weeks although individual cuttings were observed for up to 6 weeks where development appeared to be continuing.

5.2.1.4   *Quantitative description of flower bud development*

Development of individual flower and leaf buds was made using a scale of ten development stages (Table 5.1 and Fig. 5.1). This scale was extended from that of Fleckinger (Fleckinger, 1955) by subdividing Fleckinger's first stage (Stage A) into three new stages to increase the linearity of measured development with respect to time, particularly under experimental conditions. Fleckinger's alphabetic index was also replaced by a numeric scale to simplify graphical presentation of data and to permit scaling of numerical values for stages to represent actual stage transit times. A parallel scale was used to describe leaf bud development.

Numeric values of the augmented scale were subsequently adjusted to create a near-linear rate of progression through the stages of the development scale under constant temperature conditions. The adjustments were based on twice-weekly observation data describing bud development on three collections of cuttings made from Cambell, Fernhill and Sterling orchards on 30 June, 17 July and 31 July 1992. These had been forced at 20°C as part of the survey of relative bud development (Section 5.2.2.2). Rates of bud development when these three collections were forced indicated that dormancy had been largely alleviated by the time of collection. Data from the collections were pooled and

Table 5.1   Descriptions of phenological stages of apricot flower bud development, modified from those of Fleckinger (1955).

Stage	Appearance	Fleckinger	Nominal	Adjusted [z]
		Numeric stage value		
Dormant	No visible signs of bud growth	-	0	0.0
Movement	Separation of bud scales		1	1.5
Cup	Initial protrusion of sepals above scales	A	2	3.0
Bullet	Broadening of exposed sepals		3	4.2
Red Bud	Expansion and rounding of sepals	B	4	4.9
Pink Bud	Initial protrusion of petals above sepals	C	5	5.5
Balloon	Expansion and rounding of petals	D	6	6.0
Anthesis	Presentation of anthers and stigma	E	7	6.2
Petal Fall	Abscission of petals	F	8	7.4
Pistil Swell	Expansion of pistil beyond corolla cup	G	9	9.0

[z] Nominal scale values adjusted for difference of observed versus expected frequencies (under assumption of constant progression through stages) in development stage classes. Average scale for 'Royal Rosa', 'Sundrop' and 'Trevatt' apricot flower buds calculated from observed frequency data for budwood collected 30 June, 17 July and 31 July 1992 and forced at 20°C.

0 (0.0)
Dormant

5 (5.5)
Pink Bud

1 (1.5)
Movement

6 (6.0)
Balloon

2 (3.0)
Cup

7 (6.2)
Anthesis

3 (4.2)
Bullet

8 (7.4)
Petal Fall

4 (4.9)
Red Bud

9 (9.0)
Pistil Swell
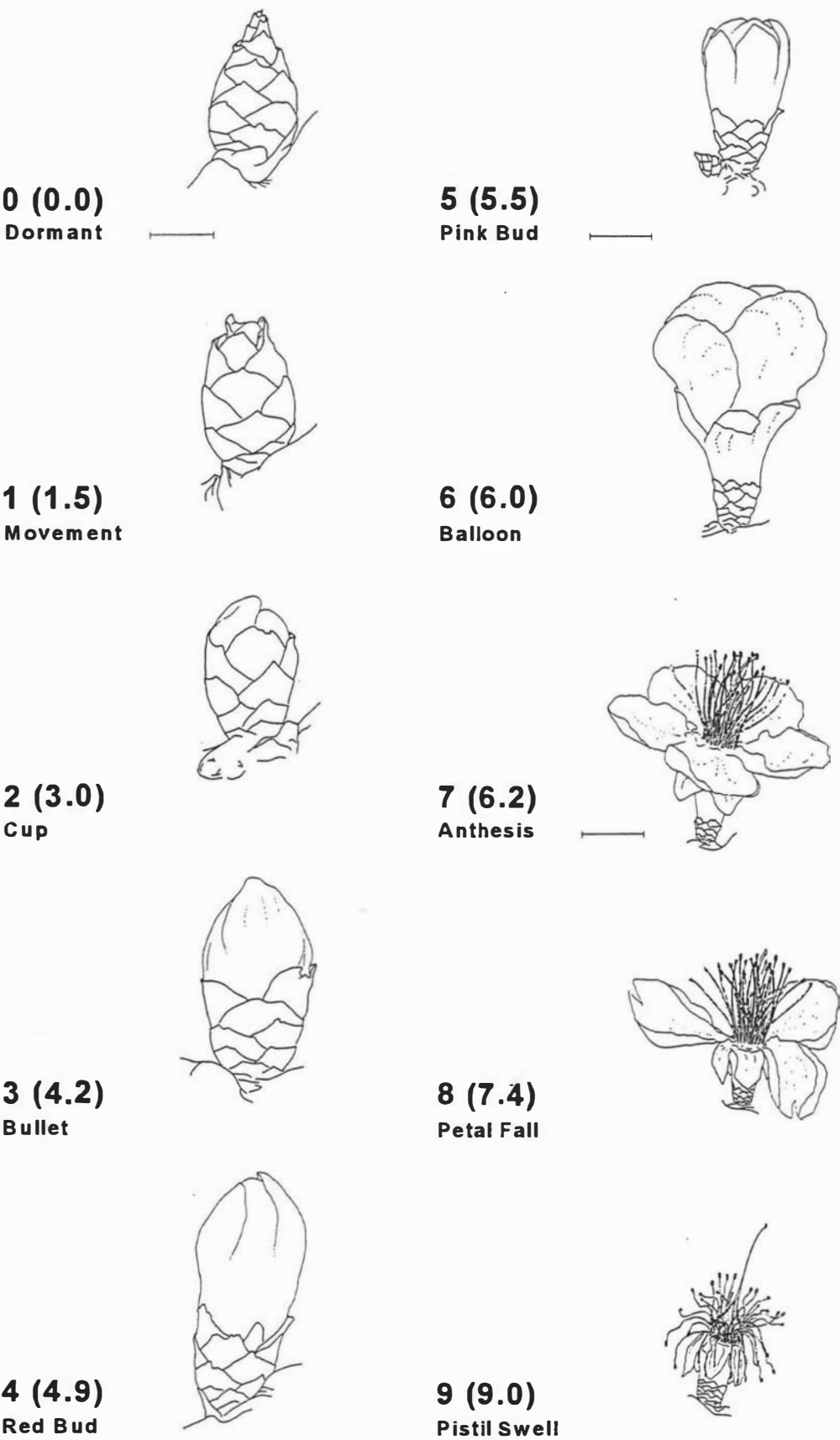
Figure 5.1   Flower bud growth stages used to describe bud development of 'Royal Rosa', 'Sundrop' and 'Trevatt' apricots in orchards and on forced cuttings. (Adjusted stage values in parentheses. Bars represent 2.5 mm: stages 0 – 4; 5 mm: stages 5 and 6; 10 mm: stages 7 – 9.)

the frequency with which observations of each development stage had been made was used to estimate the time spent by buds within each stage during the period of forcing. Each stage value was adjusted by multiplying the nominal stage value by the ratio of the observed versus expected cumulative frequencies to the stage. Expected frequencies were calculated assuming an equal expectation for each stage (i.e. a constant rate of progress through development stages). Hence, s_i' the adjusted stage value, is given by

$$ s_i' \quad = \quad \frac{\displaystyle\sum_{i=0}^{i} f_{Obs}}{\displaystyle\sum_{i=0}^{i} f_{Exp}} \cdot s_i \qquad\qquad (5.1) $$

where s_i is the nominal stage value (0 to 9) and f_{Obs} and f_{Exp} are the observed and expected frequencies of buds whose development lay between stages s_{i-1} and s_i. Only cuttings with buds whose complete development from Stage 0 ('Dormant') to Stage 8 ('Petal Fall') was observed were included in calculations to equalize the expected frequencies for each stage over the period of forcing. Data for 40% ('Trevatt') and 60% ('Royal Rosa' and 'Sundrop') of all cuttings were therefore included in calculations.

The individual bud development scales were used as the basis on which to describe the development of bud populations. Population development stage values numerically equivalent to values for individual bud development were attained when $\geq 50\%$ of buds had reached the respective development stages (i.e. population Stage 3 implies $\geq 50\%$ buds at development Stage 3). Three fractional stages were interpolated between Stage 0 and Stage 1 to increase discrimination during the earliest (and most prolonged) period of bud break (Table 5.2). The distribution of development as buds approached bloom meant that Stage 5 (50% of buds at 'Pink Bud') usually corresponded to 1% bloom, and Stage 6 (50% of buds at 'Balloon') to 5% Bloom.

Table 5.2   Interpolated development stages of bud populations used during early apricot floral bud break.

Development of bud population	Interpolated stages	
	Nominal (s)	Adjusted (s')
5-10% buds at Stage 1	0.25	0.38
10-25% buds at Stage 1	0.5	0.75
25-50% buds at Stage 1	0.75	1.13

5.2.2   **Experimental Studies**

5.2.2.1   *Bud development on 'Sundrop' spurs & extension shoots*

In 1991, flower buds on one-year-old budwood from a five-year-old 'Sundrop' tree at Massey University Fruit Crops Unit orchard (FCU) were forced to compare the time at which buds borne on extension shoots emerged from dormancy with the timing of buds borne on spurs. Collections were made twice a month from May 1 to July 31. At each collection a pair of branches, at least one metre long and bearing one-year-old spurs was removed from the tree. At the same time, a pair of one-year-old extension shoots, also at least one metre long was collected. In each case, one branch or shoot was less than 1.5 cm in diameter while the other greater than 1.5 cm. Five cuttings, each at least two nodes long and carrying at least four flower buds, were cut from each branch or shoot. The cutting were then placed in water and forced at 20°C (see Section 5.2.1.1).

A corresponding set of branches for storage at low temperature was collected from the same tree on May 1. These branches were wrapped in moist newspaper, covered with perforated black polyethylene plastic sheeting and stored at 7°C for up to 60 days. At regular intervals paired branches (one >1.5 cm and one <1.5 cm) of both shoot types were removed from storage, forced and the bud development recorded. The experiment was analyzed as a nested factorial design (factors: chilling regime, budwood type, and branch size with forcing date nested within regime, type and size) using PROC GLM (SAS Institute, 1989). Observations of bud break fraction were transformed to normits (z-values corresponding to the cumulative probability under the normal distribution equal to the original proportion) before analysis to improve the distribution of residuals. Time to bud break was analyzed as speed of development, the reciprocal of days to bud movement. Buds which failed to move during forcing were given a rate value of 0 days^{-1} (i.e. $1/\infty$ days).

5.2.2.2   *Bud development in Hawkes Bay apricot orchards*

Apricot budwood was collected from three Hawkes Bay commercial orchards during the winter of 1992 to observe the emergence of flower buds from dormancy under natural conditions. Two orchards were located on the Heretaunga Plains near Bridge Pa (Campbell Orchards) and Fernhill (Fernhill Farm Orchard, Rex Graham Associates) and

the other (Stirling Orchards) near Bayview north of Napier (Fig. 5.2). All trees were at least five-years-old, grafted on peach rootstocks and were bearing commercially. In mid-April 1992, 45 healthy representative 'Royal Rosa', 'Sundrop' and 'Trevatt' trees were selected in each orchard. Trees of each cultivar were then randomly allocated to eight sets of five trees for budwood collection while development on the remaining five trees was observed in situ over the period of bud wood collection and natural bloom.

On each tree two representative branches of sufficient size to yield two 10-15 cm cuttings, each carrying about 10 flower buds, were selected on April 24. One branch was removed immediately for storage at low temperature while the other was left for later collection after exposure to natural winter conditions (Table 5.3). Budwood was sampled twice a month at approximately fortnightly intervals through to the end of July by which time bud break was well advanced. A branch carrying at least 100 buds on short (5-10 cm) shoots ('Royal Rosa' & 'Trevatt') or spurs ('Sundrop') was also selected on each tree
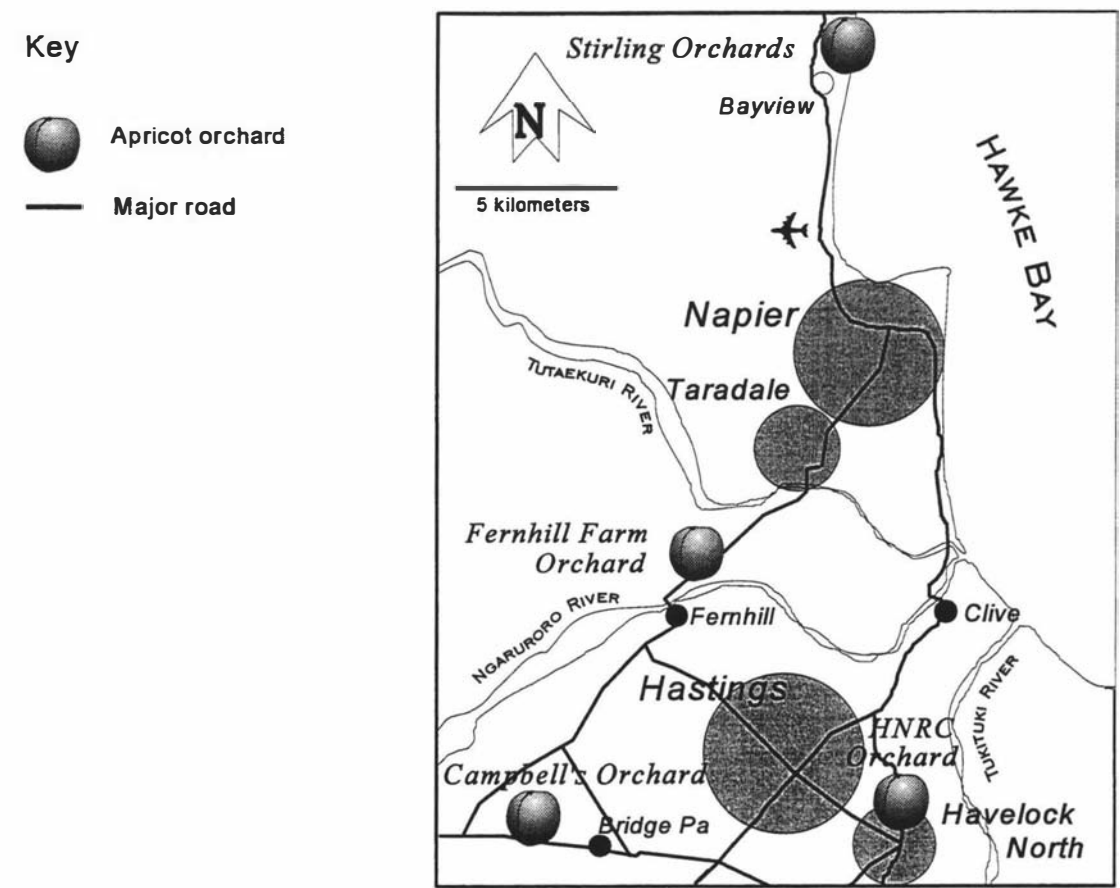
Figure 5.2 Map of Napier/Hastings area of Hawkes Bay showing locations of apricot orchards sampled for budwood during 1992 (Campbell's Orchard, Fernhill Farm Orchard and Stirling Orchards in relation to the orchard of Havelock North Research Centre.

observed in situ and labelled. Bud development was recorded from the beginning of July using the scales outlined in Tables 5.1 and 5.2. Progress of bloom was monitored until the end of August. For storage branches were recut under water, all leaves were removed and then branches were stood in water for 24 h minimise water stress. Branches were wrapped in perforated black polythene sheeting and placed at 7°C. Successive removals from storage were made until the duration of low temperature exposure (Table 5.3) substantially exceeded dormancy chilling requirements predicted by 'Utah' chill unit models for each cultivar. Leaf-fall and hardening of budwood occurred during April around about the time the first chill units began to accumulate. Budwood collected before this time in earlier preliminary experiments appeared insufficiently hardened to prevent visible shrivelling during storage.

Accumulated 'chilling' and simulated bud development at each orchard were calculated using air temperature data from two New Zealand Meteorological Service recording stations in Hawkes Bay. Air temperatures at Campbell and Fernhill Farm orchards were estimated from hourly records of air temperature at Havelock North Meteorological Station (D9668A/D9668B). Missing values in small gaps (2-4 h) in sensor records were estimated by linear interpolation between the nearest recorded values. Missing values in a few larger gaps were estimated from daily maximum and minimum temperature records using a sine-exponential model of diurnal temperature variation (Section 5.2.1.1). Air temperatures for Stirling Orchards, Bayview were estimated from air temperature recordings at Napier Airport (Station D96484) supplied by the National Institute of Water and Atmospheric Research. Hourly values were estimated by interpolation from cubic splines fitted to three-hourly recordings using Splus Version 3.2 (Statistical Sciences Inc., 1993). In both cases, air temperature data were adjusted using regression functions which described the temperature difference between the recording site and orchard observed during a period of up to one month between June and August 1992 (Table 5.4).

Table 5.3   Forcing dates of 'Royal Rosa', 'Sundrop' and 'Trevatt' apricot budwood cuttings.

Budwood sample [z]	0	1	2	3	4	5	6	7
Field	April 24	May 7	18 May	2 June	16 June	30 June	17 July	31 July
Cool-stored, 7°C	-	May 6	May 13	May 21	May 28	4 June	10 June	17 June
Duration (h)	-	288	456	648	816	984	1128	1296

[z] 'Field' budwood samples collected from three Hawkes Bay orchards April-July 1992 and corresponding 'cool-stored' budwood collected in April 1992 and given equivalent hours of 'chilling' at 7°C.

Table 5.4　　　Regression equations describing the temperature relationships between two Hawkes Bay meteorological stations and three apricot orchards used for budwood collection.

Orchard - Meteorological station	Regression equations [z]	n	r^2	Signif. [y]
Campbell - Havelock North (2 June- 16 June 1992)	$T_{Campbell} = -1.04 + 1.245\, T_{HvlNth}$	304	0.93	***,***,***
Fernhill Farm - Havelock North (17 June- 29 June 1992 & 5 August- 19 August 1992)	$T_{Fernhill} = 0.19 + 0.981\, T_{HvlNth}$	287	0.93	***,ns,***
Stirling - Napier Airport (30 June- 31 July 1992)	$T_{Stirling} = 0.30 + 0.986\, T_{NapAir}$	241	0.91	***,ns,***

[z] All orchard temperature sensors housed in Stephenson screens.
[y] ns,*,**,***: Overall regression, intercept (b_0) and slope (b_1) non-significant or significant at $P<0.05, P<0.01$ and $P<0.001$ respectively.

Orchard temperatures were recorded using a 'Taupo F' data-logger (Solid State Electronics, Lower Hutt) reading twin LM35 temperature-sensing diodes (10 mV/°C) housed in standard Stephenson screens. Temperature sensors were calibrated against the Havelock North Meteorological station temperature sensor over a 20°C range. Three screens were used: one positioned at 4.0 m, one at standard screen height 1.5 m above ground level, and another near ground level (0.2 m). Exposed grass temperature was also recorded with twin sensors laid directly on the grass. Regression equations describing the relationship of orchard temperature to corresponding recording station temperature were determined using PROC REG of SAS (SAS Institute Inc., 1989).

The effects of cultivar and orchard location on bud response to forcing and its relationship to time of bud wood collection were analysed using PROC GLM of SAS (SAS Institute Inc., 1989). Four bud development parameters were studied: bud fresh weight at the start of forcing determined from a subsample of 10 randomly-selected flower buds, the number of days at 20°C required to reach 50% bud break, the final fraction of bud break after four weeks of forcing, and the maximum numeric development stage reached by buds which initiated growth. Numeric development scale values were adjusted according to Table 5.1. Data for the final collection from Stirling Orchards (31 July) and the final two collections from Campbell and Fernhill Farm orchards (17 July and 31 July) were omitted from analyses as bud development was too advanced for meaningful comparison with other collections. Change in the various bud development characteristics was analysed by linear regression after transformation of

original data. Bud fresh weight was analysed as $fwt^{1/6}$, based on the assumption that growth rate was constant in one dimension. Time to 50% bud break and maximum development stage reached during forcing were described empirically by exponential and Gompertz growth functions respectively. Cubic polynomials were used to describe the temporal pattern of final number of buds developing during forcing after percentage data had been transformed to normits. Equations for each cultivar/site combination were then differentiated to identify the position (and height) of bud break maxima and minima relative to collection date. Stepwise multiple regression was then performed using PROC REG of SAS (SAS Institute Inc., 1989) to investigate the relation-ship between time of bud break at the three orchards and regression parameter estimates for bud fresh weight, days to 50% bud break, final bud break fraction and maximum development stage reached during forcing as well as with the date of 50% leaf fall.   Parameters tested included: date of 50% Leaf Fall; intercept (b_0) and slope (b_1) for regression of bud fresh weight (as $fwt^{1/6}$); intercept and slope for regression of number of days at 20°C taken to reach 50% bud break (as $\log_e[1/days]$); intercept and slope of final bud development stage reached (as $\ln(\ln[s'_{max} / s'_{final}])$) where $s'_{max} = 9$ and $s'_{final} = $ final adjusted bud development scale stage; combined bud break proportion after forcing of May 7 and May 18 collections ('May bud break') and for June 2 and June 16 collections ('June bud break'). Dummy variables for cultivar effects were subsequently fitted to investigate within-cultivar variation under the assumption that the relationship between date of bud break and the independent variables was the same for each cultivar. Date of bud break was calculated as the intercept with the x-axis (time) from linear regressions of observed bud development (expressed using the adjusted numeric bud development scale). Date of 50% Leaf Fall was calculated from quadratic equations fitted to leaf fall stage data using PROC REG.

5.3   Results

5.3.1   Quantitative Description of Flower Bud Development

Frequency distributions describing development of buds forced at constant 20°C showed that frequencies with which buds were observed within each development stage differed from those expected if transit times for each stage were constant (χ^2=381, 16 df: P<0.001). Bud abscission before 'Petal Fall' was common on 'Trevatt' cuttings and, since only buds which developed fully from 'Dormant' to 'Petal Fall' were used to determine observed stage frequencies, fewer data for buds of 'Trevatt' were therefore included in the analysis. Histograms for 'Royal Rosa', 'Sundrop' and 'Trevatt' (Fig. 5.3a-c) show a steady decrease in observed frequencies from nominal Stage 0 ('Dormant'). As a result, numbers of buds observed at Stages 4, 5 and 6 ('Red Bud', 'Pink Bud' and 'Balloon') were lower than expected for each cultivar. This confirmed an initial observation that buds passed more rapidly through these later stages in comparison to the earlier stages.

Slow passage of flower buds through early development stages meant numeric values of early stages increased when adjusted for the difference between observed and expected frequencies (Fig. 5.3d-f, Table 5.5). In contrast, numeric values for later stages fell due to much shorter periods spent at the 'Pink Bud' and 'Balloon' stages than represented by the numerical difference between nominal scale values. 'Anthesis' (nominal Stage 7) was represented by Stage 6.0 on the adjusted scale for 'Sundrop'. Relative frequencies for 'Royal Rosa' and 'Trevatt' did not differ from each other (χ^2=12.1, 8 df, non-significant) but together differed from those of 'Sundrop' (χ^2=58.7, 16 df, P<0.001). This

Table 5.5   Adjusted numeric scale values for 'Royal Rosa', 'Sundrop' and 'Trevatt' flower bud development stages adjusted to linearise measured development rate at constant 20°C.

Cultivar	0^z	1	2	3	4	5	6	7	8	9
				Nominal stage value						
'Royal Rosa'	0	1.5	2.8	3.9	4.6	5.4	5.9	6.2	7.4	9.0
'Sundrop'	0	1.5	3.0	4.4	5.0	5.4	5.8	6.0	7.4	9.0
'Trevatt'	0	1.5	3.1	4.3	5.0	5.7	6.1	6.3	7.4	9.0

^{z}: Stage names- 0='Dormant', 1='Movement', 2='Cup', 3='Bullet', 4='Red Bud', 5='Pink Bud', 6='Balloon', 7='Anthesis', 8='Petal Fall', 9='Pistil Swell'.
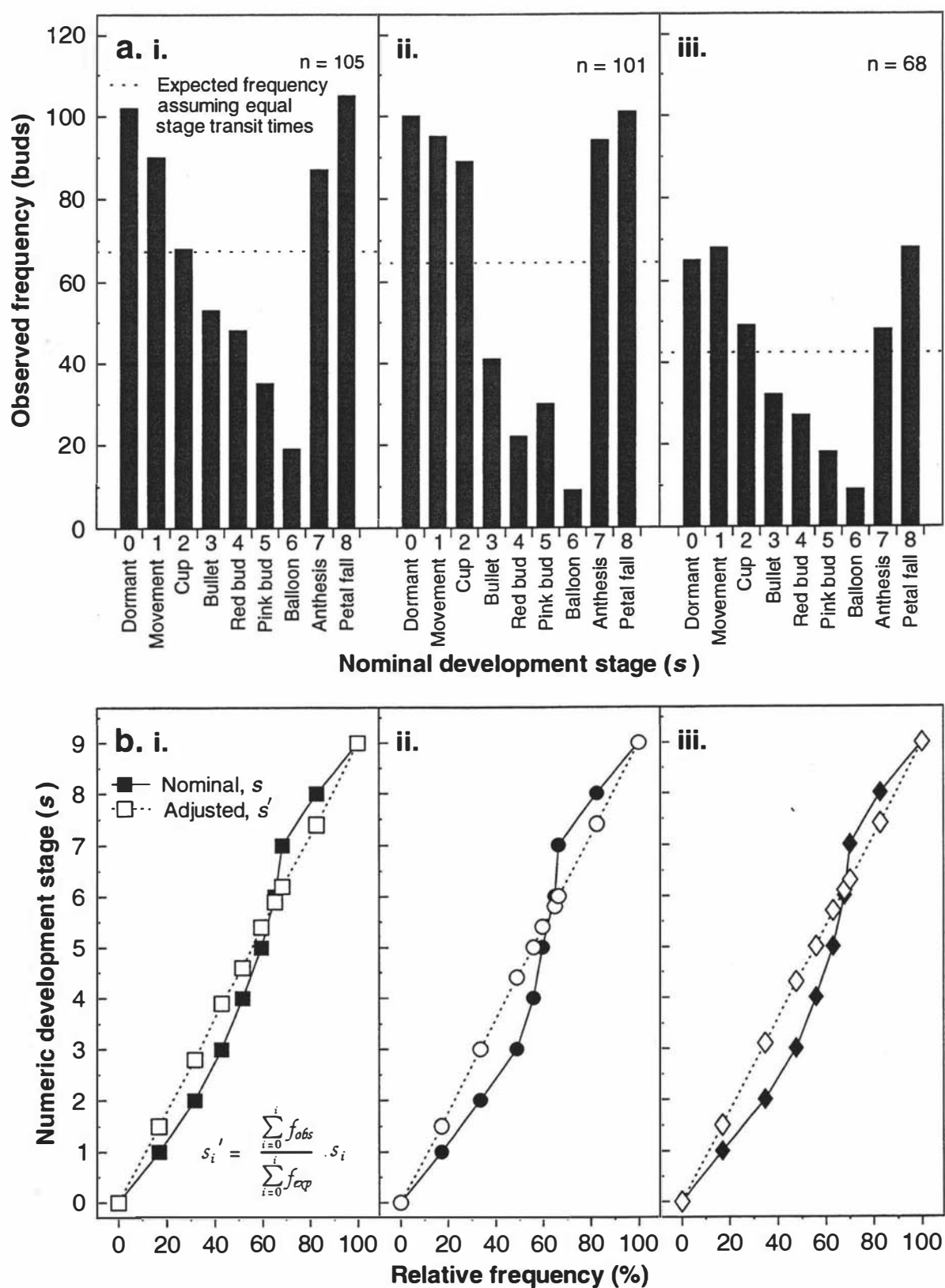
Figure 5.3   Observed frequency of apricot flower bud development stages and corresponding adjusted numeric development scale. Cultivars: i). 'Royal Rosa'; ii). 'Sundrop'; iii). 'Trevatt'.
a). Observed frequency distributions for buds incubated for four weeks at 20°C and observed twice-weekly from 'Dormant' to 'Petal Fall' stages.
b). Adjustment of numeric values of development scale using observed / expected frequency ratio. (Budwood collected from Campbell, Fernhill and Stirling orchards, 24 April-31 July 1992.)

was due to high observed frequency of 'Sundrop' flower buds in 'Cup' stage (nominal stage 2) relative to 'Bullet' and 'Red Bud' stages (nominal stage 3 and 4) compared with frequencies for 'Royal Rosa' and 'Trevatt' buds.   This probably reflected biased categorising of buds introduced by slightly different bud morphology of the three cultivars. Adjusted scales were individually calculated for each cultivar (Table 5.5) and a common averaged scale (Table 5.1) used for analyses of bud development to simplify comparison between cultivars .

5.3.2   Winter Temperatures in Apricot Growing Regions

There were notable differences between chill hour and chill unit accumulation at the Hawkes Bay and other sites for which estimates of winter chilling were calculated (Fig. 5.4).   Chill hour sums were more variable than those of 'Utah' chill units.   In Hawkes Bay, total chill hour accumulations fell by over 600 h (~30%) as proximity to the sea increased. This was due to lower winter temperature maxima at Waipukurau and warmer minima at Napier Airport (Fig. 5.4a.i-iv). Differences in chill unit accumulation were smaller, especially between Havelock North, Hastings and Napier Airport. Chill unit (CU) accumulation also varied less between the other New Zealand sites. Sites had accumulated 1500 to 1700 chill units accumulated by July whereas chill hour sums ranged from 750 h (Palmerston North) to 2000 h (Cromwell). Chill hour accumulation at Cromwell was rapid due to the relatively cold winter of Central Otago and, unlike other sites, the chill hour sum exceeded that for chill units from June onwards. With the exception of this site, chill hour sums for other New Zealand sites were comparable to those for Hawkes Bay but chill unit sums were higher, averaging 1500 CU by July versus 1300 CU in Hawkes Bay.

Of the international sites, accumulations for Bendigo and Fresno most closely resembled those for New Zealand sites as mean maximum and minimum temperatures over the winter period are comparable. However, accumulations for Penticton and Naples were substantially different.   At Penticton, cold winters during which average maximum temperatures are below 7°C cause very rapid chill hour accumulation.   However, temperatures are sufficiently low to reduce the rate of chill unit accumulation, a reflection of the original climatic situation for which the 'Utah' chill unit model was designed. Chill
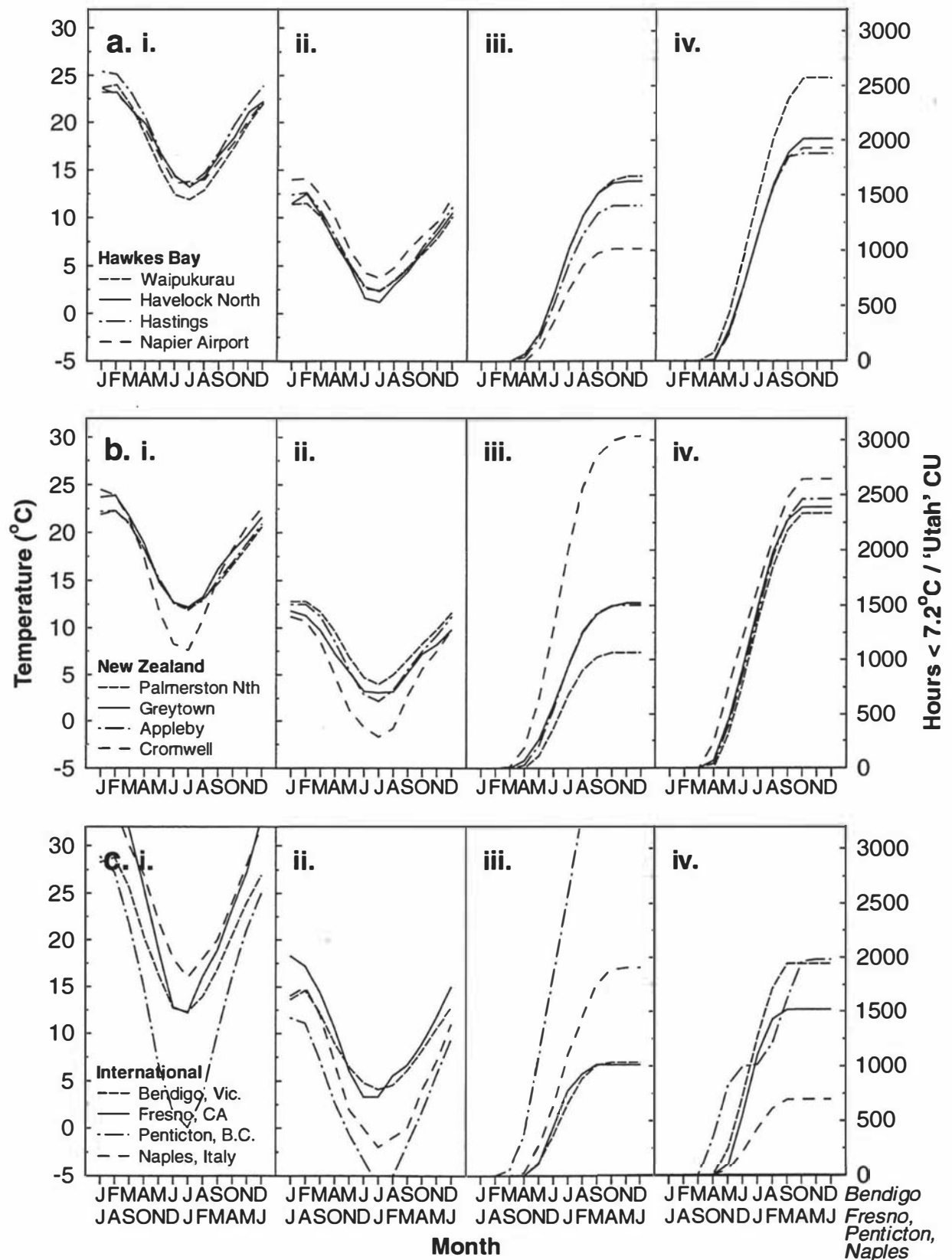
Figure 5.4   Comparison of winter 'chilling' accumulation at four Hawkes Bay sites with other New Zealand and international apricot growing areas. Variables: i). Monthly mean maximum temperature; ii). Monthly mean minimum temperature; iii). Estimated chill hour (temperature $< 7°C$) accumulation; iv). Estimated 'Utah' chill unit accumulation.

a). Hawkes Bay sites;   b). Other New Zealand sites;   c). International sites.

hours also accumulate rapidly at Naples due to low winter minima, but, by comparison, chill unit accumulation is low due to the 'chill negating' effect of relatively high average maxima.

5.3.3 Analysis of 'Utah' Chill Unit Model Performance

5.3.3.1 Prediction of 5% Bloom

'Utah' chill unit models for 'Royal Rosa', 'Sundrop' and 'Trevatt' (Fig 5.5) suggested that the three cultivars have similar chill requirements for the completion of 'rest', respectively 900, 950 and 800 'Utah' chill units for 'Royal Rosa', 'Sundrop' and 'Trevatt'. Corresponding heat requirements for development between 'rest' completion and 5% Bloom for which the coefficient of variation was minimised were respectively 3180, 3880 and 5050 GDH°C. Analysis of variance indicated that these cultivar-specific heat requirements differed significantly (Table 5.6). These chill unit models therefore suggest that the differences in time of bloom of the three cultivars are due mainly to differences in the rate at which flower buds develop from their release from 'rest' or endodormancy to anthesis. The contrasts indicate that flower buds of 'Royal Rosa' reach 5% Bloom sooner than do those of 'Sundrop' because of a greater response to heat during bud development. By comparison, buds of 'Trevatt' apparently take longer than those of 'Sundrop' to reach anthesis because their development is less responsive to heat.

Model precision was, however, reduced by high variation in the heat sums for the period from estimated completion of 'rest' to 5% Bloom. Error coefficients of variation (C.V.)

Table 5.6   Analysis of variance of GDH°C estimates from 'Utah' chill unit models for 'Royal Rosa', 'Sundrop' and 'Trevatt' derived from bloom data for HNRC, 1984 to 1991.

Source	df	Type IV MS [z]
Model	9	1924224 ***
Cultivar	2	7071805 ***
Year	7	443482 *
Residual: Error	13	108180
R^2		0.92
Contrasts		
'Royal Rosa' vs 'Sundrop'	1	1901788 **
'Trevatt' vs 'Sundrop'	1	4706964 ***

[z] Datum missing for 'Sundrop', 1991.
*,**,*** Variance components and contrasts significant at $P<0.05$, $P<0.01$ and $P<0.001$ respectively.
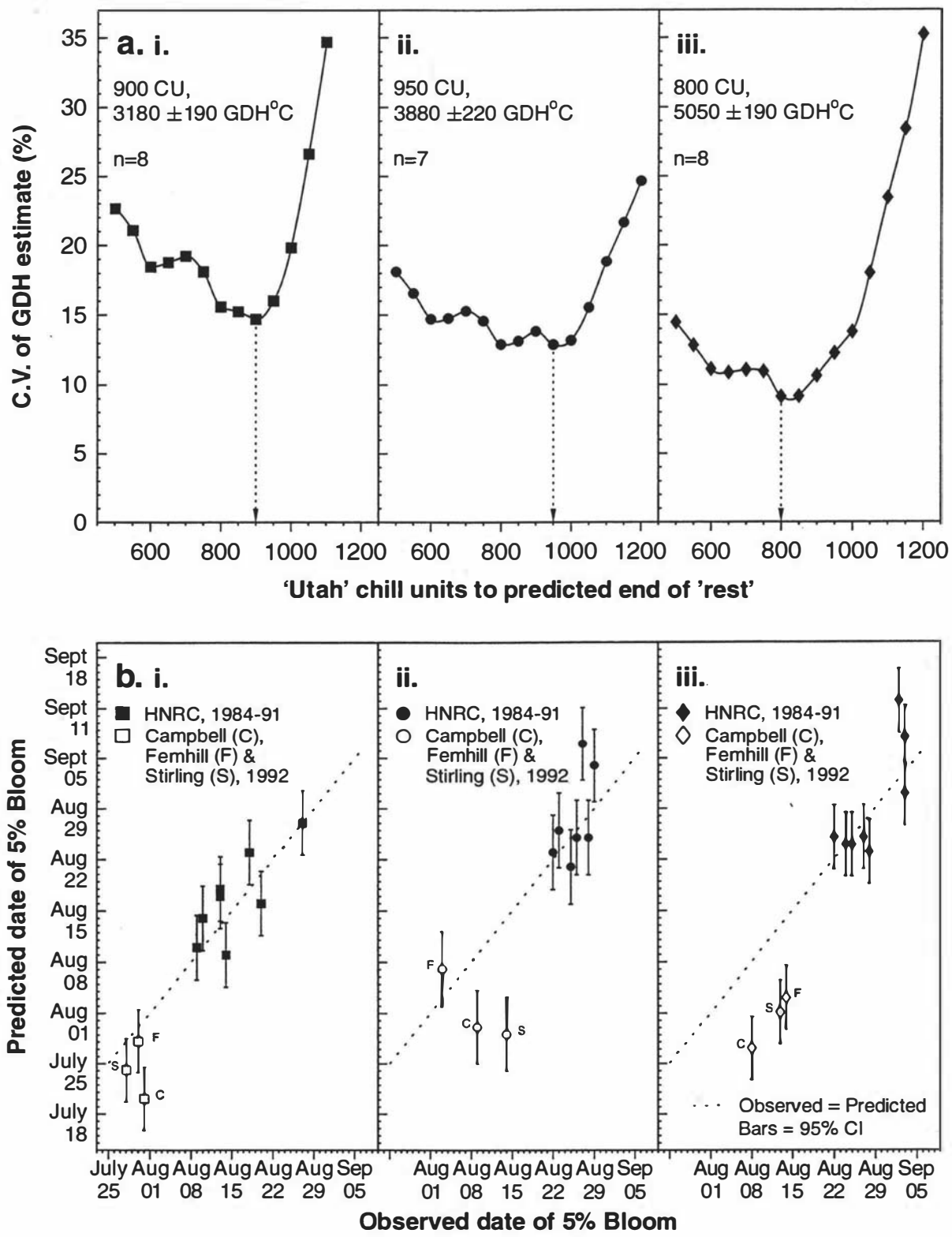
Figure 5.5   'Utah' chill unit requirements for three apricot cultivars and comparison of observed dates of 5% Bloom with predictions by corresponding models: Cultivars: i). 'Royal Rosa'; ii).'Sundrop'; iii). 'Trevatt'.

a). Estimation of chill requirements at minimum coefficient of variation of GDH$^\circ$C using bloom data for HNRC, 1984-91. Accumulation start date = March 1, Chill fixation period = 20 h, GDH$^\circ$C base temperature = 4°C (Atkins & Morgan, 1990).

b). Comparison of observed and back-predicted dates of 5% Bloom for HNRC orchard, (1984-1991) and independent predictions for Campbell, Fernhill Farm and Stirling Orchards (1992).

for GDH°C estimates were high and, at their minimum, ranged from 10% for 'Trevatt'
to 15% for 'Royal Rosa' (Fig. 5.5a i-iii). Initiating chill unit accumulation at April 1 and
May 1 rather than at March 1 had little effect on the error C.V., at best reducing it from
15% to 14% for 'Royal Rosa'. Precision of model predictions was therefore at best ±4-5
days (95% confidence interval). Model accuracy was also unsatisfactory (Fig. 5.5b i-iii).
Observed dates failed to fall within the 95% confidence interval of the predicted date
both when the models were used to back-predict onto the original data set (HNRC, 1984-
1991) and when they were used to predict independently-observed dates (Campbell,
Fernhill Farm and Stirling Orchards, 1992). Overall accuracy was poorest for the models
describing the phenology of 'Sundrop' and 'Trevatt' flower buds. For 'Sundrop', the error
between observed and predicted dates was as high as +11 days (HNRC, 1989) and
-16 days (Stirling Orchards, 1992) while for 'Trevatt', the largest errors were +11 days
(HNRC, 1986) and -12 days (Campbell and Stirling Orchards, 1992).

The accuracy of these models did not improve appreciably when performance was
assessed on the basis of ability to predict relative flowering behaviour (Table 5.7). While

Table 5.7   Accuracy of prediction for divergence of 5% Bloom between 'Royal Rosa' -
'Sundrop' and 'Sundrop' - 'Trevatt' at HNRC, 1984-1990 backpredicted by 'Utah' chill unit models
onto the original data, and also for independently-observed dates at Campbell, Fernhill Farm and
Stirling orchards in 1992.

| Site and Year | | 'Royal Rosa' - 'Sundrop' | | | 'Trevatt' - 'Sundrop' | | |
| | | Bloom divergence | | | Bloom divergence | | |
		Observed	Predicted	Error	Observed	Predicted	Error
HNRC	1984	-5	-5	0	3	2	1
	1985	-9	-17	8	-1	-1	0
	1986	-11	-12	1	4	9	-5
	1987	-13	-8	-5	-1	-1	0
	1988	-12	-9	-3	2	1	1
	1989	0	-11	11	7	1	6
	1990	-15	-7	-8	6	6	0
Campbell	1992	-9	-10	1	-1	-3	2
Fernhill	1992	-4	-10	6	11	-4	15
Stirling	1992	-17	-5	-12	-1	3	-4
	σ			7.2			5.6
Mean error [z]				5.5			3.4
	r^2			0.09			0.01

[z] Mean of absolute values of difference between observed and predicted divergence of 5% Bloom.

error of predicted bloom divergence was as low as 0 to 2 days in a third of all instances, average error was much higher. Error of predicted divergence averaged 5.5 days for the pairing of 'Royal Rosa' and 'Sundrop' and 3.4 days for 'Sundrop' and 'Trevatt'. However, absolute error of predicted bloom divergence was as high as 12 days and 15 days respectively. Consequently, the models did not describe flower bud development in Hawkes Bay with sufficient accuracy to permit confident prediction of relative bloom phenology for assessment of pollenizer suitability.

5.3.3.2   Accuracy of chill requirement estimates

Initial investigation of release of apricot flower bud endodormancy demonstrated that budwood type significantly effected apparent chilling requirement but revealed no clear indications of physiological transition at 900-1000 CU. Analyses of variance for fraction and speed of bud break (proportion of buds moving and reciprocal of days to Stage 1) showed that more flower buds on 'Sundrop' spurs began visible development than did buds on extension shoots (Table 5.8). On spurs, final bud break increased steadily and by the end of July 75% of flower buds showed visible development ('Movement' or

Table 5.8   Analyses of variance for development of forced 'Sundrop' spur and extension shoot budwood collected from FCU May-August 1991.

Source	Bud Break (%) ^{z}		(Days to 'Movement') $^{-1}$	
	df	Type III MS	df	Type III MS
Model	47	1.89 ***	47	0.0396 ***
Chilling	1	2.77 ns	1	0.0003 ns
Residual 1: Date (Chilling)	10	3.14	10	0.0462
Budwood type	1	11.02 *	1	0.6803 **
Chilling×Budwood type	1	0.01 ns	1	0.0007 ns
Residual 2: Date×Type (Chilling)	10	1.73	10	0.0478
Size	1	3.71 ns	1	0.0685 *
Residual 3: Date×Size (Chilling)	10	1.21	10	0.0107
Chilling×Size	1	0.19 ns	1	0.0250 ns
Budwood type×Size	1	0.49 ns	1	0.0219 ns
Chilling×Budwood type×Size	1	0.04 ns	1	0.0139 ns
Residual 4: Date×Budwood type ×Size (Chilling)	10	0.96	10	0.0051
Residual: Error	189	0.71	416	0.0032
R^2		0.40		0.58

ns,*,**,*** Variance components non-significant or significant at $P<0.05$, $P<0.01$ and $P<0.001$ respectively.
^{z} Bud break fractions transformed to normits for analysis of variance.

greater) within four days of forcing (Fig. 5.6a i). By contrast, most buds on extension shoots remained tightly closed, whatever the date of collection.

Flower buds on spurs also showed signs of movement significantly faster than those on shoots (Table 5.8). Prior to mid-June, the initial speed of development (i.e. the inverse of time to bud break) remained very low and bud break typically did not occur within the 5 week forcing period for buds on either budwood type. However, the average speed with which buds on spurs showed signs of growth increased progressively from mid-June (which corresponded to the accumulation of around 500 'Utah' chill units). By the final sampling date some flower buds on spurs had already reached 'Movement' (Stage 1). By contrast, initiation of bud development on extension shoots was very slow and only towards the end of July did average time to bud break approach 14 days (Fig. 5.6b.i). Cutting diameter also affected speed of bud break (Table 5.8). Flower buds on thin cuttings (diameter 0.8 to 1.5 cm) showed signs of movement significantly faster than buds on thick cuttings (diameter 1.5 to 2.5 cm).

Final fraction of buds moving which did not increase with duration of cool-storage at constant 7°C, either on extension shoots or on spurs (Fig 5.6a ii). Speed of bud break on extension shoots and spurs stored initially displayed a similar response to duration of low temperature as naturally chilled budwood (Fig 5.6b ii). On extension shoots, speed of bud break was very slow regardless of time in cool-storage whereas on spurs it initially increased. Time to reach 'Stage 1' dropped from four weeks (May 5 collection, no cool-storage), to about 14 days after 430 h at 7°C and to about 7 days after 812 h. Speed of bud break on spurs then fell unexpectedly at storage durations beyond 812 h, probably due to bud abscission which affected over half of buds by 1440 h of storage. Some bud swelling occurred in cool-storage but this was usually associated with formation of callus-like tissue at the base of the bud. Buds with callus tissue on spurs or shoots almost always abscised. Those buds forced later therefore represented a subsample of buds remaining after other buds (probably those which were faster developing) had abscised.

Flower bud development on forced cuttings of 'Royal Rosa', 'Sundrop' and 'Trevatt' budwood collected from Campbell, Fernhill Farm and Stirling orchards (Fig. 5.8) did not clearly support the chilling requirements estimated from historical bloom data for HNRC.
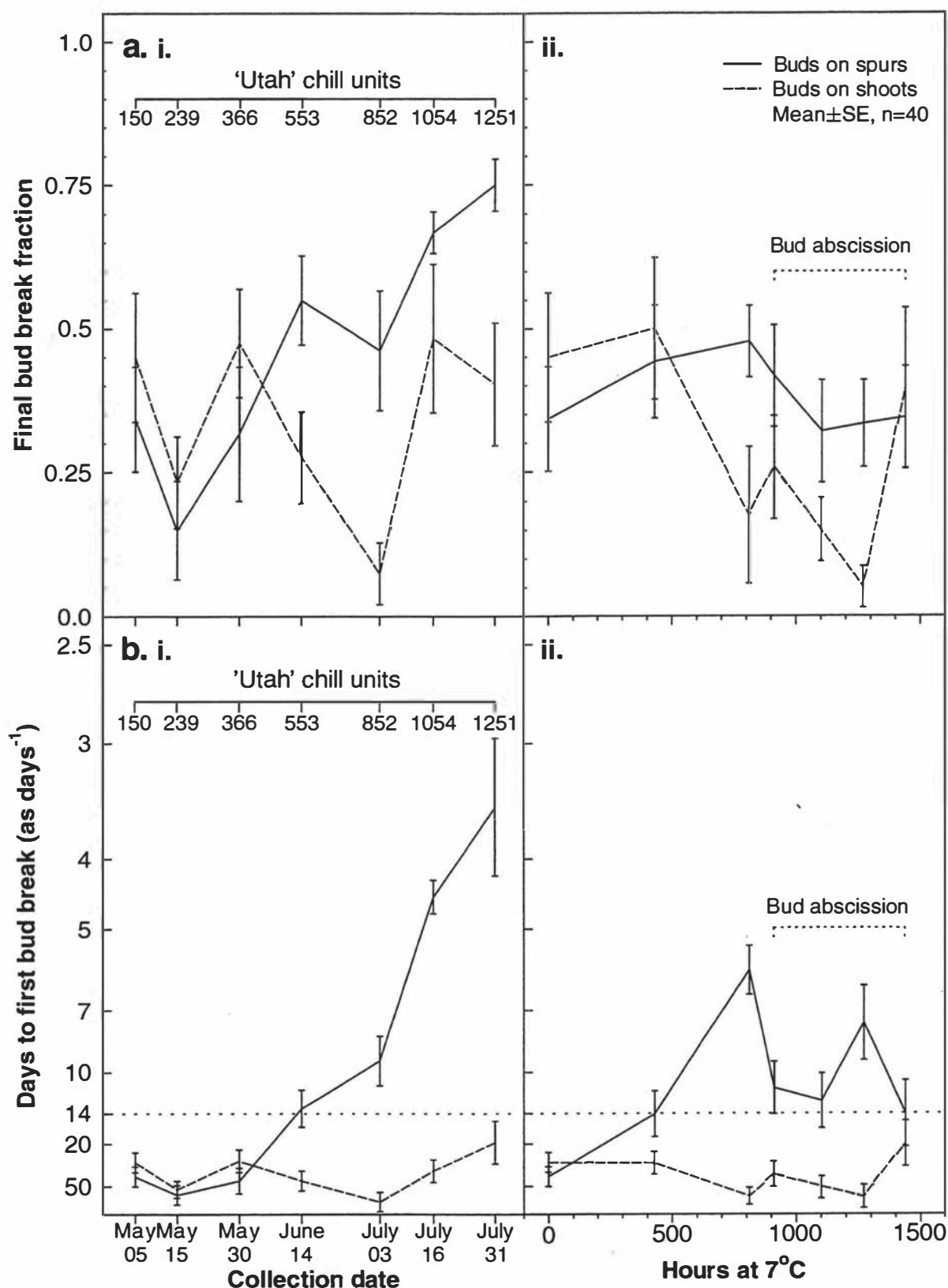
Figure 5.6   Development of forced 'Sundrop' flower buds on spurs and extension-shoots after exposure to natural winter temperatures at FCU or cool-storage at continuous 7°C. a). Final fraction of flower buds showing signs of growth: i) Field collected; ii) Cool-stored. b). Days to first bud break plotted as reciprocal (days^{-1}): i) Field collected; ii) Cool-stored.

Table 5.9   Fresh weight and pistil length for 'Royal Rosa', 'Sundrop' and 'Trevatt' apricot flower buds collected from Campbell, Fernhill Farm and Stirling orchards, 22 April 1992.

Cultivar	Bud fresh weight (mg) [z]		Pistil length (mm)	
'Royal Rosa'	8.9	a	0.61	a
'Sundrop'	11.4	b	0.75	c
'Trevatt'	9.6	a	0.68	b

[z] Means within columns followed by different letters significantly different at $P<0.05$ (n = 60). Separation by Ryan-Einot-Gabriel-Welsch multiple range test.

