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FLOWER DEVELOPMENT OF THE CHINESE GOOSEBERRY (*ACTINIDIA CHINENSIS* PLANCH.) AND SOME FACTORS INFLUENCING IT

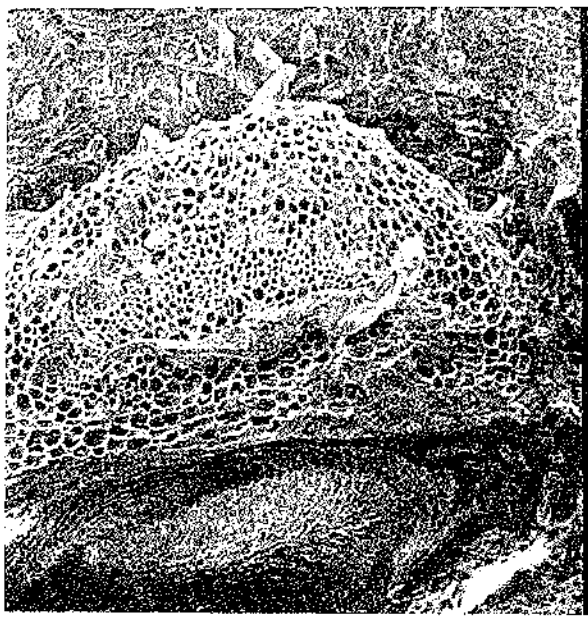
A thesis presented in partial fulfilment
of the requirements for the degree of
Master of Horticultural Science at
Massey University

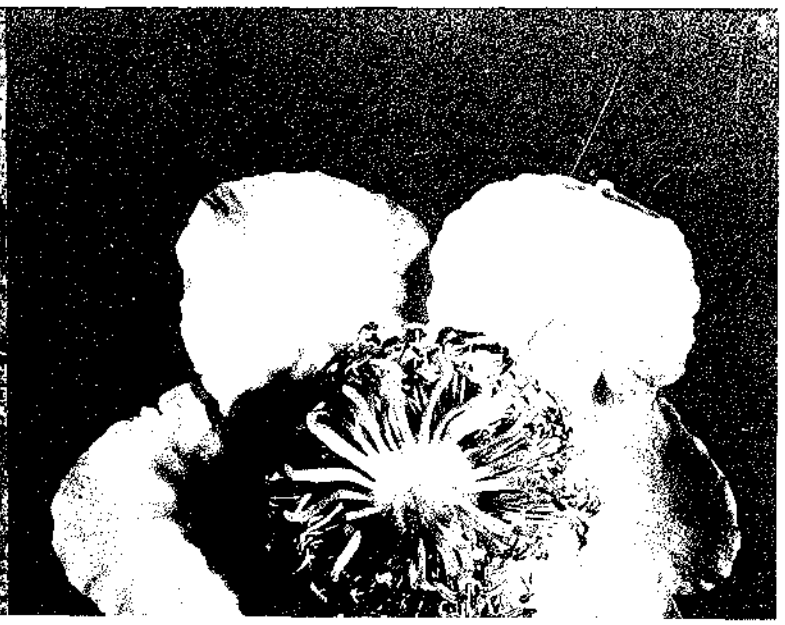
DAVID JOHN BRUNDELL

1973

Frontispiece

top	Hayward shoots, full bloom stage
bottom left	Uninitiated flower primordium, Hayward
bottom right	Terminal flower, Hayward





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Chapter 1

REVIEW OF LITERATURE

FLOWER DEVELOPMENT IN TEMPERATE AND SUBTROPICAL FRUIT TREES AND VINES

A. INTRODUCTION

It has long been known that flower buds are formed in most fruit trees during the season prior to that in which they bloom, and knowledge concerning factors which influence this phenomenon are helpful to an understanding of the growth and cropping behaviour of fruit trees and vines.

Less information has been obtained on the physiology of flowering in fruit trees and vines than on herbaceous annuals. This is due to problems associated with their size, juvenility and their lack of response to specific flowering stimuli such as photoperiod or vernalization.

There has been much confusion in the literature concerning the terminology relating to the change from the vegetative to the reproductive state. The following terminology after Thomas (295), and based on definitions by Evans (87), will be used throughout this thesis.

Flower evocation refers to the physiological changes at the apex caused by the accumulation of flower-forming factor(s).

Flower initiation occurs when there are visible changes at the apex.

What has been called initiation by some authors is a general term and by recent terminology could cover either evocation or initiation.

B. THE FLOWERING PROCESS

Organogenic studies of floral development in woody perennials are difficult to categorise into any logical sequence because of the diverse and varied way in which flowering is expressed.

Classically, the flower can be regarded as a compressed determinate shoot in which the sepals, petals, stamens and carpels (and the sterile staminodes and carpellodes, where present) are successive lateral organs. At flowering the vegetative shoot apex, whether terminal or lateral, undergoes various physiological and structural changes and becomes

directly transformed into either a single flower or an inflorescence (109, 149,243,264). The principal differences between vegetative and reproductive apices are in their different patterns of growth. Growth in the vegetative apex is normally indeterminate, whereas in a reproductive apex, growth is determinate (243).

During the growing season of woody perennials, buds are produced terminally on a long or short shoot (spur), or laterally (axillary) in the axil of a leaf. These may be either vegetative or floral (simple) and/or mixed. There are no leaves associated with the flowers of simple buds although the bud scales may expand and persist as in the cherry (58). Within a mixed bud, flowers may be arranged terminally or laterally. The type and position of floral buds are generally characteristic of that species. Flower buds on apricot, plum, peach, cherry and almond are simple and are borne laterally on new shoots and, to varying extents on spurs. A single bud may produce one flower (peach, apricot and almond), one to three flowers (plum) or more than three flowers (cherry). Apple and pear flower buds are mixed and usually found terminally in shoots or spurs but may be lateral on shoots. On expansion, buds produce leafy shoots which terminate in flowers. The quince is similar, but, on bud expansion a single flower instead of a cluster is produced at its apex. Flower buds of the Chinese gooseberry, *Actinidia chinensis* Planch. are axillary, and flowers are formed in the axils of leaves and bracts but never in the apex which remains vegetative (190).

While it is possible to categorise the flowering habits of many species and cultivars into one or another of several groups (106,157), such classifications are arbitrary as there are overlapping and borderline cases. Individual flower buds of citrus may be produced laterally or terminally and may be simple or mixed, with flowers either terminal or in axils of leaves or bracts (157). Grape flower buds are mixed buds that are formed from lateral buds on shoots of the current season. Flower clusters appear to be lateral but are initially formed terminally, and, while still in the bud, they assume a lateral position by the development of a subterminal axillary meristem.

The timing of flower initiation, which varies between species and cultivars is largely controlled by internal factors (69,99), but may be modified by the external environment (159,217). The observed time of flower initiation, as reported by various workers varies depending on the criteria used to describe the change to the reproductive condition (6,99, 135,256). Moreover some workers refer to inflorescence initiation, and others to flower initiation processes which may be separated by an

interval eg., several weeks in apple (99) and several months in grape (330). In most deciduous fruit trees flower bud initiation usually occurs in mid to late summer, 6 - 12 months prior to bloom, when the bud has completed much of its development. It is generally associated with the cessation of shoot growth and leaf expansion. (30,32,58,99,207). Fulford (99) observed that flower initiation in apples was intimately related to the pattern of bud development and occurs after several bud-scales of the terminal bud have been formed, and when the leaves preceding the bud scales were fully expanded. Generally, flower initiation for stone fruits is later than that for pome fruits (30,32).

In contrast with pip and stone fruits, flower initiation in the grape vine is not connected with a cessation of shoot growth (183). Inflorescence initiation generally commences in mid summer (33,330), and depends on the position of the winter bud on the cane (14,29,33,285,330), and the position of the inflorescence or the condensed shoot within the bud (285). Most workers (29,33,183,285,330), state that flowers are initiated on the already formed clusters in the spring, but a few report a large proportion of floral meristems forming sepals in the summer preceding the season of flowering (6,14).

Compared with temperate deciduous fruit trees and vines, the time of flower bud initiation in subtropical evergreen fruit trees is late and takes place about the commencement of a growth flush only a few weeks prior to bloom. (1,135,256). As a result it is frequently not possible to distinguish between a flower bud and a purely vegetative one before it opens, either from its size or position. Like most deciduous fruit tree crops, the bloom period is usually in the spring, but in some cultivars and in some localities this may occur at other times of the year. In California, avocado cultivars of the Guatemalan race normally bloom in the spring and early summer, whereas many cultivars and seedlings of the Mexican race normally bloom in the autumn (271).

Once the flower primordia are initiated, development of the floral parts takes place acropetally, viz., the order of development is sepals, petals, stamens and pistils. Development may be slow and interrupted (eg., by a winter period) as in most temperate fruit trees or rapid as in citrus and subtropical fruit trees.

C. GROWTH AND FLOWERING CHARACTERISTICS OF *ACTINIDIA* SPECIES

Li (190) has carried out a taxonomic review of the genus *Actinidia*.

He described the species as being:

'Climbing shrubs, glabrous, strigose or tomentose, the indumentum of stellate or simple hairs; pith solid or lamellate; bark often with linear lengthwise lenticels; winter buds very small, enclosed in the swollen base of the petiole. Leaves simple, alternate, usually long-petiolate, serrate or dentate, rarely entire, penninerved, the costa usually sulcate, the veinlets reticulate, usually in cross bars; stipules minute, obsolete or absent. Flowers white, yellow, or reddish, polygamous or dioecious, usually 5- or 4-merous, in axillary often pseudoumbellate cymes of few or many flowers, sometimes solitary; bracts generally present, minute, 1 or 2 at the apex of the peduncles. Sepals 5, rarely 2 - 4 imbricate, rarely valvate, free or slightly connate at the base, persistent. Petals 5, rarely 4 or more than 5, convolute, thin. Stamens numerous, in pistillate flowers usually with shorter filaments and smaller sterile anthers; filaments slender; anthers versatile, attached at the middle, reflexed in bud, usually divaricate at base, dehiscing lengthwise, yellow, brown, or purple. Disc absent. Ovary free, superior, tomentose or glabrous, ovoid, cylindrical, or bottle-shaped, many-celled; ovules attached on the central axis; styles many (15 - 30), free, persistent, radiating, elongating after flowering, the tip stigmatic, excurrent; rudimentary ovary in staminate flowers very small, with minute styles. Fruit a berry, glabrous or sometimes hairy, globose or oblong, spotted with lenticels or not, containing raphides. Seeds numerous, small, biconvex, oblong, immersed in pulp; testa cartilaginous, reticulate-pitted, dark when dry; albumen copious; embryo comparatively large, cylindrical, straight, the cotyledons short.'

Li (190) also gives a detailed taxonomic description of the species *A. chinensis*. He states that they are:

'Climbing shrubs to 8m.; branches reddish brown, with paler oblong lenticels, the young branchlets brownish-pubescent or setose; pith large, lamellate, whitish or yellowish. Leaves thin- or thick-chartacious, those of the sterile branches broadly ovate to elliptic, very shortly acuminate to cuspidate at apex, those of flowering branches suborbicular, shortly cuspidate, rounded or truncate at apex, rounded to more or less cordate at base, 6 - 17 cm. long, 6 - 15 cm. broad, the margins minutely denticulate, the teeth produced by tips of veinlets, the upper surface dark green,

more or less puberulous, more densely so on the costa and nerves, or densely scabrid-hispid throughout, the lower surface very pale, densely whitish-stellate-tomentose, the costa veins subconspicuous above, raised and distinct beneath, the secondary nerves about 5 - 8 per side, strongly patent, straight or arcuate-ascending, anastomosing, the branchlets ending in the marginal teeth, the veinlets in parallel crossbars, more or less conspicuous; petioles 3.5 - 7.5 cm. long, more or less densely pubescent. Inflorescences in few-flowered cymes, from axils of fallen leaves, pubescent; peduncles about 1.5 cm. long; pedicels 1 - 2 cm. long; bracts minute, linear. Flowers orange-yellow, the staminate slightly smaller; sepals 5, sometimes 3 or 4, ovate-oblong, about 8 - 10mm. long and 6 - 8 mm. wide, obtuse to acute at apex, brownish-tomentose without; petals 5, broadly obovate, shortly clawed, rounded at top, about 1.4 - 1.5 cm. long, 1 - 1.2 cm. broad; stamens very numerous, the filaments filiform, unequal, about 5 - 10 mm. long, the anthers oblong, 1.5 mm. long, acute to obtuse at apex, slightly sagittate at base; ovary subglobose, about 6 - 7 mm. across, densely brownish-villose, the styles linear, about 5 - 6 mm. long. Fruit subglobose to ellipsoid, about 3 cm. across, densely brownish-hirsute all over; seeds oblong-ellipsoid, 2 - 3 mm. long, foveolate-reticulate.'

Flowering is reported to be in mid to late summer in Britian (61) but in New Zealand *A. chinensis* regularly flowers in the late spring.

Little has been recorded on the course of flower development in *Actinidia* species. The only report on the flower initiation process in any *Actinidia* species has been on *A. kolomikta*. (171). The nature of the floral buds of *A. kolomikta* and their location within the vine are similar to *A. chinensis* and there are no external morphological differences between floral and purely vegetative buds. Kolbasina (171) states that initiation commences during the growing season, and by the end of summer there are axillary cones of flowers with undifferentiated floral parts in the completely formed floral bud. The buds remain in that state during winter and only in the spring, at the opening of the buds, does subsequent differentiation of the flowers start.

Development in the spring is rapid and an embryonic inflorescence consisting of three flowers, a fairly large apical one and two very small lateral ones, are formed. In staminate inflorescences the lateral flowers remain undifferentiated until the apical flower has developed petals and the stamens and pistil are forming and then development is

rapid. In pistillate inflorescences however, the lateral flowers remain undifferentiated and finally absciss.

Androecial and gynoecial development in staminate and pistillate apical flowers is initially the same but eventually differes. In staminate flowers the stamens continue to elongate and develop but growth of the ovary stops, whereas in pistillate flowers gynoecial development continues but the stamens remain underdeveloped with short filaments. By full bloom, which is in late spring (171), subsequent development results in flowers that are functionally pistillate or functionally staminate.

D. THE RELATIONSHIP BETWEEN VEGETATIVE AND REPRODUCTIVE GROWTH AND THE EFFECT OF SHOOT REMOVAL

Seedlings of most woody plants exhibit a juvenile period during which flowers cannot be induced, and, in most tree fruit crops, this delay in flowering may last for a number of years (53,304). This delay varies greatly between and within different species (157). Juvenility, as a general topic, and specifically to fruit trees, has been reviewed a number of times in recent years (269,304,311,333). As well as its theoretical importance, studies of the factors which cause and influence juvenility are of considerable practical significance, especially those factors which may shorten that phase. (12,88,149,166,262,288).

For breeding purposes and in commercial fruit growing, various techniques has been used to considerably shorten the juvenile phase, and the lag in bearing. These include breeding and selection, controlled environments and various cultural practices and shock treatments such as girdling, freezing, drought, root pruning, excessively heavy chemical treatments and grafting on to mature trees or dwarfing root stocks (149,197,262,333).

In temperate and subtropical fruit tree crops, once flowering has commenced and the juvenile phase is over, a more or less regular annual pattern of flowering is set up. The regularity of repeated bloom depends on how successfully the reproductive tissues can compete with other plant sinks for essential metabolites. Although the actual mechanisms are still obscure, tracer studies have established that plant hormones play a dominant role in determining the direction of movement of organic metabolites and in establishment of sink source relationships (197).

Ant agonism between vegetative growth and flower formation is a widely held theory among plant scientists, and certain observations are in agreement with this belief. Flower development in temperate fruit tree crops

occurs about the time of cessation of shoot growth and leaf expansion (31). In biennial bearing trees a positive correlation exists between the increment of spur growth and the percentage of flower buds differentiated when trees in both the 'off' and 'on' years are considered together (69). Low light intensity increases internode length and reduces flower initiation in apricots (155). Apple spur mutants, which arise as chance bud mutations of the parent cultivar, are used commercially and are generally characterised by reduced vegetative growth, short internodes and enhanced precocity (322). A stimulation of flower bud formation along with a supression of shoot growth in many fruit tree crops follows treatments with growth retardants (35,82,197,212), and the converse with certain growth stimulants (31,42,212).

However in many of these instances there is no proof for a close causal relationship and a number of observations suggest that the promotion of flowering is not always associated with retardation of shoot growth (180, 197). For example, growth retardants (35,216) and growth inhibitors (199) promote flowering in various fruit trees without a corresponding reduction in vegetative growth. Similarly in apricots, high levels of nitrogen increased both flower initiation and internode length (156).

While these observations suggest that flower evocation and shoot growth should be regarded as partially independent processes (197), flower development cannot be considered in isolation from the rest of the plant.

The removal of the apical region of the growing shoot (tipping or topping) has been used in grapes to increase set and yields (67,68,195, 265,293). However, little has been reported on its effects on flower development. Thomas (293) reported that flower bud formation was stimulated in the Sultana grape by tipping around bloom but in subsequent seasons yields progressively declined due to reduced vigour. He and others (see 195) have concluded that tipping should not be practised as a means of increasing yields because of its debilitating effect on vegetative growth. Loomis (195) on a more vigorous cultivar however obtained increased yields over a 5 year period by bloom time tipping.

Following damage by spring frosts or hail, Antcliff et al.(17) found that fruitfulness in Sultana grape buds was higher overall and the distal region of the canes was more fruitful. However, canes formed on vines damaged by frost or hail much later in the season had fewer fruitful buds in the proximal region and a lower overall fruitfulness. To compensate for such tendencies, more buds should be left on canes at winter pruning (17). Early summer pruning of apple trees prolongs vegetative growth and

delays flower bud formation (58). Depending on the maturity of the wood, mid or late summer pruning may cause a flower bud to form at the next distal leaf left on the shoot. However, this influence of pinching or summer pruning of shoots does not increase the tendency of other buds to become flower buds (58).

Decapitation of the main shoot of the mango also causes flower evocation in the laterals; in intact shoots those laterals become vegetative laterals (257). Evocation takes place in the axillary buds within 4 days after decapitation and initiation rapidly follows. However, flowering only takes place if leaves are left on the main stem. These effects have been explained in terms of an auxin-florigen antagonism or to the inhibitory action of the main shoot when it is in active growth (see 179).

E. THE ROLE OF LEAVES AND BUD SCALES AND THE EFFECT OF DEFOLIATION

Leaves are necessary for flower formation and their importance in flower initiation has been stressed by many workers (69,103,125,198). Although Fulford (99) could find no evidence for the requirement of a critical leaf area for flower initiation on apples, when the whole tree was considered, defoliation experiments on grapes (183) and on ringed branches of both apples and cherries (69) showed that a certain number of leaves had to have been formed before floral initiation would occur. Further, in several fruit trees, including apples (95,99), pears (8), plums (261), cherries (238), apricots (210), grapes (206), mangos (257), olives (103), and citrus (103), removal of leaves either mechanically or by chemical treatment, results in a reduction of flower bud initiation.

As well as reducing flowering with pre-initiation treatment, defoliation treatments during the post initiation period can also curtail effective flowering. In the apple the removal of the expanding spur leaves in the spring prior to bloom reduces fruit set and subsequent yield (19,191).

In one-year-old grape hardwood cuttings, inflorescence growth usually ceases soon after bud burst and the inflorescence shortly shrivels and abscises. Removal of the basal leaves to the leaf adjacent the inflorescence as soon as they appeared, enabled growth and development of the inflorescence to take place(224). By pruning to a single inflorescence Mullins(224) was able to obtain bunches containing up to 100 grapes within 12 weeks from planting. In field grown vines however, defoliation 2 weeks before bloom markedly reduced set by greatly reducing pollen viability (from 38% to 4%) as well as upsetting gynoecial development (328). Both phenomena can be

explained in terms of competition. Leaves contribute little to early growth on hardwood cuttings and are importers of photosynthates (224). Competition for nutrients and metabolites is much greater at that time, ence the localised removal of leaves eliminates a strongly competitive 'sink' from the developing inflorescence. Removal of mature leaves however reduces set by removing a source of photosynthates. While removal of leaves has a pronounced effect in reducing initiation and later development in the defoliated area, up to 50% of the leaf in the apricot (210) and apple (133), 25% in the plum (305) and over 90% in the olive (125), has to be removed for appreciable initiation inhibition to occur.

Defoliation and observational studies support the theory that the influence of the leaf is localised. Defoliation experiments have shown that the inhibition of flower formation occurs only in the treated portion (125,198). Heinicke (143) has observed in the apple that buds in the axils of small mature leaves remain small and dormant, or give rise to weak spurs which result in a reduced bloom, whereas larger mature leaves usually have well developed buds in their axils. As well as leaves, the other organs within the bud have recently been recognised as playing an important role in the flower forming process (3,96,270).

Bud scales, which enclose the flowers prior to expansion, are formed by the withering of the lamina and petiole of the leaf primordia. They have been shown to be physiologically active and increase in both size and weight (3). Abbott (3) and Schneider (270) suggest that they provide not only a protective covering to the bud, but also act as a buffer against resumption of growth. Abbott (3) further speculates that indirectly, through the absence of laminae, they account for the abrupt cessation of axis extension, and for the proliferation of lateral meristems which leads to the inception of inflorescence development. In storing nutrients, bud scales provide a reserve upon which the early growth of the bud can be sustained, but until senescence they ensure against premature bud break by competitive resorbtion.

From defoliation studies on apples, Fulford (99) found evidence of a self regulating system of factors controlling the development of buds and the ability to form flowers. This was based on the inhibitory nature of rapidly expanding organs as they affected the plastochrone, the time between the initiation of successive leaves or other organs in the bud.

In the past, such studies were interpreted purely in terms of nutrient supply. However growth substance and radioactive trace studies have shown that those early theories were incomplete (19,254). Using $^{14}CO_2$ on

apricot leaves, Minnis (210) showed that the radioactivity moved throughout the plant. Although the radioactivity accumulated to higher concentrations in the buds than leaves, and values were generally higher in the axillary bud of the labelled leaf, other buds sometimes had higher levels, especially when immature leaves were treated. Further, the fact that buds lacking a subtending leaf accumulated ^{14}C from other treated leaves as readily as buds with leaves intact suggest that the subtending leaf is not the sole source of carbohydrates and that it is not essential to enable the bud to attract metabolites from the rest of the plant. As well, the work on apples by Fulford (97,98,99) indicates that the patterns of bud development are too precise to be explained solely in terms of nutrition. Similarly, post initiation defoliations suggest that results be explained on a hormonal rather than a photosynthetic basis (19).

Endogenous growth substances, which are present in leaves are known to play an important role in flower formation (see section on role of growth regulators).

F. THE ROLE OF CARBOHYDRATES AND MINERAL NUTRIENTS

High levels of carbohydrates in fruit trees have, for a long time, been shown to be conducive to flowering (69,96,128,133,208,234,291). Further, flowering may be enhanced by treatments such as girdling, root restriction, root pruning and crop removal, which increase levels of carbohydrates in the shoot (80,234,249). Conversely, treatments which deplete levels of carbohydrates, such as leaf removal, shading and crop retention, reduce the tendency to form flower buds (192,234).

However, while much effort has been expended in establishing the role of carbohydrates in the flowering process, no evidence has been forwarded that they play a causal role. In fact, there is evidence to suggest that the initiation of the flowering process may precede the accumulation of carbohydrates and the variations in their levels are rather a consequence than a cause of flowering (see 200). However, may workers have produced conflicting resulsts. While Lewis et al (189) reported that levels of carbohydrates were different in the 'on' and 'off' years of biennial bearing oranges, levels continued to fluctuate when the trees were brought into annual production by chemical fruit thinning. Recent studies have shown girdling did not increase levels of carbohydrates in young cherries (54), and neither low light intensities or partial defoliation of apple trees significantly reduce carbohydrate reserves (249). Many workers

have reported that if carbohydrate levels had altered following treatments such as defoliation, shading, girdling or defruiting, their effects were small in magnitude and disappeared before growth resumed in the following spring (144,164,175).

These reports, along with work on forestry trees, which suggest that flower initiation may precede the accumulation of carbohydrates (200), lead to the conclusion that there is no direct causal role of carbohydrates in the flower initiation process.

A long held theory used to explain flower initiation has been the carbon/nitrogen (C/N) ratio. The theory, first proposed in 1918 by Kraus and Kraybill (174), suggests that flowering would be favoured if there was a high C/N ratio in the plant. Conversely, vegetative growth would be favoured if the ratio was low. Although this theory has been widely accepted, current evidence does not support it.

Many reports show that application of nitrogen fertilizers can stimulate flowering in deciduous (13,40,41,58,78,323,325) as well as evergreen (79) fruit trees, and that flowering is favoured by high nitrogen levels in tree shoots and buds (234).

As well as species differences, the type of nitrogen supplied and its time of application in relation to the growth phase of the tree have been shown to be important and explains much of the confusion existing in the literature on its effects on growth and flowering (78,114,156,327). Generally spring applications of nitrogen do not affect flower formation (78), while late summer application (post initiation) results in stronger more fertile blossom (326,327) resulting from increased longevity of the embryo-sac (148).

Several studies indicate increased flowering following phosphorus applications (18,93,94,263) and some indicate a positive correlation with levels applied (90,91). Reduced flower bud formation reportedly has resulted from various nutrient deficiencies (40,41,307).

G. THE ROLE OF THE REST PERIOD AND THE EFFECT OF TEMPERATURE

As well as a juvenile stage during which plants will not reproduce, woody plants characteristically have a distinct rest period between evocation and anthesis. The phenomena of dormancy and rest have been reviewed on a number of occasions in recent years (266,302,313). Samish (266) defines 'bud dormancy' (or quiescence) as the condition when growth is stopped by unfavourable external conditions such as cold temperature,

and 'rest' when growth will not proceed normally even in a favourable environment and is due to internal factors.

In deciduous fruit trees the onset of rest in the buds takes place acropetally along a lateral and occurs about the time the leaves subtending them become fully expanded (58). Before the onset of rest, lateral buds do not grow due to a correlative inhibition imposed by the shoot apex (apical dominance), the leaves subtending those buds, or both (58). The removal of imposed correlative inhibition by defoliation, decapitation, or both, has been used to determine the time of onset of rest in spur and shoot buds (58,255).

For most deciduous trees it has been shown that rest is due to a chilling requirement which must be satisfied before the buds will burst normally (60). Species and cultivars vary in their chilling requirements to terminate rest. Generally grapes and some peach cultivars have a low requirement, while apple and pear cultivars have a high requirement. Insufficient chilling, which occurs in many fruit growing areas with mild winters, leads to serious disorders collectively termed delayed foliation, which may make commercial crop production impracticable (282). Such disorders include delayed opening of buds, and irregular blossoming with a large percentage of buds failing to open at all. Of those that open, many flowers may have deformed female parts and a low pollen viability (282). When the percentage of deformed flowers is high, fruit set and yields will be poor (268). Further, such conditions lead to an early decline of the tree (268).

For many cultivars, particularly peaches and apricots, the amount of chilling needed has been determined, and the region in which they can be grown with a reasonable expectation of success have been defined (267). Chandler (60), quantified the term ' chilling requirement' where it was used to mean the total amount of cold required to break rest and was based on two assumptions:

(a) The existence of a threshold temperature above which rest will not be affected; and

(b) The effects of all temperatures below that threshold were equal.

Although temperatures above the accepted critical threshold of 7.2^{o}C acquire rest breaking activity (320), many workers have found that high temperatures prevent the breaking of dormancy and oppose the positive effect exerted by low temperatures (36,237). In some species other temperatures eg., 6.0^{o}C in peach (84), have maximal rest-breaking effect with a decline in efficiency as the temperature changes in both directions (268). Temperatures approaching freezing, result in decreased efficiency

(see 84). Further diurnally fluctuating temperatures can enhance the termination of rest (84). Because the termination of rest follows an optimum curve, 'weighted chilling hours' instead of the general 'chilling hours' have been proposed as a chilling measurement criterion (84).

The responses to chilling are perceived by the buds of the tree (173), and both vegetative and floral buds require chilling to break the rest period (320). Frequently there can be a difference in chilling requirements between flower and leaf buds within one cultivar, with vegetative buds usually having a greater chilling requirement (320).

Wareing and Saunders (313), in their recent review on dormancy, related the control of rest to changes in levels of endogenous growth substances; simply, rest being imposed by a build up of inhibitors and terminated when inhibitor levels fall and/or growth promotor levels rise.

Light also affects the rest period. Early investigators mentioned the negative effect of direct sun radiation during winter and emphasized the beneficial effect of winter shade. The shading effect was explained by lowering bud temperatures (319). However light is also involved directly in the termination of rest (85) although, in the peach at least, the light requirement is confined to leaf buds only; flower buds open freely in the dark (268). The light requirement seems to be related to the phytochrome system as it can be satisfied by short exposures of low intensity red light and be reversed by subsequent far-red illumination (268).

The advantage of limited light over the dormant period is ecologically significant. Compared with lower latitudes, in areas where delayed foliation is a problem, not only are winters milder, but also days are longer and light intensities over the winter greater. Further, as temperatures in the spring rise more slowly at lower latitudes, bud burst is later and therefore occurs during a much longer day.

In regions where delayed foliation is a problem, several materials have been used commercially to break rest in fruit trees (84,282). Such compounds include dinitroorthocresol (DNOC), winter oil (sometimes fortified with DNOC) and thiourea. Several workers have also reported positive results with GA (306) and cytokinins (315,321) although in some species, eg., in the grape, GA delays bud break (314).

As well as influencing dormancy, temperatures can directly influence flowering. In the grape the number of flowers initiated in the bud was closely related to the maximum temperature recorded over a period of 4 hours per day (rather than the temperature summation) during a 3 week period before the apex of the bud changed to the reproductive condition (49,50).

Little initiation occurred at 13°C, but increased to a maximum at 30 - 35°C. (Higher temperatures were not tested.) However, once initiation had occurred, there was little appreciable affect of temperature on fruitfulness (51). Similarly, apricots grown under controlled environments initiated more flowers at higher (24°C) than lower (16°C) temperatures (210).

Flowering in some fruit trees however is favoured by low temperatures. The olive has an obligate requirement for low temperatures (125,169). However, winter chilling is not essential for the resumption of vegetative growth (136). This situation is completely different from most fruit trees where flower initiation takes place in the previous summer and the winter chilling period serves only to overcome the rest period of buds (139). In the olive, controlled temperature environments showed that flowering was completely inhibited above 16°C (124). Diurnal temperature fluctuation modifies the response (22) and the length of the chilling period can be influenced by temperature (126). Further, incomplete chilling results in aberrant development with a large proportion of blooms with small non-functional pistils. Low temperatures favour pistil development (22). The chilling response is restricted to the stem and buds only, and to the portion of the tree exposed to the low temperature. There is evidence that themoinduction in the potential flower buds of olive, is accompanied by an increase in gibberellins and a reduction in inhibitors while there is little change in hormone levels in potential vegetative buds (23,24, 140). Citrus also have a low temperature requirement and high temperatures will inhibit flowering (147,219). Moss (219) has stated that at least 4 weeks of inductive cool temperatures are required to initiate flowers. This was a quantitative rather than a qualitative effect as, in the field, such conditions would not be limiting.

H. THE ROLE OF HORMONES AND THE EFFECT OF APPLIED GROWTH REGULATORS

There is little doubt that the flowering of plants is under chemical control since qualitative and quantitative changes of plant growth substances occur during flower induction and development. However, which changes are the cause and which are the result of flowering, have not been established. Largely due to the variation between species and cultivars in flowering behaviours, the classic concept of a specific flowering hormone (florigen), produced in the leaf and received in the bud, has never been popular in polycarpic plants. The flower forming process is now thought to involve a sequence of events, and each stage in this progression of events is influenced independently by internal and external

factors (87,295) ie. each stage would be determined by the hormonal balance at the initiation site, but would also be modified by nutritional and environmental factors. Much effort has been expended in trying to characterise the regulators involved in the flowering process and has followed two main courses, viz. by following the level of endogenous hormones and/or by studying the effects of applied growth regulators.

From such studies, all classes of regulators have been implicated in the flowering process although their precise role is not always clear eg. in many long day rosette plants and some conifers, gibberellins markedly and consistently promote flowering (see 180), whereas in pip fruits (76, 118,123,212), stone fruits (42,65,82,152), citrus (111,150,217,220,229), grapes (13) and tropical (163) and subtropical (24) fruit trees gibberellic acid inhibits flowering. In fruit trees, it has been postulated that flowering may only follow a reduction of endogenous gibberellins (111,197).

The other classes of growth regulators are less consistent in their effect on flowering. Various auxins have reportedly promoted flowering in the olive (23) litchi (274) as well as the pineapple (see 179), with a correlated reduction of vegetative growth. Triiodobenzoic acid (TIBA), a supposed auxin antagonist promoted flowering in apples (83,116), citrus (167,216) and grapes (see 167). Further benzothiazole-2-oxyacetate (BTOA) a compound with a structure similar to IAA, stimulated flowering in some citrus cultivars (216,217). It was thought to be an anti-auxin and acted in a way similar to drought, lower temperatures or root pruning (216). Later studies suggested it may act in a way similar to the purine derivative, kinetin (289).

Although cytokinins have not, as yet, been implicated directly in the flowering process they are effective in releasing lateral buds of apples from dormancy imposed by the terminal bud, and in breaking of winter dormancy (62,244,324).

Various inhibitors have been isolated in plants and have been implicated in the flowering process either directly (88) or indirectly by their influence on rest (313). In the olive abscisic acid (ABA) inhibits flowering (23) and levels of ABA and other inhibitors alter in buds during floral development (24).

Various growth retardants affect, sometimes spectacularly, the growth and flowering of fruit trees. As well as reducing the juvenility phase (35), they may increase the number of flower buds in apples (34,35,74,83, 197,213), pears (35,74,119,212), plums (214), peach (82), cherry (301), citrus (215,216,217,229). Generally retardants tend to delay flowering by delaying bud break (35,83,120,121,290).

There is some evidence that the retardants can act directly on flowering as bloom can be markedly increased without an appreciable effect on shoot growth (35,74). The mode of action of growth retardants has not been fully determined as they can affect aspects of auxin (63,178,258,263), gibberellin (56,77,165), and cytokinin (279) metabolism, as well as interacting with sterioids (240). Others postulate retardants act by altering the levels of basic metabolities, which in turn influence growth regulatory substances, and in turn modify growth (5).

I THE ROLE OF LIGHT AND THE EFFECT OF SHADE

Most fruit trees are considered photoperiodically day length neutral. (48,58,216). Although flower initiation in apples (113) and apricots (210), have been reported to be greater in long days than short days, the response to day length was not marked and flowering was not eliminated in short days. While Moss (219) has shown that the sweet orange was insensitive to day-length at low temperatures, Lenz (186) indicated some photoperiodic response at moderate temperatures. As the delay in flowering increased as the photoperiod increased, the reported lack of response under longer photoperiods may have been an artifact and flowering may have occurred if the experiment had not been terminated. Field observations show that flowering can occur during the long days of summer (186).

There are many reports showing the effect of different light intensities on flower initiation. In the apple (142,239), apricot (155), peach (175) and grape (26,52,205), low light intensities resulting from shading experiments, naturally by cloudy weather or within the tree canopy, have been shown to reduce or prevent flower bud formation. Further, fruitfulness in grape vines have been related to the number of hours of bright sunshine during the time of inflorescence initiation (125).

The time, duration and intensity all influence the effect of shade on flower development (205). In the grape, only heavy shading (73%) significantly depressed yields (205). May and Anticliff (205) showed that heavy shading, over a critical period of at least 4 weeks between early November and mid December (about the time of inflorescence initiation), was required to significantly reduce vine fruitfulness (number and size of infloresence) the following year. Shading for less than 4 weeks over the creitical period or only before or after that period did not depress fruitfulness.

In apples, ligher shading (with cheesecloth or muslin cloth) applied earlier (at bloom, ie. prior to evocation, compared with around initiation for grapes) for a shorter period (2 weeks) severely depresses flower bud

formation (239). Five weeks shading (80%) from, just before bloom, reduced blossom by approximately 25% and continuous shade over the whole season, reduced it to practically nil (20). Further, flower bud development was affected and fruit set was considerably reduced in both treatments. Similar treatments, extended to the second year, further reduced blossom and set (20).

The precise reason for the reduction in flowering is not altogether clear. May (203) showed that shading of individual buds of grapes (and not leaves) reduced fruitfulness in such buds and concluded that shading may reduce bud fruitfulness, at least partly, by affecting development of the leaf primordia inside the bud. In the soyabean, darkening of young leaves reduces their import of assimilates and prevents them from reaching full size which leads to their abscission (299). Insufficient import of assimilates was considered to be a cause in the grape as, up to that stage, the inflorescence was the weakest 'sink' of the shoot system (203). Although little has been documented on the effects of light on endogenous growth substance levels in fruit trees, they are likely to play a role as studies on other plants have shown light can affect auxins and gibberellins (89,182).

J. OTHER FACTORS INFLUENCING FLOWER DEVELOPMENT

Other factors, some being experimental manipulations, also influence flower formation.

I THE EFFECT OF WATER

A period of restricted water supply prior to initiation has proved to be beneficial in pears (7) and citrus (104,229). In Sicily and Israel such a technique is used commercially to obtain out-of-season lemons (see 217). Water deficiency during floral development however may reduce the flowering potential (44,138).

The mechanism of evoking flowers through water stress is not clear, but it is thought to be linked with a suspension of growth (154), by upsetting C/N ratio (58) or upsetting endogenous growth substances (217, 229).

II THE EFFECT OF GIRDLING

Girdling (or cincturing) has been used to help determine the time of flower evocation in a number of fruit tree crops (1,21,58,103,105,125,330),

to reduce the juvenile period (58,69,74,232) and to stimulate flowering (61,232,296).

In the olive, girdling, just prior to evocation increases the percentage of perfect flowers, fruit set and yeidls (134). The long term effects of girdling are generally deleterious largely due to effects of increased cropping (294).

III THE EFFECT OF THE CROP

The presence of fruit on the tree strongly influences flowering behaviour (69,233) and in many species and cultivars, often results in the familiar pattern of biennial bearing (69). Thinning of the blossom or early thinning of a substantial part of the crop have helped minimise biennial bearing (69,70,141,235,236), as have growth regulators (see section on growth regulators, above), and judicial pruning to maximise the leaf:fruit ratio (137).

Biennial bearing has been explained solely in terms of carbohydrate reserves (161,236), but this theory is incomplete as carbohydrate reserves do not always follow crop levels (189). It is now accepted that the problem is largely hormonal in nature (57,99,197,220) as the crop, particularly the seeds, are rich in growth substances (64).

IV THE EFFECT OF GRAVITY

It has long been claimed that the horizontal training of fruit trees checks vegetative growth and promotes flowering (110,129,298). However, there is evidence in the apple to the contrary (162,194). Further, in the grape (201,204) and apricot (210), vertical growth tended to enhance flower formation.

It therefore seems that the effect of gravity is at least partly species dependent, and by the conflicting reports, especially on the apple, is possibly also cultivar dependant.

Chapter 2

MATERIAL AND METHODS

A. INTRODUCTION

Little has been presented in the literature on the development of flowers of the Chinese gooseberry, or on factors which may influence this process. Accordingly information was sought, on 3 aspects: The morphology of flower development; flower distribution on different vines; as well as the effect of various environmental factors on flower development.

Experimental work on the physiology of flowering and fruiting in woody plants is often made difficult by the size of mature fruit trees and vines. A way of overcoming some of the difficulties inherent in research with woody plants has been to use small test plants; that is, plants with essentially the same flowering and fruiting characteristics as field grown fruit trees or vines, but which are more easily handled in the glasshouse or growth room (9,11,47,107,185,224,285). A method, devised by Davison (72) using dormant hardwood cuttings to investigate the physiology of flowering in Chinese gooseberry was used and is described.

As well as cuttings, field grown vines were also used for investigations of factors influencing flowering.

B. EXPERIMENTAL PLOTS AND SAMPLING TECHNIQUES

I EXPERIMENTAL PLANTINGS

Experimental vines were selected from a commercial orchard growing at Kumeu, Auckland. The planting consisted of mature vines on seedling root-stocks and trained along 3-wire fences orientated in a north-south direction. The block was mainly the Hayward cultivar (35 vines), as well as lesser numbers of Bruno (7 vines), an unknown cultivar, possibly Abbott (14 vines), and 14 unnamed staminate vines. From the overall growth habits, it was established that the staminate vines consisted of clones and one, consisting of five vines, was selected for observational studies. This was tentatively named Alpha (see Ch.6). Studies were also carried out on the Hayward cultivar.

The D.S.I.R. Fruit Station at Oratia, Auckland was also used as a

source of Monty wood as well as for the flower distribution studies on the named pistillate and staminate cultivars. The Chinese gooseberry block, established in the 1950's, is a collection of named commercial cultivars (227). All the main pistillate and staminate cultivars are present, and are trained along single, or 3-wire fences.

II SAMPLING TECHNIQUES AND PARAMETERS RECORDED

(a) Flower developmental studies (1971)

Samples were obtained from Hayward and Alpha growing at Kumeu. From mid August (19/8/71), sampling was carried out at weekly intervals until close to full bloom, except for the period around bud burst when flower development was rapid and sampling was reduced to 5 day intervals.

For each cultivar at each sample date, about 5 laterals, chosen at random, were cut just past the second node from the last fruiting stalk. Laterals were approximately 6-8 nodes long for Hayward, and 13-20 nodes long for Alpha. In early September (10/9/71), approximately 80 comparable, potentially fruiting laterals, per cultivar were tagged for later sampling. Prior to bud burst, buds at nodes 3, 5, and 7 for Hayward, and nodes 5, 9, and 13 for Alpha were dissected under the binocular microscope.

