ASPECTS OF FRUIT GROWTH AND ROOTSTOCK / SCION INFLUENCE ON FIELD PERFORMANCE IN KIWIFRUIT (*Actinidia deliciosa* (A. CHEV.) C.F. LIANG et A.R. FERGUSON var. *deliciosa*).

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JUAN GUILLERMO CRUZ CASTILLO

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ABSTRACT

The influence of nine *Actinidia deliciosa* (A. Chev.) C.F. Liang *et* A.R. Ferguson var. *deliciosa* rootstocks and four 'Hayward' strains on the growth and cropping performance of kiwifruit vines four, five, and six years after grafting was determined. Multivariate analysis of variance on phenotypic data was an effective technique to distinguish main effects of rootstock and scion and the interactions between the two. Canonical Variate Analysis was particularly useful for distinguishing between root systems, 'Hayward' selections and their interaction on the basis of field performance. This statistical technique was highly effective in summarizing the complex relationships of the data and provided a useful method of reducing the dimensionality of the problem. A rootstock effect on plants topworked on root system 4 (male) was characterised by high field performance, as expressed by high floral bud burst and high yield of large size fruit in each of three seasons. Own rooted vines had the highest field performance in one season. Own rooted 'Hayward' B strain had a large trunk diameter and high yield in comparison to the other three own rooted 'Haywards', in two seasons. In contrast, when strain 'B' was topworked across eight root systems the vines produced a low yield of small fruit in two seasons. 'Hayward' A as a scion achieved the best field performance in yield and fruit sizing across eight root systems in two seasons. Root system and scion interactions were characterised by differences in 'Hayward' selection effects on individual root systems, and root system effects on individual 'Hayward' selections. In particular scion performance on root system 9 differed significantly, as did the effect of rootstock on the scion selection 'Hayward' D.

Fruit from some vines had a significant increase in percentage of soluble solids and fruit firmness at harvest, and during storage. Scion effects on percentage of soluble solids present at harvest were lost after fifteen weeks of cold storage. Conversely, in some cases, significant interaction between rootstock and scions on that variate were found only after a period of fruit storage. Rapid fruit softening during storage occurred in some rootstock scion combinations, particularly 'Hayward' C on its own roots and three of the eight rootstocks.

The effects of early summer partial defoliation on fruit size, return bloom, and carbohydrate content of 'Hayward' kiwifruit vines were studied. An arbitrary distinction was made between shoots arising from the 'replacement cane zone' (RCZ), the wide horizontal area between the T-bar support wires, and the fruiting zone (FZ), comprising all growth arising outside the T-bar support wires. A 75 % defoliation of new shoots in the RCZ significantly reduced mean fruit size 13 and 7 g, in the RCZ and FZ, respectively, and starch content of the shoots as determined in March. The treatments did not significantly alter the root starch content over several dates sampled. The return bloom of the vines was significantly reduced by 50 and 75 % defoliation.

Pre-anthesis factors and early fruit growth were important in determining final fruit size. Ovaries from early opening flowers had significantly greater fresh weight than late ovaries. Cell number and cell size in the inner and outer pericarp of the ovary at anthesis were similar for early and late opening flowers but core cell number was significantly higher for ovaries from early flowers. At commercial

harvest, the cell number in the outer pericarp of fruit from early flowers was greater than fruit from late flowers. When treated with the synthetic cytokinin CPPU (N-(2-chloro-4-pyridil)-N-phenylurea), fruit from early flowers achieved a larger fruit size than fruit from late flowers.

Fruit weight response to the synthetic cytokinin CPPU was enhanced when applied in combination with GA_3 (gibberellic acid) + 2,4-D (2,4-dichlorophenoxyacetic acid) in three seasons. In treated 'Hayward' fruit, the relative thickness of the outer pericarp was increased, and the inner pericarp decreased. Low and high seeded fruit treated with the hormone mixture had mean fresh weights of 102 and 136 g, respectively, compared with 47 and 90 g in untreated fruit. In kiwifruit inner pericarp cultured *in vitro* there was no callus growth in the absence of hormones, even when seed were present. A mix of 2,4-D + GA_3 + BAP (6-benzylaminopurine) stimulated callus growth. In the presence of 2,4-D + GA_3, seeds or BAP increased fruit callus growth and reduced the phytotoxicity effect of abscisic acid (ABA).

The uptake of ^{14}C-CPPU and ^{14}C-CPPU + 2,4-D + GA_3 by 'Hayward' kiwifruit, and the distribution of radioactive label in fruit tissues was examined. After 21 days the recovery of radioactivity was significantly greater from fruit treated with mixture compounds to CPPU alone. At commercial harvest radio-active metabolites of CPPU were on average 6.2 and 4.8 ppb (fresh weight basis) for soluble and insoluble acetone fractions, respectively. Of this activity, 90 % was present on the skin, and 10 % in the flesh.

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CHAPTER 1.

GENERAL INTRODUCTION.

Kiwifruit (*Actinidia deliciosa* (A. Chev.) C.F. Liang *et* A.R. Ferguson var. *deliciosa*) is a member of the family Actinidiaceae. It is a deciduous vine, usually growing on the edges of forests on the hills and mountains of southern and central China. Since it was introduced to New Zealand from China in 1904, kiwifruit plantings in New Zealand have increased rapidly, from 440 ha in 1970 to 16000 Ha in 1990 (Sale, 1991). In 1992 world production of kiwifruit was 793,000 tonnes with Italy and New Zealand each producing about 270,000 tonnes (Costa *et al.*, 1991). At present, New Zealand's share of the international kiwifruit market returns NZ$500 million per year.

'Hayward' is the only female cultivar commercially grown in New Zealand for export. Export markets prefer this cultivar due to its size, eating qualities and storage characteristics (Sale, 1991). A major aim in 'Hayward' kiwifruit production is to profitably obtain high yields of export quality fruit. Higher returns per tray are consistently obtained for large fruit.

Many aspects of kiwifruit vine management can strongly influence the profitability of a kiwifruit orchard. Some practices, such as fruit thinning (Cooper and Marshall, 1990 b), irrigation (McAneney *et al.*, 1991), and pollination (Hopping, 1990) to control fruit size

have been well documented. The impact of other standard practices are not fully understood, for example, the importance of rootstock and scion in vine performance. For many years seedlings of 'Bruno' have been the most widely used rootstocks for kiwifruit in this country because of the claimed high and uniform germination and strong vigour of this cultivar (Lawes, 1990). Field observations have indicated large variation in performance (for example, in fruit yield and/or fruit size) between vines with an apparently identical micro-climate (Lawes *et al*, 1986). It seems likely those differences are influenced by the seedling rootstocks, 'Hayward' scions, and/or the interaction between the two (Woolley *et al.*, 1988). There are few published reports of rootstock effects in kiwifruit (Cruz-Castillo *et al.*, 1991 a, b). No published comparisons of 'Hayward' scion selections or rootstock and 'Hayward' scion interaction effects are available.

Kiwifruit growers in New Zealand are sometimes reluctant to use cutting-grown plants, either as fruiting plants or as rootstocks, as many consider that a seedling rootstock gives rise to a vine which grows more rapidly and is both stronger and more productive. However, there is no clear evidence that kiwifruit cutting-grown plants on their own roots are inferior in the orchard (Lawes, 1990).

Root systems can also influence the postharvest quality and storage potential of fruit commodities. In grapefruit and orange (Wutscher, 1979) rootstocks have increased the total soluble solids of the fruit after harvest. In apple, fruit maturity at harvest was advanced (Yadava and Doud, 1989), and fruit firmness after storage increased (Autio, 1991) with the use of specific rootstocks. In New

Zealand, there is considerable interest in identifying factors most responsible for influencing kiwifruit losses in storage (Hopkirk and Clark, 1992). However, little attention has been given to root system effects on postharvest quality and storage potential of kiwifruit.

While the rootstock-scion combination may influence vine growth, precocity, fruit size, and fruit storage, there are other factors that could affect crop characteristics. For example, fruit size may be affected by seed number, ovary size at anthesis, production of photoassimilates from the leaves, and the application of growth regulators.

Fruit growth is highly dependent on the seed number (Hopping, 1976). It has been demonstrated that seeds are a source of plant growth regulators (Moore, 1989). Large variations in the relationship between fruit size and seed number indicate that other factors may be important in fruit sizing. For instance pre-anthesis factors such as ovary size at anthesis may significantly influence the final fruit size. In peach (Scorza *et al.*, 1991), apricot (Jackson and Coombe, 1966), and also kiwifruit (Lai, 1987) fruit from early opening flowers are larger at harvest than those from late blooms. In strawberry (Cheng and Breen, 1992) cell number at anthesis was important for achieving superior fruit growth.

Crop yield depends on an adequate production of photoassimilate by the leaves (Lai, 1987). Regions of assimilate accumulation are known as sinks (see Chapter 4). The strength of the various carbon sinks within the vine can be investigated by defoliation studies but little is known about the carbohydrate costs of

supporting growth of the different organs after a partial kiwifruit vine defoliation.