Leaf fall at these sites had occurred from mid-April to mid-May with no consistent cultivar or site differences (Fig. 5.7a i-ii). Mean flower bud fresh weight and pistil length within buds showed no consistent differences between sites when buds were sampled at leaf-fall although there were significant differences between cultivars (Table 5.9). Sample-to-sample (between-tree) variation in fresh weight at each sampling was considerable. Bud fresh weight and pistil length were greatest for 'Sundrop' flower buds. 'Trevatt' pistils were intermediate in size and those of 'Royal Rosa' the smallest. Bud fresh weights for these two cultivars were similar. 'Utah' chill unit sums from 1 March and GDH°C sums from 16 June (980, 904 and 800 CU at Campbell, Fernhill Farm and Stirling orchards respectively) were very similar for two of the Heretaunga Plains orchards, Campbell and Fernhill Farm whereas, at Stirling Orchards near Bayview, chill unit accumulation was slower and heat accumulation faster (Fig. 5.7b i). Daily tempera-ture maxima at the three orchards over winter and spring were very similar (Fig. 5.7b ii) but temperature minima (Fig. 5.7b iii) were consistently higher at Stirling Orchards which lies within 0.5 km of the sea (Fig. 5.2). Inter-site differences in chill and heat unit accumulation were therefore probably mainly due to differences in temperature minima.

The appearance of a distinct transition from dormancy to growth depended on how bud development was measured. Bud fresh weight (measured at the start of forcing) initially increased slowly for all three cultivars (Fig. 5.8a i). Significant increases only occurred after June 16 which coincided with the accumulation of 800-1000 CU, depending on orchard site (Fig. 5.7b i). The time required for cuttings to reach 50% bud break (analysed as speed of bud break, days^{-1}) showed a similar transition after June 16 (Fig. 5.8a ii). Both site and cultivar influenced the level and change in speed of bud break (Table 5.10) which increased more slowly at Stirling Orchards and more rapidly
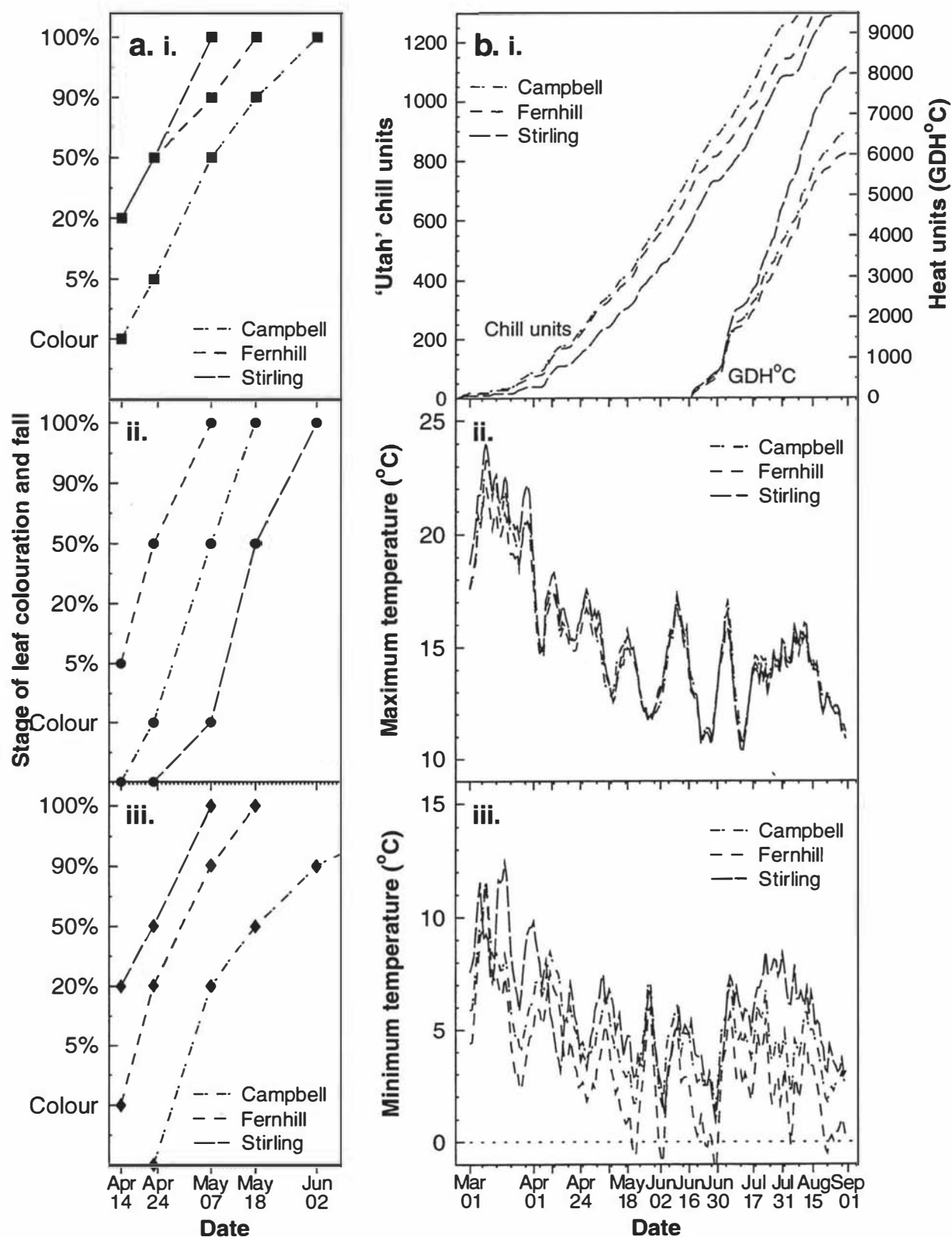
Figure 5.7   Apricot leaf fall phenology and air temperature conditions for three Hawkes Bay orchards, March-August 1992.

a). Leaf-fall phenology. Cultivars: i. 'Royal Rosa'; ii. 'Sundrop'; iii. 'Trevatt'. (Colour = Clearly visible colouration of leaves.)

b). Air temperature data: i. 'Utah' chill unit accumulation from 1 March and Growing Degree Hour accumulation from 16 June; ii. Daily maximum air temperature (7 day average); iii Daily minimum air temperature (7 day average).

for 'Royal Rosa' and 'Trevatt'. In contrast, changes in the proportion of buds initiating development and the final (maximum) development stage of those buds after forcing suggested a more gradual transition from dormancy to growth. Final develop-ment stage increased linearly from near zero (no development) for buds collected on April 24 to an adjusted stage value of over 7.4 (petal fall) by June 30 for each of the three cultivars (Fig. 5.8c i). The rate at which it increased varied among cultivars, probably because of differences between 'Royal Rosa' and 'Trevatt' since estimate comparisons indicated no significant difference between 'Sundrop' and these cultivars (Table 5.10). The comparisons also indicated that final development stage reached was initially higher for 'Royal Rosa' than for 'Sundrop'. However, variation between cuttings of the third, forth and fifth collections (May 18, June 2 and June 16) was substantial and this reduced the precision of the analysis.

Early signs of transition from dormancy were also visible in the change of bud break fraction with collection date (Fig. 5.8d i). The pattern of change was complex and was affected by both site and cultivar effects, the cultivar effect being stronger (Table 5.10). (On this basis, the data for the three sites were pooled in Fig. 5.8 to simplify graphical presentation since interest was primarily on differences between cultivars for which the different sites provided replicated observations. In addition, site effects for fresh weight and final development were non-significant.) For 'Royal Rosa' and 'Sundrop', an early rise in number of buds beginning visible development during forcing was followed by a minima in early June which preceded the rise towards to final floral bud break proportion of 80-90% on July 31 (Fig. 5.8d i). By this time, bud break and development towards bloom was well advanced at all three sites. 'Royal Rosa' had reached 5% Bloom in each case while development of flower buds on 'Sundrop' and 'Trevatt' had reached stages between 'Cup' (Stage 2) and 'Red Bud' (Stage 5). Importantly, the fraction of buds developing on cuttings from 'Sundrop' trees remained low (10-25%) until after June 16. In contrast, significantly more buds (30-45%) began visible development on 'Royal Rosa' cuttings after the initial sampling on April 24. For 'Trevatt', however, bud break rose relatively quickly to over 40% by early June and then increased only slowly after that.

Results from the forcing of cuttings after cool-storage suggest similar conclusions as to relative chilling requirement though the absolute duration of chilling required is less clear
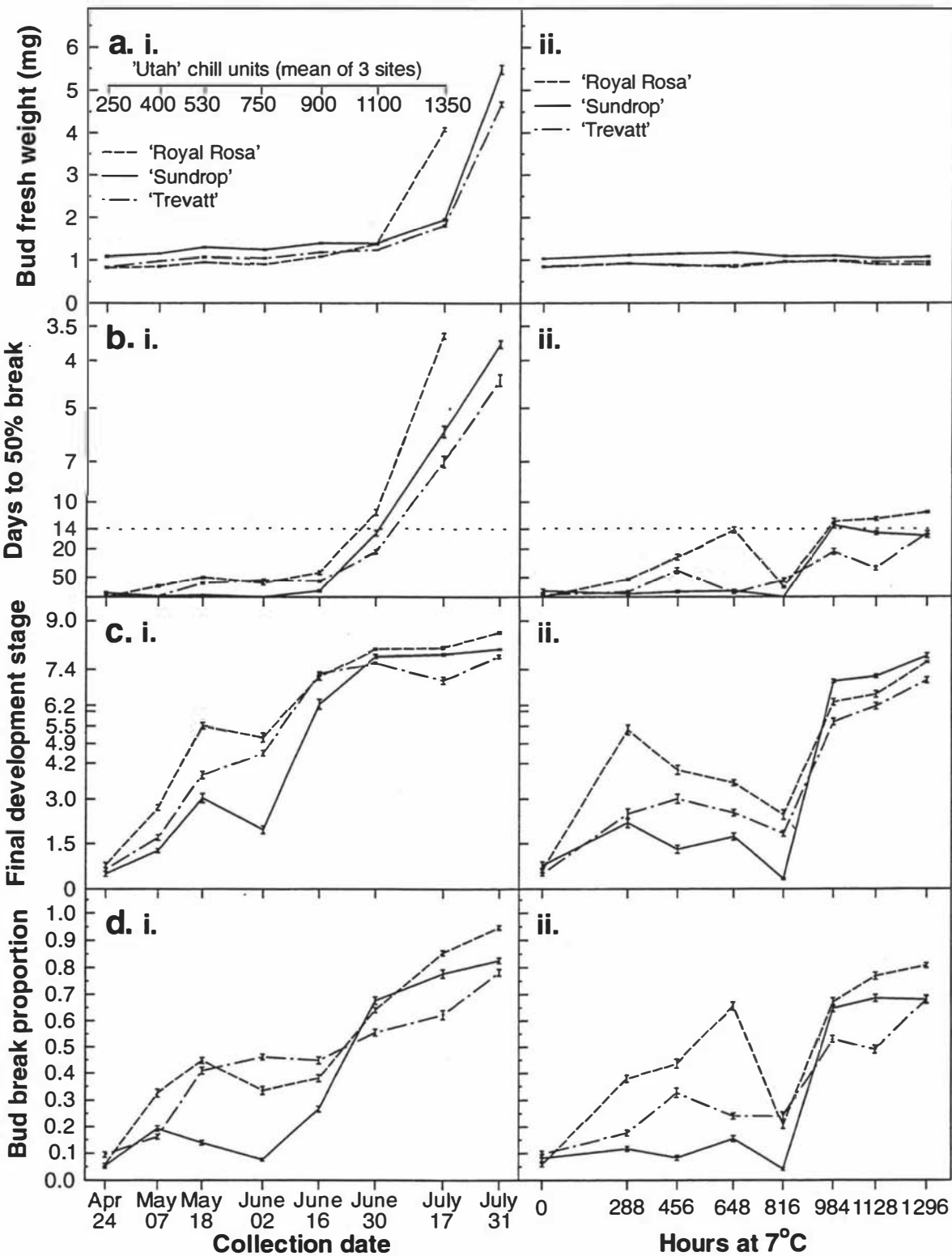
Figure 5.8   Flower bud development on 'Royal Rosa', 'Sundrop' and 'Trevatt' budwood from Campbell, Fernhill Farm and Stirling orchards. Mode of low temperature exposure: i). Natural winter conditions, 24 April- 31 July 1992; ii). Cool-storage at $7^{\circ}C$ from 24 April. a). Bud fresh weight at start of forcing; b). Days to 50% budbreak (plotted as reciprocal, days^{-1}); c). Final (maximum) bud development stage reached on adjusted numeric scale, 'Anthesis' = 6.2; d). Final proportion of buds showing visible growth. (Forcing temperature: $20^{\circ}C$. Means ±SE)

Table 5.10   Analyses of variance for bud break and development on cuttings of 'Royal Rosa', 'Sundrop' and 'Trevatt' floral budwood collected from Campbell, Fernhill Farm and Stirling orchards, 24 April to 30 June 1992 and forced at 20°C for four weeks.

Source	df	Bud fresh weight [z] Type III MS	Speed of bud break [y] Type III MS	Final bud dev. stage [x] Type III MS	df	Fraction of bud break [w] Type III MS
Model	20	33.24 ***	0.441 ***	54.49 ***	38	193.84 ***
Girth	1	0.49 ns	0.011 ns	0.52 ns	1	0.11 ns
Girth×Cultivar	2	1.85 ns	0.025 ns	2.11 ns	2	152.57 ***
Site	2	0.67 ns	0.371 ***	0.38 ns	2	44.61 ***
Cultivar	2	2.95 *	0.005 ns	4.99 *	2	153.91 ***
Site×Cultivar	4	2.19 ns	0.194 ***	2.49 ns	4	24.74 ns
Time	1	107.62 ***	3.790 ***	858.03 ***	1	556.56 ***
Time×Site	2	1.49 ns	0.396 ***	0.84 ns	2	48.60 *
Time×Cultivar	2	1.09 ns	0.201 **	6.17 ***	2	34.90 ns
Time×Site×Cultivar	4	0.50 ns	0.199 ***	2.90 ns	4	9.50 ns
Time^2	-	-	-	-	1	308.33 ***
Time^2×Site	-	-	-	-	2	38.18 *
Time^2×Cultivar	-	-	-	-	2	60.72 **
Time^2×Site×Cultivar	-	-	-	-	4	6.02 ns
Time^3	-	-	-	-	1	312.33 ***
Time^3×Site	-	-	-	-	2	31.10 ns
Time^3×Cultivar	-	-	-	-	2	93.18 ***
Time^3×Site×Cultivar	-	-	-	-	4	7.01 ns
Residual: Error	196	0.94	0.032	1.23	169	11.79
R^2		0.65	0.84	0.82		0.80
Estimate comparisons: Intercept, b_0 [v]						
'RR' – 'Sd'	1	-0.14 ns	0.27 ns	5.24 **		
'Tv' – 'Sd'	1	-0.36 *	0.23 ns	2.50 ns		
Stirling – others	1	0.02 ns	0.58 ***	-0.27 ns		
Campbell – Fernhill	1	-0.03 ns	0.01 ns	0.13 ns		
Estimate comparisons: Slope, b_1 [v]						
'RR' – 'Sd'	1	0.0022 ns	0.022 ***	0.078 ns		
'Tv' – 'Sd'	1	0.0014 ns	0.019 ***	-0.010 ns		
Stirling – others	1	-0.0018 ns	-0.027 **	-0.021 ns		
Campbell – Fernhill	1	0.0002 ns	-0.005 ns	-0.008 ns		

ns, *, **, ***   Variance components and regression intercept contrasts non-significant or significant at $P<0.05$, $P<0.01$ and $P<0.001$ respectively for fixed effects analysis of variance.

[z] Analysed as $\sqrt{}$(bud fresh weight at start of forcing).

[y] Analysed as $\log_e$(1/ days to 50% bud break at 20°C). Smaller values = slower bud break.

[x] Final (maximum) adjusted numeric bud development stage reached during four weeks of forcing at 20°C.

[w] Final (maximum) fraction of buds breaking during four weeks of forcing, analysed as normits.

[v] Performed as paired t-tests on parameters for transformed data.

(Fig. 5.8 i vs ii). The development of buds on 'Sundrop' cuttings, expressed using each
of the three development indices (speed of bud break, final development stage and
fraction of bud break) displayed a marked change after exposure to 900 hours at 7°C
(Fig. 5.8b-d). This duration of chilling was additional to possible chilling accumulated
during the period preceding budwood collection on April 24 (calculated by the
MAGICCU programme on the basis of air temperature data for each site). After 900 h
at 7°C, bud break on 'Sundrop' cuttings was reached within approximately 14 days
(Fig. 5.8b ii), final development rose dramatically from near zero to 'Petal Fall'
(Fig. 5.8c ii) and bud break proportion from under 10% to almost 70% (Fig. 5.8d ii).
These figures may, however, exaggerate the magnitude of the transition since bud
development was unexpectedly poor for the cuttings forced after 816 h at 7°C. For
'Royal Rosa' and 'Trevatt' a clear transition from dormancy was only seen in the trends
presented by the final development index. This again coincided with 900 h at 7°C.
However, before 900 h, buds of both 'Royal Rosa' and 'Trevatt' developed more
frequently, faster and further than did those of 'Sundrop'. Buds on 'Royal Rosa' budwood
displayed the greatest capacity for development. 'Sundrop' buds were larger at the start
of forcing than those of 'Royal Rosa' and 'Trevatt' by 10-20% throughout the 7°C storage
period (Fig. 5.8a ii). Bud fresh weight did not increase significantly during this time.

A fourth index of development investigated as a measure of dormancy alleviation was
the rate of bud development displayed after buds had begun visible movement. However,
collection date and duration of cool-storage had no effect on the development rate of
buds which progressed at least two nominal stages (i.e. beyond Stage 2, 'Cup'). Most
developing buds progressed at rates of between 0.4 and 0.6 adjusted scale units per day,
irrespective of previous duration of low temperature exposure. The main effect of low
temperature was therefore on capacity to start visible development at 20°C (fraction of
bud break), on the speed with which this occurred (speed of bud break) and on the extent
of development once started (final development stage, cf Table 5.10). Thus, the dormant
physiological condition did not appear to have a persistant effect on buds once
development was able to begin.

If any of the developmental indices calculated from budwood forcing are related to
changes in the temperature response then it might be expected that it will be related to

Table 5.11 Equation and analysis of variance for multiple regression of date of bud break for 'Royal Rosa', 'Sundrop' and 'Trevatt' flower buds at Campbell, Fernhill Farm and Stirling orchards, July 1992, on date of leaf fall and parameters describing bud development at 20°C.

Regression equation for date of bud break pooled over cultivars

$$y = 109.7 + 0.417\,x_1 - 36.2\,x_2 \qquad \text{where } y = \text{date of bud break, March 1} = \text{day 1}$$

Source	Cultivars pooled		Cultivars separate	
	df	Type II MS	df	Type II MS
Intercept (x_0)	1	2189.90 ***	1	2086.23 ***
Cultivar	-	-	2	30.67 ns
Regression	2	209.8 **	2	112.59 *
Date of 50% Leaf-fall (x_1) [z]	1	165.1 **	1	64.22 +
Bud break proportion (x_2) [y]	1	213.9 **	1	47.06 +
Residual: Error	6	11.18	4	9.11
R^2		0.86		0.92

ns, +, *, **, *** Variance components non-significant or significant at $P<0.1$, $P<0.05$, $P<0.01$ and $P<0.001$ respectively.

[z] Expressed as Julian date (March 1 = day 1).

[y] Average bud break proportion for May 7 and May 18 budwood collections.

date of bud break in the field for each of the nine cultivar / site combinations. Similarly, if the fulfillment 'Utah' chill unit requirements is physiologically significant then early chilling requirement fulfilment should be presaged by more advanced development as measured by forcing development indices. Multiple regression of date of bud break on regression parameter estimates for bud fresh weight, speed of bud break and final development stage, plus the average bud break fractions on budwood collected in May and June ('May bud break' and 'June bud break') was therefore performed. This indicated a significant relationship between date of bud break in the field (in July 1992) and the corresponding date of 50% Leaf Fall (in April) and 'May bud break' (Table 5.11). Other regression parameters were not significantly related to date of bud break. Overall (combining data for the three cultivars and sites) date of bud break in the field was delayed 0.4 day for each day's delay in date of 50% Leaf Fall and was advanced by 3.6 days for each 10% increase in bud break on cuttings collected in May. Parameter estimates were not significant at $P<0.05$ (though significant at $P<0.1$) when individual regressions were fitted for each cultivar using the same two parameters but since the overall pattern remained they suggested a similar relationship accounted for some variation between sites in date of bud break. Similar multiple regressions of 'end of rest'

dates predicted by the 'Utah' models on bud development parameters were non-significant. The particular bud physiological condition that determines the fraction of bud break on budwood collected in May (the begining of low temperature exposure in the field, Fig. 5.7b) therefore appears to influence time it takes to initiate visible development.

5.3.3.3   Accuracy of heat requirement estimates

Daily air temperature maxima and minima over the 4 weeks before 5% Bloom (the period of visible bud development) were similar for each cultivar (Table 5.12) but year to year variation was significant. On average, this period included 75% of heat accumulation to 5% Bloom for 'Royal Rosa', 62% for 'Sundrop' and 48% for 'Trevatt'. Heat units (above 4°C) accumulated at a rate of 100-150 GDH°C per day over this period. Year to year variation in average daily maxima was as high as 2.1°C for the period preceding 5% Bloom of 'Royal Rosa' (Fig. 5.9a i) and 3.4°C for that before 5% Bloom of 'Sundrop' .and 'Trevatt' (Fig. 5.9a ii,iii). Greatest variation in average daily minima was 3.4°C for 'Royal Rosa' and 2.1°C for 'Sundrop' and 'Trevatt' (Fig. 5.10a i-iii).

Analysis of variance of GDH°C sums had indicated that the estimates of heat required to reach 5% Bloom for each cultivar were significantly different (Table 5.6) but also that part of the imprecision associated with those estimates was due to a significant year effect on GDH°C sums. In some years the bud development on all three cultivars was relatively fast from estimated rest completion to 5% Bloom compared with to heat accumulation over the same period which lowered GDH°C sums below average. In other

Table 5.12   Analyses of variance for daily air temperature maxima and minima for the four weeks preceding 5% Bloom of 'Royal Rosa', 'Sundrop' and 'Trevatt' apricots, HNRC 1984-1991.

Source	df	Daily maxima Type IV MS	Daily minima Type IV MS
Model	9	33.04 ***	26.63 ***
Cultivar	2	13.06 ns	4.01 ns
Year	7	53.90 ***	43.42 *
Residual 1: Cultivar×Year	13	4.32 ns	11.79 ns
Residual 2: Error	621	5.99	11.38
R^2		0.16	0.08

ns,*,**,*** Variance components and contrasts non-significant and significant at $P<0.05$, $P<0.01$ and $P<0.001$ respectively for mixed model analysis of variance: Year = random effect.
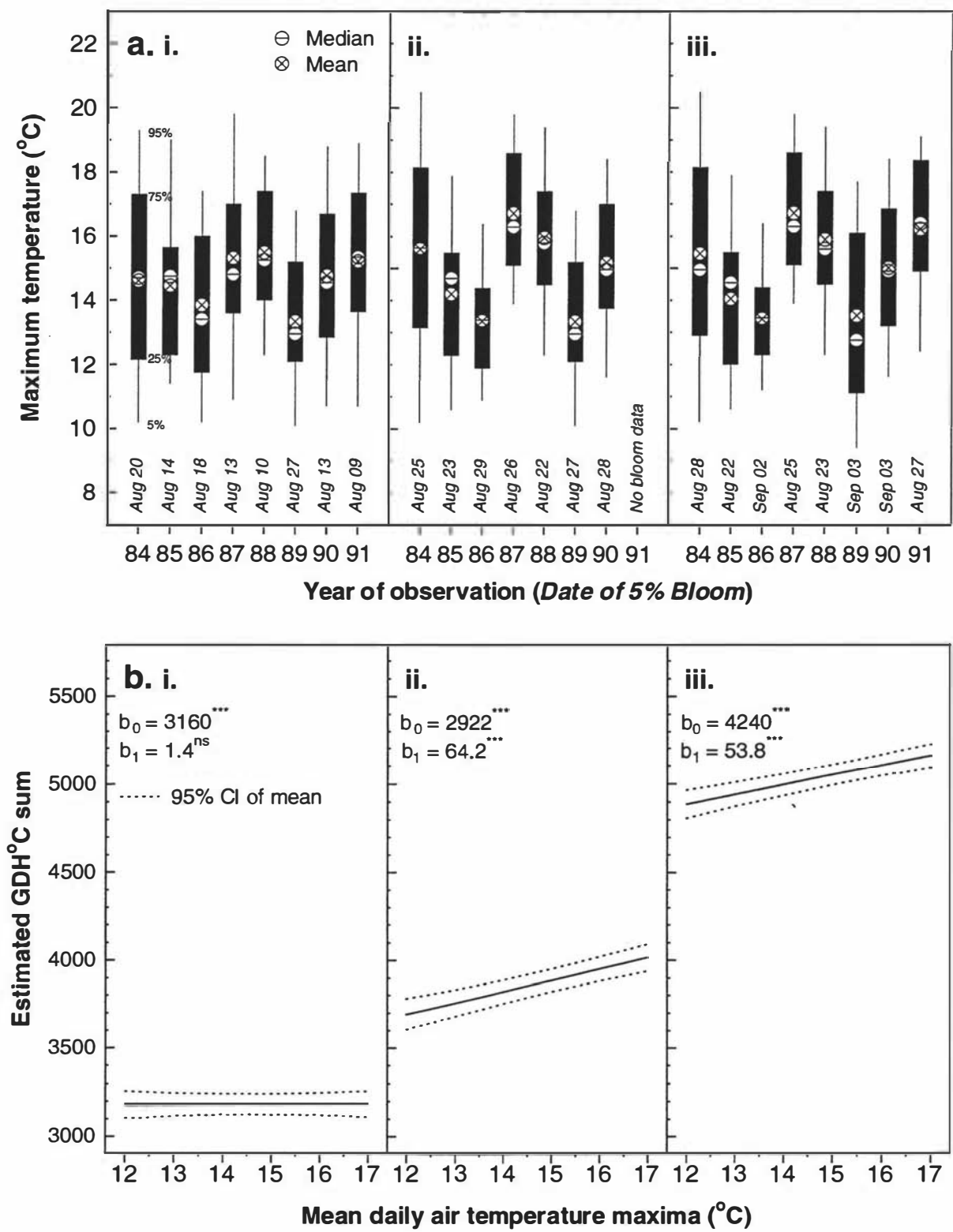
Figure 5.9   Distributions of daily air temperature maxima and their effect on $GDH^{\circ}C$ estimates of three 'Utah' chill unit models: Cultivars: i). 'Royal Rosa'; ii).'Sundrop'; iii). 'Trevatt'. a). Dates of 5% Bloom at HNRC from 1984 to 1991 and 'box and whisker' plots of daily temperature maxima for the preceding four week period.
b). Regressions of model $GDH^{\circ}C$ estimates for 5% Bloom on mean daily temperature maxima for the four weeks before 5% Bloom at HNRC, 1984-91. ([ns, ***]: Parameter estimates non-significant or significant at $P<0.001$.)
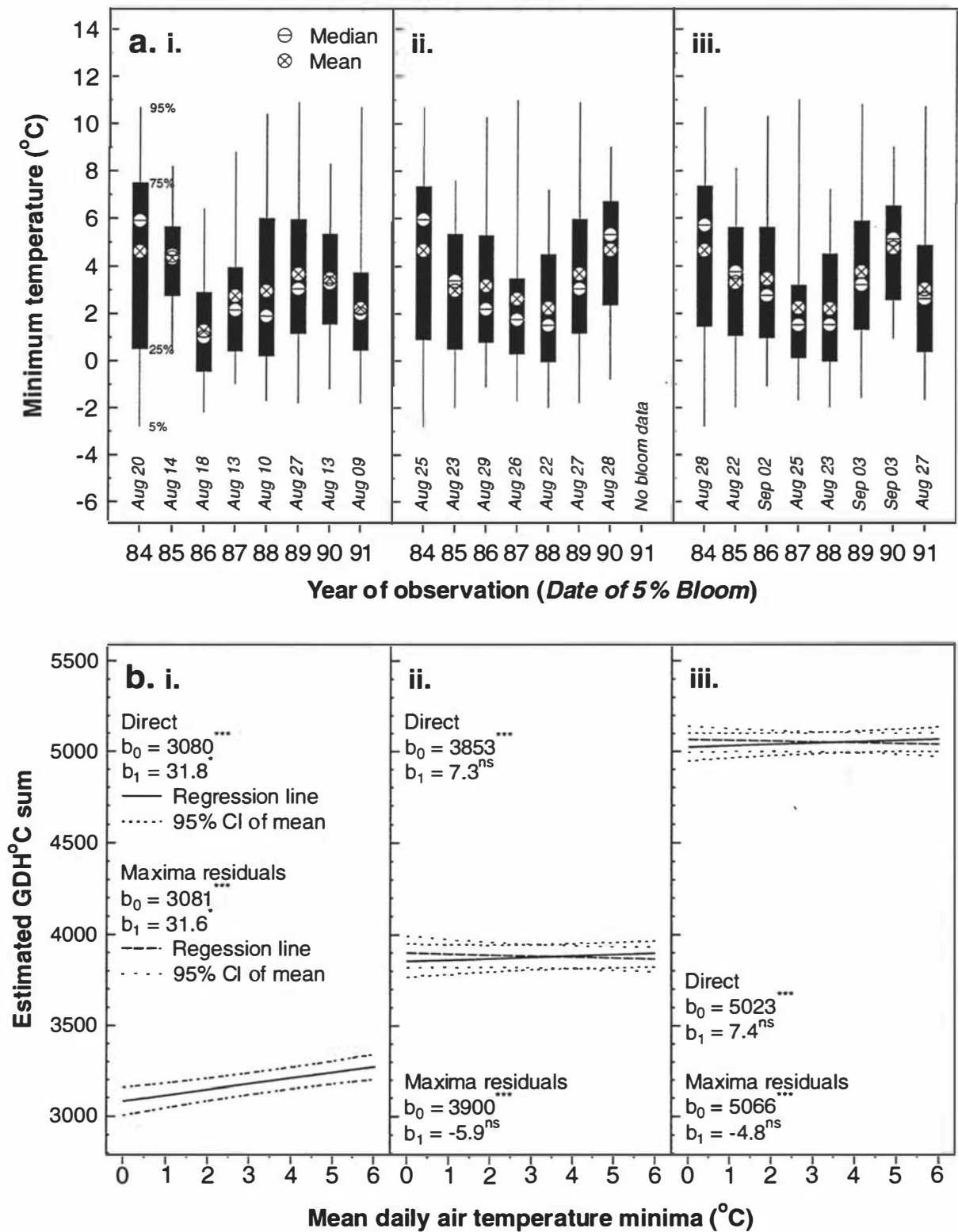
Figure 5.10   Distributions of daily air temperature minima and their effect on GDH$^{\circ}$C estimates of three 'Utah' chill unit models: Cultivars: i). 'Royal Rosa'; ii).'Sundrop'; iii). 'Trevatt'. a). Dates of 5% Bloom at HNRC from 1984 to 1991 and 'box and whisker' plots of daily temperature minima for the preceding four week period.

b). Regressions of model GDH$^{\circ}$C estimates for 5% Bloom on mean daily temperature minima for the four weeks before 5% Bloom at HNRC, 1984-91: Direct = regression of estimates on mean minima; Maxima residuals = regression of estimates on minima independent of maxima effect. ($^{ns, *,}$ *** : Parameter estimates non-significant or significant at $P<0.05$ and $P<0.001$ respectively.)

Table 5.13   Analyses of variance for linear regressions of GDH°C sums for 'Royal Rosa', 'Sundrop' and 'Trevatt' chill unit models on daily temperature maxima, daily minima and daily minima after removal of effect of maxima during the month preceding 5% Bloom at HNRC, 1984-1991.

Source	df	Daily maxima Type I MS	Daily minima Type I MS	Daily minima with maxima residuals [z] Type I MS
Model	5	81608872 ***	80177348 ***	549347 **
Cultivar	2	198990952 ***	198990952 ***	0 ns
Temperature	1	6748771 ***	1875397 **	397865 ns
Cultivar×Temperature	2	1656841 ***	514720 ns	1174435 **
Residual: Error	638	182190	193409	177884
R^2		0.78	0.76	0.02

[z]   Daily maxima and minima significantly correlated, $r = 0.25$, $P < 0.001$.
ns, **, ***   Variance components non-significant or significant at $P<0.01$ and $P<0.001$ respectively.

years, development of all three was relatively slow which raised GDH°C sums above average. In this regard, linear least squares regression showed that GDH°C sums were sensitive to both daily air temperature maxima and minima over the four week period that preceded 5% Bloom (Table 5.13). The regressions of GDH°C sum on daily maxima accounted for slightly more variation than those on daily minima ($P<0.25$). Regression of GDH°C sum residuals (from the regression on daily maxima) with daily minima also accounted for a significant portion of variation. This indicated that the effect of daily minima was independent of that of daily maxima and not merely due to the small but significant degree of correlation between daily maxima and minima ($r=0.25$, $P<0.001$).

The regressions showed that heat accumulation for 'Royal Rosa' was unaffected by daily air temperature maxima in the four weeks before anthesis (Fig. 5.9b i) whereas that for 'Sundrop' and 'Trevatt' showed a positive relationship (Fig. 5.9b ii,iii). Hence, for these two cultivars, GDH°C sums were relatively high in years when daily maxima were warmer than average during the pre-bloom period while, when they were low, GDH sums were also relatively low. The accuracy of the 'Sundrop' and 'Trevatt' models was therefore sensitive to variation in average daily temperature maxima during mid and late GDH°C accumulation to the order of about one day for every 2°C change of mean daily maximum from that of HNRC in 1984-1991 (14.4°C). The accuracy of the 'Royal Rosa' model appears less sensitive in this respect.

Daily minima during the four weeks before bloom did not affect heat unit accumulation to bloom for 'Sundrop' and 'Trevatt' whether or not the effect of daily maxima was first removed (Fig. 5.10b ii,iii). However, for 'Royal Rosa', GDH°C accumulation was positively related to mean daily minima, years with higher minima being associated with higher GDH°C sums (Fig. 5.7b i). The relationship between GDH°C sum and daily minima was maintained after the removal of the effect of daily maxima. Therefore, heat units accumulated rapidly relative to actual flower development in years with high minima, while, in cool years, heat unit accumulation was relatively slow. However, the 'Royal Rosa' model proved less sensitive to temperature variation than the 'Sundrop' and 'Trevatt' models, the error for 'Royal Rosa' being only one day for every 3-4°C variation in temperature minima.

Comparison of actual rates of bud development at Campbell, Fernhill Farm and Stirling orchards in 1992 with that predicted by air-temperature based GDH°C also suggested that the heat unit index used did not accurately predict actual development. In 1992, first bud development on 'Royal Rosa', 'Sundrop' and 'Trevatt' apricots was observed in late June at Campbell and Fernhill Farm orchards on the Heretaunga Plains (Fig. 5.11.a i&ii), and about two weeks later at Stirling Orchards, Bayview (Fig. 5.11 a iii). Analysis of variance indicated that regressions of adjusted phenological stage data against chronological time accounted for the majority (91%) of observed variation (Table 5.14). When the regressions were performed against cumulative GDH°C from 16 June (the date of first bud observations and approximately coincident with predicted 'end of rest') the variation accounted for by the regression on time did not increase (Table 5.14) but instead declined slightly. Reduced linearity is particularly noticeable for 'Trevatt' at Fernhill Farm orchard (Fig. 5.11b ii) and all three cultivars at Stirling Orchards (Fig. 5.11b iii). This was the reverse of the situation expected if GDH°C accumulation accurately weighted the passage of time for the rate of bud development at temperatures experienced. Air temperature-based heat accumulation above a 4°C base temperature was therefore not accurately simulating the rate of apricot buds as the rate of actual development did not relate closely to day-to-day variation in GDH°C accumulation.

Furthermore, comparison of observed flower bud development at Campbell, Fernhill Farm and Stirling orchards in 1992 with predicted development also indicated that
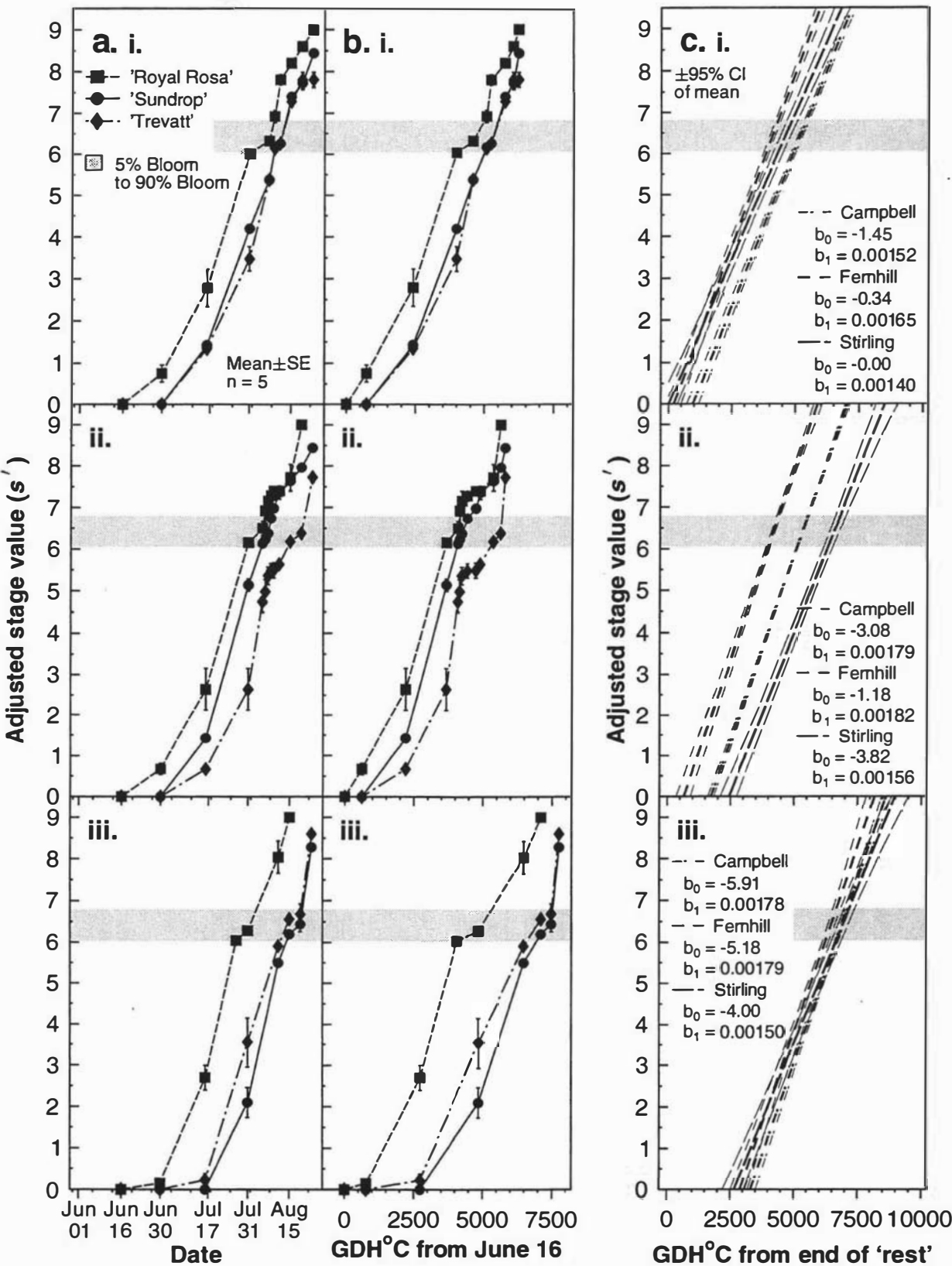
Figure 5.11   Progress of flower bud development on 'Royal Rosa', 'Sundrop' and 'Trevatt' apricots at three Hawkes Bay orchards, June to September 1992.

a). Chronological development. Orchards: i. Campbell; ii. Fernhill Farm; iii. Stirling.

b). Thermally-weighted development (GDH°C). Orchards: i. Campbell; ii. Fernhill Farm; iii. Stirling.

c). Development from end of 'rest' date predicted by 'Utah' chill unit models. Cultivars: i. 'Royal Rosa'; ii. 'Sundrop'; iii. 'Trevatt'.

Table 5.14   Analysis of variance for effects of orchard and cultivar on rates of flower bud development on 'Royal Rosa', 'Sundrop' and 'Trevatt' apricots at three Hawkes Bay orchards, June to September 1992.

Source	df	Chronological days Type III MS	GDH°C from June 16 Type III MS	GDH°C from end of 'rest' Type III MS
Model	17	125.11 ***	124.17 ***	124.17 ***
Orchard	2	5.23 ***	6.98 ***	2.70 ***
Cultivar	2	7.30 ***	29.00 ***	40.33 ***
Residual 1: Orchard×Cultivar	4	0.23 ns	1.64 ***	2.92 ***
Time	1	1875.63 ***	1815.70 ***	1815.70 ***
Time×Orchard	2	4.47 ***	5.04 ***	5.04 ***
Time×Cultivar	2	2.88 ***	3.21 ***	3.21 ***
Time×Orchard×Cultivar	4	0.14 ns	0.18 ns	0.18 ns
Residual 2: Error	362	0.28	0.33	0.33
R^2		0.95	0.95	0.95

ns, ***   Variance components non-significant or significant at $P<0.001$.

cultivar-specific GDH°C estimates did not relate closely to the actual duration of visible bud development. The conceptual model which underlies the use of chill units makes the assumption that bud development does not begin until the required duration of 'chilling' is experienced. From this point, buds become responsive to warm (>15°C) temperatures and the speed with which buds reach the phenological stage of interest is reflected in the size of the GDH°C estimate. Low GDH°C estimates imply rapid development from 'end of rest' and higher GDH°C estimates imply slow development. Hence, since 'Royal Rosa' has the lowest GDH°C estimate (3180 GDH°C), development of 'Royal Rosa' buds from predicted 'rest' completion to bloom should be the most rapid while that of 'Trevatt' buds (5050 GDH°C) should be the slowest.

This was not the case for the three cultivars observed in 1992 at the three Hawkes Bay orchards. The CU and GDH°C estimates for the three 'Utah' chill unit models suggest that 'Royal Rosa', 'Sundrop' and 'Trevatt' have similar chilling requirements whereas the heat requirements for bloom differ significantly (Fig. 5.5). Hence, if the models accurately describe flower bud development on the three cultivars then variation in the rate of bud development should be visible in the field. However, ninety percent of the variation observed in date of 5% Bloom at the three orchards in 1992 was accounted for

Table 5.15   Rates of bud development of 'Royal Rosa', 'Sundrop' and 'Trevatt' apricot flower buds at Campbell, Fernhill Farm and Stirling orchards, 16 June to 23 August 1992.

Cultivar	Development rate [z] (Stage / 1000 GDH°C)		Orchard	Development rate (Stage / 1000 GDH°C)	
'Royal Rosa'	1.52	a	Campbell	1.70	a
'Sundrop'	1.72	b	Fernhill Farm	1.75	a
'Trevatt'	1.69	b	Stirling	1.49	b

[z]   Means within columns followed by different letters significantly different at $P<0.05$.   Separation by Ryan-Einot-Gabriel-Welsch multiple range test.

by variation in date of bud break leaving the remainder (only 10%) due to differences in bud development rate. Average rates of development for the three cultivars in the field were visibly similar (Fig. 5.11c i-iii). Bud development rates for 'Sundrop' and 'Trevatt' which differ by 30% in their GDH°C estimates were the same, and together were significantly higher (instead of lower) than those for 'Royal Rosa' (Table 5.15). Development rates also varied significantly between sites and were slower for each 1000 GDH°C accumulated at Stirling orchards than at the other two sites. The difference in development rates between 'Royal Rosa' and the other two cultivars and Stirling Orchards and the other two sites represented up to 5-6 days difference in the time required to reach 5% Bloom from the date of bud break.

In contrast, the delay between predicted 'end of rest' and first visible bud development was very variable, both between cultivars and between orchards. For 'Royal Rosa' and 'Sundrop', bud break occurred, on average, 650 and 1729 GDH°C after predicted 'end of rest' (Table 5.16), significantly less than for 'Trevatt' which on average broke bud

Table 5.16   Dates of bud break for 'Royal Rosa', 'Sundrop' and 'Trevatt' apricots at three Hawkes Bay orchards in 1992 and GDH°C sums from predicted 'end of rest' to bud break.

Orchard Cultivar	Date of bud break in 1992 [z]			GDH°C from predicted 'end of rest'			
	Campbell	Fernhill	Stirling	Campbell	Fernhill	Stirling	Mean [y]
'Royal Rosa'	26 June	26 June	29 June	1191	488	270	650 a
'Sundrop'	8 July	4 July	17 July	2022	911	2253	1729 a
'Trevatt'	9 July	11 July	14 July	3545	3097	2591	3078 b
LSD$_{(0.05)}$			11 days			1575	

[z]   Dates and GDH°C sums calculated as x-axis intercepts of linear regressions of adjusted bud development stage on chronological and thermal time (GDH°C accumulation).
[y]   Means followed by different letters significantly different at $P<0.05$. Means separation by Ryan-Einot-Gabriel-Welsch multiple range test.

3078 GDH°C after predicted 'end of rest'. Variation within delay figures was also substantial, being as high as 1000 GDH°C between the lowest and highest figures for each cultivar. The difference between observed and predicted development therefore strongly suggests that the 'Utah' chill unit models derived from HNRC bloom data do not accurately describe the phenology of apricots at other orchards in Hawkes Bay.

5.4   Discussion

This study was intended to determine whether 'Utah' chill unit-based models of bloom phenology accounted satisfactorily for cultivar and orchard differences in the times of bud break and bloom of 'Sundrop', 'Royal Rosa' and 'Trevatt' apricots in Hawkes Bay. This objective was assisted by the use of phenological regression to describe bud development based on a phenological scale which took account of different stage durations. Adjustment of scale values does not appear to have been performed in other phenological studies. Stage differentiation is generally based on readily distinguishable morphological or physiological characteristics rather than the passage of time (Gepts, 1987) and most, if not all, established scales use alphabetic or evenly-spaced numeric scale values (Brown and Abi-Fadel, 1953; Fleckinger, 1955; Gepts, 1987; Guerriero et al., 1986; Tabuenca, 1968). Consequently, the unadjusted (nominal) scales are inherently non-linear (Guerriero et al., 1986; Tabuenca, 1968) and apparent rates of development (expressed as scale stages per unit time) vary throughout the scale making comparisons between relative rates of development difficult. Stage value adjustment to reflect actual rates of passage through stages addresses this issue by equalising the apparent development rate under constant temperature conditions over the range of the scale. Use of the resulting adjusted scale under varying temperature conditions is then meaningful so long as it may be assumed that the response of development rate is substantially the same over the range of the scale. This assumption appears reasonable for the limited developmental distance (bud break to just beyond bloom) covered by the scale used in this study.

Scale adjustment based on the ratio of observed and expected frequencies at constant temperature has application to many types of phenological development, and the required manipulation is very simply performed prior to (and as an integral part of) standard statistical analysis. In this study it had three significant consequences. Adjustment of numeric phenological scales for bud development of 'Royal Rosa', 'Sundrop' and 'Trevatt' effectively linearized apparent development rates as illustrated by the progress of bud development at the three orchards in 1992 (Fig. 5.11a i-iii). By this means unbiased estimates of actual first visible bud development could be made by extrapolation to the x-axis (development stage = 0) with reasonable precision (±5.5 days or better) even

though visits to orchards in the early period of bud break were made only every two weeks. The technique allowed unbiased comparison of development rates between collections despite limited development by earlier collections and indicated that final bud development reached by buds forced at 20°C increases almost linearly from late April to late June (Fig. 5.8c i). Scale adjustment therefore facilitates analysis of phenological data series, especially in relation to the calculation of development rates and interpolation between known points. In addition, it should make simulation of bud development easier since the entire course of bud development may be described in the form of a single linear equation, using chronological or thermally-weighted time as independent variables.

The chill unit models for 'Royal Rosa', 'Sundrop' and 'Trevatt' were unexceptional when compared with other previously published models. The chill requirements estimated by minimization of error C.V. (900, 950 and 800 CU for 'Royal Rosa', 'Sundrop' and 'Trevatt' respectively) are similar to figures previously published for European and American apricots which typically require 700 to 1200 hours below 7°C to initiate normal spring bud development (Brown and Abi-Fadel, 1953; Tabuenca, 1968,1979) or 700 to 1300 CU (Ashcroft et al., 1977; Bailey et al., 1982; Tabuenca, 1979). The corresponding heat requirements (3180, 3880 and 5050 GDH°C) were also very similar to those reported for 'Tilton' apricot and other deciduous fruit species (Ashcroft et al., 1977). The poor precision of the models was disappointing as was their accuracy when they were used to predict bloom dates in other Hawkes Bay orchards (Fig. 5.5b i-iii). However, here again model performance was similar to that achieved by other 'Utah' models for *Prunus* species. Chill unit accumulation did not accurately predict apricot bud development under fluctuating temperature conditions in New Jersey (Bailey et al., 1982). Model precision was also limited for the original chill unit models published. For instance, error C.V. ranged from 9.9% to 13.6% for the apricot, plum, peach and cherry models presented by Ashcroft et al. (1977), equivalent to the range observed for the Hawkes Bay models.

The models may have served the purpose of pollenizer selection if they had proved capable of predicting relative times of 5% Bloom (bloom divergence) of pairs of cultivars with an accuracy that was within the timeframe likely to affect pollen transfer. In this situation absolute accuracy of prediction is less important than reliable simulation of the

relative flowering behaviour of different cultivars. However, as Table 5.7 shows, the models proved no more accurate when assessed on the basis of predicted bloom divergence whether data were back-predictions (HNRC, 1984-1990) or independent tests (Campbell, Fernhill Farm and Stirling orchards, 1992). In 5 of 18 instances divergence errors were at least a week (in some cases considerably more), sufficiently large an error to seriously affect the reliability of predicted pollenizer pollen-flow to 'Sundrop'.

In does not appear that much of the imprecision and inaccuracy is attributable to differences in orchard conditions and management. Different rootstocks as well as use of growth regulators can affect time of bud break (Kaska, 1978; Tabuenca, 1976) but in this study all trees were reported to be on peach rootstocks and only one group ('Royal Rosa' at Stirling orchards) had been treated with a growth regulator (Cultar). Flower buds on different branch types differed in their times of bloom (Fig. 4.6) and bud break (Fig. 5.6) but, since the models predicted 5% Bloom, it is not likely that pruning regimes which altered the number of later blooming buds on long extension shoots would have affected accuracy. In addition, such differences do not account for errors in back-predictions onto the HNRC data set. The small size of flower buds on long extension shoots in comparison with those on spurs suggested that bud size might underlie some of the difference in bud break timing. However, multiple regression of dates of bud break on a range of developmental indices indicated that fresh weight did not account for a significant proportion of the variation in date of bud break, whether or not the overall cultivar effect on date of bud break was first removed (Table 5.11).

Furthermore, the forcing studies (Figs. 5.6 & 5.8) showed that flower bud development in Hawkes Bay prior to bud break is comparable to that observed in other apricot growing regions. The large variation in bud fresh weight was very similar to that of 'Reale d'Imola' (Guerriero et al., 1986), as was the rise in bud weight in relation to date and estimated chill requirement (Brown and Kotob, 1957; Guerriero et al., 1986; Tabuenca, 1964,1968). Time to 50% Bud Break was similar to that observed for other apricot cultivars in other regions (Carraut, 1968; Guerriero et al., 1986) and final level of bud break attained when flower buds were forced was ultimately as good, if not better than observed in other studies (Carraut, 1968; Guerriero et al., 1986; Guerriero and Bartolini, 1991; Scalabrelli et al., 1991). Other forcing experiments have also produced

the 'peak-then-dip' pattern of final bud break proportion (Carraut, 1968; Guerriero and Bartolini, 1991) although the reason for this phenomenon is not clear.

The difference between model predictions and observed bud development also cannot be attributed to inadequate winter chilling in Hawkes Bay orchards. The survey of chill accumulation (using chill hour and 'Utah' chill unit indices) showed that while numbers of chill hours varied considerably amoung Hawkes Bay sites, chill unit sums were relatively stable (Fig. 5.4). Comparison of chill and chill unit figures indicated that around 800 h below 7°C had accumulated by mid-June under Hawkes Bay conditions or around 1200 CU. By these indices, chilling accumulation in Hawkes Bay was similar to that at other coastal New Zealand sites. Differences in accumulated chilling only grew as climates diverged markedly from that of Hawkes Bay. Thus, whereas patterns of accumulation at Fresno and Bendigo were similar to Hawkes Bay, that for Penticton was markedly different. Some caution, however, is needed in interpreting the chilling estimates since accumulations were based on monthly mean temperatures. For instance, average chill unit accumulations for Havelock North, Hastings and Napier Airport were practically identical (Fig. 5.4a iv) whereas chill unit sums calculated from hourly tempera-tures in 1992 (Fig. 5.7b i) indicate less chill accumulation at Stirling orchards near the sea than at Campbell and Fernhill Farm orchards further inland on the Heretaunga plains.