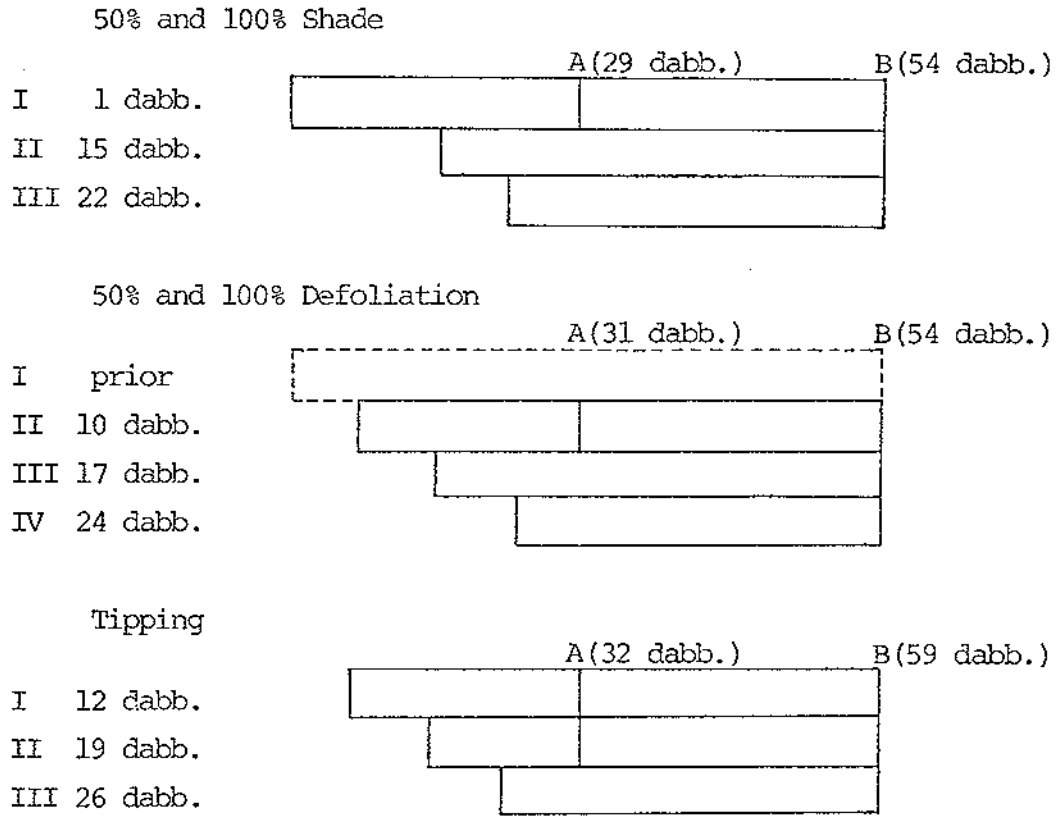
It became apparent around bud burst that some of the buds selected for recording would remain dormant and if included in averages would not give a true indication of the state of bud development. Accordingly, additional comparable bursting buds (shoots) on the selected laterals were tagged for later sampling. To ensure enough buds (shoots) for later samplings, extra shoots at a similar stage on neighbouring laterals, were also tagged. From bud burst onward, approximately 14 buds (later shoots) from between 5-7 laterals chosen at random from the orchard, were obtained at each sampling date; 10 buds (shoots), chosen at random, were dissected and recorded.

For each treatment and sample date the following parameters were recorded: The number, size and character of each leaf or leaf primordium, the direction of the phyllotactic helix, the length and basal diameter of the shoot, and the type, stage and dimensions of each axillary structure.

(b) Field experimental studies (1971)

A number of treatments, graphically set out below, were applied to Hayward shoots on laterals comparable to those used in the flower development study. A number of defoliation, shading and tipping treatments were applied prior to bloom (I,II,III,IV). All treatments were sampled close

to bloom (B) but some were subsampled earlier, approximately 30 days after bud durst (dabb.) (A).



Laterals were 8-10 nodes long and the basal 2 nodes were not treated. Ten to 15 shoots (replicates) from 5-8 laterals chosen at random were planned for each sample. Two treatments were applied on each lateral to minimise the quantity of wood removed: All shading treatments were applied on the terminal portion (approximately nodes 6-10) and defoliation and tipping treatments on the basal portion (approximately nodes 3-6) of each lateral.

Prior to bud burst (11/9/71), 200 laterals were tagged and tied to the horizontal to maximise bud burst.

Defoliation

Shoots (buds) were continuously defoliated. Defoliation prior to bud burst entailed the removal of the outer 10 scales and leaf primordia. Using a pair of secateurs the corky protection around the bud was removed, and using the thumbnail and forefinger, the outer scales and leaf primordia were cleanly broken away. Using 10 xs eye piece, any of the 10 outer leaf primordia remaining were amputated with a scalpel. The operation was carried out on an overcast day and the whole bud was covered with grease to

prevent drying out.

The post bud burst defoliation treatments involved either removing all the leaf lamina (complete or 100%) or the distal half (partial or 50%) of each leaf up to the terminal bud commencing on the appropriate date. Once shoots had been defoliated, new leaves that developed were similarly treated twice a week until they were to be sampled.

Shading

Bags, either 25 x 50 cm. (for sample A) or 30 x 70 cm. (for sample B) were made from single layers of plastic meshing of 40-44% absorbance (light or 50% shade) or black Italian cloth of 99% absorbance (heavy or 100% shade) as measured spectrophotometrically at 200-700 millimicron wavelengths. Bags were fitted at the appropriate time over the terminal portion of the selected laterals by pinning and taping the open side to the lateral and were supported by means of wires attached to either bamboo poles, one of the training wires, or to other laterals (Fig.26) so as to prevent the enclosed shoots from being damaged.

Tipping

Tipping involved the removal of the apical one centimeter of the shoot, which included only the tightly folded apical bud.

A more extensive experiment was planned for each treatment but had to be modified because bud burst was extremely poor and uneven. Because of the variability, all buds on selected laterals were indexed around bud burst and, on the basis of evenness were tagged for later sampling. As the number of suitable shoots per lateral was lower than required, comparable shoots from neighbouring laterals were also tagged at this stage for later use.

On sampling (removing the treated shoots from the laterals) shoots were stored in polythene bags at $4^{\circ}C$ until they were recorded. For each treatment and sample date, the same parameters (where applicable) used for the flower development study, were recorded. As well, for all defoliating treatments, the number of leaves removed on each date (twice weekly after the treatments commenced) were recorded.

(c) Single node hardwood cutting studies

(i) Tipping, shading and defoliating treatments (1971)

Approximately 100 potentially fruiting laterals, taken on September

14th, from Hayward vines grown at Kumeu were used to make 160 uniform single node cuttings. Each cutting was about 15 cm. long. The top was cleanly cut approximately 2 cm. above the bud and covered with grease to prevent drying out. Any lower buds which were present were amputated with a scalpel and the wound covered with grease. The cuttings were stored at $4^{\circ}C$ overnight. Cuttings were removed from the cooler the following day, the base angle cut and placed in test tube racks sitting in trays of half-strength Hoagland's solution to a depth of 5 cm. in an unheated, unshaded glasshouse (Fig.25). To prevent the growth of algae in the light exposed trays, black polythene sheeting was laid over the lower rung of the test tube rack just above the surface of the liquid with the cuttings inserted through the polythene into the solution. The Hoagland's solution was changed twice a week.

A number of treatments (plus controls) listed below were applied to the resulting shoots. Ten replicates (cuttings) were used for each treatment.

The treatments were:

(i) 50% continuous defoliation starting 5 dabb.
(ii) " " " " 10 "
(iii) 100% " " " prior to bb.
(iv) " " " " 5 dabb.
(v) " " " " 10 "
(vi) 50% continuous shade starting prior to bb.
(vii) 100% " " " " " "
(viii) Tipping at 5 dabb.
(ix) " " 9 "
(x) " " 13 "
(xi) " " 15 "
(xii) " " 17 "

Except for the 50% and 100% shading treatments, the 10 racks contained one cutting of each treatment distributed at random. The 50% and 100% shading treatments, of necessity, were in separate racks; the former in a wire cage covered with the same plastic meshing as used in the field, the latter under an inverted cardboard box covered with black polythene placed under the glasshouse bench.

Data was recorded from the controls at 5, 7, and 20 dabb., and all treatments, including the controls, were destructively sampled at the first signs of the buds withering (approximately 25 dabb.). Apart from the shading treatments, operations were generally similar to those carried out in the field. The pre-bud burst defoliation was executed under a binocular

miscroscope using a scalpel. Once commenced, all later defoliations were treated every second day until they were to be sampled.

For the non destructive recordings carried out on the controls at days 5, 7, and 20 after bud burst, the number and dimensions of the open leaves, and the length of the shoot were recorded. For the destructive sample at approximately 25 dabb., the same parameters used for the field treatments were recorded on each treatment as well as the controls.

(ii) Chilling treatments (1972)

A preliminary study on single node cuttings (from Monty vines), prepared as previously described but, taken in mid April (12/4/72, 2 months before leaf fall) and placed in continuous light at 25°C, showed that it was possible to force them into growth. On that finding, an experiment was devised to test the effect of chilling on flower bud growth and development at different sample dates.

Four chilling treatments (10, 20, 30 and 40 days at 4°C) plus control were planned for every 21 days commencing early May (2/5/72) using the cultivars Hayward and Alpha from Kumeu, and Monty from Oratia.

All sample dates for Monty were seven days later (commenced 9/5/72) than for Hayward and Alpha. At this time leaf fall had not yet occurred. Five cuttings per treatment were used, ie. on each date 25 cuttings per cultivar were prepared from potentially fruiting laterals. Each treatment was placed in separate beakers containing distilled water and stored at 4°C (in a polythene bag to prevent desiccation) for their allotted time and then placed in a 25°C growth room under continuous light.

After the third sample date it was noted from earlier records that it would be advantageous to include a 50 day chilling treatment. However, it was not possible to implement 5 chilling treatments (A, B, C, D, E) until sample date 4, as previous samples had been collected. By that stage, the 40 day chilling treatment for sample date 1 had already been carried out, but for sample dates 2 and 3, the assigned 40 day chilling treatments were transferred to the 50 day treatments, ie. treatments 1E, 2D, and 3D were omitted.

Sample dates (1-7) continued until just prior to bud burst (last sample date 5/9/72 for Hayward and Alpha and 12/9/72 for Monty).

For each cultivar, sample date and treatment, the number of days when half the replicates reached the stage of bud burst (Fig. 3), the percentage of buds that burst, and the character and dimensions of the structure in each reproductive axil were recorded.

(d) Flower distribution survey (1971)

An attempt to quantify differences in flowering characteristics of the staminate vines at Kumeu was made on the basis of their flower distribution characteristics. As well as comparing these vines with each other, they were also compared with the only two named staminate cultivars which were growing at Oratia.

On the same basis, a comparison was also made between the important commercial pistillate cultivars. All pistillate cultivars chosen for this survey were growing at Oratia. These observations were carried out during the blossom period (late November) 1971. For each vine, the number of flowers in each flowering axil per shoot were recorded, as was the ratio of the burst shoots to the total number of nodes for each lateral. Also, the rate of flower opening for the staminate vines were compared with the Hayward cultivar growing at Kumeu.

The percentage bud burst parameter gave an indication of the number of flowers per vine, and was based upon the assumption that all shoots along a lateral were fruitful, and to the same extent. Analysis of this on the Hayward cultivar (Table 2), as well as observations showed this to be the case, except in two situations. Reduced or non-fruitful shoots arise when bud burst occurs at a time later than the normal spring burst (Fig.14), and when shoots arise from basal axillary buds along a lateral (Fig.15), or from adventitious buds on the stem or trunk (water shoots). These were not included in the data and hereafter, percentage bud burst per lateral refers only to fruitful shoots.

As the amount of wood furnishing each vine varied it was not always possible to have the same number of shoots or laterals (replicates) per vine. Further, it was not possible to have the same number of vines per cultivar.

III TERMINOLOGY

The following terminology, relating to the flowering characteristics of the Chinese gooseberry will be used throughout this thesis.

A 'shoot' is present during 3 seasons. In the first season, when enclosed in the bud, it is termed a bud; in its second season, when it extends and matures, it is termed a shoot; and in its third, when it now carries fruiting shoots, it is termed a lateral.

Buds (or shoots) at nodes on laterals are numbered acropetally, commencing from the node immediately past the most distal flowering axil.

Axils on shoots are numbered acropetally commencing from the lowest

(outermost) bud scale.

The Chinese gooseberry inflorescence is potentially a compound dichasium and 2^{o}, 3^{o}, or 4^{o} laterals are used to characterise the order of lateral flowers present (see Fig.17).

'Bud burst' is that stage of early shoot development when the shoot (which is still enclosed within the outer bud scales) emerges from the corky tissue that surrounds the bud. For descriptions of stages of early shoot development see Fig.3.

The term 'days after bud burst' occurs repeatedly and has been abbreviated to dabb.

Chapter 3

THE COURSE OF FLOWER AND SHOOT DEVELOPMENT

A. INTRODUCTION

Little has been recorded on the development of floral buds in *Actinidia* species apart from the report on inflorescence development in *A. kolomikta* by Kolbasina(171).

In the present report, development of the flower buds of Chinese gooseberry for one growing seaon (1971/72) is described. The main commercial cultivar Hayward, as well as the staminate clone Alpha, both growing at Kumeu, were used for this study.

At the same time, details of the correlated vegetative development are noted and these will be described first.

In this account the development of the new bud on a current seasons' shoot up to the winter rest period is described. Subsequently the bud burst and shoot growth in the following spring is detailed, as is the development of its axillary flowers.

B. EXPERIMENTAL OBSERVATIONS AND RESULTS

I BUD GROWTH

(a) Bud development

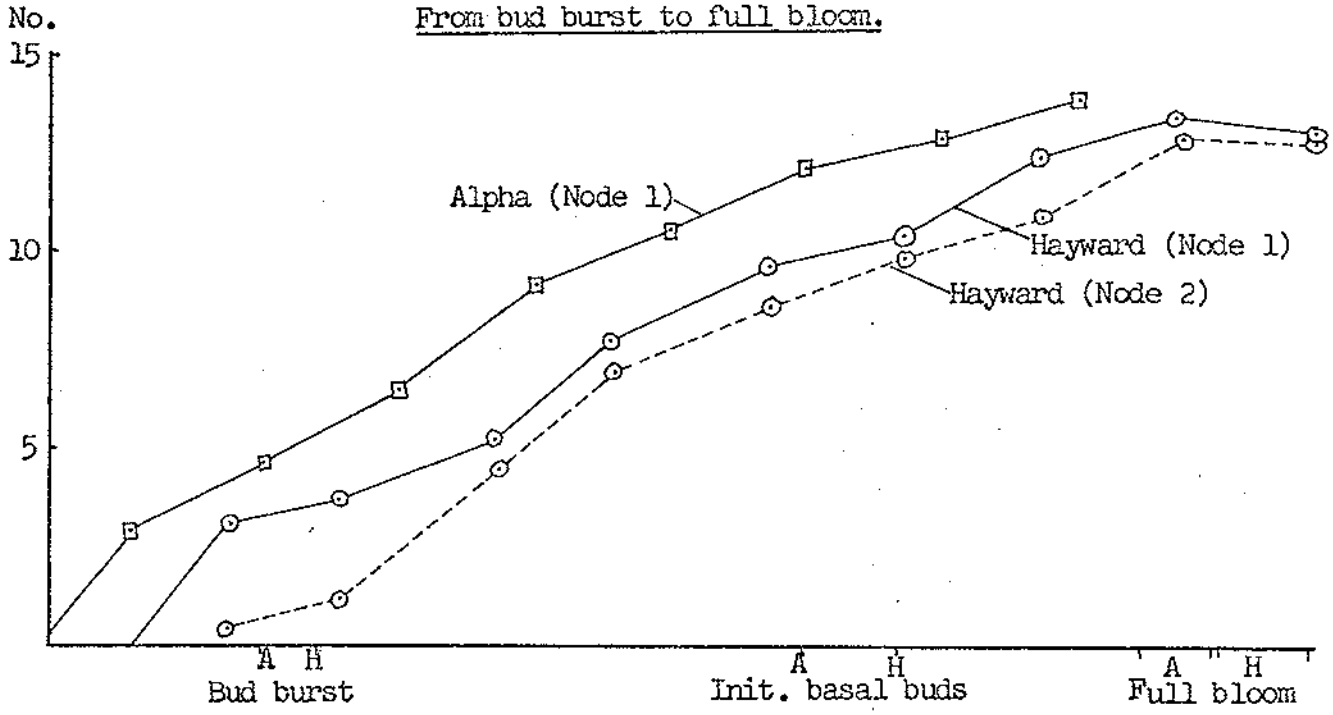
Chinese gooseberry buds are mixed buds, that is, both leaves and flowers develop from the same bud. Buds generally form on a current shoot in the axils of the leaves distal to the last flowering axil.

Leaf primordia first began to initiate in the lowest leaf axil (node 1) at the time of bud burst (Fig.1a) of the current flowering shoot. The production of leaf primordia was rapid, the plastochrone in the phase to full bloom being approximately 4 days. Characteristic lanate hairs densely coat the outer (lower) bud scales and leaf primordia soon after their initiation. Leaf primordia in the second node (distal to the last flowering axil) were initiated approximately 3 days after node 1 and generally contained one fewer leaf primordia at each sample date (Fig.1a).

Fig.1

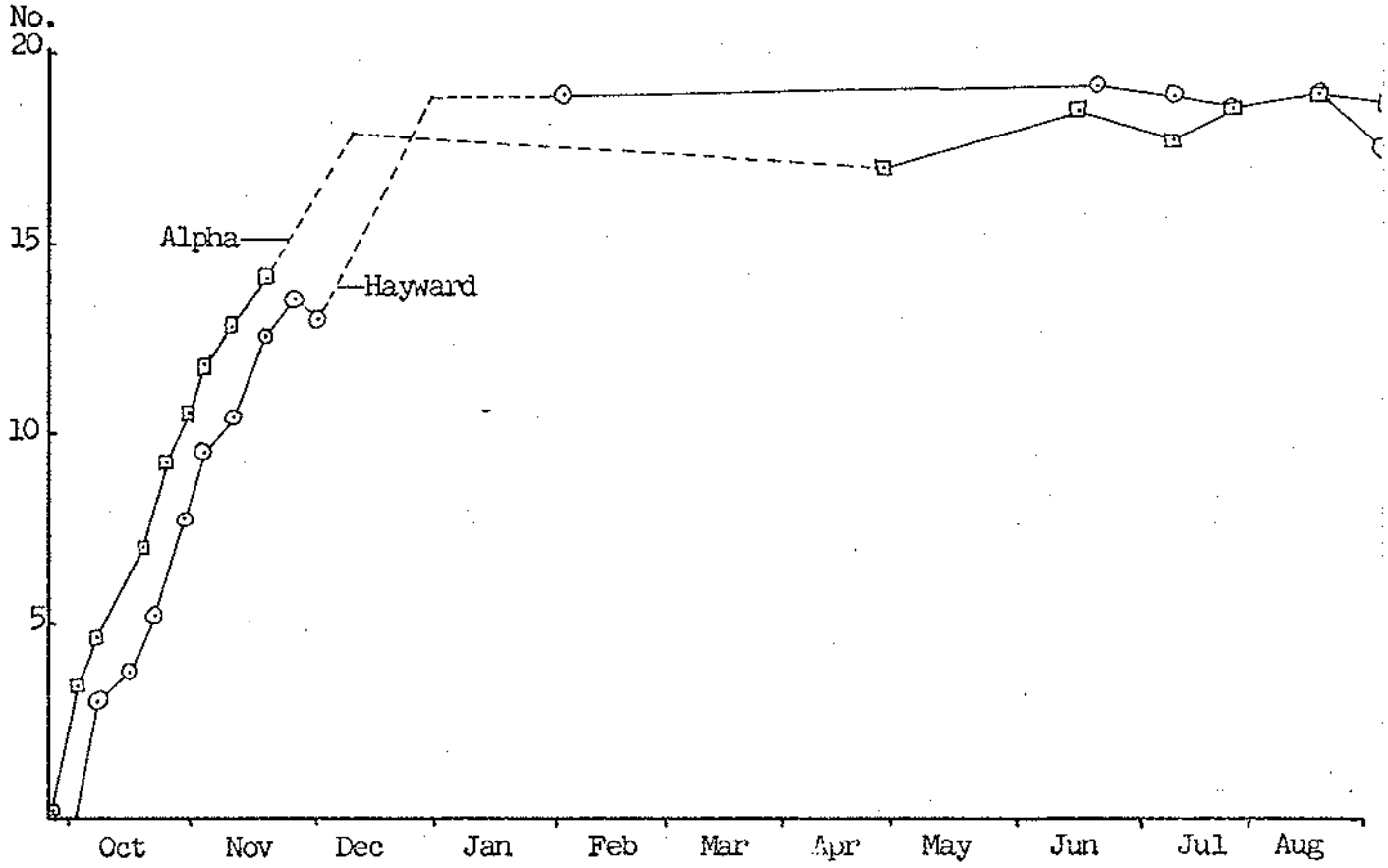
Number of leaf primordia in the new bud of Hayward and Alpha.

(a)



(b)

For the 1971/ 72 season.



By full bloom, approximately 13 leaf primordia for Hayward (10/11/71), and 14 for Alpha (18/11/71) were present (Fig.1a). By this time also, the outer (lower) primordia had become scale-like in size and shape, but had not become suberised. Leaf primordia continued to be produced rapidly until mid summer when production virtually ceased. By the end of January (24/1/72), 19 leaf primordia were present in Hayward buds, and the 3 lower (or outer) leaf primordia had become buds scales (Fig.1b). Throughout late summer further bud scales were formed.

In the axils of the newly formed outer bud scales and leaf primordia of the new bud, further buds, termed basal buds, were initiated. These were first initiated in early November, approximately 40 days after bud burst (Fig.1a). For Hayward, this occurred when 10 leaves and leaf primordia had been initiated in the new bud, and for Alpha when 12 leaves or leaf primordia had been initiated.

Basal buds occurred in up to 5 (Hayward), or 3 (Alpha) axils on a shoot and, by full bloom basal buds themselves contained 3 (Hayward) or 2 (Alpha) leaf primordia. Development of these buds continued slowly over the summer. As well as the basal buds in the outer (lower) axils of the developing bud, further meristems developed in the inner axils. These meristems increased in size throughout the season but remained uninitiated (Fig.1l).

(b) The winter bud

By winter, the bud contained up to 22 leaf formations (average 19 for Hayward, and 18 for Alpha) inserted in a spiral sequence. In Hayward, these consist of 3 - 4 bud scales, 2 - 3 transition leaf (semi-scale semi-leaf) and approximately 15 leaf primordia. In Alpha, these consist of 2 - 4 bud scales, 2 - 4 transition leaves and approximately 15 leaf primordia (Fig.2). The actual numbers of each leaf type depended upon the position of the bud on the lateral. Buds that were further along the lateral had fewer bud scales and transition leaves. Approximate dimensions of bud scales, transition leaves and oldest leaf primordia were 4.3 x 2.1 mm., 2.8 x 1.7 mm., and 2.0 x 2.0 mm., respectively. Dense lanate hair coated the outer bud scales up to the leaf primordium at approximately axil 11. In Alpha, these hairs characteristically protruded beyond the apical oriface of the corkly tissue enclosing the bud (Fig.3). Veins were also visible on leaf primordia bearing lanate hairs. From approximately axil 12 to the apex, leaf primordia lacked lanate hairs and showed no veins. The outer two bud scales in both Hayward and Alpha were attached to the side wall of the

Fig.2

Leaf primordia dissected from the winter buds of Hayward and Alpha

A Hayward, leaf primordia 1 - 16

B Alpha, leaf primordia 1 - 16

C Hayward, detailed

(a) bud scale

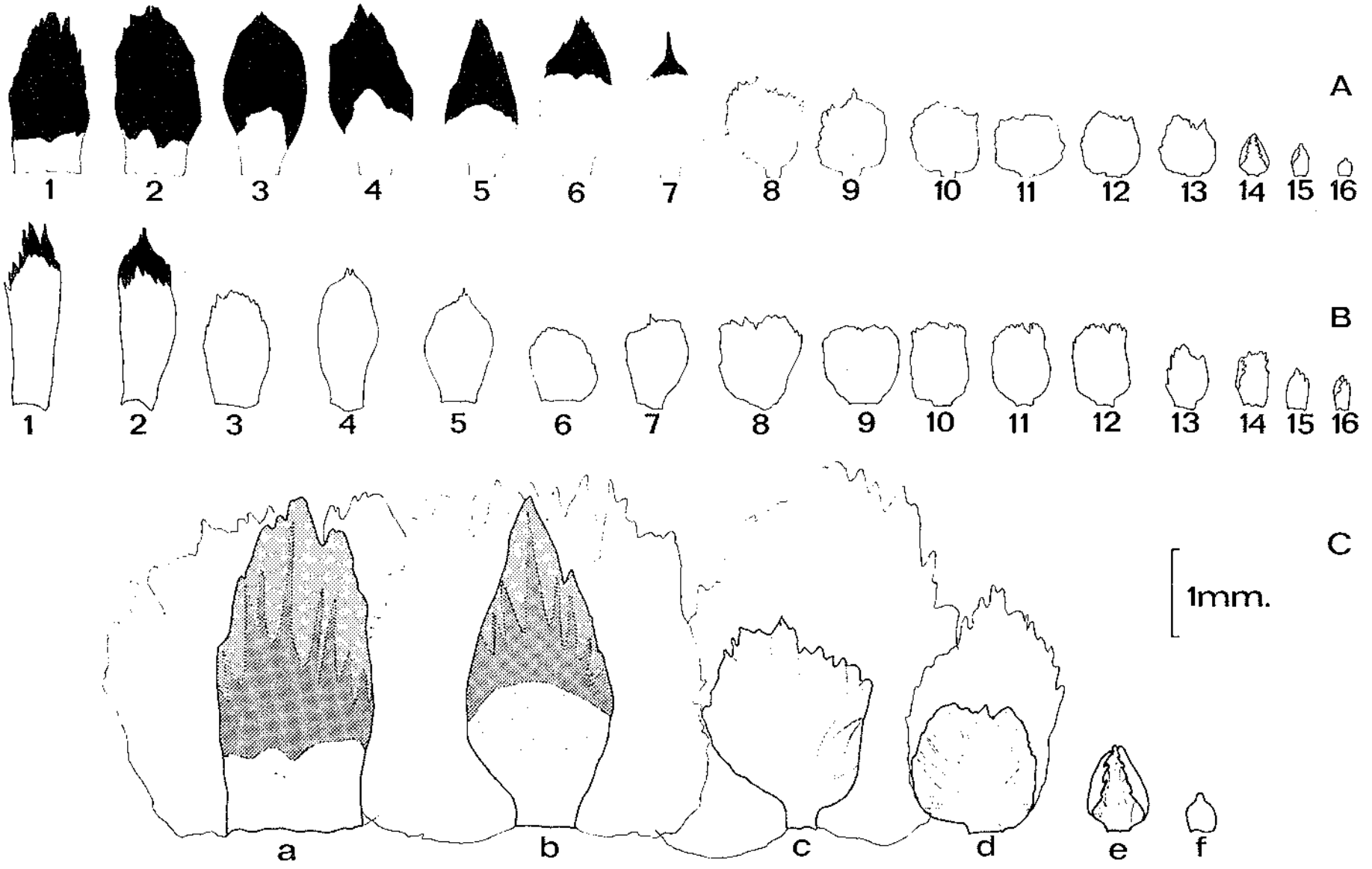
(b) transition leaf

(c) unfurled leaf

(d) unfurled leaf

(e) leaf primordium

(f) leaf primordium


A
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
B
1
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3
4
5
6
7
8
9
10
11
12
13
14
15
16
C
1mm.
a
b
c
d
e
f

corky covering which almost completely surrounds the bud, and arose away from the main central axis. These outer two bud scales were almost opposite each other and were always positioned in a plane at right angles to the lateral. The diameter of the winter bud, enclosed in the swollen base of the petiole, was up to 8.5 mm.

Basal bud development, which continued over the growing season in the outer axils of the new bud, was more advanced in Hayward than in Alpha. There were more axils containing such buds in Hayward, and each basal bud contained more leaf primordia. The outer (lower) two axils contained, on the average, 9 and 6 leaf primordia respectively in Hayward (Fig.24), and about 3 and 1 leaf primordia in Alpha. By winter, the outer leaf primordia of the basal buds in the outer two axils were suberised and had lanate hairs on their outer surface similar to the leaf primordia of the current years' bud.

In the winter bud, apart from the basal buds in the outer 2 - 3 axils of both Hayward and Alpha, the axillary meristematic areas in the inner (higher) axils remain uninitiated (Fig.24). These uninitiated meristematic domes varied in size; increasing from 3.0 x 1.5 mm., at axil 5 to a maximum of 4.0 x 2.0 mm., at axil 8, and then decreasing gradually to axil 12 where the domes were no longer visible. These meristematic domes were also a lighter colour than the predominately translucent green of the surrounding tissues.

II VEGETATIVE GROWTH

(a) Bud burst

The first indication of renewed growth of the winter bud was evident in late September at bud movement. 'Bud swell' in Alpha was approximately 5 days ahead of Hayward (25/9/771). Bud burst was estimated to have taken place 5 - 6 days after bud swell (Alpha 25/9/71, Hayward 1/10/71) and, after a lag of 10 days, the leaves unfurled ('open cluster'). (For descriptions and times of early shoot developmental stages recognised, see Fig.3). Later shoot development stages were identified by the number of days after bud burst (dabb.).

Particularly noticeable in Hayward was the large proportion of buds which failed to burst; only approximately 46% developed into shoots (see Ch.6). On the other hand, 57% of Alpha buds developed into shoots. Bud burst in Alpha extended over approximately 5 - 7 days, but in Hayward was straggly and extended over approximately 10 - 15 days. Observations

Fig. 3

Shoot bud development, from the 'dormant' stage to the 'advanced open cluster' stage.

A	Hayward (Pistillate)
B	Alpha (Staminate)
d	dormant
bs	bud swell
abs	advanced bud swell
bb	bud burst

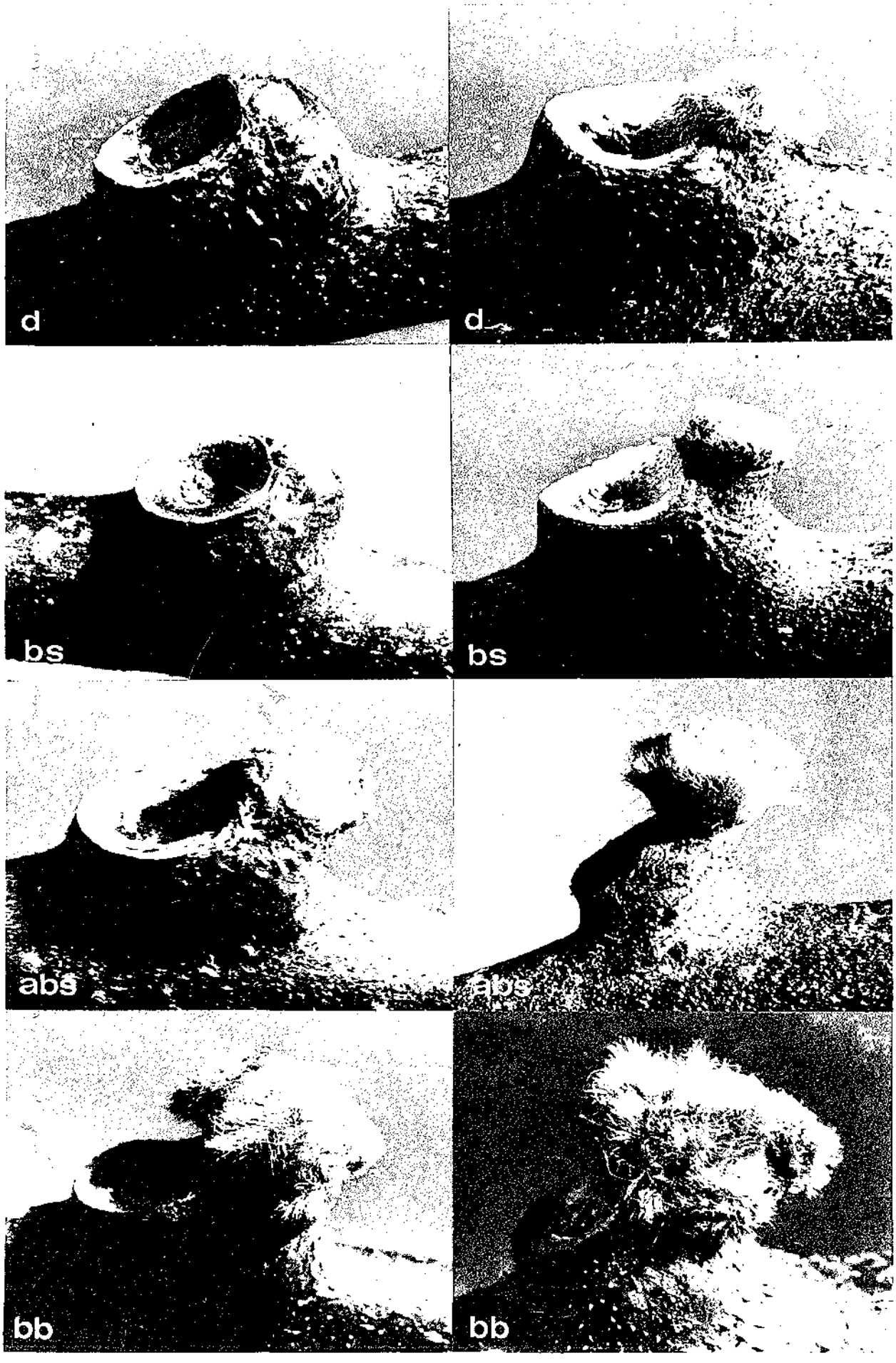
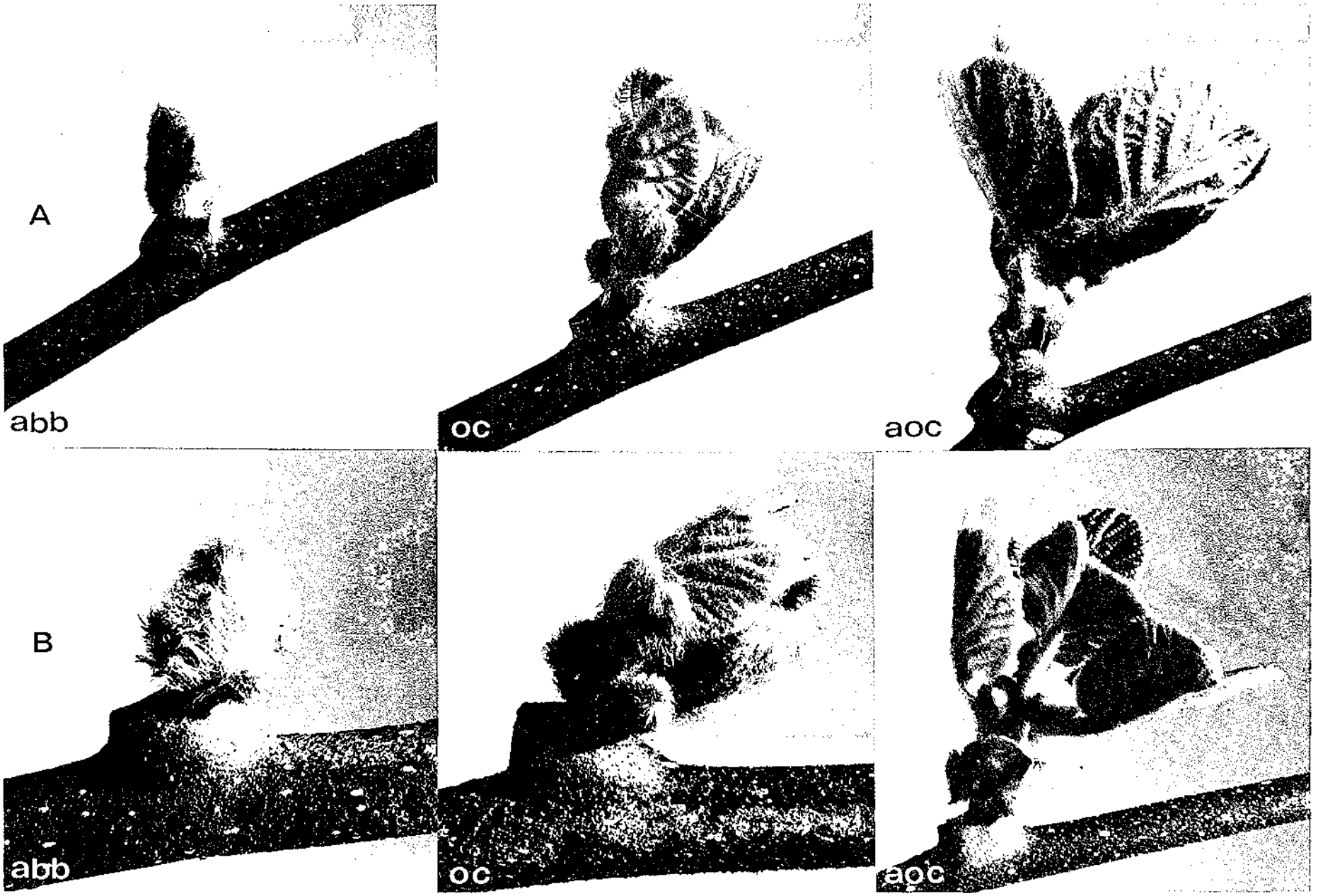

d
d
bs
bs
abs
abs
bb
bb

Fig. 3

Shoot bud development, from the 'dormant' stage to the 'advanced open cluster' stage.

A	Hayward (Pistillate)
B	Alpha (Staminate)
abb	advanced bud burst
oc	open cluster
aoc	advanced open cluster


A
abb
oc
aoc
B
abb
oc
aoc

indicated that there was a lower percentage bud burst on long laterals than on short laterals. The chances of development of a bud were also governed by its position on the lateral. Buds positioned on the underside of the lateral rarely burst or if they did, they did not develop further.

(b) Shoot development

(i) Extension growth

From the time the leaves unfurled from the bud development of the growing shoot was rapid. From 'advanced open cluster' (15 dabb.), mean shoot length (of 10 shoots) increased rapidly to a length of 15 - 20 cm., at approximately 20 dabb. (Fig.4). From this time however, some shoots terminated their extension growth following apical bud desiccation and abscission (Fig.6). The reason for this determinate type of growth is not known as all shoots chosen were in similar positions on the lateral and at similar stages of development when they were tagged at bud burst. Non-determinate shoots reached a length of 40 - 50 cm., by full bloom and determinate shoots an average length of about 20 cm. (Fig.4).

General observation indicated that Alpha produced a much greater proportion of vigorous non-determinate shoots throughout the growing season than other cultivars. Hayward shoots on the other hand are characteristically less vigorous than those on other cultivars.

The lack of terminal bud formation was also observed. On termination of extension growth the apical bud only, or the terminal portion of the shoot desiccates and abscisses (Fig.16).

(ii) Thickening growth

Over the period to full bloom, the diameter at the base of the growing shoot increased to about 7 mm. (Fig.5). By winter the basal diameter of the shoot (lateral) reached 8 - 10 mm.

(c) Leaf development

(i) Heteroblastic changes

The Chinese gooseberry displays heteroblastic changes in the morphology of leaves along a shoot. Differences in size and shape were noticeable in the winter bud (Fig.2), but became even more apparent after bud burst when the leaves expanded (Fig.7).

Leaf size and shape: All leaves remained simple. There was a characteristic pattern of leaf expansion for each axil. The lower or outer leaves

Fig.4

Non-determinate and determinate shoot growth in Hayward and Alpha.

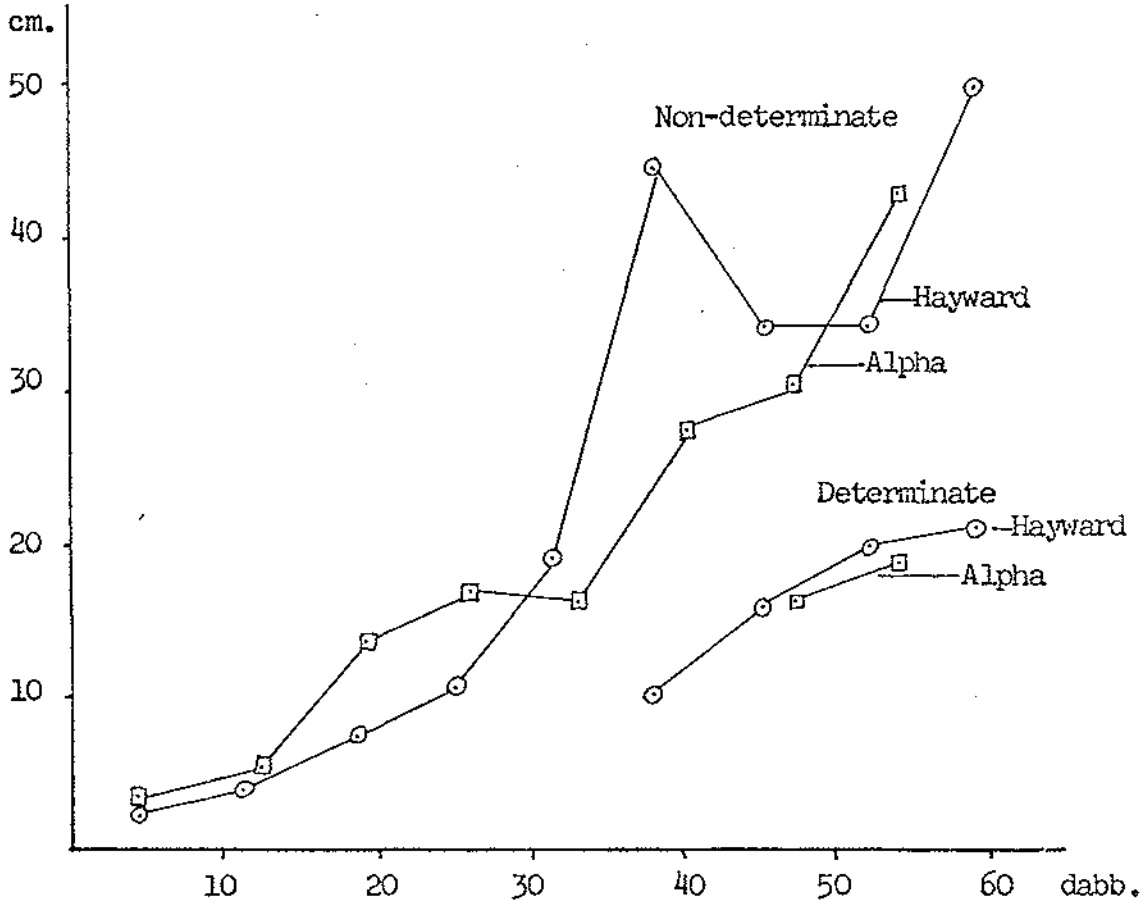


Fig.5

Thickening of the shoot in Hayward and Alpha.