The use of exogenous plant growth regulators for experimentally increasing fruit size has been used in many tree fruit species. Hopping (1976) applied a range of hormones to kiwifruit, but obtained only a small increase in fruit size. Okamoto *et al.* (1981), called attention to the fact that certain substituted phenylureas were very effective cytokinins. Iwahori *et al.* (1988), and Ogata *et al.* (1989), showed that the synthetic cytokinin substance CPPU (N-(2-chloro-4-pyridyl)-N-phenylurea) increased the size of kiwifruit, and similar effects were described by Lawes and Woolley (1990) in New Zealand.

Three related areas of kiwifruit physiology where investigated in this thesis. 1. The contribution of the scion, the rootstock, and the interaction between the two on field performance of 'Hayward' vines four, five, and six years after propagation were investigated. Multivariate statistical techniques such as multivariate analysis of variance, and canonical variate analysis were used to characterise such effects. This project was carried out from 1988-91 with vines at the Fruit Crops Unit, Massey University.

This study also presents data on fruit quality (total soluble solids and fruit firmness) at harvest and after storage for different 'Hayward' selections both own rooted, and topworked on selected clonal kiwifruit rootstocks.

2. The effect of flowering date within kiwifruit vines on the ovary and final fruit size was evaluated during three seasons. The consequences of a partial defoliation on fruit sizing, vegetative growth and bloom return, and seasonal content of vine carbohydrates were also evaluated.

3. Five aspects of the application of growth regulators were investigated: a) The effect of different plant growth regulator combinations on the fruit of 'Hayward' and 'Kramer Hayward' kiwifruit; b) The effect of a hormone mixture on the growth of different tissues in a kiwifruit; c) The uptake, distribution and harvest residues of ^{14}C-CPPU in 'Hayward' fruit; d) the effects of seeds and growth regulators on the growth of kiwifruit; and e) The fruit size response to CPPU of fruit from early and late flowers.

CHAPTER 2.

AN INVESTIGATION OF THE EFFECT OF CLONAL ROOTSTOCK AND 'HAYWARD' SCION SELECTION ON FIELD PERFORMANCE OF KIWIFRUIT (*Actinidia deliciosa* (A.Chev.) C.F. Liang *et* A.R. Ferguson var. *deliciosa*) VINES, USING MULTIVARIATE ANALYSIS TECHNIQUES.

1. Introduction.

The kiwifruit industry in New Zealand is based on the cv. Hayward (Sale, 1990 a). For many years seedlings of 'Bruno' have been the most widely used rootstocks for kiwifruit in this country because of the uniform and claimed high seed germination and strong vigour of this cultivar (Lawes, 1990). Kiwifruit growers in New Zealand have held that seedling rootstocks give rise to vines which grow more rapidly and are both stronger and more productive. However, field observations have indicated large variation in performance (for example, in fruit number and/or fruit size) between vines in an apparently identical micro-climate (Lawes *et al*, 1986). It seems likely these differences are influenced by the rootstock seedlings, the 'Hayward' scions, and/or the interaction between the two (Woolley *et al.*, 1988).

There is little published information regarding rootstock effects in kiwifruit (Cruz-Castillo *et al.*, 1991 a, b), and most studies record work in which various sources of 'Hayward' were used as the

fruiting scion. There is no clear evidence that cutting-grown plants on their own roots are inferior in performance compared with grafted kiwifruit vines (Lawes, 1990). We initiated this work with the hypothesis that own rooted vines, root systems, 'Hayward' strains, and the interaction between root systems and scions influence fruit productivity during the first years of production in the orchard. Thus, in this work the contribution of the scion and the root system, and the interaction between the two on the field performance of kiwifruit vines 4, 5, and 6 years after grafting was studied. There are biometrical methodologies to study rootstock and scion effects, for example, Rives (1971), Tubbs (1977), Lefort and Legisle (1977), and Lider *et al.* (1978). However, those univariate techniques focus on narrowly defined sections of highly integrated systems involving intercorrelated variates. Thus, multivariate analysis of variance, and canonical variate analysis were used to characterise the combined effects of the different selected root systems and scions measured response variates, and to demonstrate its applicability and potential in rootstock and scion research.

2. Literature Review.

2.1. Rootstock effects.

The economic and practical importance of rootstock effects on tree growth and fruit production has been recognised for many years. Rootstocks have been used in the culture of several fruit tree

species, and the horticultural performance of the scion cultivar has been affected in several ways.

Rootstocks have been recorded as affecting the scion in various species of fruit tree in the following ways.

(A) Leaf growth and development (Kanadia, 1979; Ferree and Barden, 1971; Barden and Ferree, 1979; Schechter *et al.*, 1991).

(B) Photosynthesis (Kubota *et al.*, 1990; Sharma and Singh, 1989; Morinaga and Ikeda, 1990; Southey and Jooste, 1992; Ferree, 1992).

(C) Water consumption (Natali *et al.*, 1985)

(D) Morphological changes in the xylem and phloem of the trunk (Rogers and Beakbane, 1957; McKenzie, 1961; Lockard, 1976; Yadava and Doud, 1978; Vasconcellos and Castle, 1994).

(E) Mineral nutrition and mineral element distribution (Embelton *et al.*, 1962; Jones and Pate, 1976; Sarič *et al.*, 1977; Dodanis, 1977; Wutscher, 1979; Hanson and Perry, 1989; Viti *et al.*, 1990; Sharma and Chauhan, 1991; Taylor and Dimsey, 1993).

(F) Responses to plant growth regulators (Jackson *et al.*, 1983; Voltz and Knight, 1986; Zeller *et al.*, 1991).

(G) Fruit setting (Zelleke and Kliewer, 1979; Jackson *et al.*, 1983; Brown and Wolfe, 1992; Stevens and Westwood, 1984).

(H) Control of tree growth (Carr, 1966; Tubbs, 1973; Robitaille and Carlson, 1976; Lockard and Schneider, 1981; Ferree, 1988; Forshey and Elfving, 1989; Autio *et al.*, 1991).

(I) Biennial production (Hoblyn *et al.*, 1936; Monselise and Goldschmidt, 1982; Crane and Iwakiri, 1986).

(J) Blossoming date (Yadava and Doud, 1989; Durner, 1991; Harber *et al.*, 1992; Durner and Goffreda, 1992).

(K) Flower density (Yadava and Doud, 1989; Schechter *et al.*, 1991; Hirst and Ferree, 1993; Wang *et al.*, 1994 b).

(L) Yield (Wolf and Pool, 1988; Warrington *et al.*, 1990; Fallahi *et al.*, 1990; Cruz-Castillo *et al.*, 1991 b; Wells, 1992).

(M) Basal suckering (Autio and Lord, 1988; Glucina *et al.*, 1992; Ferree, 1992).

(N) Precocity (Tydeman, 1937; Webster, 1980; Schmidt and Gruppe, 1988; Palmer, 1992; Cruz-Castillo *et al.*, 1991 a; Lesser *et al.*, 1993).

(O) Fruit weight (Cummins, 1972; Parnia *et al.*, 1988; Wutscher and Bistline, 1988 b; Cruz-Castillo *et al.*, 1992; Gregoriou and Economides, 1993; Prior *et al.*, 1993; Hussein and Slack, 1994; Layne, 1994).

(P) Fruit shape (Shaw, 1936; Cummins, 1975).

(Q) Fruit maturity (Yadava and Doud, 1989; Escalona *et al.*, 1989; Martin *et al.*, 1975; Wutscher, 1979; Brown and Wolfe, 1992; Westwood, 1978; Fallahi *et al.*, 1985; Lord, *et al.*, 1985; Barden and Marini, 1992).

(R) Fruit firmness in storage (Autio, 1991; Cruz-Castillo *et al.*, 1991 a; Brown and Wolfe, 1992).

(S) Fruit physiological disorders (Barden, 1988; Raese, 1989).

(T) Fruit juice composition (Ough *et al.*, 1968; Zelleke and Kliewer, 1979; Cirami *et al.*, 1984; Lipe and Perry, 1988; Wutscher and Bistline, 1988 a; Foott et al., 1989).

(U) Fruit colour (Wutscher and Bistline, 1988 b; Drake *et al.*, 1988).

(V) Tolerance to soil pests (Renaud *et al.*, 1988; Sale, 1990 b; Gabor *et al.*, 1990; Nesbitt, 1974; Rom and Carlson, 1987; Walker *et al.*, 1991; Esmenjaud *et al.*, 1994).

(W) Tolerance to unfavourable environmental conditions (Cummins and Norton, 1974; Layne, 1974; Chaplin *et al.*, 1974; Micke and Schreader, 1977; Yelenosky and Wutscher, 1985; Parnia *et al.*, 1988; Sherman *et al.*, 1991; Striegel and Howell, 1991; Alvino *et al.*, 1994).

(X) Longevity (Lider *et al.*, 1978; Okie *et al.*, 1994).