A more significant source of error may be the use air temperature to approximate bud temperatures for calculation of chilling and heat unit accumulation. This is indicated by the effect of daily temperature maxima in the four weeks preceding bloom of 'Sundrop' and 'Trevatt' on the size of GDH°C estimates from the predicted 'end of rest' to 5% Bloom. For these cultivars, GDH°C summation above a base temperature of 4°C is sensitive to variation in the temperature conditions under which summation occurs. This is possibly the result of the elevation of actual bud temperature above air temperature (Landsberg et al., 1974) which probably alters the apparent response of development to temperature (Fig. 5.12). Where bud development has a temperature optimum within the range of bud temperatures normally experienced then elevation of bud temperatures during the day by radiant heating (and, to a lesser extent, depression of bud temperatures at night due to radiant cooling) will alter the effective base temperature for GDH°C
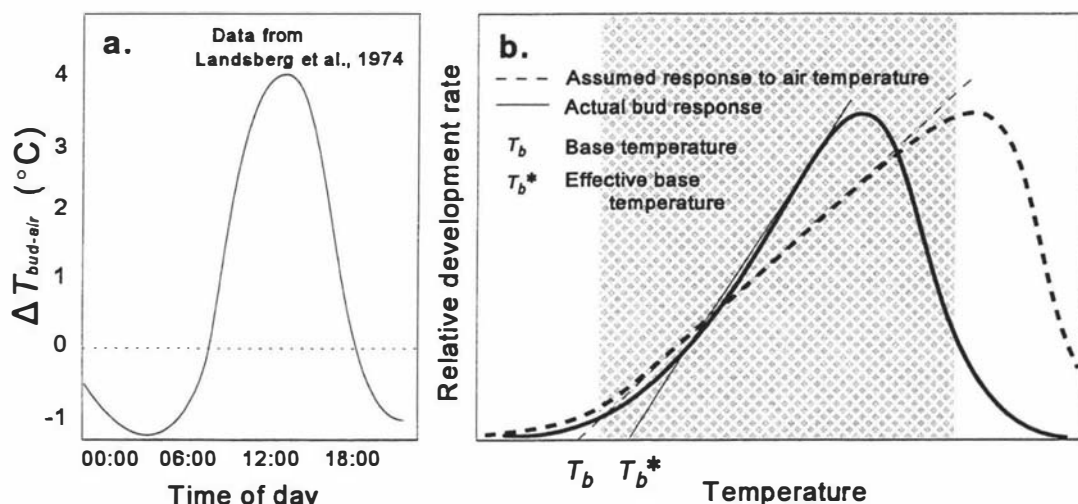
Figure 5.12   Divergence of bud temperature from air temperature and probable effect on the apparent relationship between temperature and development rate.
a.   Diurnal cycle in the difference of bud temperature from air temperature.
b.   Raising of effective base temperature for GDH°C accumulation due to effect of air/bud temperature divergence on apparent response of development rate to temperature.

accumulation in the manner shown. Greater acceleration of the development of 'Sundrop' and 'Trevatt' flower buds by warm temperatures relative to the response of 'Royal Rosa' may therefore mean that a base temperature of 4°C is too low for 'Sundrop' and 'Trevatt'. Likewise, it is possible that faster development of 'Royal Rosa' buds at low temperatures relative to that of 'Sundrop' and 'Trevatt' could account for its characteristic early blooming as well the greater influence of daily temperature minima on heat unit sums for 5% Bloom of 'Royal Rosa' (Fig. 5.10). The use of air temperature to calculate chill units is probably also biased by excessive accumulation of chill units at temperatures above the optimum chilling temperature caused by the heating of buds above air temperature (Lombard and Richardson, 1979).

Additional error may be due to the inaccurate prediction of the timing of emergence of buds from dormancy. Results of the forcing experiments failed to show a consistent transition in developmental potential that might be interpreted as evidence for a relatively discrete physiological change induced by a critical duration of low temperature (chilling) as assumed by the 'Utah' model. Increase in bud fresh weight has been used in the past as an index of dormancy for apricots (Tabuenca, 1964; Tabuenca, 1968). By this index, buds collected from Hawkes Bay in 1992 showed signs of a transition around June 30 which could be interpreted as the end of dormancy. This corresponded to the accumulation to 900-1000 CU (Fig. 5.8a). Time to 50% bud break reached 14 days, a

long-established threshold value (Samish, 1954), at around this time (Fig. 5.8b). Comparison with field bud development collected at the same time as forcing was performed (Fig. 5.11a) indicates that these transitions coincided with bud break in the field or immediately preceded it. This close relationship is clearly to be expected with bud fresh weight but the increased speed of bud break could be interpreted as a sign of the physiological change which made bud break possible. Speed of bud break, measuring the initial rate of development, might therefore be a sensitive index of dormancy alleviation since, in Hawkes Bay, sufficient heat is present even in mid-winter to permit growth as soon as it is possible. However, if this is the case, then it would be necessary to assign 'Trevatt' the highest chill requirement of at least 1000 CU, with 'Sundrop' and 'Royal Rosa' requiring progressively less chilling. This is a quite different pattern to that of the model estimates.

However, if final extent of development is used as an index of dormancy alleviation then the relative timing of the transition for dormancy of the three cultivars is again different. This index assumes that the extent of development at what is otherwise a growth-promoting temperature is dependent on the alleviation of an enduring effect of endodormancy which persists after the initiation of growth. An example of this effect is the phenomenon of 'physiological dwarfism' due to insufficent chilling of peach seeds (Frisby and Seeley, 1993a). Similar effects on growth of shoots have been interpreted in terms of gibberellin biosynthesis (Frisby and Seeley, 1993b), in the movement of nutrients towards and within the bud tissues (Gendraud and Lafleuriel, 1983) or in other metabolic changes necessary for sustained growth (Balandier et al., 1993b). By this index, the chilling requirement of 'Trevatt' flower buds is intermediate to those of 'Royal Rosa' (lowest) and 'Sundrop' (highest). A similar sequence of relative chilling requirement was suggested by final bud break proportion (Fig. 5.11d i). The data suggest early, though partial, alleviation of endodormancy for 'Royal Rosa' and 'Trevatt' after accumulation of as little as 400-500 CU whereas significant alleviation for 'Sundrop' only begins to occur after the accumulation of around 900 CU. Of the statistics describing the change in these indices between April 24 and June 30, only the average bud break on forced cuttings collected in May was significantly related to the date of bud break ultimately observed in the field in late June to early July (Table 5.11). This difference could reflect the different climates under which the three cultivars were selected but,

whatever the case, the relative pattern of bud break potential presented by these two indices during this period again did not match the relative chill requirements estimated statistically for the 'Utah' models.

These results are able to be compared with the statistically-derived estimated of chill requirement so long as the development of forced buds provides a valid picture of the physiological status of buds in the field. However, several aspects of the forcing technique, as generally used, mean that comparisons must be done with care. First, the constant temperature conditions used for forcing are quite unlike those experienced naturally by buds. Varying forcing conditions can alter the proportion as well as the speed of bud break (Latimer and Robertaille, 1981) and hence this factor alone could distort results, especially at higher temperatures ($25°$-$30°C$). Second, the cuttings used (10-15 cm, 10 flower buds) are also relatively small explants and the process of removal from the rest of the plant may itself alter the potential response of the buds (Latimer and Robertaille, 1981). This appears not to be due to wound-induced ethylene (Paiva and Robertaille, 1978) but rather to removal of relationship with the rest of the plant. The implications of removal from the whole plant then depend on whether it is considered that correlative influences are integral to dormancy induction and maintainance (Dennis, 1994). Third, it is not immediately clear which of the five developmental indices used in this study (maximum extent of development, its rate before visible bud growth and its continuing rate afterwards, the population fraction undergoing development and change in bud fresh weight) is most closely linked to changes in temperature response during dormancy alleviation since we still lack an adequate understanding of the physiology of dormancy.

Despite this, the results of the forcing studies still do not appear to support the statistically-derived chill requirements. These model parameters may therefore have little physiological significance apart from a coincidental association with the general period of early bud break. Chill unit accumulation did not accurately predict the initiation of bud development in late winter / early spring and since this was the major determinant of time of bloom then model inaccuracy is probably largely a result of the inability of the chill unit index to accurately simulate alleviation of apricot flower bud endodormancy. The physiological meaning of the $GDH°C$ estimate determined for each

of the apricot cultivars is therefore also unclear. For 'Sundrop' and 'Trevatt', the periods following estimated 'end of rest' incorporate time during which buds are still dormant as well as a later period of active development normally associated with heat unit accumulation. The validity of the assumption of constant temperature response throughout the period of GDH°C accumulation (Wang, 1960) is therefore questionable. The delay between calculated 'end of rest' and observed bud break did not relate to bud fresh weight or length of pistil (Table 5.12) since these were both smallest for 'Royal Rosa', the earliest cultivar, and greatest for 'Sundrop' which was intermediate in timing. Rates of visible bud development (Table 5.14) were also unrelated to GDH°C requirements estimated statistically from the HNRC data set. These vary by up to 1870 GDH°C (over 50% of the heat requirement for 'Royal Rosa') which contrasts with the small proportion of variation in date of bloom attributable to development rate independent of date of bud break. This again suggests that the chill unit model parameters are arbitrary and non-physiological.

Therefore, in conclusion, this study demonstrated that phenological models based on 'Utah' chill unit accumulation were unable to accurately simulate apricot flower bud development and bloom phenology under Hawkes Bay conditions. Model inaccuracy appeared to result from i): failure of chill unit accumulation to adequately predict the initiation of bud development in late winter / early spring and ii): failure of heat unit accumulation to adequately simulate bud response to environmental conditions once development had begun. The poor accuracy and low precision may in part be attributable to the use of air temperature in place of actual bud temperature to simulate bud development. However, lack of unequivocal evidence for a consistent, defined transition from bud endodormancy (which would support the assumptions underlying the 'Utah' model) suggests that the biphasic nature of models utilising 'Utah' chill units as an index of endodormancy alleviation is not suited to simulation of apricot bloom phenology in Hawkes Bay.

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Chapter 6
A Bud Dormancy Model Proposal

6.1 Introduction

Phenological models could provide an efficient method to assess pollenizer suitability if reliable prediction of relative apricot bloom phenology were possible. Such models could be established on the basis of historical bloom records or the results of budwood forcing. However, the accuracy and precision of 'Utah' chill unit models proved unsatisfactory (Chapter 5). The simplifications inherent in the chill hour index and the coarse time intervals used in Bidabé's method (Bidabé, 1963) also mean neither of these models is likely to offer significantly greater accuracy and precision. Chill hour accumulation provides a convenient method of (manually) summarising differences between average seasonal and regional temperature regimes but the arbitrary upper threshold to chill hour accumulation (7°C, 45°F) does not accurately reflect the actual temperature response of dormant buds (Erez and Lavee, 1971; Erez and Couvillon, 1987). In most cases the rate of a complex physiological processes such as growth responds to temperature progressively without sudden thresholds (Berry and Raison, 1982; Precht et al., 1973). Furthermore, simple chill hour accumulation does not take effect of diurnally cyclic temperatures (Couvillon and Erez, 1985; Erez et al., 1979). The relationship between the Bidabé model and the physiology of dormancy alleviation is also unclear, and, as originally formulated, it uses only daily temperature maxima and minima rather than hourly temperatures.

Modifications of the chill unit concept have been proposed to improve its performance and incorporate subsequent findings relating to bud physiology. These include changes in the effectiveness of chill accumulation as buds develop (Andersen, 1992; del Real Laborde et al., 1990) and an alternative method of calculating chill unit accumulation, the 'Dynamic' model (Fishman et al., 1987a,b). However all the models are based on the fundamental assumption that the time of bloom is controlled by two distinct sequential developmental processes with independent responses to temperature. The first process, dormancy alleviation, has a relatively low temperature optimum (i.e. a chilling

requirement) and the second, bud development, a relatively high temperature optimum. In most cases the simulated temperature response within each phase is identical across cultivars and species and therefore attention centres on the duration of both phases as the characteristic by which genotypes are differentiated. The principal difference between the models is the manner in which dormancy alleviation is simulated. With the exception of the 'Dynamic model' all use an empirical relationship of temperature to dormancy alleviation which lacks an explicit   physiological basis.   Temperature response is therefore probably specific to a given situation or cultivar and systematic consideration of differences between cultivars (and also as buds develop) is not possible.

An alternative approach to modelling the transition from dormancy to growth outlined in this chapter may yield models better suited to application in diverse climates and, in particular, to simulation of apricot bloom phenology under Hawkes Bay conditions. The pronounced change from chilling accumulation to heat accumulation that is a feature of existing phenology models appears well-suited to species whose transition from dormancy to active growth occurs rapidly or to climates with pronounced seasonal temperature differences. However, this is not always so and forcing apricot budwood (Chapter 5) showed that the aspects of bud physiology which determine bud break and development change progressively (Fig. 5.6b and Fig. 5.8c,d). Moreover, apricots bloom in late winter (August) in Hawkes Bay. At Havelock North, mean temperatures from April to June were 13.5°, 10.5° and 8.1 °C and, in July and August, were 7.6° and 8.7°C (New Zealand Meteorological Service, 1983). Hence temperatures during chill unit accumulation in April to June are warmer than those in July during heat unit accumulation prior to bloom.

Temperatures from late autumn to early spring therefore constantly fluctuate within a range that both promotes and impedes dormancy alleviation and are always sufficiently warm to allow growth should it become possible. Under these conditions simulation of winter bud development by means of a continuous progressive 'physiological shift' in temperature response (Saure, 1985) may prove more successful. Accurate representation of the effects of relatively high temperatures (i.e. non-'chilling' temperatures) as part of a diurnal cycle on dormancy alleviation is also important since temperatures during much of the period of alleviation are relatively warm. Furthermore, if simulation of both

longer-term seasonal change in temperature response and of short-term diurnal temperature responses was based on hypotheses derived from the normal thermodynamics of cellular metabolism then testable physiological predictions could also result from model simulations. Finally, any alternative model ideally should not require historical bloom records that include many years of observations. Such data for apricots in Hawkes Bay is scarce, greatly limiting the range and speed with which models may be developed. Determination of cultivar-specific model parameters from budwood forcing data (which can be obtained more rapidly) may provide an alternative avenue for model development.

An attempt to develop such a model is presented in this chapter. The concept of a discrete transition between successive physiologically distinct dormant and active states after a temperature-weighted time period, an assumption fundamental to the 'Utah' chill unit model, is replaced with an alternative framework. A continuously-varying potential growth response, reflecting an underlying 'physiological shift', is used to simulate developmental response to seasonal changes in temperature. Dormancy is interpreted as the failure to achieve a potential growth rate due to some external and (or) internal cause which can be partly or completely overcome (Rees, 1981). It is therefore modelled as a quantitative phenomenon in which the rate of bud growth is a function of a progressively less restricted capacity to grow under the conditions experienced in Hawkes Bay during winter and spring. Temperature is assumed to be the principal determinant of growth rate. Phenological progress is therefore modelled as the integral of the growth rate determined by the simulated interaction of the progressively-altering bud temperature response and ambient temperature.

6.2   Model Concepts

6.2.1   Structural Avoidance of Temperature Stress

The cultivated apricot is believed to have originated in the mountains of North and Northeastern China and it also occurs in the Tien Shan mountains in western China and in Kirgizstan (Mehlenbacher et al., 1991). In this area, wild apricot forests grow to an altitude 1060 m and survive winter temperatures as low as -43°C (Thompson, 1991). Apricots are also naturalised within a region which includes Central Asia, Afghanistan, Kashmir, Iran, Turkey and Trans-Caucasia. In all these regions apricots face two consecutive unfavourable seasons since hot, arid summers and autumns are followed by severely cold winters. The growing season is confined to spring, which is short and moist, and to early summer. In contrast, late summer and winter both bring environmental stress due first to high temperature and drought in summer and then freezing conditions in winter which plants must either avoid or tolerate by physiological acclimation (Levitt, 1980). Exposed shoot and floral meristematic tissues are at particular risk of freezing damage as well as dehydration in summer and winter and it is for these that dormancy provides a key mechanism of stress tolerance and avoidance.

Dormancy possibly increases the capacity for bud tissues to tolerate temperature stress. Low temperature has a direct physiological effect through changes in the positions of chemical and biochemical equilibria, changes in the rates of motion of molecules, changes in concentrations of the components in a mixture resulting from phase separations, membrane lipid phase change affecting membrane permeability and enzyme activity (Simon, 1981). Biological macromolecules are also only functional over a limited temperature range (Berry and Raison, 1982) and thus conformational changes at low temperature, effects on allosteric enzymes, failure of protein assembly and dissociation of enzymes into subunits, may all reduce enzymatic activity at low temperature. In addition, increased oxygen solubility at low temperature and low water content induced by freeze concentration can greatly accelerate oxidation of compounds such as β-carotene and vitamin A (Franks, 1981). Lowered metabolic activity in dormant tissues means the potential effects of these deleterious processes are reduced.

Early horticultural study of cold hardiness in fact suggested that physiological acclimation necessary for survival of freezing temperatures relied on the development of dormancy in late summer and autumn to repress bud metabolism and induce changes such as sugar accumulation which facilitated cold acclimation (Chandler, 1954). Attainment of the capacity to tolerate freezing stress does occur close to the transition from paradormancy to endodormancy (Ketchie, 1985; Nissila and Fuchigami, 1978; Seibel and Fuchigami, 1978) and both are induced by short days and low temperature (Dormling, 1993; Andrews and Proebsting, 1986; Kobayashi et al., 1982). However, cold acclimation has been induced independently of dormancy induction by controlled exposure to low temperature (Irving and Lanphear, 1967a). Also, herbaceous species which lack a dormant phase can survive limited freezing and display signs of low temperature acclimation in the form of altered protein metabolism (Guy, 1990). Physiological changes associated with dormancy therefore probably do not lead directly to cold acclimation which evidence shows is an active (rather than passive) process.

Instead, dormancy ensures the survival of meristematic tissues by providing a mechanism of stress avoidance. In this respect it is the anatomy of dormant buds that is vital since it confines lethal ice crystal formation to regions away from freezing-sensitive primordia. Ice nucleation for most plant tissues begins on the plant exterior or else within the apoplasm on the cell wall surface and in water transporting elements. This causes a water potential gradient by which water moves out of the cell to the apoplastic solution or to ice crystals in the cortex and scales of dormant buds (Layne, 1992; Levitt, 1980; Steponkus, 1990). Lack of vascular continuity and the formation early in freezing of a 'dry region' at the base of primordia may protect primordia by inhibiting ice propagation (Ashworth, 1989; Layne, 1992). The principle stress imposed by freezing is therefore dehydration as water moves out of the cell to freeze while intracellular ice formation is invariably lethal (Ashworth, 1989; Layne, 1992). Meristematic and other cells normally remain in the liquid phase even when temperatures are substantially below $0\,°C$. In *Prunus*, intracellular ice only forms after deep supercooling of the cellular solution to -27° to -31°C (Kadir and Proebsting, 1994; Quamme, 1974). In general, buds quickly lose the capacity to tolerate freezing once dormancy is lost and growth begins (Edgerton, 1954; Irving and Lanphear, 1967b; Litzow and Pellet, 1980; Proebsting, 1970; Valkonen et al., 1990). For instance, the cold hardiness of peach flower buds does not rise above a

minimum level until buds are able to initiate rapid growth (Proebsting, 1963).   Short periods of warm temperatures during winter cause only limited deacclimation due to thawing and water redistribution (Andrews et al., 1987). Final loss of hardiness and the capacity to deep supercool occurs in early bud swell (Andrews et al., 1983; Andrews and Proebsting, 1986), possibly because vascular differentiation allows ice crystal propagation into developing tissue (Ashworth, 1989; Ashworth et al., 1992; Proebsting et al., 1982).

Dormancy in winter therefore avoids damage to freezing-sensitive meristems by maintaining the anatomical integrity of the protective bud structure during the period when temperatures are lowest. But if it is the structure, rather than the physiology, of dormant buds that ensures their protection then it is possible that the physiological characteristics of the bud tissues may change progressively during dormancy alleviation without that protection being jeopardised.   For instance, cold acclimation in metabolically-active tissues and in dormant buds involves specific protein synthesis (Guy, 1990).   Physiological change leading to altered temperature response may therefore occur independently of significant anatomical alteration during dormancy. This possibility provides the key to an alternative approach to modelling dormancy alleviation and winter bud development in apricots which is elaborated in this chapter.

6.2.2   Dormancy in a Cyclic Environment

In summer, correlative inhibition of vegetative bud growth by the shoot apex and leaves limits potentially sensitive new growth of apricots (Ramsay et al., 1970). But, since leaves are lost prior to winter and terminal growth ceases, an alternative form of dormancy is necessary to prevent growth during winter and avoid freezing injury to sensitive meristematic tissue. In deciduous trees such as apricots this is provided by an endogenously-regulated form of dormancy (endodormancy) which prevents bud development in autumn and which requires a sustained exposure to 'chilling' (non-subzero low temperature) for its alleviation.

Low temperature alleviation of endodormancy illustrates the general need for plants to the maintain synchrony between their development and the seasonal environmental cycle. Plant development does not occur in an entirely random environment but occurs in one

therefore potentially 'predictable' since variation which occurs periodically provides information that permits anticipation of subsequent change. For instance, the initial stages of stress may elicit acclimation to more severe stress which typically follows. Alternatively, the stimulus of an agent physically unrelated to the factor necessitating an acclimative response may act as an 'environmental token' (Levins, 1969).

Three environmental parameter cycles have potential to provide information for positioning plant development with respect to seasonally-imposed stress: photoperiod, ambient temperature and soil moisture availability. Of these cycles, photoperiod provides the most regular seasonal signal which is especially pronounced at high latitudes. Short days may therefore be the principal factor inducing dormancy and cold acclimation in many northern trees such as *Populus* and also *Picea* and *Pinus* species from temperate and boreal climates (Dormling, 1993; Sakai and Larcher, 1987). However, ambient temperature itself may be the most efficient seasonal signal at low to moderate latitudes and in mountainous areas. Thus, cold hardening of *Pinus* species from warm temperate regions is a response to falling temperature. This seasonal signal also induces bud dormancy in broad leaved evergreen trees in warm temperate Japan (Sakai and Larcher, 1987). The reasons for this are fourfold: 1). Seasonal variation in mean temperature is also substantial so that temperature trends between seasons are pronounced; 2). Adverse temperature conditions (both too high and too low) represent a direct threat in the plant's native habitat; 3). Mountainous regions are characterised by sharply different temperature micro-environments due to marked variation in altitude and aspect that is independent of change in photoperiod. Dormancy is an inherited characteristic and therefore population dispersal in such regions requires a dormancy mechanism sensitive to such environmental variation; and 4). The seasonal temperature cycle is generally subject to less inter- and intra-seasonal variation than other cyclically-imposed environmental stresses (e.g. drought stress). As a seasonal signal, ambient temperature therefore has a direct relationship to a major environmental stress, as well as greater amplitude and less susceptibility to noise (i.e. better signal/noise ratio) than other potential signals and hence the narrowed range of temperature which advances dormancy alleviation represents an effective strategy for coordinating development with the seasonal temperature cycle.

Seasonal development of species from temperate climates is also regular and linear. The sequence of the three characteristic types of dormancy, paradormancy, endodormancy and ecodormancy (Lang et al., 1985,1987) therefore holds an implicit linkage to seasonal cycles but an explicit linkage is also possible. Thus, while dormancy has been described solely as a growth phenomenon (Lang et al., 1987; Wareing and Phillips, 1981), it has also been interpreted as a growth limitation imposed by progressive restriction of the temperature range at which it will occur (Vegis, 1964). Vegis notes that full dormancy is commonly preceded by a period in which the loss of the capacity to initiate rapid growth is readily overcome by moderate temperatures and long days (or continuous light). Gradually, attempts to induce active growth fail, and then the plant has reached the true dormancy that requires special treatments to overcome (Vegis, 1964).

However, Vegis (1973) also noted that in some cases, even at the time of lowest growth activity, or at the strongest depression of growth, plants are only in a state of relative or conditional dormancy. Thus during the whole of the rest period they have retained the ability to grow, although only within a narrow range of external conditions. Vegis pointed out that the growth response of buds and other organs as they emerge from dormancy is determined by the combination of ambient conditions and the limits of a plant's potential response range. Growth can start before completion of after-rest if the conditions of the ambient environment are within the range to which the otherwise dormant organs can respond positively. Initially this range is very narrow, but it widens progressively as dormancy is alleviated as, for example, during stratification when the temperature range for germination gradually widens. Vegis (1973) also notes that each stage of tulip ontogenesis, from organ initiation to flower stem elongation, has its own temperature optimum which rise steadily as the bulb develops towards bloom.

6.2.3   'Chilling' as a Seasonal Signal

This interpretation of endodormancy as a progressive depression and recovery of the temperature range for development suggests that ambient temperature itself acts as the key seasonal regulator of plant growth. Endodormancy acts as a 'brake' which holds the developmental cycle in a constant relative position to the environmental cycle. Low non-freezing temperatures, which occur predominantly during the seasonal transition periods (spring and autumn) in a continental climate, function as the environmental 'signal' which

releases the brake on the developmental cycle. The principal requirement of this thermal growth regulation scheme is that the temperature range or 'window' in which growth may occur departs from the environmental temperature range for at least some period in the seasonal cycle. If this is the case then growth is restricted to the periods of intersection between the two ranges. This may occur if the response range- the 'thermal response window'- is unchanging through the environmental cycle or is itself cyclic (Fig. 6.1). It is, however, most likely that the restriction of growth has the greatest synchronising effect when the response window itself cycles out of phase with the environmental cycle. This is because this situation allows the widest response window at the same time as preventing growth at both the environmental cycle maxima and minima.

Such an analysis indicates the key role of temperatures in the mid range of the environmental cycle as signals of relative cycle position. Indeed, the interaction of the two cycles could theoretically provide sufficient information for the synchronisation of growth independently of any additional environmental signal such as photoperiod. (This is not to deny that additional signals such as photoperiod play a significant role in the 'real world' control of development but merely to illustrate the information available to plants in a regularly cycling environment.) Not only are cycle intersections thermally distinct from non-intersection (non-growth) periods, they are also themselves distinguished from one another. First, where the response window is unchanging (Fig. 6.1a), intercepts are distinguished by the temperature trend direction, declining during the first intercept period, rising during the second. Second, if the response cycle is more than
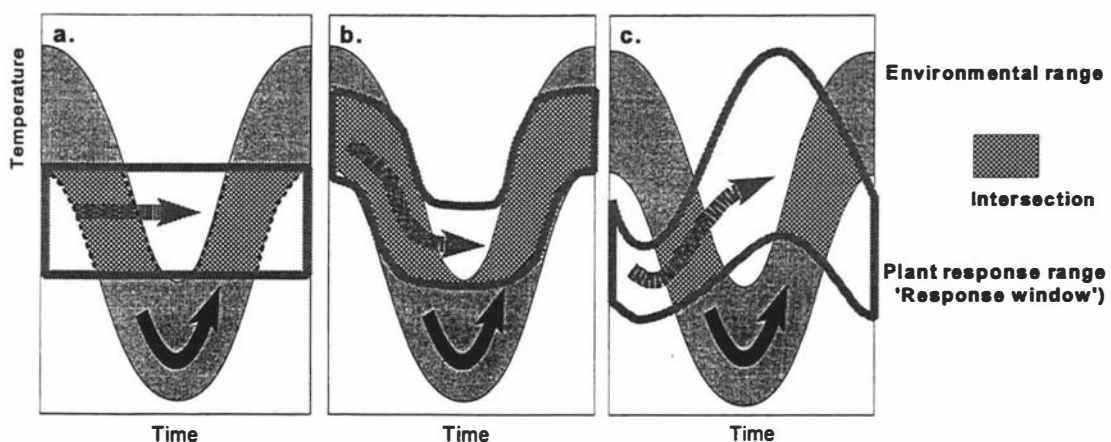
Figure 6.1   Illustration of the role of response range width and relative phase position of the ambient and response cycles as regulators of plant growth. a). Constant growth response range, intersections distinguished by declining and rising temperature trends; b). Growth response cycle in phase with ambient cycle; c). Growth response cycle out of phase with ambient cycle.

180° out of phase with the temperature cycle (i.e. it leads it- Fig. 6.1c), then additional differentiation is potentially provided by the temperature range during the intercept period. The first (declining) intercept period is characterised by a relatively low temperature range and the second (rising) intercept period by a relatively high range. A sequence of four temperature periods may be recognised: 1). high then declining temperatures, 2). low mid-range temperatures, 3). very low then rising temperatures, 4). high mid-range temperatures. The temperature requirements for development of peaches illustrates the differentiation of the two intercept periods. Weinberger (1967) suggests that the annual growth of a peach tree occurs in two stages: one stage in which a flush of growth and fruiting occurs, requiring high temperatures, and another where low temperatures are required for normal development of buds.

Under natural conditions the seasonal temperature sequence does not vary. Therefore, growth during relatively cool conditions following sustained high temperatures 'indicates' the approach of the temperature cycle minimum. Likewise, exposure to the same temperature range after the temperature cycle minimum then may be 'interpreted' to indicate a rising temperature trend. Exposure to mid-range temperatures after sustained exposure to high temperature could therefore initiate cold acclimation as well as initiating the expansion of the response window to allow growth during the high intercept period. Growth conditions during the second intercept period (high mid-range temperatures) then initiate contraction of the thermal response window and consequently prevent further growth by inducing dormancy. Consequently, the information content of this sequence enables regulation of growth and development so that adaptive structures such as dormant buds are in place before the arrival of an 'anticipated' stress. Progressive variation of a plants temperature response therefore provides a method of maintaining the synchronisation of development with the environment cycle in which the low temperature intercept period (endodormancy) acts a developmental 'control point'.

The simplistic situations illustrated in Fig. 6.1 can be made more 'life-like' if the informational content of ambient temperature is overlaid by thermal effect of temperature on the kinetics of development. Plants are poikilotherms and hence, insufficient thermal energy (too low a temperature) will limit growth and probably also any change in developmental temperature response. Thus, exposure to very low temperatures during

the seasonal cycle minimum is effectively an hiatus between the two intercepts. No change in window size is then likely to occur. This has the result that the two intercept periods are equivalent to continued mid-range temperature exposure. A similar situation may also apply when temperature is too high for developmental response.

A more 'life-like' presentation is possible (Fig. 6.2). Severe winters in continental regions within which apricots grow naturally mean the amplitude of the ambient temperature cycle is greater than that of the response range (Fig. 6.2a). Cycles intercept twice in this situation with separate periods of low intercept development (LID) and high intercept development (HID). Chill unit phenology models recognise this temporal separation by using 'chilling' accumulation as a developmental index during the first period (which in cold climates coincides with autumn) and heat unit accumulation during the second period (spring). Periods between the two intercepts are distinguished by the limiting factor which restricts growth. Following LID, growth is limited by insufficient warmth (environment-limited development or 'ecodormancy') and following HID, it is limited by the plant's inability to respond to prevailing temperatures (plant-limited development or 'endodormancy'). Sequential arrangement of LID and HID therefore restricts growth leading to low temperature-sensitive stages of development the part of the seasonal cycle least likely to cause low temperature stress. Fig. 6.2b illustrates the merging of LID and HID caused by reduction in amplitude of the ambient temperature cycle (higher minimum temperatures). The result is the formation of a continuous development period in which temperature response progressively shifts from that characterising LID to that of HID. Rather than ceasing during the temperature cycle minimum, growth therefore continues at a low rate throughout advancing developmental stages such as bud break.

'Chilling' appears to act as a signal of both declining and also rising temperature trends within this scenario. The high amplitude temperature cycle of continental climates means temperatures in the 'chilling' range are typically experienced during the periods of transition during the temperature cycle- during autumn and spring. Thus, exposure to 'chilling' represents relative coolness in autumn and relative warmth in spring. Plants might therefore respond differently to mid-range temperatures (i.e. chilling) occuring at different times in the seasonal cycle. For instance, chilling temperatures typically

a. Higher and Lower Intercepts Separate

b. Higher and Lower Intercepts Merged

Seasonal cycle type

- Temperature cycle
- Response window

Development type

- Lower intercept
- Higher intercept
- Environment-limited (*ecodormancy*)
- Plant-limited (*endodormancy*)
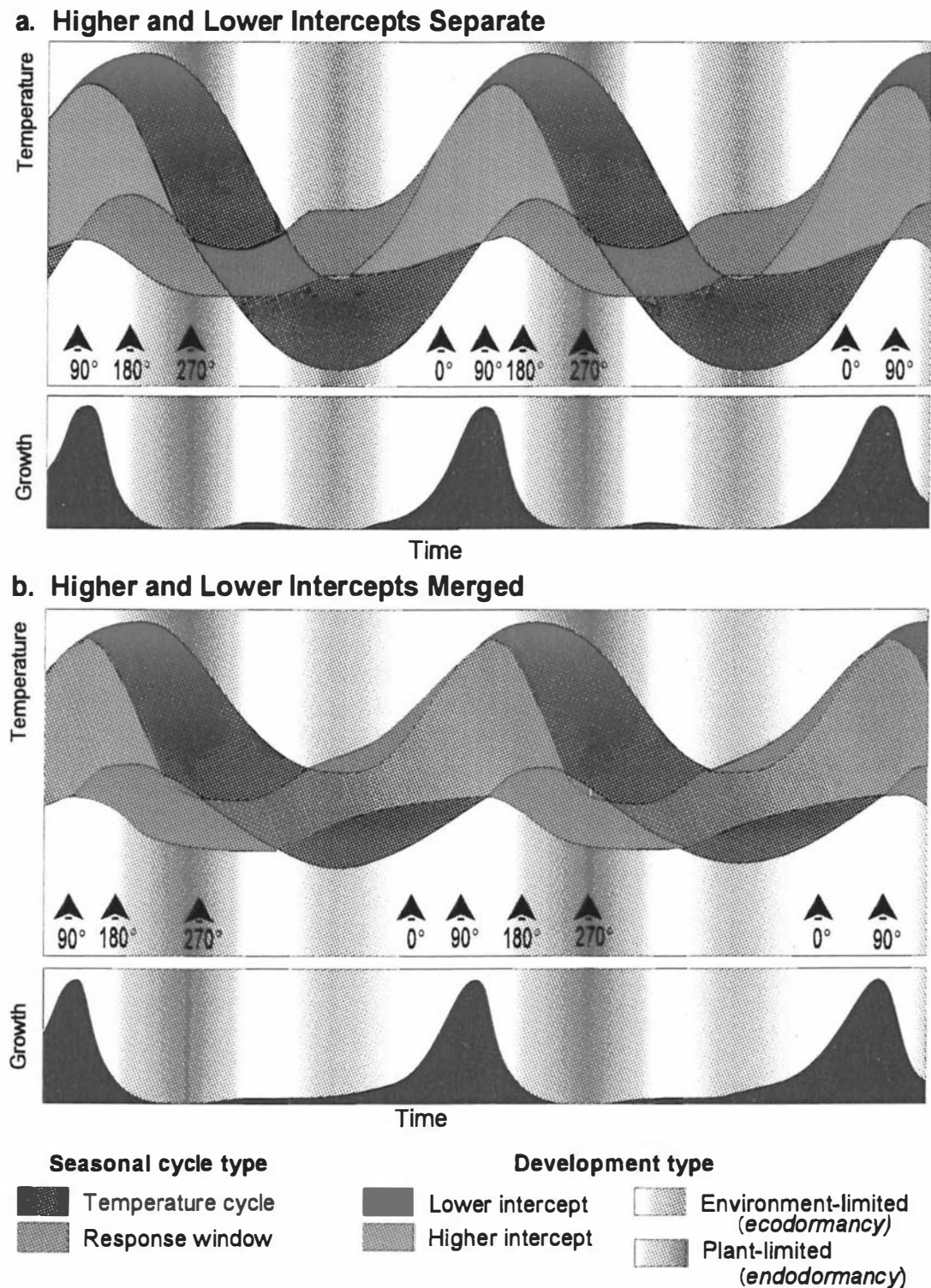
Figure 6.2   Schematic interpretation of the induction and release of bud dormancy illustrating merging of higher and lower intercept development periods ('chilling' and heat accumulation) as the amplitude of the seasonal temperature cycle is reduced.   a). Higher and lower intercept periods separate, plant-limited and environment-limited development periods distinct ; b). Higher and lower intercepts merging, plant-limited and environment-limited development periods connected. Degree Growth Stages from Kobayashi et al., 1982: 0° = Spring Bud Break; 90° = Maturity Induction Point: 180° = Vegetative Maturity: 270° = Maximum Rest.

alleviate dormancy (Vegis, 1964) but, for red-osier dogwood, low temperatures in autumn initially reduce the capacity to break bud (Kobayashi et al., 1982). In this case it appears that exposure to chilling is a signal of cooling used to 'anticipate' the potential stress of winter. Conversely, mid-range temperatures experienced in early spring (which in chill unit phenology models are counted as 'chilling' and therefore considered low temperature exposure) may actually represent relative warmth and a rising temperature trend. This is likely if conditions in autumn allow only partial completion of LID and further mid-range temperature exposure in spring is necessary to lift the response window. Such a situation would be advantageous where temperatures fluctuate greatly in winter or if exposed buds experience higher than average temperatures due, for instance, to radiative heating during fine weather. In these cases the 'prematurely' warm conditions will be unable to stimulate precocious growth until substantial exposure to mid-range temperature ('chilling') signals that it is truly getting warmer.

This dual role of mid-range temperatures is illustrated in Fig. 6.3 in relation to seasonal acclimation of potential growth rate and cold hardiness for cold winter situation in which LID and HID are separate. As temperature falls 'chilling' initially provides a cooling signal (blue arrow) which may promote deepening of dormancy as well as the first stages of cold hardiness development. Average temperatures then drop sufficiently to permit at least partial completion of low intercept development (LID), the principal effect of which is to raise the thermal response window again. However, mid-range temperatures in spring (i.e. further 'chilling') are relatively warm compared to the temperatures of mid winter. They therefore, paradoxically, signal an upward temperature trend (red arrow) resulting in further recovery of the thermal response window and loss of cold hardiness as growth begins before bud break ($0°GS$). This suggests that the distinction of plant responses to 'chilling' and 'heating' is overly simplistic and potentially misleading.

The distinction between chilling and heating is further reduced as amplitude of the seasonal temperature cycle is reduced. This is because a rise in average winter temperatures, alters the intensity and also the position in the seasonal cycle of the climatic signal provided by what are mid-range temperatures in a continental climate. Initially, a moderate increase in average winter temperatures (representing a climate with 'cool' winters, Fig. 6.4a) amplifies the 'chilling' signal by increasing the proportion of

Thermal Environment: Cold Winter Climate
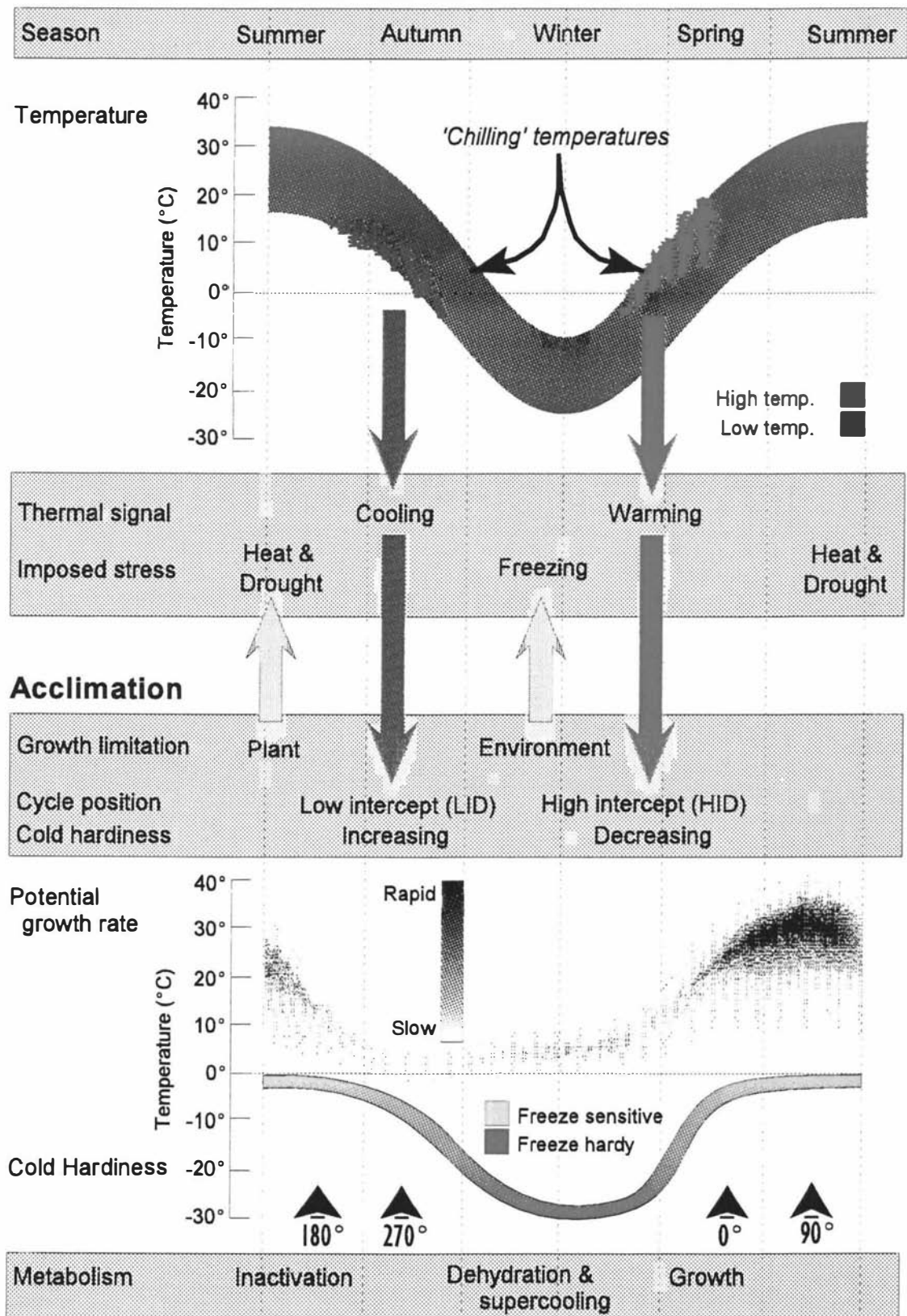
Figure 6.3   'Chilling' as a seasonal signal of declining and rising temperature trends for the synchronisation of plant growth with the ambient temperature cycle. I. Relationship of 'chilling' to cyclically-induced growth limition, potential growth response range, cold acclimation and tissue metabolic activity in a cold winter climate Degree Growth Stages from Kobayashi et al., 1982 (See Fig. 6.2 for definitions).

a. Cool winter climate
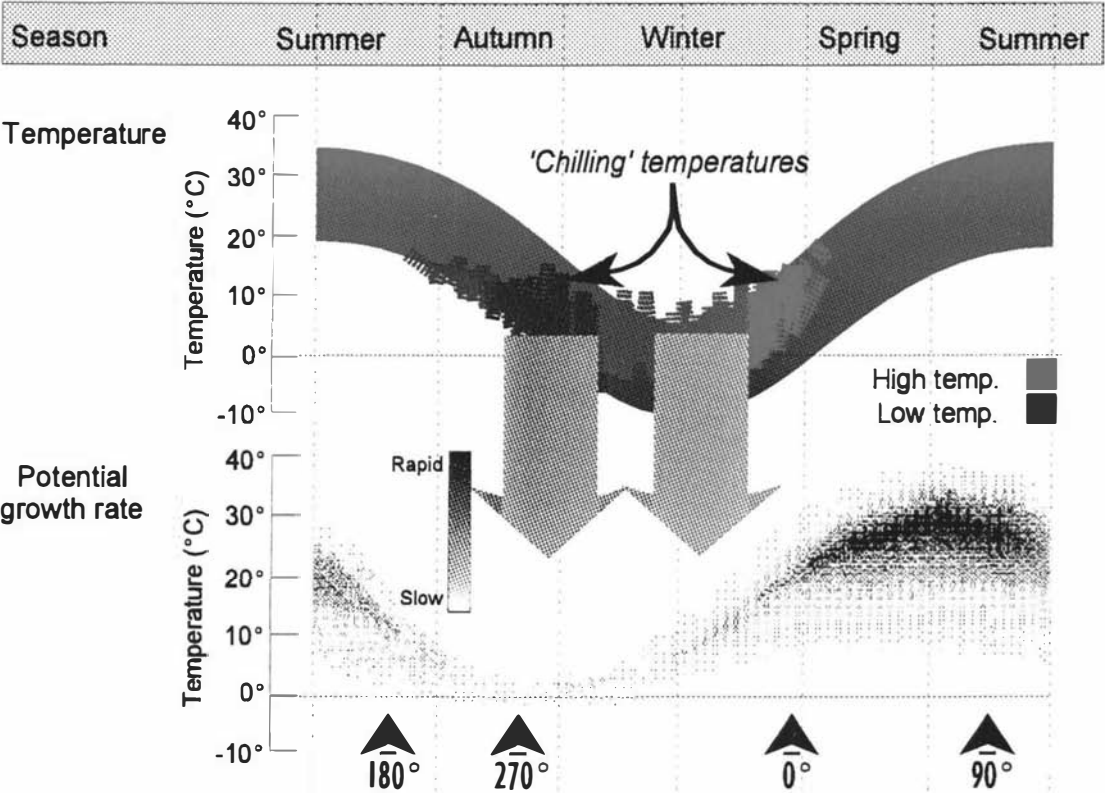
b. Mild winter climate
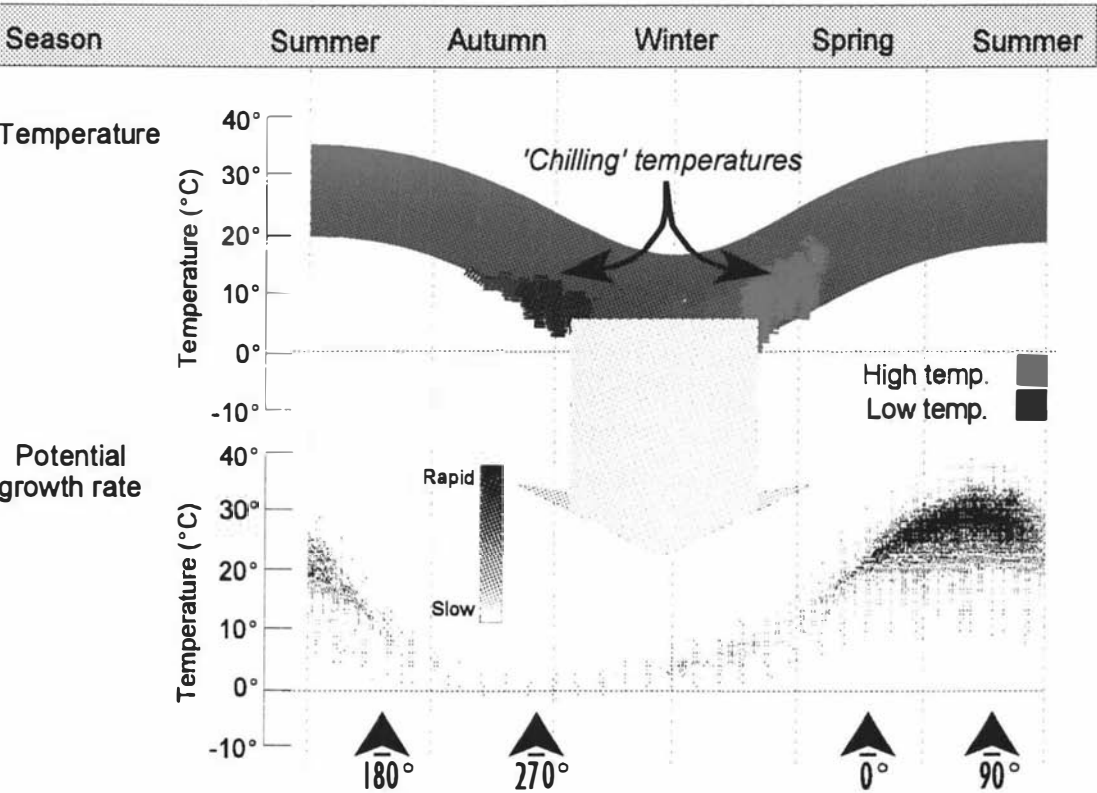
Figure 6.4   'Chilling' as a seasonal signal of declining and rising temperature trends for the synchronisation of plant growth with the ambient temperature cycle. II. Relationship of 'chilling' to potential growth response range in a cool and mild winter climate Degree Growth Stages from Kobayashi et al., 1982 (See Fig. 6.2 for definitions).

time spent in the 'chilling' temperature range (broadened blue and red arrows). Development is therefore advanced by the combined informational and thermal effect of temperature and, as a result, bud break (represented by $0°GS$) is brought forward.

However, a further increase in average winter temperatures (representing a climate with 'mild' winters, Fig. 6.4b) diminishes the 'chilling' signal. This is due not only to fewer hours mid-range temperatures but also because higher temperatures which are experienced with mid-range temperatures in a diurnal cycle are known to have an inhibitory effect on the low temperature development of buds (Erez et al., 1979). The effect of mid-range temperatures as seasonal signals is therefore weakened (or negated entirely if daily temperature maxima are high enough). The result is that the two signals are degraded and merge. Consequently, development is delayed because the response window is unable to recover as fast as ambient temperatures rise in spring. Ambient temperatures remain for the most part above that required for the maximum rate of growth. The time required to reach a given stage of development is prolonged and the start of bud growth in spring is delayed. A method of quantitatively representing the progressively changing effect of temperature on bud development, under such conditions especially, could yield a better and more comprehensive approach to understanding and modelling bud development and apricot bloom phenology.

6.3   Model Equations

6.3.1   A Modified Arrhenius Dormancy Model

The proposed model is based on two major assumptions. First, it is assumed that bud development from the point of deepest dormancy to bud break and beyond to flowering can be described using a single index of developmental position, l, expressed in terms of arbitrary 'development units' (d.u.). Units for l are arbitrary since the precise relationship between bud development and quantitative bud characteristics such as bud size, cell division or respiration rates and growth regulator levels are not known. Second it is assumed that the rate of bud development is a function of temperature, T and an index of developmental capacity, C, which represents the capacity of the bud to develop further as determined by its temperature and current developmental position. Hence

$$\frac{dl}{dt} = k = C \cdot f(T) \tag{6.1}$$

where k is the instantaneous rate of development. If it is also assumed that the overall rate of development throughout this period may be simulated as though it was controlled by a single enzyme-catalyzed reaction, then its dependence on temperature is

$$f(T) = A e^{-E_a/RT} \tag{6.2}$$

which is the Arrhenius equation describing potential growth rate where A is a constant (units: d.u. / unit time), E_a is the apparent activation energy, R is the Gas Constant (8.314 J K^{-1} mol^{-1}) and T is absolute temperature.

The relationship of C to temperature and developmental position may then be simulated by assuming that the enzyme is sensitive to high temperature during dormancy and that declining sensitivity is a key aspect of dormancy alleviation (Salisbury and Ross, 1969). This may be represented using a model of enzyme temperature-dependence presented by Johnson and Thornley (1985). Thus, if the enzyme can exist two forms, an active form favoured by lower temperatures and an inactive form favoured by higher temperatures, then ΔG, the free energy for transformation from the active to inactive form is

$$\Delta G = \Delta H - T\Delta S \tag{6.3}$$

where ΔH is the change in enthalpy for conversion of the enzyme from the active to inactive form and ΔS the corresponding change in entropy for the inactivation. The

Boltzmann energy distribution function then indicates that f_A , the fraction of enzyme molecules in the active form, is given by

$$f_A = \frac{1}{1 + e^{-\Delta G/RT}} \tag{6.4}$$

If either ΔH or ΔS change with developmental position then Equations 6.3 and 6.4 may be combined to represent the dependence of bud developmental capacity on temperature and developmental position: i.e.

$$C = \frac{1}{1 + e^{\Delta S/R} e^{-\Delta H/RT}} \tag{6.5}$$

The overall relationship of growth rate to temperature is described by

$$k = \frac{A e^{-E_a/RT}}{1 + e^{\Delta S/R} e^{-\Delta H/RT}} \tag{6.6}$$

This modified Arrhenius relationship yields an overall growth rate response curve with an optimum temperature where the product of developmental capacity and potential growth rate is maximal. The position and size of the maximum for this optimum temperature then depend on values given to E_a, ΔS and ΔH. A 'physiological shift' in temperature response associated with dormancy alleviation (Kobayashi et al., 1982; Saure, 1985) could therefore reflect a progressive change in the relationship between temperature and C, the developmental capacity. For instance, a change in ΔH from a relatively low initial value ΔH_0 to a higher new value ΔH_1 would result in a rightward lateral shift in the relationship between C and temperature and a consequent similar shift in the optimum temperature for growth (Fig. 6.5a). If E_a and ΔS remain unchanged the shift is also marked by an increase in the rate of growth at the optimum temperature.