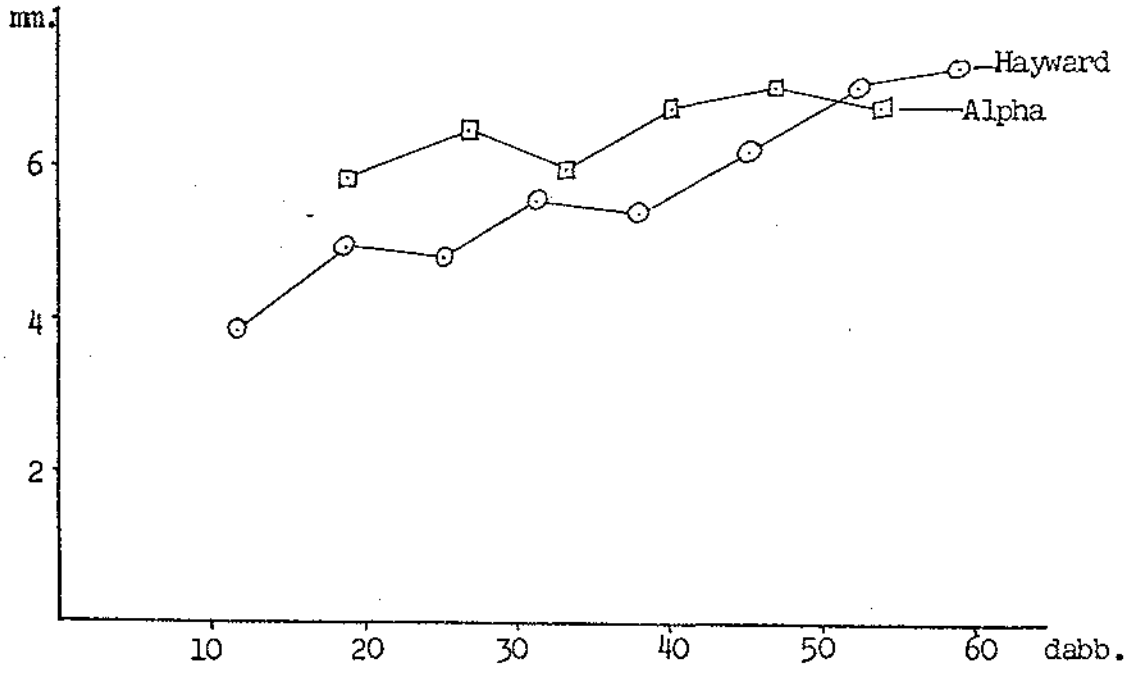


Fig.6

Non-determinate and determinate shoots of Hayward (38 dabb.) and Alpha (47 dabb.).

A Non-determinate shoot growth

B Determinate shoot growth

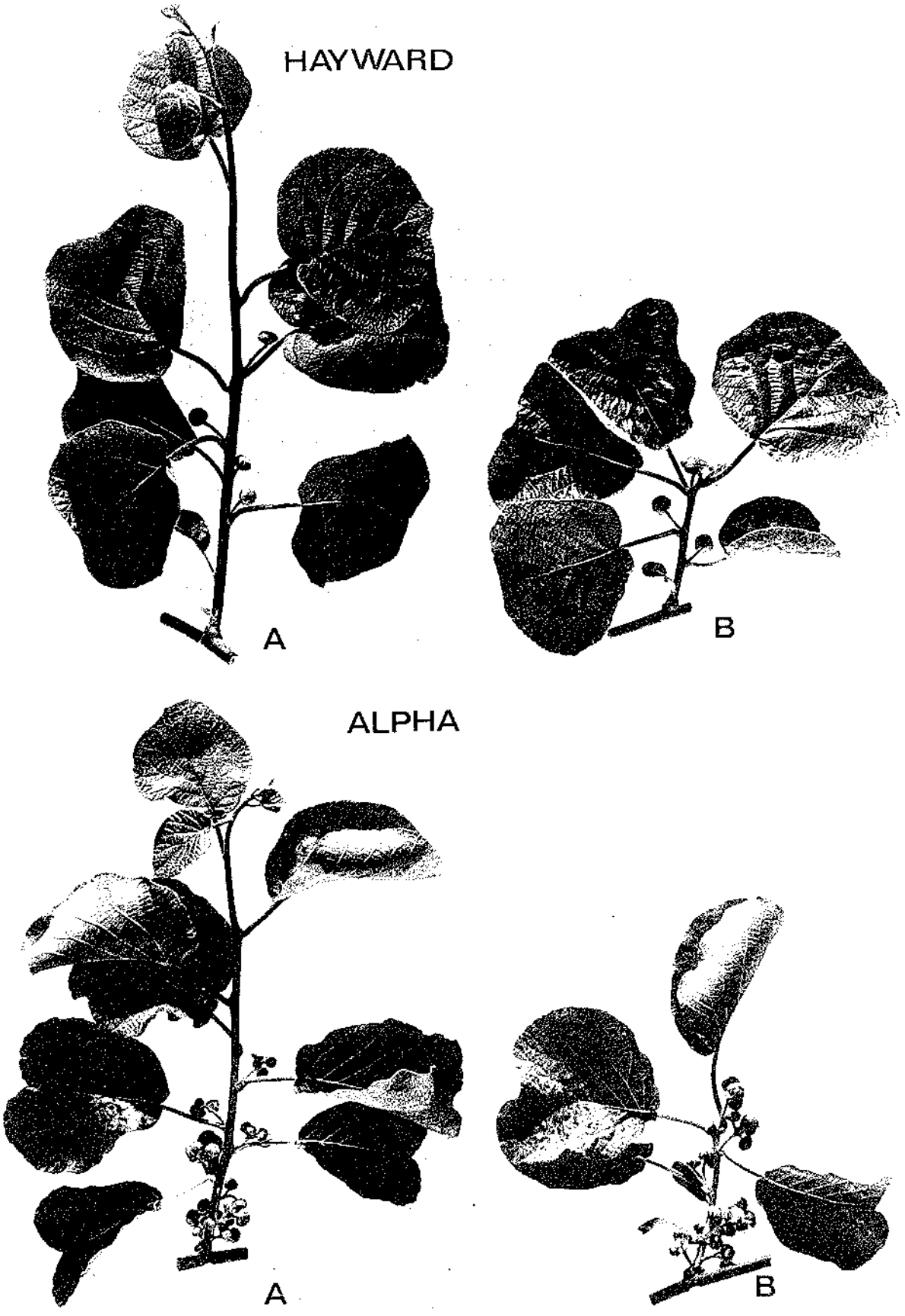

HAYWARD
A
B
ALPHA
A
B

Fig.7

Heteroblastic leaf development in Hayward and Alpha.

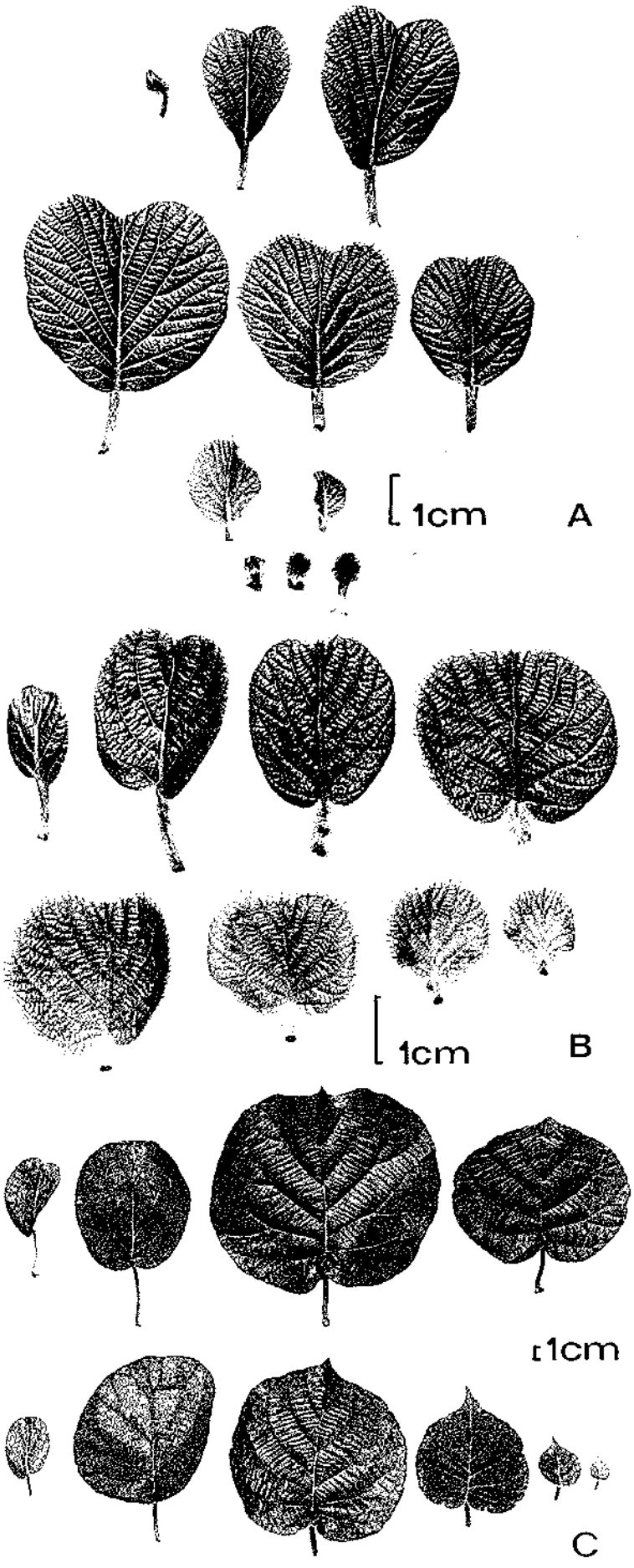
A Alpha ('advanced open cluster' stage), developing leaves 5 - 12

B Hayward ('advanced open cluster' stage), developing leaves 2 - 12

C Hayward (full bloom stage)

top row determinate shoot, leaves 5,7,8 and most distal

bottom row non-determinate shoot, leaves 5,7,8,12,13,14


1cm
A
1cm
B
1cm
C

(bud scales and outer transition leaves) made only limited growth and abscissed soon after bud burst. From the inner (lower) transition leaves (axil 4) to approximately leaf 9, there was an increase in the actual size of each leaf (Figs. 7 and 8). Size was generally maintained for all subsequent fully expanded leaves, except on determinate shoots where there was a rapid decrease in size over the last 2 - 3 leaves (see determinate shoot, Hayward, Figs. 6 and 7).

The smaller leaves at the lower (outer) axils were approximately 4.0 x 2.5 cm., (see Fig.6 on determinate and non-determinate shoots of Hayward). The leaf breadth measurement at different dates gave an indication of the growth rate of individual leaves along the shoot (Fig.8). Figure 8 shows that, except for the smaller leaves at the lower axils, there was a rapid increase in size for approximately 30 days, then the growth rate slowed until the ultimate size (approximately 12.0 x 13.5 cm., in both Hayward and Alpha) was reached. The length:breadth ratio (shape) followed the same pattern as for leaf size (Fig.7). From the outer bud scales the length:breadth ratio decreased from 2:1 to just under 1:1 at approximately leaf 8 where it was maintained unless growth terminated. When growth terminated, the ratio rapidly increased to 3:2, corresponding with the decrease in the ultimate size of the leaf.

Mature leaves along the shoot showed the following specific changes in shape.

Leaf apices: A gradual change from emarginate (transition leaves), to retuse (leaves 8 - 10), to apiculate (from approximately leaf 11 on).

Leaf bases: A less gradual change from attentuate (inner transition leaves), to cordate (higher leaves).

Leaf margins: Became denticulate, although the inner transition leaves might be entire.

Leaf and petiole surfaces: As described previously, lanate hairs covered the backs of leaves in the winter bud and the young developing shoot. On maturing leaves, the lower surfaces became covered with stellate hairs. The upper surface developed bristles which were limited to the main midrib and the later veins. The petiole and stem became also covered with bristles.

(ii) Leaf production

Following a lag of approximately 5 - 10 days after bud burst, there was sudden rise in the number of opening leaves. The same rate of opening continued for the next 15 days (Fig.10). From approximately 20 dabb., the rate was lower but steady until the termination of shoot growth.

Fig.8

Changes in leaf lamina growth at each axil along a shoot up to bloom.
(Hayward)

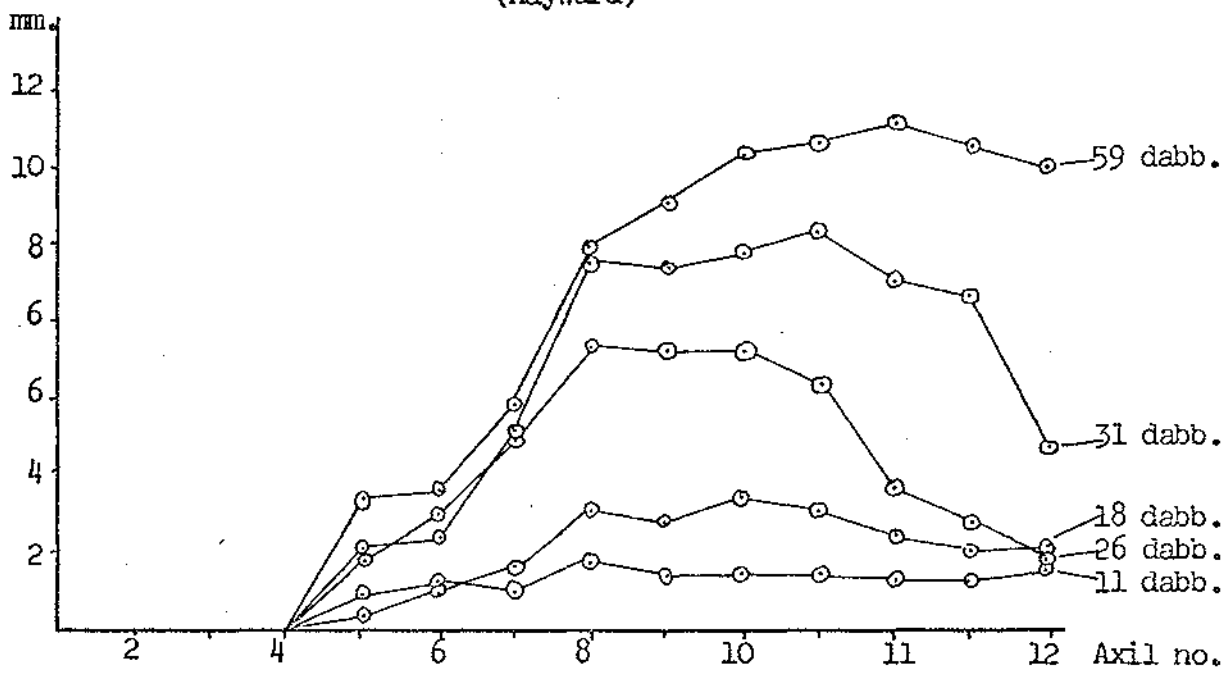


Fig.9

Changes in shoot length to each axil along a shoot up to bloom.
(Hayward)

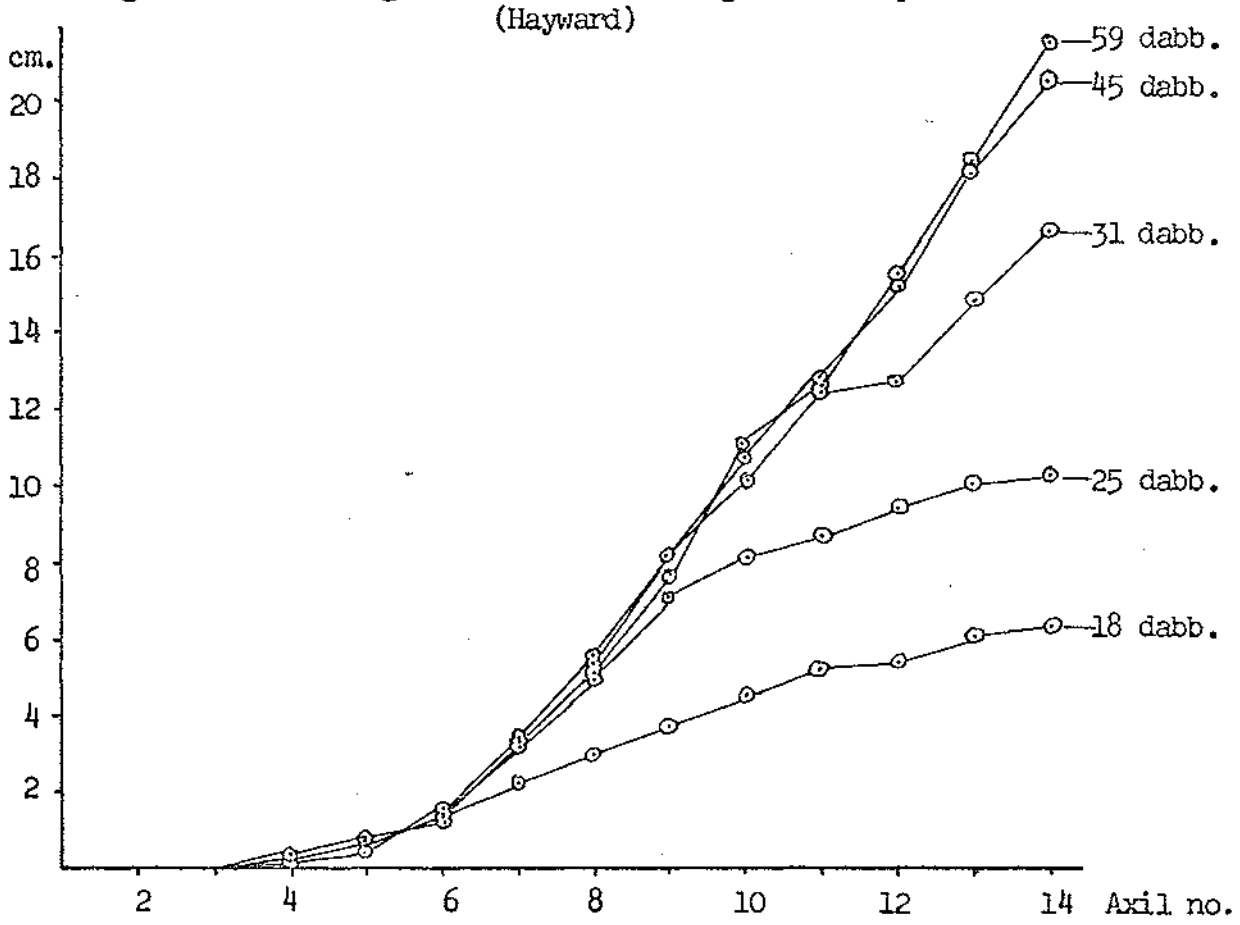
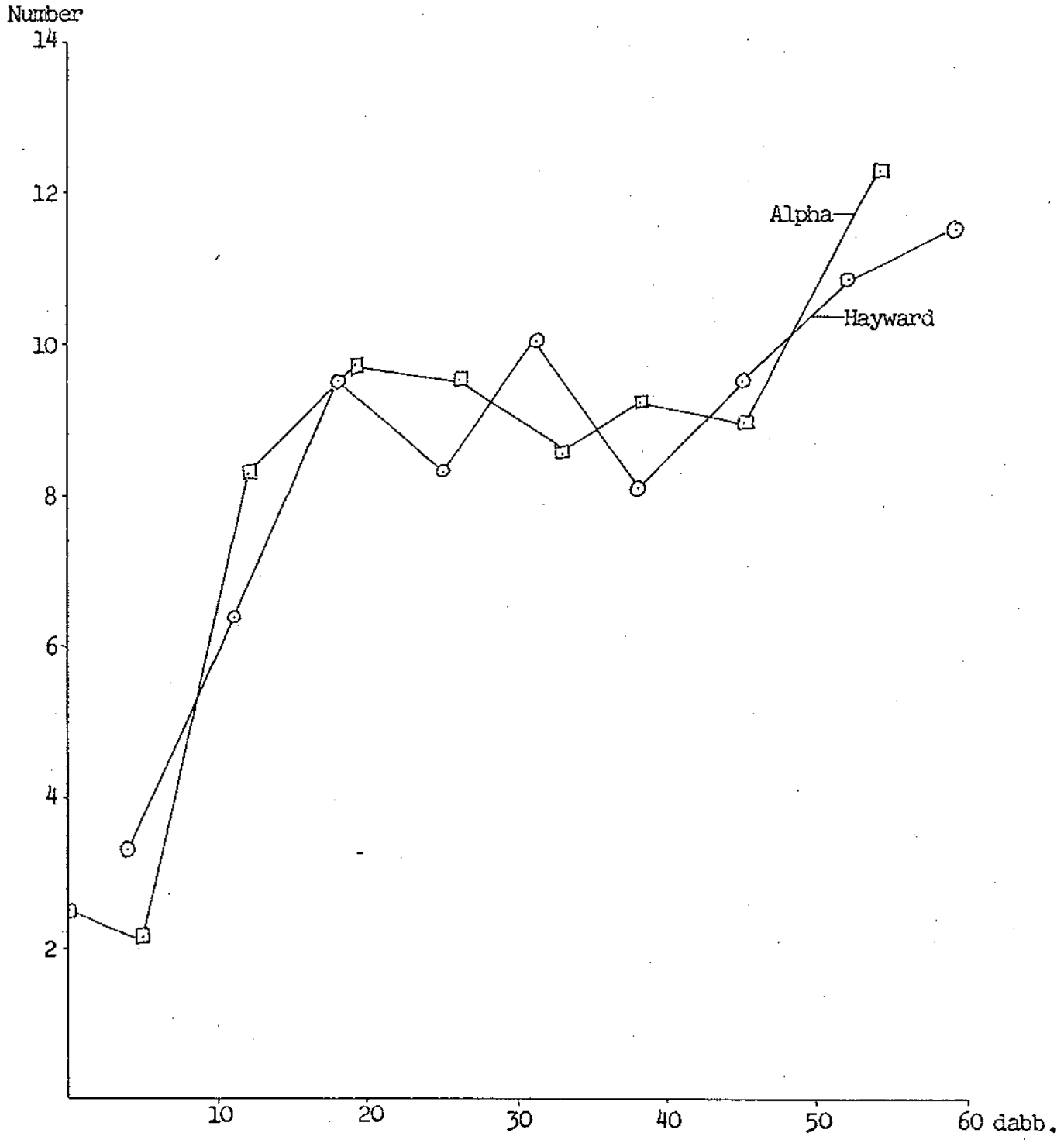


Fig.10

Rate of leaf opening up to bloom in Hayward and Alpha.



For extending shoots in both Hayward and Alpha, there were always approximately 14 leaf primordia in the apical bud.

(d) Internode development

The internode lengths along a shoot were shown to be closely related to the size of the leaf (see Fig.9). Internodes expanded as leaves matured but remained small between leaves that made only limited growth ie., there was a pattern along the shoot. Internodes at the base were very short, and rapidly lengthened to approximately axil 8, and remained constant, unless the size of the leaf was reduced (determinate shoot) when the internode very rapidly shortened.

(e) Basal bud development

(i) Number of basal buds

By bud burst, it became possible to identify the nature of the meristem in each leaf axil. Prior to bud burst, only the outer 2 - 3 axils had produced distinguishable structures (basal buds), the rest remained uninitiated (see Fig.24). Basal buds could occupy up to 5, but usually 4, outer leaf axils in Hayward, and up to 4, but usually 2 axils in Alpha. The actual number of basal buds per shoot, like the number of bud scales and transition leaves, depended on the position of the shoot on the lateral (Table 1). Results on fruiting laterals of Hayward showed that the number of basal buds per shoot decreased significantly, from a mean 4.2 at node 1, to 2.8 at node 8.

(ii) Post bud burst development

Basal buds, produced in the lower axils during the previous season, continued to develop slowly during growth of the current shoot. While no more leaf primordia were initiated in the lower axils, the upper (or inner) axil basal buds continued to initiate leaf primordia. By full bloom, these basal bud axils had up to 5 leaf primordia. These upper (inner) basal buds remained hairless. By full bloom also, the outer scale leaves, of the lower (outer) basal buds themselves had axillary meristems, but they remained uninitiated.

Basal buds do not usually length unless stimulated, as eg., by damaging of the shoot or the hard pruning of a lateral (Fig.15).

Table 1

The effect of nodal position along a lateral on the number of basal bud axils per shoot in Hayward

Node	Mean	Signif.
1	4.2	A *
2	4.1	A B
3	3.7	A B C
4	3.6	A B C
5	3.6	A B C
6	3.5	A B C
7	3.4	A B C
8	2.9	B C
9-17	3.1	C

Analysis of variance, multiple comparison of vines by Tukey's method.

Mean of 11 shoots, chosen at random from tagged shoots used for flower development studies.

* Values with no letter in common are significantly different at the 1% level.

III REPRODUCTIVE GROWTH

(a) Flower bud development

(i) The course of terminal bud development

All potentially reproductive meristems in the leaf axils were still at the uninitiated stage in early September (Fig.11, Stage 1). The first discernible changes in the reproductive meristems (in the leaf axils immediately above those containing basal buds) occurred just prior to bud movement in the spring.

There was a rapid increase in volume of the meristematic region (Fig.11, Stage 2). In Hayward, this occurred around September 20th, and in Alpha, 10 days earlier. From Stage 2 on, development was rapid, and parts appeared in an acropetal order at successive higher levels. Within 5 days, a pair of protuberances appeared at the base of the primordium (Stage 3) which usually later formed into bracts and the subtending lateral flowers. Bracts and the associated lateral primordia were not always present however at that stage.

The sepals primordia, the first primordia to appear on the floral meristem, arose as a shorl of 5 - 7 papillae on the side of the meristematic dome (Stage 4). This stage was reached (in both Hayward and Alpha) when shoot buds were at the ' advanced swell' stage. As the sepal tips met over the top of the developing bud they changed from a translucent white to an opaque light green colour and became densely covered with deep red hirsute hairs.

Within 5 days after bud burst, petals were initiated between, and inner to the sepals bases just before the sepals met to enclose the structure (Stage 5).

Stamen initials appeared almost immediately after petal initiation as two whorls in Hayward, and as three whorls in Alpha (Stage 6). The whorls were initiated in rapid succession (the outer whorl first), and was completed by the 'advanced bud burst' stage.

At the time of stamen initiation of the terminal flower, the sepal whorl was being initiated on lateral flower primordia.

As the petals curved inwards and the tips interlaced and turned light green, the stigma was initiated as a convoluted whorl around the periphery of the apical dome (Stage 7). This occurred as the leaves were unfurling from the shoot bud ('open cluster'), some 10 dabb. By this stage also, the developing lateral flowers had initiated their petal whorl.

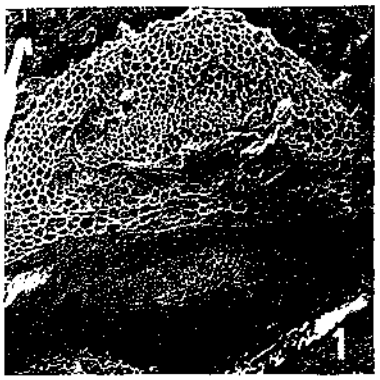
The stigmal convolutions became deeper and longer and it was not until

Fig.11

Flower bud development stages in Hayward and Alpha

H Hayward (Pistillate)

A Alpha (Staminate)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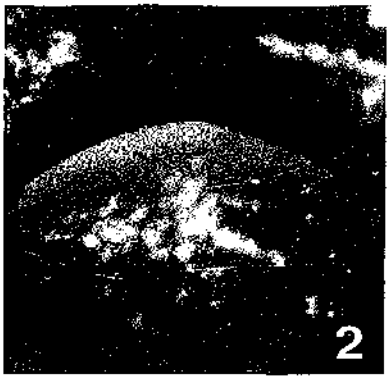
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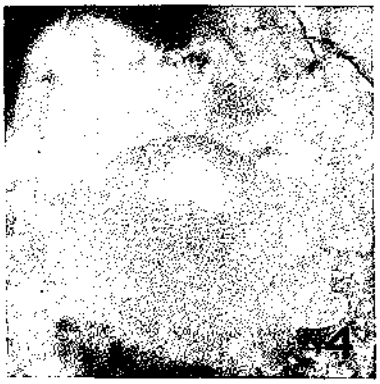
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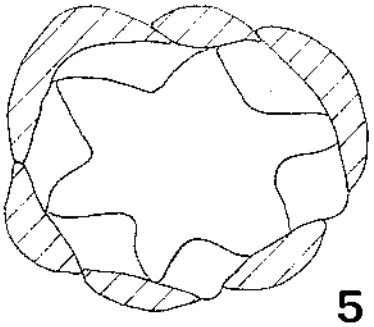
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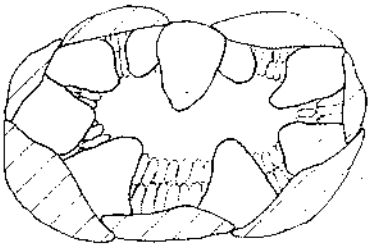
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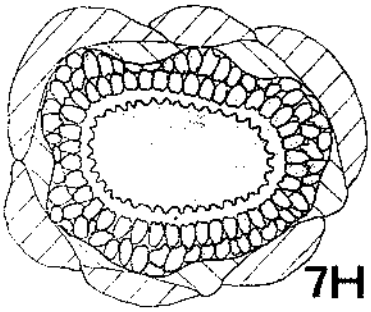
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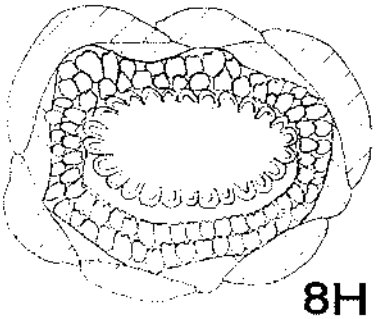
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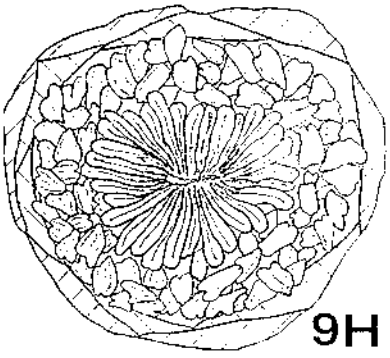
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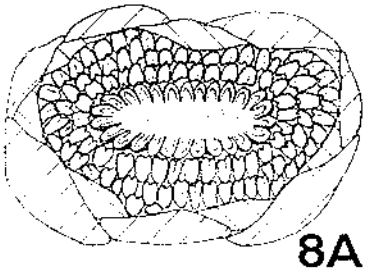
7A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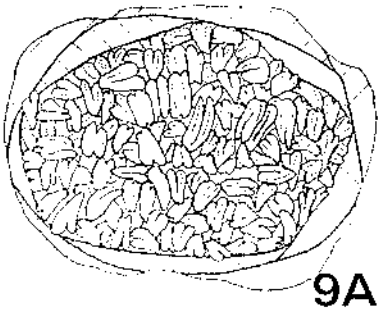
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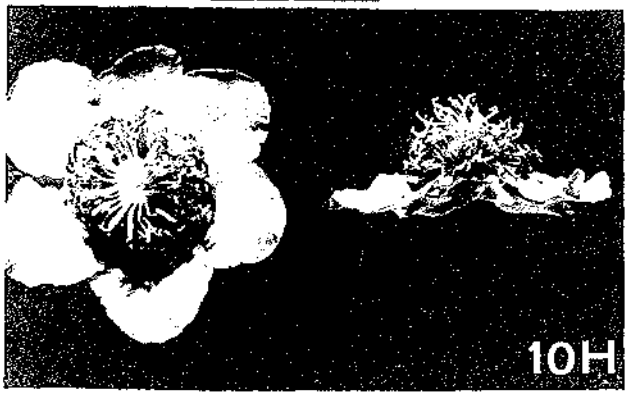
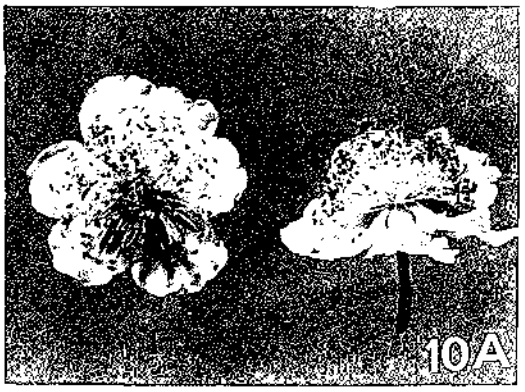

10H


10A

this stage that differences between the pistillate Hayward and staminate Alpha became apparent.

In the pistillate cultivar Hayward, the stigmal whorl rose forming a gynoecial plateau above the developing stamens (Stage 8).

The outer region of the gynoecial area continued to rise at a faster rate than the central portion, leaving that portion of the gynoecium to appear depressed. As that occurred, the stigmal lobes lengthened and the superior ovary formed in the central column beneath the stigmal whorl. This occurred approximately 18 dabb., and expansion of the ovary continued steadily to full bloom (Fig.20).

Stamens expanded slowly from their inception, and differentiated into anthers and filaments approximately 35 dabb., but the filaments remained short. By the time the loculi were first discernible in the ovary (45 dabb.), the anther heads had developed into the characteristic two lobed, four loculed structure, and pollen grains formed therein shortly after. By this time, sericeous hairs covered the ovary wall, the short style and the central portion of the stigma. Shortly after the loculi were first discernible, the ovules were initiated in the multilocular ovary (Stage 9). As a result of further flower development and expansion the sepals, which had previously completely encased the flower bud, began to separate to reveal the petals.

Shortly after the petals became externally visible, the stigmal lobes separated from each other and the distal upper surfaces became sticky. At this time also, separated pollen grains were observed in the anther heads, and the stamen filaments expanded rapidly, especially over the last five days before bloom.

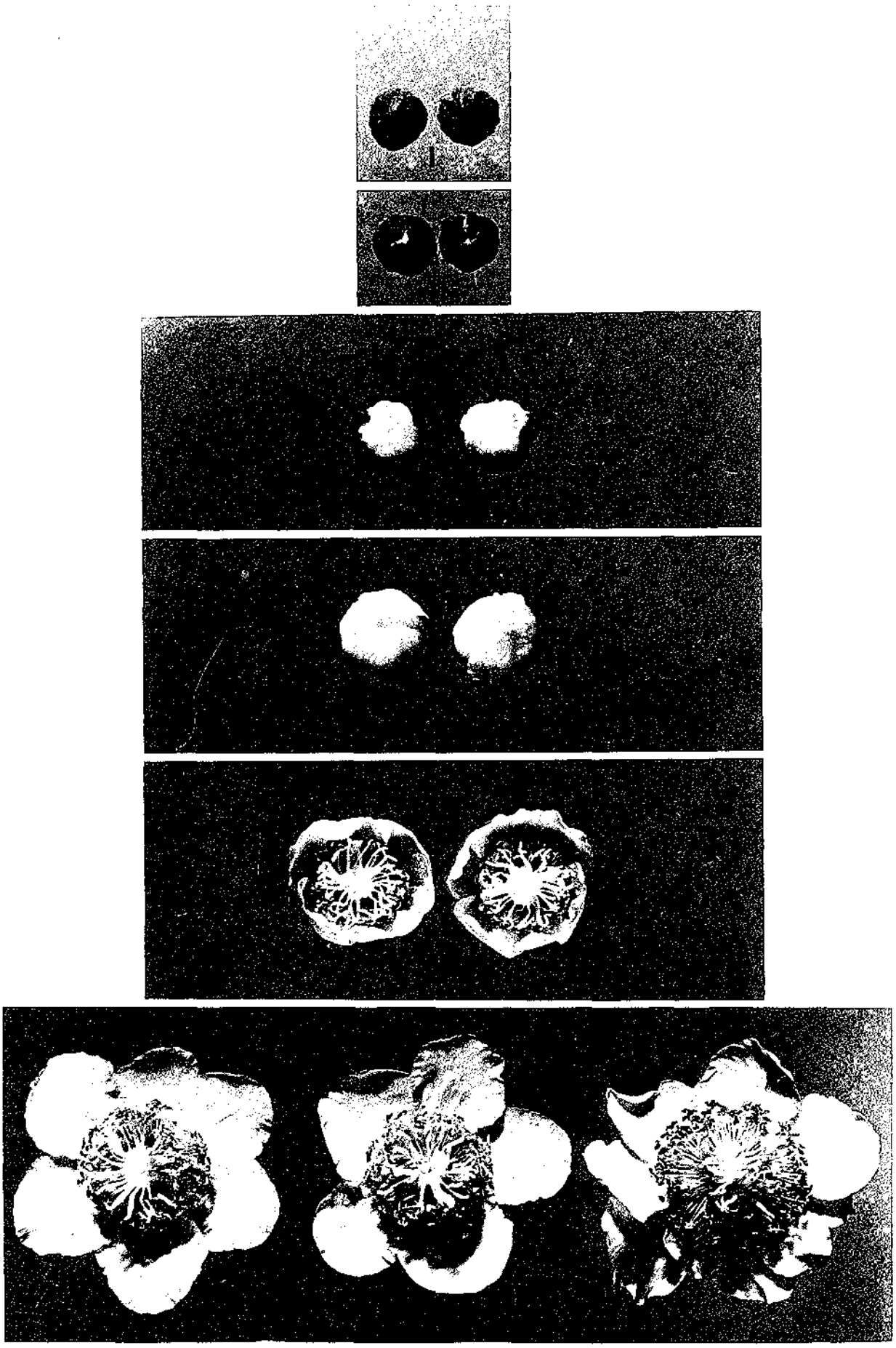
The full bloom stage (Stage 10) in Alpha occurred 54 dabb., (18/11/71) and in Hayward, 59 dabb., (30/11/71). The bloom period extended over 5 - 7 days in Hayward and 10 - 15 days in Alpha (see also Ch.6).

The final sequence of flower bud development in Hayward was arbitarily classified into a number of stages (I - VI), based on the external morphology of the bud (Fig.12). Commencing when the petals were first externally visible, these external developmental stages were compared with the growth of the various flower parts (Table 3). From stages II - IV development was steady, taking approximately 10 days. The final 2 stages (V- VI) to full bloom however were rapid and occurred within 36 hours, depending on the weather.

Early flower bud development in the staminate clone Alpha was similar to that in the pistillate cultivar Hayward. Differences in the course of

Fig.12

Late flower bud development ('split calyx' stage to full bloom), Hayward.



flower bud development in Alpha however, became apparent from the time the stigmal whorl was initiated (Stage 7).

Although the stigmal whorl was actually initiated in Alpha and the lobes lengthened slightly and even widened at their proximal ends (Stage 8), further gynoecial development was strictly limited. The gynoecial structure in staminate flowers did not expand and become elevated above the plane of the stamens as in the pistillate flower. Instead, the gynoecial structure appeared to consist only of vestigial stigmal lobes (Stage 8). By this stage (26 dabb.), the stamens had differentiated into anthers and filaments and by 35 dabb., the anthers had developed into the 2 lobed, 4 loculed structure, similar to anthers in pistillate flowers.

Pollen grains were first seen formed in the anthers shortly after locular formation. By that time, the anthers had almost completely covered the gynoecium (Stage 9). External flower development was similar to Hayward although petals were visible beneath the parted sepals earlier, some 18 days before bloom. The filaments of the stamen lengthened rapidly approximately 5 days prior to bloom, at the time the flower bud was rapidly unfurling (Stage 10).

(ii) Aborted (aberrant) flower bud development

It became apparent, soon after flower initiation (just prior to bud movement), that flower primordial development in some axils, (in both pistillate and staminate flowers) was abnormal.

While some of these aberrant structures ceased growth at various stages up to bloom, most made only limited development. Such aberrant development could be predicted at the uninitiated primordial stage. Instead of the normally symetrically swollen floral primordia (Stage 1), a variety of uninitiated primordial shapes were later shown to cease development (Fig.13a upper line, also Fig.24 axil 4). By the time normal flower buds had reached Stage 5 (5 dabb.), the aberrant structures ceased growth, without having initiated petals (Fig.13a, lower line).

Where development ceased at stages well after the immediate post initiation period, development prior to their cessation of growth appeared to be normal. Such late aborting buds usually abscissed when their growth stopped, but those aberrant structures which made only limited early growth persisted to full bloom.

In both Hayward and Alpha, most of the aberrant structures were found in the lowest reproductive axils. The frequency of such structures in Hayward was noticeably greater than in Alpha (Fig.19b). In Hayward structures in up to 3 reproductive axils were aberrant, whereas in Alpha

Fig. 13

Abnormal flower development.