Although it is recognised that rootstock selection offers the potential for improving kiwifruit yields and/or profitability, there are few reported trials regarding rootstock influences on kiwifruit. In California (USA) male kiwifruit seedlings were used as rootstocks because of high vigour in comparison to female seedlings (Weet, 1978). Viti *et al.* (1990), evaluated the effect of different soil lime concentrations on growth of own-rooted and grafted kiwifruit vines growing in artificial conditions. None of the own-rooted 'Hayward' plants subjected to the highest calcium carbonate concentrations survived. However a high percentage of 'Hayward' vines grafted on the rootstock 'D 1' (a male seedling of 'Bruno') survived. In an early evaluation of rootstock effects in kiwifruit, Lawes, Woolley, Zhu and Cruz (1990), detected two rootstocks with high, and two with low field performance characteristics. Lowe and White (1991) reported increased flowering and yield of kiwifruit vines grafted on the rootstock 'Kaimai', a clonal selection of *A. hemsleyana*. Seeking causes of enhanced flower production by kiwifruit rootstocks, Lowe *et al.* (1992), studied the root anatomy of several species of *Actinidia* topworked with 'Hayward'. 'Kaimai' was characterised by having the greatest proportion of bark area occupied by idioblasts. They also analyzed bark carbohydrate levels in the rootstocks, and found a reduction in starch in 'Kaimai' in the spring, which suggested differences among rootstocks in the way carbohydrates are mobilised from bark tissue during spring. The concentration of starch in the 'Hayward' scion was not affected by the rootstocks. These results suggest that the mode of action of kiwifruit rootstocks may be

different from the action of size-controlling rootstocks used in the apple industry, where dwarf rootstocks have a thicker bark (phloem) and higher starch levels (Beakbane and Thompson, 1947; Lockard and Schneider, 1981). Hopping *et al.* (1991), investigated kiwifruit rootstocks propagated from roots taken from high-producing vines growing in established orchards. He determined root:shoot ratios (dry weight) of those rootstock plants. Further rootstock plants were grafted with the cv. Brodie. Rootstocks with low root:shoot ratios produced the greatest number of 'Brodie' fruit of large size. Hopping *et al.* (1991), explained the yield increases as a result of rapid vine establishment and increased cane numbers, rather than a rootstock effect on increased floral bud break or flowers per bud. In contrast, 'Kaimai' has the distinct effect of increasing flowering (Lowe *et al.* , 1992).

2.2 Own-rooted kiwifruit vines.

Despite the lack of any clear evidence that kiwifruit cutting-growing vines are inferior to plants produced by topworking 'Hayward' onto 'Bruno' seedlings (Lawes, 1990), it is this latter method of propagation that is preferred by growers in New Zealand. In other tree fruit species own rooted plants have performed just as well as those grown from seedlings, or even better. Sarooshi *et al.* (1982) showed that the 7-year cumulative yields of the own rooted grape 'Muscat Gordo Blanco' was equal or better than when grafted on rootstocks. Callensen and Larsen (1990) demonstrated that young plants of the apple cvs. Ingrid Marie, Lobo, and Summerred yielded heavier crops on their own roots than when grafted on M26 rootstock. Singh *et al.* (1990), found that 'Sand Pear' growing on its

own roots came into bearing two years earlier than those grafted on wild root suckers.

In New Zealand, Lawes, Woolley, Zhu and Cruz (1990), found that young kiwifruit vines on their own roots in the field performed as well as, or better, than grafted plants. According to Weet (1978), in California (USA) nurserymen produce more kiwifruit vines from cuttings, than from grafted seedlings. He indicated that no disease-resistant or dwarfing rootstock had been discovered for kiwifruit vines, and that there was no advantage to the kiwifruit grower to prefer one type of plant over another for either of these reasons. In grape, topworked vines had more extensive root growth than own rooted vines (Nagarajah, 1987). However, in kiwifruit there is no evidence to support the concern that own-rooted plants have 'poor' anchorage and reduced drought tolerance (Lawes, 1990). Further studies of the field performance of own-rooted kiwifruit vines are necessary to clarify any benefit in productivity.

2.3 'Hayward' variability in kiwifruit production.

The kiwifruit industry in New Zealand is based on the cv. Hayward (Sale, 1990 a). According to Zhu (1990) 'several 'Hayward' mutations have been claimed in New Zealand over the past decade.'

Lawes *et al.* (1986), and Woolley *et al.* (1988), reported that individual vines monitored over a number of years showed considerable variation in their ability to size their fruit. These differences were not accounted for by dissimilarities in fruit seed

number. They pointed out that the vine variation could reside either in the 'Hayward' scion or in the rootstock. Studies on scion effects on kiwifruit vines could contribute to identifying a clone of 'Hayward' that maximises the yield of exportable fruit across a diversity of rootstocks.

2.4. Rootstock scion interactions.

The understanding of rootstock and scion relationships are of importance to basic plant physiology for the light it may throw upon basic root-shoot interactions as well as in horticultural productivity.

Glenn and Scorza (1992) using reciprocal grafts of tall and dwarf peach trees studied rootstock and scion interaction effects on tree growth. They found the scion characteristics (tall or dwarf) determined the phenotype of the tree irrespective of the rootstock. Tubbs (1976) studied rootstock and scion interactions in apple, quince, and cherry. He found the growth contributions by scion and rootstock were largely additive. The scion-rootstock interaction was often statistically non-significant. In subsequent work, Tubbs (1980) determined the relative growth rate of apple clones worked as both scion or rootstock, and confirmed the additive relationship between the growth influences of rootstock and scion. In cucumber, non-significant interactions between scion and rootstock on fruit production have been also observed (Zijlstra *et al.*, 1994).

The ability of specific wine grape rootstock-scion combinations to improve fruit productivity was emphasised by Rives

(1971), who described consistent significant rootstock-scion interactions on fruit yield and fruit weight. Ough *et al.* (1968) studied rootstock-scion interaction of grapevines on wine making. They found significant interactions on the ammonia and total nitrogen concentration of the grape juice, and concluded that the choice of rootstock for a specific cultivar can alter the juice composition significantly.

No research has yet been carried out to determine if there is an interaction between rootstock and scion in the growth and yield of kiwifruit.

2.5. Multivariate analysis of variance (MANOVA).

Multivariate techniques have in common statistical models that simultaneously analyze multiple measurements on the individuals under investigation (Hair *et al*, 1987). While the original derivations of most of these techniques were carried out around fifty years ago, the comparatively recent growth of computer technology has revolutionized multivariate statistical analysis and it is now being applied in a number of disciplines. In many horticultural studies measurements are made of a number of different attributes. In the analysis of experimental work in this discipline, little enthusiasm for those techniques was apparent in the early 1980's (Swallow, 1981). Recently, several authors have found these techniques useful in understanding the responses to the treatments employed in horticultural research (Yourstone and Wallace, 1990; Lawes, Woolley, Zhu and Cruz, 1990; and Perez-Gonzales, 1992).

The analysis of variance (ANOVA) has proved to be the most widely used and useful approach to study differences among several populations or treatments (Steel and Torrie, 1980). However, ANOVA handles only one dependent variable. If one wants to deal with many characters together, a multivariate ANOVA (MANOVA) is needed. MANOVA is the statistical technique concerned with analyzing the variance of multiple measurements on several populations (Hair *et al*, 1987).

The data for performing a MANOVA are assumed to be multivariate normal in distribution, and with the same covariance matrix for each population (Cliff, 1987). Procedures to assess multivariate normality, and homogeneity of the covariance matrix are readily available in the statistical computer package SAS (SAS Institute, 1991 b).

According to Cole and Grizzie (1966), MANOVA has proved to be a unified approach with all the power and flexibility of ANOVA. In agricultural research MANOVA has been used in several ways, for example in the analysis of sequential observations on grazing animals and perennial plants (Evans and Roberts, 1979), and to evaluate the effects of photoperiod and temperature on node development in beans (Yourstone and Wallace, 1990). Zhu (1990) used MANOVA in kiwifruit breeding to evaluate the superiority of cross combinations between a number of different parent vines. Yourstone and Wallace (1990), and Zhu (1990), following a MANOVA performed a canonical variate analysis to obtain scores for means comparison.

Chapter two

2.6. Canonical variate analysis (CVA).[1]

Because MANOVA cannot make a comparison of means, or provide information on the relations among the several variates studied (Kshirsagar, 1972), CVA has been employed for these purposes. The history, methodology, and applications of CVA will be briefly reviewed.

In horticultural research the relationships between a number of complex characteristics are often studied. Canonical variate analysis (CVA) is a multivariate statistical research tool capable of identifying differences among groups of individuals (or treatments), and improving the understanding of the relationships among the several variates measured within those groups.

The groups are defined *a priori* by some criterion external to the set of variates measured, for example rootstocks (Cruz-Castillo *et al.*, 1992; 1994), carbohydrate status of nursery trees (Prins *et al.*, 1990), supermarket for floral customers (Behe *et al.*, 1992), origin of wines (Forina *et al.*, 1986), species of trees (Majer *et al.*, 1992), or cultivars of swede (Cole and Phelps, 1979), bluegrass (Bruneau *et al.*, 1987), and cowpea (Fernandez and Miller, 1985). CVA has not been used extensively in horticultural research (Cruz-Castillo *et al.*, 1992).

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[1] Papers published in Acta Horticulturae (Cruz-Castillo *et al.*, 1992), and accepted by HortScience (Cruz-Castillo *et al.*, 1994) are attached at the end of this thesis.