If developmental distance, a measure of the relative development position of a bud, is denoted by l, then the developmental position relative to some point i is given by the integral of development rate with respect to time

$$l_{ij} = \int_{t_i}^{t_j} k \, dt \tag{6.7}$$

where t_i and t_j mark the ith and j[th] points in time over which integration is performed and l_{ij} the developmental 'distance' covered in that time. If t_i then represents a convenient
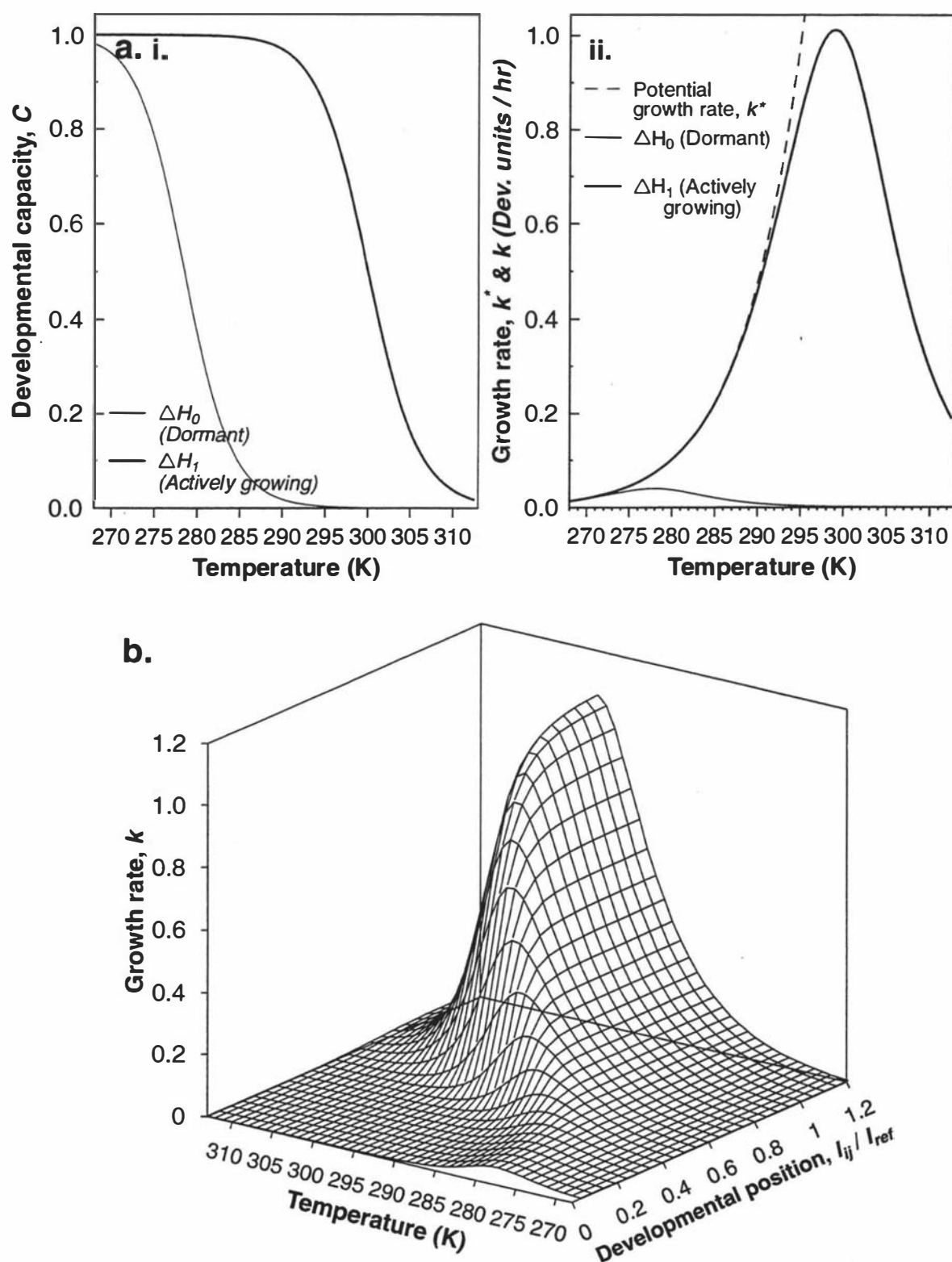
Figure 6.5   Simulation of temperature and development-dependent bud growth rate using a modified Arrhenius dormancy model incorporating a 'physiological shift'.
a). Modified Arrhenius function for simulated dormant and actively growing buds: i). Developmental capacity, C at two levels of enthalpy of inactivation; ii). Potential growth rate and actual growth as determined by C. (E_a=12500, $\Delta S/R$=100, $\Delta H_0/R$ = 27850, $\Delta H_1/R$ = 30000). b). Response surface illustrating dependence of growth rate on temperature and relative developmental position.

initial starting point (eg the time of deepest dormancy) and t_j any time thereafter, and if l_{ref} is the integral to a specific developmental reference point, then the ratio l_{ij} / l_{ref} may be used as an index describing relative developmental position at any point in time. Therefore, $l_{ij} / l_{ref} = 0$ at the initial starting point when $t_j = t_i$ and $l_{ij} / l_{ref} = 1$ some time later when the reference point (eg the full release of dormancy) has been reached. The relationship between temperature, T, relative developmental position l_{ij} / l_{ref}, and growth rate, k, is then described by a three-dimensional surface (Fig. 6.5b).

For enzymes, the free energy associated with inactivation, ΔG, is dominated by the enthalpy, ΔH, since the contribution of $T\Delta S$ is generally small (Johnson and Thornley, 1985). Change in C is therefore more sensitive to alteration of ΔH, the change in enthalpy for the conversion from the active to inactive state, than it is to alteration of ΔS, the change in entropy associated with enzyme inactivation. Hence, if it is assumed that E_a (the apparent activation energy for the reaction) is unchanging, then the position and size of the maximum growth rate (optimum temperature) is determined by variation in ΔH, the enthalpy of inactivation. ΔH may therefore be used as a quasi-physiological parameter which may be progressively varied to empirically simulate the upward shift in the temperature optimum of growth rate which is observed as dormancy is alleviated. Consequently, if ΔH is able to vary from ΔH_0, its initial value when dormancy is deepest to ΔH_1, its value at the reference point where dormancy is fully released, then

$$\Delta H_j = \Delta H_0 + D_j \cdot (\Delta H_1 - \Delta H_0) \tag{6.8}$$

where ΔH_j and D_j are the enthalpy of inactivation and the relative depth of dormancy at time t_j and D_j ranges from $D_j = D_i = 0$ at the initial time point (deepest dormancy) to $D = 1$ for full release and D_j is a function of l_{ij}.

The modified Arrhenius relationship (Equation 6.5) implies that C (the denominator) reaches equilibrium instantaneously. However, under supra-optimal temperature conditions growth and metabolic activity appear to decline progressively rather than immediately (Rank et al., 1991; Tutty et al., 1994). Rapid metabolic adjustment appears even less likely after periods of supra-optimal temperature when C will be low. Therefore, to damp the rate of change in C, an additional condition is imposed such that when temperatures rise, only a portion of developmental capacity is lost per unit time C

while potential increase in C due to falling temperature is damped by weighting the rate of increase by C: i.e.

$$\frac{dC}{dt} = \begin{cases} q \cdot \dfrac{dC^*}{dt} & (\dfrac{dT}{dt} > 0) \\[4mm] C \cdot \dfrac{dC^*}{dt} & (\dfrac{dT}{dt} < 0) \end{cases} \tag{6.9}$$

where dC^*/dt represents the potential instantaneous change in C and q is the proportion of activity respectively lost per unit time (eg 80%). Decline in C is therefore exponential while recovery is autocatalytic.

In summary, bud growth rate is a function of temperature and two physiological state variables l_{ij}, the relative developmental position and C , the developmental capacity. Change in l_{ij} describes development during both alleviation of endodormancy and spring bud growth and thereby also determines relative dormancy, D_j and the seasonal change in the optimum temperature for bud growth. The position of the temperature optimum in relation to the temperature at time t_j then determines the value of the second state variable, C, which integrates the developmental and temperature effects on growth rate. C is affected directly by temperature but also by developmental position. Thus, as developmental position changes, the relationship of C to temperature also changes. Initially, moderate temperatures in the range $10°$-$15°C$ cause marked depression in C, whereas after alleviation of dormancy (simulated by change in l_{ij}) the same temperature range causes C to approach 1.00 (i.e. full developmental capacity). Hence, a key feature of the proposed model is that the simulated relationship of growth rate to temperature is continuous and is dependent on state variables describing both short-term (diurnal) and long-term (seasonal) changes in bud physiology.

6.3.2   Application to Phenology Modelling

For practical simulation of dormancy alleviation and bud growth in spring the duration between times t_i and t_j is divided into j-i periods. Equation 6.6 is then approximated by

$$d_{ij} \;=\; \sum_{t=i}^{j} v_t \tag{6.10}$$

where d_{ij} is the developmental distance covered between times t_i and t_j, and v_t is the average rate of development for the tth time interval. Hence

$$d_{ij} \;=\; \sum_{t=i}^{j} \frac{A\,e^{-E_a/RT_j}}{1 + e^{\Delta S/R}.e^{-\Delta H_j/RT_j}} \tag{6.11}$$

where T_j is the mean temperature for the jth period, ΔH_j is the enthalpy of inactivation at the development stage reached at time t_j, and where $d_{ij} = d_{ref}$ when dormancy is fully alleviated.

Calculation of ΔH_j therefore requires a function to relate relative dormancy, D_j to developmental position, d_{ij}. Since the actual developmental-dependence of dormancy alleviation is not known several potential relationships between D_j and position d_{ij} relative to d_{ref} are proposed. The simplest is a piecewise linear relationship:

$$D_j \;=\; \begin{cases} \dfrac{d_{ij}}{d_{ref}} & (d_{ij} < d_{ref}) \tag{6.8 a} \\[2em] 1 & (d_{ij} \geq d_{ref}) \tag{6.8 b} \end{cases}$$

Alternatively, more complex functions could replace Equation 6.8 a to describe the relationship between relative dormancy and developmental position between D_j=0 and D_j=1. Power and logistic functions such as

$$D_j \;=\; (d_{ij}/d_{ref})^r \tag{6.9 a}$$

$$D_j \;=\; \frac{1}{1 + e^{[a - b.(d_{ij}/d_{ref})^r]}} \tag{6.9 b}$$

could be used where r is a parameter determining the shape of the response of relative dormancy to development and where a and b are constants in the logistic function with appropriate values selected to cause D_j to rise from very near 0 to very near 1.00 as

d_{ij} / d_{ref} moves from, respectively, 0 (initial point) to 1 (the reference point). Values of $a = 5$ and $b = 10$ were used in all calculations. When $r = 1.0$, equation 6.9a simplifies to a simple linear function and equation 6.9b to a logistic function. When $r < 1$, D_j is initially more sensitive to developmental position compared to the simple linear and logistic functions, whereas when $r > 1$, D_j is initially less sensitive (Fig. 6.6b). Varying the relationship between dormancy alleviation and developmental position provides one possible method by which cultivars could be distinguished using the model parameters

For convenience, $D_i = 0$ was arbitrarily defined as a 'standard' depth of dormancy at the point when dormancy is deepest, used as an initial point for simulation. Higher or lower values (i.e. $D_i > 0$ and $D_i < 0$) then represent initially deeper or shallower dormancy in which the thermal response window is more or less depressed. This being the case then

$$D_j^{'} \;=\; D_i \;+\; (1 - D_i) . D_j \tag{6.14}$$

where $D_j^{'}$ is the adjusted relative dormancy value, D_i is the initial depth of dormancy and D_j describes bud dormancy later at time t_j as a function of d_{ij} / d_{ref}. Varying D_i is a second method by which cultivar-specific differences in response to temperature may be represented within this model (Fig. 6.6a). In addition, each of four modified Arrhenius equation parameters, E_a, ΔH_i, ΔH_{ref}, ΔS could theoretically vary between cultivars or species and thereby account for observed differences in patterns of dormancy alleviation and flowering. However, for simplicity, only D_i, the initial depth of dormancy, and s, the parameter determining the shape of the relationship between development and relative dormancy are proposed at this point as cultivar-specific model parameters (Fig. 6.6a,b). E_a and ΔS plus the initial and reference values of ΔH are fixed as constants (Table 6.1) across both cultivars and developmental stages.

Table 6.1   Parameter values for the modified Arrhenius equation (Equation 6.5) which provide three different temperature optima widths for the simulated growth rate response.

Parameter	Broad optimum	Intermediate optimum	Narrow optimum
A	3.95×10^{18} s^{-1}	2.49×10^{18} s^{-1}	2.25×10^{18} s^{-1}
E_a / R	12500 K	12500 K	12500 K
$\Delta H_0 / R$	20750 K	27850 K	41950 K
$\Delta H_1 / R$	22250 K	30000 K	45000 K
$\Delta S / R$	75 K	100 K	150 K
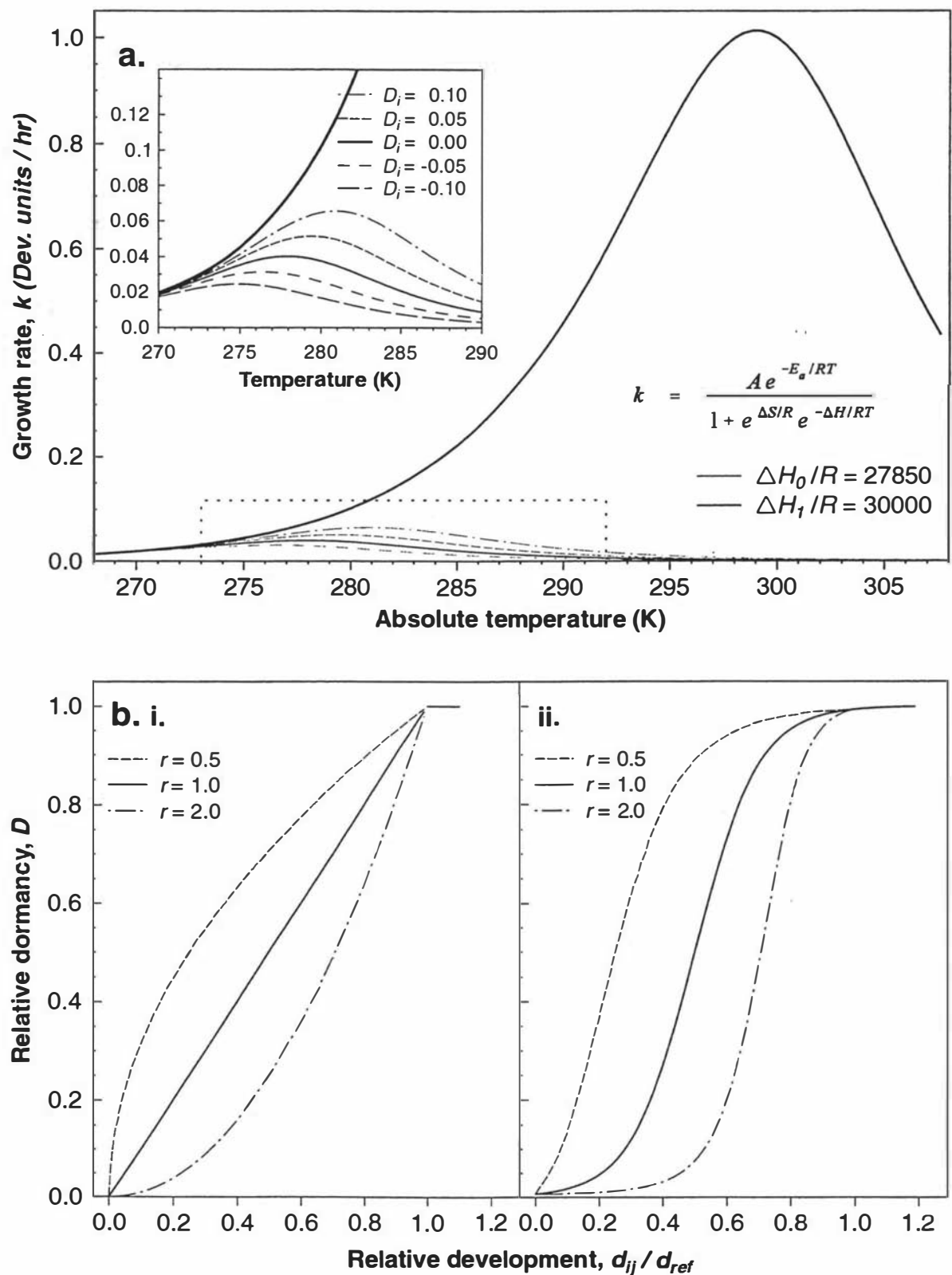
Figure 6.6   Alternative strategies for representing different cultivar-specific responses of bud growth rate to ambient temperature within the proposed model.

a). Representation of variation in initial depth of relative dormancy, D_i.

b). Linear, power and logistic relationships between relative dormancy, D_j, and relative developmental position, d_{ij} / d_{ref}: i). $D_j = (d_{ij} / d_{ref})^s$; ii). $D_J = 1 / (1 + e^{[a - b(d_{ij}/d_{ref})^r]})$, $a = 5$, $b = 10$.

Values for E_a, ΔS, ΔH_0 and ΔH_1 were chosen so that the function relating growth rate, k, to temperature had a maximum at 5°C (278 K) when dormancy was deepest ($D_j = 0$) and a maximum at 25°C (308 K) when dormancy was fully released ($D_j = 1$). The value of the Arrhenius constant, A, was chosen so that the maximum growth rate at 25°C when development reached the point at which dormancy was fully alleviated was equal to 1.00 (Fig. 6.5a). The shape of the relationship between developmental capacity, C, and temperature depended on the value given to the entropy of inactivation, $\Delta S/R$. When $\Delta S/R = 100$ K, C declines from 1 (full capacity) to 0 (nil capacity) over a temperature range of about 15°C. Sensitivity of C to temperature is higher when $\Delta S/R = 150$ K (temperature range ~10°C) and lower when $\Delta S/R = 75$ K (temperature range ~20°C). The value of E_a is within the range of apparent activation energies observed in plant systems (40-120 KJ mol$^{-1)}$ as are values for ΔS, ΔH_0 and ΔH_1 belonging to constant sets 1 and 2 (typically $\Delta S/R = 85$ K, and $\Delta H/R = 25{,}000$ K: Berry and Raison, 1982). Values for ΔS, ΔH_0 and ΔH_1 in set 3 of Table 6.1 are, however, higher than average.

An iterative procedure similar to that used for the 'Utah' chill unit model was used to determine d_{phen}, the developmental distance to a phenological stage, and optimal values of D_i or r for different cultivars based on several years of historical phenology data and corresponding temperature data. This involved:

i).   Estimation of likely values for d_{ref}, the developmental integral to full release of bud dormancy for either r or D_i. Selection of variation in initial depth of dormancy, D_i or of the relationship of dormancy alleviation to development (determined by r) reflected a subjective judgement based on available experimental data and field observations.

ii).   Calculation of the relative developmental distance (d_{if}/d_{ref}) to the observation dates for each record and combination of d_{ref} by summing the average hourly growth rates over the period from deepest bud endodormancy (mid-late autumn) to the particular phenological stage of interest. A standardized calendar start date (e.g. March 1) is probably satisfactory instead of exact determination of the date of deepest endodormancy since model equations minimise simulated development while temperatures are mild.

iii).   Independent analyses of variance on the relative development integral for each combination of model parameter values using phenological stage as a classification variable. Both the standard error or the error coefficient of variation allow identification of the best initial model since expected error variance is zero when simulated development exactly matches actual development.

6.4   Discussion

This study sought to establish an conceptual framework for a model of dormancy alleviation and bud development based on an analysis of the ecological significance of dormancy and distinct from durational models of dormancy such as the 'Utah' chill unit phenology model. The 'PHYSHIFT' model ultimately derived from this analysis uses one of two physiological scenarios that have been proposed to account for the positive effect of low temperature on bud and seed dormancy. The first of these is illustrated by the 'Dynamic model' of dormancy alleviation proposed by Fishman et al. (1987a,b). This scenario explains the promotion of dormancy alleviation by low temperature by means of a process analogous to that suggested for vernalization (Purvis and Gregory, 1952). A two-step process is proposed in which reversible formation of a thermally-unstable precursor leads to formation of a 'dormancy breaking factor' after a critical level of the precursor has accumulated. The promotive and inhibitory effects of temperature arise from the changing response of the overall process as it reflects the effect of temperature upon the relative rates of formation and decay of the precursor. This mechanism accounts for the chill unit response curve, the dual effect of moderate temperatures on dormancy alleviation and the effect of cycle length when high temperatures are cycled with low temperature (Fishman et al., 1987b).

The second scenario which is used in the 'PHYSHIFT' model outlined in this chapter explains the promotive effect of low temperature in terms of two distinct and possibly independent processes with different relationships to temperature, one of which promotes development, while the other causes its inhibition (Saure 1985). In dormant buds, the effect of the inhibitory process over-rides the promotive process thereby preventing development. Dormancy alleviation is due to a progressive diminishment of the inhibitory process under continued exposure to low temperature. The characteristic bell-shaped temperature-dependence of dormancy alleviation is then interpreted in terms of stress imposed by supra-optimal temperature in the range of what is otherwise the 'normal' range for growth (Salisbury and Ross, 1969). This perspective emphasizes the very rapid rate at which inhibition of dormancy alleviation grows as temperature rises. For instance, the 'Utah' chill unit weighting scale falls from a maximum at 6°-7°C to zero at 12°-14°C and continues to become increasingly negative beyond this point

(Richardson et al., 1974). The high temperature sensitivity (Q_{10}) required of any process which might impede development in this manner rules out purely physical processes (eg diffusion or leaching) as key mechanisms and is more suggestive of processes which occur during cellular deterioration at high temperature (Christophersen, 1973). Salisbury and Ross (1969) suggest that enzyme denaturation may be involved and this is the physiological hypothesis implied by the model presented in this chapter. Parallels can be drawn with high temperature induced rosetting in biennials due to inhibited stem elongation and the subsequent low temperature requirement for bolting (Ohkawa et al., 1994). Breaking of dormancy therefore may not involve any special low temperature process but rather the alleviation of growth inhibition due to supra-optimal temperatures.

This alleviation process could have been integrated within a biphasic chill unit-type model by requiring complete removal of the inhibition before growth could begin. Two separate scales would then be needed, one to describe the rise in developmental capacity, the other describing subsequent growth. However, a single developmental scale was used to describe dormancy alleviation and bud development and to replace separate chill unit and heat unit indices since it better reflects the nature of the 'temperature stress' scenario. This is because the principal effect of the inhibitory process is to prevent progress of the developmental process which ultimately alleviates the inhibition. The situation is therefore one of negative feedback. Only one positive process occurs (summarised under the category 'growth') which itself induces the progressive physiological shift (Saure, 1985) which simulates dormancy alleviation. In this respect the proposed model is similar to a model of apple fruit bud development (Landsberg, 1974) in which growth rate is a function an empirical dormancy index and the temperature-weighted passage of time (i.e. heat unit accumulation). The model is consistent with observations of a number of species which indicate that the relationship between development and temperature alters if the modelled period of development is sufficiently extensive (Porter and Delecole, 1988; Pollock and Eagles, 1988). This phenomenon is readily handled in the proposed model by means of the function which relates simulated temperature response to developmental position on the scale. Continuity of movement along this scale without dramatic steps also appears consistent with the results of budwood forcing experiments (Chapter 5) which suggest that the potential for bud break and extensive development increase progressively over winter (Fig. 5.6b and Fig. 5.8c,d).

Introducing the concept of a progressive 'shift' in the temperature optimum has the consequence that   temperature integral (CU and GDH°C sums) are no longer the principal parameters by which the phenology of different cultivars is interpreted. With Utah chill unit-type models, there is a single, fixed relationship between temperature and development which is simulated by summing the thermally-weighted passage of time (Table 6.2). Such models (Richardson et al., 1974; Shaltout and Unrath, 1983) plus other similar phenology models incorporating alleviation of dormancy (Bidabé, 1963; Cannell & Smith, 1983; Fishman et al., 1987a) are therefore biphasic. The developmental distance from dormancy induction to budbreak (or flowering) is divided into two distinct phases within each of which a constant temperature-development relationship applies. Phenological differences between cultivars and species are reflected in the duration required to reach a particular stage of interest and therefore sums to the same stage for different cultivars differ. Large heat or chill unit sums indicate slow development and conversely, smaller sums indicate more rapid development. Consequently, accumulated CU or GDH°C on a given day can only be compared relative to the total required.

The alternative adopted by the PHYSHIFT model proposed in this chapter is to regard the developmental distance between phenological stages as constant. Consequently, it is the rate with which that distance is covered which varies between cultivars. The model therefore has parallels with the Degree Growth Stage model of cold acclimation and dormancy development (Kobayashi et al., 1982) which divides the annual development cycle into 360° and places four phenologically-significant events at the cardinal points of the compass (0°, 90°, 180°, 270°). Submodels with different coefficient for different genotypes simulate development between the cardinal points which are located in the same position for each plant. For the proposed model, different relative development rates are achieved by varying D_i, the initial depth of dormancy, or r, the parameter determining the dependence of dormancy alleviation on developmental distance. Hence, the simulated growth rate of a cultivar with relatively shallow initial dormancy ($D_i > 0$), or relatively high initial sensitivity to developmental position ($r < 1$), is more rapid than

Table 6.2   Two alternative methods of modelling cultivar-specific phenological differences.

Model type	Temperature-dependence of growth rate	Integral of growth rate to same stage of development
Chill unit	Fixed	Variable
PHYSHIFT	Variable	Fixed

growth for a cultivar with deeper dormancy ($D_i < 0$) or low initial sensitivity to developmental position ($r > 1$).

Application of the proposed model to distinguish the causes of phenological differences between cultivars therefore focuses on the relative depth of dormancy and its relationship with relative developmental position rather than the relative duration of dormancy. Unlike chill unit-type models there is no fixed relationship between the passage of time and the integral used to simulate development. Consequently, developmental events occurring at regular intervals while temperature is constant need not be separated by identical growth rate integral (i.e. developmental distances). If the simulated temperature response changes between otherwise identical time periods (either in the optimum temperature for growth or in its sensitivity to developmental position) then the simulated developmental distance covered during that period will also differ. For instance, change in developmental position during the latter part of an extended period of chilling at, say, 8 °C, will be greater than that during the initial period since the physiological shift simulated in the intervening period means the buds are now more responsive to warmth.

The actual numerical values given to the growth rate, k, (and therefore also d_{ij} and d_{ref}, the growth rate integral to time t_j and to the time when dormancy alleviation is complete) are arbitrary and are ultimately determined by the value given to A, the Arrhenius constant. This value was chosen to make $k = 1$ at 25 °C for the selected set of values for E_a, ΔS and ΔH_{ref} (Table 6.1) to simplify comparison of growth rates relative to the maximum rate possible. The value of d_{ref}, the growth rate integral by which development position is relativised with respect to the point at which dormancy is completely alleviated, is therefore directly affected by the value given to A. Higher values of A necessarily lead to higher values of d_{ref}. It is also affected by the values of D_i and r and therefore comparisons between the respective values of D_i and r for different cultivar models only have meaning for a common value of d_{ref}.

The proposed model is also distinguished from existing chill unit-type models in that periods of supra-optimal temperature do not reverse any development which has already occurred. Rather, periods of supra-optimal temperature only affect the potential for subsequent development. Thus, while C, the developmental capacity, may rise or fall in response to diurnal temperature variation, change in d_{ij} / d_{ref}, the relative develop-

mental position, is always positive. The concept of 'chilling negation', used previously (Erez et al., 1979a) to account for inhibition of dormancy alleviation by periods of high temperature, is therefore not used in the proposed model. This concept implies that low temperature exposure creates a labile physiological state in dormant buds that may be erased by subsequent periods of high temperature until it is 'fixed' hours later. The concept simplifies selection of starting dates for chill unit accumulation since significant accumulation only begins only after the frequency of high temperature interludes declines sufficiently to permit 'fixation' of accumulated chill units. Thus, in chill unit models, the negative effect of high temperature is retroactive, effectively erasing a developmental change (chilling accumulation) which has already occurred. Its significance is entirely dependent on the prior existence of 'unfixed' chilling. In contrast, the PHYSHIFT model assumes that supra-optimal temperature only has an effect on the potential for development subsequent to exposure to high temperature. This type of carry-over effect is observed when stem elongation and respiratory activity are precisely measured before and after transfer to new temperature levels (Rank et al., 1991; Tutty et al., 1994). Carefully-designed controlled temperature experiments involving appropriate cyclic temperature regimes may be able to determine whether dormant buds respond similarly or whether developmental negation better describes bud response. The results might also indicate whether dormancy alleviation involves alleviation of an inhibition (PHYSHIFT model) or redressing a deficiency by the creation of a new condition or substance necessary for growth (chill unit models).

The physiological validity of this and the other hypotheses underlying the PHYSHIFT model framework is likely to have a significant effect on its generality. This is turn affects its value for assessment of pollenizer suitability since 'portability' of cultivar-specific models from one region to another greatly enhances the database on which predictions can be made. In this respect, the ecological significance of dormancy as a mechanism to avoid the lethal effects of temperatures well below 0°C highlights the large difference between the climate of Hawkes Bay and the continental regions to which apricots are indigenous. The Hawkes Bay climate also differs markedly from that of Central Otago, the main apricot growing region in New Zealand as do the climates of regions from which apricot cultivars grown in Hawkes Bay are drawn (Chapter 5). However, the simplifications and assumptions implicit in empirical devices such as the chill unit mean they are most likely to perform well in only a few of these situations. In

contrast, a more general model of apricot phenology, suited to a range of cultivars and environments and which allows extrapolation of data from one region to another, will require greater flexibility and physiological realism.

The proposed model does offer a very large measure of flexibility.   There are numerous model constants which could be systematically (or arbitrarily) altered to improve the fit of the model to individual data sets. However, the validity of physiological conclusions drawn from relative parameter values depends on whether the simple inactivation process which is modelled adequately encompasses the mechanism by which the temperature response of dormant buds is determined. For instance, study of regulation of metabolic systems such as that of photosynthesis indicates that a variety of coarse and fine control methods determine overall activity (Raven, 1981). In this respect, the model does not integrate the effects of other environmental factors such as water status, photoperiod, light intensity, light quality and rainfall (Brown 1953; Erez et al., 1968; Gilreath and Buchanan, 1979; Romberger, 1963; Westwood and Bjornstad, 1978) but the fact that all may affect bud development and dormancy alleviation suggests control of dormancy and is likely to be much more complex reflecting the interaction of a number of component sub-processes. The model also does not reproduce the promotion of bud development caused in some cases by brief exposure to high temperatures (i.e. 40°-50°C) nor does it address the possibility that the optimum temperature for development may be higher during the day than at night (Robertson, 1968). Consequently, the modified Arrhenius response used in the proposed model is probably best regarded as an empirical simulation of the overall temperature-dependence of observed growth rate rather than a strict physiological description. Independent investigation of the physiological hypotheses underlying the model is needed before precise physiological meaning can be given to the model parameters. This is, however, not a possibility with other chill unit models, the 'Dynamic' model (Fishman et al., 1987a) excepted.

Furthermore, the model does not address the issue of the level of integration at which the control of temperature response operates, either within the bud itself or within the plant as a whole. The simple structure of the model assumes buds act as units and suggests that all tissues respond to temperature uniformly without interaction. However, dormant buds possess a substantial degree of differentiation and it is possible that the growth of all tissues may not be equally suppressed. Particular tissues may play a more active role in

the regulation of growth than others. This is suggested by research which shows that translocation to the bud is influenced by changes to membrane permeability in the tissue directly below the bud (Gendraud and Laflueriel, 1983). Hence, the observed temperature response may reflect the response of a critical but localised process rather than one which is common to all bud tissues. If this is the case then unsynchronised change in temperature response of flower bud parts could, for instance, be responsible for flower bud development anomalies reported in some climates (Guerriero and Bartolini, 1991). Measurement of relative rates of transport and incorporation of labelled carbohydrate or other tracers into various bud tissues might indicate the level of organisation within the bud at which the observed temperature reponse is determined.

The interaction of the bud with the metabolism of the whole plant is also not explicitly considered by the model. This point is highlighted by the recent differentiation of the 'classical' (or hormonal) and 'French' (or correlative) schools of dormancy research (Dennis, 1994). The fundamental simplicity of a single enzymatic mechanism acting as the sole control point for temperature response suggests that in this respect the PHYSHIFT model fits readily within the purview of the 'classical' school. Molecular techniques proposed for the study of dormancy (Lang, 1994) may in future identify the metabolic site the physiological shift proposed. However, enzymatic inactivation alone appears to be a rather coarse method of control in comparison with the more subtle methods of metabolic control which regulate complex process such as photosynthesis (Raven, 1981). Furthermore, dormancy may be controlled by the interaction of short and long range correlative influences (Balandier et al., 1993; Crabbé, 1990; Gendraud and Laflueriel, 1983). In both these situations the Arrhenius temperature response function of the proposed model is then most probably not a precise mechanistic representation but an empirical description of the response of dormant buds. Such an empirical approach may ultimately prove to be the more efficient modelling approach given the potential complexity of a fully-mechanistic model if the processes underlying the physiological shift are more complex than those assumed by the PHYSHIFT model. Resolution of this issue will require comprehensive experimental study which compares the progressive physiological changes of whole plants and single bud explants, not only under a single artificially-constant temperature regime but also at a variety of temperature levels and cyclic temperature treatments.

6.5   References

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Chapter 7
Modelling Apricot Flower Bud Development

7.1 Introduction

The quantitative dormancy paradigm and resulting PHYSHIFT model presented in the previous chapter represents a distinct break from other models of dormancy and bud development. The suggestion that dormancy alleviation reflects a progressive change in temperature response is, in itself, not new and has been made previously on the basis of experimental observation (Vegis, 1964) and physiological speculation (Saure, 1985). The general concept has also been used empirically as the basis for modelling of bud development (Cannell and Smith, 1983; Landsberg, 1974). However, these and other models are fundamentally durational in that a common temperature integration scheme is the principal method of developmental simulation and genotypic differences are expressed in terms of time periods of temperature exposure. Most adopt a bi-phasic approach, distinguishing a low temperature (chilling) response from a subsequent high temperature response (Bidabé, 1967; del Real Laborde et al., 1990; Gilreath and Buchanan, 1981; Richardson et al., 1974; Shaltout and Unrath, 1983). The proposed PHYSHIFT model is also distinctive in that it does not assume that low temperature acts through a process which creates a special dormancy breaking factor as assumed for the 'Dynamic' model (Couvillon and Erez, 1985; Fishman et al., 1987a). Rather it assumes that low temperature promotes development during winter dormancy by progressively removing the inhibitory effect of high temperature on bud metabolism as proposed by Salisbury and Ross (1969) and Saure (1985). Hence, in this respect it is also distinguished from the 'Dynamic' model.

At this point it is not possible to assess the validity of the hypotheses underlying the PHYSHIFT model since data describing the physiology of dormancy are still sparse. Nor is it possible to predict its accuracy under Hawkes Bay conditions if it were to be

used as an entirely empirical model for apricot bloom phenology. However, the differences between the PHYSHIFT and other dormancy models mean it is possible the new model may respond to specific temperature conditions in a manner quite different to that observed and therefore fail entirely to simulate the actual process of bud break and development. For instance, the inability of the 'Utah' chill unit model to accurately predict bud break under cyclic temperature conditions is well established (Couvillon and Erez, 1985; Erez and Couvillon, 1987) whereas the performance of the 'Dynamic' model appears more satisfactory (Fishman et al., 1987b).

By contrast, there has been no systematic investigation of a model incorporating a progressive 'physiological shift'. This chapter therefore presents an initial comparison of development simulated by the proposed PHYSHIFT model with actual bud development under known temperature conditions as an evaluation of the model's hypotheses. The comparison was based on a set of experimental temperature regimes that were used to establish the inadequacy of the 'Utah' model under cyclic temperature conditions (Couvillon and Erez, 1985; Erez et al., 1979; Erez and Couvillon, 1987). The results from this set of experiments were also used to justify the physiological hypothesis underlying the 'Dynamic' model. Hence, simulations by the proposed model also test the assertion by the creators of the 'Dynamic' model that 'chilling enhancement' and 'negation' at the same high temperature in a diurnal cycle can be explained only when two antagonising reactions are promoted by the same temperature at the same time (Couvillon and Erez, 1985).

7.2   Methods and Materials

7.2.1   PHYSHIFT Simulation Program

The equations comprising the proposed model were compiled as PHYSHIFT.EXE, a DOS computer program for IBM-compatible computers, using Borland Turbo Pascal 6.0 (Appendix 2). The program simulated dormancy alleviation from temperature data files representing either simulated controlled-temperature experiment treatments or temperature files for periods corresponding to bloom phenology records (Fig. 7.1). For

File type		File contents	
▯	Text file	hrtemp01.dat	Hourly temperature data
		arrheniu.con	Arrhenius equation constants
▭	Executable file	iteratio.par	Iteration parameters (d_{ref} & D_i)
		example.exp	Temperature files & experimental data
		example.phn	Temperature files & phenological data
		example.rcd	Simulation log file
		example.out	Hourly or daily simulation values
		example.fin	Final simulation values

Figure 7.1   Flow diagram for simulation of dormancy alleviation and bud growth by PHYSHIFT model program using temperature regimes which represent experimental treatments and field temperature conditions corresponding to phenological records.

convenience, the model calculations were based on hourly temperature values. However, this time interval (relative to the total duration of simulation) also corresponded to that giving the minimum numerical integration error for the simple (Euler) integration method employed to measure development progress (Thornley and Johnson, 1990). Filenames for temperature data files collectively comprising the temperature regimes of a controlled-temperature experiment or those corresponding to a set of phenological records were stored in files ('.exp' and '.phn' respectively) along with the dates of 5% and 90% Bloom in the case of phenological data files (Appendix 3). Values for the Arrhenius equation constants (A, E_a, ΔS, ΔH_0, ΔH_1) and iteration parameters for d_{ref} and D_i were stored in separate files. The names of these files, data specifying the response of dormancy alleviation to development (i.e. the form of the physiological shift: linear or logistic, plus the value of r), and the name of the file storing temperature data filenames were then stored together in the main input file ('.inp') the name of which could be passed to PHYSHIFT.EXE as a command line parameter along with output options. The program calculated values of developmental distance, d_{ip} relative dormancy, D_j and developmental capacity, C_j for each combination of d_{ref} and D_i specified. Values of d_{ip} D_j and C_j could be output in several ways: hourly, daily (at 24:00 hours), as a final summary at the end of a simulated experimental temperature regime, or (for comparison with phenological data) daily for the period preceding date of a phenological record.

7.2.2   Model verification

Confirmation that the proposed model reproduced the general pattern of bud response to cyclic temperatures was based on results of temperature regimes drawn from published controlled-environment experiments (Table 7.1). These studies (Erez et al., 1979; Couvillon and Erez, 1985; Erez and Couvillon, 1987) illustrate the effect of constant and cyclic temperatures on dormancy alleviation in leaf and flower buds of peach (*Prunus persica* (L.) Batsch) and, in particular, effects of various characteristics of cyclic temperature regimes. These characteristics include: the relative level of the temperature maximum in the cycle, the overall cycle duration, the duration of the high temperature maximum, the position of the high temperature cycle in the total period of chilling and the relative level of the low temperature minimum in a diurnal cycle. The original figures are presented in Appendix 4. Compable data for apricots are not yet available.

Table 7.1   Details of simulated controlled temperature treatments used to compare output from the proposed PHYSHIFT model with actual dormancy alleviation and bud development.

Regime	Details of simulated conditions	Reference	Appendix 4
Constant	Constant temperature, 0° to 22°C	Erez and Couvillon, 1987 (Fig. 1)	Fig. 1
Cyclic 1 (Maxima level)	16 h at 6°C cycled with 8 h at 7° to 26°C in a 24 h diurnal cycle	Erez and Couvillon, 1987 (Fig. 3)	Fig. 2
Cyclic 2 (Cycle duration)	Exposure to 4°C cycled with 24°C in 2:1 ratio under 1,3,6 & 9 day cycles	Erez et al., 1979b (Fig. 3)	Fig. 3
Cyclic 3 (Maxima duration)	Exposure to 4°C cycled with 0, 2, 4, 6 and 8 h at 20° or 24°C in a 24 h cycle	Couvillon and Erez, 1985 (Fig 2)	Fig. 4
Cyclic 4 (Cycle timing)	16 h at 4°C cycled with 8 h at 15°C, in first, second and last third of chilling	Erez and Couvillon, 1987 (Fig. 4)	Fig. 5
Cyclic 5 (Minima level)	16 h at 15°C cycled with 8 h at 0°, 4° and 6°C in a 24 h cycle	Erez and Couvillon, 1987 (Fig. 2)	Fig. 6

The simulated response to constant temperatures between 0°C and 22°C of the PHYSHIFT model was investigated using a standard 50 day duration (1200 h) as had been used by Erez and Couvillon (1987). In each case, the 50 day exposure was followed by 14 days at 22°C to simulate a period of forcing. Final developmental distance was calculated to permit comparison with observed floral and vegetative bud break fraction on 'Redhaven' peach plants in the original experiment (Erez and Couvillon, 1987: Fig. 1). The relative sensitivity of simulated development to initial relative dormancy, D_i was investigated under this constant temperature environment. The effect of altering the relationship between developmental distance and relative dormancy so that the 'physiological shift' function was linear, power or logistic was also investigated, as was changing the value given to r, the parameter which determined the shape of the physiological shift. More detailed comparison of the time course of the simulated response was performed for three selected temperatures (4°, 8° and 12°C) to visualise the daily progression of relative developmental distance, relative dormancy and developmental capacity. The effect of varying the duration of constant temperature before submitting plants to forcing was also investigated for temperatures between 0°C and 22°C for durations of 33, 50 and 75 days (792 h, 1200 h and 1800 h). In each case,

the initial period of exposure was followed by 14 days at 22°C. Durations represented insufficient, marginal and sufficient low temperature exposure to alleviate dormancy.

The response of three model variables was measured: d, the developmental distance covered within the period of the simulated experiment, D, the relative dormancy corresponding to the developmental distance covered at any given time during that period, and C, the developmental capacity. When C was calculated daily, the level at midnight (00:00) at the completion of the high temperature period was used as a representative value for comparison. Identification of optimum values for D_i, d_{ref} and Arrhenius equation constants (E_a, ΔS, ΔH_0, ΔH_1) which minimised the error between observed and predicted development was not attempted since the material used in the studies on which this analysis was based varied between experiments. Appropriate values for d_{ref} were not known and therefore each simulation was run using six sets of model parameters consisting of factorial combinations of two relative dormancy levels (D_i=0.00 and D_i=0.05, equivalent to initial low temperature optima of around 5°C and 7°C) and three values for d_{ref} which varied as the value given to r and the nature of the relationship between developmental distance and dormancy alleviation was altered. Results presented are those derived using the values for Arrhenius equation constants which yielded a growth rate temperature optimum of intermediate width (Table 6.1).

Investigation of the effect on model behaviour of the level of the cycle maximum in a simulated diurnal cycle followed the pattern of treatments used by Erez and Couvillon (1987). Floral and vegetative bud break fraction on 'Redhaven' peach was the variable measured in the original experiment. Final developmental distance was calculated for simulated temperature regimes where low temperature exposure (6°C) was interrupted with an 8 h period of warmer temperature at 7°C to 26°C for a duration of 75 cycles (1800 h). In each case, the simulated low temperature treatment period was followed by 14 days 'forcing' at 22°C. Diurnal temperature cycles were 'square-waves' in which transitions to a new temperature were immediate and not progressive. The start of the low temperature period was used as the beginning of the cycle so that the high temperature period always followed the low temperature period. 1200 h constant 4°C and 6°C were used to represent control regimes as in the original experiment. Daily values of relative development distance, the corresponding value for relative dormancy

and the developmental capacity at that point were calculated to produce response profiles for the entire simulated 6°C / 18°C temperature regimes. Hourly response profiles were also calculated for two temperature regimes, 6°C / 18°C and 6°C / 22°C.

Investigation of the behaviour of the model under cyclic temperature conditions was completed by consideration of the effects of total cycle length, duration of the high temperature period and level of the low temperature period on final developmental distance at the completion of the combined low temperature and forcing period. Simulation of varying total cycle duration involved temperature regimes used by Erez et al. (1979). In this experiment, lateral and terminal vegetative bud break on 'Redhaven' peach plants was measured after chilling at 4°C during which low temperature conditions were cycled with 24°C in a constant 2:1 exposure time ratio while total cycle duration ranged from 1 to 9 days. Simulation of varying the high temperature exposure duration (assuming a 'square-wave' diurnal temperature cycle) used temperature regimes from an experiment in which vegetative bud break had been measured after 'Redhaven' peach plants were chilled at 4°C and periodically warmed to 20°C or 24°C for durations between 2 h and 8 h in a 24 h cycle (Couvillon and Erez, 1985).

The effect of changing the time at which plants experienced warm period interruptions to chilling was investigated using temperature treatments from a study of floral and vegetative bud break fraction on 'Redhaven' peach plants (Erez and Couvillon, 1987). Bud break had been measured after plants had received 1200 h at 4°C but in those treatments where plants were exposed to cyclic temperature conditions, warm period interruptions occurred in the first, second or last third of chilling. A continuous 4°/15°C cyclic treatment was also included. Finally, investigation of the proposed model's behaviour when the minimum temperature of a temperature cycle was progressively varied used the temperature regimes from a study of lateral vegetative bud break fraction on 'Coronet' peach plants (Erez and Couvillon, 1987). Bud break had been measured after 900 h of low temperature exposure in which the daily temperature cycle minima were varied between 0° and 6°C while the cycle maxima remained at 15°C. In all investigations the simulated cyclic temperature treatment was followed by 14 days at 22°C to reproduce the effect of forcing which was part of the original experiments.

7.2.3   PHYSHIFT Apricot Bloom Phenology Models

Initial investigation of the behaviour of the PHYSHIFT model under field conditions used hourly data series describing air temperature at HNRC (Havelock North Meteorological Station, D96689) from March 1 to September 30 in 1988 and 1989. These years were chosen for the temperature conditions they displayed.   Daily temperature maxima were higher in the autumn of 1989 than in 1988 while, in winter, temperature maxima were higher in 1988 than in 1989.   A simple piecewise linear relationship between developmental distance and relative dormancy was assumed (i.e. $D_j = d_{ij} / d_{ref}$, $d_{ij} \leq d_{ref}$; $D_j = 1$, $d_{ij} > d_{ref}$; $r = 1$) and the same values for d_{ref} (120, 150 and 180) were used as for previous simulation of experimental temperature regimes. Daily values for C, D and d_{ref} were calculated to follow the simulated alleviation of dormancy and subsequent growth of buds over the winter period.

Provisional PHYSHIFT phenology models were developed for 'Royal Rosa', 'Sundrop' and 'Trevatt' apricots using bud development observations made at Campbell, Fernhill Farm and Stirling orchards in 1992. The models assumed that the response of dormancy alleviation to development from the initial starting point was linear ($r = 1$, as above) and that the differing phenology of the three cultivars reflected differences in the initial level of dormancy and the rate at which dormancy was alleviated, determined by d_{ref}. Values for initial dormancy were $D_i = -0.2$ to $D_i = 0.1$ (0.025 increments representing initial temperature optima at deepest dormancy of 1°C to 7°C respectively). Values of d_{ref} were $d_{ref} = 60$ to $d_{ref} = 180$.

The 'best' model for each cultivar was selected by identifying the values of D_i and d_{ref} which minimised the coefficient of variation for d_{ij} / d_{ref} at 5% Bloom. This procedure reflects an assumption that each cultivar reaches an equivalent phenological stage at the same developmental distance from the initial point of deepest dormancy at all sites. Simulated development corresponding to 5% Bloom was calculated by regressing the bud development stages (expressed as adjusted stage values, s') against the corresponding simulated development value. A logarithmic model, $s' = b_0 + b_1.\ln(d_{ij} / d_{ref})$, satisfactorily approximated the relationship between adjusted phenological stage and

simulated development over the range of values of D_i and d_{ref} ($R^2 = 0.97$ to $R^2 = 0.99$). Least squares regression was performed using PROC REG of SAS (SAS Institute, 1989). Simulated development at 5% Bloom was calculated as

$$(d_{ij}/d_{ref})_{5\% \, Bloom} = e^{\left(\frac{6.05 - b_0}{b_1}\right)} \qquad (7.1)$$

where b_0 and b_1 are the regression parameters for the intercept and slope respectively and 6.05 is the adjusted phenology scale value corresponding to 5% Bloom.

7.3   Results

7.3.1   PHYSHIFT Simulation of Bud Development

7.3.1.1   Constant temperature conditions

Simulations run using 1200 h constant temperature regimes demonstrated that the
PHYSHIFT model did reproduce the 'bell-shaped' temperature response reported for
dormancy alleviation. The simulations were run for temperatures between $0°$ and $22°C$,
followed by a 14 day (336 h) period of 'forcing' at $22°C$, and at two values of initial
dormancy ($D_i = 0.00$ and $D_i = 0.05$) and three values of r (0.5, 1.0 and 2.0) under the
assumption that the linkage between dormancy alleviation was a linear function of
developmental distance (Fig. 7.2b), a power function (Fig. 7.2a,c) or a logistic function
(Fig. 7.3). Each variable altered the shape of the simulated response curve in a
distinctive manner. Varying r, the parameter controlling the shape of the physiological
shift' function, had the effect of altering the relative duration of the developmental period
which is characterised by a low temperature optimum in comparison to the time spent
with a higher optimum. When r was low ($r=0.5$; very rapid initial alleviation of
dormancy), the simulated developmental response showed a broad temperature optimum
with an apparent maximum (under the treatment regimes imposed) of $12°$ to $17°C$,
depending on values for d_{ref} and D_i (Fig. 7.2a i-iii). As r was increased (i.e. relatively
slower initial dormancy alleviation) the breadth and position of the apparent optimum
temperature range for bud growth over the duration of the experiment changed. The
position of the optimum declined on average by about $5°C$ when r was increased to 1.0
(Fig. 7.2b) and dropped by a further $4-5°C$ when r was increased to 2.0 (Fig. 7.2c). At
the same time, the breadth of the optimum also fell, reducing from $10-15°C$ to as little
as $5°C$.

Lessening the initial depth of dormancy ($D_i=0.00$ to $D_i=0.05$, equivalent to raising the
initial growth response temperature optimum by about $2°C$) affected the simulated
development response asymmetrically, favouring development at temperatures higher
than the apparent optimum while having little effect at temperatures below the optimum.
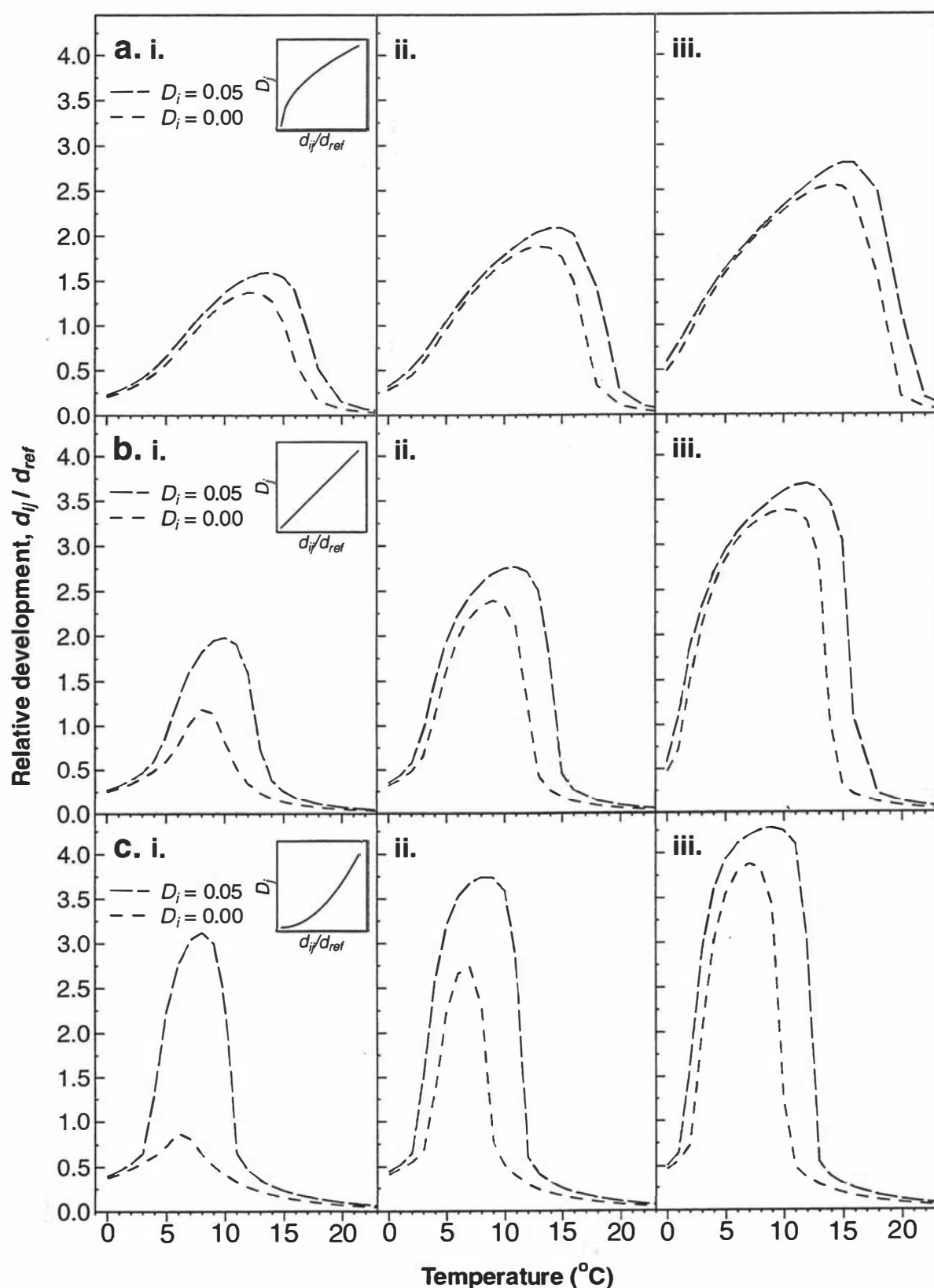
Figure 7.2   Bud development after 50 days (1200 h) constant temperature conditions and 14 days 'forcing' at 22°C simulated by the PHYSHIFT model using linear or power functions to relate dormancy alleviation to developmental position. (E_a = 12500 K, $\triangle S/R$ = 100 K, $\triangle H_0/R$ = 27850 K, $\triangle H_1/R$ = 30000 K.)

a). r=0.5: i). d_{ref} = 300; ii). d_{ref} = 250; iii). d_{ref} = 200. b). r=1.0; i). d_{ref} = 180; ii). d_{ref} = 150; iii). d_{ref} = 120. c). r=2.0; i). d_{ref} = 110; ii). d_{ref} = 100; iii). d_{ref} = 90. (Inset figures represent relationship between dormancy alleviation and developmental position.)