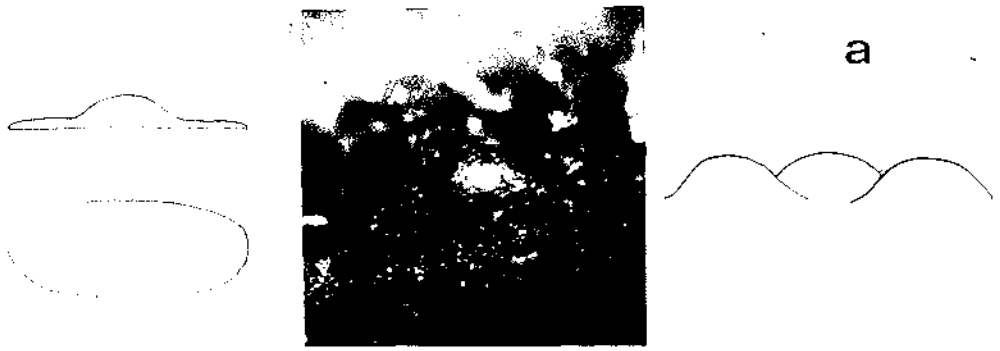
(a) Aberrant flower bud development, Hayward and Alpha

top line uninitiated state

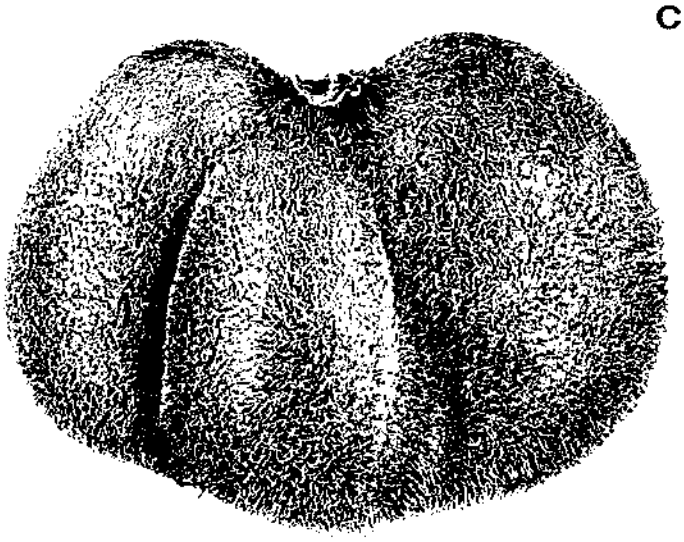
lower line maximum development

(b) Fasciated fruit, Hayward

(c) Fasciated fruit, Hayward


a


b


c

aberrant structures occupied on the average fewer than 1 axil. Further, by full bloom, the number of structures, which aborted at stages well after flower initiation (late abortions) were almost nil in Alpha, but in Hayward made up to 50% of the total aborted axils.

Although the primordia in the lower reproductive axils normally cease development or abort, a low frequency (less than 1%) of such primordia develop, bloom (Fig.13b) and set fruit (Fig.13c). These were characteristically fasciated due to the checking of development of the terminal flower bud with a fusing of flowers. In some cases, these fasciated fruit appear to be formed by the fusion of more than 3 flowers suggesting that Hayward, like Alpha is capable of initiating tertiary (3^{O}) lateral flower buds (Fig.17).

Environmental factors apparently influence this phenomenon as the frequency of these faciations is greater in some seasons than others.

It was also observed that the few buds which were stimulated into growth much later than normal did not carry flower buds (Fig.14). It was not determined whether aberrant reproductive structures were present in axils on those shoots.

(iii) Lateral flower bud development

The pattern of lateral flower bud formation was similar to that of terminal flower buds, but at all stages, development lagged behind that of the terminal flower bud.

In both Hayward and Alpha, the sepal primordia of secondary lateral flowers (see Fig.17) were initiated when the stamen whorl was forming in the terminal flower. However in Hayward, virtually all of these lateral flower buds ceased development before the stage of petal initiation. Secondary lateral flower buds in Hayward however occasionally develop and bloom (Fig.18). In some pistillate cultivars and in most staminate vines this development is characteristic (see Ch.6).

Tertiary flowers were initiated (see Fig.17) in Alpha, but not in Hayward. The delay in initiation of tertiary lateral flowers in Alpha was not as great as the delay in the initiation of secondary lateral flowers, and occurred when the secondary flower buds had initiated their petals and the terminal flower bud was at Stage 8.

Although relative development was more rapid in the lateral flowers, lateral flowers always bloomed after the terminal flower (Fig.18).

Fig.14

Late shoot development, Hayward.

Fig.15

Stimulation of a basal bud into growth in Hayward.

Fig.16

The terminal portion of a dormant Hayward shoot (lateral).

A Determinate shoot

B Non-determinate shoot

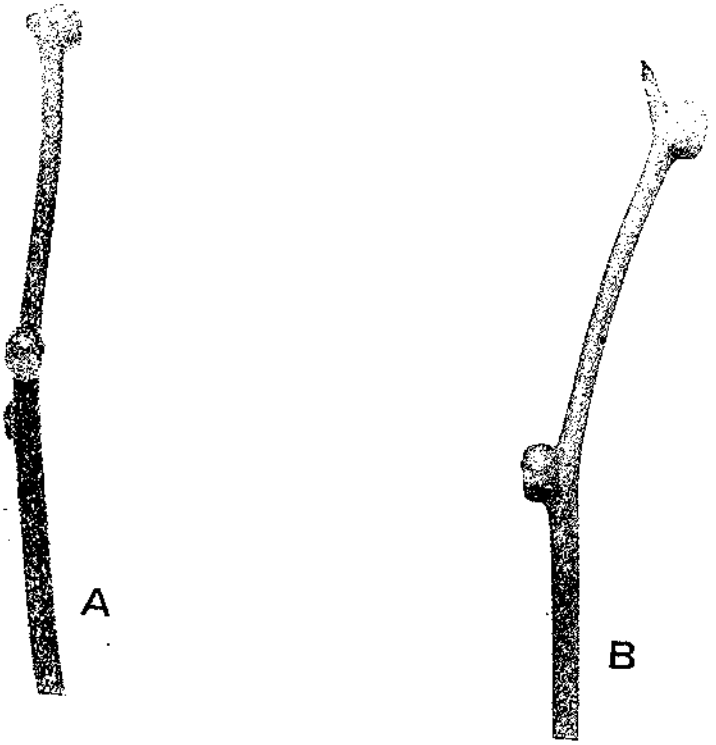
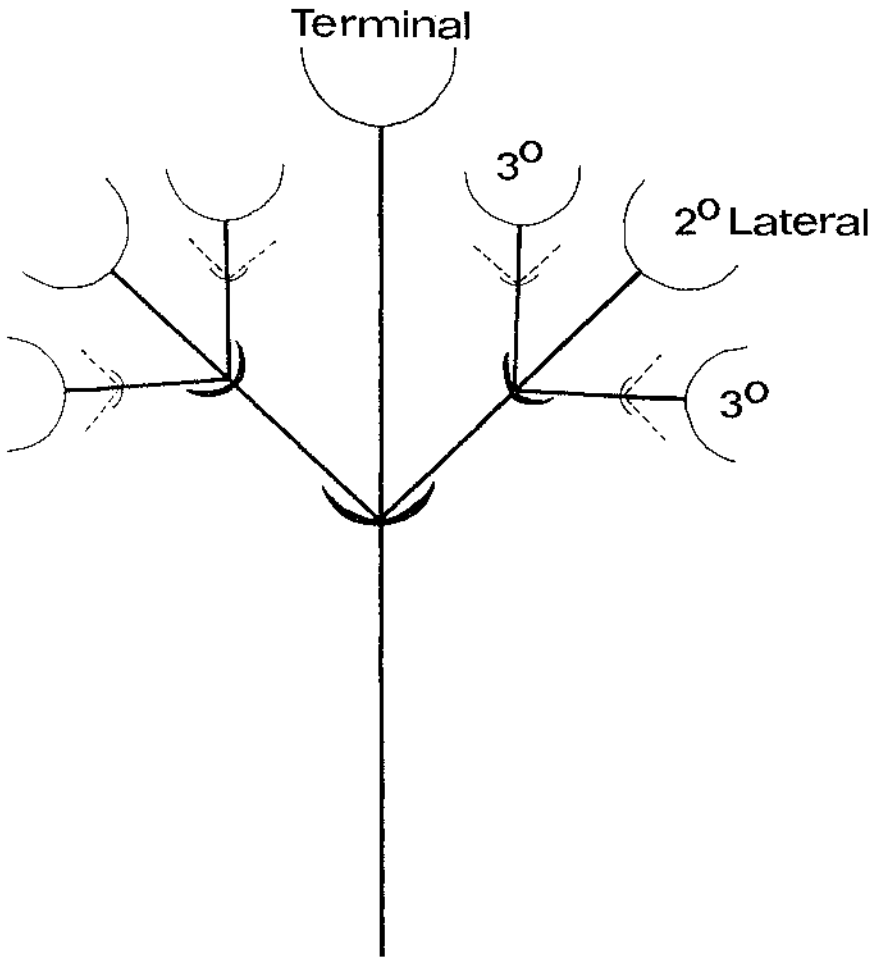

A
B

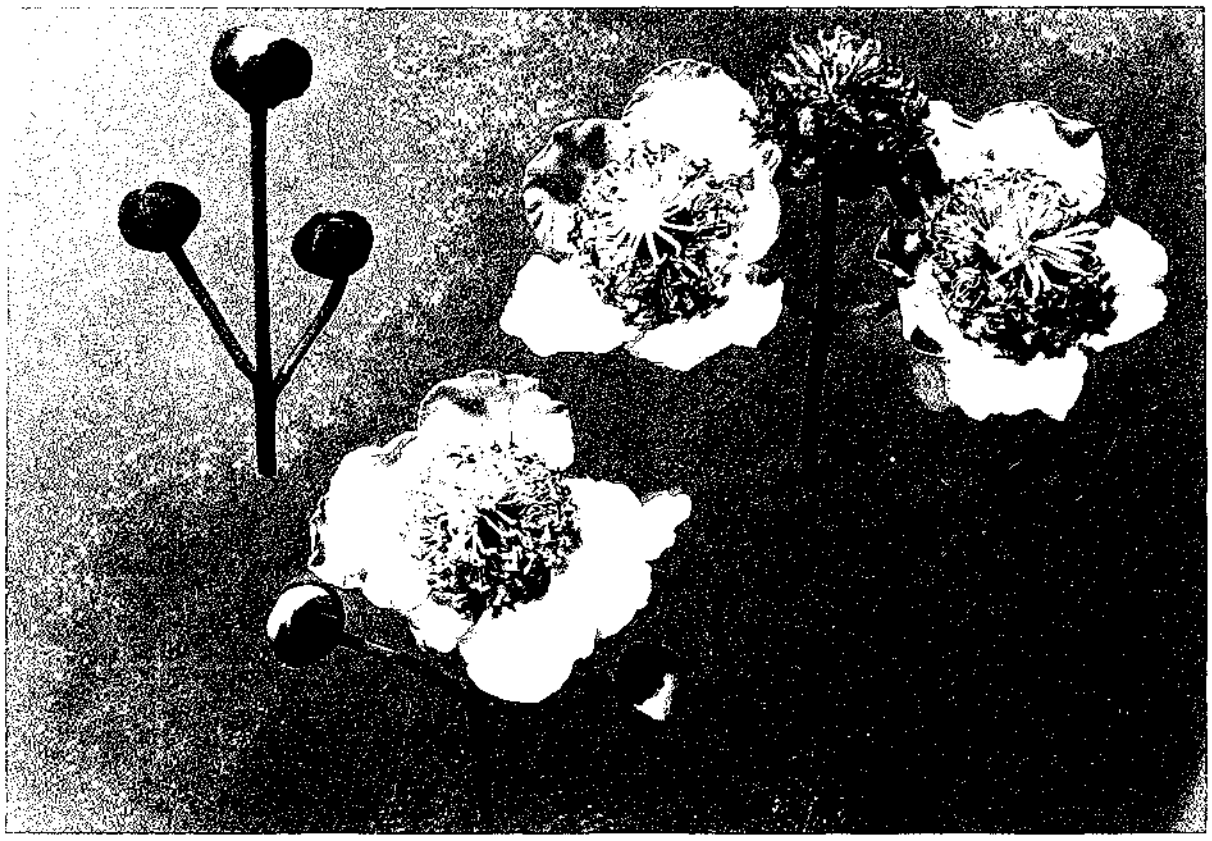
Fig.17

Diagramatic representation of a Chinese gooseberry inflorescence (compound dichasium).

Fig.18

Lateral flower bud development, Hayward.


Terminal
3°
2° Lateral
3°



(b) Flower distrubtion

(i) Number of reproductive axils per shoot along a lateral

Although basal buds developed in the outer leaf primordia (bud scales) of the winter bud, the fate of the primordia in the axils of the inner (lower) leaf primordia could not be determined until initiation commenced, at bud movement in the spring.

By bud burst, it became apparent that the reproductive region on a shoot was between the most distal axil with a basal bud and the lowest axil containing the new bud. The exact position of this region on the shoot depended on the number of axils with basal buds. Although it was shown that in Hayward, the number of basal bud axils depended on the position of the shoot on the lateral (Table 1), the number of reproductive axils was found to be independent of such positional effects (Table 2).

(ii) Number of functional flower axils per shoot

At various stages in the course of flower bud development some flower buds ceased growth and aborted (see earlier). In Hayward, the number of flowering axils per shoot, which were still functional, decreased from approximately 7.2 at initiation to approximately 4.5 at bloom (Fig.19a). In Alpha, the corresponding number of functional flowering axils was 8.2 at initiation and 7.7 at bloom (Fig.19b). These trends correlated with the number of aborted reproductive axils.

(iii) Variation in flower bud development along a shoot

From the time of initiation, there was a variation in the size of the flower buds along a shoot. Prior to initiation, the size of the uninitiated primordium seemed correlated with size of the leaf primordium subtending it, ie., the larger outer leaf primordia generally had larger flower primordia in their axils (Fig.21). However once initiation had commenced and the flower buds grew, a different pattern emerged; the zone of maximum size shifted to the upper reporductive axils. This was due to the almost complete abortion of the flower structures in the lower axils at this time. There were consistent differences in the stage of flower bud development in axils along a shoot right from the early initiation stage. This could be related to both primoridal and later flower bud size. This led ultimately to a consistent sequence of flower opening. In both Hayward and Alpha the Coefficient of Concordance (286) between orders of opening were significant at the 1% level. With aborted axils excluded,

Table 2

The effect of nodal position along a lateral on the number of reproductive axils per shoot in Hayward

Node	Mean	Signif.
1	7.6	A*
2	7.1	A
3	7.1	A
4	7.7	A
5	7.3	A
6	7.4	A
7	6.7	A
8	7.7	A
9-17	7.0	A

Analysis of variance, multiple comparison of vines by Tukey's method.

Mean of 7 shoots, chosen at random from tagged shoots used for flower development studies.

* Values with no letter in common are significantly different at the 1% level.

Fig.19

The number of normal flowering axils per shoot,
the number of aborted (aberrant) flowering axils per shoot,
and the number of reproductive axils per shoot.

(a)

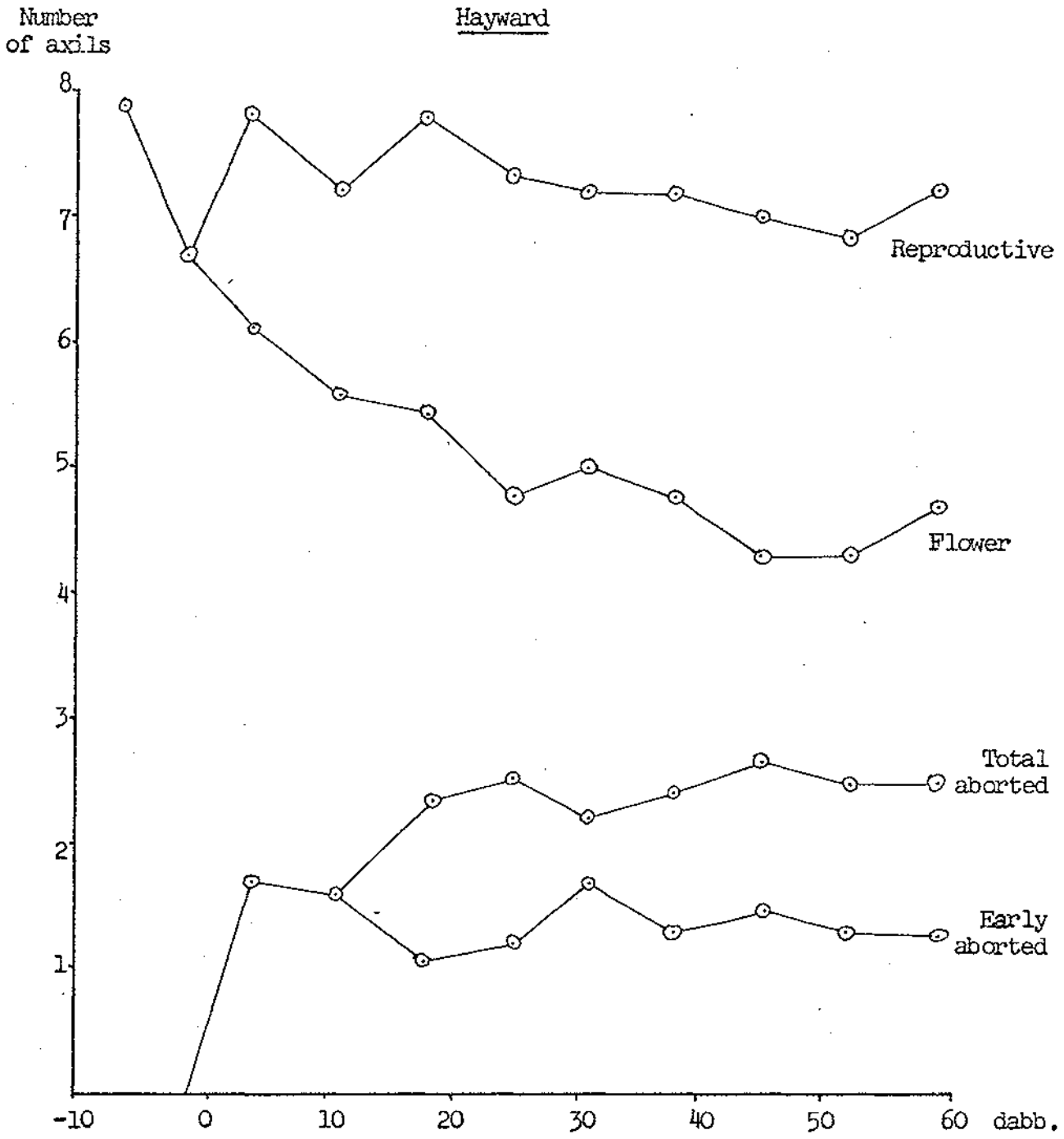


Fig.19

The number of normal flowering axils per shoot,
the number of aborted (aberrant) flowering axils per shoot,
and the number of reproductive axils per shoot.

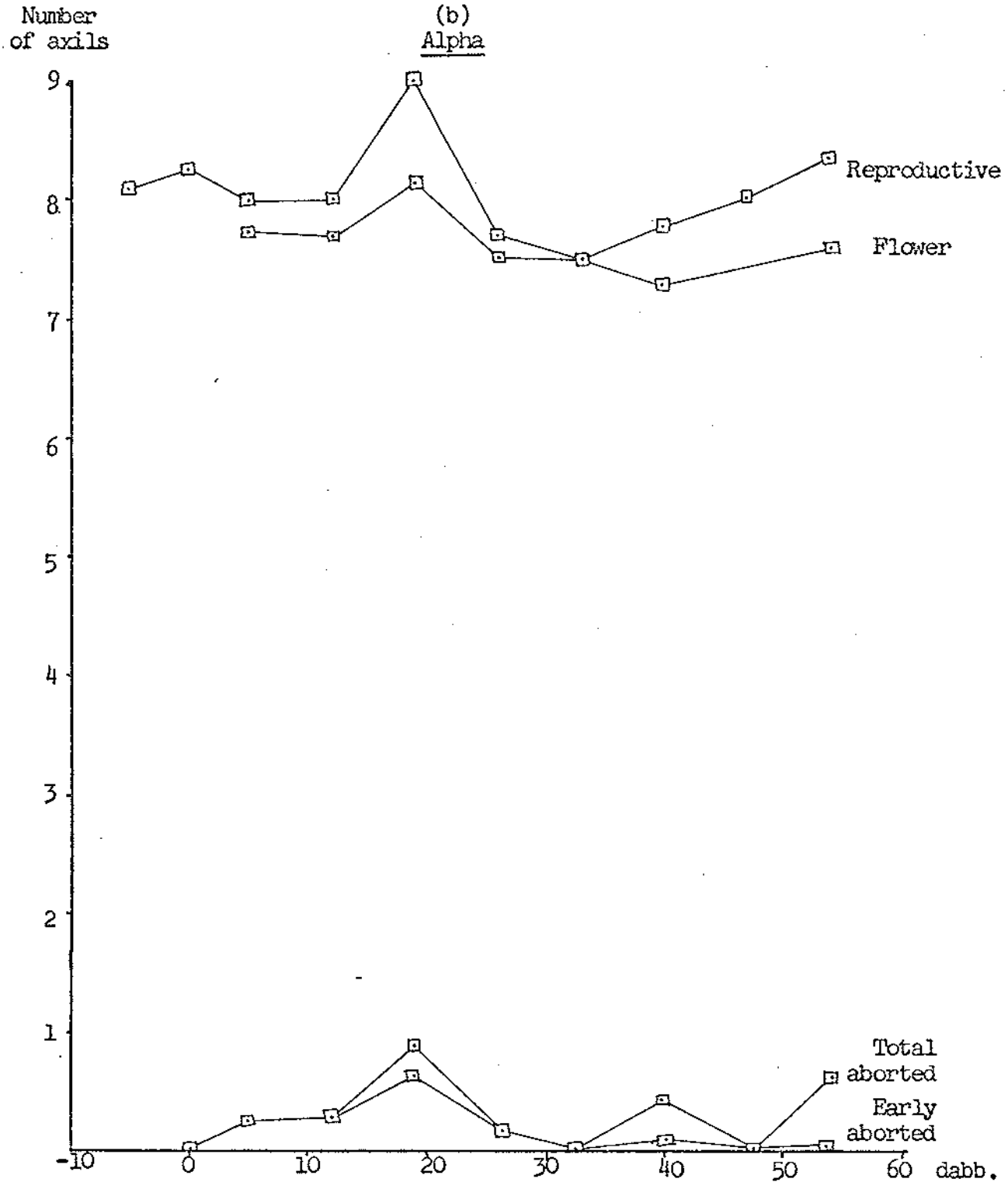


Fig.20

Flower bud growth at each reproductive axil along a shoot in Hayward.

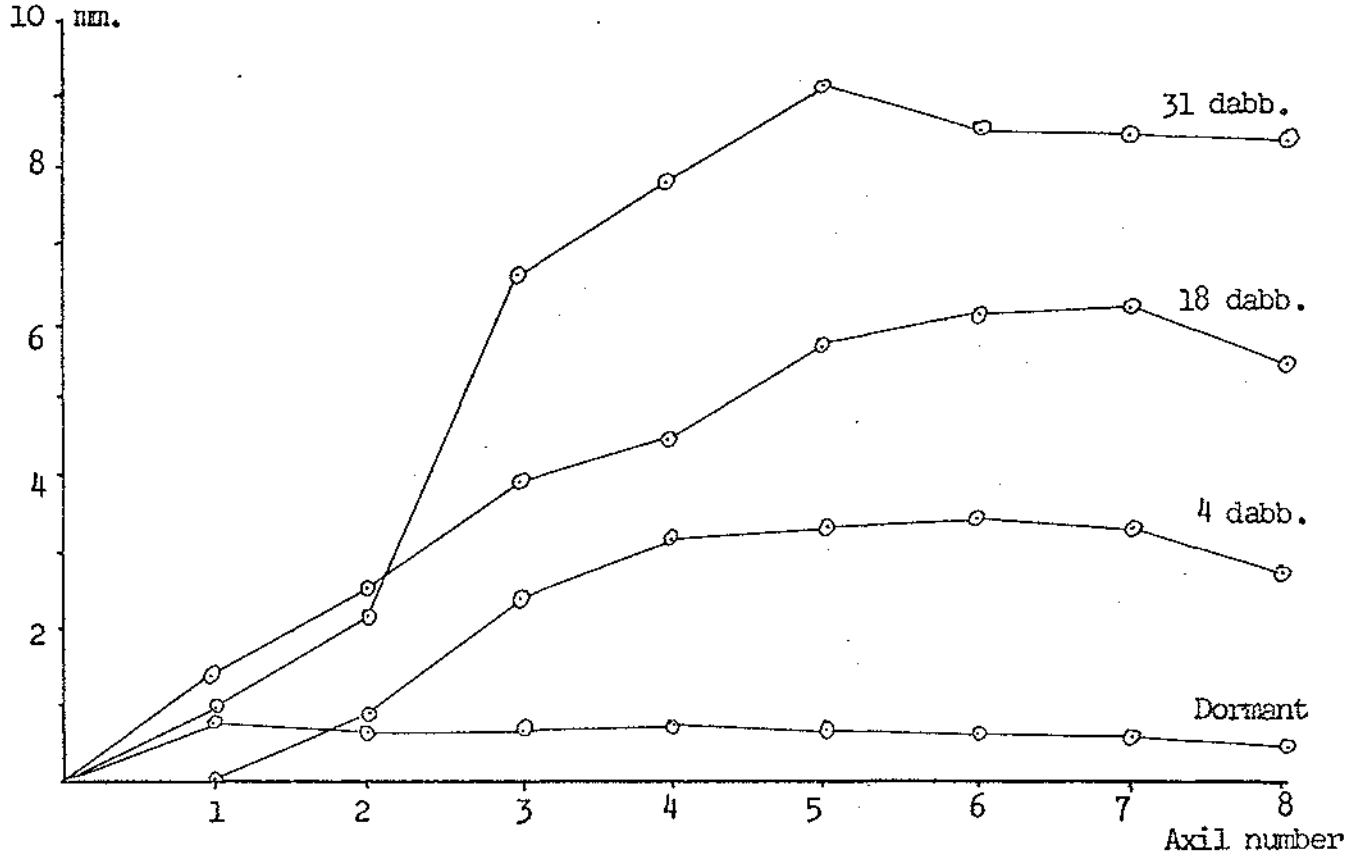
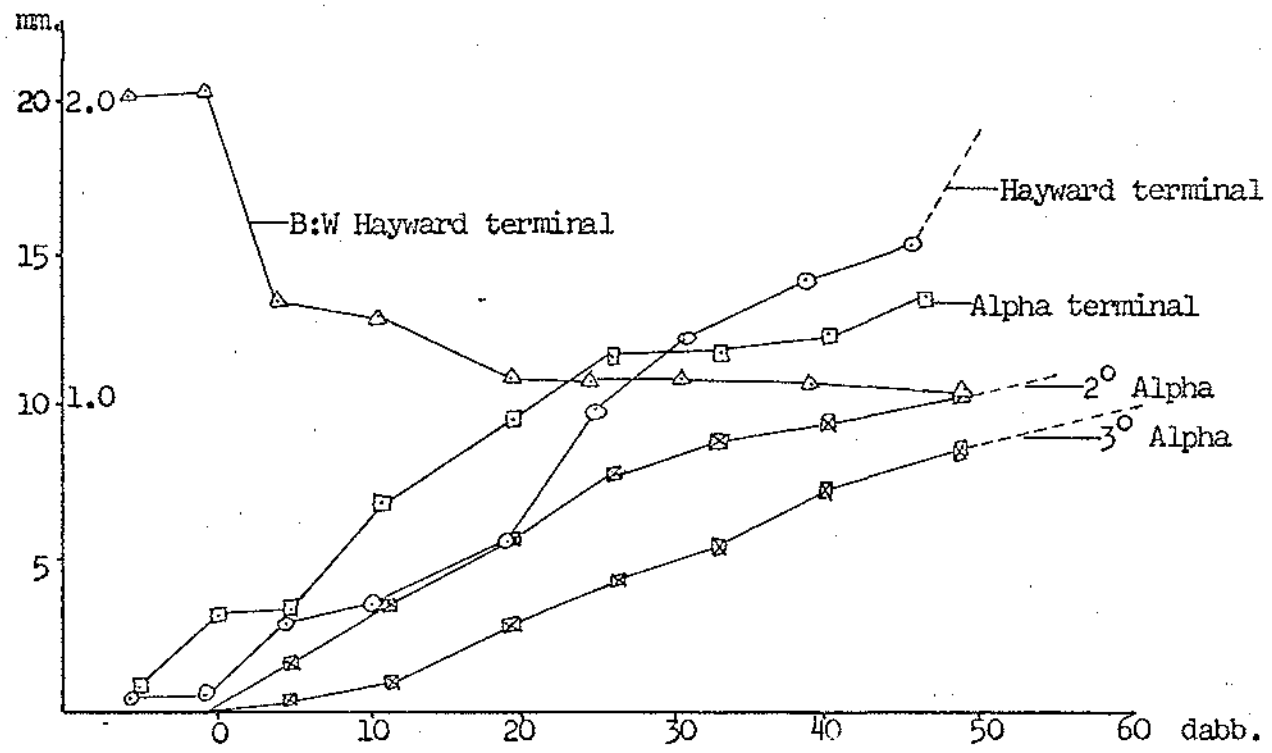


Fig.21

Flower bud growth per shoot in Hayward and Alpha terminal flower buds, Alpha 2^{o} and 3^{o} lateral flower buds, and the change in the Hayward terminal flower bud breadth : width ratio with growth.



the order of flower opening (flower axil numbered from the base of the shoot) was:

Hayward	4 - 1 - 2 - 3
Alpha	7-6-5-2-1-4-3

Also noted were variations in the numbers of individual flower components. These were generally related to the shape of the flower bud. While such data were not reported for Alpha, in Hayward, flower buds at the base of a shoot tended to be more oval than those further up the shoot.

The number of sepals and petals in normal flowers were generally slightly greater at the base and numbers observed varied from 5 - 7 (see Stage VI, Fig.12). The breadth:width ratio of the ovary in the buds decreased up the shoot giving changes in ovary shape similar to trends seen with flower buds. Where fasciated flowers (Fig.13a) were present however, the bud and ovary was markedly oval with breadth:width ratios of over 2:1 and noticeably more sepals and petals (up to 14) were present.

(c) Flower bud growth patterns

(i) Flower bud growth

Bud breadth was used as an index of flower bud growth. For Hayward the mean flower bud breadth per shoot increased from 0.4 mm., in its uninitiated state in the winter bud to approximately 15.2 mm., at the stage when the calyx split to reveal the petals (52 dabb., Fig.20). Over that period also the breadth:width ratio for Hayward decreased from 2.1:1 to 1.1:1 (Fig.21). For Alpha, the mean terminal bud breadth per shoot increased from 0.4 mm., (uninitiated) to 13.5 mm. (47 dabb., Fig.21).

Secondary lateral buds in Hayward generally made only limited growth and development (see earlier) and reached a maximum breadth of less than 5 mm., before aborting. In Alpha however, secondary and tertiary lateral buds increased in diameter from their initiation, to 10.2 mm., and 8.5 mm., respectively when the terminal bud reached the split calyx stage. (Fig.21). To the same stage of calyx split, it was estimated that bud breadth for the secondary and tertiary lateral flower buds would be 11.0 and 9.8 mm., respectively (Fig.21).

The average size of the flower bud to the external bud development stage and the flower bud stage is represented graphically in Figure 22. By advanced open-cluster (Fig.3) and flower bud stage 8 (Fig.11), 15 dabb., mean flower bud breadth was 4.6 mm., and the breadth:width ratio was 1.18:1 (Fig.22). The changing bud shape is clearly demonstrated.

Fig.22

Early (up to 15 dabb.) flower bud growth and the change in the flower bud breadth:width ratio in Hayward as related to the external shoot bud stage and to the flower bud development stage.

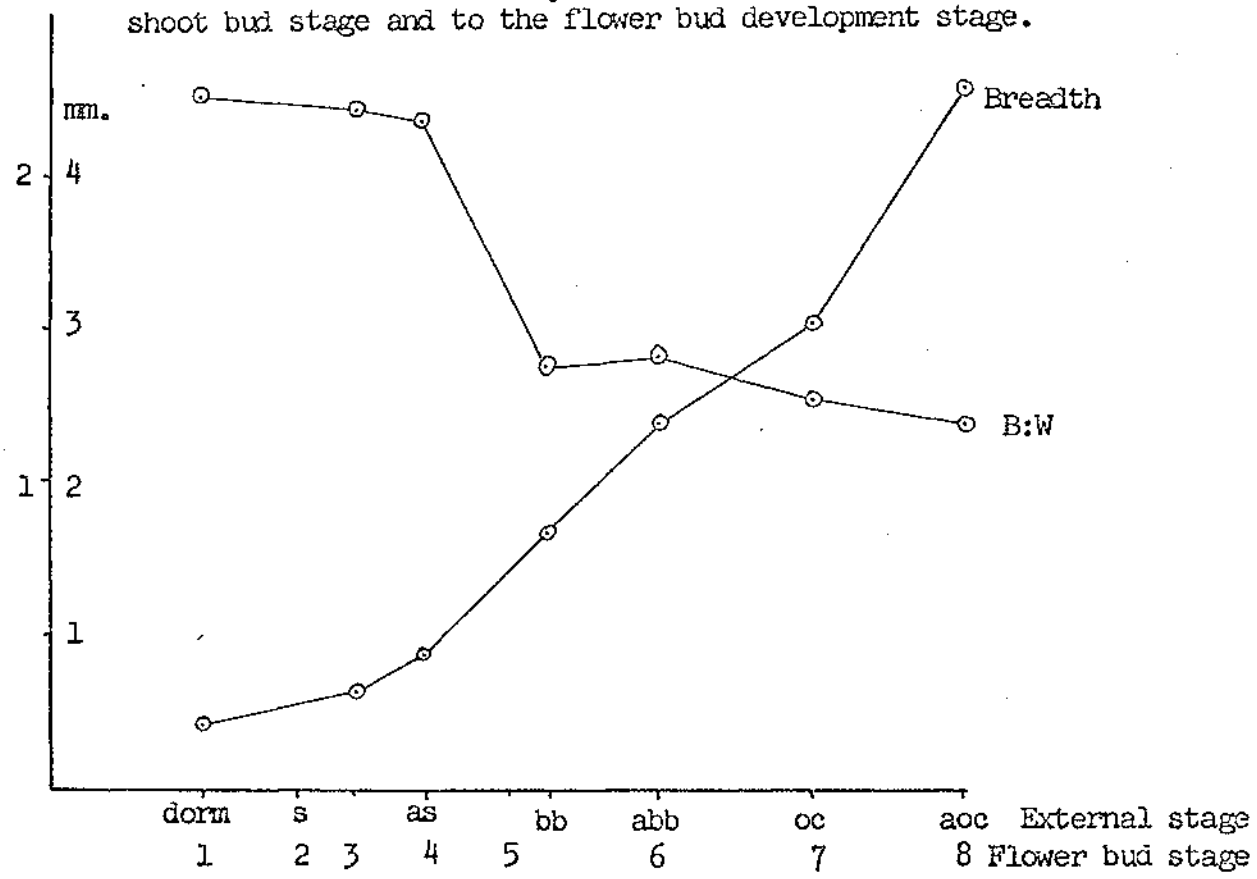
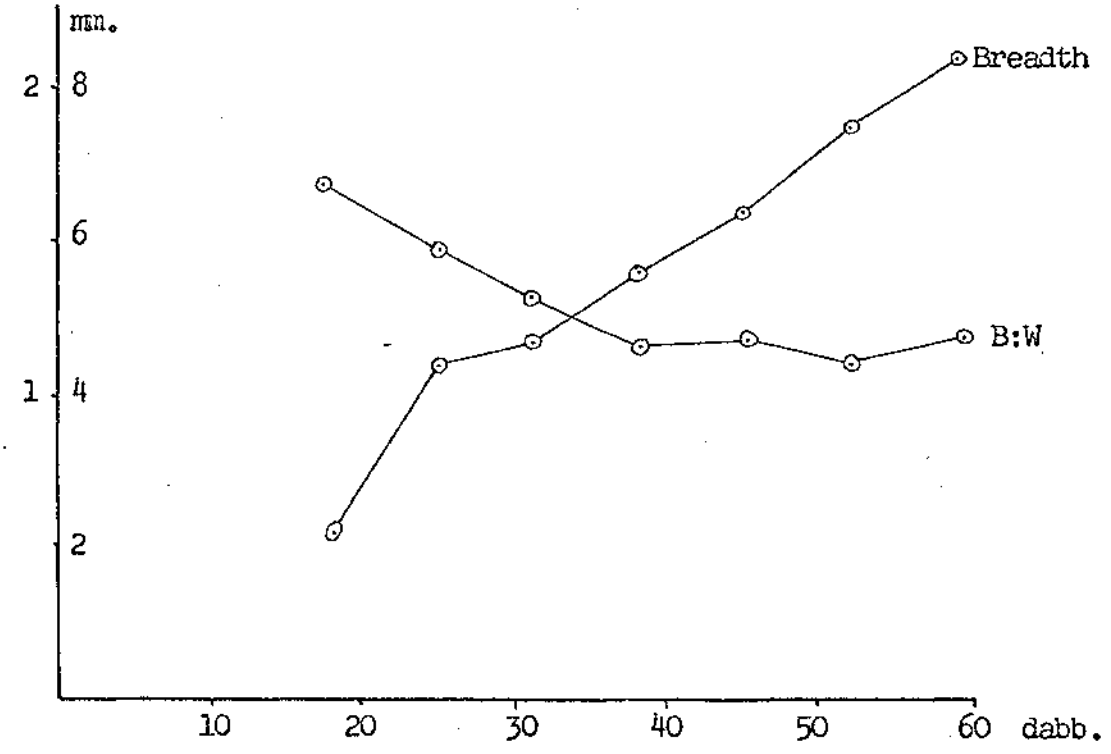


Fig.23

Ovary growth per shoot and the change in the mean ovary breadth:width ratio per shoot in Hayward.



(ii) Ovary Growth

The ovary was first formed in Hayward approximately 20 days after bud burst. The mean cross section dimensions increased from 2.1 x 1.3 mm., at that date to 8.3 x 7.0 mm., at bloom (Fig.23). Over that period, the breadth:width ratio decreased from 1.6 to 1.2, indicating a change in shape as with the complete bud.

(iii) Growth of flower parts over later stages of development

The rate of growth of the various flower components in Hayward are correlated with the external stages of late flower development (Table 3). From the time the calyx split, bud breadth increased from 14.9 mm., to 26.5 mm., just prior to opening, and to a diameter of 67 mm., at full bloom.

Over that period the ovary increased in breadth only from 7.09 mm., to 8.15 mm. The stigmal diameter increased rapidly from 4.78 mm., at late flower development (Stage II) to 10.83 mm., at bloom (Stage VI). While the mean anther size increased steadily over this period, the filament length increased rapidly, especially over the 2 days prior to bloom (Table 3). These comparisons emphasize the rapid development of the flower parts in the 10 days preceding blossoming.

(iv) Quantitative differences between terminal and lateral blooms

Terminal and lateral flower buds differed in size (Fig.21). One of the factors showing this difference in size was the significantly fewer petals in lateral flowers than in terminal flowers (Table 4). The mean number of petals in Alpha terminal flowers and lateral flowers respectively was 7.8 and 5.8.

IV PHYLLOTAXIS

(a) Description of the phyllotaxy

In the Chinese gooseberry, leaves and leaf primorida are arranged in a spiral on the stem (Fig.24). Various systems of spiral phyllotaxis are recognised (309). An earlier method, based on the divergence angle between the leaves, expressed the phyllotaxis as a fraction of a circle. If two exactly superimposed leaves were separated by b internodes and there existed a turns of the genetic spiral between them, then the

Table 3

The growth of the flower parts of Hayward over the ten days preceding bloom.

Stage (a)	Days to bloom	Flower (mm.)				Pistil (mm.)				Stamen (mm)		
		Bud			Stalk	Ovary			Stigma	Anther		Filament
		bth.	wth.	b:w	lth.	bth.	wth.	b:w	diam.	lth.	bth.	lth.
I	10	14.9	14.2	1.1	4.4	7.1	6.5	1.1	4.7	2.8	1.2	3.4
II	8	15.2	14.5	1.1	4.7	7.1	6.5	1.1	4.8	3.4	1.2	4.0
III	5	18.8	18.3	1.0	6.2	7.4	6.9	1.1	7.5	3.8	1.3	5.2
IV	2	26.5	24.2	1.1	5.6	7.5	7.0	1.1	9.7	4.3	1.3	6.5
V	0.5	59.3	56.8	1.0	5.8	7.5	6.9	1.1	10.3	4.1	1.4	10.3
VI	0	67.9	65.3	1.0	6.5	8.2	7.3	1.1	10.9	4.1	1.4	11.3

(a) See Fig.12

Table 4

The relationship between the number of petals in terminal flowers and lateral flowers at each flowering axil along a shoot in Alpha*

	Terminal flowering axil								
Shoots	1	2	3	4	5	6	7	8	Mean number per shoot
a.	8	9	6	10	7	8	8		7.7
b.	8	8	7	10	8	6	8		7.8
c.	10	8	8	10	7	6	9	8	8.2
d.	7	8	8	12	10	6			8.5
e.	6	6	11	8	8				7.8
f.	10	6	7	6	10	6	9	7	7.6
g.	7	7	8	7	7	6	7		7.0
Mean no. per axil	8.0	7.4	7.8	9.0	8.1	6.3	8.2	7.5	7.8

	Lateral flowering axil								
Shoots	1	2	3	4	5	6	7	8	Mean number per shoot
a.	6	6	6	6	5	5			5.7
b.	6	6	5						5.7
c.	5	7	5	5	5	6	6	5	5.5
d.	6	6	6						6.0
e.	5	5	5						5.0
f.	5	6	6	5	5				5.4
g.	5	5	5						5.0
Mean no. per axil	5.5	5.9	5.4	5.3	5.0	5.5	6.0	5.0	5.5

* Analysis by the Sign Test

Petal number in terminal flowers significantly greater (5%) than in lateral flowers,

where n = 7 (number of pairs of observations.)

r = 0 (number of pairs where lateral mean is greater than terminal mean.)