The problem addressed with CVA is how well it is possible to separate or discriminate two or more groups of individuals, given quantitative measurements of several variates on these individuals. Johnson and Wichern (1992), and Mardia *et al.* (1979), reported that this technique was first used by Fisher in 1936, and is also known as Fisher's discriminant analysis, or canonical discriminant analysis (SAS Institute, 1989). CVA can be defined as a multivariate statistical technique which determines linear functions of quantitative variates that maximally separate two or more groups of individuals while keeping each group as compact as possible (Manly, 1986). This approach leads to the determination of a number of uncorrelated canonical variates (CVs) or canonical discriminant functions. They are defined as linear combinations of the original variates that best separate the means of groups of observations relative to the within-group variation (Rencher, 1992). The first CV, CV 1, gives the maximum possible variation between groups with respect to within group variation, and therefore reflects group differences to the greatest degree possible; CV 2 captures as much as possible the group differences not displayed by CV 1, subject to the condition that there is no correlation between CV 1 and CV 2. CV 3, uncorrelated with CV 1 and CV 2, reflects as much as possible the group differences not displayed by CV 1 and CV 2 and so on. The maximum number of CVs obtainable is equal to the number of variates or 1 less than the number of groups, whichever is smaller (Manly, 1986). CV standardized scores (having zero means and unit variances) of each individual in the data-set can be obtained for these CVs to further illustrate the group differences. The first few CVs are an incomplete summary of the original sample information (Johnson and Wichern, 1992), but the hope is that they are sufficient to

account for most of all the important group differences (Manly, 1986). If three or less CVs are needed for this purpose, then the CV scores of the groups can be plotted to show the differences between them. The graphical presentation of the groups may become unfeasible when a large number of groups are to be discriminated. In such a situation, a simple multiple comparison test such as Duncan's multiple range test (Steel and Torrie, 1980) may be administered to differentiate the groups.

2.6.1. Assumptions for CVA.

The data for performing a CVA should be replicated within and between the groups. Standardization prior to the analysis is not required (Kshirsagar, 1972). The outcome of a CVA is not affected in any important way by the scaling of individual variables (Manly, 1986). The major assumption under which CVA operates is the homogeneity of the within-group covariance structure of all the groups under investigation. Failure of this assumption reduces the reliability of the significance test performed to determine the number of CVs that are adequate to represent the data, when using the likelihood ratio criterion approximation (Kshirsagar, 1972). This test of significance also requires that within the groups, data are multivariate normally distributed. However, the normality assumptions underlying CVA are not considered to be very important when empirical evidence is sought (Cliff, 1987), thus CVA may be used descriptively when it is derived from non normal data. Procedures to assess multivariate normality, and homogeneity of within group covariance matrices, for example Bartlett's test, are

readily available in SAS (SAS Institute, 1991 b). Krzanowski (1988) indicated that Bartlett's test is very sensitive to non normality, so may not be very reliable to evaluate homogeneity of covariance matrix before performing CVA. He also pointed out that if the non-homogeneity is not very marked there is no reason not to perform CVA.

2.6.2. Conducting the analysis.

For performing CVA the SAS (SAS Institute, 1989) system is popular and the software can be used in different ways. More specifically the CANDISC procedure of SAS is dedicated for CVA, and for this reason it has been used in this study. The CANDISC procedure performs CVA by finding the smallest number of potential linear combinations of the original variates that maximally discriminate the group means. In other words, the first linear combination is derived to maximise the multiple correlation with the group structure. This maximal correlation is called the first canonical correlation between the variates and the group structure. The second linear combination is found such that it is orthogonal to the first and has the second highest canonical correlation between the variates and the groups. This procedure is continued until the canonical correlation becomes insignificant or the maximum number of potential CVs have been found (Kshirsagar, 1972).

The coefficients of the linear combination are the canonical weights of the original variates and they provide information about the discriminatory power of each variate. The canonical coefficients or weights are usually standardized for interpretation purposes (SAS

Institute, 1991 b). For each CV the CANDISC procedure outputs the eigenvalue which is the ratio of between-group variation to the pooled within-group variation. These eigenvalues indicate the relative percentage of the degree of separation between the groups accounted for by the corresponding CVs (Manly, 1986).

Furthermore, the CANDISC procedure also produces for each CV the standardized canonical scores for individuals in each group. As explained earlier, it is worthwhile to plot these scores for the first two or three CVs to provide a visual display of the groups and to illustrate the discriminating power of each CV in separating the groups. The plots may also be useful for identifying the outliers in the data (Afifi and Clark, 1990). When there are many groups under study and the group separation is difficult to observe on the graphs, analysis of variance (ANOVA) followed by an independent multiple comparison test can be performed using the scores of important CVs.

2.6.3. Interpreting the CVs.

A distinction can be made between interpreting each CV and evaluating the contribution of each original variable to that CV. To rank the variables in order of their contribution to the function, the absolute values of the standardized canonical coefficients are used, while the signs of these coefficients are taken into account to characterise the function (Rencher, 1992). Both situations are illustrated by an example on kiwifruit vines taken from Cruz-Castillo *et al.* (1992), where five response variates were measured on 'Hayward' vines, own rooted and also topworked on eight different

rootstocks. Let x_1 denote the number of fruits removed to give a constant crop load, x_2 = % of flowers occurring in a compound dichasium at full bloom, x_3 = number of flowers per shoot, x_4 = yield (kg/vine), x_5 = % fruit ≥ 98 g fresh weight (large fruit size). The first canonical variate was given by:

$$CV\ 1 = -0.47x_1 - 0.34x_2 + 0.25x_3 + 0.84x_4 + 0.70x_5,$$

in which the absolute values of the coefficients rank the variables. The higher values of the canonical coefficients of x_4 and x_5 indicate that the separation between the rootstocks was most strongly influenced by total yield and fruit size. With their signs a high CV 1 value signifies a rootstock characterised by high yield of large fruit. If, however these coefficients had been negative, then CV 1 would have been influenced strongly by a low yield of small fruit. In both cases, the relative contribution of each variable is the same but the interpretation is different.

The use of correlations between the CVs and the original variables helps to enhance the interpretation of the CVs (Afifi and Clark, 1990). These correlations indicate how each predictor variable in an univariate way contributes to that discriminant function (Rencher, 1992), and they are useful in understanding the relationship between the original variables and the CVs. These correlations are referred to as the 'total canonical structure' in the CANDISC output. When some of the original variates are highly intercorrelated, the correlations of the total canonical structure and the standardized canonical coefficients of the CV can be quite different. When this occurs some statisticians find it simpler to make inferences using the correlations rather than the coefficients of the CVs (Afifi and Clark, 1990). However, it is important to realize that the correlations of the

total canonical structure merely show the importance of each variate independent of all the other variables, without providing information about the multivariate contribution of that variate. In contrast, in standardized form, the canonical coefficients of each CV provide information about the joint contribution of the variables to that CV (Rencher, 1992).

The objective of this chapter is to demonstrate the applicability of CVA in root system and scion research, and evaluate effects of root systems, scions, and any rootstock-scion interaction on the field performance of 'Hayward' kiwifruit vines.

3. Material and Methods.

The experiment was carried out at the Fruit Crops Unit a research and commercial orchard at Massey University, Palmerston North. The kiwifruit vines had been topworked in 1985 with selected material from commercial 'Hayward' kiwifruit orchards. Vines from Hawkes Bay and Horowhenua selected for propagation were on seedling rootstocks and were growing close together in the same block. Observations during two previous seasons had identified the vines as 'good' or 'poor', producing a high yield of large fruit, or low yield of small fruit, respectively. On the basis of vine differences in those characteristics, four pairs of contrasting vines were selected for the propagation of the experimental plants. Root material from three 'good' (large fruit, high yield) and four 'poor' (small fruit, low yield) source plants was induced to produce entire plants that were the root

system clones and which may vary in their effects on scion behaviour. Similarly, 'Hayward' scion material from two of the 'good' and two of the 'poor' vines was propagated to give plants on their own roots. These four 'Hayward' selections were also topworked on the seven clonal root systems and on 'Bruno' seedlings. The root and shoot cuttings were mist propagated as described by Sale (1990 a). Each root system-scion combination was replicated six times across the four scions (24 plants/root system, or 54 plants/'Hayward' selection).

Originally the 'Haywards', and the root systems were selected from the orchards of Mr. Desborough in Levin, and Mr. Edilsen and Mr. Evans in Hastings. The 'Haywards' were named as Desborough E, Edilsen 1, Desborough G, and Edilsen 12. In this work, they were renamed as A, B, C, and D, respectively. The first two selections were taken from 'good' vines, and the last two from 'poor' vines. The nine root systems were named 'own roots', 'Bruno' seedlings, Desborough A, Desborough E, Evans 2, Evans 3, Desborough G, Desborough F, and Edilsen 12. The last seven root systems were renamed as root systems number 3, 4, 5, 6, 7, 8, and 9, respectively. Root systems from 3 to 5 were derived from 'good' vines, and from 6 to 9 were taken from 'poor' vines.

The vines were trained on a T-bar trellis system, and planted at a spacing of 5.0 x 2.5 m on a sandy loam soil. A male polleniser vine (M51 or M52) was planted after every third female vine, in each row. For each vine, data were collected for percentage bud burst, percentage floral bud burst (calculated as percentage of total buds in the same way as percentage bud burst), and mean number of flowers per current shoot in early spring. These horticultural attributes were

determined on two current season replacement canes of about similar size situated randomly on each side of the vine. Trunk diameter was measured in spring at 70 cm above the ground, in the seasons 1988-89, and 1989-90. Fruit number, vine yield, and mean fruit size per vine in the 1988-89 season were obtained by counting and weighing each fruit (including non-export sized fruit) on an electronic balance connected to an Epson HX20 computer. In the following two seasons 1989-90 and 1990-91, the total crop of each vine was counted, and weighed in the field using a Salter 236 thermoscale, and the mean fruit size was determined from a randomly selected subsample of 60 fruit (including non-export sized fruit) taken from two canes.