The breadth of the optimum temperature range was increased in this way by 2-3 °C, depending on values for r and d_{ref}. The value given to d_{ref} also had a pronounced effect on the developmental position reached at the conclusion of the simulated experiment since it affects the absolute rate at which dormancy is alleviated. Increasing d_{ref} represents an increase in the developmental distance to full dormancy alleviation. Therefore, simulated development was less advanced at the time of transfer to the 'forcing' conditions when d_{ref} was relatively high for each value of r. In the extreme case (Fig. 7.2c i: D_i=0.00), dormancy was still sufficiently deep (i.e. there had been little upward movement in   growth rate temperature optimum) that the simulated growth response on transfer to 'forcing' was completely suppressed.

Simulations run with a logistic function linking dormancy alleviation to developmental distance (Fig. 7.3) displayed slightly narrower apparent temperature optima ranges at the conclusion to the temperature treatment than did those using a linear or power function linkage (Fig. 7.2). Sensitivity to d_{ref} was again greatest at high values of r (i.e. relatively slow initial dormancy alleviation). The effect of increasing d_{ref} by 50% was relatively small when $r = 0.5$ compared to the dramatic effect of increasing d_{ref} by 25% when $r = 2.0$. In the first case, maximum developmental distance (d_{ij}/d_{ref}) increased on average from 1.5 to 3.0 and the range of temperatures at which significant growth had occurred by the end of the temperature regime from 3°-12°C to <0°-15°C (Fig. 7.3a i-iii). However, in the second, maximum development increased on average from under 1.0 (Fig. 7.3c i) to almost 4.0 and the range of temperatures at which significant growth occurred from a very restricted range at 6°C to, at greatest, 3°-11°C. Sensitivity to D_i was also greater for $r > 1$ (slow initial dormancy alleviation) than for $r < 1$ (rapid initial dormancy alleviation). For $r < 1$ (Fig. 7.3a and also Fig. 7.2a), changing D_i from 0.00 to 0.05 had the uniform effect of increasing the apparent responsiveness of simulated growth to higher temperatures but for $r > 1$ (Fig. 7.3c and also Fig. 7.2c), the alteration to D_i in some cases made the difference between significant development at the conclusion of the simulated experiment or almost none at all.

When the simulation results are compared with the original experimental results under similar constant temperature regimes (Erez and Couvillon, 1987: Appendix 3, Fig. 1), the
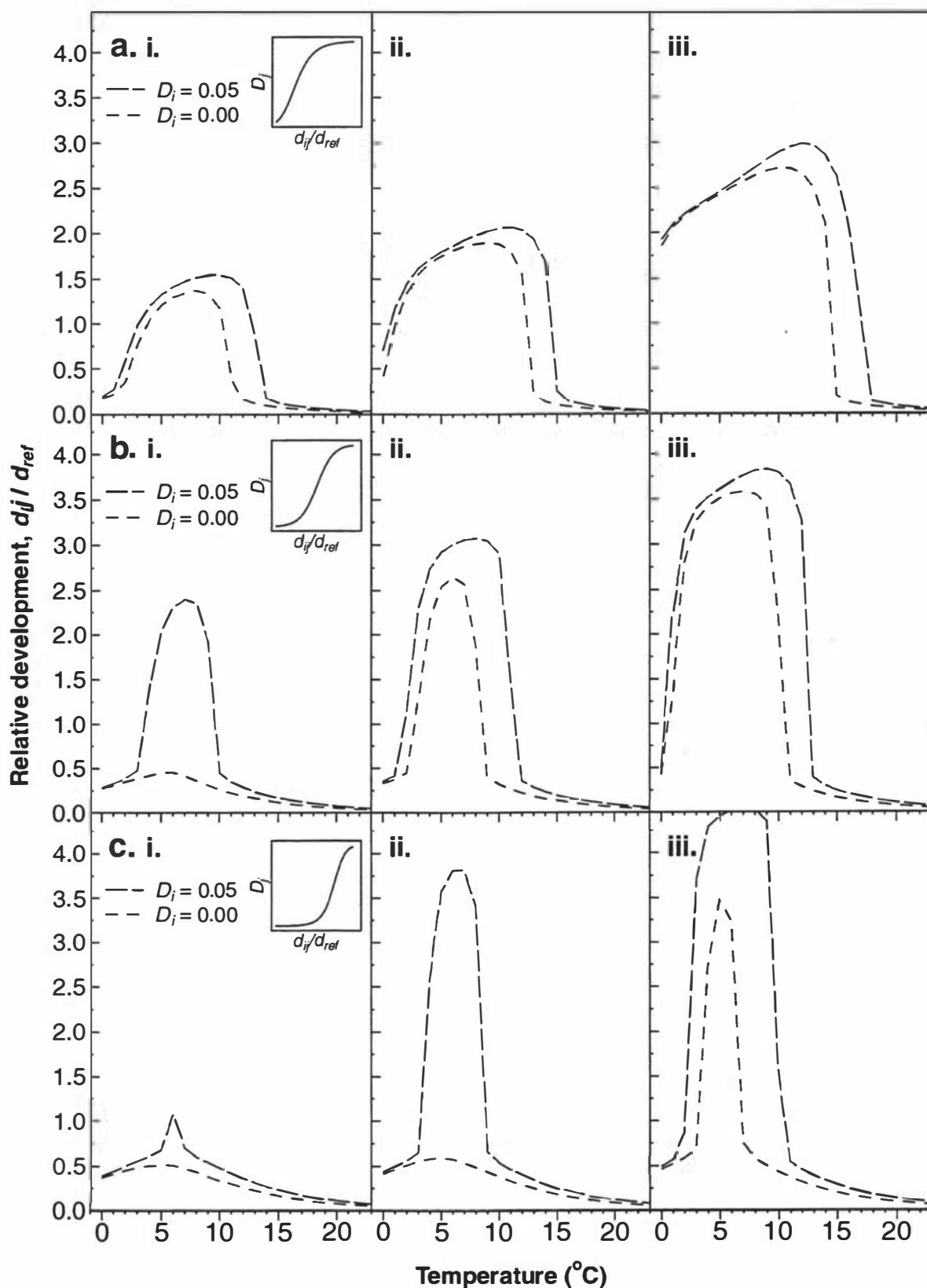
Figure 7.3 Bud development after 50 days (1200 h) constant temperature conditions and 14 days 'forcing' at 22°C simulated by the PHYSHIFT model using a logistic function to relate dormancy alleviation to developmental distance. (E_a = 12500 K, $\triangle S/R$ = 100 K, $\triangle H_0/R$ = 27850 K, $\triangle H_1/R$ = 30000 K.)

a). r=0.5: i). d_{ref} = 300; ii). d_{ref} = 250; iii). d_{ref} = 200. b). r=1.0; i). d_{ref} = 180; ii). d_{ref} = 150; iii). d_{ref} = 120. c). r=2.0; i). d_{ref} = 100; ii). d_{ref} = 90; iii). d_{ref} = 80. (Inset figures represent relationship of dormancy alleviation and developmental position.)

logistic linkage between dormancy and developmental distance did not improve simulation of bud break. Changing the value of r from $r = 1.0$ also did not improve the reproduction of the response of bud break to temperature and the difference between the curves for vegetative and floral bud break could be readily represented by different combinations of values for D_i and d_{ref}. A simple linear relationship ($D_j = d_{ij} / d_{ref}$) between dormancy alleviation and developmental distance was therefore used for subsequent investigation of the simulated response to experimental temperature regimes. The same investigation of model behaviour under constant temperature conditions was conducted using the two alternative Arrhenius equation parameter sets (Table 6.1) which provided both a broader and narrower optimum temperature range for simulated growth rate. The response of simulated development at the end of the experimental temperature regimes was consistent with the underlying Arrhenius growth rate response (respectively broader and narrower) but neither represented a substantial improvement over the response for the intermediate set illustrated.

The daily response profiles for C, D_p and d_{ij} / d_{ref} at 4°, 8° and 12°C illustrated the effects of D_i and d_{ref} on development and dormancy alleviation in more detail (Fig. 7.4 and Fig. 7.5). The values of D_i and d_{ref} (0.00 or 0.05 and 120, 150 or 180 respectively) were those used previously (Fig. 7.2). At 4°C and $d_{ref} = 120$, $D_i = 0.05$ (Fig. 7.4b i) initial developmental capacity was 70% of potential but it increased progressively as dormancy was alleviated. Alleviation had progressed substantially ($D_j = 0.60$) at transfer to 22°C (simulated forcing) and simulated growth accelerates under the warmer conditions. Depression of C on transfer was limited and of short duration but indicated the forcing temperature was still supra-optimal at this point. With $d_{ref} = 150$ (i.e. more extended suppression of growth rate temperature optimum, Fig. 7.4b ii), dormancy alleviation at transfer was slightly less advanced ($D_j = 0.57$) and therefore C suffered slightly greater initial depression before recovery. However, in both cases, continued growth at the new temperature was possible, and therefore the physiological shift necessary to completely alleviate dormancy was able to occur and rapid development began after only a short delay. Developmental capacity did not ever reach 100% since, even with dormancy fully alleviated (i.e. $\Delta H_j / R = \Delta H_1 / R = 30{,}000$ K), 22°C was sufficiently high a temperature to induce significant 'enzyme inactivation' (as presumed by the model's mechanistic
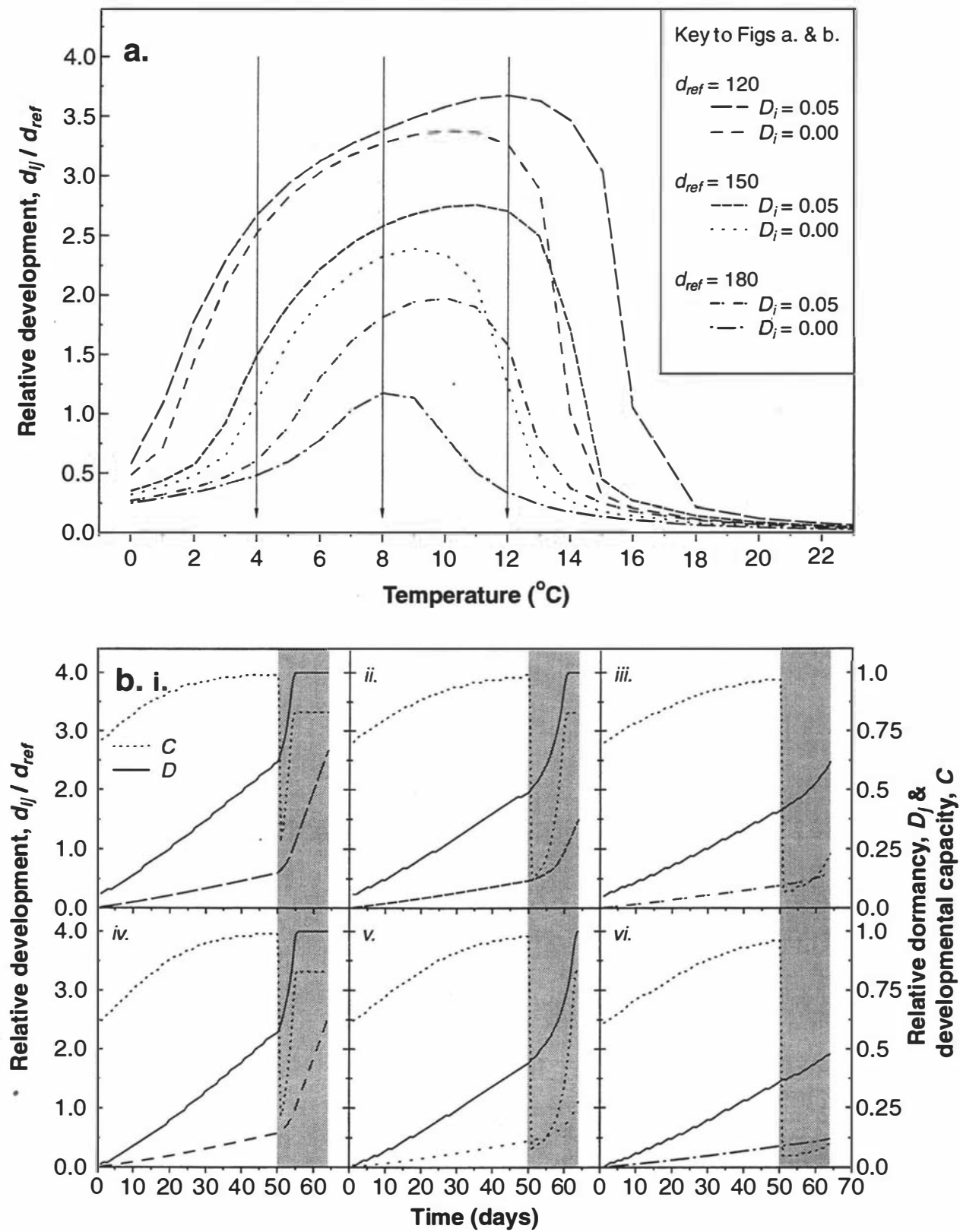
Figure 7.4   PHYSHIFT simulation of bud development under constant temperature regimes. I.
a). Simulated development relative to reference point reached after 50 days (1200 h) constant
temperature followed by 14 days forcing at 22°C.
b). Simulated development profiles at 4°C, including response of developmental capacity and
relative dormancy: i). & iv). d_{ref} = 120; ii). & v). d_{ref} = 150; iii). & vi). d_{ref} = 180. (Shaded region =
period of forcing at 22°C).

hypothesis) and therefore loss of developmental capacity. The effect of transfer to 22°C was increasingly marked with d_{ref} = 150 and d_{ref} = 180 (Fig. 7.4b ii,v and Fig. 7.4b iii,vi) where alleviation at transfer was less than 50% and 40% complete respectively. Exposure to 22°C suppressed C considerably before it began to rise again towards the end of the 14 days forcing due to continued slow development.

At 8°C (Fig. 7.5a), comparatively rapid dormancy alleviation and development meant that dormancy alleviation was either complete at transfer or sufficiently advanced at each set of parameter values to permit almost immediate acceleration of growth after transfer. In each case, C was markedly reduced by exposure to 8°C and in one case (Fig. 7.5a vi) it still had not reached 1.00 at the simulated transfer to forcing. However, in each case, dormancy was fully alleviated after 14 days forcing at 22°C. Speed of alleviation noticeably accelerated around D_j = 0.2 as C rose from its initial value and approached 1.00. This occurred after about 20, 25 and 30 days at 8°C when D_i = 0.05 and d_{ref} = 120, 150 and 180 respectively but was delayed by about 10 days when D_i = 0.00.

The greatest contrast between profiles for D_i = 0.00 and D_i = 0.05 was observed at 12°C at which temperature final development differed considerably (Fig. 7.5b and Fig. 7.4a). Simulated developmental capacity was initially strongly suppressed by exposure to 12°C (C = 0.09-0.12) but the relatively high temperature also meant that growth was able to occur relatively quickly. Therefore, although growth was initially very slow, it was able to accelerate to a much greater extent prior to forcing than it could at either 4°C or even 8°C. For D_i = 0.05 and d_{ref} = 120 (Fig. 7.5a i), developmental capacity, C, approached 1.00 after 40 days and alleviation was complete before 50 days. Alleviation was slower for d_{ref} = 150 and for d_{ref} = 180, it was insufficient to permit immediate acceleration of growth on transfer. However, with D_i = 0.00, dormancy alleviation was only sufficient to permit immediate acceleration of growth when D_{ref} = 120 (Fig. 7.5b i). At the highest value of d_{ref}, alleviation was insufficient to permit any acceleration at 22°C within the 14 days at the forcing temperature (Fig. 7.5b iii).

The PHYSHIFT model predicted that the duration of the initial constant temperature strongly influences the apparent range of effective 'chilling' temperatures as well as the
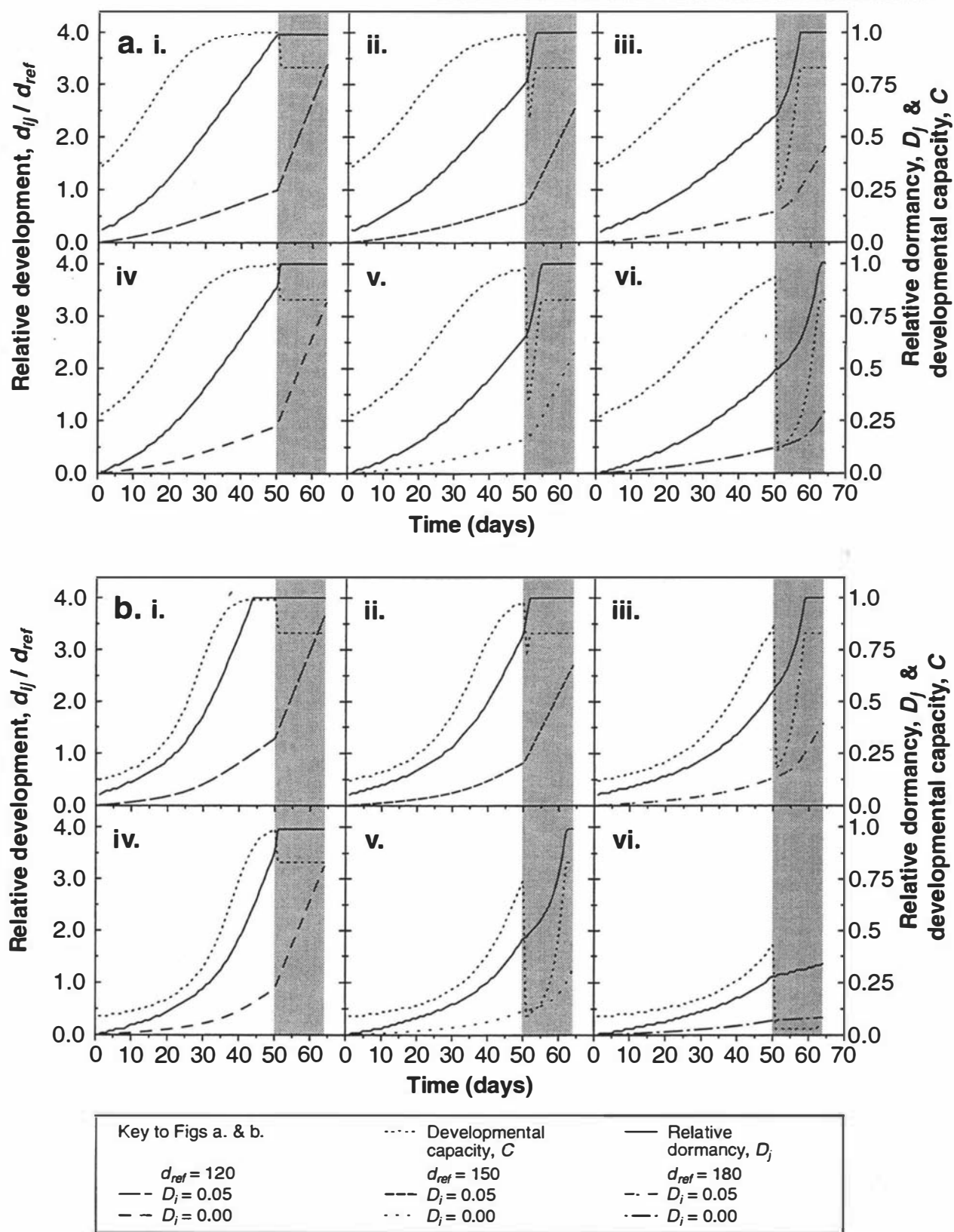
Figure 7.5   PHYSHIFT simulation of bud development under constant temperature regimes. II. (Shaded region = period of forcing at 22°C)

a). Simulated development profiles at 8°C, including response of developmental capacity and relative dormancy: i). & iv). d_{ref} = 120; ii). & v). d_{ref} = 150; iii). & vi). d_{ref} = 180.

b). Simulated development profiles at 12°C, including response of developmental capacity and relative dormancy: i). & iv). d_{ref} = 120; ii). & v). d_{ref} = 150; iii). & vi). d_{ref} = 180.

extent of growth after forcing. This effect is illustrated for 'chilling' durations of 33, 50 and 75 days constant temperature exposure and 'forcing' (Fig. 7.6a). The effect of changing the duration of exposure was very similar to that of changing d_{ref}. The apparent optimum range for stimulation of growth centred on 8°C, shifting upwards to 12°C as duration of exposure increased. At the same time there was also a broadening of the effective range from a narrow band around 8°-10°C after 33 days to 1°-16°C after 75 days. Differences between simulations at $D_i = 0.00$ and $D_i = 0.05$ were most pronounced above 8°C and when forcing occurred after 33 days.

The PHYSHIFT model also predicted that changing the forcing temperature will affect the range of temperatures which apparently promote dormancy alleviation and bud development (Fig. 7.6b). When 14 days forcing at 20°C followed 50 days simulated exposure to temperatures between 0° and 24°, the apparent effective range of temperatures for dormancy alleviation ranges from about 3° to 13°-15°C (depending on values given D_i and d_{ref}). If the forcing temperature was increased to 25°C (the optimum temperature for growth after full alleviation of dormancy), the final extent of development increased at the centre of the effective range but at the same time the width of the apparent effective range narrowed. The narrowing was greater still when the forcing temperature was 30°C (supra-optimal at the Arrhenius constants used for simulations: cf Fig. 6.1). This was due to marked depression of C at the higher forcing temperatures when dormancy was only partly alleviated by the time of transfer. Diminished capacity for growth outweighed the increase in potential growth and consequently, final development at the end of forcing was reduced.

7.3.1.2   Cyclic temperature conditions

The PHYSHIFT model was able to simulate several effects of cyclic temperature regimes, including those induced by varying cycle maximum and minimum temperatures, the total duration of the cycle and the duration of the high temperature period within the cycle. The model reproduced the apparent promotion of dormancy alleviation by diurnal cycling with higher temperatures (Fig. 7.7a). Although temperatures above 15°C inhibited growth when imposed constantly (Fig. 7.2b), such temperatures enhanced growth when cycled for 8 h with 6°C in a 24 h cycle. All promotive cyclic regimes
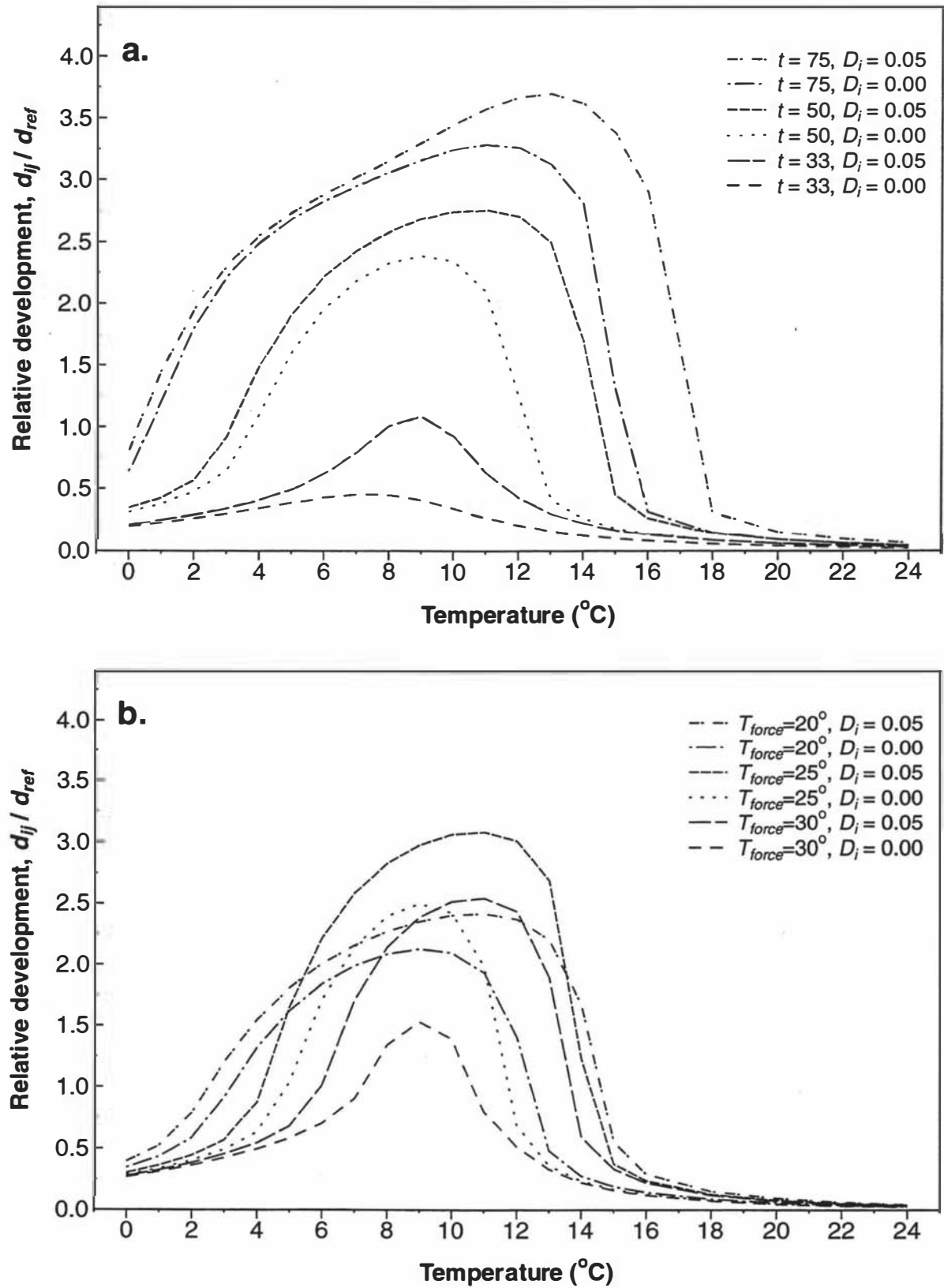
Figure 7.6   Simulated effect of duration of constant temperature exposure and of forcing temperature on the apparent temperature range which promotes development (d_{ref} = 150). a). Simulated relative developmental position after 33, 50 and 75 days constant temperature exposure and 14 days forcing at 22°C. (t = duration of exposure.) b). Simulated relative developmental position after 50 days constant temperature exposure and 14 days forcing at 20°, 25° and 30°C. (T_{force}= forcing temperature.)
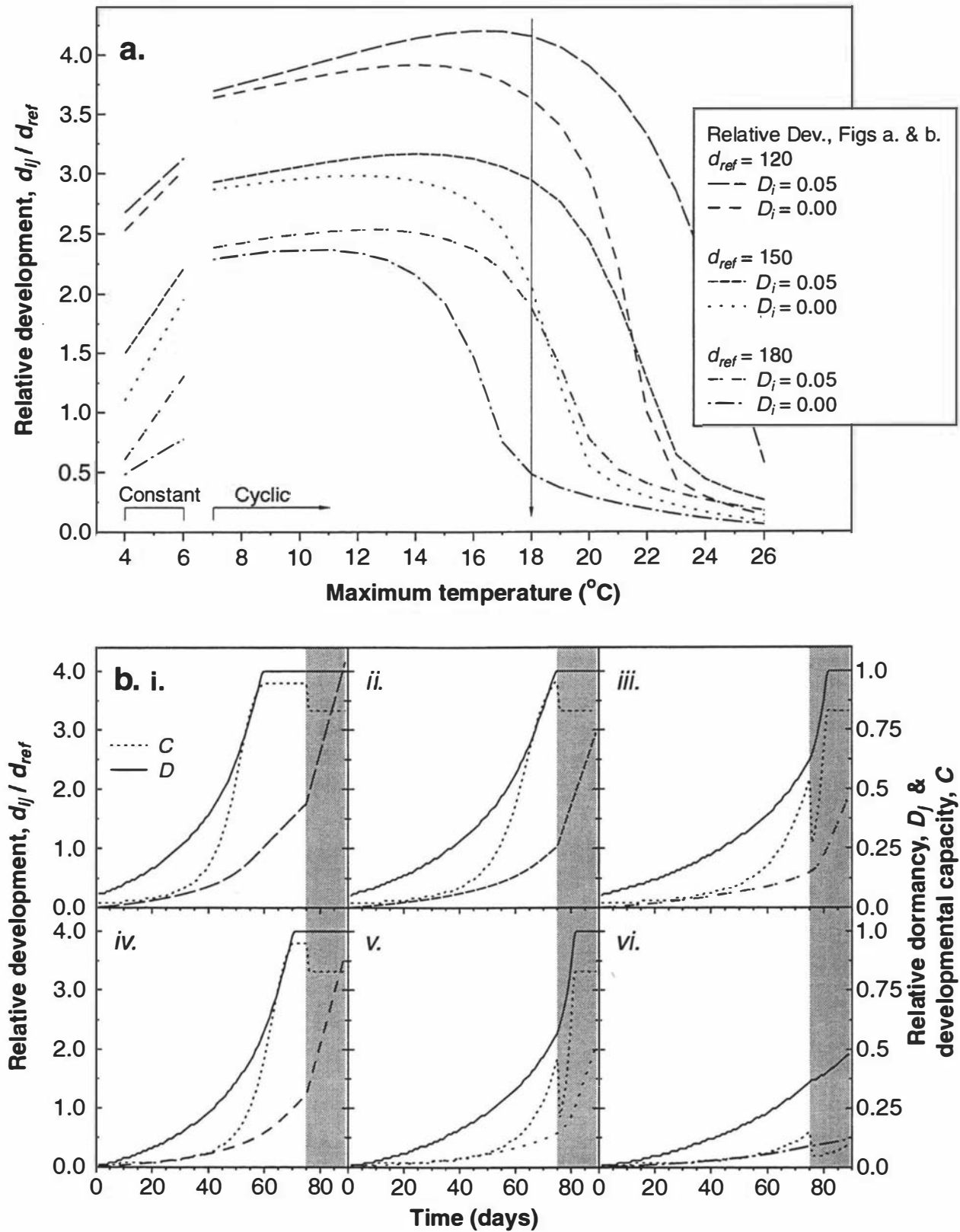
Figure 7.7   Simulation of enhanced bud dormancy alleviation due to cyclic diurnal tempertures. a). Simulated development after 1800 h raised temperature cycle and 14 days forcing at 22°C. (Temperature cycle: 16 h, 6°C / 8 h, raised temperature. Controls: 1200 h 4°C and 6°C constant temperature .)

b). Simulated development profiles at 6°C / 18°C including response of developmental capacity and relative dormancy. (Shaded region = period of forcing. 6°C / 18°C indicated in Fig. a by arrow.)

displayed greater development at the end of forcing (1800 h plus 14 days) than did the two constant temperature controls which included the same number of hours at low temperature (1200 h). The general response was similar to that reported for peach (Erez and Couvillon, 1987: Appendix 3, Fig. 2) except that the model tended to exaggerate the final development achieved at lower values of d_{ref} and predict greater promotion above 15°C than was observed in the actual experiment. At d_{ref} = 120 and D_i = 0.05 the model predicted greatly enhanced development when 20°C is cycled with 6°C whereas bud break on 'Redhaven' was actually reduced by this temperature regime relative to the 4° and 6°C constant temperature controls.

Daily profiles for the 6°C/18°C temperature regime (Fig. 7.7b) illustrate why 'moderate' temperatures appear to promote simulated development when they are cycled with a lower temperature. Two distinct phases were present in each profile where enhanced development was observed before transfer to 22°C. The first was characterised by a slow growth rate before the rise in C. This was followed by the second in which growth accelerated. This was due to depression of C, and therefore growth, by the periods at 18°C experienced before full dormancy alleviation. After alleviation, these periods of relative warmth had little or no impact on C and therefore accelerated growth. When alleviation did occur, it was also quicker than it was at constant temperature (Fig. 7.4b) due to the increasing acceleration of the 'physiological shift' by the 18°C period as dormancy was progressively alleviated.

The diurnal cycles of developmental capacity at several stages of dormancy alleviation illustrated the relative effects of moderate temperatures (15°-18°C), which appear to promote development when cycled with low temperatures, and 'high' temperature (>20°C) which are inhibitory (Fig. 7.8). Under the 6°C/18°C regime (D_i = 0.05, d_{ref} = 150) developmental capacity on days 9 and 10 recovered to the maximum level for 6°C within the 16 h low temperature period, permitting significant growth to occur (Fig. 7.8a i). 18°C still depressed developmental capacity on days 49 and 50 but by days 74 and 75, simulated dormancy alleviation had progressed sufficiently that 18°C was now fully promotive and C was only slightly depressed at the higher temperature. Growth therefore occured rapidly after transfer to forcing at 22°C. The general pattern
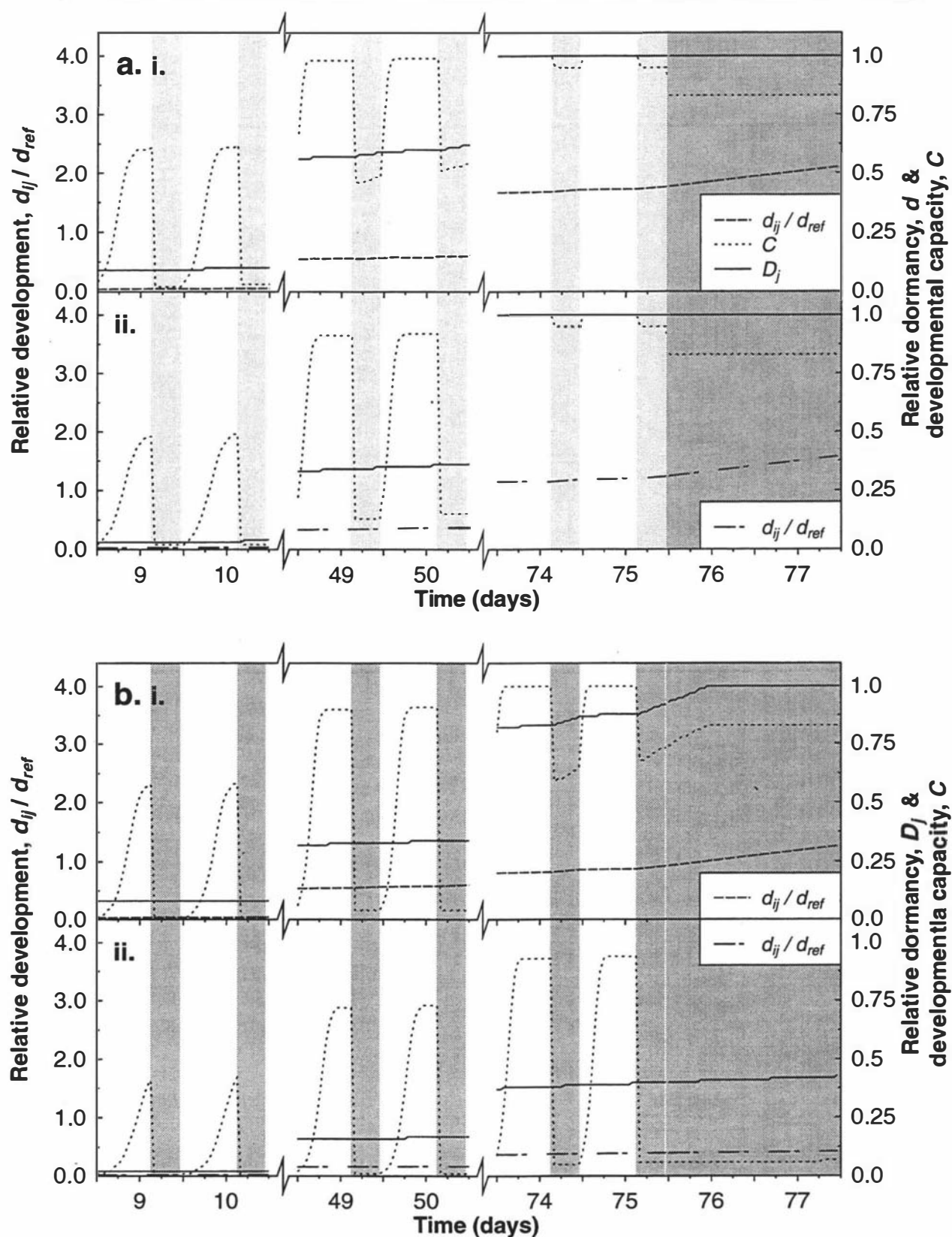
Figure 7.8　　PHYSHIFT simulation of diurnal bud response profile under two cyclic temperature regimes at two levels of initial relative dormancy (d_{ref} = 150). a). Simulated diurnal profiles, 75 days (1800 h) at 6°C / 18°C (16h / 8h). i). D_i=0.05, ii). D_i=0.00 (Light shading = period at 18°C, dark shading = forcing period at 22°C) b). Simulated diurnal profiles, 75 days (1800 h) at 6°C / 22°C (16h / 8h). i). D_i=0.05, ii). D_i=0.00 (Dark shading = period at 22°C)
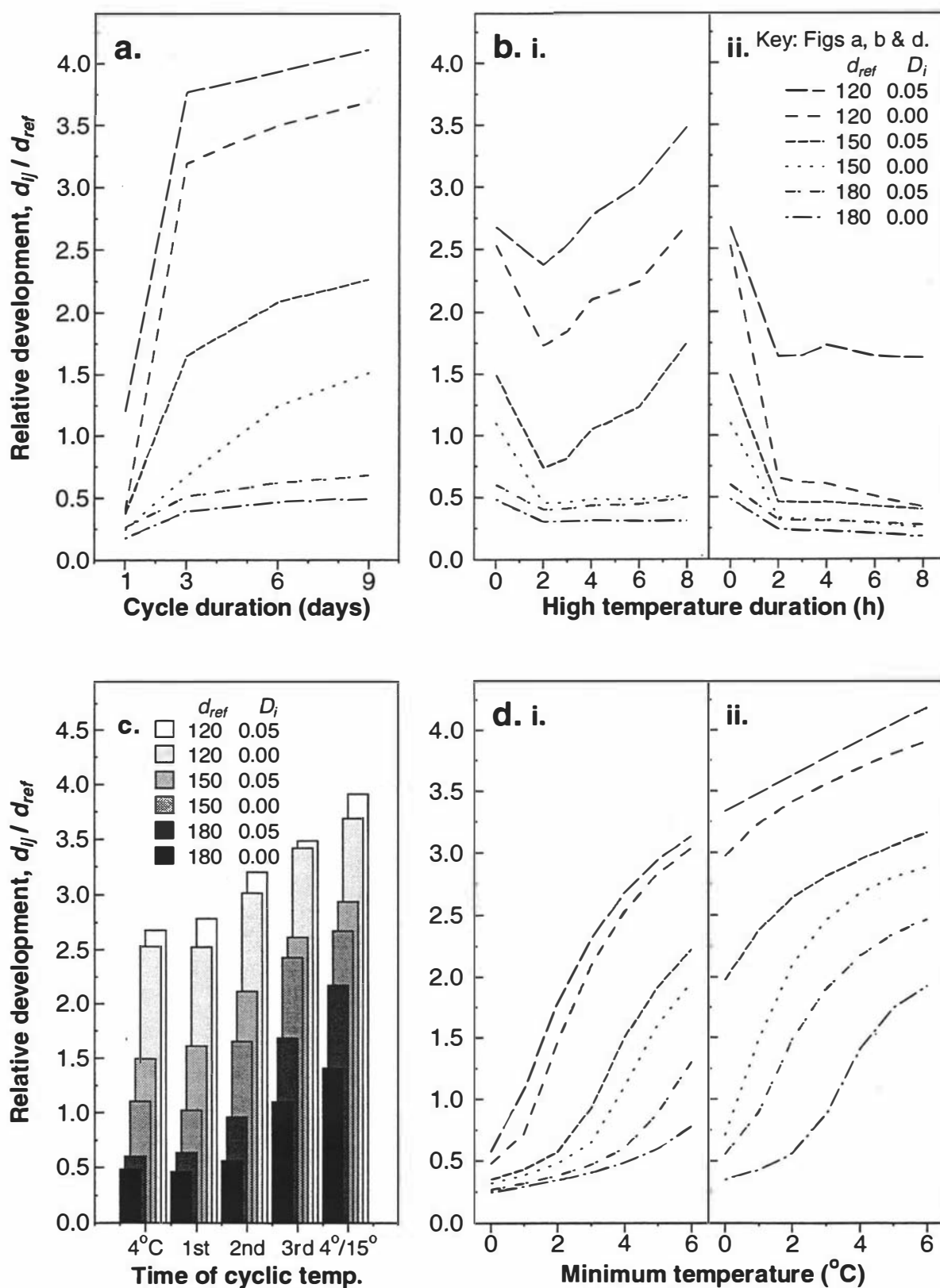
Figure 7.9 Simulation of a range of experimental cyclic temperature regimes: a). Overall duration of cycle, 3:1 low:high temperature ratio; b). Duration of high temperature period: i). $4^{\circ}C/20^{\circ}C$, ii). $4^{\circ}C/24^{\circ}C$; c). Timing of $4^{\circ}/15^{\circ}C$ 16h/8h cyclic period (first, second or last third of estimated 'Utah' chill unit requirement); d). Varying minimum temperature: i). constant temperatures, ii). same temperatures in 16h / 8h cycle with $15^{\circ}C$ maximum temperature.

was the same for $D_i = 0.00$, although development is slower and C was markedly depressed by 18°C on days 49 and 50 (Fig. 7.8a ii). By contrast, C was depressed by the high temperature period throughout the 75 days of the 6°C/22°C regime at both $D_i = 0.00$ and $D_i = 0.05$ (Fig. 7.8b i,ii). Growth was therefore slower at 6°C when cycled with 22°C than it was when cycled with 18°C and dormancy alleviation was thus also slower. With $D_i = 0.00$, depression of C by the 22°C period was sufficient to almost entirely prevent growth (Fig. 7.12b ii).

Other PHYSHIFT simulations under cyclic temperature regimes produced responses in agreement with some, but not all, of the results for the original experiments. Increasing cycle duration from 24 h to 3, 6 and 9 days increased the final development at the conclusion to the forcing period (Fig. 7.9a). Response to increased cycle duration was greatest at low d_{ref} (most rapid dormancy alleviation) and fell as d_{ref} increased. At $d_{ref} = 120$ and $d_{ref} = 150$, the general pattern of response compared closely to the original results (Appendix 4, Fig. 3) but at $d_{ref} = 180$ the simulated response was too low. Agreement between simulated and experimental results was not observed as the high temperature duration was reduced from 8 h to 2 h (Fig. 7.9b). Simulated growth was accelerated strongly towards the end of the cyclic period when the cycle maximum was 20°C. The simulation therefore showed a positive relationship between cycle maximum duration and final development, completely unlike that actually observed (Appendix 4, Fig. 4). When the maximum was 24°C, simulated growth was strongly inhibited whatever the duration at all values of d_{ref} and D_i except $d_{ref} = 120$ and $D_i = 0.05$. This, again, compared poorly with the bud break observations from the actual experiment.

In contrast, simulations in which the timing of a period of cyclic temperatures was varied in relation to the overall chilling duration (Fig. 7.9c) did produce a pattern of response that compared well with experimental results (Appendix 4, Fig. 5). Progressively delaying a period of 4°C/15°C cyclic temperatures increased the development distance covered by the end of forcing as in the actual experiment. The change was due to depression of C by the 15°C period when it occurred early in the chilling treatment. However, when the cyclic temperature period came later after partial or full alleviation of dormancy, 15°C no longer depressed developmental capacity and hence accelerated

growth. Overall response to change in d_{ref} and D_i was consistent with that observed in other simulations (higher final development with lower d_{ref} and higher D_i). A moderate level of similarity between the model and experimental results was also seen when the minimum temperature cycled with 15°C was progressively raised from 0°C to 6°C (Fig. 7.9d). In the actual experiment, exposure to 15°C cycled with 0°, 4° and 6°C enhanced the capacity of the lower temperature to alleviate dormancy. At the parameter values used, enhanced development at the end of forcing was also observed when 15°C was cycled with low temperature, especially at 0° and 2°C. However, the degree of enhancement was dependent on the rate at which dormancy was alleviated and was greatest when d_{ref} = 120 and limited at low temperature when d_{ref} = 180.

7.3.1.3   Field temperature conditions

PHYSHIFT simulations of bud development based on air temperature at Havelock North Meteorological Station predicted that bloom of 'Royal Rosa', 'Sundrop', and 'Trevatt' was earlier in 1988 than it was in 1989 (Table 7.2). This agreed with actual development since 1988 and 1989 were respectively early and late years for apricot bloom at Havelock North Research Centre (HNRC). The difference between the dates of 5% Bloom in the two years for 'Royal Rosa', 'Sundrop' and 'Trevatt' differed by 5-17 days. The difference between the dates at which the developmental position d_{ij}/d_{ref} = 2.0 (an arbitrary value) was reached varied by 12-16 days, depending on the value given d_{ref} (which determined the rate at which dormancy was alleviated). Simulated development therefore differed by a similar degree between years although differences induced by changes in the value of d_{ref} alone did not precisely duplicate the individual differences between cultivars.

Table 7.2   5% Bloom dates for 'Royal Rosa', 'Sundrop' and 'Trevatt' at Havelock North Research Centre in 1988 and 1989 compared with the dates at which an arbitrary developmental position was reached by three illustrative models with different rates of dormancy alleviation.

Year	Date of 5% Bloom			PHYSHIFT: d_{ij}/d_{ref} = 2.0 [z]		
	'Royal Rosa'	'Sundrop'	'Trevatt'	d_{ref}=120	d_{ref}=150	d_{ref}=180
1988	9 Aug	20 Aug	23 Aug	22 Jul	18 Aug	6 Sept
1989	26 Aug	25 Aug	2 Sept	7 Aug	2 Sept	18 Sept
Difference	+17 days	+5 days	+10 days	+16 days	+16 days	+12 days

[z] Arbitrary value for d_{ij}/d_{ref} used to approximate 5% Bloom. Model parameters: r = 1, D_i = 0.00, E_a/R = 12,500 K; $\Delta S/R$ = 100 K; $\Delta H_0/R$ = 28,750 K; $\Delta H_1/R$ = 30,000 K.
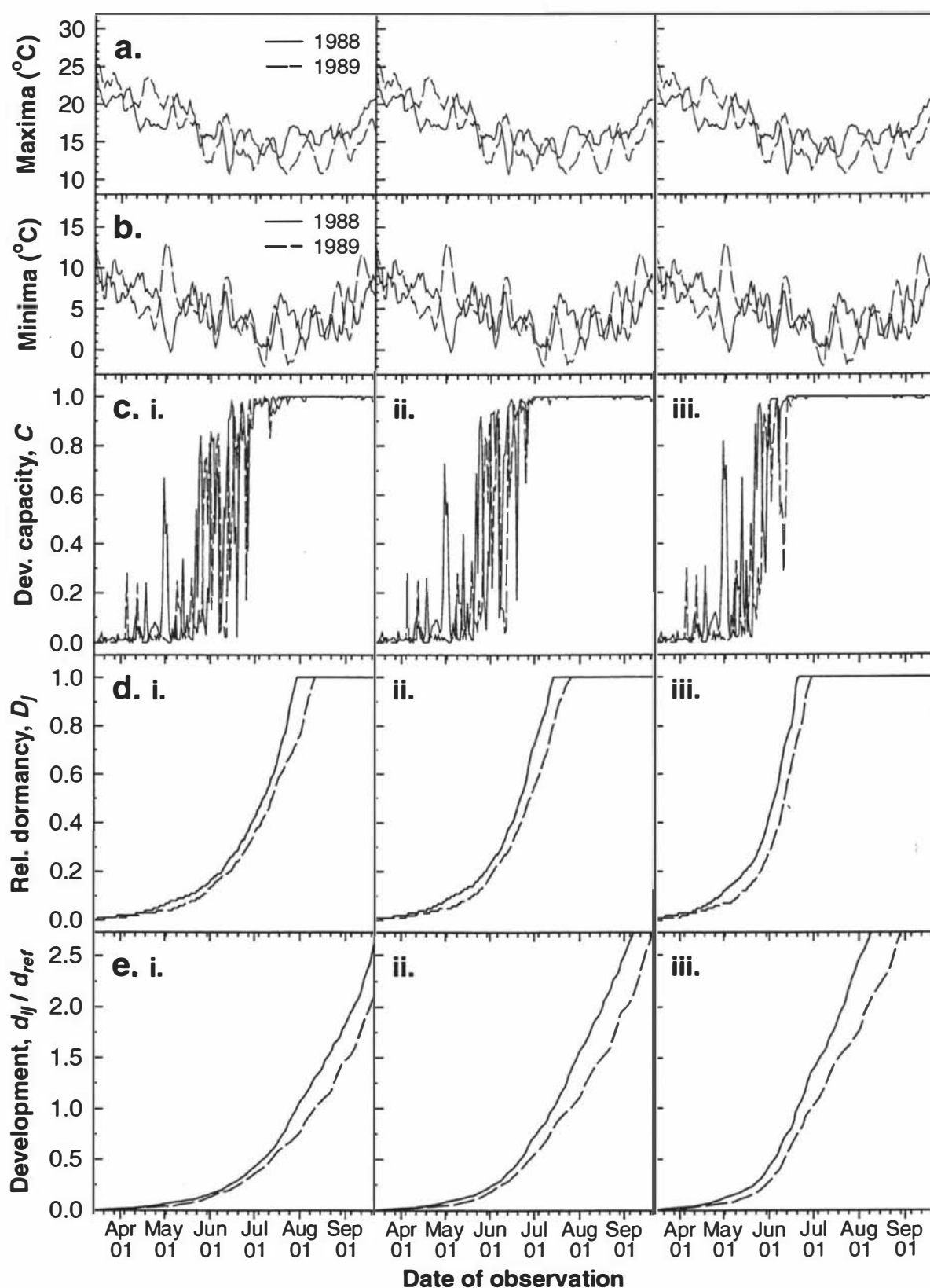
Figure 7.10   Response of three PHYSHIFT variables to air temperature data for Havelock North in 1988 and 1989 for D_i = 0.00 and three rates of dormancy alleviation set by d_{ref}. a). Daily temperature maxima (7 day average). b). Daily temperature minima (7 day average). c). Developmental capacity, C, estimated at midnight: i). d_{ref} = 180; ii). d_{ref} = 150; iii). d_{ref} = 120. d). Relative dormancy, D_j: i). d_{ref} = 180; ii). d_{ref} = 150; iii). d_{ref} = 120. e). Simulated development relative to reference point, d_{ref}: i). d_{ref} = 180; ii). d_{ref} = 150; iii). d_{ref} = 120.

Profiles of developmental capacity, relative dormancy and developmental position illustrate the effect of the two years on model output (Fig. 7.10). Temperatures in the two years differed principally during autumn (April-May), when average daily maxima 1989 were 2-3 °C warmer than in 1988, and during late winter/early spring (July-August) when daily maxima in 1989 were 2-3°C cooler (Fig. 7.10a,b). As a consequence, developmental capacity levels tended to be higher in autumn of 1988 than they were in 1989 at each of the values of d_{ref} investigated (Fig. 7.10c i-iii). In each case, periods with high daily maxima depressed C whereas periods with low maxima allowed C to reach high levels, even before dormancy was fully alleviated. Higher developmental capacity in 1988 during autumn than in 1989 therefore permitted more rapid growth and hence caused earlier dormancy alleviation in 1988 than in 1989 (Fig. 7.10d). Dormancy was completely alleviated by the start of August with $d_{ref} = 180$ (Fig. 7.10d i) but was a month earlier with $d_{ref} = 120$ (Fig. 7.10d iii).

7.3.2   PHYSHIFT Models of Apricot Bloom Phenology

Initial dormancy levels estimated for PHYSHIFT models fitted to flower bud development data for 'Royal Rosa', 'Sundrop' and 'Trevatt' apricots at Campbell, Fernhill Farm and Stirling orchards were very similar. In each case the initial temperature optimum for growth at the point of deepest dormancy was 2°C or 2.5°C (Table 7.3). The principal difference between the models was the distance over which dormancy was alleviated as development was simulated. This ranged from a distance of 60

Table 7.3   Characteristics for PHYSHIFT models fitted to bud development data for 'Royal Rosa', 'Sundrop' and 'Trevatt' apricots at Campbell, Fernhill Farm and Stirling orchards in 1992.