Fig.2b

Distribution of the phyllotaxis spiral
of the dissected winter bud of Hayward.
(2b)

Clockwise helices (Solid lines)
1,3,5,7,9,11,13.
2,4,6,8,10,12,14.

Anticlockwise helices (Dotted line)
1,4,7,10,13.
2,5,8,11,14.
3,6,9,12,15.

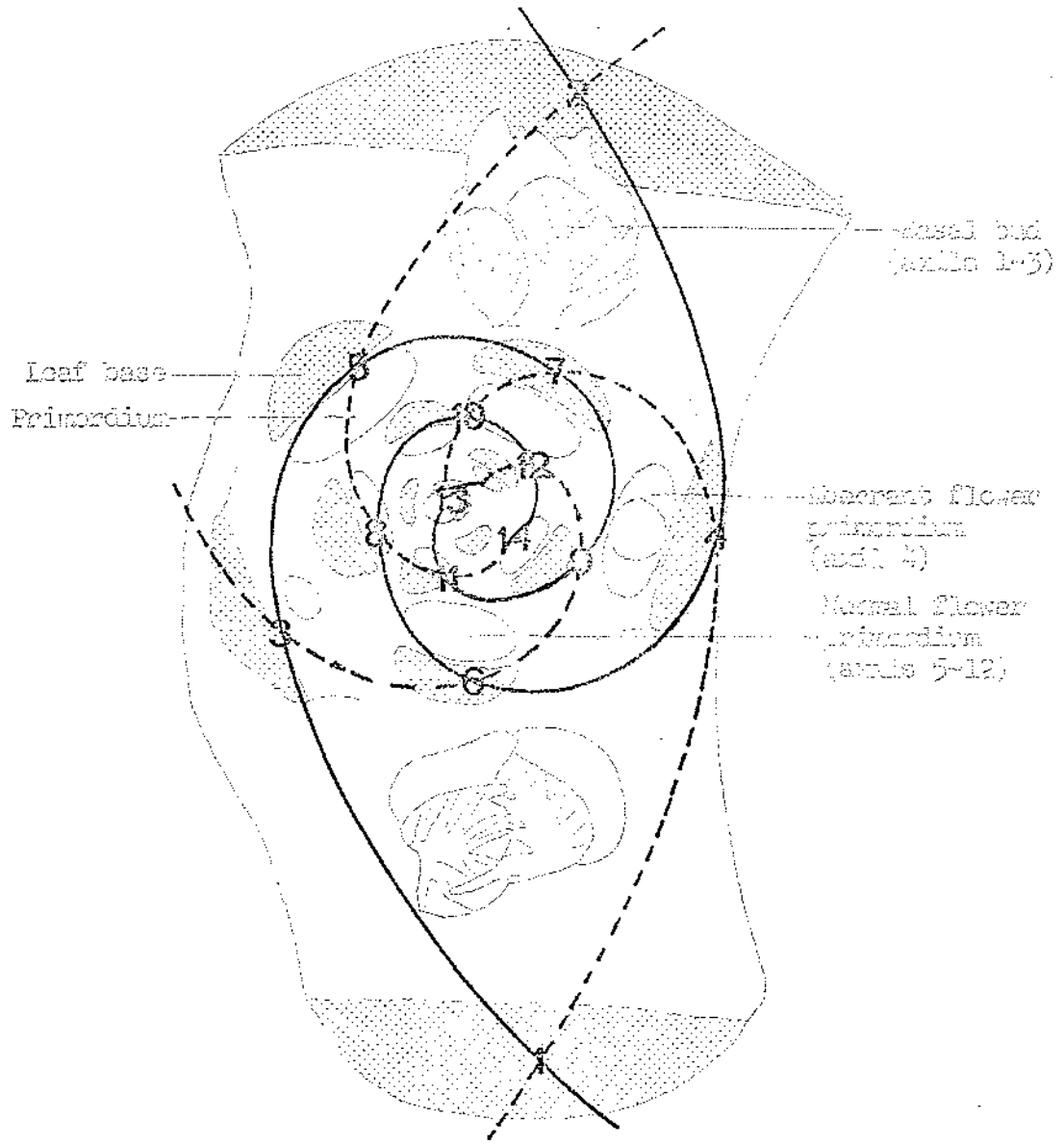
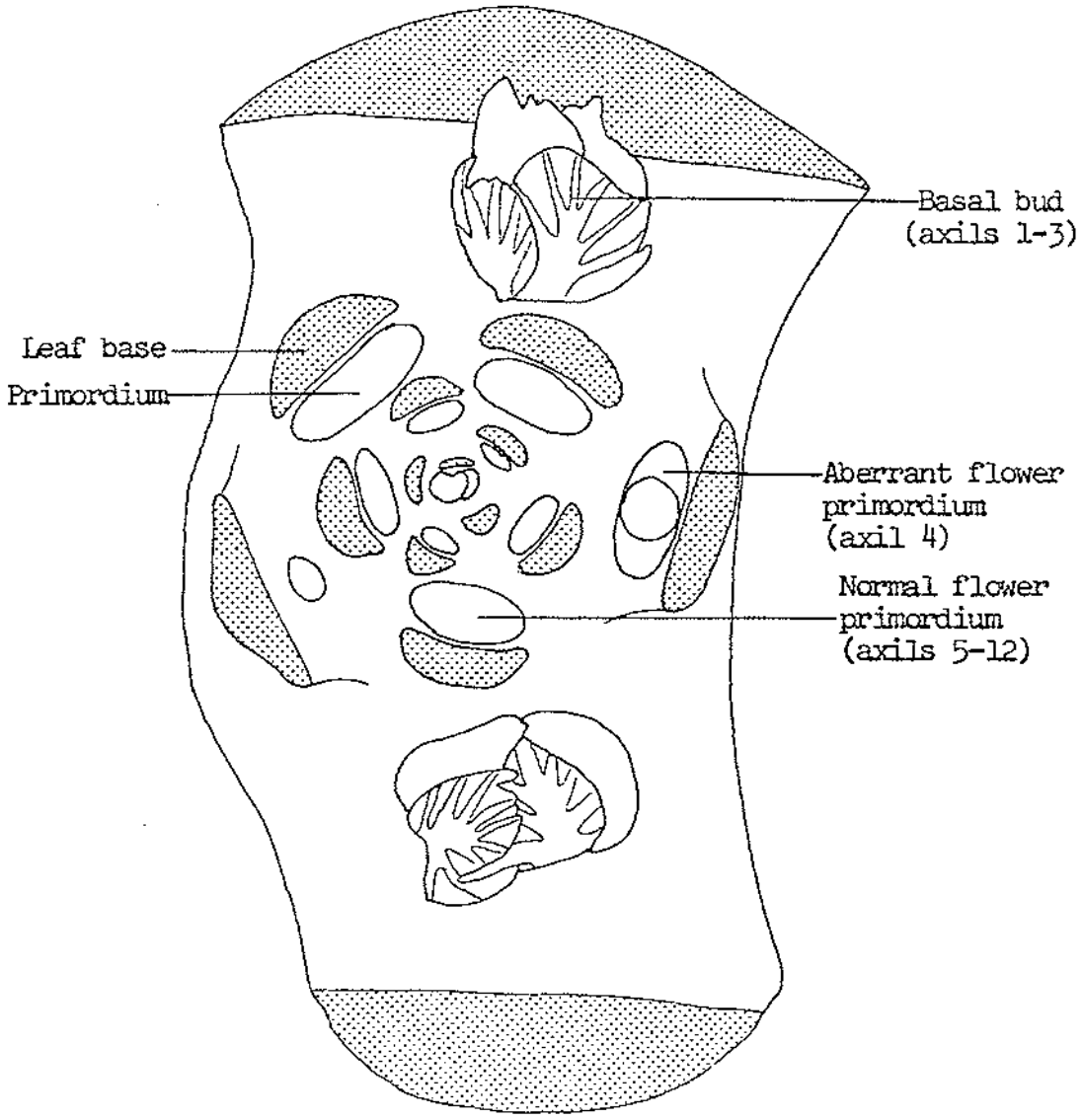


Fig.24

Characterisation of the phyllotactic spiral
of the dissected winter bud of Hayward.

(2+3)

Clockwise helices (Solid lines)	Anticlockwise helices (Dotted line)
1,3,5,7,9,11,13.	1,4,7,10,13.
2,4,6,8,10,12,14.	2,5,8,11,14.
	3,6,9,12,15.



divergence was represented by *a/b*. For the Chinese gooseberry, this is 2/5 as leaf 6 superimposes leaf 1 after two turns of the spiral (Fig.24). This description is now less favoured since leaves are rarely superimposed on the stem.

The other common method of characterising a phyllotaxis is by reference to the sets of parastichies (helices) that may be recognised when the shoot is viewed from the top. By counting the number of these parastichies in each direction, the phyllotaxis can be described. For Chinese gooseberry this is 2 + 3 (Fig.24).

Two anomolies in the phyllotactic spiral of Chinese gooseberry were observed. In a number of cases (less than 5%) the ascending order of progressively younger leaves was slightly altered: A younger and therefore later initiated leaf was sometimes observed to be lower on the shoot than the leaf formed immediately before. (See both determinate and non-determinate Hayward shoots, Fig.6.) The other, much less frequent (less than 1%) anomoly observed, was the changing of the direction of the phyllotactic spiral.

(b) Direction of the phyllotactic helix

Wardlaw (309), in his review on the organisation of the shoot apex, stated that in plants a spiral phyllotaxis, the direction of the genetic spiral in the primary shoot, is usually considered to be randomly determined and for many plant species it occurs in a 1:1 ratio. The direction of the spiral in lateral shoots may be independent of the main shoot and also randomly distributed. However, in many species a negative correlation exists between the direction of the spirals of the lateral shoots and that of the main axis (antidomy). The opposite case (homodromy) occurs, but is much less frequent.

From the examination of buds and shoots of both Hayward and Alpha, it was found that the direction of the phyllotactic helix could be either 'clockwise' or 'counter-clockwise' (interpreted as the ascending directions of the foliar helix observed from above).

The aim of this study was to examine the frequency of the direction of the genetic spiral of the bud (or shoot) and to relate it to the direction of the spiral of the lateral. These relationships were examined on separate vines. Relevant data were obtained from the buds and shoots used in the flower development study of Hayward. Analysis of the results of buds (or shoots), showed that there was a significant association between the direction of the spiral on the lateral and that of the bud (or shoot) (Table 5). The spiral direction was not found to be a specific

Table 5

The relationship between the direction of the phyllotactic spiral of the bud (or shoot) and that of the lateral in Hayward.

	Clockwise lateral	Anticlockwise lateral	Total
All clockwise buds	10 (6.3)*	2 (5.7)	12
Some clockwise, some anticlockwise buds	8 (7.3)	6 (6.7)	14
All anticlockwise buds	4 (8.3)	12 (7.6)	16
Total	22	20	42

* Number of buds (or shoots) observed. In brackets, numbers expected if occurrence of clockwise or anticlockwise helices was random. (Laterals with only one bud (or shoot) excluded.)

Goodness of fit $\chi^2_2 = 9.7$ (P less than 1%).

Table 6

The relationship between the direction of the phyllotactic spiral of the bud (or shoot) and of the lateral, and that of the vine in Hayward.

	Vines with all laterals in same direction (excluding those with only one lateral)	Vines with only one lateral and some vines with some laterals in opposite directions from others	Total
All buds in same direction as parent lateral	11 (12.6)*	11 (9.4)	22
Some buds one direction, some buds in other direction	10 (8.0)	4 (6.0)	14
All buds in opposite direction to parent lateral	3 (3.4)	3 (2.6)	6
Total	24	18	42

* Number of buds (or shoots) observed. In brackets, numbers expected if there was no significant association. (Laterals with only one bud (or shoot)excluded.)

Goodness of fit $\chi^2_2 = 1.8$ (P greater than 20%).

property of individual vines, the various types being found on each vine. Further, the strength of the bias towards one spiral direction was not found to be a specific property of individual vines (Table 6).

C. DISCUSSION

Little has been reported previously on different aspects of flowering and associated vegetative growth in the Chinese gooseberry. It is of interest to relate the characteristics found in this study on the Chinese gooseberry to those in other crops having similar fruiting and growth habits.

The grape is a crop which has been widely studied and is, in many respects, similar to the Chinese gooseberry. Both are deciduous vines which carry their crop on one year old wood in the axils of leaves at the base of a shoot. In view of a report on flower development in *A. kolomikta* (171), it was inferred at the commencement of this study that, as with grapes and most deciduous fruit crops, it should be possible to observe developing flowers in the Chinese gooseberry bud during the season previous to flowering. However from this study of *A. chinensis* over the 1971/72 growing season, it is apparent that there were a number of features in the flowering habit of this species that are peculiar to the Chinese goosebery.

Bud Growth

As with grapes, leaf primordia were initiated in the next years' fruiting bud soon after bud burst although the rate and the final number formed by winter was greater in Chinese gooseberry. In grapes, the number of leaf primordia initiated increases to reach a maximum of 10 - 15 depending on the cultivar by approximately 100 dabb. (51,202). In Chinese gooseberry, approximately 18 leaf primordia had been initiated by that time (Fig.1).

A number of workers on different crops have reported changes in the rates of leaf primordia initiation in fruiting buds and have related such changes to the inception of flowers (51,99,202). In a number of grape cultivars, a lag in both the increase in fresh weight of leaf primordia (51,202), as well as in the rate of initiation (51) around the 50 - 75 dabb., period have been related to the timing of inflorescence initiation. In the Gordo cultivar, 6 leaf primordia were initiated at that time, and the first bunch primordium start forming at the same time as the fifth or

sixth leaf on the bud axis (51).

In a series of papers on the apple, Fulford (97,98,99), also showed that the timing of flower determination was related quite precisely to the pattern of terminal bud development. However, this pattern was different from that in grapes. Instead of flower initiation being associated with a lag in leaf primordia development (ie., a long plastochrone), Fulford (99) showed in apples that, as well as depending on the presence of bracts, this phenomenon was dependent on a short plastochrone (5 - 7 days).

Unlike the situation in grapes and apples no marked changes in the rates of leaf primordia production were found in Chinese gooseberries. There may have been a short lag in the Hayward variety at 60 dabb., but this could possibly have been associated with ovary growth as this lag occurred around the bloom period but was not found in the staminate clone Alpha (Fig.1). Although no samples were taken between bloom and mid January, it was deduced, from the slope of the curve prior to bloom and from the number of leaf primordia in the bud by mid January, that the rate of production of leaf primordia continued until the maximum was reached (estimated to be around the end of December). This is comparable to the situation in grapes (51,202).

The structure of the resting (winter) bud varies between fruit tree crops and depends upon the position of the bud on the shoot and on the position of flowers within the bud.

As in citrus (172) and grapes (329), terminal buds never form in the Chinese gooseberry (Fig.16), the growing apical bud of the shoot, and sometimes the terminal portion of the shoot itself, desiccates and abscisses at various times during the season (Figs.16a and 16b). The axillary buds of the Chinese gooseberry are less prominent than in many other crops as they are enclosed in the swollen base of the petiole (Fig.3). Both the Chinese gooseberry and the grape possess basal (lateral) buds. The Chinese gooseberry may possess up to 5 basal buds (Table 1) but usually only the outer 2 develop leaf primordia by winter (Fig.24). These do not usually develop into shoots unless the primary growing point is damaged (Fig.15). Under commercial growing conditions these buds usually remain dormant for approximately 3 - 4 years when they can be stimulated into growth (maiden laterals) in the renewal system of pruning, by the removal of the primary lateral system at or near its base (92).

Vegetative Growth

As in the grape (329), but unlike most deciduous fruit trees bud burst in the Chinese gooseberry is late. The first signs of bud movement was in early September, and general bud burst did not take place until the end of that month. In some cultivars, especially Hayward, but burst was extremely poor (see Ch.6) and uneven. The reason for the uneveness in bud burst could, in part, be due to climatic factors as the winter prior to 1971 was milder than average, possibly indicating some chilling requirement. As well it was observed that buds at nodes on the undersides of a lateral did not burst.

Following a lag of approximately 10 dabb., leaf production and extension growth proceeded rapidly (Figs.4 and 10). Figures for these parameters were extremely variable. This was largely due to two factors. Firstly, the data were obtained from different plants at each date (as material was destructively sampled). Secondly, a variable number of the tagged shoots had terminated their growth by each sample date. An attempt was made to minimise the variation by separating those shoots which had terminated their growth from those that had not (Fig.4) although there was no indication initially of shoots either ceasing growth or continuing.

The shoot length varied widely in Chinese gooseberries. Although no terminal bud was produced, some shoots had ceased extension growth by 40 dabb., making only 10 cm. of growth (Figs.4 and 6), while others continued growth throughout the season. Shoots of approximately 10 meters in length have been reported on vigorous clones where growth has not been checked. The reason for the variation in shoot length is not known as both types of shoots result from apparently similar shoots tagged at bud burst. Generally, Hayward is a less vigorous cultivar with fewer non-determinate shoots. Lateral shoots in that cultivar generally cease growth by mid December, 80 dabb. (71).

Like many species, the Chinese gooseberry displays heteroblastic leaf development along a shoot (Figs.2 and 7). This development was apparent in the winter bud (Fig.2), but became more obvious after shoot growth had commenced (Fig.7).

Although there were differences in heteroblastic development between Alpha and Hayward (eg., there were fewer bud scales and transition leaves in Alpha), general patterns were similar. In both Alpha and Hayward, the size of each leaf and length of each internode depended upon the position of the leaf in the bud or shoot and upon the position of the bud or the lateral, a situation comparable with other plants (15).

The number of basal buds in both Hayward and Alpha depended on the position of the bud along a lateral. Buds closer to the base of a lateral contained a greater number of axils possessing basal buds (Table 1). Alpha had fewer basal bud axils than Hayward and this was apparently associated with the number of scales and transition leaves.

Reproductive growth

It is well known that in most deciduous fruit tree and vines species flowers or inflorescences are initiated in the summer preceding their flowering and fruiting (30). On the other hand, in evergreen temperate and sub-tropical fruit trees, flower initiation takes place only a few weeks before bloom and is often associated with resumption of growth (103, 135,256).

In *A. kolomikta*, it has been reported, that (171) by the end of summer lateral cones of flowers with undifferentiated floral embryo are present in the completely formed floral bud.

In *A. chinensis* however, the present study has shown that, although axillary primordia were present in the potentially reproductive region of the winter bud, they remained uninitiated (Fig.24). It was not until just before growth was resumed in the late spring that discernable changes in those primordia were noted.

The timing of flower initiation in the Chinese gooseberry appears to be atypical of most deciduous plants where almost fully formed inflorescences and flowers are present in the bud by winter (171). The pattern found in the Chinese gooseberry however can be partially compared with that in the grape where, although the inflorescence (which consists of the main body of the cluster and bracts with branches and sub-branches in their axils) is initiated during the previous summer, individual flowers, on already formed clusters are not initiated until the spring (247). A similar situation to that in the grape is also reported for *A. kolomikta* (171). The timing and pattern of flower initiation in the Chinese gooseberry seems most closely related to that found in evergreen temperate and subtropical fruit trees (103,135,256).

Once the flower primordia were initiated in the spring, flower development was extremely rapid and continuous and, within 30 days of initiation, the ovary was being formed. The sequence of initiation of the flower parts was generally similar to most other species. Within a given flower, the sepals were the first to develop, followed by the petals, stamens, and lastly, the pistil with its multi-locular ovary.

Up to the time of stigma initiation, the pattern of flower development was similar for both the pistillate Hayward and the staminate Alpha. Instead of the gynoecium continuing to develop, as in Hayward, the staminate gynoecium developed little and remained vestigial.

Early stages of androecial development in Hayward (and other pistillate cultivars) seemed to be normal; the stamens developed into anthers and filaments similar to staminate flowers. However in Hayward (and other pistillate cultivars) the pollen grains which form in the anthers remain sterile (272).

Thus, in the Chinese gooseberry the pattern of sex-expression follows the more normal angiosperm pattern where the flower begins as a potentially hermaphrodite primordium; functional unisexuality then results from unbalanced growth, with only the androecium or the gynoecium completing development (15). The cause of unisexuality in plants is not fully understood. Although it is thought likely to be hormonal, studies on a wide range of woody plants indicate that the hormonal status controlling sexuality is species specific (157).

At various stages of flower development, it was found that buds at some axils ceased further development, and in some cases abscissed (Fig.19). The frequency of aborted (or aberrant) axils was comparatively high in Hayward compared with Alpha (Fig.19).

Most of the flower buds (primordia) destined to abort ceased development soon after bud burst, when sepals were being initiated in normal flowers. These early abortions mostly occurred in the lower axils of the shoot immediately above the last axil containing a basal bud. Further, it was possible to deduce, from the shape of the primordium at initiation, which would shortly cease development (Fig.13a top line). For those flower buds which aborted at later stages, it was not possible to predict their fate as numbers were not great (especially in Alpha), their position on the shoot was not apparent, and development seemed normal up to their cessation of growth.

The cause of this aberrant flower development is not fully understood although it also occurs, to a greater or lesser degree, in many angiosperms (including fruit trees and vines) and gynosperms (99,156,202). Evidence from the position of aberrant axils on the shoot did not allow any deductions, as to the internal factors which were responsible for such development. However, it was deduced that, sometimes structures in those axils which abort early could develop and form flowers. Those flowers were usually fasciated (Fig.13b) and were likely to result when the development of the terminal flower primordium in those axils was only slightly checked

with the laterals continuing development. It is known that the frequency of such fasciated flowers varies between seasons, possibly indicating some environmental influence.

Other experimental results quoted elsewhere (Ch.4 and 5), however indicated that the quantity and/or the quality of the factors forming flowers could be altered by specific treatments (as measured by the number of normal flower buds). The fact that staminate vines are more fruitful than pistillate vines could also possibly indicate variations in the quantity and/or quality of flowering stimulii between clones.

In Hayward, while lateral buds were initiated, virtually all of them ceased development soon after their petals were initiated. In the staminate Alpha, secondary and tertiary lateral flower buds were initiated, and a large proportion of them developed to bloom. As some staminate vines had up to 9 flowers in an inflorescence (Ch.6), it was concluded that the inflorescence in the Chinese gooseberry vines was potentially a compound dichasium (Fig.17).

Lateral flowers, although initiated after the terminal flower, developed at a faster rate, and bloomed approximately 3 days after the terminal flower. As well, lateral flower buds were always smaller (Fig.21) and contained fewer petals (Table 4).

In the Chinese gooseberry the reproductive region of a shoot occupied approximately 7 axils in Hayward and 8 axils in Alpha (Fig.19), and was not influenced by the distance from the base of the lateral (Table 2). In the grape however, there are usually only 1 - 3 reproductive axils (33,329) and further, not all buds are fruitful (29). Barnard (29) showed in the Sultana cultivar, that the proportion of buds that were fruitful were low towards the base of the lateral (cane), and increased progressively outwards, and again decreased towards the distal end in all but very short canes.

Phyllotaxis

Wardlaw (309) states that the commonest form of phyllotaxis is the spiral form. Chinese gooseberry possess this form and can specifically be defined as 2/5, or (2 + 3) spiral. As in many plant species with a spiral phyllotaxis, the spiral in Chinese gooseberry may either be clockwise or counter-clockwise. However, unlike most species with a spiral, there was a positive correlation between the spiral on a Chinese gooseberry shoot (or bud) and that of the lateral (homodromy) (Table 5). The more usual cases are a negative correlation (antidromy), or an independent association (309).

The reason for the two observed anomolies in the phyllotactic spiral of Chinese gooseberry are not known although these occurred in the regions of the shoot where there was a change in either the vegetative or the reproductive state. Where a younger and therefore later initiated leaf was lower on the shoot than the leaf formed immediately before, this only occurred at the uppermost flowering axil (see both determinate and non-determinate Hayward shoots, Fig.6). Where the phyllotactic spiral changed direction, it did so around axil 5, around the region that the shoot changed from the vegetative to the reproductive state. Changes in the phyllotactic patterns along a shoot occur repeatedly in other plants although the reasons for this phenomenon are not understood (309).

Chapter 4

THE EFFECT OF DEFOLIATION, SHADING, AND TIPPING ON FLOWER DEVELOPMENT AND CONCURRENT VEGETATIVE GROWTH

A. INTRODUCTION

A major factor governing yield in fruit trees and vines is that of determining the partition of metabolites between the various reproductive and vegetative growth centres (127,131). Over the early period of spring growth the competition between the various growth centres for available metabolites is particularly intense and how successfully a growth centre can compete for limited supplies depends upon their relative activity or sink capacity (127,131,176,250).

Autoradiographic and other studies have shown that the initial shoot growth is dependent upon photosynthate mobilised from reserves within the parent plant or vine (46,224,250,310,331). In the grape, Hale and Weaver (127) have shown that as soon as a leaf commences exporting metabolites, movement is acropetal to the young leaves and shoot apex which constitute powerful sinks, but with continuing growth of the shoot and the production of new leaves, metabolite movement becomes bidirectional at first and then basipetal. This basipetal movement occurs during the prebloom period. However, during the prebloom and bloom period, a normal grape shoot appears to be independent of others for supply of photosynthates (254).

The actual cause of the metabolite movement is not completely understood, but it is known that growth substances play a vital role as powerful mobilising agents (254), and they are synthesised (to a greater or lesser extent) in the various growth centres within the plant (87,115,254).

By eliminating or reducing the effectiveness of the various sinks and sources within the plant using such manipulations as defoliation, girdling, shading, tipping, deblossoming, and the use of growth substances, the partition of metabolites within the plant can be altered (67,224,252,254). Such manipulations may be carried out on whole trees and vines, as well as on cutting material (see Ch.1).

While the main Chinese gooseberry cultivar Hayward produces large fruit, it does not numerically bear heavily. Hayward typically has fewer axils bearing flowers and fewer flowers at each axil than other cultivars

(Ch.6).

To gain information on some of the factors affecting the development of flowers in the Chinese gooseberry, a number of defoliation, shading, and tipping treatments were applied to shoots growing from isolated single node cuttings as well as to individual shoots on field grown vines.

A number of statistical tests were applied to the collected data. Because of the limited capacity to make the many observations recorded, the data accumulated in the study of the normal sequence of development (Ch.3) was used as control figures for this series of experimental manipulations. This data was utilised by fitting a least squares regression line to the records (collected at 5 - 7 day intervals up to bloom) used for the Hayward flower development studies (Ch.3). The regression equation for each parameter, along with an estimation of its goodness of fit are set out below. The value predicted by this line at the sample date in question and the standard error of this prediction were used as the defining parameters of a normal distribution, from which values were randomly selected.

Parameter	Mean control values used for each sample date	Regression Equation	Error of Prediction as % of prediction
Number of effective flowers	see Fig.19a	Y= 5.872 - 0.027x	22
Average ovary size	see Fig.23	Y=13.819x + 21.638	12
Number of open leaves	see Fig.10	Y= 0.114x + 5.043	28
Average leaf size	Unpresented	Y= 0.191x - 0.131	19
Total number of leaves	Unpresented	Y= 0.007x + 11.604	17
Shoot length	see Fig. 4	Y= 0.591x - 2.220	65
Shoot thickness	see Fig. 5	Y= 0.067x + 3.260	16
Number of leaf primordia	see Fig. 1a	Y= 0.207x + 2.276	18

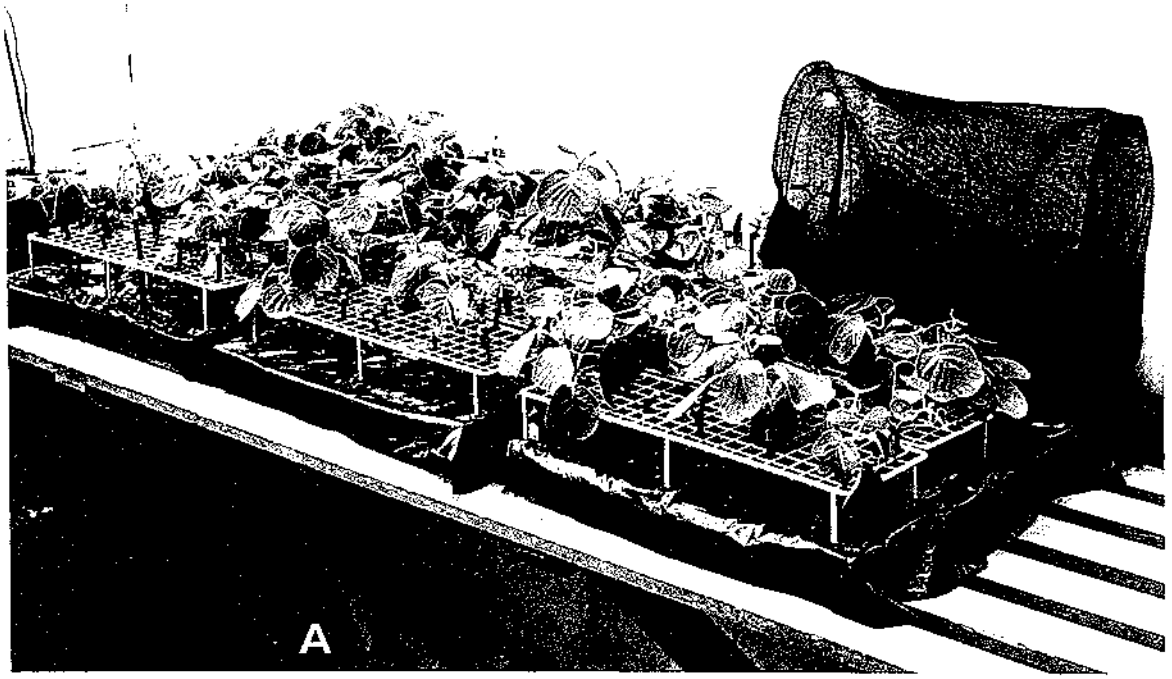
Where possible an analysis of variance, followed by Duncan's Multiple Range Test (286) was carried out on the single node cutting data as well as on the field data (using the treatment and generated control replicates). Where the data did not meet all the criteria for the analysis of variance (when for example the data were not homogeneous using Bartlett's Test (284) for homogeneity), even after the logrithmic and square root transformation, the analagous, non parametric Kruskal-Wallis Test (286), was used to test for overall statistical significance, followed by Dunnett's Test (81) to test treatments against the control.

Fig.25

Defoliation, shading and tipping treatments on Hayward single node cuttings.

Fig.26

The shading treatment (50% shade) applied to Hayward shoots in the field.


A


B

B . EXPERIMENTAL OBSERVATIONS AND RESULTS

Because of various experimental problems it was not possible to include in the results all the treatments and all the replicates originally applied to the tagged shoots. In the field, none of the buds receiving the prior to bud burst defoliation treatment grew. This seemed mainly due to sunscald and desiccation even though the treatment was carried out on an overcast day and the wound was covered with grease. A large number of the shoots (replicates) in the shading treatments (especially the heavy shade) rotted inside the bags. As well, a number of replicates in the defoliation and tipping treatments were lost due to wind and other mechanical damage.

Again, although the single node cuttings were selected for evenness prior to burst, a number of the cuttings (replicates) in most treatments either did not burst their buds or made only limited (abnormal) growth.

In all analyses, the number of replicates used are included in the tables.

The overall effects on reproductive and vegetative growth can be seen in Fig.27 (single node cuttings sampled 25 dabb.) and Fig.28 (field studies, sampled close to bloom).

I REPRODUCTIVE GROWTH

(a) Number of flowers per shoot

The total number of reproductive axils per shoot were, not unexpectedly, (see Ch.3 and 5) similar for all treatments (Table 7). The influence of the treatments on reproductive development can be seen in the number of normal flowers per shoot (or the complementary number of aborted or aberrant axils) at each sample date.

Single node cuttings

Generally, complete defoliation increased, total shading reduced, and tipping had little effect on the number of flower buds per shoot (Table 7a). Partial defoliation and partial shading treatments were generally without effect.

A significant trend was evident in the complete defoliation treatments where the earlier the commencement of the treatment the greater was the promotion. The number of flower buds per shoot was increased from 4.1 (Control) to 5.6 (commenced 10 dabb.) to 6.3 (commenced 5 dabb.) to 7.3 (commenced prior to bud burst).

Fig. 27

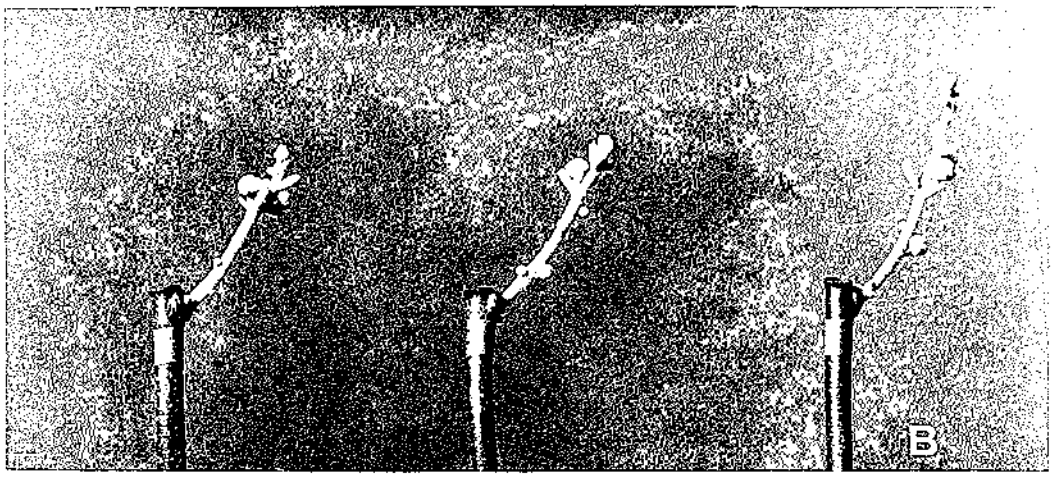
The effects of defoliation, shading and tipping on the growth and development of Hayward single node cuttings, sampled 25 dabb.

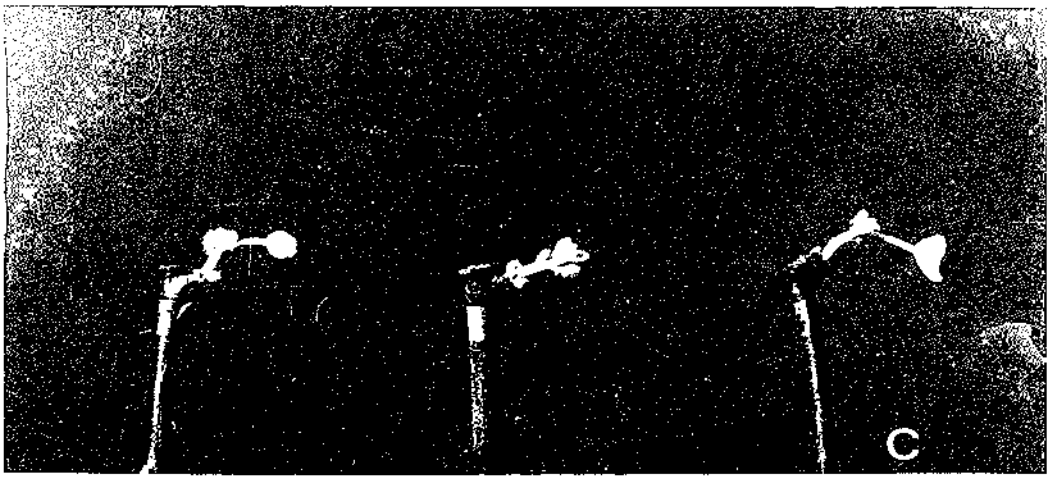
A Control

B Defoliation (100% started prior to bud burst)

C Shading (100% started prior to bud burst)

D Tipping (started 9 days after bud burst)


B


C


D

Fig. 28

The effects of defoliation, shading and tipping on the growth and development of field grown shoots of Hayward, sampled close to bloom.

A Defoliation (100% started 17 dabb.)

B Shading (100% started 1 dabb.)

C Tipping (started 19 dabb.)


A
B
C

Table 7

The effects of defoliation, shading, and tipping treatments on the number of reproductive axils per shoot, the number of flowering axils per shoot, in Hayward.

(a) Single node cuttings.

		DEFOLIATION					SHADE		TIPPING				
		50%		100%			50%	100%					
	Cont	5d.	10d.	Prior	5d.	10d.	Prior	Prior	5d.	9d.	12d.	15d.	17d.
Number of reproductive axils	7.1	7.5	7.3	8.7	7.3	7.0	7.2	7.9	7.3	7.0	8.0	7.3	7.9
Number of aberrant axils	2.9	2.9	2.6	1.3	1.0	1.4	2.6	6.2	5.7	2.8	3.9	2.9	2.9
Number of replicates	20	10	10	6	9	10	10	7	9	9	10	10	10
Number of flower buds	4.2	4.7	4.7	7.3	6.3	5.6	4.6	1.7	4.7	4.3	4.1	4.4	5.0
Number of replicates	20	10	10	6	9	10	10	7	9	9	10	10	10
Significance 5% level	d*	cd	cd	a	ab	bc	cd	e	cd	d	d	cd	cd
Significance 1% level	C	C	C	A	AB	BC	C	D	C	C	C	C	CD
Average flower bud size (mm.)	3.2	3.4	2.9	4.8	4.9	3.7	3.1	5.1	3.1	3.0	2.8	3.9	3.5
Number of replicates	20	10	10	6	9	10	10	7	9	9	10	10	10
Significance 5% level	a‡	a	a	a	a	a	a	a	a	a	a	a	a

(b) Field studies.

Sample date A (see Ch.2)	DEFOLIATION			SHADE			TIPPING		
		50%	100%		50%	100%			
	Cont	10d.	10d.	Cont	1d.	1d.	Cont	12d.	19d.
Number of reproductive axils	-	7.1	7.1	-	7.1	8.1	-	6.7	7.2
Number of aberrant axils	-	1.5	1.3	-	2.2	2.8	-	1.7	2.4
Number of replicates	-	9	10	-	12	11	-	11	10
Number of flowers	4.9	5.6	5.8	4.6	4.9	5.4	5.4	5.0	4.8
Number of replicates	10	9	10	12	12	11	11	11	10
Significance 5% level	b	ab	a	a	a	a	a	a	a
Significance 1% level	A	A	A	A	A	A	A	A	A
Average ovary size	4.6	3.9	4.6	4.3	4.2	4.4	4.5	4.9	4.5
Number of replicates	10	9	10	12	12	11	11	11	10
Significance 5% level	a	a	a	a	a	a	a	a	a

One way analysis of variance followed by Duncan's Multiple Range Test.

* Treatments with no letter in common are significantly different at that level.

‡ After the logrithmic transformation.

Sample date B (see Ch.2)	DEFOLIATION							SHADE							TIPPING			
		50%			100%				50%			100%						
	Cont	10d.	17d.	24d.	10d.	17d.	24d.	Cont	1d.	15d.	22d.	1d.	15d.	22d.	Cont	12d.	19d.	26d.
Number of reproductive axils	-	6.8	6.7	7.4	7.0	7.1	7.0	-	6.8	6.3	6.5	6.7	6.7	6.3	-	7.1	7.2	7.4
Number of aberrant axils	-	2.2	2.2	2.6	2.2	2.2	2.1	-	2.3	2.4	2.1	2.9	3.2	2.4	-	2.2	2.2	2.2
Number of replicates	-	14	12	13	17	9	14	-	23	7	11	11	6	7	-	11	15	13
Number of flowers	4.3	4.6	4.5	4.8	4.8	4.9	4.9	4.1	4.5	3.9	4.4	3.8	3.5	3.9	4.3	4.9	5.0	5.2
Number of replicates	16	14	12	13	17	9	14	16	23	7	11	11	6	7	15	11	15	13
Significance 5% level	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Average ovary size	7.8	7.4	7.5	7.8	7.4	8.1	7.6	7.4	7.6	7.2	8.0	6.9	7.2	7.3	8.5	8.3	7.9	7.7
Number of replicates	16	14	12	13	17	9	14	16	23	7	11	11	6	7	16	11	15	13
Significance 5% level	a	a	a	a	a	a	a	ab	ab	b	a	b	b	b	a	ab	bc	c
Significance 1% level	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A

Field studies

Treatments had little effect on the number of flowers per shoot (Table 7b). However certain trends were evident although no statistical significance showed.

Defoliation appeared to slightly increase flowering at both sample dates, the trend being greater with the more severe treatments. The earliest complete defoliation treatment (10 dabb.) increased the number of flowers per shoot from 4.9 to 5.8 at the early sample date and, by the bloom sample date, from 4.3 to 4.8.

Shading slightly increased flowering at the early sample date (the effect being more marked with the heavier shading), but by full bloom partial shading was without apparent effect and heavy shading slightly decreased flowering.

Tipping treatments were without effect at the early sample date, but by bloom appeared to slightly increase flowering.

(b) Average ovary or flower bud size per shoot

Single node cuttings

Defoliation, particularly complete defoliation, appeared to increase the average flower bud size per shoot (although trends were not significant); the treatment prior to bud burst increased the average size from 3.2 mm. to 4.8 mm. (Table 7a). Further, total shading slightly increased the average flower bud size (to 4.4 mm.).

Partial shading and tipping treatments were generally without effect.

Field studies

Defoliation and shading treatments had little effect on average ovary size per shoot at either sample dates although total shading seemed to have a slightly depressing action at the bloom sample (Table 7b). For both defoliation and shading treatments slight trends were generally apparent with both application date and treatment severity; ie. the earlier and/or more severe the treatment, the more marked the effect (depression).

Although the earliest tipping treatment (12 dabb.) increased average ovary size slightly (but not significantly) at the early sample date, average ovary sizes for all tipping manipulations were slightly decreased (but not significantly) by the bloom sampling (Table 7b). This bloom time effect was more marked with successively late tipping treatments.