Throughout the experiment vines were winter and summer pruned as in commercial orchards. In vines presenting $\simeq$ 8.5 m^2 canopy, lateral and flat fruit were thinned off to leave about 35, 40, and 45 fruit / m^2 canopy, for the first, second, and third seasons, respectively. These crop loads were defined to observe vine yield capacity and sustainability of the fruit production.

Multivariate analysis of variance (MANOVA) with a factorial arrangement (root systems and scions) in a completely random design was performed in each of three kiwifruit growth seasons to determine multivariate main effects and interactions for 'Hayward' selections and root systems. In the first two seasons, nine root systems and four 'Hayward' selections were evaluated. In the third season of experiments, three root systems across two 'Hayward' selections were analyzed. These vines were selected to contrast 'poor' and

'good' field performers on the basis of the results obtained in the first two seasons investigated.

Analyses of variance (ANOVA) in a completely random design, and CVA were performed on the root systems across the 'Hayward' selections, and on the 'Hayward' selections across the root systems (excluding own rooted vines) to evaluate scion effects. In the seasons where significant root system and scion interactions from the MANOVA were obtained, additional ANOVAs, and CVAs were carried out on either root systems or 'Hayward' selections among 'Haywards' or root systems, respectively. Only root systems or 'Haywards' having a significant likelihood test, and/or a relatively large percentage of the degree of separation between groups are shown. For example, the CVA for root systems in the 1990-91 season was not interpreted for this reason. In the three seasons of experiments a small number of vines were not included in the analyses because they were grafted in 1986 or 1987. Fruit number was not included in the CVA because it was highly correlated ($P = 0.01$, and $r \geq 0.95$) with fruit yield, and when it was included it was difficult to interpret the CVA. Afifi and Clark (1990) showed when some of the original variates are highly intercorrelated, the standardized canonical coefficients of the CVA can be difficult to interpret.

The SAS procedures ANOVA and GLM (SAS Institute, 1989) were used for performing ANOVA with balanced and unbalanced data, respectively. For analysing multivariate data, GLM was used for MANOVA, and CANDISC (SAS Institute, 1989) for CVA.

4. Results

The MANOVA indicated significant differences amongst the nine root systems and four 'Hayward' scions in the first two seasons (Table 2 - 1). In the final season when only three root systems and two 'Hayward' scions were considered significant differences among the root systems were obtained but the scion effects were non-significant ($P \leq 0.14$). The interaction was significant at 5 % level in the first, but not in the second ($P \leq 0.09$) and third ($P \leq 0.12$) seasons (Table 2 - 1). However the interaction between the 'Hayward' selections and the root systems in the second season should not be ignored as it shows some evidence of significance at 10 % level.

4.1. Root system effects across four different 'Hayward' selections.

4.1.1. 1988-89 season.

The F test for comparisons from independent ANOVAs, together with the least square means (used for ANOVA with unbalanced data (SAS Institute, 1991 a)), and standard error of the least square means of the measured variates for the vines on different root systems are presented in Table 2 - 2. The vines on the different root systems were significantly different in trunk diameter, yield, and fruit weight. The greatest trunk diameter, and yield were achieved by own rooted vines. In contrast, vines on the root systems 7, and 9 presented the smallest trunk diameter, and the lowest yield,

Table 2 - 1. Multivariate analysis of variance in vine performance for root system, and 'Hayward' scion selection. Nine root systems and four 'Haywards' with six response variates were analysed in 1988-89, and 1989-90. Three root systems and two 'Haywards' with five response variates, were analysed in 1990-91.

1988-89 Season	Value	F	df	Wilks' Lambda P > F
Root systems	0.27	2.78	48	0.0001
'Hayward' selections	0.59	2.87	18	0.0001
Interaction	0.17	1.33	138	0.0125
1989-90 Season				
Root systems	0.47	2.76	48	0.0001
'Hayward' selections	0.67	3.77	18	0.0001
Interaction	0.39	1.16	144	0.0927
1990-91 Season				
Root systems	0.44	2.48	10	0.0167
'Hayward' selections	0.72	1.85	5	0.1384
Interaction	0.56	1.65	10	0.1186

Table 2 - 2. Least square means (± standard error of the least square means) and analysis of variance (ANOVA) for the response variates measured across four 'Hayward' selections own rooted, and topworked on eight different kiwifruit root systems. 1988-89 season.

Root systems	N[4]	% Bud burst	% Floral bud burst	Number of flowers per shoot	Trunk diam. (mm)	Yield (Kg/vine)	Fruit number	Mean fruit weight (g)
1 Own roots[1]	18	54.4 (1.6)	88.1 (2.6)	3.3 (0.1)	27.5 (0.7)	39.1 (3.7)	333 (30)	120.0 (2.1)
2 'Bruno' seedlings	13	58.1 (1.7)	86.5 (3.0)	3.6 (0.2)	25.2 (0.1)	33.8 (3.6)	308 (36)	112.1 (3.4)
3[2]	17	58.9 (2.4)	87.2 (2.3)	3.3 (0.1)	23.9 (0.9)	31.1 (2.6)	276 (31)	114.0 (2.6)
4 (male)[2]	11	57.2 (2.1)	87.2 (3.2)	3.1 (0.2)	27.1 (0.1)	28.1 (4.7)	238 (39)	123.7 (4.4)
5[2]	15	53.9 (2.1)	85.9 (3.3)	3.3 (0.2)	24.2 (0.6)	26.7 (3.3)	227 (33)	119.4 (2.9)
6[3]	16	57.1 (1.3)	88.9 (2.3)	3.3 (0.1)	24.3 (0.6)	29.9 (2.8)	257 (32)	115.8 (2.4)
7[3]	11	49.3 (3.0)	83.4 (3.7)	3.5 (0.2)	22.2 (0.6)	25.8 (4.3)	236 (39)	115.8 (5.6)
8[3]	15	56.8 (1.9)	81.3 (3.4)	3.4 (0.1)	26.5 (0.7)	29.4 (3.2)	267 (33)	112.3 (2.6)
9[3]	14	53.6 (2.3)	84.2 (3.6)	3.1 (0.2)	25.7 (0.7)	22.6 (3.2)	207 (34)	112.5 (2.6)
ANOVA significance								
Root systems		NS	NS	NS	*	*	NS	*

[NS, *]Non-significant or significant at $P \leq 0.05$, respectively.
[1]Least square means of four 'Hayward' selections on their own root.
[2]Root system derived from 'good' vines which produced high yield of large fruit.
[3]Root system derived from 'poor' vines which produced low yield of small fruit.
[4]Number of individuals.

respectively. Root system 4 (male) had the largest mean fruit weight with a value of 123.7 g. There were no significant differences in fruit number across the nine root systems. However, by orthogonal contrast own roots was significantly different ($P \leq 0.05$) from vines on rootstock 9. ANOVA did not show how the different root systems compared with respect to all the variates measured, and how those variates may be associated among themselves.

A CVA was carried out to characterise the field performance of vines on the different root systems. Thus, with data for six variates, and nine root systems the maximum number of CVs obtainable was five. The significance of the likelihood test showed the first two CVs might be used for interpretation. These functions accounted for 70 % of the total variation among the root systems (Table 2 - 3). CV 1 had a canonical correlation of 0.58 (Table 2 - 3). This value shows the highest possible multiple correlation of the response variates with the root system. The eigenvalue of 0.50 explained 51 % of the variation between the respective root systems across four 'Hayward' selections (Table 2 - 3). This indicates that the root systems differed most widely on CV 1. The standardized canonical coefficients of CV 1 (Table 2 - 3) showed larger absolute values for the variates number of flowers per shoot, trunk diameter, and mean fruit weight. The signs of these coefficients indicated that root system discrimination was highly influenced by large trunk diameter, low number of flowers, and large fruit size. These variates individually also showed high correlations (r) with CV 1 compared with other variates (Table 2 - 3). Thus, on a grouping and on an individual basis number of flowers per shoot, trunk diameter, and mean fruit weight contributed markedly to the differences among root systems.

Table 2 - 3. Standardized canonical coefficients (SCC), and correlation coefficients (r) between the canonical variates (CVs) and the measured variates of nine different root systems across four 'Hayward'selections. A Canonical Variate Analysis was performed each season. Canonical correlation values, eigenvalues, percentage of variance explained by eigenvalues, and likelihood are also shown.