Model parameters [z]	'Royal Rosa'	'Sundrop'	'Trevatt'
Initial dormancy, D_i (temp. optimum)	-0.150 (2°C)	-0.125 (2.5°C)	-0.125 (2.5°C)
Distance to full alleviation, d_{ref}	60	180	120
Minimum C.V. (at 5% Bloom)	3.8 %	10.2 %	0.28 %
Prediction details			
Average distance: 50% Bud Break, $\overline{d}_{BBk}/d_{ref}$	2.66	0.22	0.91
Average distance: 5% Bloom, $\overline{d}_{5\% Bloom}/d_{ref}$	4.51	0.43	1.77
95% Confidence Interval	±0.17	±0.04	±0.05

[z] Model constants: $r = 1$, $E_a/R = 12,500$ K; $\Delta S/R = 100$ K; $\Delta H_0/R = 28,750$ K; $\Delta H_1/R = 30,000$ K.
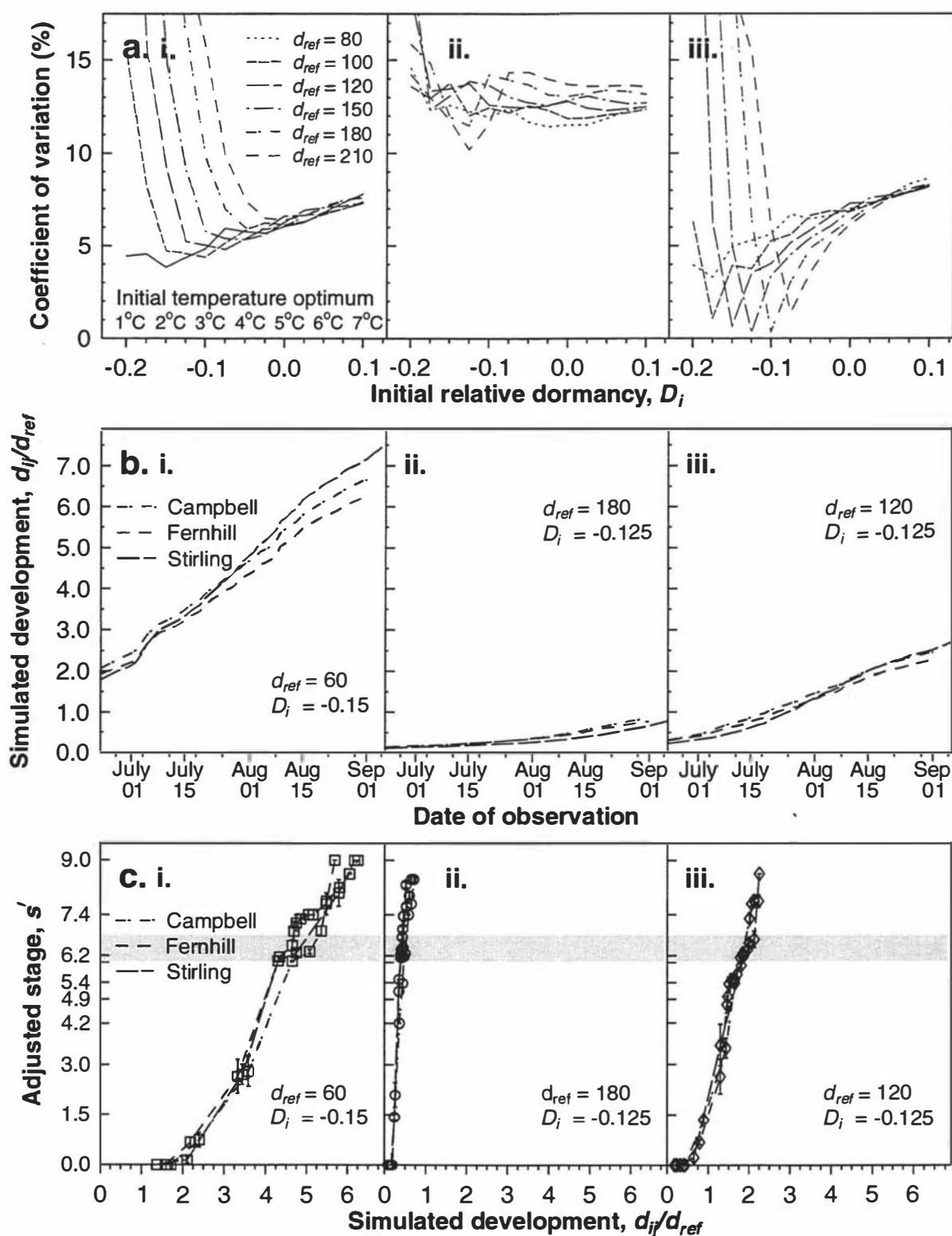
Figure 7.11   Derivation of PHYSHIFT models for 'Royal Rosa', 'Sundrop' and 'Trevatt' bud development from observed phenology at Campbell, Fernhill Farm and Stirling orchards in 1992.
a). Coefficient of variation for model fit at Campbell, Fernhill Farm and Stirling orchards in 1992 at different levels of d_{ref} and D_i: i). 'Royal Rosa'; ii). 'Sundrop'; iii). 'Trevatt'.
b). Simulated development profiles for 'best' models at Campbell, Fernhill Farm and Stirling orchards in 1992: i). 'Royal Rosa'; ii). 'Sundrop'; iii). 'Trevatt' ($d_{ij}/d_{ref} = 1$ = full dormancy alleviation).
c). Relationship of observed phenology to simulated development for Campbell, Fernhill Farm and Stirling orchards; i). 'Royal Rosa'; ii). 'Sundrop'; iii). 'Trevatt' ($d_{ij}/d_{ref} = 1$ = full dormancy alleviation, shading = 5% Bloom to 90% Bloom).

development units to full dormancy alleviation for 'Royal Rosa' to 180 units for 'Sundrop'. (One development unit (d.u.) is equivalent to the developmental distance covered in one hour at 25°C after full alleviation of dormancy.) However, the adequacy with which simulated development represented actual development varied substantially between the cultivar models. Model error coefficients of variation ranged from a surprisingly low value of 0.28% for 'Trevatt' to just over 10% for 'Sundrop' (Table 7.3). Minimum C.V. for 'Royal Rosa' was intermediate at 3.8%. For 'Royal Rosa' and 'Trevatt' the surfaces describing the relationship between D_i, d_{ref} and error C.V. displayed a regular trough associated with the minimum value (Fig. 7.11a i,iii) whereas, for 'Sundrop', the form of the surface was less regular and changed less rapidly with D_i and d_{ref} about the higher minimum value (Fig. 7.11a ii).

Development profiles for the three cultivars at each of the three sites illustrate the effect of varying d_{ref} and therefore the rate of dormancy alleviation (Fig. 7.11 b). For 'Royal Rosa', simulated development was well advanced (d_{ij}/d_{ref} = 2: i.e. d_{ij} = 120) at each site by the beginning of July (Fig. 7.11b). Bud break occurred very early in July at which point simulated development had reached 2.66±0.17 relative to d_{ref}, the distance required for full dormancy alleviation, or alternatively, 160±10 d.u. from the initial point of deepest dormancy (Table 7.3). 5% Bloom, which occurred on average in the second week of August, coincided with a relative developmental distance of 4.51±0.17 or 270±10 d.u. Over the period up to the beginning of September simulated development was almost linear, increasing at a slightly faster rate (but from a lower initial level) at Stirling orchard in Bayview than at Campbell and Fernhill Farm orchards on the Heretaunga Plains.

By comparison, the developmental distance covered during the winter and spring period in simulations by the 'best' models for 'Sundrop' and 'Trevatt' (i.e. those with the lowest error C.V.) was much more limited. For 'Sundrop', the relative developmental distance had yet to reach 1.0 by the end of September indicating the model predicted that dormancy was incompletely alleviated when bloom had been reached mid-August. 5% Bloom coincided with a relative developmental distance of 0.43±0.04 or 77±7 d.u. The linear linkage between dormancy alleviation and development means that the

simulated temperature response of growth at this point ($D_j = 0.43$) had a maximum at 14°C. For 'Trevatt', simulated development was more advanced at the beginning of July (relative development averaged 0.2) and reached just over 2.0 by the beginning of September. Consequently, although the PHYSHIFT model predicted that dormancy was still affecting the temperature response of 'Trevatt' buds at bud break in mid-July ($\overline{d}_{BBk}/d_{ref} = 0.91 \pm 0.05$), it predicted that dormancy had been fully alleviated by 5% Bloom ($\overline{d}_{5\% \, Bloom}/d_{ref} = 1.77 \pm 0.05$ or $\overline{d}_{5\% \, Bloom} = 212 \pm 9$ d.u.).

The difference between the simulated development profiles predicted by each cultivar model was highlighted when the adjusted phenological stage data (see Chapter 5 for method of adjustment) for the three cultivars at each site were plotted against simulated relative developmental distance, d_{ij}/d_{ref} (Fig. 7.11 c). For 'Royal Rosa', development from 50% Bud Break ($s' = 1.5$) to 5% Bloom ($s' = 6.05$) occurred between $d_{ij}/d_{ref} = 2.5$ and $d_{ij}/d_{ref} = 4.5$ on the simulated relative development scale. Phenological stages were reached slightly faster (for the same change in simulated development) at Campbell and Fernhill Farm orchards than they were at Stirling orchard. By contrast, for 'Sundrop' all observed development from 50% Bud Break to 5% Bloom occurred with the span of less than 1.0 on the simulated relative development scale. The relationship for 'Trevatt' was intermediate to the other two cultivars. A large range in developmental position relative to dormancy alleviation was therefore predicted by the 'best' PHYSHIFT models fitted to phenological data for the three Hawkes Bay orchards. This conflicts with the expectation that equivalent bud development stages of genetically related cultivars such as 'Sundrop' and 'Royal Rosa' should not differ greatly in their developmental position relative to dormancy alleviation ($d_{ref} = 1.0$). Application of the three 'best' models to predict times of bloom at HNRC for the years 1984 to 1991 resulted in estimates of the date of 5% Bloom that were consistently 2-3 weeks late. A key element of the PHYSHIFT model therefore inadequately simulates apricot flower bud development under field conditions.

7.4   Discussion

This initial evaluation of the PHYSHIFT model of dormancy alleviation and bud growth presented in the previous chapter shows that it reproduces the general form of bud response to constant and cyclic temperature regimes.   The phenomena reproduced include i). a 'bell-shaped' low temperature enhancement of bud development (Fig. 7.2), similar to the 'Utah' chill unit curve (Richardson et al., 1974) but with developmental inhibition by high temperature replacing negative chill unit accumulation; ii). apparent enhancement of the promotive effect of low temperatures when cycled with moderate temperatures (Fig. 7.7), similar to that found for peach (Erez and Couvillon, 1987); iii). the limited effect of extended temperature cycle duration (Fig. 7.9a) as originally observed (Erez et al., 1979); iv). greater promotion of dormancy alleviation by moderate temperatures experienced late in chilling (Fig. 7.9c) as Erez and Couvillon (1987) observed and v). more effective dormancy alleviation when temperatures below 6°C were cycled with moderate temperatures (Fig. 7.9d) again as found for peach (Erez and Couvillon, 1987).   The model also correctly predicted the relative order of bloom of apricots at HNRC in two climatically-contrasting years (Table 7.2 and Fig. 7.10).

These effects were reproduced using a simple linear linkage between temperature response and developmental position (the physiological shift involved in dormancy alleviation) and a limited range of values for D_i and d_{ref}. Simulations by the model also illustrate two responses to constant temperature that so far are untested experimentally on *Prunus* species.   The first of these is the apparent broadening of the range of growth promoting temperatures and rise in optimum temperature as duration of exposure to low temperatures increases (Fig. 7.6a).   The second is the apparent dependence of the effective temperature range on forcing temperature (Fig. 7.6b).   These features arise as the direct consequence of the basic mechanistic assumptions that underlie the model without any additional hypotheses.   Thus, the PHYSHIFT model proposed in this study presents a promising combination of mechanistic plausibility, flexibility and fidelity of reproduction under a range of experimental temperature regimes.

It is likely the present results represent a performance baseline from which refinement of model constants and parameter values will improve accuracy of simulation. Values for Arrhenius constants were selected from the range observed for plants (Berry and Raison, 1982) in order to create a initial temperature response profile that appeared physiologically plausible. However, alternative values (illustrated by sets 1 and 3, Table 6.2) could prove more appropriate. Raising the value of ΔS, for instance, not only narrows the width of the optimum temperature range but also increases the depression of developmental capacity and hence growth by supra-optimal temperature. Periods of high temperature interrupting periods of low temperature would therefore have a greater negative impact. Lowering ΔS would have the opposite effect. By comparison, the effect of changing E_a is only significant if it changes as part of the physiological shift simulated by the model since the main effect of an across-the-board increase to E_a is an increase in the numerical value the growth rate which can be offset by change to A, the Arrhenius constant. Changing E_a as part of the physiological shift alters the rate of development at the low temperature optimum and so is equivalent to changing d_{ref} in its effect on the rate at which dormancy intensity changes with respect to duration of temperature exposure. Lowering initial E_a increases the rate of initial rate of growth and so has a similar effect to lowering d_{ref}, which, by reducing the developmental distance to full dormancy alleviation is equivalent to increasing the rate of development. This could provide a means of reducing by one the number of parameters in the model. Change in d_{ref} at constant E_a, used to represent variable absolute developmental distance covered at constant maximum potential rate, could be replaced by use of change in E_a at constant d_{ref}, meaning a constant absolute developmental distance would be covered at a variable maximum potential development rate.

Reproduction of results from simulated experimental temperature regimes would also be improved if D_i, the initial level of dormancy (and by implication, the initial values for ΔH), was reduced as the 'best' models fitted to bud development data from Hawkes Bay orchards show. These models are characterised by values of D_i of -0.125 and -0.150, considerably lower than the values used for simulation of experimental temperature regimes. With $D_i = 0.00$ and $D_i = 0.05$ the initial optimum temperature for development is about 5° and 7°C respectively. This corresponds to the maximum of the bell-shaped

'Utah' chill unit accumulation curve. However, this curve represents an average response over the entire period of dormancy alleviation whereas the progressive upward shift integral to the PHYSHIFT model means that the mean optimum temperature over the equivalent period is higher. Consequently, the temperature range which apparently promoted dormancy alleviation and bud development to the greatest extent after 50 days exposure (Figs. 7.2, 7.3, 7.6) was higher than that observed experimentally (Appendix 4, Fig. 1) and the apparent effectiveness of temperatures below 6°C fell (Fig. 7.9d). The exaggerated promotion of growth when temperatures in the range 18°-24°C were cycled with low 'chilling' temperatures (Fig. 7.7) also stems partly from this problem.

Refining the dynamics of change in C could contribute to further improvement in this area since the mechanisms used in the proposed model (instantaneous decline in C, autocatalytic recovery) probably over-estimate the rate of adjustment to new temperature regimes. This is most clearly shown by failure of the PHYSHIFT model to accurately reproduce bud response to an experimental temperature regime where the high temperature duration in a diurnal cycle was progressively lengthened (Fig. 7.9b: cf. Appendix 4, Fig. 4). Rapid autocatalytic recovery of developmental capacity led to prediction of early dormancy alleviation by the model when the cycle maximum temperature was 20°C. This temperature was insufficiently high to greatly depress C and at high temperature durations of 4-8 h the rapid recovery resulted in the over-prediction of bud development during the later stages of the temperature treatment before forcing. In contrast, the extended depression of developmental capacity at 24°C prevented almost all development whatever the cycle duration.

It is possible that deepening initial dormancy (lower initial optimum temperature response) might have improved model accuracy in this situation. However, the sharp difference in response between the 20°C and the 24°C regimes suggests that the dynamics of either or both the decline and recovery of developmental recovery are overly sensitive to temperature change. By comparison, acclimation of mitochondria from dormant tulip bulbs to 5°C after incubation at 17°C took one to two weeks and decline in activity was also slow (Kanneworff and van der Plas, 1994). Slow recovery is suggested by the failure of a 2°/15°C square-wave diurnal temperature cycle to promote

of olive flower initiation whereas a similar sine-wave temperature cycle was promotive (Hartmann and Whistler, 1975). It is also suggested by the relatively slow response of other plant systems (e.g. tomato cells: Rank et al., 1991; flower stem elongation: Tutty et al., 1994) to temperature transitions. Hence, damping the response of C would probably improve the models accuracy in this situation by allowing limited development at short durations of 24°C, as observed in the actual experiment. It might also delay dormancy alleviation and the exaggeration of development when low temperatures are cycled with more moderate temperatures. The extent of damping could be assessed by comparing the effects of cyclic temperature regimes with complementary 'saw tooth' profiles (i.e. slow rise / rapid fall vs rapid rise / slow fall) with differing wavelength (cycle periods). Such experiments would require repeated assessment of developmental position throughout the period of cyclic temperature duration to produce a dormancy alleviation time series to which to fit the model. Unfortunately there are few cyclic temperature experiments where progressive assessment of dormancy alleviation has been made. In most cases, only bud break at the conclusion of the experiment is reported. It is therefore not possible to distinguish the potentially opposing effects of, for instance, warm temperatures at the beginning and end of a cyclic temperature regime.

Such experiments would also show more clearly the relationship of relative developmental position (d_{ij}/d_{ref}) with dormancy alleviation and bud temperature response. This should also improve model performance. An instantaneous transition from dormancy to active growth (with a corresponding change in bud temperature response) lies at one extreme and could be described by a discontinuous function. A model based on such a linkage would display many of the characteristics of the biphasic 'Utah' chill unit model (Richardson et al., 1974) and the 'Dynamic' model (Fishman et al.,1987a). The simple linear relationship used for these initial investigations lies at the other extreme, representing a slow, progressive transition from dormancy to active growth. It was therefore used to maximise the contrast between the proposed model and such biphasic models. In comparison, the logistic function represents an intermediate linkage form. Observed development was better simulated under constant temperature conditions (Figs. 7.2 and 7.3) when initial change in dormancy was slow and transition to full dormancy alleviation therefore more rapid ($r > 1$). This might be interpreted as evidence

that the temperature range does not widen gradually as initially suggested (Vegis, 1964) but rapidly and synchronously with chilling requirement fulfilment (Seeley, 1990). However, poorer performance by linear and other low-r models probably reflects the overly high initial dormancy values used in these preliminary simulations. This is because the principal effect of increasing r is to delay the rise in temperature optimum, the equivalent overall effect to deepening the initial level of dormancy.

The simulation results do not indicate whether a linear or logistic linkage is the more appropriate representation of the underlying physiological shift hypothesised to be responsible for dormancy alleviation. The failure of linear PHYSHIFT models based on 1992 bud development data to adequately predict 5% Bloom at HNRC may reflect inappropriate linkage between development and temperature response. However, it probably also reflects the error incurred by using air temperature rather than bud temperature to model bud development (Landsberg et al., 1974) as discussed in Chapter 5 with regard to the Utah chill unit models. Bud break data from 1992 forcing results (Fig. 5.8d i) suggest that a physiological shift for 'Sundrop' might best take a logarithmic form while the shift for 'Royal Rosa' and 'Trevatt', though more complex, might be described by a linear or power function ($r < 1$). This might explain the superior precision of the best 'Royal Rosa' and 'Trevatt' models (Table 7.3) over that for 'Sundrop'. However, the progressive increase in final development stage reached after buds of 'Royal Rosa', 'Sundrop' and 'Trevatt' flower buds from Hawkes Bay orchards were forced in 1992 (Fig. 5.8c i) could be used as evidence to support a linear relationship. Models fitted to phenology data for these orchards in the same years also indicate the model precision was best for 'Trevatt' (Table 7.3) for which the relationship between maximum development and date of forcing was most nearly linear (Fig. 5.8c i). Simulations using a linear linkage and field temperature data (Fig. 7.10) indicated that the transition from relatively deep dormancy ($D_j < 0.2$) to full alleviation ($D_j = 1$) could occur within as little as five weeks (Fig. 7.10d iii). A linear linkage therefore does not preclude apparently rapid change in temperature response. Furthermore, an apparently sigmoidal change in bud response to duration of temperature exposure (del Real Laborde et al., 1990) does not necessarily mean that the underlying relationship between dormancy alleviation and

developmental position is identical.   Slower dormancy alleviation after an initial rapid rate (i.e. $r < 1$) could produce a similar sigmoidal response of dormancy alleviation.

Lack of a clear physiological link between temperature response and the behaviour of forcing parameters such as time to bud break, maximum development and bud break fraction represents a major barrier in this respect. Investigation of PHYSHIFT models fitted to forcing data describing bud break and bud development could provide a way forward, if only by excluding possible alternatives. However, such study would require explicit consideration of the relationship between simulated development and the development of bud populations within which the characteristics of buds can differ considerably. This is because change in population descriptors such as percent bud break is a reflection of change in the distribution of buds as well as in the underlying physiological change of individual buds which is actually simulated by the model. For instance, progressive increase in probability of bud break for an individual bud may be linear but, if the distribution of rates of increase for the different buds in a population is clustered about a mean value, then the overall response will tend to be sigmoidal. Conversely, where different buds differ widely in their probability of bud break then the overall change in bud break fraction will appear more gradual. Such study would also need to recognise that bud break alone is not necessarily an accurate indicator of dormancy status since the capacity for subsequent development after forced premature bud break may be seriously restricted (Frisby and Seeley, 1993).

Investigation of the link between the degree of bud morphological development and bud physiology could also yield useful information, particularly if the PHYSHIFT model is to simulate the response of bud populations. Buds on different parts of a tree differ in their morphological development but all must be able to tolerate the stress imposed by the same adverse conditions over winter. Hence, the effectiveness of an environmental signal such as chilling would seem to be greatest if the same physiological response entailed by dormancy alleviation is made by all buds. All buds on a tree might therefore, be expected to recover from the deepest depression of their thermal response window at the same rate irrespective of their morphological development. Later bud break by some buds therefore reflects the need for more extensive growth before development is visible

rather than a slower recovery in the response window and therefore slower growth. However, the assumption which underlies the PHYSHIFT model is that physiological development, as indicated by changing temperature response, is directly linked to the morphological development which culminates in bud break and anthesis.   This is consistent with the observation that bud break on shoots which continue growth late into summer is delayed relative to those that cease growth early (Chandler and Tufts, 1934). Application of the PHYSHIFT model to a population of buds predicts therefore that the developmental temperature optimum of buds which are morphologically advanced will rise earlier than those which are retarded. This suggests that initiation of cell division and cell enlargement prior to bud break should occur earlier in larger buds on spurs than in the smaller buds on extension shoots. Investigation of these two alternatives may also indicate the most effective manner in which bud preconditioning (e.g. the effect of summer weather conditions) could be integrated within the PHYSHIFT model.

The present results do, however, confirm that simulating dormancy alleviation by means of a progressive shift in temperature response reproduces most of the effects of the modelled temperature regimes. Modelling dormancy alleviation, bud break and bud development therefore does not necessarily require the biphasic approach used in the 'Utah' and 'Dynamic' models (Fishman et al., 1987a; Richardson et al., 1974). The PHYSHIFT model also demonstrates that it is possible to describe the general response of dormant buds to constant and cyclic temperatures without dependence on the two-step labile precursor model initially proposed to explain vernalization (Purvis and Gregory, 1952). Apparent enhancement of the effectiveness of exposure to low temperature by short periods of moderate temperature was used by Couvillon and Erez (1985) as evidence to support their contention that chilling enhancement and negation, obtained by exposure of buds to the same high temperature in a diurnal cycle, can be explained only when two antagonising reactions are promoted by the same temperature at the same time. They therefore attribute the promotive effect of cycled moderate temperatures to the accelerated creation of a dormancy breaking factor. However, enhancement of bud break on both apple and peach trees by periodic exposure to 15°C is increased if it occurs after exposure to constant low temperature whereas similar exposure to 15°C before a period of constant low temperature reduces bud break (Erez and Couvillon, 1987; Young,

1992). This is not the result expected if bud response to temperature remains the same throughout the period of dormancy alleviation as assumed by biphasic dormancy models which use the concept of a chilling requirement. In contrast, the pattern of development predicted by the PHYSHIFT model when the period of cyclic temperatures was progressively delayed (Fig 7.9c) compares well with Erez and Couvillon's results (Appendix 4: Fig. 5). The promotive effect of moderate temperatures cycled with low temperature can therefore be interpreted as accelerated growth late in incubation period brought about during the warmer period. Hence, this result, and those from other simulations, provide preliminary evidence that the general form of the PHYSHIFT model will simulate the temperature response of apricot and other deciduous fruit tree flower buds during dormancy alleviation and bud development.

7.5   References

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8.1   Project Overview

The results presented within this thesis represent a wide range of observational, experimental and theoretical data describing the reproductive biology of apricots. They are, however, unified by two themes. The first arose from the horticultural basis of the project: the investigation of unreliable fruit set on 'Sundrop' apricot in Hawkes Bay. Hence, primarily, the project was intended to identify the main biological and climatic factors influencing success of fruit set on 'Sundrop' apricots. This involved two broad areas of study: 1) pollen tube growth and pollen transfer and 2) pollenizer bloom phenology (Table 8.1). The second theme was the use of mathematical modelling to describe and analyse factors influencing fruit set on 'Sundrop'. This arose from the goal of establishing a framework within which the impact of climatic and biological factors might be quantitatively analysed. The formulation of two mathematical models were

Table 8.1   A listing of the research objectives achieved in this study of the control of fertilization, pollenizer pollen transfer and pollenizer bloom synchrony as factors influencing reliability of fruit set on 'Sundrop' apricot in Hawkes Bay.

Control of Fertilization and Pollenizer Pollen Transfer

1. Compare the relative significance of pollen tube self incompatibility and low temperature to success of fruit set.

2. Determine whether 'Sundrop' displays cross incompatibility with 'CluthaGold', a closely related cultivar and potential pollenizer.

3. Confirm the presence of sufficient numbers of potential pollen vectors in 'Sundrop' blocks to achieve cross pollination under Hawkes Bay conditions.

4. Compare the duration of floral lifespan with those of stigmatic and ovule receptivity as factors restricting the success of cross pollination

5. Investigate effect of pollenizer bloom synchrony on fruit set and estimate optimum degree of pollenizer bloom divergence from bloom of 'Sundrop'.

Control of Pollenizer Bloom Synchrony

1. Assess the precision and accuracy of 'Utah' chill unit models as predictors of relative apricot bloom phenology in Hawkes Bay.

2. Establish the conceptual basis for an alternative form of bloom phenology model, concentrating on relative depth of dormancy and a progressive shift in temperature response.

3. Formulate the mathematical and computational expression of this alternative model.

4. Conduct initial evaluation of the performance of the model.

important steps towards the quantitative analysis of the interaction between self incompatibility and climate on apricot yields.

The order in which the results of this investigation have been presented follows the logic of the experimental investigation from factors immediately connected with fruit set to those more distant and preliminary. Thus, controlled pollination experiments which investigated pollen tube growth in 'Sundrop' flowers (Chapter 2) demonstrated that microgametophytes from 'Sundrop' pollen generally fail to penetrate styles of 'Sundrop' flowers and that this prevents fruit set under Hawkes Bay conditions. Tubes from the same pollen were, however, able to penetrate styles of 'Trevatt' and 'CluthaGold' apricot flowers. Study of apricot pollen tube growth at five constant temperatures between 5° and 25°C suggested that the penetration failure was not due to adverse temperature conditions since self pollen tube penetration was strongest at 10° and 15°C, temperatures typical of Hawkes Bay during apricot bloom. These results therefore confirmed that the need for cross pollination of 'Sundrop' (Wood, 1983) is due to a self incompatibility syndrome.

These results also emphasized the importance of pollenizer pollen transfer to the success of fruit set on 'Sundrop'. Observation of foraging activity on 'Sundrop' trees in bloom (Chapter 3) indicated that 'Sundrop' flowers were well visited by honey bees and also showed that foraging activity was highly weather-dependent. However, calculated estimates of the foraging activity required to set a 'Sundrop' crop indicated that number of bee visits needed to set a crop could be achieved by provision of hives within the range recommended for similar deciduous crops. Lack of foraging activity alone was not preventing fruit set, as long as flower visits by foragers could bring about cross pollination. Thus, insufficient numbers of pollenizers or excessive pollenizer bloom divergence could be contributing to unreliable fruit set.

In this respect, analysis of bloom records indicated that relative times of bloom of apricots in Hawkes Bay and other North Island sites varied considerably from year to year (Chapter 4). Hence, an assessment of the effect of pollenizer bloom divergence on cross pollination appeared necessary. This issue had not been addressed previously for apricots. Delayed pollination experiments showed that the duration of receptivity of

'Sundrop' flowers was the same as petal lifespan. Therefore a simple model of pollenizer pollen transfer based on cumulative bloom was used to establish a preliminary estimate of the optimum pollenizer bloom divergence for 'Sundrop'. This model indicated that optimum time of pollenizer bloom was slightly (1-2 days) behind that of the main cultivar. Shortening the duration of bloom had little effect on the probability of cross pollination apart from the increased risk of disruption by adverse weather that a shorter time period carries. A long period of pollen release by pollenizer and main cultivar (e.g. 4 days) advanced the optimum time of pollenizer bloom by about one day relative to the bloom divergence when pollen release was shorter (2 days). In contrast, a long period of floral receptivity on the main cultivar (e.g. 7 days) delayed optimum bloom divergence from near synchrony with the main cultivar when floral receptivity was short (3 days) to almost three days behind the main cultivar. Importantly, significant opportunity for cross pollination was still predicted when the pollenizer bloomed as late as six days after the main cultivar. By these criteria, 'Trevatt' (the most commonly-used pollenizer cultivar) appeared satisfactory under most, though not all, conditions.

This pollen transfer model indicated that reliable bloom divergence from 'Sundrop' represents an important consideration for selection of pollenizer cultivars for 'Sundrop' and any other self incompatible apricot cultivars. The Utah chill unit (CU) index was a poor predictor of dormancy alleviation for apricots growing in Hawkes Bay (Chapter 5) and the resulting Chill Unit / Growing Degree Hour models were not sufficiently accurate to reliably identify suitable new pollenizer cultivars. These results lend weight to experimental evidence (Erez and Couvillon, 1987) that the Utah chill unit index does not adequately describe dormancy alleviation under mild and cyclic temperature conditions. This has led some researchers to modify the chill unit concept (del Real Laborde et al., 1990; Fishman et al., 1987a,b) but a different modelling approach was adopted in this study. This arose from an analysis of the ecological significance of bud dormancy and of the potential for seasonal temperature transitions to synchronise the development of deciduous plants with annual environmental cycles (Chapter 6). This suggested that temperature-mediated alleviation of dormancy could be modelled by a progressive shift in bud temperature response.

A mathematical model of dormancy alleviation was formulated on the basis of this analysis. It incorporated a single development index to describe dormancy alleviation and bud development, and a modified Arrhenius function (Johnson and Thornley, 1985) to describe the relationship of growth rate to temperature throughout that period. Initial model evaluation (Chapter 7) confirmed that the resulting PHYSHIFT model was highly flexible and could reproduce many of the responses that dormant buds of *Prunus* species display to constant and cyclic temperature regimes. The results suggest that when properly calibrated, and given improved conversion of air temperature data into bud temperatures, this alternative phenological model may offer more reliable prediction of relative bloom timing for the purpose of pollenizer selection than conventional chill unit-type models. Thus, horticulturally, the project represents a retro-gressive analysis of the processes influencing the critical event of fruit set in apricots, namely fertilization. Methodologically, it represents an attempt to bring the power and rigour of a quantitative modelling approach to bear on the practical problem of selecting suitable pollenizers in a new and changeable environment.

8.2 Experimental Implications

8.2.1 Apricot Self Incompatibility

Self incompatibility in *Prunus* is a gametophytically-determined trait (de Nettancourt, 1977). The capacity of a pollen tube to penetrate the style in which it is growing depends on whether the self incompatibility (*'S'*) genotype of the haploid microgametophyte which produces the pollen tube matches either of the *'S'* alleles of the diploid style. Cultivars which share the same alleles therefore can be mutually self incompatible and the existence of multiple *'S'* alleles means groups of such cultivars which are unable to act as reciprocal pollenizers can exist. The practical implications of this genetically-determined situation for pollination of sweet cherries and almonds are well documented (Way, 1968; Kester et al., 1994) but there has been no comparable study of the genetics of self incompatibility in apricots. The genotypes of self incompatible apricot cultivars have yet to be established and the extent to which cross incompatibility is likely to affect to suitability of pollenizer combinations is therefore unknown.

Many identified self incompatible cultivars appear to reflect the repeated use of 'Perfection', or its off-spring, in North American and related breeding programs. They therefore presumably share the same *'S'* alleles which suggests that the number of *'S'* alleles may be limited. However, their frequency in what are generally regarded as self fertile cultivars is also not known. *'S'* alleles may have been fortuitously absent from apricots initially introduced to Europe with the result that most potential genotypes are fully self fertile. It is equally possible that early cultivation of very limited numbers of apricot trees in English and French gardens in the seventeenth to nineteenth centuries (Roach, 1985) and selection for productivity under frequently adverse spring weather conditions has 'inadvertently' selected for at least partial self compatibility from within a population containing a number of potential self incompatible genotypes.

Active *'S'* alleles may therefore still be relatively common within older 'European' cultivars such as 'Blenheim', 'Hemskirke', 'Luizet', 'Moorpark' and 'Peach'. The self incompatibility of some 'Moorpark'×'Sundrop' hybrids indicates that 'Moorpark', though itself self compatible, carries an active *'S* allele while the self incompatibility of 'Paviot'

suggests that 'Luizet' also may carry an allele. The use of germplasm from other eco-geographical groups to incorporate desirable fruit characteristics and improved disease resistance into breeding programmes is also likely to increase the incidence of self incompatibility. The self incompatibility of some Spanish cultivars is, for instance, thought to be due to interbreeding of local varieties with introduced North African apricots (Garcia et al., 1988). These are commonly self incompatible (Mehlenbacher et al., 1991; Valdeyron and Crossa-Raynaud, 1956). It is also likely to increase the frequency of 'S' alleles in self compatible cultivars. Whether this is likely to be significant in a commercial orchard environment probably depends on conditions. Possession of a single active 'S' allele reduces the probability of self fertilization by preventing penetration by the fifty percent of self pollen tubes which carry that allele. It would also reduce pollen tube penetration in styles of other cultivars which also share the allele. Widespread possession of 'S' alleles could therefore begin to affect fruit set when pollen viability or pollen transfer is low. This second issue appears of particular concern in Hawkes Bay due to the weather conditions during bloom and given the increasing number of self incompatible cultivars. Screening of cultivars for their 'S' genotype, either by reciprocal cross pollination or by molecular techniques, would provide important practical information for pollination purposes as well as for breeding.

Cross pollination increases fruit set on many self fertile apricot cultivars (Cappellini and Limongelli, 1981; Dimitrovski, 1976) which suggests that a low level of self pollen tube inhibition occurs already in ostensibly self compatible cultivars. This raises the issue of the incidence of so-called 'cryptic' self incompatibility in apricots as well as other *Prunus* species. In some species such as legumes, controlled self pollination causes self fertilization but slow growth by self pollen tubes prevents them from effecting fertilization after mixed pollination. This is caused by maternal selection against self tubes which is expressed as relatively more rapid penetration by tubes arising from cross pollination (Jones, 1994; Weller and Ornduff, 1977). As a mechanism for promotion of outcrossing the phenomenon has the benefit of permitting fertilization and seed set in the absence of cross pollen but preventing self fertilisation in its presence. In this form of self incompatibility recognition and inhibition of self tubes can occur at or in the ovule itself (Cooper and Brink, 1940; Kendrick et al., 1984). The report that self pollen tubes

penetrate styles of 'Tokaloğlu' apricot, a Turkish cultivar, but fail to penetrate the ovule micropyle (Gülcan and Askin, 1991) may therefore be significant in this regard.

The structure of *Prunus* flowers appears particularly suited to the expression of this form of breeding system. 'Cryptic self incompatibility' is a specific instance of the more general phenomenon of gametophytic competition in which pollen tube genotype influences reproductive success (Mulcahy et al., 1983; Spira et al., 1992). Its potential significance is greatest where the number of pollen tubes exceeds the number of ovules and there is opportunity for pollen tube competition to occur. It is therefore significant that the limited number of ovules in individual flowers of *Prunus*, the relatively long styles characteristic of this genus and the trumpet shape of the transmitting tissue which narrows towards the entrance to the ovary all enhance opportunities for gametophytic competition. This suggests that 'cryptic' self incompatibility could be a feature of the original breeding system of species or populations of *Prunus* which apparently lack normal self incompatibility when hand pollinated.

The significance of 'cryptic' self incompatibility in an orchard environment is threefold. First, the effective pollination period (EPP) for self pollination may be shorter than for cross pollination. This is because growth of self pollen tubes is retarded, with the result that ovules may senesce before fertilization occurs. Providing pollenizers may therefore improve pollination reliability even where controlled hand pollination indicates cultivars are self compatible. This possibility is consistent experiments where open pollination of apricots consistently gave better fruit set than self pollination (Cappellini and Limongelli, 1981). However, this hypothesis has not been investigated for apricots nor does it appear to have been tested for other crops which have a similar self incompatibility system.

Second, 'cryptic' self incompatibility may lessen the benefit derived from warm conditions during bloom if deposited pollen shares the same 'S' alleles as the style. EPP duration is a function of the combined response of pollen tube growth rate and ovule senescence to temperature (Sedgley, 1989). High temperatures promote rapid pollen tube growth but at the expense of more rapid ovule senescence. Thus, if warm conditions accelerate ovule senescence more than they do pollen tube penetration then high temperatures shorten EPP duration and the differential temperature sensitivity of pollen

tube growth and ovule senescence modulates compatibility.   For 'Sundrop', the temperature experiment reported in Chapter 2 indicated that low temperatures (<15°C) favoured self pollen tube penetration whereas high temperatures (>15°C) inhibited self pollen tube penetration. High temperature did not reduce penetration of 'CluthaGold' and 'Goldrich' pollen tubes even though the genetic relationship between these cultivars means they may share one or more 'S' alleles with 'Sundrop' (cf Table 1.1).

Third, 'cryptic' self incompatibility probably increases the foraging activity required to set a satisfactory crop on apparently self compatible cultivars. This situation has been observed on almonds with low self compatibility (Weinbaum, 1985). Fruit set appeared to be favoured by relatively high stigmatic pollen deposition which ensures the presence of pollen tubes able to overcome stylar inhibition and achieve fertilization.   In this regard, the absence of a high temperature effect on penetration of 'CluthaGold' and 'Goldrich' pollen tubes down 'Sundrop' styles (Chapter 2) possibly reflected the many pollen grains deposited on the hand pollinated stigmas. This ensured that numerous pollen grains with 'S' alleles different to those of the style were present on each stigma but this need not be the case under natural conditions which may restrict the number of pollen grains deposited or the timing of deposition.   These three possibilities again suggest that genetic screening of apricot cultivars for self incompatibility genotype may yield information that leads to selection of more effective pollenizer combinations.

Ultimately, the effectiveness of self and cross pollination as agents of fruit set are linked to the reproductive strategies displayed by apricots. *Prunus* species produce very large numbers of flowers which might suggest that, with suitable conditions and appropriate management, potential fruit set could be substantial. Despite this, less than half the flowers usually set fruit (Guitian, 1993; Kester and Griggs, 1959) but poor pollination or flower quality (however measured) are not necessarily to blame. Patterns of energy allocation within the plant itself also present the major limitation to yield. The energy allocated to overall reproductive effort and to the respective sexual functions of flowers under natural conditions reflects the reproductive strategy of a species or population (Charlesworth and Morgan, 1991). For instance, a study of wild *Prunus mahaleb* (Guitian, 1993) has shown many flowers are produced but do not set fruit and that supplementary pollination did not increase fruit set. Guitian therefore suggested that,

rather than providing the plant with opportunities to exploit unusually favourable conditions (an option with obvious horticultural significance), the excess flowers allowed selective abortion of 'poor quality' fruits (Stephenson, 1981) or provided a reserve supply of ovaries in case of high mortality during the flowering period (Ehrlén, 1991).

Such naturally-established patterns of energy allocation can remain even after domestication and human selection (Mione and Anderson, 1992). The apparent potential for substantial fruit set need not imply therefore that it is attainable, even after selection for higher energy allocation to reproductive effort. In this regard, patterns of sexual function displayed by *Prunus* follow those observed in other less-domesticated genera. Dioecious and self incompatible species commonly have higher pollen : ovule ratios than self compatible species, due both to greater pollen production and less energy allocated to ovaries and ovules (Evenson, 1983). This pattern presumably reflects the reproductive advantage gained for self incompatible genotypes by trading off reduced floral receptivity (female function) against maximized pollen distribution (male function). This appears still to be observed in *Prunus* (including apricots) where self incompatibility is frequently associated with lower pistil length and higher stamen numbers (Surányi, 1976). Species or populations in *Prunus* displaying self incompatibility might therefore also be characterised by higher pollen viability and lower ovule viability than those characterised by self compatibility due to genetically-determined energy allocation strategies. Problems with fruit set caused by the association of self incompatibility and short ovule lifespan in sweet cherries, almonds and plums (Stösser and Anvari, 1982; Pimienta and Polito, 1982; Keulemans and van Laer, 1989) suggest this could be the case. Naturally-determined patterns of energy allocation might also imply that ovule viability is less likely to limit fruit set in predominantly self compatible species such as peaches and 'European'-type apricots. This hypothesis has yet to be explicitly tested for apricots. However, it implies that including germplasm from predominantly self sterile, outbreeding populations such as those of Central Asia (Mehlenbacher et al., 1991) may not only increase the incidence of self incompatibility but also shorten the average EPP. Such a combination would exacerbate the difficulties of cross pollinating apricots in Hawkes Bay.

8.2.2 Dormancy Depth versus Dormancy Duration

The dormancy concepts developed in this study for the modelling of apricot bloom phenology have implications for the wider study of dormancy in other deciduous crops and possible dormancy in general. Modern horticultural study of dormancy has been dominated by the twin concepts of the chilling requirement, the minimum duration of low temperature exposure needed for dormancy alleviation and the chilling hour as the index of alleviation. Both are North American in origin and reflect the southward expansion of the North American deciduous fruit industry. Experience of crop loss due to severe cold in northern regions directed attention towards the issue of cold hardiness and placed study of dormancy induction in the context of acclimation to low temperature (Proebsting, 1963; Fuchigami et al., 1977; Kobayashi et al., 1982). However, in southern regions, delayed foliation and erratic flowering of deciduous fruit trees focused attention on a minimum duration of low temperature as an agent to release dormancy and permit "normal" development. The chilling hour index provided a numerical measure of that duration by which to differentiate cultivars for breeding purposes in these regions (Weinberger, 1950a).

A flow diagram summarising the history of ideas underlying horticultural modelling of dormancy illustrates the origins and development of the chilling requirement concept, the key component of the 'Utah' chill unit model (Fig. 8.1). The importance of the dormancy/ rest metaphor for the contrasting phases of meristematic cycle to the development of the chilling requirement concept is obvious. However, what is particularly striking is the virtual independence of the derived concepts of the chilling hour and chill unit from physiology and biochemical thermodynamics, particularly as it is represented in the Arrhenius temperature equation. Even the heat unit, which pre-dates quantitative study of dormancy by over a century and which does have a physiological basis, appears not to have contributed directly to their development. Instead, the crucial step in the develop-ment of quantitative horticultural modelling of dormancy was the 'borrowing' of the index by which relative dormancy was described from meteorology and engineering. This was the 'heating degree day', a calculating device involving summation of days with mean (or minimum) temperatures below a threshold temperature ($40°$ or $45°F$, $4.4°$ or $7.2°C$).

This index provides a simple method of quantifying relative building heating requirements in different environments. It has a mechanistic significance in this situation since it is a direct measure of the required duration of heating. And, as an empirical measure of dormancy, the approach was also well suited to the situation to which it was originally applied- quantitative differentiation between peaches on the basis of their relative requirements for low temperature exposure. This was the case for four reasons: 1). The index was closely linked to mean winter temperatures in southern United States when an appropriate threshold (45 °F) was selected but, unlike mean temperature, it required minimal recalculation (Weinberger, 1956); 2). It represented the temporal aspect of

Time	Concept	Application	Source
1700	Temperture summation above a threshold	Phenology (Heat Units)	de Réaumur
1800	Physiological distinction of dormancy from growth	Dormant 'state'	Not known
	Temperature dependence of reaction rates	Arrhenius Equation	van't Hoff and Arrhenius
1900	Environmental control of dormancy	Low temp. alleviation	Howard and others
	Temperature summation below a threshold	Heating degree days	Not known
1920	Minimum duration of low temp. for bud break	Chilling requirement	Chandler, Coville, Horne and others
1930		Index of winter chilling	Hutchins and others
	Irreversible transformation by low temperature	Vernalization	Lysenko and others
1950	Reversibility of low temperature effect	Vernalization model	Purvis &Gregory
	Temporal index of chilling requirement	Chilling hour	Weinberger
1960	Reversibility of chilling effect	Chilling negation	Weinberger and others
	Continuously varying temp. response range	Temp. response window	Vegis
1970	Prediction of sensitivity to freezing injury	Weighted chilling hour (Utah' Chill Unit Model)	Richardson and others
1980	Continuously varying physiological condition	Physiological shift	Saure
	Critical precursor level	'Dynamic' model	Fishman, Erez and others
1990	Tissue sensitivity	Modified chill unit accumulation	Seeley and others
	Dormancy described by Arrenius function	PHYSHIFT model	

Figure 8.1 A schematic history of horticultural bud dormancy concepts with particular reference to the development of the concept of a chilling requirement and of chill unit-type phenology models in distinction to the antecedents of the PHYSHIFT model.

development, an issue the selection of cultivars for early bloom had highlighted (Yarnell, 1944); 3). The absence of physiological indicators of dormancy meant that only phenom-enological and correlative descriptions of bud development was possible (Chandler et al., 1937; Reinecke, 1936); and 4). Detailed analysis of temperature response was not feasible since facilities for large scale control of environmental conditions were not yet available. The successful peach and nectarine breeding programme to which the chilling requirement concept contributed (Childers and Sherman, 1988; Diaz, 1992; Lloyd, 1992) testifies to its validity as a tool for the purposes for which it was originally intended.

Despite its obvious benefits, it is important to note the possible implications of the pragmatic origins of the chilling requirement concept. The key feature of the conven-tional definition of the chilling requirement is that it is a measure of time and is therefore presented, almost exclusively, as an index of relative dormancy duration. It uses a temperature-weighted time scale to differentiate between genotypes with what are regarded to be otherwise identical temperature responses during the exposure duration. The aspect of relative depth of dormancy (i.e. varying temperature responses) is not encompassed by the concept. However, the potential for accurate comprehension of any partially-understood phenomenon is greatly affected by the goals which direct its study. Limited, pragmatic objectives usually reflect a need to describe a single element within a narrow context and therefore will not necessarily yield an understanding that adequately encompasses another. Moreover, generalisations from a limited line of inquiry may ultimately prove misleading. This is particularly likely when a partial understanding is developed in an environment which removes the phenomenon from its original context.

Both these situations apply to the development of the durational chilling requirement and the chill unit as bases for the quantitative description of dormancy. It is therefore quite possible that the durational chilling requirement concepts used as the basis for the 'Utah' and other chill unit type models have little direct connection to the actual physiology of dormancy. The chilling hour index then relies for its accuracy on two general facts: 1). that most processes occur more slowly as temperature falls and 2). that, in certain climates, lower temperatures at the extremes of a diurnal cycle may be experienced for a shorter period than temperatures in its mid range. A cultivar with a deeper depth of dormancy, caused by a lower 'chilling' optimum, therefore appears to have a longer

duration of dormancy. Firstly, because its optimum rate of dormancy alleviation is slower, and secondly, because the period when alleviation may occur is also shorter.

Hence, theoretically, cultivar chilling requirements established from field data and the corresponding optimum chilling temperature for those cultivars should be negatively correlated. Cultivars with relatively high optimum chilling temperatures for initial release of dormancy would thus display shorter chilling requirements. There is some evidence to suggest that this is the case for 'low chill' and 'high chill' peach and nectarine cultivars (Gurdian and Biggs, 1964) and also for apricots (Tabuenca, 1979) but this issue has not been systematically investigated.

The accuracy of the 'Utah' chill unit models in Hawkes Bay may therefore be inherently limited for the reason that they are based on a spurious physiological interpretation of dormancy phenomena in which dormancy duration (measured in chilling hours or chill units) acts as an inadvertent cipher for depth of dormancy. This is not because the dormancy metaphor itself excludes the concept of relative depth of dormancy or dormancy intensity. In a very early study of the phenomenon, Howard (1910) comments that "the dormant state varied very greatly with the different species, not only in point of the duration of rest, but also in the degree of its intensity" and that "the rest period is more profound during its earlier stages than it is later and that the plants were able to overcome their dormant state with greater and greater ease as the season advanced." Howard therefore recognised that dormancy could vary in intensity, especially since attempts to stimulate dormant buds relied on varying combinations of relatively drastic treatments. However, the practical significance of the end of dormancy and the results of forcing under relatively warm conditions (regarded as "normal" growth temperatures), along with the impact of common observation, emphasized dormancy duration.

This interpretation also reflects the assumption that dormant buds are in a distinct physiological state which contrasts with that of growing buds. This now conventional perspective can be seen in the phenomenological approach of early studies of dormancy. For instance, Howard (1910) reports many species were very difficult to "awaken from their resting state, even under severe treatment, while others would eventually make some growth merely under the influence of warmth." A qualitative physiological

difference between growing and dormant buds (metaphorically awake and asleep) requiring the action of an agent to initiate conversion from one state to the other is therefore envisaged. Analogies with seed dormancy, the termination of which can be abrupt, and the use of failure to grow to in a single 'conducive' environment as a test of dormancy emphasized the apparent differentiation of states.

This dual-state interpretation of dormancy led directly to the inference that flower buds of deciduous fruit trees display a substantial period of 'true dormancy', weeks in duration, in which there is complete, though temporary, suspension of growth. For instance Howard concluded that "each species, and possibly each variety, has a certain number of days during which it will not grow under natural conditions." Subsequent study of the promotion of dormancy alleviation by low temperature ('chilling') was defined almost exclusively in terms of the time required for chilling to 'break' dormancy, converting the bud from one state to another, thus allowing growth to proceed 'normally' (Chandler and Tufts, 1934; Reinecke, 1936; Weinberger, 1950a,b). Weinberger (1950a) notes that recognition of a time interval necessary for buds to complete their processes before the rest period is broken was essential in determining chilling requirements.

Modelling dormancy in terms of the duration to an hypothesized transition between alternative states is thus now conventional practice. It does, however, have a number of corollaries which distinguish it from the approach adopted by the PHYSHIFT model formulated in this study. The first of these is that chilling accumulation reflects a physiologically-distinct period of bud development which is distinguished from normal growth by a characteristic temperature response. Low temperature acts exclusively to remove the 'rest influence' and therefore temperature response is uniform throughout the period. Second, that transition from dormancy to growth occurs over a relatively short period and is sufficiently distinct that its recognition is independent of method used to determine the end of dormancy. Third, that the 'rest influence' affects the flower bud in its entirety, preventing all but very limited growth until dormancy is almost completely 'broken'. Consequently, the developmental distance from the end of dormancy to bud break and any subsequent stage is fixed and independent of the manner in which 'chilling' is accumulated. And fourth, the promotive effect of 'chilling' is potentially reversible since it is not related to actual bud development, but to a condition imposed on it. In

many cases the physiological hypotheses implicit in both perspectives have yet to be tested.

The first corollary implied by the conventional description of dormancy, that of a distinct and uniform chilling response, contrasts with the progressively changing temperature response which underlies the PHYSHIFT model. This alternative perspective was originally proposed by Vegis (1964) who argued that a progressive narrowing and broadening of the temperature range for development was fundamental to the temperature response of dormant buds. This description has, however, received little support from North American researchers whose work belongs predominantly to what has been called the 'classical' (i.e. American!) school (Dennis, 1994). The idea of a durational chilling requirement is consistent with this approach which regards dormancy as a relatively simple phenomenon with discrete causes. Work within this school has therefore sought to isolate the hormonal triggers for dormancy induction and release. Between these two points bud temperature response is determined by that of the process alleviating the 'rest influence'. It is therefore relatively constant until growth is possible.

In contrast, Vegis' progressive concept of dormancy is more consistent with the perspective of what has been described as the 'French' school of dormancy research (Dennis, 1994). Studies by these predominantly European workers have focused on the short and long-range factors affecting correlative development and plant form. Dormancy is thus regarded as but one part of the complex rhythmical cycles of plant growth. However, in neither case have the dynamics of the temperature response of dormant buds during chilling been investigated thoroughly. Very few studies explicitly address the issue, despite its relevance to phenological modelling. In one (Brown and Abi-Fadel, 1953) the conclusion was that temperature response of apricot buds did not change but the methods and experiments used lacked precision. By comparison, a study of black currants requiring long durations of chilling (Plancher, 1983) suggests that temperature response does change. The optimum temperature level for these was 0°C after 600 h exposure, but moved upwards to reach 3°C by 2400 h. Bud break during this period increased from 30% to 91%. At 9°C, bud break after 600 h was less than 5% and reached 46% by 2400 h.