II VEGETATIVE GROWTH

(a) Leaf growth

For shading and tipping treatments, the number of open leaves per shoot gives an estimate of leaf production. For defoliation treatments this was not practical and an estimate of leaf production was obtained by summing the number of leaf axils (up to the uppermost defoliated leaf) per shoot at each destructive sample date. This total included the scale and transition leaves (Ch.3) at the base of the shoot.

Heavy shading of single node cuttings resulted in shoot growth that was completely chlorotic (Fig.25). While the pigment content was low in heavily shaded shoots in the field, green pigmentation was present, even when shading commenced prior to bud burst.

(i) Leaf production per shoot

Single node cuttings

Shading, especially heavy shading decreased the number of open leaves (Table 8a and Fig.27).

Clearly the number of open leaves per shoot in the tipping treatment would be decreased, an effect proportional to the earliness of tipping.

All the defoliation treatments promoted leaf production, especially the complete treatments (Table 8a and Fig.29a).

Figure 29a which shows the effect of defoliation on leaf production was obtained by recording the number of leaves removed over the experimental period. After 25 dabb., leaf production following complete defoliation prior to bud burst (18.2) was significantly greater than that from later complete defoliation treatments which in turn were still significantly greater than that from the control (11.1).

Field studies

As with the single node cuttings, shading treatments decreased leaf production (Table 8b). The effect was more marked with more severe shading and with time of treatment commencement. While light shading had little effect on leaf production by the early sample date, severe shading (from bud burst) significantly decreased the number of open leaves per shoot, from 8.1 to 5.6 (Table 8b). At the bloom recording both partial as well as severe shading showed significantly decreased leaf production.

The act of tipping clearly reduced the number of open leaves per shoot.

While partial defoliation had little effect on leaf production,

Table 8

The effects of defoliating, shading, and tipping on the number of open leaves (or the total number of leaves) per shoot and the average leaf size per shoot in Hayward

(a) Single node cuttings.

		DEFOLIATION					SHADE		TIPPING				
		50%		100%			50%	100%					
	Cont	5d.	10d.	Prior	5d.	10d.	Prior	Prior	5d.	9d.	13d.	15d.	17d.
Number of open leaves	6.8						6.0	3.4	5.7	5.4	7.6	6.8	8.2
Number of replicates	20						10	7	9	9	10	10	10
Significance 5% level	a‡						a	b	a	b	a	a	b
Average leaf size (cm.)	4.5						4.4	1.9	5.4	5.0	4.2	4.6	4.5
Number of replicates	20						10	7	9	9	10	10	10
Significance 5% level	bc*						bc	d	a	ab	c	bc	bc
Significance 1% level	AB						B	C	A	AB	B	AB	AB
Total number of leaves	11.1	11.9	11.8	18.2	13.3	14.1							
Number of replicates	20	10	10	6	9	10							
Significance 5% level	c	c	c	a	b	b							
Significance 1% level	D	CD	C	A	BC	B							

(b) Field studies.

Sample date A (see Ch.2)	DEFOLIATION			SHADE			TIPPING		
		50%	100%		50%	100%			
	Cont	10d.	10d.	Cont	1d.	1d.	Cont	12d.	19d.
Number of open leaves				8.1	8.8	5.6	10.2	8.1	8.0
Number of replicates				12	12	10	11	11	10
Significance 5% level				a	a	b			
Significance 1% level				A	A	B			
Average leaf size (cm.)				5.2	6.5	3.2	5.9	7.8	7.6
Number of replicates				12	12	10	11	11	10
Significance 5% level				b	a	c	b	a	a
Significance 1% level				A	A	B	B	A	A
Total number of leaves	14.2	14.4	16.3						
Number of replicates	10	9	10						
Significance 5% level	a	a	a						

One way analysis of variance followed by Duncan's Multiple Range Test.

‡ In this case analysis of variance was not applicable. A Kruskal-Wallis Test was used followed by Dunnett's Test for significance with the control.

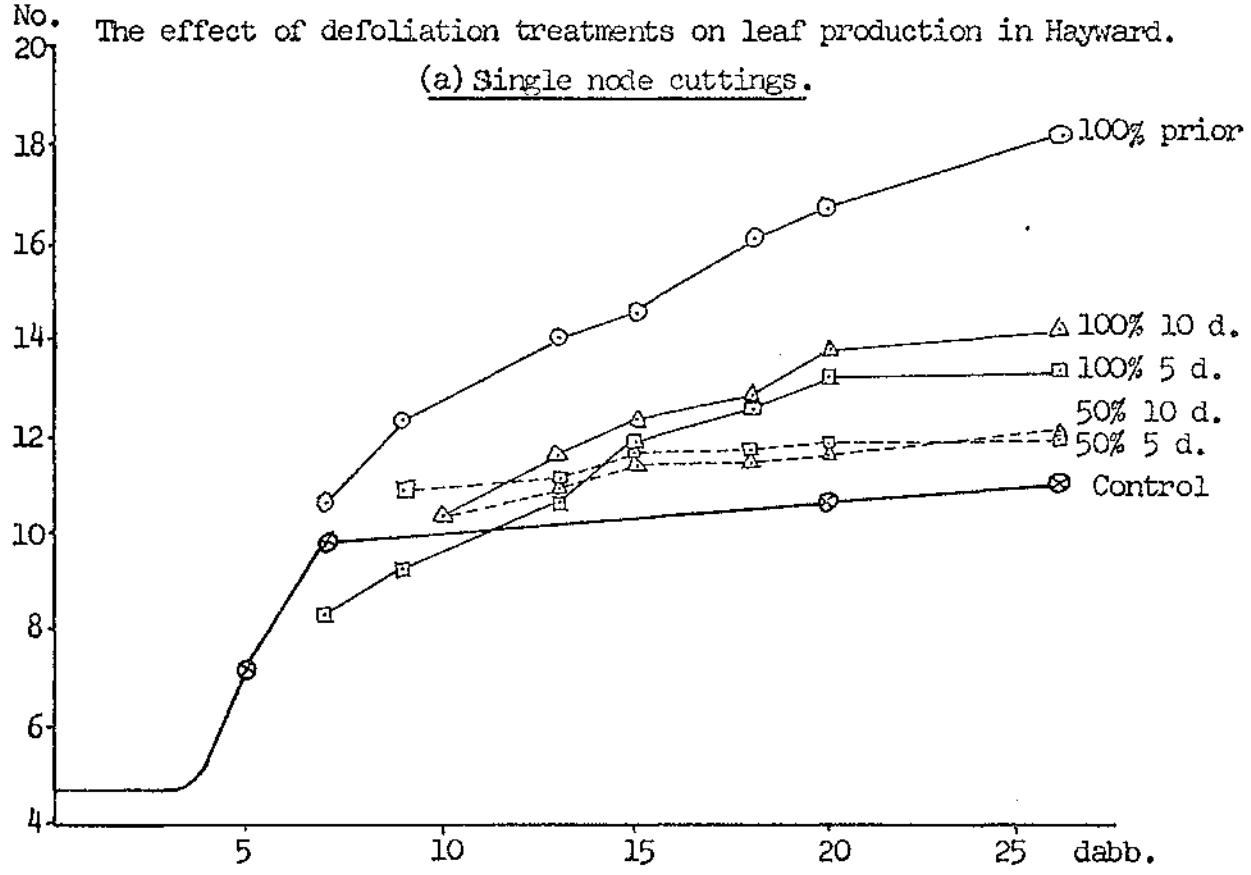
* Treatments with no letter in common are significantly different at that level.

Sample date B (see Ch.2)	DEFOLIATION							SHADE							TIPPING			
		50%			100%				50%			100%						
	Cont	10d.	17d.	24d.	10d.	17d.	24d.	Cont	1d.	15d.	22d.	1d.	15d.	22d.	Cont	12d.	19d.	24d.
Number of open leaves								11.7	7.8	8.9	9.7	6.3	6.3	2.7	11.9	7.6	8.0	8.3
Number of replicates								16	20	7	11	6	3	3	15	11	14	13
Significance 5% level								a	bc	abc	ab	c	c	d				
Significance 1% level								A	B	AB	AB	BC	BC	C				
Average leaf size (cm.)								10.2	9.7	9.5	9.8	4.5	3.7	6.6	10.4	10.3	9.2	10.6
Number of replicates								16	20	7	11	6	3	3	15	11	14	13
Significance 5% level								a	a	a	a	c	c	b	a	a	a	a
Significance 1% level								A	A	A	A	C	C	B	A	A	A	A
Total number of leaves	15.7	15.6	14.3	15.9	18.7	22.2	17.4											
Number of replicates	16	14	12	13	17	9	14											
Significance 5% level	c	c	c	bc	b	a	bc											
Significance 1% level	BC	BC	C	BC	AB	A	BC											

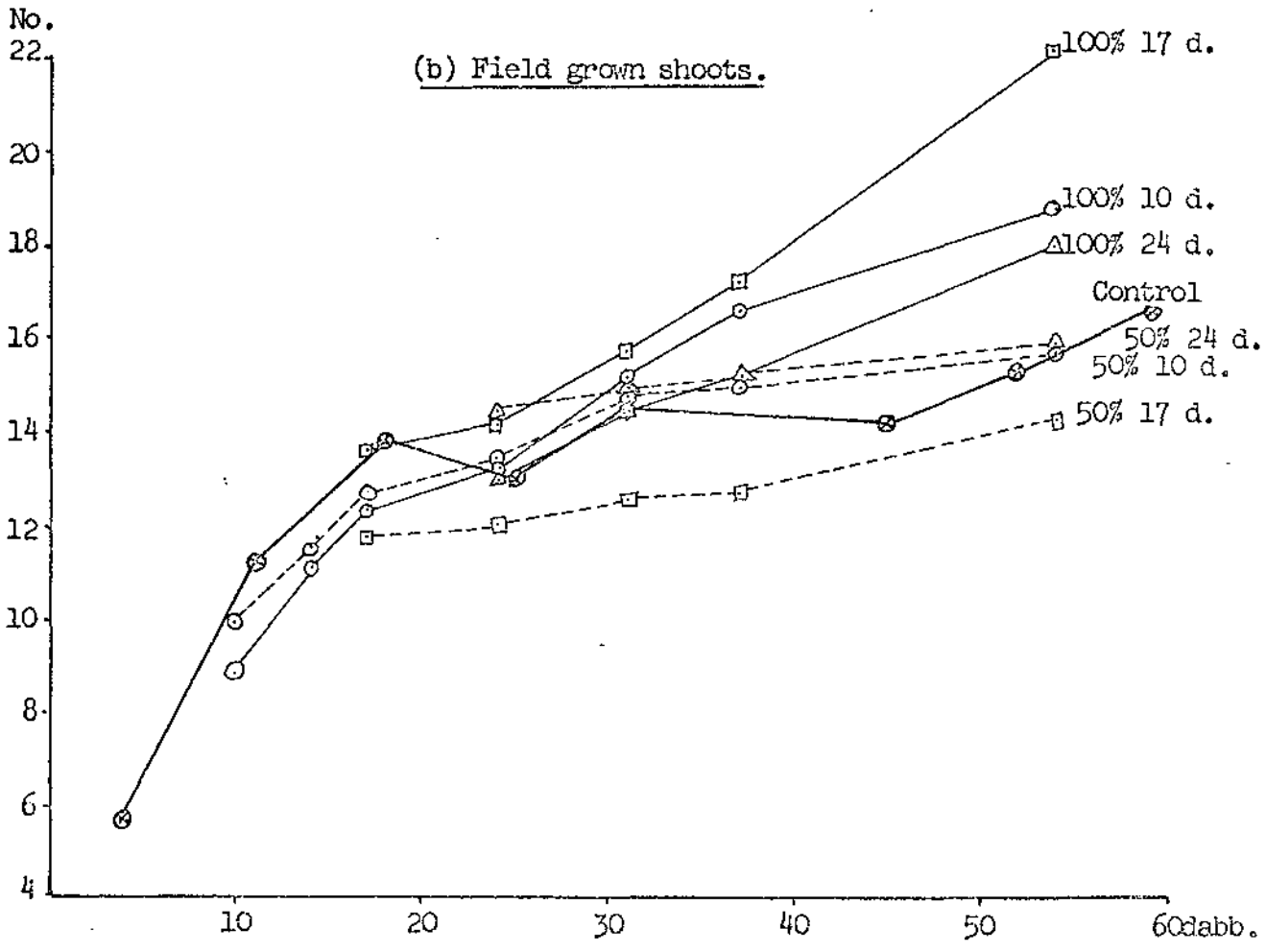
Fig.29

The effect of defoliation treatments on leaf production in Hayward.

(a) Single node cuttings.



(b) Field grown shoots.



complete defoliation increased the number of leaves (Fig.29b). By the early sample date, the trend had become apparent and by bloom the 10 dabb., and 17 dabb., treatments were significant (Table 8b).

(ii) Average leaf size per shoot

The average leaf lamina breadth per shoot was used as an index of average leaf size.

Single node cuttings

Total shading greatly reduced the average leaf size per shoot from 4.5 to 1.9 cm. while partial shading had little effect (Table 8a).

Tipping treatments slightly increased the average leaf size per shoot, an effect more noticeable for the earlier tipping treatments.

Field studies

As with the single node cuttings heavy shading reduced greatly, although not significantly, the average leaf size (Table 8b). This effect was noticeable at the early sample date as well as at the bloom sampling. Partial shading was without apparent effect.

Tipping treatments slightly promoted average leaf size at the early sample date, but by bloom little differences from the controls were evident.

(b) Shoot growth

(i) Shoot length

Single node cuttings

Defoliation treatments generally promoted shoot length (Table 9a). This effect was particularly noticeable for the defoliation treatment prior to bud burst.

Total shading, on the other hand appeared to retard shoot growth although not significantly. Partial shading was without effect.

The effect of tipping was more noticeable in stopping shoot growth with early treatments.

Field studies

As the variability of the control data was so high (for mean values, see Fig.4; the error of prediction as a percentage of the prediction being 65%), no analyses were carried out on this parameter.

In contrast with the single node cuttings, defoliation (especially complete) appeared to retard shoot growth (Table 9b). Complete defoliation

Table 9

The effects of defoliation, shading, and tipping on the shoot length and thickness in Hayward.

(a) Single node cuttings.

		DEFOLIATION					SHADING		TIPPING				
		50%		100%			50%	100%					
	Cont	5d.	10d.	Prior	5d.	10d.	Prior	Prior	5d.	9d.	13d.	15d.	17d.
Shoot length (cm.)	5.3	6.3	6.9	8.2	5.3	6.0	5.4	3.0	5.6	4.8	5.8	5.2	7.0
Number of replicates	20	10	10	6	9	10	10	7	9	9	10	10	10
Significance 5% level	bc*	ab	ab	a	bc	ab	bc	c	b	bc	b	bc	ab
Significance 1% level	A	A	A	A	A	A	A	A	A	A	A	A	A
Shoot thickness (mm.)	4.0	4.1	4.0	4.2	4.1	4.0	3.8	3.5	4.3	4.0	4.2	4.1	4.4
Number of replicates	20	10	10	6	9	10	10	6	9	9	10	10	10
Significance 5% level	a	a	a	a	a	a	a	a	a	a	a	a	a

(b) Field Studies.

Sample date A (see Ch.2)	DEFOLIATION			SHADING			TIPPING		
		50%	100%		50%	100%			
	Cont	10d.	10d.	Cont	1d.	1d.	Cont	12d.	19d.
Shoot length (cm.)	16.1	12.7	10.6	14.9	16.5	15.6	16.7	14.1	14.4
Number of replicates		9	10		12	11		11	10
Shoot thickness (mm.)	5.2	4.8	4.8	5.3	5.1	4.9	5.3	5.8	5.2
Number of replicates	10	10	9	12	12	11	11	11	10
Significance 5% level	a	a	a	a	a	a	a	a	a

Sample date B (see Ch.2)	DEFOLIATION						SHADING						TIPPING			
		50%			100%			50%			100%					
	Cont	10d.	17d.	24d.	10d.	17d.	24d.	Cont	1d.	15d.	22d.	1d.	15d.	22d.	Cont	12d.	19d.	24d.
Shoot length (cm.)	29.7	29.6	22.4	27.0	20.0	29.7	19.6	29.7	19.8	22.1	28.3	33.0	47.2	12.8	32.6	14.9	15.0	20.3
Number of replicates		14	12	13	17	9	14		20	7	11	4	2	5		11	15	13
Shoot thickness	7.4	6.3	6.0	6.4	5.2	5.7	5.8	7.0	5.6	5.9	6.5	5.9	5.6	5.5	7.2	6.7	6.5	6.8
Number of replicates	16	14	12	13	16	9	14	16	18	7	10	11	6	7	13	11	13	13
Significance 5% level	a#	b	b	b	b	b	b	a	bc	bc	ab	bc	bc	c	a	a	a	a
Significance 1% level								A	B	B	AB	B	B	B	A	A	A	A

One way analysis of variance followed by Duncan's Multiple Range Test.

In this case analysis of variance was not applicable. A Kruskal-Wallis Test was used followed by Dunnett's Test for significance with the control.

* Treatments with no letter in common are significantly different at that level.

starting 10 dabb., retarded shoot length from 16.1 to 10.6 cm. at the early sample date and by bloom was 20.6 cm. compared with the control value of 29.7 cm.

Also in contrast with the single node cuttings, shading appeared to have little effect on shoot growth; figures were inconsistent. As with the single node cuttings, tipping reduced (expectedly) shoot growth, the size of the reduction being related to the earliness of tipping (Table 9b).

Defoliation treatments had a marked influence on internode growth. In the field, the average internode length (mean shoot length ÷ mean total number of leaves) was greatly decreased by all complete defoliation treatments; the earliest (10 dabb.) treatment reducing the average length from 1.89 cm. (control) to 1.09 cm. Partial defoliation appeared to have little effect.

In the single node cuttings however, defoliation treatments, even complete defoliations, only slightly reduced internode growth. This was because shoot growth was increased (Table 9a)(along with leaf production) and not decreased as was generally the case in the field (Table 9b). The average internode length for the prior to bud burst treatment was 0.45 cm. (compared with 0.48 cm. for the controls).

(ii) Shoot thickness

The diameter of the base of the shoot was used as an indication of shoot thickening.

Single node cuttings

Generally defoliation had little effect on shoot thickness although the treatment prior to bud burst appeared to have a slightly promotive effect (Table 9a).

Shading slightly retarded thickening only when the treatment was severe.

Shoot thickness was generally unaffected by all the tipping treatments.

Field studies

Defoliation as well as shading inhibited shoot thickening, an effect directly related to the intensity of the treatment and to the length of time the treatments were applied (Table 9b).

Tipping slightly promoted shoot thickening at the early sample date but by the bloom sampling was slightly retarded.

III NEW BUD DEVELOPMENT

The number of leaf primordia in the axil immediately distal to the uppermost flowering axil were recorded to assess the effect of treatments on new bud development. It is these buds that develop into flowering shoots next year.

Single node cuttings

Complete defoliation stimulated new bud development; the earliest treatment increased significantly the number of leaf primordia from 6.8 to 9.8 (Table 10a). Partial defoliation however appeared to decrease slightly bud development.

Shading greatly decreased bud development with the total shading treatment decreasing numbers from 6.8 to 3.8.

As early (5 dabb., and 9 dabb.) tipping removed all the axils containing the developing buds no data were available from these treatments. No consistent trends were evident following later tipping.

Field studies

Defoliation appeared to have little effect at the early sample date, but by the bloom sampling complete defoliation significantly decreased bud development, while partial defoliation appeared to slightly increase bud development (Table 10b).

Both shading treatments promoted significantly bud development at the early sample date, but by the bloom sampling bud development was decreased significantly.

As the tipping treatments on shoots in the field were carried out later than on the single node cuttings this parameter could be recorded for all treatment dates. Tipping treatments promoted significantly bud development at the early sample date but by the bloom sampling this increase was not significant.

C. DISCUSSION

It seems highly probable that the pattern of metabolite movement in the Chinese gooseberry is basically similar to that of other deciduous fruit trees and vines.

The overall situation in the case of the single node cuttings is less complex than in the field studies. The shoot is physiologically isolated and there are fewer growth centres competing for essential metabolites and

Table 10

The effects of defoliation, shading, and tipping on the number of leaf primordia in the new bud in Hayward.

(a) Single node cuttings.

		DEFOLIATION					SHADING		TIPPING				
		50%		100%			50%	100%					
	Cont	5d.	10d.	Prior	5d.	10d.	Prior	Prior	5d.	9d.	13d.	15d.	17d.
Number of leaf primordia	6.8	6.1	6.7	9.8	7.9	8.8	5.0	3.8	-	-	6.4	8.0	6.9
Number of replicates	20	9	10	6	8	8	9	6	-	-	9	8	10
Significance 5% level	cd	cd	cd	a	bc	ab	d	e	-	-	cd	bc	c
Significance 1% level	BC	BCD	BC	A	AB	AB	CD	D	-	-	BC	AB	BC

(b) Field treatments.

Sample date A (see Ch.2)	DEFOLIATION			SHADING			TIPPING		
		50%	100%		50%	100%			
	Cont	10d.	10d.	Cont	1d.	1d.	Cont	12d.	12d.
Number of leaf primordia	8.9	8.8	9.1	7.9	10.4	9.6	8.5	10.6	10.1
Number of replicates	10	9	10	12	12	10	11	11	10
Significance 5% level	a*	a	a	b	a	a	b	a	a
Significance 1% level	A	A	A	B	A	AB	A	A	A

Sample date B (see Ch.2)	DEFOLIATION							SHADING							TIPPING				
		50%			100%				50%			100%							
	Cont	10d.	17d.	24d.	10d.	17d.	24d.		1d.	15d.	22d.	1d.	15d.	22d.	Cont	12d.	19d.	24d.
Number of leaf primordia	12.8	13.9	14.3	13.6	10.1	11.1	10.9	13.7	11.8	11.9	12.7	11.6	10.5	10.5	13.9	15.0	14.6	15.5
Number of replicates	16	14	12	13	17	9	12	16	16	7	10	11	2	6	14	11	14	12
Significance 5% level	b	ab	a	ab	c	c	c	a#	b	b	a	b	b	b	a	a	a	a
Significance 1% level	A	A	A	A	B	B	B								A	A	A	A

One way analysis of variance followed by Duncan's Multiple Range Test.

In this case analysis of variance was not applicable. A Kruskal-Wallis Test was used followed by Dunnett's Test for significance with the control.

* Treatments with no letter in common are significantly different at that level.

treatment effects on the cutting are not influenced by the effects of other shoots, or by other growth centres (eg. roots) in the parent vine.

Studies on unrooted grape cuttings have shown that there is little (if any) increase in the total dry weight of the shoot and cane (46) and studies on pre-rooted cuttings indicate that there is little increase in total dry weight of the cuttings during the first month after bud burst (224). This may suggest that the growth of the shoot system in the Chinese gooseberry is largely dependent on reserves in the cane.

During the pre-bloom and bloom period, developing flower buds have only limited abilities to attract metabolites and are weak sinks compared with the shoot apex, developing leaves and other growth centres (eg. roots) in the parent vine (127,131,224).

Defoliation

Leaves, during their expansion phase contribute little to growth and are importers (sinks) rather than net suppliers of metabolites (67,169). In many deciduous perennial plants, Wardlaw (310) and others (127,176,188, 252) have found that a leaf does not become a contributing organ until it has reached one-third to one-half its final area. However, leaves, particularly very young leaves, are known producers of auxins (27,164,332), gibberellins (102,115,164) and inhibitors (332) and their removal would cause a deficiency of those substances.

The effects of leaf removal on the various growth centres may be interpreted in terms of photosynthate redistribution and/or in terms of hormonal responses.

In the single node cuttings the total leaf area per shoot was still expanding rapidly for a large proportion of the experimental period and the effects of continuous defoliation on such shoots indicated just how strong an influence expanding leaves had on growth and development. The effects were related to the severity of the treatment, and to the length of time the treatment was applied. While the partial (distal 50%) defoliation treatments were generally stimulatory, their effects may not be proportional to the leaf area removed as the remaining proximal portion of the leaf would likely have some sink capacity.

The stimulatory effects of defoliation on reproductive development in the single node cuttings corresponded with that found in rooted grape cuttings (224). In rooted grape cuttings, Mullins (224) showed that inflorescence growth usually ceases soon after bud burst, but by removing the leaves (up to the axil containing the one inflorescence that was allowed to remain), the inflorescence survived to bloom and was able to set

fruit. This was explained in terms of the inability of the inflorescence to compete with the leaves and other organs for available food supplies.

A similar explanation, based on competition, is likely to be the reason for the greatly stimulated flower numbers and average flower bud size in Chinese gooseberry cuttings as the result of defoliation (Table 7a).

Like the grape, flower evocation had already commenced (Ch.5) and the effects of defoliation in the Chinese gooseberry cuttings probably would have been to divert metabolites, that would otherwise have been channeled into leaf growth, into developing flower buds. The greatly increased number of flower buds per shoot was the result of stimulating some of those flowering axils into growth which normally (see Ch.3) would have aborted early (Table 7a).

In cases where evocation is stimulated, for example, when tomato seedlings are continually defoliated from emergence, the effects have been explained largely in hormonal terms as even the presence of one leaf greatly reduced the stimulation (291). A flowering inhibitor was thought to be present in the leaves and its removal by continuous defoliation produced the stimulation.

When individual shoots in the field were continuously defoliated the pattern was however different to that found in the single node cuttings.

As most of the leaves were still expanding at the early (31 dabb.) sample date (see Ch.3), the significant increase in the number of flowers per shoot was probably due to the elimination of a competitive net sink (Table 7b). Early defoliation removes organs which would later provide metabolites for the growing flowers. Therefore it may have been expected that, by bloom, the number of flowers per shoot would have been reduced especially by the continuous total defoliation treatments. Results showed that this was not the case (Table 7b) and suggests that metabolites were imported from outside the treated shoot as shown for grapes (252).

Various vegetative parameters of shoot growth were affected by continuous defoliation and results generally agreed with those reported in other fruit trees (19,27,102,115,164). The greatly stimulated leaf production (Fig.29, Table 8), also reported in the apple (19,164) is likely to be due to the removal of some inhibiting substance(s) present in leaves and/or to the greater continued attraction of metabolites to the shoot apex some of which otherwise would have been channeled into leaf growth.

Internode growth was greatly inhibited by continuous defoliation, an effect especially marked in individual shoots in the field as shoot growth

was also inhibited (Table 9b). These effects have also been reported in the apple (164). As immature leaves act as metabolic sinks (310) their removal might then be assumed to free metabolites for growth elsewhere (eg. to internodes). Since defoliation in Chinese gooseberry causes a reduction in internode length, this implies the effects of a specific factor(s) as postulated in apple stems by Barlow and Hancock (27). Since gibberellins are synthesised in very young leaves (102,115,164), and will promote internode growth when exogenously applied (115,164,254), a deficit of these substances may be the cause of the decreased internode growth and have since been proposed to constitute a major part of Barlow and Hancock's inhibitor (102,115,164).

The stimulation of shoot growth, as the result of continuous defoliation in the single node cuttings contrasts to its inhibition in the field and could be due to a number of factors. If factors governing leaf production and internode growth were (partially) dependent on reserves or metabolites, they may be relatively more available in single node cuttings. Again, the sink capacity of the apex may be greater compared with that in the field. The fact that the average internode growth in the single node cuttings was less inhibited (approximately 90% compared with approximately 65% in the field for complete defoliation treatments) may be the result of lower internode growth factor (higher gibberellin) levels (27) in the detached shoot. This may either be because levels produced in single node cutting leaves were relatively lower compared with that in the field and/or the leaves were removed before relative maximum levels were produced. As leaves in the single node cuttings were removed at an earlier stage of development, some support for this latter theory comes from the finding that, in the apple, maximum GA levels per leaf were not attained until they had reached one half their ultimate size, and that levels in folded immature leaves were even lower than those in full sized leaves (164). This view is further supported by the finding that the defoliation prior to bud burst (where a large proportion of the leaves removed were at the folded immature stage and less) resulted in the least reduction of internode growth (compared with both the total defoliation treatments on other single node cuttings and with all similar defoliations in the field).

The axillary buds, in which next years' flowering shoots will form are greatly influenced by their subtending leaves (28,127). The stimulation of axillary bud development by continuous defoliation in single node cuttings is probably the result of modification of the pattern of metabolite movement within the shoot by the elimination of a powerful competing

sink (young leaves). In the field this situation may have been the case when shoot growth was largely dependent upon reserves mobilised from the parent vine, as evidenced by the stimulation recorded at the early sample date. When the leaves became net exporters however, continuous total defoliation would remove this source of metabolites and would greatly curtail axillary bud development and this is what was recorded at the bloom sample.

In the grape, axillary buds have been shown to be a minor sink during the prebloom and bloom periods compared with the developing flower clusters (127,254). In the Chinese gooseberry, this same possibility was supported by the finding that, whereas axillary bud development in defoliated shoots in the field was inhibited by the bloom record, flower bud growth was not.

Shading

The influence of shading on overall growth and development would be expected to be generally less definitive compared with defoliation as the sink and source capacity of the leaves are not completely eliminated, although when comparing heavy shading (as used in the single node cuttings), the effects may not differ greatly from total defoliation. The effects of shading however are more complicated than those of defoliation as (unlike the other treatments) all the various growth centres are likely to be influenced to a greater or lesser degree by the shading treatments per se.

The effects of shading on growth and development (in the cutting material and in the field) were generally not marked unless the treatments were severe. As with total defoliation, differences in the effects of severe shading on reproductive development were found between the single node cuttings and individual shoots in the field (Table 7). In the single node cuttings, total shading severely reduced the number of flower buds per shoot. This was due to the large scale abortion of the flower buds, mainly over the later part of the experimental period; possibly either due to a relative reduction in the sink capacity of the developing flower buds and/or to a reduction in the levels of available reserves (248).

The shading of individual shoots in the field however did not result in this reduction in flower numbers per shoot - even at the bloom sample date (Table 7b). As with defoliation, shading individual shoots may have induced the transfer of assimilates to the developing flower buds from outside the treated shoot, an effect reported in grapes (254). The overall sink capacity of the flower buds may have been lowered by severe shading as the average ovary size per shoot was slightly reduced by servere shading. (In the single node cuttings, the average flower bud size per shoot of

those remaining was actually increased, presumably because of the extensive abortion of a large proportion of buds.)

Overall vegetative development was only retarded greatly when shading was severe; light shading on individual shoots was either without apparent effect or was slightly stimulatory (Table 8 and 9). Leaves on shoots severely shaded prior to their expansion made only very limited growth, probably did not become photosynthetic (especially in the single node cuttings), and usually abscissed. This effect, also noted in other fruit trees (210), shows that the factors required for the maintenance and growth of leaves are not produced under very low light intensities and are not readily translocated from leaves on other shoots receiving adequate light.

This possibly suggests that the factors for leaf growth are more specific than for flower bud growth as shading had much less effect on flower bud development than leaf development. This also possibly suggests that shading may alter the relative competitiveness of the two sinks (favouring the flower buds).

Shoot thickening was greatly retarded (Table 9), presumably as the leaves on shaded shoots were of low capacity for photosynthesis.

Although the severe shading may initially stimulate axillary bud development (possibly due to a modification of metabolite movement within the shoot), the effects (like those of total defoliation) were, by the final recording shown to be greatly inhibitory (Table 10). This indicates the considerable influence of the subtending leaves. Similar inhibitions of bud development by severe shading have been reported for grapes (203).

Tipping

The shoot apex, a powerful metabolic sink, influences the pattern of photosynthate movement within the plant, and its removal can greatly modify that pattern (67,68,127,195,252,254). In grapes, tipping can greatly improve fruit set although results are often variable (67).

Present results on the Chinese gooseberry showed that tipping was generally without effect. One reason for the lack of response (in both the single node cuttings as well as in individual shoots in the field) may be the fact that only the shoot apex was removed and the still expanding leaves which remained are probably still a strong competitive sink for metabolites. This explanation was put forward by Coombe (66) when he stated that in some circumstances on the grape, topping (the removal of 6 inches or more of the shoot) produced a greater response than tipping.

Again, the overall lack of response from tipping of individual shoots in the field may have resulted in the movement of metabolites from the

treated shoot to neighbouring untreated shoots rather than to the other growth centres (sinks) within the treated shoot. In a slightly different study, Quinlan and Weaver (254) showed this to be the case where individual grape shoots were tipped and deblossomed.

Because of the possible atypical responses when applying treatments to individual shoots in the field and the many impracticalities of treating whole vines in the field it would be of considerable practical benefit to obtain small test plants for such an investigation into the physiology of flowering and fruiting of *A. chinensis*. While the use of the single node cuttings is of benefit caution is required in extrapolating the responses to the field situation (where a shoot does not become self sufficient and the leaf area is effectively mostly a net importer). The use of dormant one year old cuttings would still be the ideal system if roots could be induced without the loss (abortion) of the flower buds as cuttings could be collected, stored and used throughout the year. Future research may find that the level of competition immediately after bud burst (which is the critical period) may be sufficiently reduced by inducing roots prior to the bursting of the shoot or by defoliating up to the last flowering axil while roots were being initiated. These methods have been used in grapes to obtain small test plants (46,224).

Although Hayward comprises over 90% of the Chinese gooseberry plantings, a cultivar like Monty would be more suited for such test plant flowering studies. This is because its buds burst more readily and it normally bears larger numbers of flowers (Ch.6). Any treatment effect would therefore be more readily noticed.

Chapter 5

THE EFFECT OF CHILLING ON THE TERMINATION OF REST AND FLOWERING

A. INTRODUCTION

Certain species, notably the olive (124), have a chilling requirement for flowering evocation. As well, many deciduous fruit tree species have a chilling requirement to terminate the rest period (60).

The requirement of chilling temperatures to evoke flowering in the olive is very specific (22). Under controlled environmental conditions, at least 10 weeks at a constant temperature of 13°C were required for flowering (124), but that could be modified by diurnally fluctuating temperatures (22). However, the flowering response under controlled environmental conditions was less than that occurring naturally, and neither the mean temperature or the accumulated number of hours below a given value, eg. 7°C, adequately characterised those requirements.

The chilling requirement to overcome rest varies between fruit tree cultivars (60), but methods to quantify that requirement have not been totally successful (267). Generally, chilling requirement values vary, from a high for most apple and pear cultivars, to apparently none for some grape cultivars (60).

Nothing has been reported in the literature regarding the effects of low temperature on flower development, or on the termination of rest, in the Chinese gooseberry.

This study set out to investigate such effects using single node cuttings (previously described), taken at three-weekly intervals from late autumn to early spring, from the pistillate cultivars Hayward and Monty, and the staminate clone Alpha. At each sample date (1-7), cuttings were chilled for increasing periods (10 day intervals up to 50 days) at 4°C in the dark before being placed at 23°C under continuous light. (A.B.C.D.E. chilling treatments.) An unchilled control (0) was also included at each sample date.

It should be recognised that during the course of the sampling, the vines left in the field underwent a degree of chilling, but this was not very intensive compared with the chilling treatment.

The following are the mean of the maximum and minimum temperatures (°C)

for Oratia for 1972, covering the period when sampling was carried out (228).

Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.
18.6	15.9	12.7	9.6	10.3	9.3	12.6	13.8

The temperatures for the Kumeu samples were within 0.5°C of the Oratia values.

B. EXPERIMENTAL OBSERVATIONS AND RESULTS

I BUD BURST

(a) Days to bud burst

From the earliest sample date (early May), cuttings from all cultivars could be forced into growth without supplementary chilling (Table 11a and Fig.30). At sample date 1 without supplementary chilling, buds of Hayward , Alpha and Monty took 42, 25 and 37 days respectively for 50% of the replicates to reach the stage of bud burst (Table 11a). With later sample dates, and with increasing chilling, the length of the rest period diminished.

The response to chilling was more marked up to treatment B (20 days at 4°C), but then became less evident up to treatment E (50 days at 4°C). Chilling treatment effects were more marked at the earlier sample dates (sample dates 1 and 2) and, over the later sample dates, became less noticeable (Fig.30). These trends were especially evident in the Hayward and Monty cultivars.

(b) Percentage bud burst

There was an apparent increase in the percentage of buds that burst, both with natural chilling (sample dates) and with chilling treatments (Table 11b). This was most evident in Hayward where sample date control values increased from 60% at sample date 1 to 100% by sample date 6. Similar trends were also noted for the chilling treatments, especially at the earlier sample dates.

With both natural chilling (later sample dates) and chilling treatments, the time between the first and last buds to break was also reduced, ie. bud burst was more even at later sample dates and with increasing chilling treatments.

Table 11

The effects of the period of chilling and the date of sampling on :

(a) The days to bud burst.

(b) The percentage bud burst.

HAYWARD

Treatment / Date	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	42	31	23	20	17	-	60	60	100	100	100	-
2.	46	38	24	19	-	13	60	60	100	80	-	100
3.	36	28	26	23	-	13	80	100	100	60	-	100
4.	35	28	22	22	15	11	80	80	80	80	80	80
5.	29	21	19	11	9	9	80	80	100	100	80	80
6.	20	19	16	12	9	8	100	80	80	80	100	100
7.	13	9	9	7	7	6	100	100	100	100	100	100

ALPHA

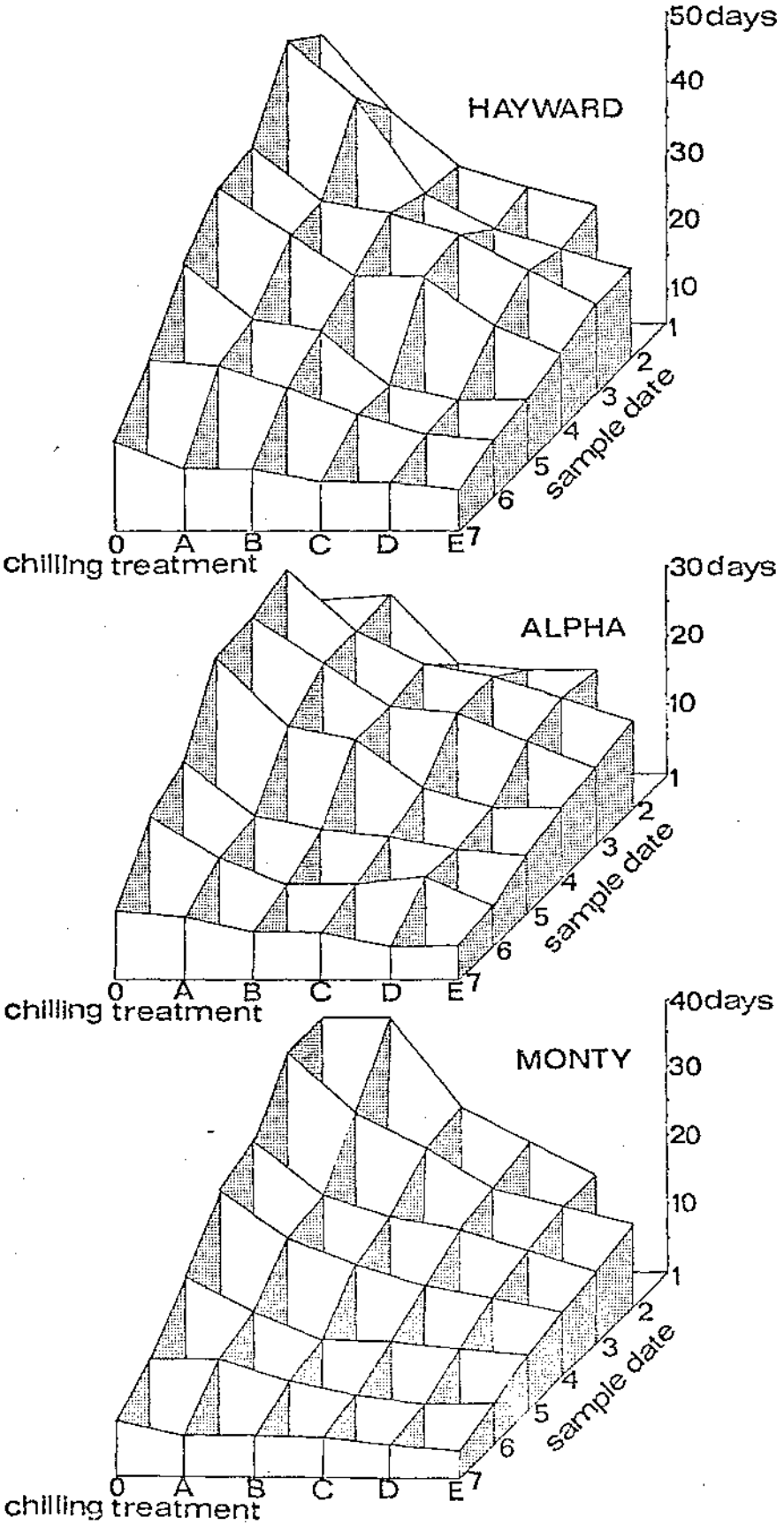
	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	25	26	16	15	15	-	100	100	100	80	60	-
2.	35	26	21	19	-	13	60	60	100	100	-	100
3.	33	26	20	19	-	11	100	100	80	100	-	100
4.	32	22	20	13	10	10	100	80	100	100	100	80
5.	22	14	12	11	9	8	100	100	100	100	100	100
6.	19	13	9	9	7	6	100	100	100	100	100	100
7.	10	8	7	7	5	5	100	100	100	100	100	100

MONTY

	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	37	37	24	19	14	-	60	100	100	100	100	-
2.	37	28	23	17	-	12	100	100	80	100	-	100
3.	29	21	18	16	-	10	100	100	100	80	-	100
4.	27	20	16	13	11	9	80	100	100	100	100	100
5.	19	14	10	10	9	8	80	100	100	100	100	100
6.	12	12	9	7	6	6	80	100	100	100	100	100
7.	8	6	6	6	5	4	100	80	100	100	100	100

Fig. 30

The effect of the period of chilling and the date of sampling on the number of days to bud burst.