Response Variables	1988-89						1989-90				1990-91[x]	
	CV 1	CV 1	CV 2	CV 2	CV 3	CV 3	CV 1	CV 1	CV 2	CV 2	CV 1	CV 1
	r	SCC	r	SCC	r	SCC	r	SCC	r	SCC	r	SCC
% Bud Burst	0.13 (NS)	0.11	-0.35 (**)	-0.67	0.66 (**)	0.76	-0.21 (**)	-0.39	0.05 (NS)	0.24	0.27 (NS)	0.34
% Floral Bud Burst	0.09 (NS)	0.28	0.20 (*)	-0.03	0.47 (**)	0.66	-0.31 (**)	-0.37	0.46 (**)	0.61	0.37 (*)	0.60
Number of Flowers per Shoot	-0.26 (**)	-0.49	0.21 (*)	0.05	-0.02 (NS)	-0.42	-0.13 (NS)	-0.42	0.21 (**)	-0.09	-0.08 (NS)	0.00
Trunk Diam. (mm)	0.79 (**)	1.09	-0.09 (NS)	-0.39	-0.26 (*)	-0.47	0.77 (**)	1.11	0.41 (**)	0.23	---	---
Yield (Kg/Vine)	0.23 (**)	-0.01	0.52 (**)	1.10	0.24 (*)	0.19	0.29 (**)	0.02	0.49 (**)	0.34	0.26 (NS)	0.68
Mean Fruit Weight (g)	0.30 (**)	0.48	0.39 (**)	0.53	0.16 (NS)	0.19	-0.07 (NS)	-0.28	0.63 (**)	0.80	0.72 (***)	1.03
Canonical Correlation Value	0.58		0.40		0.34		0.52		0.39		0.63	
Eigenvalue	0.50		0.19		0.13		0.37		0.18		0.66	
% Variance Explained by Eigenvalue	51.00		19.00		14.00		58.00		28.0		79.0	
Likelihood P > F for CVs	**		*		NS		**		*		*	

NS, *, **Non-significant or significant at $P \leq 0.05$, or 0.01, respectively.

[x]CDA performed for five response variates on three different root systems across two 'Hayward' selections.

It is important to note that the differences in number of flowers per shoot were small, the highest value among the root systems was 3.6 and the lowest 3.1 (Table 2 - 2). Therefore, in practical terms this variate may have low importance. CV 1 showed that the vines on root system 4 (male), and on their own roots achieved large canonical score means, and were significantly different from vines on the root systems 2 ('Bruno' seedlings), 3, 5, 6, 7, 8, and 9 (Tables 2 - 2, 2 - 4). Vines on root system 7 had the lowest values, which is interpreted as meaning that vines on this root system tended to have small trunk diameter, a slightly larger number of flowers, and smaller fruit size (Table 2 - 4).

For CV 2 the canonical correlation and the eigenvalue were 0.40 and 0.19, respectively. The eigenvalue accounted for 19 % of the variation between the different root systems (Table 2 - 3). According to the standardized coefficients and correlations, this CV was correlated significantly with, and primarily influenced by the characteristics of low percentage bud burst, and high yield of large fruit size (Table 2 - 3). Own rooted vines achieved the highest canonical mean scores and were significantly different from vines on root system 4 (male), 8 and 9. Root system 9 had the lowest canonical mean score (Table 2 - 4). The interpretation of CV 2 for this root system indicates high percentage of bud burst, and low yield of smaller fruit. In contrast, the least square means showed root system 9 had low bud burst (Table 2 - 2). In the standardized CV functions, each of the six measured variates had a contribution, and in CV 2 three variates showed a larger influence and thus primarily characterise this function. Sometimes the grouping arrangement of

Table 2 - 4. Mean canonical variate (CV) score of the response variates measured on nine different root systems across four 'Hayward' selections. A Canonical Variate Analysis was performed each season. In the last season, three root systems across two selections were analysed.

	1988-89				1989-90			1990-91	
Root systems	N[z]	CV 1[x]	CV 2[x]	CV 3[x]	N[z]	CV 1[x]	CV 2[x]	N[z]	CV 1[y]
Own roots	18	0.98 a	0.72 a	-0.10 abc	24	0.96 a	0.10 bcd	12	-0.08 b
2 'Bruno' seedlings	13	-0.39 b	-0.04 abc	0.02 abc	23	-0.28 b	-0.05 bcd		
3	17	-0.47 b	-0.11 abc	0.55 a	24	-0.00 b	-0.29 cde		
4 (male)	11	1.17 a	-0.20 bc	0.20 abc	19	0.65 a	0.76 a	11	1.04 a
5	15	-0.23 b	0.15 abc	0.00 abc	21	-0.44 bc	0.32 abc		
6	16	0.23 b	-0.04 abc	0.43 ab	24	-0.28 b	0.45 ab		
7	11	-1.33 c	0.57 ab	-0.50 c	24	-1.04 c	-0.11 bcde		
8	15	0.14 b	-0.45 c	-0.43 c	21	0.60 a	-0.72 e		
9	14	0.16 b	-0.66 c	-0.36 bc	24	-0.02 b	-0.36 de	12	-0.87 c

[x]Least square means with the same subscript in each column are not significantly different.
[y]Means with the same subscript in each column are not significantly different, by Duncan's multiple range test, 5 % level.
[z]Number of individuals.

the variates is difficult to explain because they reflect the mutual influence of the variates on each other (Rencher, 1992), and the interpretation of the results may be limited. Therefore, in practical terms root system 9 was characterised by low yield of smaller fruit size.

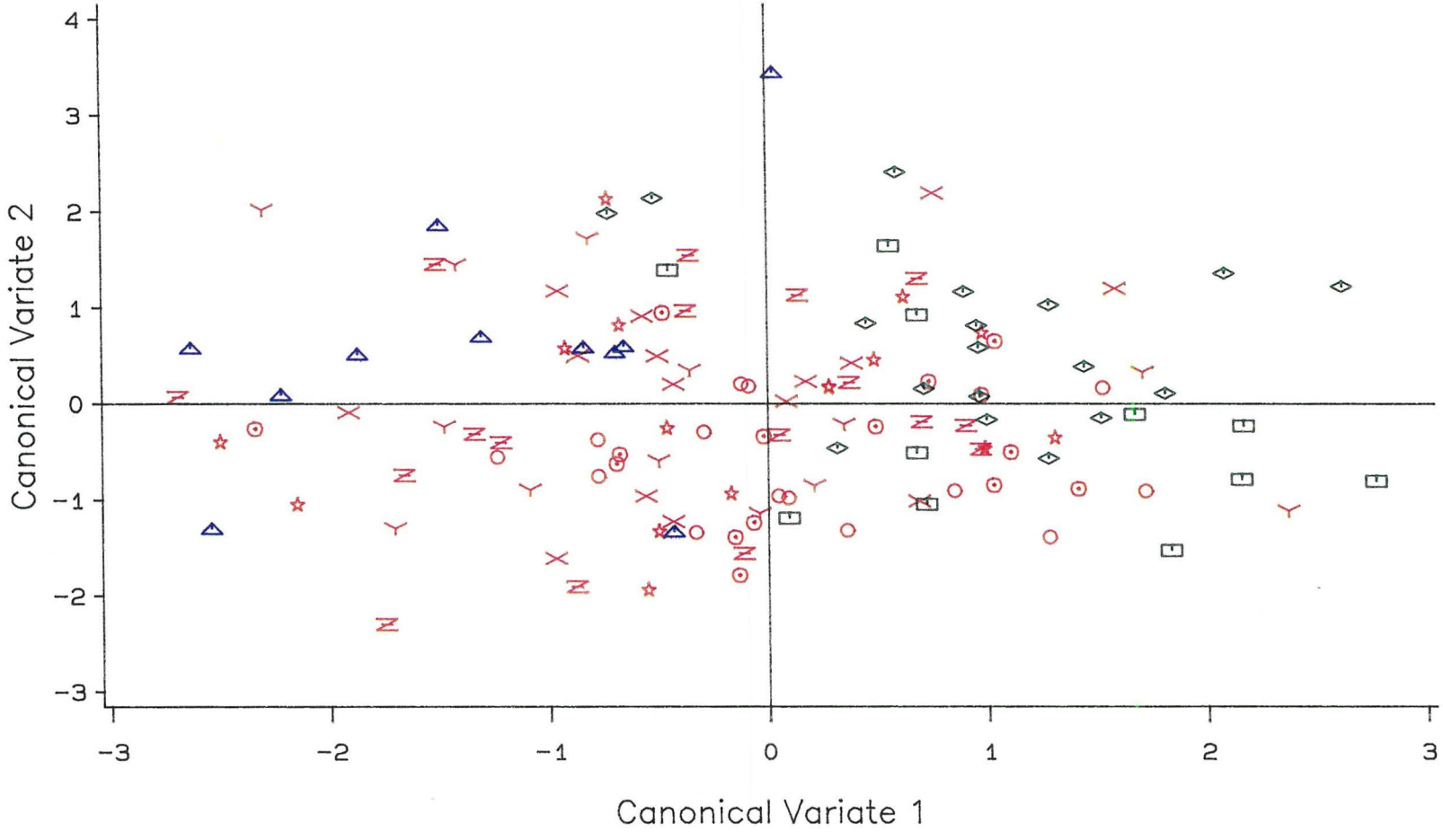
A plot of the canonical coefficient scores of the vines on the root systems illustrate the high discriminating capacity of CV 1 in separating own roots and vines on root system 4 (male), from root system 7 (Figure 2 - 1) mainly on the basis of large trunk diameter and fruit size . The CV 2 score makes a clear separation of own rooted vines and vines on root system 9. CV 2 characterised own rooted vines as having low bud burst, and high yield of large fruit size.

The third CV accounted for only 13 % of the variation among the root systems, and the significance of the likelihood test was low (Table 2 - 3), thus this CV together with the other two CVs (not shown) were not used for interpretation.