The possibility of a progressive physiological shift (Saure, 1985) which induces a change in temperature response is consistent with the extended period over which dormancy alleviation occurs and the slow, though steady, growth of peach and apricot flower buds which is evident during that time (Brown and Kotob, 1957; Chandler and Tufts, 1934; Legave, 1975; Viti and Monteleone, 1991). The concept is also consistent with the progressive increase in respiration rate in pear flower buds (Cole et al., 1982), the rise in protein, DNA and RNA in early-blooming cherry flower buds (Wang et al., 1985) and changing nucleotide metabolism in peach leaf buds (Balandier et al., 1993). A progressive physiological shift, initially towards deeper dormancy and then to greater responsiveness, would also account for changing sensitivity to exogenous gibberellin of peach and apricot buds (Hatch and Walker, 1969) and the variable effect of high temperature interruption during low temperature exposure of apple seeds and buds (del Real Laborde et al., 1990; Young, 1992). However, whether this is matched in each case by movement in the thermal response window has not been explicitly tested.

Indirect evidence for a temperature response shift is provided by the Hawkes Bay budwood forcing study performed in 1992. An unexpected 'peak-then-dip' pattern was observed in the level of forced bud break (Fig. 5.5d). The pattern was similar to that discernable in bud break time series from other apricot studies (Carraut, 1968; Guerriero and Bartolini, 1991). It could reflect an oscillation in the thermal response window as multiple regression showed that trees with higher forced bud break during the early peak ('May bud break') also tended to have earlier dates of bud break in the field (Table 5.11). The reason for the bud break pattern is not clear but it might reflect the relative rates at which the influences of para- and endodormancy recede. Such variation in temperature response could, however, greatly influence the accuracy of both chill unit and PHYSHIFT type models for apricots. A second study incorporating forcing at several temperatures is therefore needed to confirm the generality of the bud break pattern and to explicitly test whether it is related to bud temperature response.

Change in temperature response in the period leading up to bud break, the so-called 'after-rest' period (Couvillon and Hendershott, 1974), also needs further study in relation to the differences between the conventional and PHYSHIFT models of dormancy. This period is significant as it has been observed that post-dormant differences in temperature

response between species have as much impact on time of bloom as differences during dormancy (Werner et al., 1988). Substantial anatomical and physiological change occurs during this early period (Ashworth, 1984; Gardea et al., 1994a,b) but the same base temperature for GDH accumulation is normally applied over the entire period from the estimated end of dormancy to bud break and from then to anthesis. However, where the appropriate base temperature does in fact change, the physiological impact of a relatively cold period, followed by warmer period, differs from that of the reverse temperature sequence. Despite this, both are registered identically by heat unit accumulation using a single base temperature which, over the whole period, averages temperature not growth response (Wang, 1960). Wang therefore argues that base temperatures need to be related to stage of development and may be valid for as little as a week.

There is some evidence for temperature response change during this period. Appropriate base temperatures for blooming of apples appear to vary with time (Kronenberg, 1983) and heat accumulation above a base temperature that shifted from -1° in mid-winter to +8°C at full bloom successfully described apple cold hardiness (Winter, 1986) but this approach has not been used widely. Development rates of peach flower buds at 7°, 13°, 18° and 24°C (recalculated as 1/days-to-phenological-stage from reported cumulative degree-day sums) indicate that development rate at 24°C rose relative to that at lower temperatures as buds grew towards anthesis (Rom and Arrington, 1966). The optimum temperature after bud swell was higher than for the period from start of forcing to bud swell and appropriate base temperatures rose from near 0°C to around 7°C. This result is consistent with the observation that during early apricot flower bud development, temperatures at the lower end of the growth range were more 'efficient' than those at the higher end (Brown, 1960). The most appropriate base temperatures for day and night heat unit accumulation have also been found to differ (Renquist et al., 1978; Weilgolaski, 1974).

A progressively changing optimum temperature for growth is consistent with suggestions of an effect of chilling on subsequent potential development rate. For instance, Gurdian and Biggs (1964) suggest that the influence of low temperature on bud dormancy may be one of "preconditioning the tissues so that the initial response to favourable conditions is faster, and possibly, a faster sustained growth rate once it has been initiated." Sparks (1993) interpreted shortening of development times as chilling accumulated to mean that

"within the normal range of chilling received in nature, chilling, and thus rest, is rarely if ever 'completed'." Sparks therefore proposed a model in the form of a logistic relationship between heat accumulation needed for bud break and accumulated chill hours. Very similar empirical models describing the relationship between development rate and chilling accumulation have been proposed for the flushing of temperate forest gymnosperms (Campbell and Sugano, 1979; Cannell and Smith, 1983). These results may reflect a change in responsiveness as chilling is experienced. However, the unbounded temperature response described by the Arrhenius function shows that change in growth rate is as readily caused by a change in the sensitivity to temperature whereby the optimum temperature for growth is altered.

The second corollary, that dormancy alleviation is a relatively discrete event occurring over a limited time period, appears to lead to the view that identification of the end of dormancy is independent of the method used. A variety of methods have therefore been used to establish when the chilling requirement has been satisfied. Common methods include: 1). response to GA_3 (Richardson et al., 1974); 2). forcing at temperatures of 20°C and above using percent bud break (Erez and Lavee, 1971; Erez et al., 1988) or time of development to a certain stage (Gilreath and Buchanan, 1981) as indices of 'rest completion', and 3). statistical estimation by minimisation of error variance associated with estimated heat requirements (Ashcroft et al., 1977). Other researchers have also used formation of tetrads in stamens to indicate 'rest completion' (Bailey et al., 1982; Young and Houser, 1980) and rapid gain of bud fresh or dry weight (Brown and Kotob, 1957; Tabuenca, 1964,1968). However, if the end of dormancy is not a discrete event but instead a continuum of increasing responsiveness to warmer temperatures, then careful attention needs to given to criteria used to define its completion (Felker and Robitaille, 1985).

If dormant buds do undergo a physiological shift then it appears unlikely that chilling requirements calculated using such a diverse array of different methods will be directly comparable. Research objectives ultimately determine the suitability of the method but the accuracy and precision of some methods for phenological modelling is questionable. For instance, peach flower buds do not respond to GA_3 (Hatch and Walker, 1969), the determination of a start of bud weight gain is subjective (Brown and Kotob, 1957) and

the relation of tetrad formation to alleviation of dormancy varies (Viti and Monteleone, 1991; Weinbaum et al., 1988). Furthermore, if Vegis' interpretation of dormancy is valid, then bud development in response to forcing is also dependent on conditions used. Its use as an index of dormancy therefore also needs care. Vegis (1964) comments that tests to see whether the experimental material is in a state of true dormancy before the experiment are often insufficient and that growth inability in conditions which at full growth activity are favourable for growth is not a valid indication of a state of true dormancy. This is because apparent growth capacity is a function of both temperature and the temperature response range of the bud. Percentage bud break, and hence the chilling exposure required to allow 50% bud break, is therefore determined by the forcing temperature and may be longer when forcing temperatures are higher. This, however, has never been explicitly tested. The relationship between changes in populational characteristics, such as percent bud break, to the process of dormancy alleviation as it occurs in individual buds also must be considered. The appearance of continuous change at a populational level (in, for instance bud break percentage) does not rule out discrete transitions in the probability of bud break at an individual bud level.

The third corollary, that dormancy affects buds in their entirety and prevents all but very limited growth before the end of dormancy, implies that the delay between dormancy alleviation and, for instance, bud break is independent of how chilling is experienced. Despite this, flower buds are complex structures and it is possible that growth of individual parts (e.g. petals, stamens and pistil) may become responsive to warm temperatures earlier than other processes, such as vascular differentiation, which may be more closely controlled by the dormancy mechanism. For instance, pollen mother cell maturation in apricot and almond flowers is at least partly independent of potential for rapid bud break (Scalabrelli et al., 1991; Viti and Monteleone, 1991; Weinbaum et al., 1988). If different parts of a bud can develop independently, then some may develop more rapidly relative to the bud as a whole during the period of chilling accumulation as they respond to the warmer temperatures which may be experienced with chilling in the natural diurnal temperature cycle. This unregistered 'heat accumulation' will lower apparent heat sums for later phenological stages such as anthesis.

This is not a difficulty from which the proposed PHYSHIFT model is exempt (as acknowledged in Chapter 6). Its effect in this case would be to introduce a bias to the temperature response profiles calculated under particular temperature regimes. However, the situation for conventional durational models of dormancy is more complex. This is because while these models presuppose that the heat requirements from dormancy release to bud break are fixed, their nature as sequential integrals of time means they are actually inherently correlated with one another. Both chill and heat accumulation are temporal indices which divide a process of finite duration into three parts: a period covered by the first index, a period covered by the second, and a remainder in which no change occurs according to either index. The higher the proportion of the total process time in which temperatures are within the range of the two indices, the greater the probability that the duration of the two periods covered by the indices will be correlated and increase in one index (time spent in one period) will be at the expense of the other. The value of the two sums are therefore not truly independent.

Calculated heat requirements are therefore reliable estimates of the time required for development in regions where significant growth occurs only in spring, but they are probably arbitrary when determined statistically in regions with mild winters. It can not simply be concluded from the correlation of chill and heat unit sums that "buds remain under a rest influence" which reduces the efficiency with which heat promotes development and that "if chilling were completed, bud break would occur with very little heat" (Sparks, 1993). This conclusion requires knowledge of the precise developmental position of flower buds, but the actual development made from the start of forcing has rarely been established in studies on deciduous fruit crops. It is therefore difficult to validate statements such as "Buds ... kept at temperatures that are effective in breaking dormancy, but too low [it is assumed] to permit bud development, continue to increase in growth potential well after the 'minimum number' of chill units required to 'break dormancy' has accumulated." (Dennis, 1994).

If heat requirements are fixed by the development needed between dormancy release and, for example, anthesis, then they should be independent of the manner in which chilling is accumulated. In some cases it should also be independent of chilling accumulation beyond the duration of the estimated chilling requirement. This may be true when plants

are chilled at controlled low temperatures. Time till formation of pollen grains in apricot flower buds did not fall after fulfilment of chilling requirements at 3°C (Brown and Kotob, 1957). Richardson et al. (1975) also reported that peach trees, which had completed rest, failed to show signs of growth after being held for several months in chambers controlled at 4.5°C. However, the speed with which post-chilling development stages are reached after chilling can be related to the chilling regime. Exposure to low temperatures in association with short higher temperature, 'non-chilling' interruptions can reduce time to bud break (Felker and Robitaille, 1985) or tetrad formation (Scalabrelli et al., 1991). Also, times to bud break and bloom, measured in days, GDD (growing degree days) or GDH, are inversely related to chilling duration under controlled temperature and field conditions. Holding flower and vegetative buds of apple, pear, peach and sweet cherry at between 2° and 7.2°C for up to 2400 h after estimated fulfilment of the chilling requirement progressively decreased time to bud break and bloom (Couvillon and Erez, 1985a; Scalabrelli and Couvillon, 1986). Incubation of sour cherry flower buds at 5°C for up to 3000 h had a similar effect (Felker and Robitaille, 1985). Moreover, the buds ultimately reached anthesis at 5°C which showed that all stages of growth were possible at this low temperature. Under field conditions GDH estimates for full bloom of 'Springcrest' peach at three sites in Italy were almost linearly associated with chill unit accumulations except where temperatures were near zero for a large period of 'chilling' (chill hour or unit) accumulation (Pitacco et al., 1992; Scalabrelli et al., 1992). The PHYSHIFT model avoids this difficulty by regarding temperature response as a continuum so that all development is registered on the same index. The key issue is then to ensure that the simulated temperature response throughout the entire period faithfully represents plant development.

The fourth corollary, the concept of chilling 'reversibility', illustrates a major contrast between the conventional and PHYSHIFT modelling approaches. The difference is that in conventional chill unit models, high temperature reverses previously acheived alleviation of dormancy whereas in the PHYSHIFT model, high temperatures inhibit future alleviation. Both concepts were canvassed in early studies of high temperature delay of bud break. For instance, Overcash and Campbell (1955) suggested that intermittent high tempera-tures during the chilling period not only tended to counteract the chilling which has already taken place but they also depressed the cumulative effect of chilling. However, the idea that

chilling precipitates a physiological change independent of growth has favoured the second option. Weinberger (1967) subsequently remarks that "Since high maximum temperatures counteract 'chilling', the rest breaking process must be at least partially reversible." This conclusion appears to reflects an analogy with reported reversibility of vernalization due to the effect of high temperature (Purvis and Gregory, 1952).

However, the concept of reversibility, as applied to vernalization, appears to have been as much an attempt to repudiate Lysenko's genetic theory of vernalization as an hypothesis based on firm physiological evidence. Furthermore, there is still no clear physiological evidence that the dormancy alleviating effect of low temperature is actually reversed by high temperature since the locus of the chilling effect remains unknown. Despite this, the concept of 'chilling negation' is the basis of interpretation of the effect of high temperature periods in diurnal cycles (Couvillon and Erez, 1985b; Erez and Lavee, 1971; Erez et al., 1979; Felker and Robitaille, 1985). The reversibility of the chilling effect is also fundamental to the 'Dynamic model' of dormancy alleviation (Fishman et al., 1987a,b). This position is based on the argument that the observation of both chilling enhancement and negation, the consequences of exposure to the same high temperature for different durations in a diurnal cycle, "can be explained only when two antagonising reactions are promoted by the same temperature at the same time" (Couvillon and Erez, 1985b).

In contrast, the PHYSHIFT model shows that observed responses to controlled cyclic temperatures can also be explained in terms of high temperature suppression of subsequent potential development at low temperature. This was Overcash and Campbell's (1955) first alternative. In this case, the apparent enhancement of chilling by moderate temperatures or by short periods of high temperature are not due to concomitant heat unit accumulation (Felker and Robitaille, 1985) or marginal augmentation of accumulation of a thermally unstable precursor over high temperature-induced destruction (Fishman et al., 1987b). Rather, it results from growth acceleration by the high temperature period late in the alternating temperature regime compensating for initial inhibition of development. No negation of a previous chilling effect is involved. This explains the recovery of sour cherry buds exposed to 2000 h at 5°/15°C to equal the development of buds exposed to 2000 h at 5°C after buds under the cyclic regime had lagged in their development at 400 h (Felker and Robitaille, 1985). Further studies which direct careful attention to the relative

developmental stages reached at the end of corresponding cyclic and constant temperature periods, and which determine the thermal response window at these points, are required to critically distinguish between the two alternatives.

Final confirmation of the validity of a progressive alleviation of dormancy as against a discrete transition to growth depends on data on the actual physiology of bud dormancy in deciduous trees such as apricots. Dormancy alleviation coincides with numerous physiological changes (Lavee, 1973; Wang and Faust, 1988) and alone or together these might contribute to a progressive shift in temperature response directly via altered metabolism or indirectly by a change in gene expression (Lazarus, 1991). The most widely investigated changes are depletion of inhibitors, such as phenolic compounds and abscisic acid (ABA), and accumulation of growth promoters, such as auxins, polyamines, cytokinins and gibberellins (Lavee, 1973; Wareing and Saunders, 1971).

Dormant buds contain relatively high levels of phenolic compounds which are generally inhibitory to growth but evidence for their direct involvement in dormancy release is lacking (Lavee, 1973). Evidence for the involvement of ABA, at least in the early stages of dormancy, is stronger. The action of ABA is clearly involved in the induction of dormancy in seeds (Hilhorst and Karssen, 1992). It was also linked to the induction of dormancy in buds early after its discovery (El-Antalby et al., 1967). In *Prunus*, ABA accumulates in bud scales and floral tissues simultaneously with dormancy induction and autumn leaf abscission then declines after the end of rest (Ramsay and Martin, 1970). This might suggest that dormancy alleviation reflected declining levels of endogenous ABA but this is probably not the case. Maintenance of dormancy in seeds and bulbs is not always related to ABA concentration (Black, 1991; Djilianov et al., 1994; Hilhorst and Karssen, 1992). Endogenous ABA does not always rise with dormancy induction in buds (Powell, 1976), nor are declining levels consistently associated with dormancy alleviation (Corgan and Martin, 1971; Freeman and Martin, 1981; Mielke and Dennis, 1978). Application of thidiazuron to apple seedlings also did not reduce endogenous ABA despite inducing bud break (Wang et al., 1987). Furthermore, early reports of diminished ABA levels were based on bioassay techniques and may be confounded by rising promoter levels (Lavee, 1973). The presence of ABA in dormant buds may therefore relate more closely to the capacity for tolerance of winter water stress associated with freezing (Trewavas and Jones, 1991). The

endogenous level of ABA is therefore probably not an accurate guide to likely temperature response that could be used as an alternative method of deriving PHYSHIFT models for different cultivars.

Experimental evidence also indicates that dormancy alleviation does not correspond to a general rise in the endogenous levels of growth-promoting compounds. Endogenous auxin levels rise in spring but this appears most closely related to the initiation of rapid growth (Lavee, 1973; Little and Wareing, 1981). Similarly, a rapid increase in endo-genous polyamine levels only occurred as active growth resumed in *Prunus serrulata* (Wang et al., 1985) and, though levels rose in buds of 'Anna' apple after exposure to low temperature, they did not relate to capacity for bud break or flower development (Wang and Faust, 1994a). Evidence for the involvement of gibberellins (GA) is also ambivalent. Application of GA will promote germination of some seeds, but the action of GA appears restricted to the germination process only and synthesis of GA does not seem to be involved in dormancy alleviation (Hilhorst and Karssen, 1992). Application of GA to fruit trees can also promote bud break (Hatch and Walker, 1969; Williams and Stahly, 1968) and bud break induced by defoliation is also preceded by a three-fold rise in GA activity (Taylor et al., 1984). However, GA application over winter has no effect on floral bud break on peach and apricot (Hatch and Walker, 1969). Spring GA application accelerated development of underchilled 'Redskin' peach floral buds but had little effect on those of 'Redhaven' (Couvillon and Hendershott, 1974). In another peach cultivar the highest concentrations of free GA_1 /GA_3 was found in dormant flower buds in mid-winter (June) and diminished thereafter (Luna et al., 1990). It therefore appears unlikely that a rise in endogenous GA provides a simple explanation of dormancy alleviation.

In contrast, cytokinins (CK) may be more closely linked to dormancy release and bud break (Lavee, 1973; Powell, 1987). In potato, changes in the level of endogenous cytokinins are closely associated with the release of bud dormancy (Turnbull and Hanke, 1985b). Exposure to low temperature and exogenous application of cytokinins both cause equiva-lently rapid and substantial rises in endogenous CK which coincide with the transition from dormancy. In deciduous trees, CK activity in the sap falls with the onset of dormancy and rises again in spring prior to bud break (Alvim et al., 1976; Hewett and Wareing, 1973) and xylem sap showing CK activity was also able to induce bud development (Jones, 1973).

Bud break induced by defoliation is preceded by a slight rise in CK activity (Taylor et al., 1984) and exogenous application also promotes bud break (Hatch and Walker, 1969; Williams and Stahly, 1967).

However, the connection of CK to any hypothesised physiological shift again appears more complex than a simple direct linkage of endogenous level and depth of dormancy. In young potato tubers, exogenous CK induced sprouting of buds which were dormant even though endogenous CK levels were very high (Turnbull and Hanke, 1985a,b). High endogenous CK levels in the stems of apple shoots preceding defoliation also suggested CK levels were not limiting bud break (Taylor et al., 1984). A period during which dormant buds of various plant species are insensitive to exogenous cytokinins is also observed. In *Prunus avium*, injection of CK induced vegetative bud break only in late summer and not over the winter period (Arias and Crabbé, 1975). The effect was also greatest for buds at the shoot base and limited for those at the top. Similarly, application of thidiazuron, a synthetic growth regulator with cytokinin-like properties which induces vegetative bud break on apple trees (Wang et al., 1986), generally only induced bud break before apple shoots are exposed to chilling (Steffens and Stutte, 1989). And for potato, applied CK induced bud break on immature tubers during summer but a period of low temperature storage was required before buds on mature potato tubers became responsive to exogenous CK (Turnbull and Hanke, 1985a) The influence exerted by CK on the level of dormancy therefore appears to vary with tissue type and stage of develop-ment and not directly with endogenous concentration. Changing tissue sensitivity to prevailing growth regulator levels (Trewavas, 1982) may reconcile these apparently conflicting results. This approach is more consistent with the concept of dormancy advocated by French-speaking researchers (Champagnat and Côme, 1986; Crabbé, 1990) and focuses attention on metabolic changes within the bud tissue itself which might alter tissue sensitivity and therefore temperature response. In particular, evaluation of the physiological validity of the PHYSHIFT model requires further study of the way growth regulator-induced stimulation of bud break is affected by incubation temperature. If, for instance, progressive change in the response window is related to tissue sensitivity then forcing temperature may directly affect the amount of growth regulator (e.g. cytokinin) required to achieve a standard level of bud break. This could provide a simple method of measuring any progressive movement in the thermal response window.

Changes in the organisation of cellular membranes may be particularly important to temperature response in this respect (Hobson, 1981). Membrane transition temperatures are lower during the dormant period in artichoke and tulips (Chapman et al., 1979; Davies and Hobson, 1980), a transition linked to greater cold hardiness, and changes in membrane composition have recently been linked to the movement of water into cells of apple buds early in bud break (Wang et al., 1994). Altered membrane permeability in the surrounding tissue which restricts movement of metabolites to the meristem also appear related to dormancy in artichoke (Gendraud and Lafleuriel, 1983). Control of translocation to the meristem in this way would markedly affect on the potential influence of otherwise mobile growth regulators such as xylem-borne cytokinins. Such alterations to membrane composition could be caused as part of changes to the oxidative status of the buds which has been suggested as a key factor in leaf bud paradormancy alleviation (Liu et al., 1992; Wang and Faust, 1988). Wang and Faust (1988) contend that relief of correlative inhibition on apple shoots is brought about by the removal of free-radicals from bud tissue through activated peroxide-scavenging systems. The hypothesis stems from study of thidiazuron-induced bud break of non-chilled apple buds which caused marked increases in oxidative enzyme activity and in the levels of ascorbic acid and reduced glutathione (Wang et al., 1991a,b,c). Increases in catalase activity were also associated with bud break in apricot (Scalabrelli et al., 1991). In addition, exposure to low and high temperature, and the application of allyl disulphide, induced bud break in paradormant and endodormant vegetative buds on 'Anna' apple and increased ascorbic acid plus reduced glutathione whereas dehydroascorbic acid and oxidized glutathione decreased (Wang and Faust, 1994b). Related work using magnetic resonance imaging showed that thidiazuron induced the rapid conversion of water in buds from a bound form, typical of dormant buds in winter, to a free form (Faust et al., 1991). Change in the oxidative and water status of dormant buds could therefore represent the basis of the physiological shift proposed by Saure (1985) and simulated in the PHYSHIFT model.

In addition such changes would be likely to have widespread effects on the balance of metabolic activity, protein conformation and protein synthesis. Treatment of buds with thidiazuron is, for instance, immediately followed by a distinct metabolic shift of glucose-6-phosphate from the pentose-phosphate pathway to the glycolytic-TCA cycle which appears to be completed before the resumption of growth (Wang et al., 1991b). The

change from one dominant respiratory pathway (cyanide-insensitive) to another (cyanide-inhibited and low temperature-sensitive) also occurs before bloom of pear (Cole at al., 1982). Changes in the Q_{10} of apple shoot respiration during chilling (Young, 1990) would appear therefore to reflect a change from one pathway to another rather than acclimation of a single enzyme system. If such a progressive physiological shift occurs during dormancy alleviation, thereby affecting temperature response then, clearly, the Arrhenius function used in the proposed model is an empirical approximation of a suite of changes rather than a precise biochemical description of an individual adjustment. Changes in the parameters of the Arrhenius function other than ΔH (used in Chapter 7) would therefore almost certainly feature in a 'physiological shift' of the type proposed. However, the existance of measurable metabolic changes such as these may provide a means of verifying the existance of the physiological shift assumed by the PHYSHIFT model and establishing a physiological basis for any change in temperature response.

Finally, the understanding of dormancy which underlies the PHYSHIFT model suggests a need to redefine the concepts of 'endodormancy' and 'ecodormancy' proposed by Lang and his coworkers (Lang et al., 1987). This is because the conceptual framework used in the PHYSHIFT model proposes that growth is regulated by the position of the thermal response window relative to the ambient temperature range. Lang et al. differentiate between the two types of dormancy on the basis of the agent causing the lack of growth. Endodormancy therefore covers dormancy which is imposed by physiological factors within the affected structure which prevent growth when external conditions are otherwise suitable. Ecodormancy then covers those situations where dormancy is imposed by unsuitable environmental conditions (Lang et al., 1987).

Implicit in this distinction is the idea that a generalised set of environmental conditions exists which provides a universal set of conditions 'suitable' for plant growth. However, the PHYSHIFT model proposes that the thermal conditions suitable for development, if not for growth, vary progressively throughout the year. The relevance of a generalised set of 'suitable' environmental conditions is therefore questionable, at least for temperature, since the temperatures that promote development depend on developmental position. The relationship between the cycles of ambient temperature and the plant response window (Fig. 8.2) illustrate the ambiguity of the current distinction between eco- and endodormancy.

If growth only occurs during the intersections between the two cycles then it could be argued that endodormancy encompasses both the period of dormancy when the response window is above the ambient temperature range and also the period when it is below. Conditions suitable for growth are then determined by the position of response window. On the other hand, and despite assertions to the contrary, (Lang et al., 1987), it could equally be argued that ecodormancy encompasses both periods as it is unsuitable environmental conditions that ultimately prevent growth in both periods of dormancy.

This ambiguity may be avoided (and the helpful terminology of Lang et al. retained) if the concept of 'limitation' is distinguished from that of 'inhibition' and ecodormancy and endodormancy explicitly defined in terms of the factor which limits further development. Thus, a limiting factor may be said to be one which prevents the development by its absence and an inhibiting factor is one which prevents development by its presence. This qualitative concept may be extended quantitatively so that a limiting factor prevents development when it is relatively low and an inhibitory factor prevents it when it is relatively high. Then, if the plant thermal response window is low relative to the ambient temperature range, growth is limited by the potential plant response (i.e. plant limited development, PLD) whereas when the ambient temperature range is low, growth is limited by ambient temperatures (i.e. environment limited development, ELD). This concept also covers situations where the ambient range is wider than the response window and vice versa. Both paradormancy and
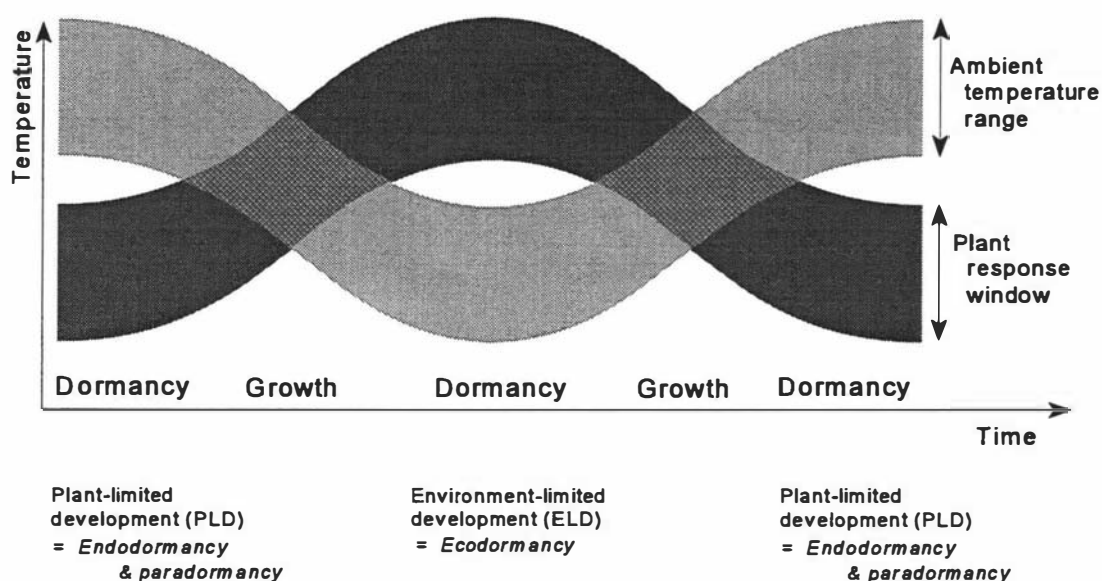
Figure 8.2   Alternation of the relative position of the seasonal cycles of ambient temperature and plant thermal response window to illustrate its role as a determinant of plant growth and the concept of limitation as the cause of dormancy.

endodormancy represent forms of PLD. The two forms of dormancy are still distinguished by the origin of the growth limitation, whether within or outside the affected structure. Ecodormancy equates with the period of ELD. In each case, reference to an arbitrary set of 'suitable' growth conditions is avoided and the cause of dormancy is defined in terms of the relative positions of the environmental and plant response ranges. The PHYSHIFT model therefore emphasizes the important point that the regulatory role of physiological factors in dormancy can be properly considered only in relation to the environment of the plant. Equally, influence of the environment as a determinant of growth rate can only be quantified with reference to a plant's seasonal developmental position.

8.3   Modelling as a Horticultural Tool

Scientific understanding develops by the proposal and testing of hypotheses within the context of an encompassing research programme. The more precisely they are stated the better the chance that a research programme will develop as the hypotheses generated by it are either refuted by subsequent testing or lead to new and novel discoveries. To this end, mathematical modelling offers the facility to precisely state the hypotheses which provide the framework of scientific knowledge (Thornley and Johnson, 1990). The attempt to do so can pin-point areas where knowledge and data are lacking as well as stimulate new ideas and experimental approaches. Explicit modelling can also help focus research to the study of particular questions and alternative hypotheses, reducing the amount of *ad hoc* experimentation. Furthermore, models can also perform a synthetic function, bringing information on different aspects of a process together, giving a unified picture as well as a convenient data summary. This is particularly true of the complex systems experienced and managed horticulturally such as that of pollination. Here, the formulation of a synthetic model means the implications of changes to the system can be investigated and described more readily (Estes et al., 1983).

Mechanistic modelling, in particular, offers a powerful tool for quantitatively describing and analysing the biological systems which underlie horticultural activity. Mechanistic models depict and predict the behaviour of the modelled system at one level of integration in terms of the interaction of its component processes at lower levels of integration. Such models have the benefit that their parameters often have a more general scientific meaning. Thus they can often deepen understanding of the system they describe even though correct reconstruction of observations is no guarantee of a model's validity (Martin and Monot, 1974). Both the pollen transfer model and the PHYSHIFT bloom phenology model presented in this thesis are, to a degree, mechanistic. In each case their output is determined by the interaction of contributory processes (change in cumulative pollenizer bloom and diurnal change in developmental capacity) whose relationships form the critical hypotheses of the models' design.

Both models, however, also display a high degree of empiricism. In essence, empirical models only describe existing data and lack any hypotheses concerning the mechanism by which the observations arose. Accuracy of representation is the primary aim while the form of the relationship is taken for granted. Thus, the Gompertz function used to describe cumulative bloom for calculating pollenizer pollen availability is entirely empirical since the parameters in the function have no biological meaning that can be applied to the mechanism describing the cumulative function. The Arrhenius function used to describe the response of growth rate to temperature is also probably largely empirical as, discussed previously, it most likely describes the overall response of a complex process rather than a single enzyme-catalysed reaction step.

In both cases, more sophisticated relationships incorporating formal mechanistic hypotheses might have replaced those used to describe cumulative bloom and overall rate response. Balancing the level of realism to ensure accuracy versus that of simplicity to ensure tractability, ease of solution and ready interpretation is the primary problem in modelling (Bailey, 1974). In this respect, the purpose and desired output of both models provided guidance. The pollen transfer model was designed to determine the effect of relative time of bloom on cross pollination. Mechanistic representation of population bloom dynamics was therefore not needed. Likewise, the PHYSHIFT model is not intended as a test of the precise physiological hypotheses supporting the form of growth rate function. Rather, it provides a method by which the ability of a continuous shift in temperature response to account for patterns of dormancy alleviation could be tested. The ultimate application of both models is also practical: selection of suitable pollenizers. Greater complexity would probably have contributed little to achieving this pragmatic goal, whatever cognitive value it might have had.

Despite this practical intent both models are still relatively complex and require the use of a computer for their implementation. In this respect digital computers are without peer as modelling tools since mathematical models are fundamentally calculating devices. They give the ability to interpolate between observed data, to extrapolate (cautiously) beyond them, and thereby, to predict behaviour in new situations that are either difficult to create experimentally or which provide critical tests of the validity of the model's hypotheses. In this way, computers facilitate the cyclic interaction between experimental and theoretical

work: i.e. 1) design of experiments; 2). collection of data; 3). data manipulation and analysis; 4) formulation or modification of a model; 5) conformation of the model to data and evaluation of the model, and then 6) simulation of new experimental conditions (Groth, 1974).

This cycle is clearly illustrated by the development and experimental implications of both the pollen transfer and PHYSHIFT models. Both models produce novel outcomes that either question the generality of conclusions drawn in specific circumstances or challenge the validity of conventional perspectives. As an example of the first point, the pollen transfer model indicates that pollenizers should begin to bloom slightly after the cultivar to be pollinated. This contrasts with conclusion drawn from experience with pears and apples (Wauchope, 1968; Williams and Sims, 1977) which suggests that these earlier recommendations may reflect the specific requirements of these crops rather than the general process of pollen transfer. It also highlights the need for fruit set measurements under controlled pollenizer pollen flow to allow calibration of the index of cross-pollination to test this subsequent hypothesis. The PHYSHIFT model illustrates the second point as a test an alternative conceptual framework for dormancy alleviation that differs in many respects from the established model. Initial evaluation (though only qualitative) indicated its ability to describe a range of dormancy phenomena which suggests that behaviour predicted by the model in as yet untried conditions may provide new information on dormancy alleviation.

The availability of low cost numerical computing capacity in the form of the personal computer also opens the way for reassessment of the adequacy of commonly-used descriptive and predictive models. Some, such as the heat unit index and simple alphabetic developmental scales may have sufficed in the past because they required little calculation. However, other more numerically-intensive models may possess significant advantages. For instance, description of response to temperature in the PHYSHIFT model by means of a differential equation has the advantage that slower development corresponds to lower rates of development. In addition the units of the model marry readily with the well developed description of biochemical reactions. In contrast, description of development using heat units has the result that slower development corresponds to higher cumulative temperature sums. The units of the model ($^\circ$C.h) have uncertain physical meaning and are

also misleading since it is not heat but temperature that is in fact being integrated. A further example of the advantage of more numerical methods is the adjusted development scale used to describe apricot bud phenology (Chapter 5) which unlike older alphabetic scales, allow application of regression techniques.

Computer-based modelling also provides the vehicle for integrating research findings with tailored data to provide decision support for orchardists (Laurenson, 1990). Thus the two models developed in the study could be integrated into a more comprehensive decision support tool for analysis of risk associated with different cultivar selection strategies and orchard layout designs (Fig. 8.3). The package could combine models describing bloom phenology (eg PHYSHIFT model), likely forager activity (Szabó, 1980), pollen transfer, fruit set, thinning and fruit growth, all driven by historical or stochastically-generated weather data sets (Buishand, 1978), with an economic analysis component to estimate
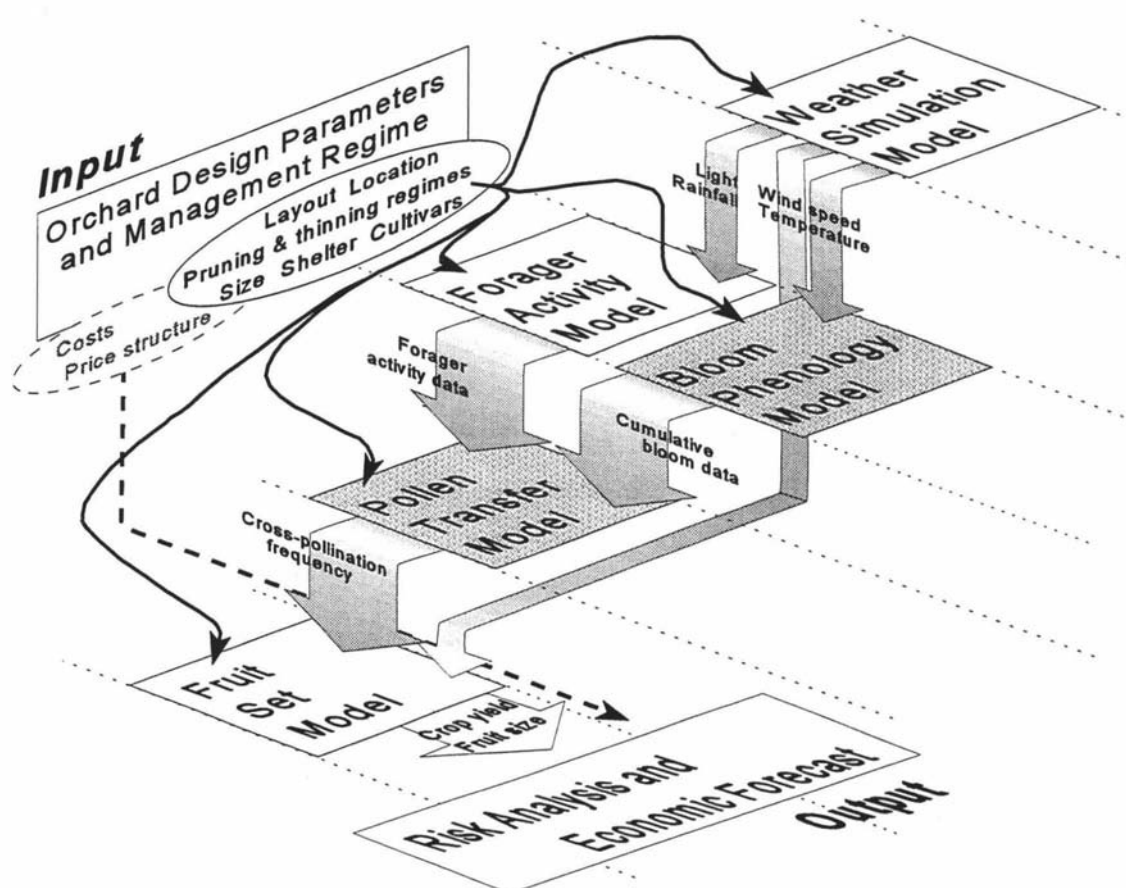
Figure 8.3   Potential integration of PHYSHIFT bloom phenology model and pollenizer pollen transfer model within a comprehensive pollination risk analysis modelling package. (Shaded models indicate those models presented in this study.)

expected crop returns. The pollen transfer and fruit components could be based on a model such as that presented in Chapter 4 or others previously published (Degrandi-Hoffman et al., 1987, 1989; Brain and Landsberg, 1981). When linked to a real-time meteorological data logger the phenology model component could give running estimates of frost sensitivity and predict the time of bloom. Calibration options could allow 'tailoring' of models to specific orchards based on annually-updated records. The package could also be used to predict the regional impact of global climate change on the performance of horticultural systems (Atkins and Morgan, 1990; Kerr, 1988).

Integration of the two models proposed in this study would require representation of the differences in bud characteristics that determine the shape of the cumulative bloom distribution within the PHYSHIFT model. Fitting the phenology model to phenological stage data (the times when 50% of buds reached a given stage of development) produces a model which predicts the development of buds with characteristics in the central range of the bud population. The shape of the cumulative bloom distribution is, however, a function of the bud population as a whole, being determined by the response of buds developing faster as well as slower than the average. In the parameters of the PHYSHIFT model this could reflect distributions in initial bud temperature response (i.e. depth of dormancy, D_i), initial developmental position (d_i) or potential development rate (determined by A and E_a). All could vary but it may be necessary to represent the distribution of only one if it was the dominant determinant of the cumulative bloom distribution. Cumulative bloom distributions for blueberries have been related to chill and heat unit accumulation (NeSmith and Bridges 1992) using Weibull functions and a similar empirical approach could also be adopted for the PHYSHIFT model. A more mechanistic approach which aimed to reproduce the effects of actual bud characteristics such as bud size might prove more useful in that it could be used to represent the effects of different pruning and tree management strategies on bloom phenology and cross pollination and also the effect of tree maturation on bloom divergence. Bud size has a significant effect on the bloom phenology of cherries (Yoshino, 1974) which suggests that initial developmental position may be important. Measuring bud size and development distributions on different shoot types at the start of winter, and as visible bud development began, could estimate both the distribution of initial developmental position and growth rate; in addition it is relatively straight-forward to accomplish.

Finally, for success the resulting information from a combined model package such as that outlined above needs to do more than duplicate users' horticultural intuition. Four criteria provide a basis for assessment: 1) economic significance; 2) sufficient variability in the phenomenon modelled; 3) possibility for action, and 4) accuracy (Waggoner, 1974). The first three criteria are probably met by the package outlined above, but the fourth, accuracy, is clearly of critical importance. In particular, the need for individual model accuracy increases as overall system complexity grows. An estimate of each individual models' precision is also vital as is the ability to integrate these to provide a confidence measure for final output. Combining models also strengthens the argument for a reassessment of common methods used in horticultural modelling. This is because attention is principally on the final output and less on the detailed structure of individual models. Hence there is less need for internal calculations to use units such as the chill unit and growing degree hour merely for the reason they are familiar to the user. Contributory models may therefore be expressed in forms which better reflect the hypotheses on which the models are built or the phenomena modelled. Practical application of computer-based mathematical models may therefore prove an effective stimulus for greater understanding in two horticulturally-significant fields of scientific research- pollination biology and dormancy physiology.

8.4   Conclusions

The research presented in this study identifies and analyses how the processes of fertilization, pollen transfer and flower bud development affect cropping in 'Sundrop' apricot orchards in Hawkes Bay. The results illustrate the strong influence weather conditions have on honey bee foraging activity but show that activity on 'Sundrop' flowers is normally sufficient to achieve satisfactory cross pollination. They also show that 'Sundrop' flowers have adequate viability and that cross pollination yields more than satisfactory fruit set. However, the results demonstrate that expression of gametophytic self incompatibility in 'Sundrop' flowers almost entirely prevents self fertilization, and thus fruit set, after self pollination. For this reason an adequate supply of pollenizer pollen is essential for significant fruit set on 'Sundrop' and hence commercial orchards require a substantial proportion of pollenizer trees relative to that of 'Sundrop'.

For existing orchards with few potential pollenizer trees, several tactical options exist to improve fruit set. The provision of adequate numbers of hives is clearly critical to achieving the necessary level of honey bee foraging activity. Calculations based on forager data collected in Hawkes Bay indicate that five hives per hectare should be sufficient where pollenizer pollen is non-limiting. Higher numbers of hives may improve pollenizer pollen transfer especially under marginal conditions. Minimizing wind speed within the orchard will also enhance bee activity while providing gaps between or under trees within the rows (Hill, 1989) may assist movement between the pollenizer and 'Sundrop' trees. Encouraging vigorous extension growth could also provide a short-term remedial measure to improve fruit set on 'Sundrop' where cross-pollination depends on an early cultivar such as 'Royal Rosa'. This is because bloom on long extension shoots can be up to a week later than the bulk of flowers on spurs and short shoots. The effectiveness of early pollenizers could therefore be enhanced by retaining, or even promoting, a proportion of extension growth, especially as trees mature.

The results also have 'strategic' significance to the design of new 'Sundrop' blocks in Hawkes Bay orchards. Fruit set on 'Sundrop' and other tree crops declines sharply as the distance from pollenizer trees increases (Free, 1962; Free and Spencer-Booth, 1964a,b;

McLaren, Fraser and Grant, 1992; Wertheim, 1991) and gradients in pollen flow are observed even within trees (Briggs et al., 1983; Jackson and Clarke, 1991). Bees also tend to forage along rows even in orchards of relatively open trees such as almonds (Ferrari, 1990). Honey bees are therefore unlikely to transfer pollen much beyond two rows. Existing blocks of 'Sundrop' in Hawkes Bay, commonly three or more rows deep with pollenizers planted only at the margins, should therefore be considered to represent a minimum pollination baseline, satisfactory when weather conditions favour pollen transfer but inadequate when they do not. This is the more likely given the common recommendation that all self incompatible trees should stand adjacent to a pollenizer (Free, 1962; Hill, 1989; Jackson, 1986; Nyútjó et al., 1982). This gives a 1:9 pollenizer ratio but these authors even recommend complete 1:1 interplanting in difficult situations.

Such high pollenizer ratios narrow the choice of potential pollenizers since they require that all cultivars are of value in their own right. Two contrasting pollenizer selection strategies are possible. The first is to use older, self compatible cultivars such as 'Trevatt' as pollenizers. It represents a lower risk/lower gain strategy since while year-to-year variation in production may be minimised, these cultivars generally have average-to-mediocre fruit quality. The second is to use recently-introduced, higher quality cultivars such as 'CluthaGold' and possibly 'Goldrich'. It represents a strategy aimed at higher average returns but since these cultivars are also self incompatible it entails a higher risk of crop loss when adverse conditions prevent adequate cross pollination. 'CluthaGold' appears the leading potential pollenizer option for 'Sundrop' since historical phenological data indicate that it blooms almost synchronously with 'Sundrop' (Glucina et al., 1990; McLaren, Lewis and Glucina, 1992). Pollination studies indicate the two cultivars are cross compatible and their close genetic relationship and similar growth form also mean they are likely to respond to variation in winter weather patterns in much the same way.

In this regard the results highlight the potential for variable pollenizer bloom divergence which further restricts the range of suitable pollenizer cultivars. The bloom divergence model of pollen transfer, developed as part of the study, indicates effective cross pollination requires pollenizers which bloom consistently in synchrony with 'Sundrop' or slightly later. However, analysis of historical bloom data showed there is considerable variation in bloom divergence between apricot cultivars in Hawkes Bay which the pollen transfer model

indicates is sufficient to significantly reduce the opportunity for cross pollination. Provision of at least two potential pollenizers, one to bloom slightly before 'Sundrop' and one to bloom slightly after, is therefore advisable to ensure full overlap with the bloom period of 'Sundrop'. Selection should be based on phenology data from sites with climates as similar as possible to the location of the new planting.

Both the pollen transfer model and the PHYSHIFT model therefore emphasise the essential importance of simple phenological observations as the foundation for scientific understanding and horticultural decision-making. Ultimately, the ideal solution for reliable production is clearly the breeding of high quality self compatible cultivars suited to Hawkes Bay. Other new cultivars arising from the New Zealand apricot breeding programme may provide faster alternatives or may themselves require pollination (McLaren, Lewis and Glucina, 1992). However, their place in an overall solution for pollination problems experienced by Hawkes Bay apricot growers can only be assessed on the basis of comprehensive phenological records. Further development of both models also requires phenological data. This would be most beneficial if it comprised measurements made in a range of New Zealand environments but all under the typical orchard conditions which the models are intended to describe and predict. Regular and systematic phenological observation covering bud break, bud development, bloom and fruit development is therefore of fundamental importance to growers and scientists alike.

Finally this study highlights the practical importance of conceptual and descriptive tools such as the models developed in this study. Both models need further testing and refinement before they can be confidently used to match cultivars for optimum cross pollination. This will require both controlled environment studies to investigate specific model details and tests under natural conditions to test their performance in commercial orchards. Substantially more analysis of orchard pollination systems is also needed before they will reliably quantify and predict pollination risk in a range of situations. However, even as they stand, the models show that the level of fruit set on 'Sundrop' reflects the direct effect of the Hawkes Bay climate on pollen transfer and also its indirect effect via its impact on relative bloom phenology.

8.5   References

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Appendix 1
Interspecific Pollination of 'Sundrop' Apricot

A1.1 Introduction

Interspecific hybridization within *Prunus* offers promise of improved disease resistance as well as novel fruit characteristics such as the combination of apricot flavour with plum-type flesh (Hall, 1991). However, poor fruit set had occurred from pollination of 'Sundrop' with non-*P.armeniaca* species as part of the HortResearch breeding programme. It was known at the outset of this study that 'Sundrop' benefited from cross-pollination (Wood, 1983). The most probable cause for this was a self-incompatibility syndrome as occurs in other Rosaceous crops such as cherries and apples. However, failure of pollen tube development can also be caused by poor gametophyte vigor or male sterility, or when hybridizing, to genetic incongruity (Hogenboom, 1975). Interspecific hybridization therefore offered the opportunity to compare 'Sundrop' pollen tube development with a range of different and potentially incompatible pollen tubes in 'Sundrop' flowers.

A1.2 Methods & Materials

In this initial trial, pollination treatments using four classes of *Prunus* pollen were selected to represent a range of genetic distance from 'Sundrop': i). 'Sundrop' self-pollination, ii). *Prunus mume* and *Prunus ansu* apricot pollens; iii). two plumcot (plum-apricot hybrid) pollens; and iv). two peach pollens. On 17 August clusters of at least 30 flowers on a mature 'Sundrop' tree at HNRC orchard were emasculated and pollinated with pollen of *Prunus armeniaca* 'Sundrop', *P. mume* 'Bungo' or *P. ansu* cv. 'Akita Omi' or with a mixture of *P. armeniaca* pollen ('Royal Rosa' and 'Trevatt'). The tree was enclosed within a sealed pollination tent to exclude bees and other insects. Pistils were collected at intervals between 1 h and 72 h post-pollination and fixed in acetic acid-ethanol (Section 2.2.1.3).

On 3 September clusters of 50 flowers distributed over eleven 5-year-old 'Sundrop' trees at FCU were emasculated and pollinated with six pollen types: *P. persica* 'Springcrest', *P. mume* 'Bungo', *P. ansu* 'Akita Omi', an unnamed dwarf flowering

peach, and two plumcots, Plumcot 'A' and Plumcot 'M'. The dwarf peach pollen was collected from a tree in a domestic garden while other pollens were collected from HNRC orchard. Pistils were bagged and collected 72 h and 1 week post-pollination. Pistil growth and fruit set were recorded at regular intervals between petal-fall in August and harvest in December.

A1.3 Results

No fruit set occurred on the 'Sundrop' tree at HNRC after pollination with either 'Sundrop' or mixed 'Royal Rosa' and 'Trevatt' pollen, or after pollination with 'Akita Omi' or 'Bungo' pollen (Table A1.1) Nearly all fruitlets had abscised by the completion of pit-hardening at the beginning of November with the exception of two fruitlets which subsequently abscised. Pistils for observation of microgametophyte development were collected up to 72 h after pollination which proved insufficient to follow tube growth to the base of the style. However, all styles contained numbers of brightly fluorescent pollen tubes by this stage. Dissection of the few (shrivelled) styles remaining on pistils collected at 3 wks indicated that in each case pollen tubes had aborted after penetrating only one quarter to one half the length of the style.

At FCU the greatest difference observed in pollen tube penetration (Table A1.2) related to pollen quality. No fruit set as a consequence of pollination with pollen of Plumcot 'A' and Plumcot 'M'. Anthers of both hybrids released limited pollen and the proportion of empty grains was particularly high for Plumcot 'M'. Few grains were retained on styles after dissection and very few tubes were counted in styles pollinated with either pollen.

Table A1.1   Abscission of 'Sundrop' fruitlets after self, cross and non-*Prunus armeniaca* pollination: Havelock North Research Centre orchard, 1990.

Pollen source	Original count	Fruit remaining		
	18 August	18 Sept.	2 Nov.	27 Nov.
'Sundrop'	104	52	1	0
'Trevatt' & 'Royal Rosa'	81	33	0	0
'Akita Omi'	122	48	1	0
'Bungo'	152	55	0	0

Table A1.2   Pollen germination, maximum tube penetration and fruit set of 'Sundrop' pistils after pollination with six foreign pollens: Massey University Fruit Crops Unit, 1990. (Mean ± SE)

Pollen source	Pollen grains	Tubes in style	Tube penetration (mm) 72 h	1 week	Fruit set Pistils	Fruits
'Bungo'	26±3 a	7±1 bc	4.1±0.4 b	12.7±0.8 a	30	1
'Akita Omi'	20±3 a	8±2 ab	8.2±1.0 a	9.9±2.1 a	30	3
'Springcrest'	26±3 a	13±3 a	4.3±0.7 b	12.5±1.6 a	30	0
Dwarf peach	32±4 a	9±2 ab	5.0±0.8 b	9.6±1.8 a	30	0
Plumcot 'A'	3±1 b	0.8±0.3 cd	2.3±1.3 c	1.8±0.8 b	30	0
Plumcot 'M'	1±1 b	0.03±0.03 d	2.3±1.3 c	-	30	0
Significance	***	***	**	***		

, * Effect of pollen type non-significant or significant at $P \leq 0.01$, $P \leq 0.001$. Means separation by Tukey's multiple range test, P=0.05.