II FLOWER BUD DEVELOPMENT

(a) Number of reproductive axils per shoot

Observations on dormant buds taken at each sample date supported the previous year's finding that flower initiation did not commence until around bud movement (Ch.3). Buds, when forced into growth (and destructively sampled 20 dabb.) were found to be in the reproductive state, as judged by number of reproductive axils present (Table 12a). Apart from a suggestion that there may be slightly fewer reproductive axils at the first sample date (early May), results generally indicated little change in the number of such axils with sample date, or with increasing periods of chilling. The average number of reproductive axils per shoot varied between cultivars from approximately 7.7 in Alpha and 7.1 in Hayward, to 6.2 in Monty.

(b) Number of aborted (aberrant) reproductive axils per shoot

The number of aborted reproductive axils per shoot generally decreased, both at later sampling dates and with increasing chilling treatments (Table 12b). There was considerable variability between the cultivars in the number of aborted axils, at all sample dates, and after increasing chilling treatments. Generally, the number of aborted axils per shoot decreased markedly, from a maximum of approximately 6 for Hayward and Monty, and 4 for Alpha over the earlier control sample dates, to approximately just over 3 in Hayward and Monty and 1 in Alpha at the last sample date. The rate of decrease was particularly noticeable in Alpha, especially over the earlier sample dates. Generally, the effect of chilling treatments on the number of aborted axils were less marked, except for Alpha where values fell markedly, particularly at earlier sample dates (Table 12b).

From the knowledge obtained during the previous season (Ch.3) it was possible to separate the structures in aborted axils into those which aborted early (ie. did not initiate petals) and those that aborted later (ie. petals present) (Table 13).

The relative number of early and late aborted axils varied between cultivars as did their rate of decrease with increasing chilling treatments and later sample dates. Generally the numbers for the early aborted axils fell over the initial 2-3 sample dates and then remained steady (Table 13).

In the Hayward and Monty, numbers of late abortions fell steadily over all the sample dates, approaching zero at later sample dates (Table 13b).

Table 12

The effect of the period of chilling on the date of sampling on :

(a) The number of reproductive axils per shoot.

(b) The number of aborted axils per shoot.

HAYWARD

Treatment Date.	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	6.3	-	5.8	6.0	8.0	-	6.3	-	5.8	6.0	8.0	-
2.	5.0	4.7	5.2	6.5	-	7.4	5.0	4.7	5.2	6.5	-	7.4
3.	7.5	6.8	8.0	7.7	-	7.6	7.5	6.8	8.0	7.7	-	6.0
4.	8.5	7.5	7.0	8.0	7.5	7.8	8.0	7.3	6.8	5.0	4.0	4.0
5.	7.8	8.8	8.6	8.8	7.8	8.0	5.3	4.0	3.4	3.8	3.5	3.0
6.	7.4	8.0	7.5	7.5	8.6	7.2	5.4	4.0	4.3	4.3	3.4	3.2
7.	7.4	8.2	8.5	9.0	7.0	8.0	3.4	3.0	3.8	3.8	3.0	3.0

ALPHA

	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	-	-	-	-	-	-	-	-	-	-	-	-
2.	7.0	6.4	7.8	8.0	-	7.4	4.7	3.7	3.2	2.0	-	2.2
3.	6.6	7.2	8.3	6.6	-	7.8	2.0	1.8	2.3	0.8	-	1.2
4.	7.6	8.5	7.4	8.0	8.0	8.0	1.8	1.8	1.0	0.8	1.4	0.3
5.	8.6	7.6	8.2	8.4	8.4	8.6	1.0	1.8	1.0	2.2	0.8	0.2
6.	8.0	7.8	8.8	8.2	8.8	8.0	2.2	0.4	1.0	1.2	1.4	1.4
7.	8.2	9.0	8.4	8.2	7.8	8.0	1.4	0.8	0.8	0	0.2	0.8

MONTY

	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	5.3	5.0	5.0	4.8	6.0	-	5.3	5.0	5.0	4.8	5.2	-
2.	6.8	6.6	6.8	6.2	-	7.0	6.8	6.6	6.5	4.4	-	4.4
3.	5.8	5.8	6.6	6.3	-	6.0	5.6	4.2	4.2	2.8	-	2.0
4.	6.3	6.0	6.2	6.0	5.8	6.6	4.3	3.8	2.4	2.0	2.2	2.6
5.	6.3	6.2	6.0	6.6	6.8	6.2	3.0	2.6	2.0	2.6	3.0	2.2
6.	6.3	6.4	6.8	6.4	6.6	6.6	2.5	2.8	2.2	2.4	2.6	2.2
7.	6.6	6.5	7.0	6.4	6.2	6.0	3.2	2.8	3.4	2.6	1.8	2.4

Table 13

The effects of the period of chilling and the date of sampling on :

(a) The number of early aborted axils per shoot.

(b) The number of late aborted axils per shoot.

HAYWARD

Treatment / Date	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	5.3	-	3.4	3.0	3.4	-	1.0	-	2.4	3.0	4.6	-
2.	4.0	3.7	5.2	5.0	-	3.6	1.0	1.0	0	1.5	-	3.8
3.	4.0	3.8	3.2	2.3	-	2.6	3.5	3.0	4.8	5.3	-	3.4
4.	4.8	2.5	1.5	1.8	1.3	3.0	3.3	4.8	5.3	3.3	2.8	1.0
5.	1.8	1.5	0.8	3.2	3.5	2.3	3.5	2.5	2.6	0.6	0	0.8
6.	2.2	2.0	3.8	3.3	3.2	2.8	3.2	2.0	0.5	1.0	0.2	0.4
7.	3.0	2.4	2.3	3.0	2.6	2.6	0.4	0.6	1.5	0.8	0.2	0.4

ALPHA

	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	-	-	-	-	-	-	-	-	-	-	-	-
2.	4.7	3.3	2.4	2.0	-	2.2	0	0.3	0.8	0	-	0
3.	1.8	1.6	2.3	0.8	-	1.0	0.2	0.2	0	0	-	0.2
4.	1.8	1.8	1.0	0.8	1.4	0.3	0	0	0	0	0	0
5.	0.8	1.6	1.0	2.2	0.8	0	0.2	0.2	0	0	0	0.2
6.	2.2	0.4	1.0	0.2	0.8	0.2	0	0	0	1.0	0.6	1.2
7.	1.2	0.8	0.6	0	0	0.8	0.2	0	0.2	0	0.2	0

MONTY

	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	3.3	3.0	2.5	2.2	1.6	-	2.0	2.0	2.5	2.6	3.6	-
2.	4.0	3.6	3.5	2.4	-	3.4	2.8	3.0	3.0	2.0	-	1.0
3.	2.2	2.6	2.4	2.3	-	1.6	3.4	1.6	1.8	0.5	-	0.4
4.	2.3	3.0	2.0	2.0	1.8	2.6	2.0	0.8	0.4	0	0.4	0
5.	2.3	2.4	1.8	2.2	2.6	1.6	0.8	0.2	0.4	0.4	0.4	0.4
6.	1.5	1.4	1.8	2.4	2.6	1.6	1.0	0.4	0.4	0	0	0.6
7.	2.8	2.5	3.4	1.6	1.6	2.4	0.4	0.3	0	1.0	0.3	0

There appeared to be an effect of chilling at the early sample dates, but this was not obvious at late sample dates as the control value approximately reached zero at that time (Table 13b).

In the Alpha group, late aborted axil totals were initially small and remained so at later sample dates.

(c) Number of flower buds per shoot

The total number of flower buds per shoot generally increased, both at later sampling dates, and with increasing chilling treatments on all cultivars (Fig.3, and Tables 14 and 16).

(i) Terminal flower buds

There were marked variations between cultivars in the number of terminal flower buds per shoot. Values for each cultivar generally increased steadily at later sample dates, and with longer chilling treatments (Table 14a).

In Alpha, 3-4 terminal flower buds per shoot were present on control cuttings taken in early May (sample date 1). It was not until sample date 4 (mid July) in Monty or sample date 5 (late July) in Hayward, that terminal flowers first appeared (Table 14a). By sample date 7 (early September), the number of terminal flower buds per shoot on control cuttings in Alpha, Hayward and Monty were 6.8, 3.8, and 3.7 respectively.

Chilling treatments increased the number of terminal flower buds in all cultivars, especially over the early sample dates. While terminal flower buds were generally not present in the control buds of Hayward until sample date 5, flower buds were present by the 50 day chilling treatment (E) at sample date 3. Similarly in Monty, where flower buds were not present in control buds until sample date 4, terminal flower buds were present by the 40 day chilling treatment (C) at sample date 2. In Alpha the number of terminal flower buds at sample date 1, increased from 3.4 with no chilling to 6.3 after 40 days chilling.

(ii) Lateral flower buds

Lateral flowers did not develop unless there was a terminal flower bud. In Alpha, lateral flower buds were present on controls from early May (sample date 1), and numbers generally increased markedly with later sample dates and increasing chilling treatments (Table 14b). The number of lateral flower buds which developed in both the pistillate cultivars was however very low. Lateral flower buds were present in Hayward and

Table 14

The effects of the period of chilling and the date of sampling on :

(a) The number of terminal flower buds per shoot.

(b) The number of lateral flower buds per shoot.

HAYWARD

Treatment / Date	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	0	0	0	0	0	-	0	0	0	0	0	-
2.	0	0	0	0	-	0	0	0	0	0	-	0
3.	0	0	0	0	-	1.6	0	0	0	0	-	0
4.	0.5	0.3	0.3	3.0	3.5	3.8	0	0	0	0	0	0
5.	2.5	4.3	4.8	4.0	4.0	4.8	0	0.5	0.4	0.8	0.3	0.3
6.	2.0	2.8	3.3	3.3	4.2	4.0	0	1.3	0	0	1.0	0
7.	3.8	5.0	3.8	4.4	4.2	4.6	0.2	0.4	1.0	0.8	0	0.4

ALPHA

	Cont	A	B	C	D	E	Cont.	A	B	C	D	E
1.	3.4	3.8	3.8	4.8	6.3	-	2.0	2.6	1.6	4.3	4.0	-
2.	3.3	4.0	4.6	6.0	-	5.2	1.7	1.7	1.4	3.0	-	5.2
3.	4.6	5.4	6.0	5.8	-	6.6	0.8	0.6	1.8	1.0	-	6.0
4.	5.8	6.8	6.4	7.2	6.6	7.8	1.0	5.5	3.4	5.2	6.6	9.5
5.	7.6	5.8	7.2	6.2	7.4	8.4	5.0	4.4	8.6	7.8	10.2	10.2
6.	5.8	7.4	7.8	7.0	7.4	6.6	4.4	9.8	6.6	6.6	6.0	8.4
7.	6.8	8.2	7.6	8.2	7.8	7.2	9.8	9.8	9.8	9.0	10.2	8.8

MONTY

	Cont	A	B	G	D	E	Cont	A	B	C	D	E
1.	0	0	0	0	0.8	-	0	0	0	0	0	-
2.	0	0	0.3	1.8	-	2.6	0	0	0	0	-	0
3.	0.2	1.6	2.4	3.5	-	4.0	0	0	0.6	1.3	-	0
4.	2.0	2.0	3.8	4.0	3.6	4.0	0	0.2	0	0.4	0	0
5.	3.3	3.6	4.0	4.0	3.8	4.0	0	1.0	0.8	0.8	0	0
6.	3.8	3.6	4.6	4.0	4.0	4.4	2.0	1.6	0	1.2	2.0	0.8
7.	3.4	3.8	3.6	3.8	4.4	3.6	0.4	2.0	2.2	0.8	2.0	0.8

Monty only at late sample dates, and chilling treatments were generally without effect.

(iii) Total number of flower buds

The total number of flower buds, the sum of terminal and lateral flower buds, was substantially higher in Alpha than Hayward or Monty (Table 15a and Figs. 31 and 32). For all cultivars, values increased markedly with later sample dates (Table 15a). Chilling treatments also increased values, especially over the early sample dates.

As the total number of flower buds at different sample dates, and after chilling treatments, was an important response, they were analysed for significance. After the square root transformation, analysis of variance with orthogonal polynomals (284) showed that, for each cultivar, there were highly significant trends for both sample date and chilling treatment effects (Table 16). These trends could be explained in terms of a linear, quadratic and an unexplained (departure) component. For the Monty cultivar only, there were significant sample date x chilling treatment interactions (Table 16).

(d) Average flower bud size per shoot

(i) Terminal flower buds

The average terminal flower bud size (breadth) generally increased both with later sample dates and with increasing chilling treatments (Table 17a). The average flower bud size in Alpha was substantially greater than those for Hayward and Monty. Bud breadth in Alpha for the control treatment at sample date 1 averaged 5.1 mm. while bud breadths for the values at the earliest sample date for Hayward (sample date 4) and Monty (sample date 3), had averaged 2.4 and 2.1 mm. respectively. At the final sample date (early September), average bud breadths for Alpha, Hayward and Monty were 7.6 mm., 4.1 mm., and 4.9 mm., respectively. With chilling, flower bud sizes increased only over the early sample dates.

(ii) Lateral flower buds

Because of lack of lateral flower buds, no trend could be examined in Hayward or Monty. On Alpha, the average size of lateral flower buds increased with later sample dates, and with chilling treatments only over the early sample dates (Table 17b). In Hayward and Monty lateral buds remained small; few grew over 3.0 mm. in breadth. In Alpha however,

Table 15

The effects of the period of chilling and the date of sampling on :

(a) The total number of flower buds per shoot.

(b) The average flower bud size (all buds included) per shoot.

HAYWARD

Treatment / Date	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	0	0	0	0	0	-	-	-	-	-	-	-
2.	0	0	0	0	-	0	-	-	-	-	-	-
3.	0	0	0	0	-	1.6	-	-	-	-	-	2.9
4.	0.5	0.3	0.3	3.0	3.5	3.8	2.4	4.0	2.7	3.2	5.2	5.1
5.	2.5	4.8	5.2	5.0	4.3	5.0	2.8	3.4	3.4	4.6	5.2	5.0
6.	2.0	4.0	3.3	3.3	5.2	4.0	4.7	3.7	3.2	3.8	4.5	3.6
7.	4.0	5.2	4.8	5.2	4.2	5.0	3.9	4.4	4.8	4.6	3.6	4.2

ALPHA

	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	5.4	6.4	5.4	9.0	10.3	-	4.2	4.1	4.6	3.9	4.5	-
2.	5.0	5.7	6.0	9.0	-	10.4	4.7	4.7	6.3	6.0	-	5.2
3.	5.4	6.0	7.8	6.8	-	12.6	6.2	7.4	6.4	6.9	-	5.5
4.	6.8	12.3	9.8	12.4	13.2	17.3	7.5	6.5	5.7	6.1	5.7	5.1
5.	12.6	10.2	15.8	14.0	17.6	18.6	6.6	6.6	5.9	6.0	5.9	5.2
6.	10.2	17.2	14.4	13.6	13.4	15.0	6.2	6.4	6.5	5.9	5.9	5.8
7.	16.6	18.0	17.4	17.2	17.8	16.0	6.1	5.9	5.3	6.2	5.6	5.6

MONTY

	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	0	0	0	0	0.8	-	-	-	-	-	3.2	-
2.	0	0	0.3	1.8	-	2.6	-	-	2.4	3.5	-	5.3
3.	0.2	1.6	3.0	4.7	-	4.0	2.1	5.1	4.5	5.7	-	6.0
4.	2.0	2.4	3.8	4.4	3.6	4.0	3.1	5.1	5.4	5.0	4.9	5.1
5.	3.3	4.6	4.8	4.8	3.8	4.0	4.8	5.5	5.8	4.3	4.6	5.0
6.	5.8	5.2	4.6	5.2	6.0	5.2	4.9	4.6	4.9	4.9	5.3	4.6
7.	3.8	5.8	5.8	4.6	6.4	4.4	4.6	5.1	4.5	4.8	4.1	4.1

Fig.31

The effect of the period of chilling and the date of sampling on the total number of flower buds per shoot.

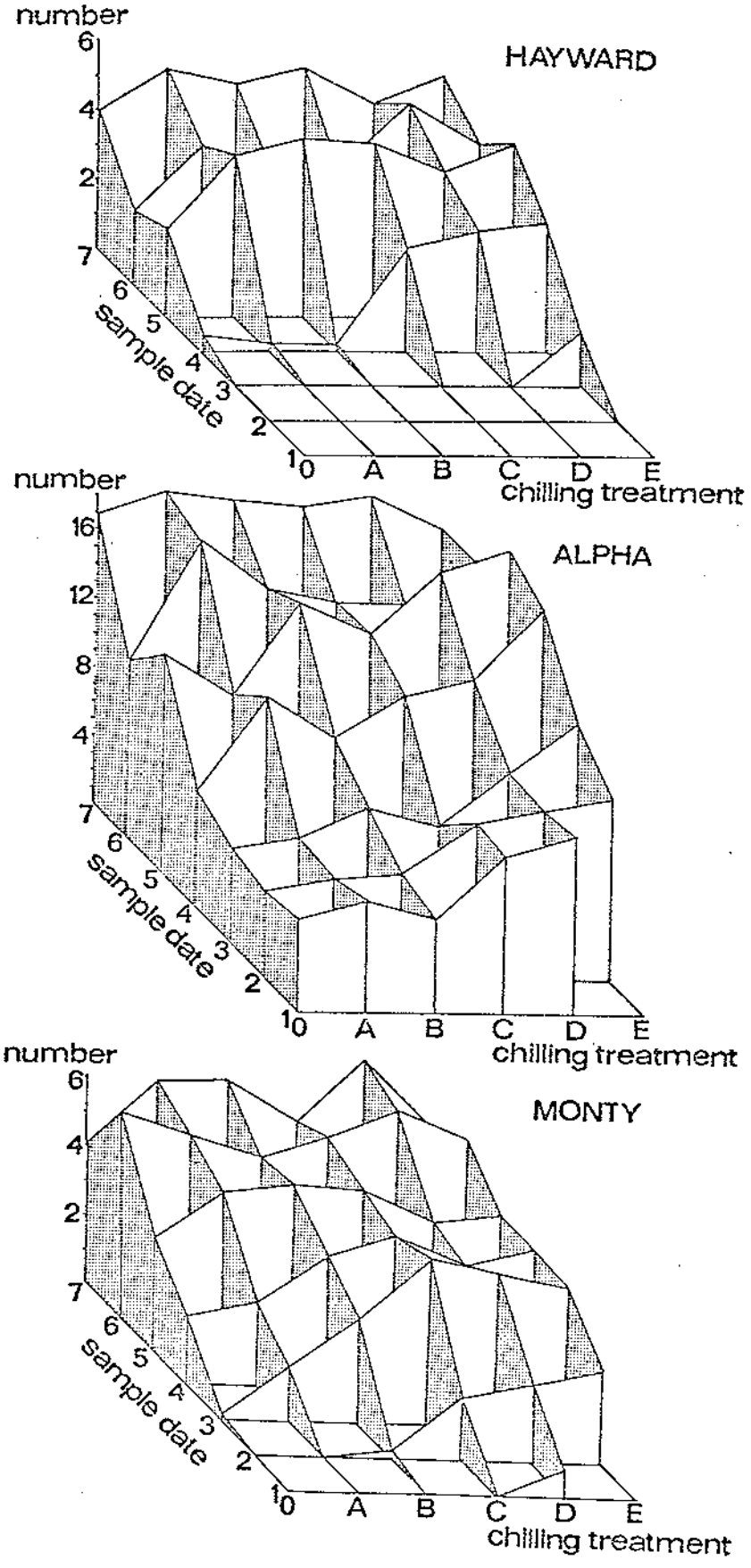


Fig.32

The effect of the period of chilling on flower bud development in different cultivars.

(a) The forcing of unchilled Hayward, Alpha and Monty buds at sample date 3 (June)

A Hayward

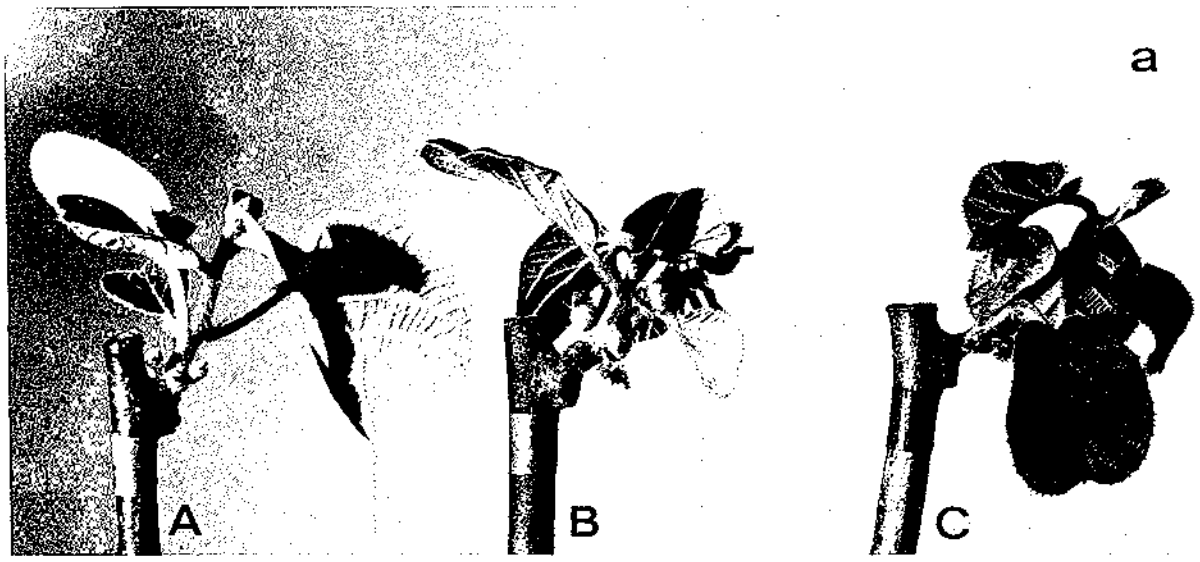
B Alpha

C Monty

(b) The effect of chilling at sample date 3 (June) in Monty

A Control

B 10 days chilling


a
A
B
C

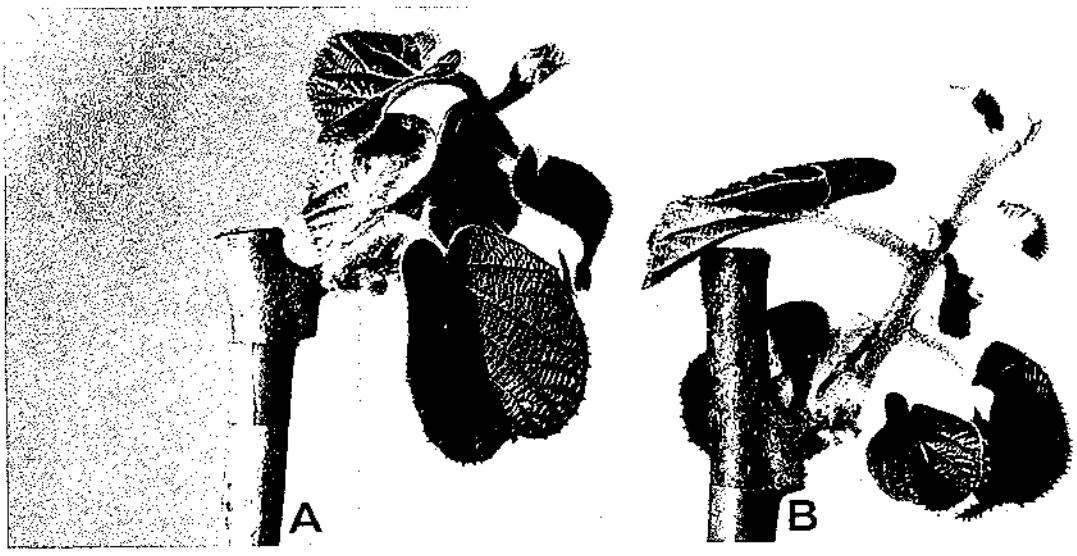

b
A
B

Table 16

Analysis of variance using orthogonal polynomals on the effects of the period of chilling and the date of sampling on the total number of flower buds per shoot (square root transformation).

	df	MS	Signif	
HAYWARD				
Treatment Linear	1	9.82	**	
Quadratic	1	0.19	NS	
Departures	3	0.20	NS	
Date Linear	1	74.31	**	
Quadratic	1	0.08	NS	
Departures	4	2.46	**	
Treatment x Date	27	0.49	NS	
Residual	78	0.32		

Data for 1E, 2D, and 3D were missing.

ALPHA				
Treatment Linear	1	7.18	**	
Quadratic	1	0.15	NS	
Departures	3	0.19	NS	
Date Linear	1	20.96	**	
Quadratic	1	0.18	NS	
Departures	4	4.95	**	
Treatment x Date	27	0.38	NS	
Residual	78	0.32		

Data for 1E, 2D, and 3D were missing.

MONTY				
Treatment Linear	1	13.11	**	Tested against interaction MS.
Quadratic	1	1.58	NS	
Departures	3	0.04	NS	
Date Linear	1	59.78	**	
Quadratic	1	3.43	*	
Departures	4	0.04	NS	
Treatment Linear x Date Linear	1	25.58	**	
Date Quadratic	1	1.61	**	
Date Departures	4	0.48	NS	
Treatment Quadratic x Date Linear	1	0.16	NS	
Date Quadratic	1	1.55	**	
Date Departures	4	0.46	NS	
Treatment Departures x Date Linear	3	0.51	**	
Date Quadratic	3	0.44	*	
Date Departures	9	0.36	*	
Residual	78	0.14		

Data for 1E, 2D, and 3D were missing.

NS = Not significant * = Significant 5% level ** = Significant 1% level

Table 17

The effects of the period of chilling and the date of sampling on :

(a) The average terminal flower bud size per shoot.

(b) The average lateral flower bud size per shoot.

HAYWARD

Treatment / Date	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	-	-	-	-	-	-	-	-	-	-	-	-
2.	-	-	-	-	-	-	-	-	-	-	-	-
3.	-	-	-	-	-	2.9	-	-	-	-	-	-
4.	2.4	4.0	2.7	3.5	5.2	5.2	-	-	-	-	-	-
5.	2.8	3.5	3.5	5.1	5.4	5.2	-	1.6	1.6	2.0	2.4	3.0
6.	4.4	4.6	3.2	4.2	5.0	3.6	-	2.3	-	-	2.2	-
7.	4.1	4.3	5.5	5.1	3.6	4.2	1.6	1.6	1.6	2.0	-	2.4

ALPHA

	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	5.3	5.8	5.8	5.8	5.8	-	1.4	1.6	1.6	1.9	2.4	-
2.	5.6	5.6	6.9	6.9	-	6.8	1.9	2.3	3.1	3.6	-	3.8
3.	7.1	7.8	6.9	7.2	-	7.0	3.4	3.7	4.3	4.6	-	3.9
4.	7.8	7.9	6.7	7.6	7.4	6.7	5.9	4.5	4.2	4.2	3.8	3.8
5.	7.6	8.0	7.6	7.7	8.0	6.7	4.8	4.4	4.4	4.3	4.4	4.0
6.	7.4	7.7	7.5	7.5	7.2	7.4	4.9	5.5	5.0	4.1	4.2	4.6
7.	7.6	7.2	7.1	7.9	7.0	7.2	5.0	4.8	3.8	4.7	4.1	4.5

MONTY

	Cont	A	B	C	D	E	Cont	A	B	C	D	E
1.	-	-	-	-	3.2	-	-	-	-	-	-	-
2.	-	-	2.4	4.0	-	5.3	-	-	-	-	-	-
3.	2.1	5.0	5.1	5.3	-	5.9	-	-	2.4	1.8	-	-
4.	2.6	5.1	5.5	5.2	4.8	5.1	-	3.2	-	2.4	-	-
5.	6.0	6.2	6.1	4.7	4.9	5.1	-	2.9	2.2	2.0	-	-
6.	5.8	5.3	4.9	5.5	6.3	4.9	3.1	3.1	-	2.5	3.2	2.0
7.	4.9	5.0	5.5	5.0	4.9	4.8	2.7	2.1	2.7	2.4	2.2	2.0

lateral flower buds increased in size from 1.4 mm. at sample date 1 to approximately 5.0 mm. at sample date 7.

(iii) Average flower bud size (all buds included)

Average bud breadth values (all buds included) per shoot were variable, but generally increased with later sample dates, and, especially at the early sample dates, increased with chilling treatments (Table 15b and Fig.33). Average values for Alpha were noticeably greater than for Hayward or Monty.

As with the data for the total number of flower buds, average flower bud breadth values (all buds included) were analysed for significance (Table 18). Because of insufficient data it was not possible to analyse the results of Hayward and Monty over all the sample dates. Analyses of variance with orthogonal polynomals (without transformation), over sample dates 4-7 in Hayward, 1-7 in Alpha, and 3-7 in Monty showed that significant sample date and chilling treatment trends occurred in only Alpha (Table 18). All the significance in Alpha values could be explained by the linear and quadratic components. Values for all cultivars had significant sample date x treatment interactions (Table 18).

C. DISCUSSION

Rest termination

Results obtained with controlled temperatures suggest that the two pistillate cultivars, Hayward and Monty and the staminate clone Alpha have a low chilling requirement to overcome bud rest. In contrast with most decidious fruit trees (267), Chinese gooseberry buds could be forced into growth before the winter, without any supplementary chilling (Table 11 and Fig.30). This was even before leaf fall. The chilling requirement to overcome rest seems comparable to the situation in the grape where cuttings of different cultivars, taken before leaf fall could also be forced into growth (16, 170). Outdoor observations, and chilling temperature summations, also indicate that many cultivars of grapes have low chilling requirements to terminate rest (10,37,60). It is probable that Chinese gooseberry buds, like the grape (16) are in a state of dormancy over the winter, the buds being prevented from bursting only by the cold temperature.

Like most other plant species, lateral buds in Chinese gooseberry generally do not burst prior to leaf fall. These are thought to be prevented from bursting due to correlated inhibition, initially through

Fig. 33

The effect of the period of chilling and the date of sampling on the average flower bud size (all buds included) per shoot.

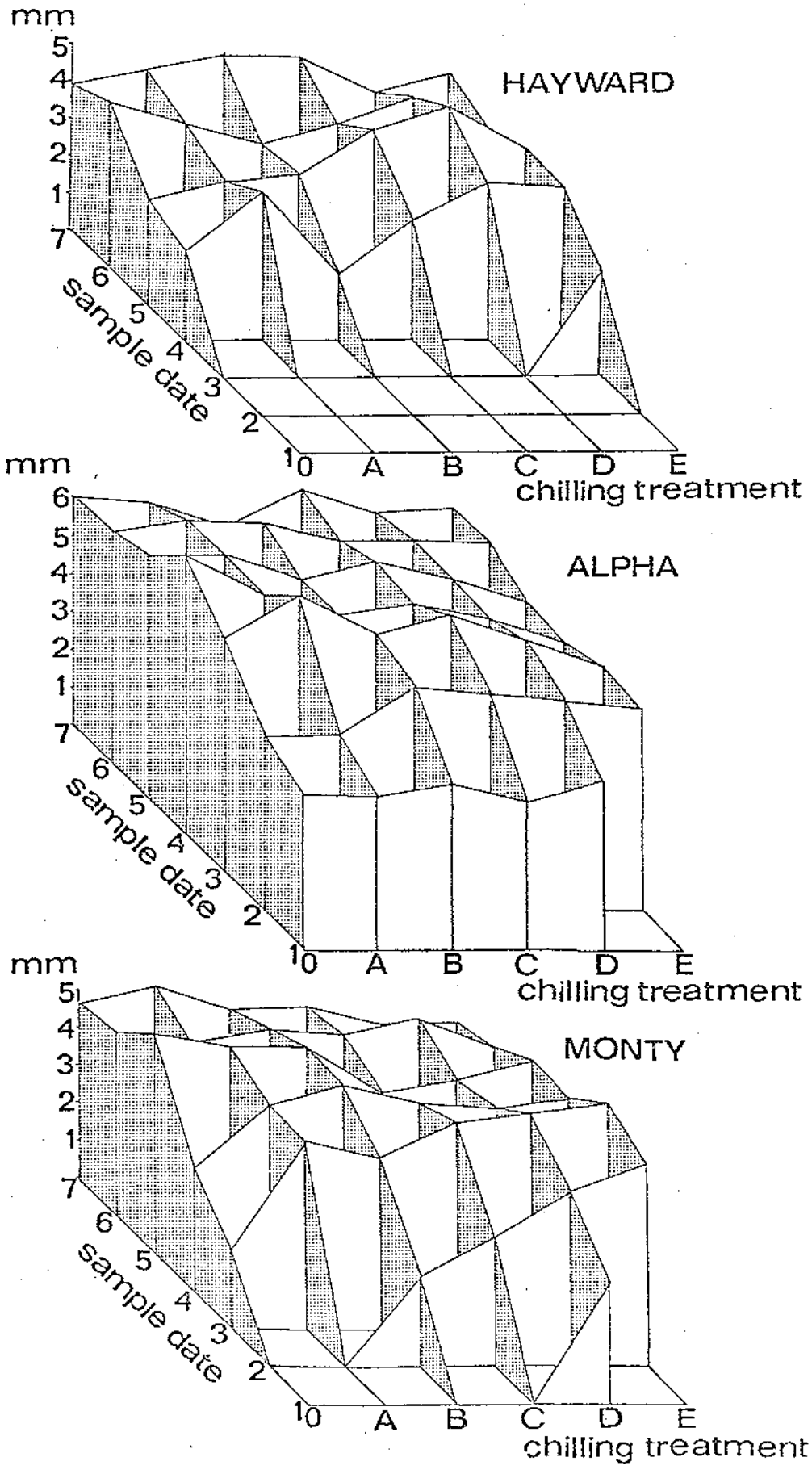


Table 18

Analysis of variance using orthogonal polynomals on the effects of the period of chilling and the date of sampling on the average flower bud size (all buds included) per shoot (no transformation).

	df	MS	Signif.	
HAYWARD (Sample dates 4-7 only)				
Treatment	5	1.4	NS	
Date	3	1.0	NS	
Treatment Linear x Date Linear	1	6.70	**	
Date Departures	2	2.32	NS	
Treatment Departures x Date Linear	4	1.81	NS	
Date Departures	5	1.64	NS	
Residual	50	0.75		

There were no data for 4Cont, 4A, and 4B, and two replicates only for 6Cont. (Insufficient data to estimate quadratic effects.)

ALPHA (All sample dates)				
Treatment Linear	1	11.86	**	Tested against interaction MS.
Quadratic	1	1.82	NS	
Departures	3	0.19	NS	
Date Linear	1	39.24	**	
Quadratic	1	58.39	**	
Departures	4	2.10	NS	
Treatment Linear x Date Linear	1	0.22	NS	
Date Quadratic	1	3.27	*	
Date Departures	4	1.48	*	
Treatment Quadratic x Date Linear	1	0.70	NS	
Date Quadratic	1	0.02	NS	
Date Departures	4	1.31	NS	
Treatment Departures x Date Linear	3	0.38	NS	
Date Quadratic	3	0.70	NS	
Date Departures	3	1.06	NS	
Residual	78	0.56		

Data for 1E, 2D, and 3D were missing.

MONTY (Sample dates 3-7 only)				
Treatment	5	0.29	NS	Tested against interaction MS.
Date Linear	1	5.15	NS	
Quadratic	1	1.23	NS	
Departures	2	2.71	NS	
Treatment Linear x Date Linear	1	2.86	NS	
Date Quadratic	1	0.30	NS	
Date Departures	2	4.43	**	
Treatment Quadratic x Date Linear	1	0.01	NS	
Date Quadratic.	1	0.13	NS	
Date Departures	2	2.20	NS	
Treatment Departures x Date Linear	3	0.95	NS	
Date Quadratic	3	1.47	NS	
Date Departures	4	2.63	**	
Residual	62	0.72		

Data for 3Cont and 3D were missing.

NS = Not significant * = Significant 5% level ** = Significant 1% level

apical dominance and subsequently by the foliage leaves (297, 312). The commercial practice of summer pruning, which destroys apical dominance, often forces distal lateral buds into growth. This tendency varies between cultivars.

In a recent review of dormancy, Wareing and Saunders (313) suggested that the onset and termination of rest was influenced by the relative amounts of endogenous growth substances (promotors and inhibitors) in buds of woody plants. One hypothesis receiving widespread support is that the decline in inhibitor levels in buds which parallels emergence from rest, are overcome by growth promotor levels, which follow an inverse relationship with the inhibitors (39,297). Bud scales have been shown to contain inhibitory substances (313), and it is thought that their removal (16,270, 297), as well as the soaking of buds in water (16,316), hastens the termination of rest by the leaching out of inhibitors. The fact that rest can be extended or hastened in grapes (16,170,316,318) and other fruit trees (242,268), by the applications of various growth regulators further implicates the role of hormones in dormancy.

There were indications that artificial chilling in the dark conditions of the refrigerator did not completely substitute for the chilling in the field. While the amount of chilling at $4^{o}C$ for 40-50 days is considerably greater than that occurring naturally, cuttings taken in the autumn (before natural chilling had commenced) and subjected to 40 days at $4^{o}C$ did not hasten the number of days to bud burst as much as control cuttings (receiving no artificial chilling) taken in the spring when most of the natural chilling had been completed (Table 11a and Fig.30). This situation has also been reported in the cranberry (260).

Flower bud development

Results suggest that the Chinese gooseberry does not have an absolute cold temperature requirement for flower evocation; the reproductive state appeared to be present on control shoots (no artificial chilling) taken in the autumn (early May, ie. without natural chilling), and generally for each cultivar, the number of reproductive axils per shoot did not increase, at later sample dates, or with chilling treatments (Table 12a).

It was not possible to characterise the temperature requirement for flowering in the Chinese gooseberry as the exact time of evocation is not known. As well as the well documented chilling requirements for flowering in the olive (124), low temperatures are generally conducive to flowering in citrus (147,154,186,219). On the other hand, higher temperatures around evocation favour flowering in the grape (49,50,51) and the apricot (210).

In the cranberry, the production of normal flowers was not only ensured by satisfaction of cold requirement, but also involved exposure of buds to temperatures above 45°F (260).

In the Chinese gooseberry the breaking of the rest period did not ensure production of normal flower buds. While cuttings taken in the autumn were able to burst even without artificial chilling, it was only in Alpha that a few normal flower buds were present. Normal flower buds did not appear in the pistillate cultivars until well into the winter (Fig.31). In all cultivars, the number of normal flower buds per shoot generally increased at later sample dates (greater natural chilling). It therefore appears that flower development in the Chinese gooseberry is a separate, though parallel, process to that of satisfaction of the rest period requirement. This has also been reported in the cranberry (260). As with the termination of rest (above), there were indications that the artificial chilling in the dark conditions of the refrigerator did not completely substitute for the chilling in the field. Further, the fact that artificial chilling at later sample dates did not increase the number of normal flower buds per shoot (there were still abberant flowering axils present), indicates that other factors, apart from chilling, are influencing flowering. Warm temperatures, day length, and light intensities are other environmental factors which influence the production of normal flowers in other fruit crops (155,205,239,260), and may influence flowering in the Chinese gooseberry.

It is well known that flower bud development can be influenced by endogenous growth substances which are synthesised by the various meristematic areas of the plant (88).

Up until mid June (sample date 3) when leaf fall occurred, the presence of leaves, which synthesise growth regulators would influence the overall hormonal balance of the vine (164). In Hayward and Monty the crop, which undoubtedly influences the hormonal balance of the vine (64), was not harvested until the May-June period (sample dates 2 and 3). The roots and growing shoots are also rich sources of plant growth regulators and, depending on the conditions (temperature), would also influence the hormonal composition of the vine (197,278). Undoubtedly the hormonal status of the vine alters over this period.

Further, the cambium actively synthesises growth regulators (230), and Skene (see 280) has shown in grape cuttings that limited cambial division takes place during cold storage. Skene (280) also raises the possibility that in the intact vine the cambium provides significant quantities of

cytokinins, especially during periods when contributions from the roots are low. Cytokinins have been shown to stimulate inflorescence size in grapes (226) and their levels in the xylem sap of grape cuttings rise during cold storage and would be available for the emerging bud (280). This may be one of the factors accounting for the stimulated flower bud production in Chinese gooseberry cuttings after chilling. Growth inhibitors, eg. abscisic acid (ABA) also influence flower production in some species (4,88) and their concentrations have been shown to decrease with cold treatment (88).

The carbohydrate status also influences the capacity of the vine or plant to produce flower buds (248). Carbohydrates accumulate in the vine over the growing season, reaching a peak around the time the leaves become non functional (sample date 3). From leaf fall, carbohydrate levels fall only slowly. In grape vine stems, the decrease in carbohydrate levels during the dormant season was about 0.5% per month (331). The composition of carbohydrates over that period changes; and there is a marked fall in starch, and a corresponding rise in sugars during winter under natural conditions, followed by a partial reversal to a second starch peak in early spring (331). In other words the carbohydrate status in the cuttings taken over the winter varies. Further, the carbohydrate composition also has been shown to alter during storage at $4^{o}C$, ie. sugars were depleted by respiration during cold storage without the starch content being affected (46).

A number of workers report that low temperatures often lead to the accumulation of carbohydrates at the shoot apex and their presence parallels the initiation of flowering (88).

Shoot and flower buds on single node Chinese gooseberry cuttings make only limited growth and by 25 dabb. begin to wither (see Ch.2). It is probable that the carbohydrate reserves become depleted (331). In the absence of roots, water vessels are no doubt soon plugged up at the basal end, helping to create a water deficit in the growing shoot.

Further the nutrient status, particularly nitrogenous reserves, alter in concentration throughout the season (246) and could conceiveably modify any flowering stimulus.

While no information is available on the causes of the chilling response (natural and artificial) in the Chinese gooseberry, it seems likely that results could be due to differences in the hormonal, carbohydrate and nutritional status in the cutting which would be changing during the course of the experiment.

There were marked differences in the results recorded between the

cultivars, especially the pistillate cultivars Hayward and Monty as compared with the staminate clone Alpha.