4.1.2. 1989-90 Season.

Four of the seven independent ANOVAs showed significant differences among the different root systems in regards to percentage of floral bud burst, trunk diameter, yield, and mean fruit weight. Own rooted vines and vines on root system 4 (male) achieved the highest values on trunk diameter and yield. Vines on root systems 4 and 6 achieved the highest mean fruit weight (Table 2 - 5). There were non-significant differences in crop load across the nine root systems. However, by orthogonal contrast vines on root system 4 with a least

Figure 2 - 1 Plot of the canonical scores of the first two canonical variates for field performance of 'Hayward' vines on nine root systems. 1988-89 Season . Root system 1 = own-rooted vines.



Root Systems 1 2 3 4 5 6 7 8 9

square mean of 528 fruit were significantly different ($P \leq 0.05$) from vines on root system 7 which had a least square mean of 392 fruit (Table 2 - 5).

The CVA indicated that 86 % of the variance among the nine different root systems was explained by the first two CVs with eigenvalues of 0.37 and 0.18, respectively (Table 2 - 3). The other three CVs are not shown due to the low percentage of the variance accounted for by them, and non-significant values from the likelihood test. Consideration of the structure and canonical coefficients of CV 1 shows it was primarily associated with large trunk diameter (Table 2 - 3). The vines on root systems 4 and 8, and the own rooted vines, achieved the highest mean score values, and were significantly different from the other vines topworked on the different root systems (Table 2 - 4).

CV 2 correlated significantly with large mean fruit weight, high yield, large percentage of floral bud burst, large trunk diameter, and large number of flowers per shoot (Table 2 - 3). The standardized values showed that this CV was mostly influenced by high percentage floral bud burst, and high yield of large fruit size. Vines on root systems 4, 5, and 6 scored high for CV 2. Root system 4 was significantly different from the own rooted vines, and vines on root systems 2 'Bruno' seedlings, 3, 7, 8, and 9 (Table 2 - 4). Vines on root systems 5, and 6 had significantly higher mean scores than vines own rooted and on root systems 3, 8, and 9 (Table 2 - 4).

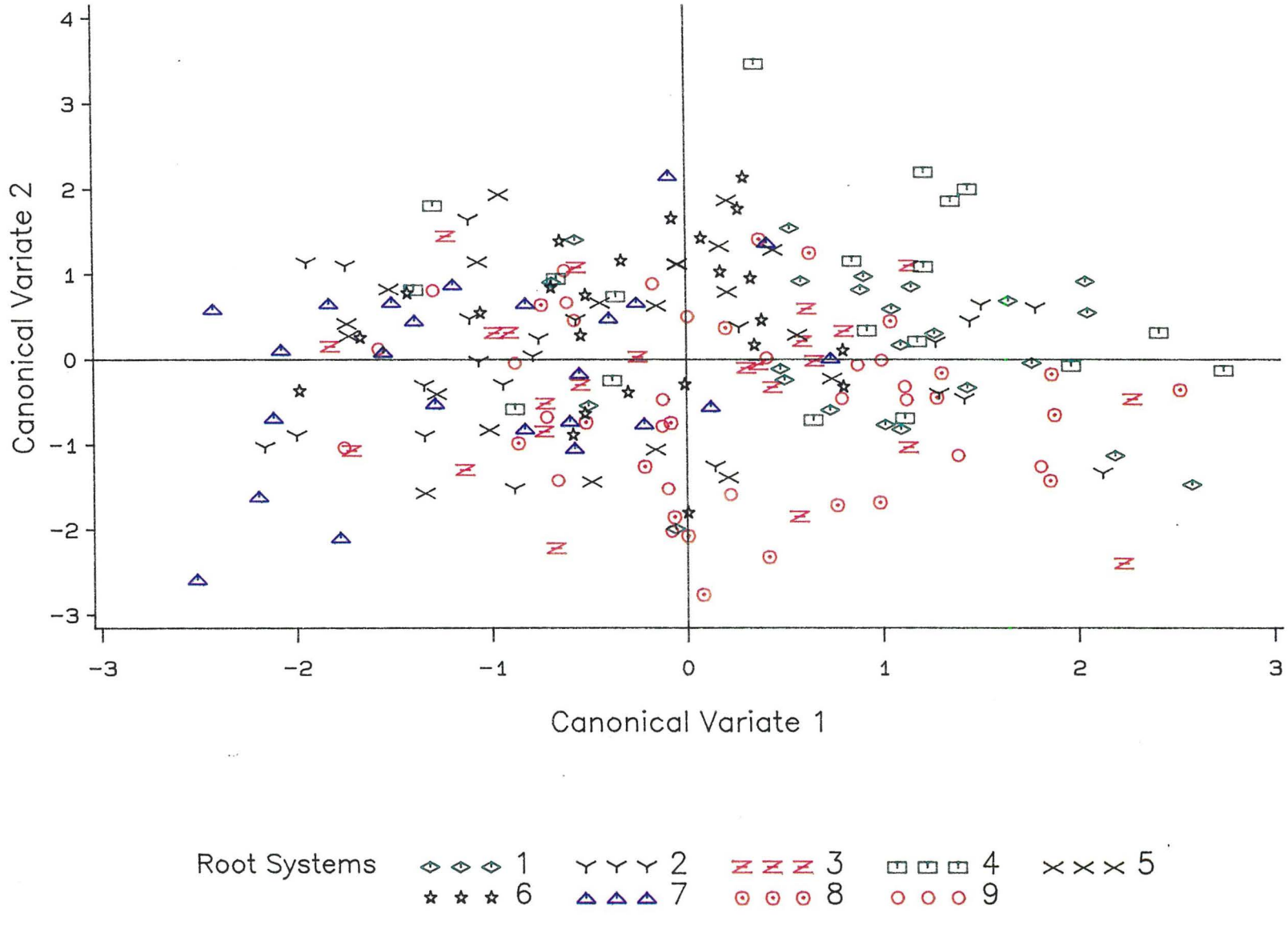
In spite of the overlapping of the scores of a few vines,

Table 2 - 5. Least square means (± standard error of the least square means), and analysis of variance (ANOVA) for the response variates measured across four 'Hayward' selections own rooted, and topworked on eight different kiwifruit root systems. 1989-90 season.

Root systems	N[4]	% Bud burst	% Floral bud burst	Number of flowers per shoot	Trunk diam. (mm)	Yield (Kg/vine)	Fruit number	Mean fruit weight (g)
1 Own roots[1]	24	55.5 (1.9)	90.3 (2.0)	3.6 (0.1)	37.8 (0.8)	49.3 (3.1)	501 (35)	96.9 (1.6)
2 'Bruno' seedling	23	56.7 (1.6)	92.4 (1.0)	3.5 (0.1)	32.2 (1.3)	40.2 (3.2)	423 (34)	97.7 (1.6)
3[2]	24	59.7 (1.5)	90.6 (1.7)	3.7 (0.1)	33.7 (1.1)	47.9 (2.6)	514 (36)	93.2 (1.6)
4 (male)[2]	19	56.3 (1.8)	93.6 (1.5)	3.6 (0.1)	37.6 (1.2)	53.0 (4.4)	528 (39)	100.5 (2.2)
5[2]	21	58.3 (1.5)	95.0 (0.9)	3.7 (0.1)	32.9 (1.0)	47.0 (4.2)	505 (37)	97.4 (2.6)
6[3]	24	59.9 (2.2)	91.6 (1.0)	3.7 (0.1)	33.8 (0.8)	49.0 (3.0)	493 (35)	100.7 (1.9)
7[3]	24	59.1 (1.7)	93.6 (1.2)	3.7 (0.1)	29.8 (1.1)	38.7 (2.8)	392 (35)	97.1 (1.9)
8[3]	21	57.5 (1.7)	86.9 (2.3)	3.5 (0.1)	34.6 (1.3)	41.8 (3.9)	467 (37)	93.0 (2.4)
9[3]	24	54.6 (1.8)	91.7 (1.8)	3.5 (0.1)	32.2 (0.8)	42.4 (2.6)	459 (34)	94.7 (1.8)
ANOVA significance.								
Rootstocks		NS	*	NS	**	**	NS	**

NS, *, **Non-significant or significant at $P \leq 0.05$, or 0.01, respectively.
[1]Least square means of four 'Hayward' selections on their own roots.
[2]Root system derived from 'good' vines which produced high yield of large fruit.
[3]Root system derived from 'poor' vines which produced low yield of small fruit.
[4]Number of individuals.

Figure 2 - 2 Plot of the canonical scores of the first two canonical variates for field performance of 'Hayward' vines on nine root systems. 1989-90 Season . Root system 1 = own-rooted vines.


Canonical Variate 2
Canonical Variate 1
4
3
2
1
0
-1
-2
-3
-3
-2
-1
0
1
2
3
Root Systems
1
2
3
4
5
6
7
8
9

CV 1 produced an adequate separation of the vines own rooted, and topworked on root systems 4 and 8, from the vines on root system 7 (Table 2 - 4, Figure 2 - 2). Some separation between vines on root system 4 and vines on root systems 8 and 9, along CV 2 is apparent (Figure 2 - 2).

4.1.3. 1990-91 Season.