By contrast, microgametophytes emerged from pollen of *P. mume* 'Bungo', *P. ansu* 'Akita Omi' and the two *P. persica* varieties and penetrated beyond the stigma into the stylar transmitting tissue. Retained grain counts and pollen tube numbers suggest comparable germination levels. Pollen tube penetration by the four cultivars was also similar (though penetration by 'Akita Omi' at 72 h appears anomalously high). and after 1 week all treatments included pistils with at least one pollen in the ovary (approximately 15 mm from the stigma). However, large numbers of highly fluorescent tubes were observed in styles from each treatment and particularly in styles pollinated by peach pollens. These pollen tubes were characterised by thickened walls with heavy callose deposition near the tube tip and typically terminated in the style.

A1.4 Discussion

Poor germination by both plumcot pollens is suggested by the low numbers of pollen grains retained on the stigma after dissection and low number of pollen tubes below the stigma. The limited growth by pollen tubes present in styles also suggests low overall viability of the hybrid pollen. In this respect the pollens of Plumcot 'A' and 'M' were identical to that of other largely sterile plum/ apricot hybrids in which chromosomal abnormalities during meiosis and abnormal spore formation have been reported (King, 1940). The initial development of other pollens was stronger. Penetration of *P. ansu* and *P. mume* pollen tubes within 'Sundrop' styles and fruit set, though limited, is

consistent with the results of more extensive interspecific crosses performed between *P. armeniaca* and these two species (Yoshida et al., 1975). In the cases reported, fruit set after interspecific crossing between these species was good as for intervarietal cross-pollinations. Greater pollen tube fluorescence and lack of fruit set after pollination with peach pollen reflects the greater genetic distance between peach (subgenera *Amygdalus*) and apricot (subgenera *Prunophora*) and suggests that genetic incongruity between style and pollen tube (Hogenboom, 1975) ultimately caused pollen tube abortion.

The better development of tubes at FCU is probably a reflection of the lower temperatures at this site during pollen tube growth. Temperatures reached 35°C in the sealed tent at HNRC which, in the light of subsequent measurements of the effect of temperature on pollen tube development, probably inhibited pollen tube growth. By contrast, daily temperatures in 1990 at FCU during bloom averaged 10°C with mean daily maxima being 13°C. Day temperatures were therefore within the optimum range for pollen tube growth.

A1.5 References

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PHYSHIFT.PAS: Dormancy Model Source Code

PASCAL source code for PHYSHIFT.EXE, compiled using Borland Turbo Pascal 6.0. PHYSHIFT.EXE and sample data files are presented in diskette inside back cover of thesis.

```pascal
PROGRAM PHYSHIFT_ARRHENIUS_DORMANCY_ALLEVIATION_MODEL;
{$G+}
{$M 40960,0,655360}
{$N+}
{$R-}

USES Crt,Dos;

CONST
  DrefArraySize = 5;
  ParamArraySize = 20;
  TempFileArraySize = 100;
  ObsArraySize = 20;

TYPE
  BEEPS = (Error, Finish, Hit, Tick);
  PARAMARRAY = Array [1..ParamArraySize] of REAL;
  OUTPUTARRAY = Array [1..ParamArraySize,1..ParamArraySize] of REAL;
  FILEARRAY = Array [1..TempFileArraySize] of PATHSTR;
  CONCATARRAY = Array [1..TempFileArraySize] of BYTE;
  OBSMATRIX = Array [1..TempFileArraySize,1..ObsArraySize] of REAL;
  NUMSTR = STRING[2];
  RESPSTR = STRING[3];

VAR
  BeepType : BEEPS;
  DRefArrSize,PhenDatPointer,InitDepthArrSize,TempFileArrSize : BYTE;
  Output : CHAR;
  DArray : OUTPUTARRAY;
  DRefArray : PARAMARRAY;
  InitDepthArray : PARAMARRAY;
  Aconst,Ea0Const,Ea1Const,DeltaH0Const,DeltaH1Const,DeltaSConst,
      ShapeNo : REAL;
  PhenDatMat : OBSMATRIX;
  TempFileArray : FILEARRAY;
  ConcatFileArray : CONCATARRAY;
  ConstantsFile,ParametersFile,ObservationDataFile : PATHSTR;
  ResponseType : RESPSTR;
  fRcd,fOutput : TEXT;

FUNCTION FileExists(FileName: string) : Boolean;
{Returns True if file exists; otherwise returns False. Closes file.}
VAR
  f: file;
BEGIN
  {$I-}
  Assign(f, FileName);
  Reset(f);
  Close(f);
  {$I+}
  FileExists := (IOResult = 0) AND (FileName <> '');
END;

PROCEDURE Beep(BeepType : BEEPS);
BEGIN
  CASE BeepType OF
    Error  : BEGIN Sound(400); Delay(300); NoSound; END;
    Finish : BEGIN Sound(1000); Delay(200); NoSound; END;
    Hit    : BEGIN Sound(200); Delay(30); NoSound; END;
    Tick   : BEGIN Sound(100); Delay(15); NoSound; END;
  END;
END;
```

```
PROCEDURE OpenFile(PathName:PATHSTR; VAR f:TEXT);
BEGIN
  {$I-}
  Assign(f,PathName);
  Reset(f);
  {$I+}
  IF (IOResult<>0) OR (PathName='') THEN
  BEGIN
    WriteLn(fRcd,'ERROR: Incorrect path or filename: "',PathName,'"');
    Close(fRcd);
    Beep(Error);
    HALT(02);
  END;
END;

PROCEDURE WriteTitle;
BEGIN
  ClrScr;
  HighVideo;
  WriteLn('PHYSHIFT Phenology Model:   Version 1.0');
  WriteLn('Paul T. Austin, Department of Plant Science, Massey
University');
  LowVideo;
  WriteLn;
END;

PROCEDURE OpenRcdFile(PathName:PATHSTR; VAR f:TEXT);
VAR
  Dir : DIRSTR;
  Name : NAMESTR;
  Ext : EXTSTR;
BEGIN
  FSplit(PathName,Dir,Name,Ext);
  Assign(f,Dir+Name+'.rcd');
  Rewrite(f);
  WriteLn(f,'PHYSHIFT Model              P.T. Austin');
  WriteLn(f,'                           Plant Science Department');
  WriteLn(f,'                           Massey University');
  WriteLn(f);
END;

PROCEDURE ReadInputFile(VAR
Constants,Parameters,ObservationData:PATHSTR;
                        VAR Response:RESPSTR; VAR Shape:REAL);
VAR
  Dir : DIRSTR;
  Name : NAMESTR;
  PathName : PATHSTR;
  Ext : EXTSTR;
  f : TEXT;
  Resp : STRING;
  Letter : CHAR;
PROCEDURE GetFileName(DataType:STRING; VAR FileName:PATHSTR);
BEGIN
  Write('Enter location of ',DataType,' data:  ');
  ReadLn(FileName);
END;

BEGIN
  FSplit(ParamStr(1),Dir,Name,Ext);
  IF Ext = '' THEN Ext := '.phy';
  PathName := Dir + Name + Ext;
  IF FileExists(PathName) THEN
  BEGIN
    OpenFile(PathName,f);
    IF NOT Eof(f) THEN ReadLn(f,Constants);
    IF NOT Eof(f) THEN ReadLn(f,Parameters);
    IF NOT Eof(f) THEN ReadLn(f,ObservationData);
    Response := '';
    WHILE (Response = '') AND NOT Eof(f) DO
```

```
      BEGIN
        Resp := '';
        Letter := '%';
        WHILE (Letter <> ' ') AND NOT Eoln(f) DO
        BEGIN
          Read(f,Letter);
          IF NOT (Letter=' ') THEN Resp := Resp + Upcase(Letter);
        END;
        IF Resp = 'LINEAR' THEN Response := 'Lin'
          ELSE IF Resp = 'LOGISTIC' THEN Response := 'Log'
            ELSE
            BEGIN
              Beep(Error);
              WriteLn(fRcd,'ERROR: Incorrect response type: ',Resp);
              Close(fRcd);
              HALT(06);
            END;
      END;
      ReadLn(f,Shape);
      Close(f);
    END;
  IF FileExists(Constants) THEN WriteLn('Constant data in:',Constants)
    ELSE GetFileName('constant',Constants);
  IF FileExists(Parameters) THEN WriteLn('Parameter data in:
    ',Parameters)
    ELSE  GetFileName('parameter',Parameters);
  IF FileExists(ObservationData) THEN WriteLn('Phenology data data in:
    ',ObservationData)
    ELSE  GetFileName('phenology data',ObservationData);
  WriteLn('Dormancy response:      ',Resp,'  Shape number:
    ',Shape:4:2);
  WriteLn(fRcd,'Constants file:        ',Constants);
  WriteLn(fRcd,'Parameters file:       ',Parameters);
  WriteLn(fRcd,'Phenology data file:  ',ObservationData);
  WriteLn(fRcd,'Dormancy response:     ',Resp,'  Shape number:
    ',Shape:4:2);
  WriteLn(fRcd);
END;

PROCEDURE CheckOutputType(VAR Out:CHAR;VAR fOut:TEXT);
CONST
  ANSWERS = ['D','F','H','P','T'];
VAR
  CmdLnPar : STRING;
  Dir : DIRSTR;
  Name : NAMESTR;
  PathName : PATHSTR;
  Ext : EXTSTR;
  Ans : CHAR;
BEGIN
  CmdLnPar := ParamStr(2);
  IF NOT (CmdLnPar = '') THEN Out := Upcase(CmdLnPar[1])
      ELSE Out := ' ';
  IF NOT(Out IN ANSWERS) THEN
  BEGIN
    Out := ' ';
    WHILE NOT (Out IN Answers) DO
    BEGIN
      GotoXY(1,9);  ClrEol;
      Write('Output mode: Hourly [h], daily [d], transfer [t], final
           [f], phenology [p] :-  ');
      Out := Upcase(ReadKey);
      WriteLn(Out);
      IF NOT (Out IN Answers) THEN Beep(Error);
    END;
  END;
  FSplit(ParamStr(1),Dir,Name,Ext);
  CASE (Out) OF
    'D' : ;
    'H' : ;
```

```
        'P' : BEGIN
                  Assign(fOut,Dir + Name + '.sum');      Rewrite(fOut);
              END;
        'F' : BEGIN
                  Assign(fOut,Dir + Name + '.fin');      Rewrite(fOut);
              END;
        'T' : BEGIN
                  Assign(fOut,Dir + Name + '.trn');      Rewrite(fOut);
              END;
    END;
END;


PROCEDURE ReadConstantsFile(Constants:PATHSTR;
                             VAR A,Ea0,Ea1,DeltaH0,DeltaH1,DeltaS:REAL);
{Reads values for A, Ea0 Ea1 DeltaH0 DeltaH1 DeltaS to variables}
VAR
   fConstant : TEXT;
BEGIN
   OpenFile(Constants,fConstant);
   IF NOT Eof(fConstant) THEN ReadLn(fConstant, A);
   IF NOT Eof(fConstant) THEN ReadLn(fConstant, Ea0);
   IF NOT Eof(fConstant) THEN ReadLn(fConstant, Ea1);
   IF NOT Eof(fConstant) THEN ReadLn(fConstant, DeltaH0);
   IF NOT Eof(fConstant) THEN ReadLn(fConstant, DeltaH1);
   IF NOT Eof(fConstant) THEN ReadLn(fConstant, DeltaS);
   WriteLn('Values of Arrhenius Equation Constants');
   WriteLn('      A =       ',A:8);
   Write('     Ea0 = ',Ea0:11:0);
   IF Ea0 > 15000 THEN WriteLn(' NOTE: High value!') ELSE WriteLn;
   Write('     Ea1 = ',Ea1:11:0);
   IF Ea1 < Ea0 THEN Write('NOTE: Ea1 < Ea0  ') ELSE Write(' ');
   IF Ea0 > 15000 THEN WriteLn('NOTE: High value!') ELSE WriteLn;
   Write('     DeltaH0 = ',DeltaH0:7:0);
   IF DeltaH0 > 100000 THEN WriteLn(' NOTE: High value!') ELSE WriteLn;
   Write('     DeltaH1 = ',DeltaH1:7:0);
   IF DeltaH1 < DeltaH0 THEN Write('NOTE: DeltaH1 < DeltaH0  ')
      ELSE Write(' ');
   IF DeltaH1 > 100000 THEN WriteLn('NOTE: High value!') ELSE WriteLn;
   Write('     DeltaS = ',DeltaS:8:0);
   IF DeltaS > 200 THEN WriteLn(' NOTE: High value!') ELSE WriteLn;
   WriteLn(fRcd,'Arrhenius Equation Constants');
   WriteLn(fRcd,'        A       Ea0      Ea1 DeltaH0 DeltaH1 DeltaS');
   WriteLn(fRcd,A:8,Ea0:8:0,Ea1:8:0,DeltaH0:8:0,DeltaH1:8:0,DeltaS:7:0);
   WriteLn(fRcd);
   Close(fConstant);
END;


PROCEDURE ReadParamsFile(Parameters:PATHSTR;
                          VAR DRefArrSiz,InitDepthArrSiz:BYTE;
                          VAR DRefArr,InitDepthArr:PARAMARRAY);
{Procedure reads parameter values for Dref and DepthNo into respective
arrays}
VAR
   fParams : TEXT;
BEGIN
   OpenFile(Parameters,fParams);
   WriteLn;
   WriteLn('Model parameter values: Developmental distance to dormancy
                                    alleviation (d_ref)');
   Write('  ');
   WriteLn(fRcd,'Model parameter values: d_ref');   Write(fRcd,'  ');
   DRefArrSiz := 0;
   WHILE NOT (Eof(fParams) OR Eoln(fParams))(DRefArrSiz<ParamArraySize) DO
   BEGIN
     DRefArrSiz := DRefArrSiz + 1;
     Read(fParams, DRefArr[DRefArrSiz]);
     Write(DRefArr[DRefArrSiz]:6:0);
     Write(fRcd,DRefArr[DRefArrSiz]:6:0);
   END;
   ReadLn(fParams);
```

```
    WriteLn;
    WriteLn(fRcd);  WriteLn(fRcd);
    WriteLn('Model parameter values: Initial depth of dormancy');
    Write('  ');
    WriteLn(fRcd,'Model parameter values: Initial depth of dormancy');
    Write(fRcd,'  ');
    InitDepthArrSiz := 0;
    WHILE NOT(Eof(fParams) OR Eoln(fParams)) AND
                                    (InitDepthArrSiz<ParamArraySize) DO
  BEGIN
    InitDepthArrSiz := InitDepthArrSiz + 1;
    Read(fParams, InitDepthArr[InitDepthArrSiz]);
    Write(InitDepthArr[InitDepthArrSiz]:6:2);
    Write(fRcd,InitDepthArr[InitDepthArrSiz]:6:2);
  END;
  WriteLn;
  WriteLn(fRcd);  WriteLn(fRcd);
  Close(fParams);
END;

PROCEDURE ReadObsDataFile(ObservationData:PATHSTR;
                          VAR TempFileArr:FILEARRAY;
                          VAR ConcatFileArr:CONCATARRAY;
                          VAR TempFilePoint:BYTE;
                          VAR PhenDatM:OBSMATRIX;    VAR
PhenDatPoint:BYTE);
{Reads names of temperature files into array and dates (Julian days)
      into observation data array}
VAR
  i,j,MinPhenDatPoint : BYTE;
  Letter : CHAR;
  fObsData : TEXT;
  PathName : PATHSTR;
  Dir : DIRSTR;
  Name : NAMESTR;
  Ext : EXTSTR;
FUNCTION StringToNumber(Str:NUMSTR) : BYTE;
BEGIN
  IF Length(Str) = 1 THEN
    StringToNumber := Ord(Str[1]) - 48
  ELSE
    StringToNumber := (Ord(Str[1])-48)*10 +Ord(Str[2])-48;
END;

PROCEDURE DateToJulianDay(Mth,Dy,Yr:WORD; VAR JDay:REAL);
CONST
  JulDays : Array [1..12] of WORD=(0,31,61,92,122,153,184,214,245,275,306,337);
BEGIN
  IF (Mth < 3) THEN Mth := Mth + 10
    ELSE Mth := Mth - 2;
  JDay := JulDays[Mth] + Dy;
  IF JDay > 306 THEN
    IF ((Yr mod 4=0) AND (Yr<>0)) THEN
      JDay := JDay - 366
    ELSE
      JDay := JDay - 365;
END;

PROCEDURE GetJulianDay(VAR f:TEXT; VAR JulianDay:REAL);
VAR
  Mth,Dy,Yr : NUMSTR;
  Month,Day,Year : BYTE;
PROCEDURE IncorrectDate(Mth,Dy,Yr:INTEGER);
BEGIN
    WriteLn;
    WriteLn('ERROR: Incorrect phenology record date at ',
                    TempFileArr[TempFilePoint],'   ',Mth,'/',Dy,'/',Yr);
    WriteLn(fRcd);
    WriteLn(fRcd,'ERROR: Incorrect phenology record date at ',
                    TempFileArr[TempFilePoint],'   ',Mth,'/',Dy,'/',Yr);
```

```
      Beep(Error);
      Close(fRcd);
      Close(f);
      HALT(03);
   END;

BEGIN
  Mth := ''; Dy := ''; Yr := '';
  WHILE ((Letter<>'/') AND (Letter<>'-')) AND NOT Eoln(f) DO
  BEGIN
    Mth := Mth + Letter;
    Read(f,Letter);
  END;
  Month := StringToNumber(Mth);
  Read(f,Letter);
  WHILE ((Letter<>'/') AND (Letter<>'-')) AND NOT Eoln(f) DO
  BEGIN
    Dy := Dy + Letter;
    Read(f,Letter);
  END;
  Day := StringToNumber(Dy);
  Read(f,Letter);
  WHILE (Letter<>' ') AND NOT Eoln(fObsData) DO
  BEGIN
    Yr := Yr + Letter;
    Read(f,Letter);
  END;
  Year := StringToNumber(Yr);
  IF ((Month>12) OR (Day > 31)) THEN IncorrectDate(Month,Day,Year);
  DateToJulianDay(Month,Day,Year,JulianDay);
END;

PROCEDURE ReadPhenDates(VAR fObs:TEXT; VAR PDatM:OBSMATRIX;
                            TFilePoint: BYTE; VAR PDatPoint:BYTE);
BEGIN
  PDatPoint := 0;
  WHILE NOT(Eoln(fObs)) AND (PDatPoint<ObsArraySize) DO
  BEGIN
    Read(fObs,Letter);
    CASE Letter OF
      ' ' : ;
      '.' : BEGIN
              PDatPoint := PDatPoint + 1;
              PhenDatM[TFilePoint, PDatPoint] := 367;
              Write(fRcd,'   .');
            END;
      '0'..'9' : BEGIN
                   PDatPoint := PDatPoint + 1;
                   GetJulianDay(fObs, PDatM[TFilePoint, PDatPoint]);
                   Write(fRcd,PDatM[TFilePoint, PDatPoint]:4:0)
                 END;
    END;
  END;
  IF NOT Eof(fObs) THEN ReadLn(fObs);
END;

PROCEDURE ReadExpData(VAR fObs:TEXT; VAR PDatM:OBSMATRIX;
                          TFilePoint: BYTE; VAR PDatPoint:BYTE);
VAR
  Blank : CHAR;
PROCEDURE IncorrectValue;
BEGIN
    WriteLn;
    WriteLn('ERROR: Incorrect observation at ',
                                        TempFileArr[TempFilePoint]);
    WriteLn(fRcd);
    WriteLn('ERROR: Incorrect observation at',
                                        TempFileArr[TempFilePoint]);
    Beep(Error);
    Close(fRcd);
```

```
        Close(fObs);
        HALT(03);
    END;

BEGIN
    PDatPoint := 0;
    {$I-}
    WHILE NOT Eoln(fObs) DO
    BEGIN
        PDatPoint := PDatPoint + 1;
        Read(fObs, PDatM[TFilePoint, PDatPoint]);
        Write(fRcd,PDatM[TFilePoint, PDatPoint]:4:0);
        IF NOT Eoln(fObs) THEN Read(fObs,Blank);
        IF (IOResult<>0) THEN IncorrectValue;
    END;
    IF NOT Eof(fObs) THEN ReadLn(fObs);
    {$I+}
END;

BEGIN
    OpenFile(ObservationData,fObsData);
    FOR i := 1 TO TempFileArraySize DO TempFileArr[i] := '';
    FOR i := 1 TO TempFileArraySize DO ConcatFileArr[i] := 0;
    FOR i := 1 TO ObsArraySize DO
    BEGIN
        FOR j := 1 TO TempFileArraySize DO
        BEGIN
            PhenDatM[i,j] := 367;
        END;
    END;
    MinPhenDatPoint := ObsArraySize;
    Write(fRcd,'Temperature File           Observation Data');
    TempFilePoint := 0;
    WHILE (TempFilePoint<TempFileArraySize) AND NOT Eof(fObsData) DO
    BEGIN
        PathName := '';
        TempFilePoint := TempFilePoint + 1;
        IF NOT Eof(fObsData) THEN
            Read(fObsData,Letter);
        IF ((Letter='&') AND (TempFilePoint<>1)) THEN
        BEGIN
            ConcatFileArr[TempFilePoint] := 1;
            Write(fRcd,' ')
        END
        ELSE
            WriteLn(fRcd);
        WHILE (Letter<>' ') AND NOT Eoln(fObsData) DO
        BEGIN
            IF NOT (Letter = '&') THEN PathName := PathName + Letter;
            Read(fObsData,Letter);
        END;
        IF (Eoln(fObsData) AND (Letter <>' ')) THEN
            PathName := PathName + Letter;
        TempFileArr[TempFilePoint] := PathName;
        IF FileExists(TempFileArr[TempFilePoint]) THEN
        BEGIN
            Write(fRcd,TempFileArr[TempFilePoint],'   ');
        END
        ELSE
        BEGIN
            Beep(Error);
            Write(fRcd,'ERROR: Cannot find"',TempFileArr[TempFilePoint],'"');
            Close(fRcd);
            Close(fObsData);
            HALT(02);
        END;
        FSplit(TempFileArr[TempFilePoint],Dir,Name,Ext);
        IF Ext = '.ehr' THEN
            ReadExpData(fObsData,PhenDatM,TempFilePoint,PhenDatPoint)
        ELSE
```

```
        ReadPhenDates(fObsData,PhenDatM,TempFilePoint,PhenDatPoint);
     IF (PhenDatPoint < MinPhenDatPoint) THEN MinPhenDatPoint :=
PhenDatPoint;
  END;
  PhenDatPoint := MinPhenDatPoint;
  WriteLn(fRcd);
  Close(fObsData);
END;

PROCEDURE DoCalculations(Constants,Parameters,ObservationData:PATHSTR;
             A,Ea0,Ea1,DeltaH0,DeltaH1,DeltaS:REAL;
             Response:RESPSTR; Shape:REAL;
             DRefArrSiz,InitDepthArrSiz,TempFilePoint,PhenDatPoint:BYTE;
             DArray:OUTPUTARRAY;
             DRefArr,InitDepthArr:PARAMARRAY;
             TempFileArr:FILEARRAY;
             ConcatFileArr:CONCATARRAY;
             PhenDatM:OBSMATRIX;
             Out:CHAR; VAR fOutput:TEXT);
TYPE
  SITESTR = STRING[4];
VAR
  i,j,PhenStgPointer : BYTE;
  DepthArray,fAArray : OUTPUTARRAY;
  EaDifference,DeltaHDifference,Temp : REAL;
  Name : NAMESTR;
  Dir : DIRSTR;
  Ext : EXTSTR;
  Site : SITESTR;
  fTemp : TEXT;
  Year,HrsElapsed : WORD;
  Day : REAL;
PROCEDURE WriteCalcsToScreen(X,Y:BYTE; FilePath:PATHSTR; Yr:WORD;
JDay:REAL);
VAR
  Name : NAMESTR;
  DIR : DIRSTR;
  EXT : EXTSTR;
BEGIN
  FSplit(FilePath,Dir,Name,Ext);
  IF (Ext <> '.ehr') THEN
  BEGIN
  IF JDay < 0 THEN
    IF ((Yr mod 4=0) AND (Yr<>0)) THEN
      JDay := JDay + 366
    ELSE
      JDay := JDay + 365;
  END;
  GotoXY(X,Y);
  ClrEol;
  Write(' ',Name,JDay:8:0);
END;

PROCEDURE OpenListFile(PathName:PATHSTR; VAR f:TEXT);
VAR
  Name : NAMESTR;
  Dir : DIRSTR;
  Ext : EXTSTR;
BEGIN
  FSplit(PathName,Dir,Name,Ext);
  Assign(f,Dir+Name+'.out');
  Rewrite(f);
END;

PROCEDURE WriteListFileHeader(Resp:RESPSTR;Constant,Param,Obs:PATHSTR;
                    DrefAr,InitDepthAr:PARAMARRAY;
                    DrefArrSi,InitDepthArrSi:BYTE; VAR f:TEXT);
VAR
  k,l : BYTE;
BEGIN
```

```
  WriteLn(f,'!Constants file:        ',Constant);
  WriteLn(f,'!Parameters file:       ',Param);
  WriteLn(f,'!Phenology data file:  ',Obs);
  WriteLn(f,'!Dormancy response:     ',Resp,' Shape number:',Shape:4:2);
  WriteLn(f,'!Arrhenius Equation Constants');
  WriteLn(f,'!      A     Ea0     Ea1 DeltaH0 DeltaH1 DeltaS');
  WriteLn(f,'!',A:8,Ea0:8:0,Ea1:8:0,DeltaH0:8:0,DeltaH1:8:0,DeltaS:7:0);
  WriteLn(f,'!Parameters');
  Write(f,'!Dref:');
  FOR k := 1 TO DrefArrSi DO
  BEGIN
    FOR l := 1 TO InitDepthArrSi DO
    BEGIN
      Write(f,'      ',DrefAr[k]:5:0,'         ');
    END;
  END;
  WriteLn(f);
  Write(f,'!Depth:');
  FOR k := 1 TO DrefArrSi DO
  BEGIN
    FOR l := 1 TO InitDepthArrSi DO
    BEGIN
      Write(f,'      ',InitDepthAr[l]:4:2,'         ');
    END;
  END;
  WriteLn(f);
  IF (Out='F') THEN Write(f,'!Filename') ELSE Write(f,'!Day');
  FOR k := 1 TO DrefArrSi DO
  BEGIN
    FOR l := 1 TO InitDepthArrSi DO
    BEGIN
      Write(f,'     D Depth  fA ');
    END;
  END;
  WriteLn(f);
END;

PROCEDURE WriteToListFile(Yr,HrsElap,Hr:WORD;JDay:REAL;
            PathName:PATHSTR;
                        DrefAr,InitDepthAr:PARAMARRAY;
                        DrefArrSi,InitDepthArrSi:BYTE;
                        DArr,DepthArr,fAArr:OUTPUTARRAY; VAR f:TEXT);
VAR
  Name : NAMESTR;
  Dir : DIRSTR;
  Ext : EXTSTR;
  k,l : BYTE;
  Depth,RelDevPos : REAL;
BEGIN
  IF (Out='F') THEN
  BEGIN
    FSplit(PathName,Dir,Name,Ext);
    Write(f,Name,' ');
  END
  ELSE
  BEGIN
    IF JDay < 0 THEN
    BEGIN
      IF ((Yr mod 4=0) AND (Yr<>0)) THEN JDay := JDay + 366
        ELSE JDay := JDay + 365;
    END;
    IF (Out='H') THEN
    BEGIN
      Write(f,HrsElap:4,JDay:4:0,Hr:3);
    END
    ELSE
      Write(f,JDay:3:0);
  END;
  FOR k := 1 TO DrefArrSi DO
  BEGIN
```

```
      FOR l := 1 TO InitDepthArrSi DO
      BEGIN
        RelDevPos := DArr[k,l]/DrefArr[k];
        Write(f,' ',RelDevPos:7:3,' ',DepthArr[k,l]:4:2,' ',
                                                  fAArr[k,l]:4:2);
      END;
    END;
  WriteLn(f);
END;

PROCEDURE WriteOutput(VAR fOut:TEXT;TempFile:PATHSTR;
                          VAR PStgPoint:BYTE; PhenDate:REAL;
                          DrefAr:PARAMARRAY; DRefArSz:BYTE;
                          DArr:OUTPUTARRAY; InitDepthArSz:BYTE);
VAR
  k,l : BYTE;
  RelDevPos : REAL;
  FileName : NAMESTR;
  Dir : DIRSTR;
  Ext : ExtStr;
BEGIN
  FSplit(TempFile,Dir,FileName,Ext);
  IF (PhenDate = 367) THEN
    Write(fOut,FileName,'   .   .')
  ELSE
    Write(fOut,FileName,PStgPoint:4,Phendate:4:0);
  FOR k := 1 TO DRefArSz DO
  BEGIN
    FOR l := 1 TO InitDepthArSz DO
    BEGIN
      RelDevPos := DArr[k,l]/DrefAr[k];
      IF PhenDate = 367 THEN
        Write(fOut,'   .   ')
      ELSE
        Write(fOut,RelDevPos:7:3);
    END;
  END;
  WriteLn(fOut);
  PStgPoint := PStgPoint + 1;
END;

PROCEDURE ReadTempFile(Ex:EXTSTR; VAR f:TEXT; VAR JDay:REAL;
                       VAR T:REAL;VAR Yr:WORD; VAR Name:SITESTR);
BEGIN
  Read(f,JDay,T);
  IF (Ex = '.ehr') THEN
  BEGIN
    Yr := 0;
    Name := 'EXPT';
    ReadLn(f);
  END
  ELSE
  BEGIN
    ReadLn(f,Yr,Name);
    IF JDay > 306 THEN
      IF ((Yr mod 4=0) AND (Yr<>0)) THEN JDay := JDay - 366
      ELSE
        JDay := JDay - 365;
  END;
  IF ((T<-50) OR (T>50)) THEN
  BEGIN
    WriteLn(fRcd,'Bad temperature at ',Name,' ',Yr,' ',JDay,': ',
                                        T:6:1,'Temp set to 10°C');
    Beep(Error);
    T := 283;
  END
  ELSE
    T := T + 273.3;
END;
```

```pascal
PROCEDURE DoAllHourlyCalcsLin(EaDiff,DeltaHDiff,Temperature:REAL);
VAR k,l : BYTE;
PROCEDURE CalcDevIncrmLin1(T,Dref,InitDepth,EaDif,DeltaHDif:REAL;
                          VAR D,fA,Depth:REAL);
VAR
  Ea,DeltaH : REAL;
  NewfA : DOUBLE;
BEGIN
    IF (D<Dref) THEN
    BEGIN
      Depth := InitDepth + (D/Dref)*(1-InitDepth);
      Ea := Ea0 + Depth*EaDif;
      DeltaH := DeltaH0 + Depth*DeltaHDif;
    END
    ELSE
    BEGIN
      Ea := Ea1;
      DeltaH := DeltaH1;
    END;
    NewfA := 1/(1+exp(DeltaS)*exp(-DeltaH/T));
    IF (NewfA > fA) THEN fA := fA + fA*(NewfA - fA) ELSE fA := NewfA;
    D := D + fA*A*exp(-Ea/T);
END;
PROCEDURE CalcDevIncrmLin2(T,Dref,InitDepth,EaDif,DeltaHDif:REAL;
                          VAR D,fA,Depth:REAL);
VAR
  Ea,DeltaH : REAL;
  NewfA : DOUBLE;
BEGIN
    IF (D<Dref) THEN
    BEGIN
      Depth := InitDepth + exp(Shape*ln(D/Dref))*(1-InitDepth);
      Ea := Ea0 + Depth*EaDif;
      DeltaH := DeltaH0 + Depth*DeltaHDif;
    END
    ELSE
    BEGIN
      Ea := Ea1;
      DeltaH := DeltaHl;
    END;
    NewfA := 1/(1+exp(DeltaS)*exp(-DeltaH/T));
    IF (NewfA > fA) THEN fA := fA + fA*(NewfA - fA) ELSE fA := NewfA;
    D := D + fA*A*exp(-Ea/T);
END;

BEGIN
  IF Shape = 1 THEN
  BEGIN
    FOR k := 1 TO DRefArrSiz DO          {All values of Dref}
    BEGIN
      FOR l := 1 TO InitDepthArrSiz DO      {All values of InitDepthNo}
      BEGIN
        CalcDevIncrmLin1(Temperature,DrefArr[k],InitDepthArr[l],EaDiff,
                 DeltaHDiff,DArray[k,l],fAArray[k,l],DepthArray[k,l]);
      END;
    END;
  END
  ELSE
  BEGIN
    FOR k := 1 TO DRefArrSiz DO          {All values of Dref}
    BEGIN
      FOR l := 1 TO InitDepthArrSiz DO      {All values of InitDepthNo}
      BEGIN
        CalcDevIncrmLin2(Temperature,DrefArr[k],InitDepthArr[l],
                    EaDiff,DeltaHDiff,
                    DArray[k,l],fAArray[k,l],DepthArray[k,l]);
      END;
    END;
  END;
END;
```

```pascal
PROCEDURE DoAllHourlyCalcsLog(EaDiff,DeltaHDiff,Temperature:REAL);
VAR
  k,l : BYTE;
PROCEDURE CalcDevIncrmLog1(T,Dref,InitDepth,EaDif,DeltaHDif:REAL;
                           VAR D,fA,Depth:REAL);
VAR
  Ea,DeltaH : REAL;
  NewfA : DOUBLE;
BEGIN
    IF (D<Dref) THEN
    BEGIN
      Depth := InitDepth + (1-InitDepth)/(1+exp(6-12*(D/Dref)));
      Ea := Ea0 + Depth*EaDif;
      DeltaH := DeltaH0 + Depth*DeltaHDif;
    END
    ELSE
    BEGIN
      Ea := Ea1;
      DeltaH := DeltaH1;
    END;
    NewfA := 1/(1+exp(DeltaS)*exp(-DeltaH/T));
    IF (NewfA > fA) THEN fA := fA + fA*(NewfA - fA) ELSE fA := NewfA;
    D := D + fA*A*exp(-Ea/T);
END;

PROCEDURE CalcDevIncrmLog2(T,Dref,InitDepth,EaDif,DeltaHDif:REAL;
                           VAR D,fA,Depth:REAL);
VAR
  Ea,DeltaH : REAL;
  NewfA : DOUBLE;
BEGIN
    IF (D<Dref) THEN
    BEGIN
      Depth := InitDepth +
(1-InitDepth)/(1+exp(6-12*exp(Shape*ln(D/Dref))));
      Ea := Ea0 + Depth*EaDif;
      DeltaH := DeltaH0 + Depth*DeltaHDif;
    END
    ELSE
    BEGIN
      Ea := Ea1;
      DeltaH := DeltaH1;
    END;
    NewfA := 1/(1+exp(DeltaS)*exp(-DeltaH/T));
    IF (NewfA > fA) THEN fA := fA + fA*(NewfA - fA) ELSE fA := NewfA;
    D := D + fA*A*exp(-Ea/T);
END;

BEGIN
  IF Shape = 1 THEN
  BEGIN
    FOR k := 1 TO DRefArrSiz DO          {All values of Dref}
    BEGIN
      FOR l := 1 TO InitDepthArrSiz DO       {All values of InitDepthNo}
      BEGIN
        CalcDevIncrmLog1(Temperature,DrefArr[k],InitDepthArr[l],
                    EaDiff,DeltaHDiff,
                    DArray[k,l],fAArray[k,l],DepthArray[k,l]);
      END;
    END;
  END
  ELSE
  BEGIN
    FOR k := 1 TO DRefArrSiz DO          {All values of Dref}
    BEGIN
      FOR l := 1 TO InitDepthArrSiz DO       {All values of DepthNo}
      BEGIN
        CalcDevIncrmLog2(Temperature,DrefArr[k],InitDepthArr[l],
                    EaDiff,DeltaHDiff,
                    DArray[k,l],fAArray[k,l],DepthArray[k,l]);
```

```
            END;
          END;
        END;
    END;

  PROCEDURE InitialiseArrays(VAR DArr,DepthArr,fAArr:OUTPUTARRAY);
  VAR
    k,l : BYTE;
  BEGIN
    FOR k := 1 TO ParamArraySize DO
    BEGIN
      FOR l := 1 TO ParamArraySize DO
      BEGIN
        DArr[k,l] := 0.0000001;
        fAArr[k,l] := 0.1;
        DepthArr[k,l] := 0;
      END;
    END;
  END;

BEGIN
  EaDifference := Ea1-Ea0;
  DeltaHDifference := DeltaH1-DeltaH0;
  IF ((Out = 'F') OR (Out = 'T')) THEN

WriteListFileHeader(Response,Constants,Parameters,ObservationData,

DrefArr,InitDepthArr,DrefArrSiz,InitDepthArrSiz,fOutput);
  FOR i := 1 TO TempFilePoint DO
  BEGIN
    IF (ConcatFileArr[i]=0) THEN
    BEGIN
      HrsElapsed := 0;
      InitialiseArrays(DArray,DepthArray,fAArray);
                              {1=Concatenate temperature files, 0=don't}
    END;
    FSplit(TempFileArr[i],Dir,Name,Ext);
    OpenFile(TempFileArr[i],fTemp);
    IF ((Out = 'D') OR (Out = 'H')) AND (ConcatFileArr[i]=0) THEN
    BEGIN
      OpenListFile(TempFileArr[i],fOutput);
      WriteListFileHeader(Response,Constants,Parameters,
          ObservationData,DrefArr,InitDepthArr,DrefArrSiz,
                                        InitDepthArrSiz,fOutput);
    END;
    PhenStgPointer := 1;
    Day := 0;
    WHILE ( ((Output = 'P') AND NOT Eof(fTemp)) OR
            ((Day < PhenDatM[i,PhenStgPointer]) AND NOT Eof(fTemp)) )
DO
    BEGIN
      IF (PhenStgPointer < ObsArraySize) AND (Output = 'P')
        AND (Day > PhenDatM[i,PhenStgPointer]) THEN
      BEGIN
        Beep(Hit);
        WriteOutput(fOutput,TempFileArr[i],PhenStgPointer,
            PhenDatM[i,PhenStgPointer],DrefArr,DRefArrSiz,
                                        DArray,InitDepthArrSiz);
      END;
      j := 0;                   {Listing for every 24 hours}
      WHILE (j < 24) AND NOT Eof(fTemp) DO
      BEGIN
        j := j + 1;
        ReadTempFile(Ext,fTemp,Day,Temp,Year,Site);
        IF Response = 'Lin' THEN
          DoAllHourlyCalcsLin(EaDifference,DeltaHDifference,Temp)
        ELSE
          DoAllHourlyCalcsLog(EaDifference,DeltaHDifference,Temp);
        IF (Out = 'H') THEN
                WriteToListFile(Year,HrsElapsed,j-1,Day,
```

```
                              TempFileArr[i],DrefArr,InitDepthArr,
                              DrefArrSiz,InitDepthArrSiz,
                              DArray,DepthArray,fAArray,fOutput);
          HrsElapsed := HrsElapsed + 1;
        END;
        WriteCalcsToScreen(50,23,TempFileArr[i],Year,Day);
        IF (Out = 'D') THEN
              WriteToListFile(Year,0,0,Day,TempFileArr[i],
                  DrefArr,InitDepthArr,DrefArrSiz,InitDepthArrSiz,
                              DArray,DepthArray,fAArray,fOutput);
      END;
      Close(fTemp);
      CASE Output OF
        'D' : IF (i=TempFileArraySize) OR (ConcatFileArr[i+1]=0)
                    THEN Close(fOutput);
        'F' : IF (i=TempFileArraySize) OR (ConcatFileArr[i+1]=0)
                    THEN WriteToListFile(Year,0,0,Day,
                              TempFileArr[i-1],DrefArr,InitDepthArr,
                              DrefArrSiz,InitDepthArrSiz,
                              DArray,DepthArray,fAArray,fOutput);
        'H' : IF (i=TempFileArraySize) OR (ConcatFileArr[i+1]=0)
                    THEN Close(fOutput);
        'P' : ;
        'T' : WriteToListFile(Year,0,0,Day,
                    TempFileArr[i],DrefArr,InitDepthArr,
                              DrefArrSiz,InitDepthArrSiz,
                              DArray,DepthArray,fAArray,fOutput);
      END;
    END;
    CASE Output OF
      'D' : ;
      'F' : Close(fOutput);
      'H' : ;
      'P' : Close(fOutput);
      'T' : Close(fOutput);
    END;
END;

BEGIN
  WriteTitle;
  OpenRcdFile(ParamStr(1),fRcd);
  ReadInputFile(ConstantsFile,ParametersFile,ObservationDataFile,
      ResponseType,ShapeNo);
  CheckOutputType(Output,fOutput);
  ReadConstantsFile(ConstantsFile,
      AConst,Ea0Const,Ea1Const,DeltaH0Const,DeltaH1Const,DeltaSConst);
  ReadParamsFile(ParametersFile,
      DRefArrSize,InitDepthArrSize,DRefArray,InitDepthArraY);
  ReadObsDataFile(ObservationDataFile,TempFileArray,ConcatFileArray,
      TempFileArrSize,PhenDatMat,PhenDatPointer);
  DoCalculations(ConstantsFile,ParametersFile,ObservationDataFile,
      AConst,Ea0Const,Ea1Const,DeltaH0Const,DeltaH1Const,DeltaSConst,
      ResponseType,ShapeNo,
      DRefArrSize,InitDepthArrSize,TempFileArrSize,PhenDatPointer,
      Darray,DRefArray,InitDepthArray,TempFileArray,ConcatFileArray,
      PhenDatMat,Output,fOutput);
  Close(fRcd);
  Beep(Finish);
END.
```

Sample Data Files for PHYSHIFT Programme

A3.1 EXAMPLE.INP: Programme Input File

```
param\arrhen02.con
param\iterat06.par
data\conti50.exp
linear 0.5
```

Arrhenius constants
Iteration parameters
Temperature regimes
Dormancy-development response

A3.2 ARRHEN02.CON: Arrhenius Equation Constants, Set 2

```
2.49e18     A
12500       Ea0
12500       Ea1
27850       DeltaH0
30000       DeltaH1
100         DeltaS
```

A3.3 ITERAT06.PAR: Iteration Parameters for d_{ref} and D_i, Set 6

```
120 150 180
0.0 0.05
```

d_{ref} values
D_i values

A3.4 CONTI50.EXP: 50 Day Constant Temperature Experiment

Temperature file   Duration
& second file   Duration   ('&' = connector)

```
tdat\00_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\01_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\02_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\03_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\04_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\05_conti.ehr 50
&tdat\22_conti.ehr 14 ...
```

... CONTI50.EXP continued.

```
tdat\06_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\07_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\08_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\09_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\10_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\11_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\12_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\13_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\14_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\15_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\16_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\18_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\20_conti.ehr 50
&tdat\22_conti.ehr 14
tdat\22_conti.ehr 50
&tdat\22_conti.ehr 14
```

A3.5 00_CONTI.EXP: Hourly Temperature File, Constant 0°C

```
Day Temp
 1 0         1 0         2 0         3 0
 1 0         1 0         2 0         3 0
 1 0         1 0         2 0         3 0
 1 0         1 0         2 0         3 0
 1 0         2 0         2 0         3 0
 1 0         2 0         2 0         3 0
 1 0         2 0         2 0         3 0
 1 0         2 0         2 0         3 0
 1 0         2 0         3 0         3 0
 1 0         2 0         3 0         3 0
 1 0         2 0         3 0         3 0
 1 0         2 0         3 0         3 0
 1 0         2 0         3 0         4 0
 1 0         2 0         3 0         4 0
 1 0         2 0         3 0         4 0
 1 0         2 0         3 0         4 0
 1 0         2 0         3 0         4 0
 1 0         2 0         3 0         .
 1 0         2 0         3 0         .
 1 0 ...     2 0 ...     3 0 ...     .     etc
```

A3.6 HNRC_SD.PHN: 'Sundrop' Phenology Data for HNRC

```
Air temp. file        5% Bloom 90% Bloom
```
```
tdat\hvl84tem.shr    08/25/84 08/28/84
tdat\hvl85tem.shr    08/23/85 09/02/85
tdat\hvl86tem.shr    08/29/86 09/09/86
tdat\hvl87tem.shr    08/26/87 09/01/87
tdat\hvl88tem.shr    08/22/88 08/29/88
tdat\hvl89tem.shr    08/27/89 09/07/89
tdat\hvl90tem.shr    08/28/90 09/07/90
```

## A3.7 HVL84TEM.SHR: Hourly Screen Air Temperature File

```
Day    Hour    Temperature
```
```
  1    1:00     10.9
  1    2:00     10.6
  1    3:00     10.3
  1    4:00     10.1
  1    5:00     10.0
  1    6:00     10.6
  1    7:00     13.2
  1    8:00     15.6
  1    9:00     17.8
  1   10:00     19.8
  1   11:00     21.4
  1   12:00     22.5
  1   13:00     23.3
  1   14:00     23.5
  1   15:00     23.3
  1   16:00     22.5
  1   17:00     21.4
  1   18:00     19.8
  1   19:00     17.7
  1   20:00     15.9
  1   21:00     14.5
  1   22:00     13.5
  1   23:00     12.7
  1   24:00     12.1
  2    1:00     11.7
  2    2:00     11.4
  2    3:00     11.1
  2    4:00     11.0
  2    5:00     10.8
  2    6:00     11.5
  2    7:00     14.3
  2    8:00     16.9
  2    9:00     19.3
  2   10:00     21.4
  .
  .
  . etc
```

Appendix 4

## Controlled-Environment Temperature Experiments

A4.1 Constant Temperature Level

Figure 1 Bud break of 'Redhaven' peach plants following exposure to 1200 hr at various continuous temperatures. (Erez and Couvillon, 1987: Fig. 1)
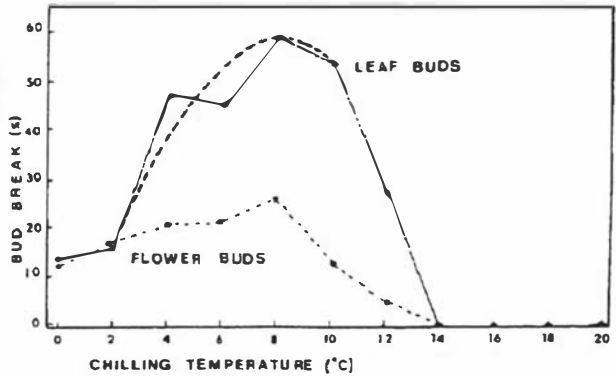

A4.2 Level of Temperature Cycle Maxima

Figure 2 The effect of exposure of 'Redhaven' peach plants to 1200 hr of continuous 4°C or 1200 hr of 6°C accumulated in a diurnal cycle (16 hr at 6°C and 8 hr at moderate temperature) on flower and vegetative bud break (closed circles, and dashed and solid lines, respectively). (Erez and Couvillon, 1987: Fig. 3)
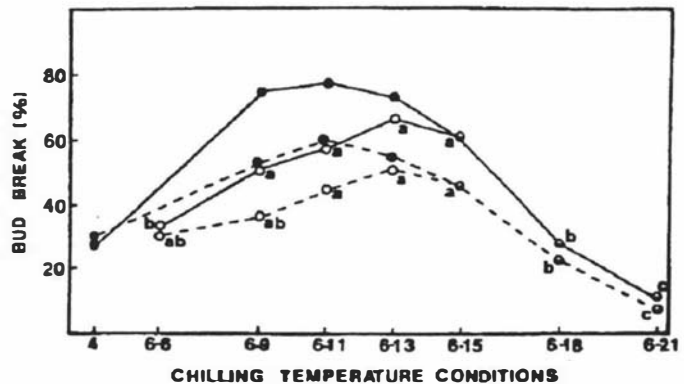

A4.3 Duration of Temperature Cycle

Figure 3 The effect of GA_3 and cycle duration on rate of lateral and terminal bud break in 2 peach cultivars, 'Redhaven' and 'Redskin'. (Erez, Couvillon and Henderscott, 1979: Fig. 3.)
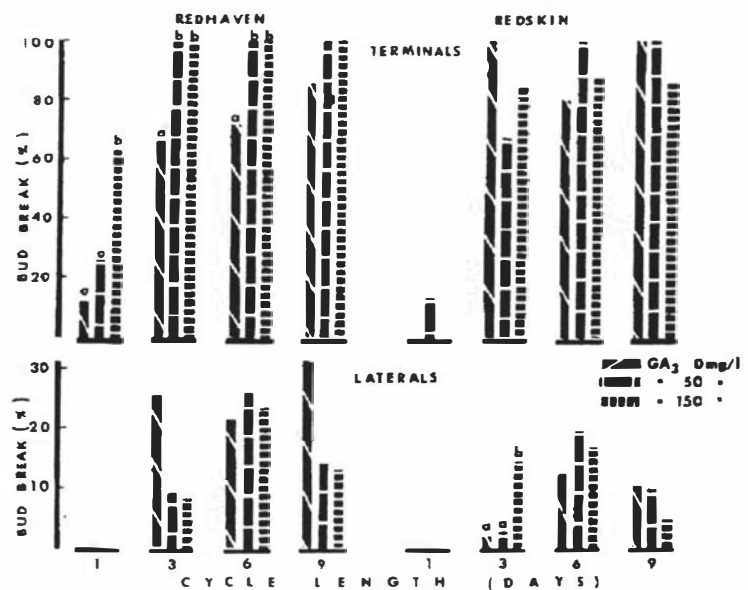
A4.4 Duration of Cycle Maxima

Figure 4   The influence of the duration of high temperature in a diurnal cycle on chilling negation in 'Redhaven' peach (vegative buds). (Couvillon and Erez, 1985: Fig. 2)
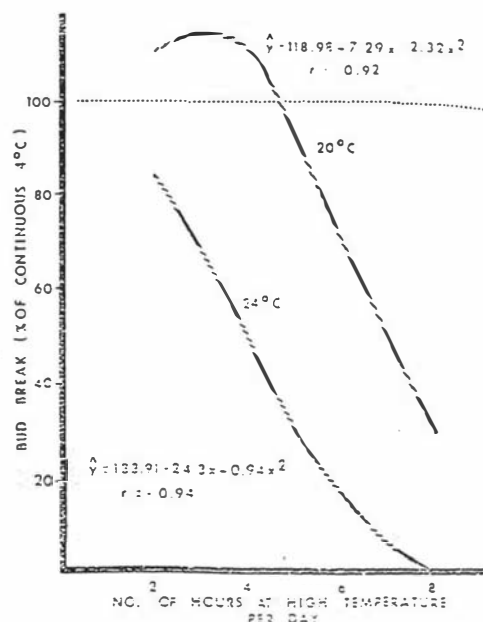

A4.5 Timing of Cyclic Temperature

Figure 5   The effect of timing (first, second, or last third of chilling requirement) of cyclic temperature (16 hr at 4°C and 8 hr at 15°C) on breaking rest of 'Redhaven' peach buds. (Erez and Couvillon, 1987: Fig. 4)
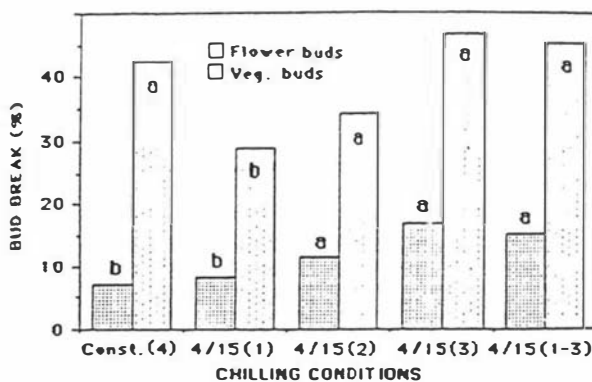
A4.6 Level of temperature cycle minima

Figure 6   The effect of exposure of 'Coronet' peach plants to 900 hr at 0°. 4°, or ·6°C, applied continuously or in a diurnal cycle with 15°C for 8 hr, on later vegetative budbreak following 28 days of forcing at 22°C. (Erez and Couvillon, 1987: Fig. 2)
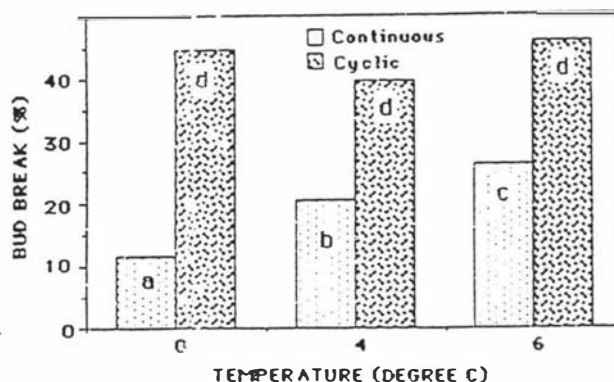
References

Couvillon, G.A. and A. Erez. 1985. Effect of level and duration of high temperatures on rest in the peach. Journal of the American Society for Horticultural Science 110:579-581.

Erez, A. and G.A. Couvillon. 1987. Characterization of the influence of moderate temperatures on rest completion in peach. Journal of the American Society for Horticultural Science 112: 677-680.

Erez, A., G.A. Couvillon and C.H. Hendershott. 1979. The effect of cycle length on chilling negation by high temperatures in dormant peach leaf buds. Journal of the American Society for Horticultural Science 104:573-576.