The fact that in both pistillate cultivars, flower buds were formed at a much later date than in the staminate clone, that there were almost no lateral buds, and that the average flower bud size was much lower, indicates some or all of the following:

(a) The hormonal, carbohydrate and nutritional requirements for pistillate flower bud development are greater.
(b) The hormonal, carbohydrate and nutritional requirements for pistillate flower bud development are more specific.
(c) The hormonal, carbohydrate and nutritional levels within pistillate plants are lower.

This situation seems comparable to that in some cucurbits where there is a trend, from underdeveloped staminate flowers, to normal staminate flowers, to normal pistillate flowers up the stem (231). That trend occurs under all conditions, but the duration of each phase, in terms of node number, can easily be modified by environmental conditions such as light (231).

The inability of Monty to produce its characteristic lateral flower buds on single node cuttings, while Alpha did so, could further support the theory of a greater and/or more specific flowering stimulus requirement for pistillate flowers. As the shoot growth in Alpha was also more vigorous than Monty (or Hayward), a greater level of carbohydrates or other reserves could also account toward the observed differences although the bulky ovary, which is produced in pistillate flowers, could modify such levels.

These studies with isolated cuttings show that differences between Hayward and Monty were not marked. However field observations show that Hayward produces virtually only terminal fruit of a large size, while Monty produces smaller fruit in clusters of three. As the number of lateral flower buds, the total number of flower buds, and their average size were similar in this study at the final sampling date, carbohydrate reserves would appear to be similar. It seems that some factor(s) not present, or present in suboptimal amounts, in the isolated system were required for lateral flower production in Monty. Such a factor(s) could originate in the root and be hormonal in nature.

Chapter 6

A SURVEY OF THE FLOWERING CHARACTERISTICS OF VARIOUS CULTIVARS AND STAMINATE VINES

A. INTRODUCTION

Lack of pollination is one of the factors limiting production of Chinese gooseberries. Without adequate fertilization the fruit does not develop to a commercial size and also has a less attractive appearance.

The degree of pollination is likely to be influenced by a number of factors including the ratio of pistillate to staminate vines in the orchard, the weather, the number and distribution of flowers on staminate vines, as well as the relative time of peak flowering between the staminate and pistillate vines.

At present there are only two named staminate Chinese gooseberry cultivars (Tomuri and Matua), although there are known to be a number of different selections in use. No survey on the detailed flowering characteristics of the staminate selections or cultivars have been reported. If these criteria can be put on a quantitative basis it may be possible to screen selections for their potential effectiveness as pollinators.

While the main pistillate cultivars of Chinese gooseberries have been described in terms of their individual flower and fruit characteristics (222), no account, quantitatively expressing the distribution of flowers on these cultivars has been reported.

A survey of the flowering characteristics was carried out on the staminate vines growing at the Kumeu orchard and were compared with the two named cultivars growing at Oratia. As well, the flowering characteristics of the important pistillate cultivars growing at Oratia were surveyed.

B. EXPERIMENTAL OBSERVATIONS AND RESULTS

I STAMINATE VINES

(a) Number of flowers and flowering axils per shoot

Ten to twenty shoots per vine were chosen at random on the staminate vines growing at Kumeu and Oratia. Analysis of results from 10 of those

shoots chosen at random showed there were significant variations in the numbers of flowers and flowering axils per shoot between vines (Table 19). The staminate vines growing at Kumeu were identified by their row positions. The number of flowers per shoot varied from 9.0 - 23.5; the named cultivars Tomuri and Matua averaging 18.4 and 19.8 flowers per shoot respectively. The number of flowering axils per shoot varied from 3.3 - 7.9 with Tomuri having 4.5 and Matua having 6.6. flowering axils per shoot.

(b) Percentage of shoots bursting per lateral

Ten or fifteen laterals were chosen at random and the number of shoots bursting and the total number of nodes per lateral were recorded and percentages calculated. The number of nodes per sampled lateral varied from 3 - 44, but the majority were between 15 - 30.

Preliminary analysis indicated that some bias was introduced by including very short laterals bearing 3 - 5 nodes because they gave a significantly higher bud break than on longer laterals. This was not unexpected. It therefore seemed justifiable to make the comparison between vines using long laterals bearing 9 or more nodes. Results on 7 such laterals chosen at random showed that there were significant differences between vines (Table 19).

Shoot burst varied from 27.2% - 68.4%, with values for Tomuri and Matua 33.5% and 52.4% respectively.

(c) Flowering index for grouped vines

From overall observations of flowering and vegetative characteristics it seemed highly probable that the 14 staminate vines originally came from 3 different vine sources. Further, none of these groups appeared to be either of the two named cultivars Tomuri or Matua. Accordingly vines, B4, B10, C7, D4 and D14 were grouped and called Alpha; vines B1 and C17 called Beta; and vines A3, A7, A11, A14, B16, C13 and D8 called Gamma. Analysis on the grouping of these vines, and for the named cultivars Tomuri and Matua, showed that there were significant differences between groups for all above parameters (Table 20).

As the density of flowers per vine is one important factor in ensuring adequate pollination, a flowering index could be effective in screening for a selection's potential as a pollinator. The flowering index would be the product of the mean number of flowers per shoot (Table 19) and the percentage of shoots bursting along a lateral (Table 19). The flowering index for the staminate vines shown in Table 21, was based upon the grouped mean values. For groups Alpha and Beta, the flowering index

Table 19

The number of flowers per shoot, the number of flowering axils per shoot, and the percentage bud burst for various staminate vines.

Vine	B4	C7	D4	D14	B10	B1	C17	Mat.	Tom.	A3	A14	D8	A7	C13	A11	B16
	Number of flowers per shoot (10 shoots).															
Mean	22.2	20.2	19.1	23.1	17.2	19.3	16.9	19.8	18.4	17.4	13.8	12.2	14.6	15.7	13.7	9.0
Signif 5%	a*	ab	abc	a	abc	abc	abc	ab	abc	abc	bcd	cd	bcd	abc	bcd	d
Signif 1%	AB	ABC	ABC	A	ABC	ABC	ABCD	ABC	ABC	ABC	BCD	CD	ABCD	ABCD	BCD	D
	Number of flowering axils per shoot (10 shoots).															
Mean	7.9	7.4	7.3	7.1	7.2	6.8	6.4	6.7	4.5	4.7	4.5	3.8	4.3	3.9	3.9	3.3
Signif 5%	a	ab	ab	ab	ab	ab	b	ab	cd	cd	cd	cd	cd	cd	cd	d
Signif 1%	A	A	A	A	A	A	A	A	B	B	B	B	B	B	B	B
	Percentage bud burst (7 laterals).															
Mean	60.7	57.5	59.0	58.1	49.6	68.4	60.7	52.4	33.5	42.8	44.0	51.7	39.5	27.2	37.0	39.3
Angle transf.	51.3	49.3	50.2	49.7	44.8	55.7	51.2	46.4	35.3	40.9	41.5	46.0	38.9	31.5	37.5	38.8
Signif 5%	ab	abc	abc	abc	abcd	a	ab	abcd	de	bcde	bcde	abcd	bcde	e	cde	bcde
Signif 1%	AB	ABC	ABC	ABC	ABCD	A	AB	ABC	CD	ABCD	ABCD	ABC	BCD	D	BCD	BCD

One way analysis of variance, multiple comparison of vines by Tukey's method.

* Values with no letter in common are significantly different at that level.

Table 20

The number of flowers per shoot, the number of flowering axils per shoot, and the percentage bud burst for grouped staminate vines.

Group	Alpha	Beta	Matua	Tomuri	Gamma
	Number of flowers per shoot, all shoots grouped.				
Mean	20.4	17.6	18.5	18.6	13.2
Number	60	40	20	20	140
Signif 5%	a*	ab	ab	ab	b
Signif 1%	A	AB	AB	AB	B
	Number of flowering axils per shoot, all shoots grouped.				
Mean	7.4	6.6	6.5	4.6	4.1
Number	60	40	20	20	140
Signif 5%	a	a	a	b	b
Signif 1%	A	A	A	B	B
	Percentage bud burst, all laterals grouped.				
Mean	56.6	63.2	52.4	33.5	40.0
Angle transf.	48.8	52.7	46.4	35.3	39.2
Number	47	26	7	7	98
Signif 5%	ab	a	abc	bc	c
Signif 1%	A	A	AB	AB	B

Analysis of variance, multiple comparison for vines followed by multiple comparison of groups by Scheffe's method.

* Treatments with no letter in common are significantly different at that level.

was greater than the existing cultivars, while group Gamma was lower.

Table 21

A flowering index of various staminate clones
(Number of flowers per lateral)

Tomuri	623
Matua	969
Alpha	1155
Beta	1112
Gamma	528

(d) Number of flowers per inflorescence

From the recorded number of flowers in each flowering axil per shoot, the number of flowers per inflorescence for each vine, as well as for each group was obtained (Table 22). There was considerable variation in the number of flowers per inflorescence, as well as the frequency of that distribution. The number of flowers per inflorescence varied from 1 - 3 in vine C7 to 1 - 9 in vine A14. There were relatively few inflorescences with greater than 3 flowers in Matua and the groups Alpha and Beta, while group Gamma and Tomuri, had a high proportion of inflorescences containing 4 or more flowers.

(e) Distribution of flowers per shoot

Using the flowering data for the same 10 or 20 randomly selected shoots per vine, the average number of flowers per inflorescence along a shoot could be calculated. Figure 34 shows the mean values for each group. For the group Gamma, and Tomuri, there was a greater number of flowers per axil spread over fewer flowering axils compared with the other groups. Matua and groups Alpha and Beta all had similar flower distribution patterns.

(f) Flower opening sequence

At 2 day intervals from 11/11/71, the proportion of flowers open were visually estimated for all the staminate vines growing at Kumeu and were compared with the Hayward cultivar in the same orchard (Fig.35). Ninety per cent bloom was reached about 5 days earlier than Hayward for

Table 22

The number of flowers in inflorescences of various staminate clones.

Flowering axils having			1	2	3	4	5	6	7	8	9	flowers
												Number of flowering axils
Matua	(20)		12*	7	100	7	3					129
		%	9.3	5.4	77.5	5.4	2.3					
Tomuri	(20)		2	10	17	28	22	8	4			91
		%	2.2	11.0	18.7	30.8	24.2	8.8	4.4			
B4	(10)		7	14	48	7	3					79
B10	(10)		17	15	36	3	1					72
C7	(10)		6	17	51							74
D4	(10)		13	13	18	7	2					73
D14	(10)		3	10	35	15	8					71
Alpha	(40)	Total	46	69	208	32	14					369
		%	12.5	18.7	56.4	8.7	3.8					
B1	(20)		23	11	104	2	0	1				141
C17	(20)		24	11	94	1						130
Beta	(40)	Total	47	22	198	3	0	1				271
		%	17.3	8.1	73.1	1.1	0	0.4				
A3	(20)		5	12	27	22	10	12	3	2		93
A7	(20)		7	12	49	12	8	1				90
A11	(20)		7	15	32	10	6	4	3			78
A14	(20)		8	11	44	15	4	3	2	0	1	88
B16	(20)		7	9	29	12	4	1				62
C13	(20)		4	12	25	18	21					80
D8	(20)		10	9	28	13	9	22				73
Gamma	(140)	Total	48	81	234	102	62	23	11	2	1	564
		%	8.5	14.4	41.5	18.1	10.1	4.1	2.0	0.4	0.2	

* Total of vine values.

Number of replicates (shoots) per vine in brackets.

Fig. 34

Number of flowers at each flowering axil along a shoot in various staminate clones

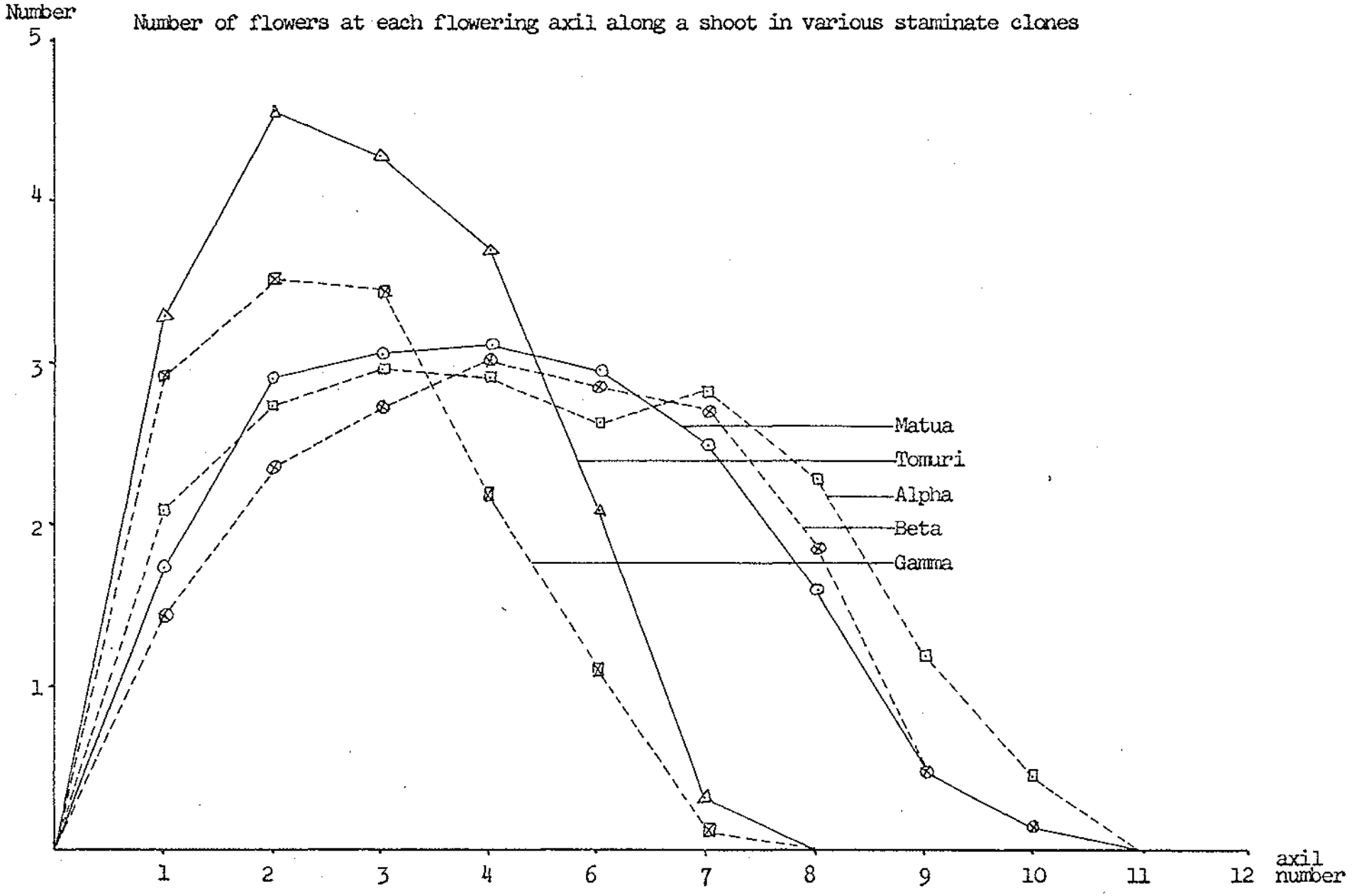
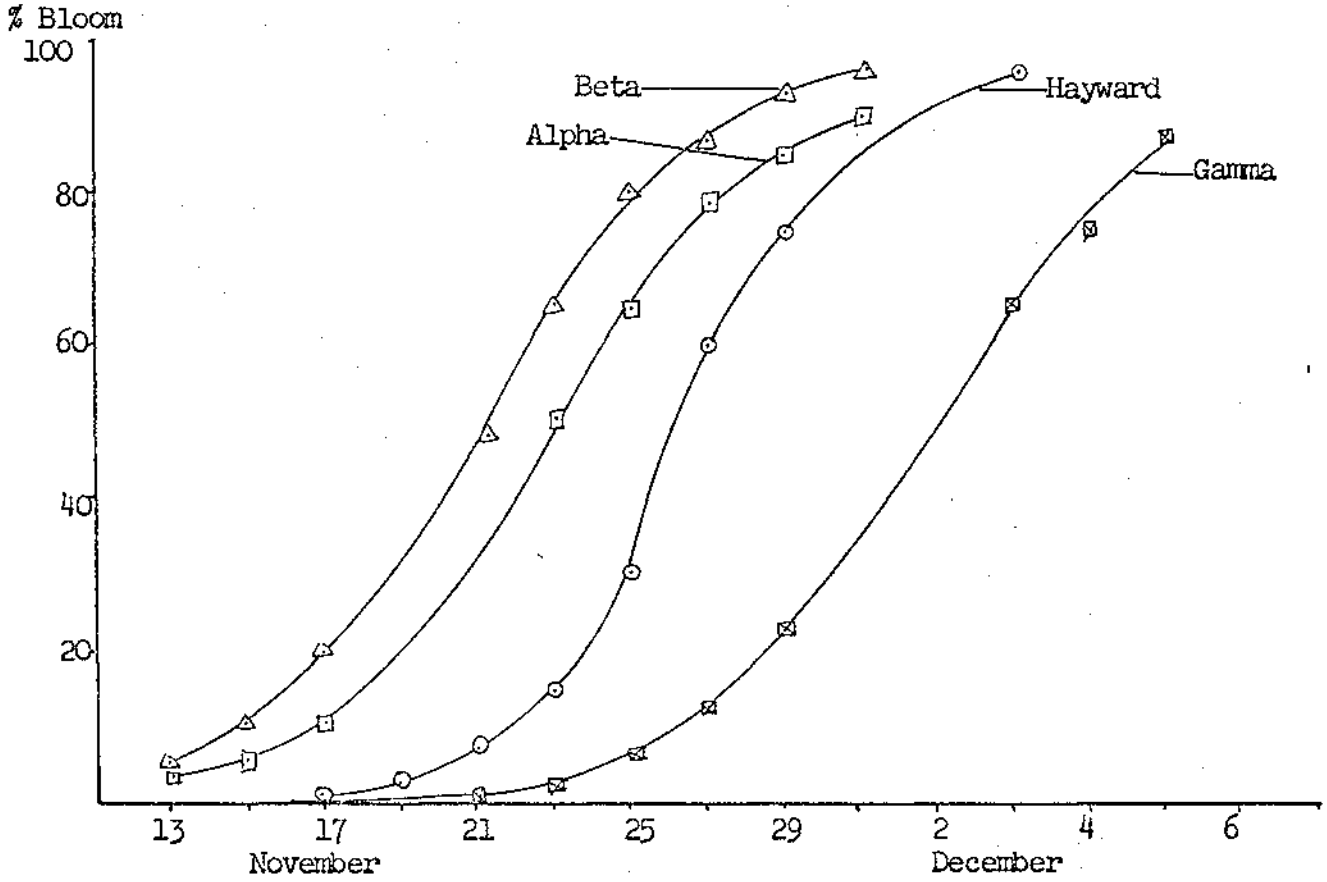


Fig.35

The flower opening sequence of various staminate cultivars compared with that in Hayward.



group Beta, 2 days earlier for group Alpha, but 8 days later for group Gamma.

II PISTILLATE CULTIVARS

(a) Number of flowers and flowering axils per shoot

Twenty shoots per vine were chosen at random on all the pistillate cultivars growing at Oratia. There were 3 vines per cultivar except for Allison where there were two. The number of flowers per shoot, and number of flowering axils per shoot for each showed considerable variation (Table 23). The number of flowers per shoot varied from 4.4 for Hayward, to 13.6 for Monty, and the number of flowering axils per shoot varied from 4.1 for Hayward to 5.7 for Bruno.

(b) Percentage of shoots bursting per lateral

Fifteen laterals per vine were chosen at random. The number of nodes per lateral varied from 4 - 27, but the majority for all vines were within the range of 10 - 20 nodes. Results showed that the percentage of shoots per lateral for Hayward (45.5%) was considerably lower than the other cultivars (70.5% - 73.8%)(Table 23).

(c) Number of flowers per inflorescence

From the recorded number of flowers in each flowering axil per shoot the total number of flowers per inflorescence could be calculated for each available vine and each cultivar (Table 24). Results showed that almost all of the Hayward flowers were borne singularly, while most of the Monty inflorescences contained 3 or more flowers.

(d) Distribution of flowers per shoot

From the flowering data for the same 20 randomly selected shoots per vine the average number of flowers in each flowering axil along a shoot could be calculated. Figure 36 shows the mean for each cultivar. Except for the upper flower axils, Monty was shown to have considerably more flowers per axil. Hayward on the other hand, generally had the fewest number of flowers per axil. Bruno had more flowers; the nature of the graph (Fig.36) showed these were more equally distributed over a larger number of axils.

Table 23

The number of flowers per shoot, the number of flowering axils per shoot, and the percentage bud burst for various pistillate cultivars.

	Hayward	Monty	Bruno	Abbott	Allison
Number of flowers per shoot (20).					
	4.7*	15.6	7.1	6.9	9.7
	4.4	13.2	7.6	7.4	8.9
	4.3	12.1	6.7	9.1	
Mean	4.4	13.6	7.1	7.8	9.3
Number of flowering axils per shoot (20).					
	4.4	5.2	5.7	3.9	5.2
	4.1	4.8	6.0	4.7	4.9
	3.8	4.4	5.5	5.7	
Mean	4.1	4.8	5.7	4.8	5.0
Percentage bud burst (20).					
	40.2	71.6	71.7	73.8	70.4
	50.6	69.4	73.3	71.7	74.8
			67.6	75.8	
Mean	45.5	70.5	70.9	73.8	72.6

* Mean of vine values.

Number of replicates (laterals) per vine in brackets.

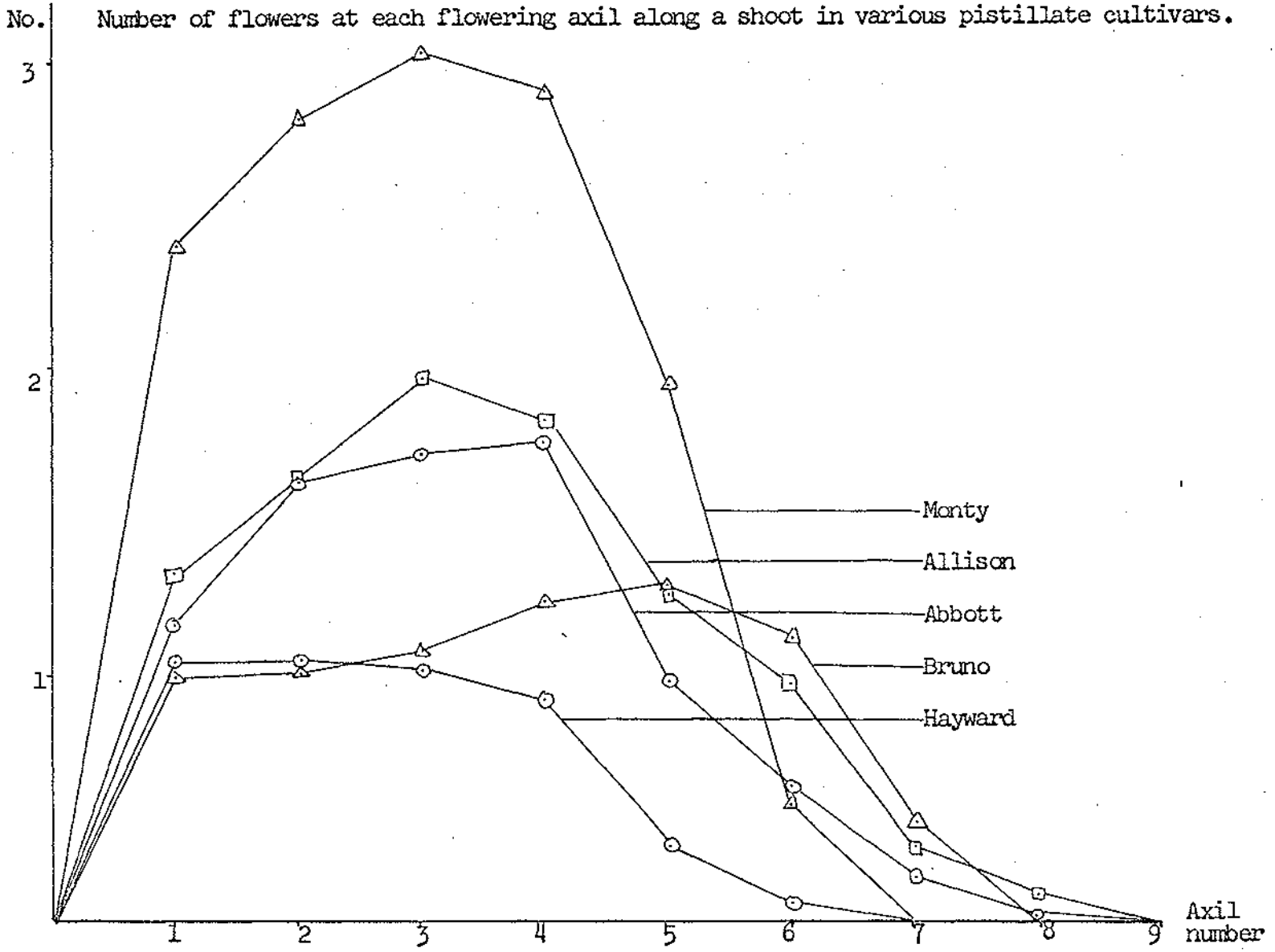
Table 24

The number of flowers in inflorescences of various pistillate cultivars.

	Flowering axils having 1	2	3	4 flowers	Number of flowering axils
Hayward	a. 83	4	1		88
	b. 76	4	1		81
	c. 70	5	1		76
	Total 229	13	3		245
	% 93.5	5.3	1.2		
Monty	a. 4	7	83	11	105
	b. 9	9	76	2	96
	c. 5	12	68	2	87
	Total 18	28	227	15	288
	% 6.3	9.7	78.8	5.2	
Bruno	a. 97	11	10		119
	b. 90	17	6		113
	c. 88	19	3		109
	Total 275	47	19		341
	% 80.6	13.8	5.8		
Abbott	a. 70	17	26		113
	b. 38	21	19		78
	c. 61	14	19		94
	Total 169	46	62		285
	% 59.3	18.2	22.5		
Allison	a. 49	18	36		103
	b. 43	28	26		97
	Total 92	46	62		200
	% 46.0	23.0	31.0		

Total of 20 shoots per vine.

Fig.36


No.
Number of flowers at each flowering axil along a shoot in various pistillate cultivars.
3
2
1
Monty
Allison
Abbott
Bruno
Hayward
1
2
3
4
5
6
7
8
9
Axil number

C. DISCUSSION

This survey set out to quantitatively separate the staminate vines and cultivars on the basis of their flowering characteristics. Analysis of the results generally did not conflict with the overall vegetative and flowering observations that the staminate vines came from three different vine sources (Table 19). Within groups Alpha and Beta, all parameters tested (number of flowers per shoot, number of flowering axils per shoot and number of burst shoots per lateral) were not significantly different from each other (Table 19). While there were no significant differences in the number of flowering axils per shoot between vines within the group Gamma, there were significantly different numbers of flowers per shoot and percentage shoots bursting per lateral.

These differences occurred only between one pair of vines for the two parameters, and the pair of vines were different for each parameter. Vine B16 had a significantly lower number of flowers per shoot than vine A3, and vine C13 had a significantly lower percentage of burst shoots per lateral than vine D8.

While other factors such as the amount of pruning, and variations in soil type or environmental conditions, might be contributing factors to the variability in that group, no real correlation was apparent. A further possibility is that other staminate selections were included in this group in spite of the fact that all appeared to be similar on overall appearance.

Analysis of the grouped vines and cultivars showed significant differences for all parameters. While there were no significant differences between groups Alpha and Beta for all parameters, they were significantly higher than Gamma in the number of flowers per shoot and percentage shoot burst per lateral. Although there were also significant differences in the number of flowering axils per shoot between groups Alpha and Gamma, there were no significant differences in that value between those groups and group Beta (Table 20).

Although climatic conditions at Kumeu and Oratia are not very different, comparison between vines growing at the two locations is not strictly exact. The staminate clones at Oratia were trained differently. They were grafted on to pistillate vines and trained along wires above them. This may have resulted in altered vigour. As well, some staminate vines in each group at Kumeu were less heavily pruned than others, but there were no significant differences in the parameters recorded. However such a quantitative comparison of new selections with some standard (the

established cultivars) is useful as an initial screening procedure for later, better based evaluations.

For the number of flowers per shoot, or percentage burst shoots per lateral, cultivars Tomuri and Matua generally had intermediate values. Neither was significantly different from each other, or from groups Alpha or Beta, or from group Gamma. Tomuri did not have significantly different number of flowering axils per shoot from group Gamma, but both Tomuri and Gamma were significantly lower than Matua and groups Alpha and Beta (Table 20).

Although Matua had slightly more flowers per shoot than the poorest staminate group Gamma, values for the staminate groups were generally far greater than for the pistillate cultivars (Tables 20 and 23). Similarly, the denser flowering staminate groups had a greater number of flowering axils per shoot than the pistillate cultivars. However, apart from Hayward, the percentage of shoot burst per lateral for the staminate groups was considerably lower than for the pistillate cultivars (Tables 20 and 23). Compared with the other pistillate cultivars Hayward showed a considerably lower number of flowers per shoot, number of flowering axils per shoot and percentage shoot burst per lateral (Table 23). The reduced number of flowers per shoot for Hayward was largely due to the virtual lack of lateral flowers in each axil (Table 24) and, to a lesser extent, the fewer number of flowering axils per shoot (Table 23). The large number of flowers per shoot for Monty was due to the high proportion of inflorescences having three or more flowers as the number of flowering axils was not greatly different from the other cultivars (Fig.36).

Compared with the pistillate cultivars, the staminate vines had a much greater range in the number of flowers per inflorescence (Tables 22 and 24).

While pistillate cultivars had up to 4 flowers per inflorescence (Table 24), all staminate groups had a least 5 flowers per inflorescence (Table 22). Tomuri had over 4% of its inflorescences with 7 flowers and one of the unnamed vines (A4), had 9 flowers in one inflorescence. This range of flowers per inflorescence is comparable with that found in *Actinidia kolomikta* where nearly 7% of inflorescences contained 7 or more flowers, and, up to 10 flowers per inflorescence were recorded (171).

The relative time of peak flowering between staminate and pistillate vines is an important factor governing the pollinator's suitability (Fig.35). Purely on grounds of flower opening time, the group Gamma is not likely to be suited as a pollinator for Hayward because its peak of bloom (50% opening) was some 6 days later than Hayward. For effective pollination, it is essential that the staminate bloom coincides with the

pistillate peak bloom. Although peak bloom for groups Alpha and Beta occurred 3 - 4 days prior to Hayward, the bloom period continues up to, and possibly after the completion of bloom in Hayward (Fig.35). The reason for this extended bloom period for the staminate vines is the fact that they possess a large proportion of inflorescences containing lateral blooms (Table 22) which open after the terminal blooms (Fig.18). Hayward on the other hand, produces virtually only terminal blooms (Table 24). This can be shown in Figure 35 where the slope of the curve for Hayward is steeper than for the staminate groups. Another way of saying this is that 10 days elapsed between 10% - 90% bloom in Hayward compared with 14 days for Alpha or Beta.

From the results, it seems groups Alpha and Beta warrant further evaluation to test their effectiveness as pollinators for Hayward. The flowering index, the product of the number of flowers per shoot and the percentage of burst shoots per lateral (Table 21), shows both groups potentially produce favourable quantities of flowers per vine, and that these open at a suitable time (Fig.35). Although evaluation of pollen germination between groups was not attempted, Davison (72) showed no consistent differences between a number of different staminate selections, including Tomuri and Matua. He further suggested that the quality of the pollen from different staminate selections was unlikely to be a factor in poor fruit set. If later evaluations show that the peak bloom period of staminate selections precede that for Hayward, it may be possible to delay or spread staminate flowering chemically, as has been shown with the growth retardant, aminozide (71).

Chapter 7

CONCLUSIONS

A number of important conclusions can be drawn when linking the observations and results from the four experimental sections. Compared with most deciduous plants flower initiation in the Chinese gooseberry occurs late in the seasonal cycle, not commencing until the resumption of growth in the spring (mid September). In this respect, the pattern is very similar to that found in evergreen temperate and subtropical fruit trees (103,135,256). Some similarities however can be seen with initiation in the grape (247) and other *Actinidia* species (171) where, although the inflorescences and bracts are initiated during the preceding summer, the individual flowers are not normally initiated until the spring.

The difference in the reported time of flower initiation between the different *Actinidia* species is interesting and warrants further investigation.

In the Northern Hemisphere where the two species, *A. kolomikta* and *A. chinensis* have been compared, the former flowers in the spring (171) while the latter flowers in mid - late summer (61). It has not been possible to investigate this point in New Zealand because, as far as is known, *A. kolomikta* has not been introduced.

While this study did not specifically set out to determine the time of flower evocation it was concluded from results of the chilling experiments (Ch.5) that evocation occurred at some time before April (2 months prior to leaf fall). Thus the sequence of flower evocation and initiation seems atypical compared with other fruit tree crops. Unlike most deciduous trees initiation is late, but unlike evergreen tropical and subtropical fruit trees, where evocation precedes initiation by only a few weeks (105,126, 271), evocation in the Chinese gooseberry occurs at least 20 weeks prior to initiation and the two events are separated by the dormant winter period. Future studies should more precisely determine the time of flower evocation. This can be determined relatively simply by defoliating and ringing techniques (105,183).

Results using single node cutting material showed that, although evocation had occurred prior to leaf fall, as shown by the full complement of reproductive axils present at that time (Table 12a), the factors that produce flowers improved in quantity and/or quality, as measured by the

number of normal flowers per axil (Fig.31), right up to the normal period of burst.

The factor(s) that produce flowers could be a build up of a positive factor(s) such as growth promotors, or to the removal of a negative factor(s) such as growth inhibitors. Research on other crops (87) suggests that the expression of flowering is unlikely to be due to changes in any one factor but to be the result of changes in the expression of several factors including both promotors and inhibitors. The fact that flowering in the Chinese gooseberry is related to the termination of rest (Ch.5) also suggests a role of both promotors and inhibitors as their relative levels in the buds are thought to determine the onset and termination of rest in woody plants (313).

Differences between cultivars, especially between pistillate and staminate cultivars, in the number of flower (buds) per shoot (Ch.6) suggests differences in the level and/or composition of the factor(s) needed for flowering. The fewer flower buds per shoot present on pistillate cultivars than on staminate cultivars (Ch.5) may suggest that the level and/or the requirement for factor(s) needed for flowering in pistillate cultivars may be greater than in staminate cultivars. The finding that pistillate cultivars finally have fewer vegetative axils and more aborted reproductive axils in a bud than staminate cultivars (Ch.3) may also give support for that theory.

Factors, emanating from outside the shoot are also likely to be involved in the formation of the flowering stimulus and could hlep to explain the lower flowering capacity of single node cuttings compared with that of shoots on a vine. This difference in the flowering capacity between single node cuttings and shoots on a vine also varies with cultivars as this was especially marked in the pistillate cultivar Monty (Table 15a and 23).

Although the Chinese gooseberry does not have an absolute low temperature requirement for flowering, chilling was found to be one environmental factor which could modify the flowering response (Ch.5). While results suggested that the Chinese gooseberry does not have an absolute cold temperature requirement for flower evocation, chilling (both natural and artificial) intensifies the flowering response. This response was due to the stimulation of growth in those reproductive axils which otherwise would have aborted. Such responses have been discussed in terms of changes in hormonal, carbohydrate and nutrient composition within the bud (Ch.5). However, the fact that articifical chilling in the dark did not completely substitute for natural chilling in the field is further

evidence that there are other factors which will influence flowering.

Once flower initiation occurred, development was extremely rapid, the ovary being present within 30 days of initiation. The pattern of flower part initiation and sex-expression is typical of most angiosperms, viz. flower parts are initiated in the order sepals, petals, stamens and lastly the pistil, and sex-expression results from the unbalanced growth of either the androecium or gynoecium from a potentially hermaphrodite primordium (Ch.3).

Large differences in the number of flowers per shoot and the number of flowers per axil between cultivars (especially between pistillate and staminate cultivars) have been recorded (Ch.6). It is of considerable interest to find that, on cultivars which characteristically have a low flowering capacity (notably Hayward), the reduced capacity is due largely to the abortion of the lateral flower buds (Ch.3). There is in fact little difference between all cultivars in the number of reproductive axils actually initiated, and lateral flower buds are initiated in all instances (Ch.3 and Table 5).

Within a growing shoot, especially a newly emerging shoot, there is intense competition between the various metabolic sinks for limited substrates. Over the prebloom period, when the developing flowers are weak metabolic sinks (127), the pattern of photosynthate movement within the shoot can be modified by the eliminating or reducing the competition between the various sinks and sources (Ch.4). It seems that results could be most readily explained in these terms. However, as will be discussed later, growth regulators also play an important role.

In the unrooted single node cuttings the shoot makes only limited growth and is likely to be supported largely from reserves within the parent stem (46,183). Defoliation studies on such Hayward cuttings confirmed the findings in other crops (310) that the developing leaves are strong sinks for metabolites and their continuous removal channels metabolites into reproductive growth (Table 7a). The resulting increased number of flowers per shoot was shown to be due to the stimulation into growth of normally aborting flowering axils and not to the development of lateral flowers. Observations in the field on Hayward showed that such lateral flower buds make only very limited growth and cease development early, shortly after bud burst (Ch.3).

The removal of a strong sink by defoliation in the single node cuttings also promoted growth and development in other ways, eg. increased axillary bud development, shoot thickening and leaf production (Ch.4). These are all

lines of evidence supporting the redirection of assimilates.

In contrast to the beneficial effects of early leaf removal were the debilitating effects of total shading which caused the premature abortion of almost all flower buds on the single node cuttings (Table 7a). Axillary bud growth, shoot thickening and new leaf production were also severely retarded.

The tipping treatments had little effect on reproductive growth in the single node cuttings (Table 7a). One reason for the lack of response was thought to be the presence of still expanding leaves on the stem. A similar situation has also been noted in grapes (312). Subsequent studies however showed that the treatments could not have been expected to affect flowering as the tippings were applied after those flowering axils and lateral flower buds destined to abort had ceased growth (Ch.3).

Not all the observed post bud burst phenomena can be explained solely in nutrient competitive terms. For example, the inhibited internode growth in defoliated Chinese gooseberry shoots (Tables 8 and 9) as well as in other crops (115,164) is thought largely to be due to hormonal factors emanating from the leaves (see Ch.4). If it were a nutrient competitive phenomenon the removal of these leaves might then be assumed to free assimilates for growth elsewhere (eg. internodes). Implication of growth substances also comes from the findings that the pattern of assimilate movement in a plant can be altered as a result of exogenous application of herbicides (188) and growth regulators (253,276).

Further, even though certain phenomena might be explained satisfactorily in terms of nutrient competition, it does not rule out the possibility that growth substances also play a role. For example, the stimulated flower development in defoliated single node cuttings (Table 7a) may be the result of the removal of some growth substance(s) (eg. gibberellins) which inhibit flower development. Similarly, the beneficial effect of tipping reported in other crops (67) may be due to the diversion of growth substances to the developing flower buds.

Treatment results on individual Chinese gooseberry shoots in the field were not as marked as may have been expected if all shoots on a vine were treated. In the experiments reported this is probably due to the translocation of assimilates from untreated to treated shoots and vice versa, an effect also reported in the grape (254). Research on other crops in fact report the inhibiting effects of whole tree defoliation (19,67,68,169) and shading (169,205) on overall reproductive growth. On the other hand, tipping treatments, principally on grapes, have improved flower development;

but to be successful however, the timing and the proportion of the shoot removed are important (67).

Apart from the treatment effects on flower bud development, the effects on new bud development are also of considerable practical significance as this is where the following year's flowers and crop originate. It is well established that leaves have a large influence on their axillary meristems (28). Any reduction in the import of water, assimilates or hormones to those buds (by the damage or shading of the leaves) could result in insufficient assimilates reaching the regions in the bud where evocation and later initiation takes place. As the developing flower buds are the weakest 'sink' in a shoot system (203), such deficiencies could result in retarded flower development leading to increased flower abortions. This theory has been suggested to account for the debilitating effects of defoliation and shading on next year's crop in the grape, which has certain similar flowering characteristics to the Chinese gooseberry (203,205,206). Although there are reports that tipping may promote next year's flowering, the long term effects that practice are generally debilitating due to loss of leaf area (293).

Present studies on the Chinese gooseberry showed that, even by bloom, defoliation and shading had an inhibiting effect on new bud development (Table 10b), which could be expected to reduce flowering next year. This would be so especially if whole vines were treated this way.

The relatively drastic treatments applied in these experiments readily induced growth changes. It is conceivable that such modifications may occur under normal cultural conditions when, for example leaves become damaged by wind, inspects or sprays, or when leaves become shaded by other leaves. While the reduction in the level of assimilates exported from such leaves may be compensated for by changes in the pattern of assimilate movement from other leaves, the final impact would obviously depend on the proportion of the shoots or leaves affected.

It seems unlikely that in practice physical treatments (like tipping) can stimulate substantially the flowering capacity of Chinese gooseberry vines as flower development studies (Ch.3) show that flower axil and flower lateral abortions occur soon after bud burst, too early for such manipulations. Future research may find however that the level of competition can be sufficiently reduced early enough to stimulate such flower buds into growth by the use of growth retarding or inhibiting chemicals. Current research in grapes has shown that fruit set can be stimulated chemically, in a way which is physiologically similar to tipping (276).

Another characteristic of the Hayward cultivar which may contribute

to its low flowering capacity is its relatively very low and uneven bud burst compared with other cultivars (Table 23). This characteristic obviously must lead to a lower overall yield. As the low bud burst phenomenon may be associated with rest termination or to some other physiological process, it may also be possible to enhance that phenomenon using some chemical method.

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