From an ANOVA performed on each of five response variates, mean fruit weight was the only variate significantly different among own roots, and root systems 4 (male) and 9 (Table 2 - 6).

The first CV explained 79 % of the variance between the different root system groups, and was mainly influenced by high floral bud burst, yield, and mean fruit weight (Table 2 - 3). Vines on rootstock 4 achieved the highest score on that canonical function, and were significantly different from own rooted vines, and rootstock 9 (Table 2 - 4). Own rooted vines had a tendency to have higher coefficients ($P \leq 0.06$) than root system 9. Although the scores of the vines had a slight overlapping, vines on root system 4 were well separated from root system 9 along CV 1 (Figure 2 - 3).

4.2. 'Hayward' scion effects across eight root systems.

4.2.1. 1988-89 Season.

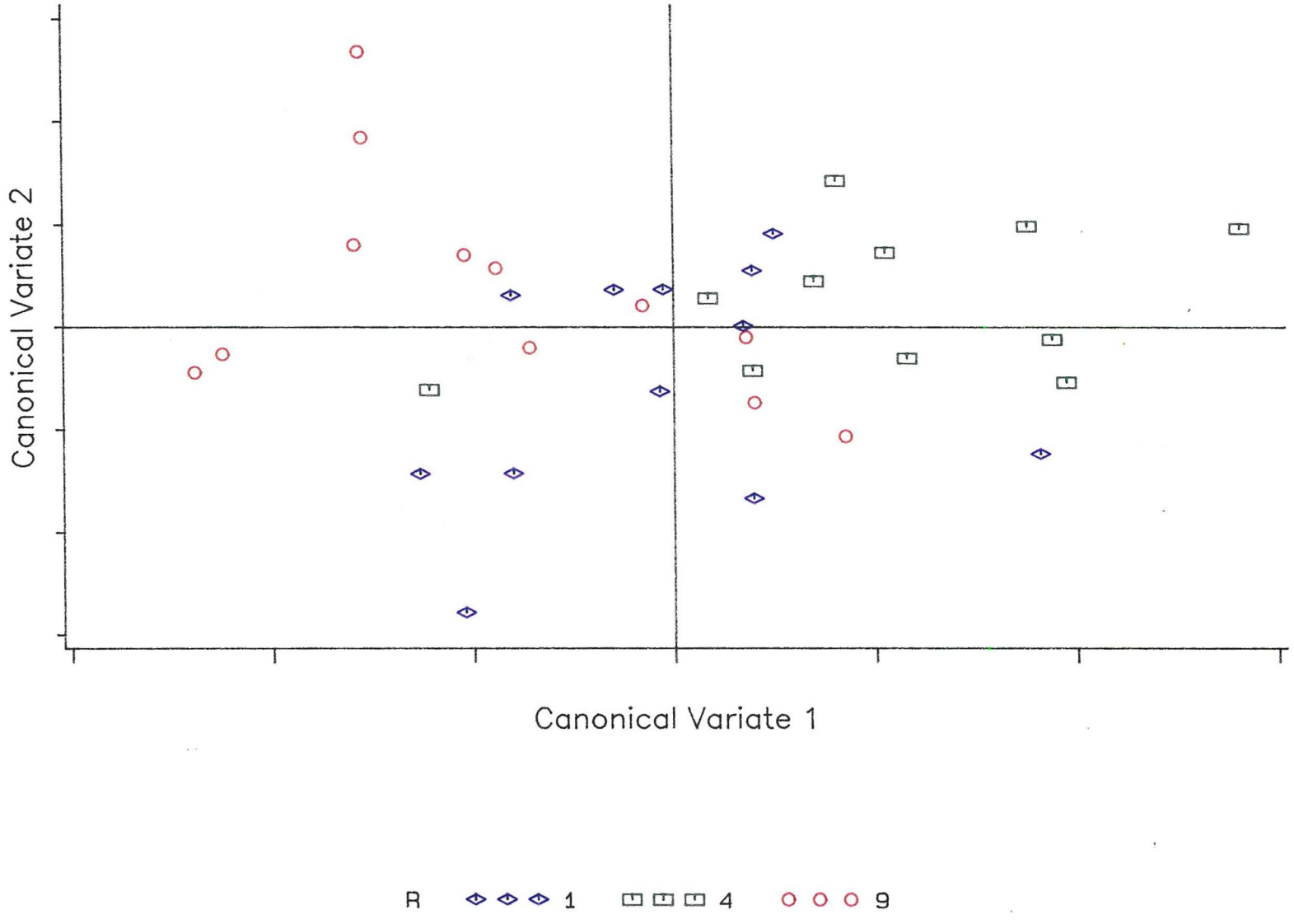
ANOVA and CVA were performed on seven and six response variates, respectively, measured on four different 'Hayward' selections topworked across eight different root systems. Own rooted systems

Table 2 - 6. Least square means (± standard error of the least square means), and analysis of variance (ANOVA) for the response variates measured across two 'Hayward' selections own rooted, and topworked on two different root systems. 1990-91 season.

Root systems	N[4]	% Bud burst	% Floral bud burst	Number of flowers per shoot	Yield (Kg/vine)	Fruit number	Mean fruit weight (g)
1 own roots[1]	12	62.0 (2.7)	68.7 (4.8)	3.6 (0.2)	33.9 (4.0)	342 (36)	100.2 (2.0)
4 (male)[2]	11	64.2 (2.9)	79.5 (3.8)	3.8 (0.3)	47.9 (6.5)	406 (37)	100.2 (2.0)
9[3]	12	61.2 (1.9)	70.3 (2.8)	3.7 (0.2)	38.3 (2.9)	396 (36)	90.8 (2.9)
ANOVA significance							
Root systems		NS	NS	NS	NS	NS	*

NS, *Non-significant or significant at $P \leq 0.01$, respectively.
[1]Means of two 'Hayward' selections on their own roots.
[2]Root system derived from 'good' vines which produced high yield of large fruit.
[3]Root system derived from 'poor' vines which produced low yield of small fruit.
[4]Number of individuals.

Figure 2 - 3 Plot of the canonical scores of the first two canonical variates for field performance of 'Hayward' vines topworked on three root systems. 1990-91 Season . Root system 1 = own rooted vines.


Canonical Variate 2
Canonical Variate 1
R
1
4
9

were excluded from the analysis to evaluate scion effects. Fruit number, yield and mean fruit weight showed significant differences among the four different 'Hayward' scions by ANOVA (Table 2 - 7).

Although the likelihood test showed only CV 1 significant, CV 2 accounted for a considerable amount of the variation (32 %), hence it was used for interpretation (Table 2 - 8). In total, the two CVs accounted for 97 % of the total variation between the four different 'Hayward' selections (Table 2 - 8).

CV 1 reached an eigenvalue of 0.22, and explained 65 % of the variation between the different 'Hayward'. The standardized canonical coefficients characterised primarily for vines having a low number of flowers per shoot, and high yield of large fruit size (Table 2 - 8). The differences in number of flowers per shoot were small with a difference of 0.4 between the higher and lower vine flower producers (Table 2 - 7). Therefore, this variate may have in practical terms low importance for discriminating among the 'Hayward' scions. The vines topworked with 'Hayward' A reached the highest mean canonical coefficient value, and were significantly different from the other 'Hayward' selections (Table 2 - 9). 'Hayward' B produced the lowest mean score, indicating a 'poor' performance in yield and fruit size (Table 2 - 9). Haywards 'A' and 'B' had similar crop load ($P \leq 0.36$) (Table 2 - 7). A plot between the first two CVs illustrated the higher discriminant capacity of CV 1 in separating the 'Hayward' selections A and B on the basis of the characteristics stated above (Figure 2 - 4).

Table 2 - 7. Least square means (± least square standard error of the means), and analysis of variance (ANOVA) for the measured response variates of four different'Hayward' selections topworked across eight different kiwifruit root systems. 1988-89 season.

'Hayward' selections	N[3]	% Bud burst	% Floral bud burst	Number of flowers per shoot	Trunk diam. (mm)	Yield (Kg/vine)	Fruit number	Mean fruit weight (g)
A[1]	33	55.0 (1.5)	83.8 (2.2)	3.1 (0.1)	24.0 (0.5)	27.8 (2.0)	230 (21)	122.1 (2.1)
B[1]	21	56.2 (1.8)	84.5 (2.3)	3.3 (0.2)	24.1 (0.6)	22.0 (2.6)	199 (26)	111.9 (2.9)
C[2]	36	55.9 (1.5)	86.4 (1.8)	3.4 (0.1)	25.4 (0.5)	31.7 (2.4)	288 (20)	113.6 (1.7)
D[2]	22	56.5 (1.3)	88.3 (2.4)	3.5 (0.1)	26.0 (0.8)	30.8 (2.3)	282 (25)	112.1 (2.3)
ANOVA significance								
'Hayward' selections		NS	NS	NS	NS	*	*	**

NS, *, **Non-significant or significant at $P \leq 0.05$ or 0.01, respectively.
[1]'Hayward' derived from 'good' vines which produced high yield of large fruit.
[2]'Hayward' derived from 'poor' vines which produced low yield of small fruit.
[3]Number of individuals.

Table 2 - 8. Standardized canonical coefficients (SCC), and correlation coefficients (significance) between the canonical variates (CVs) and the measured variates of four 'Hayward' selections topworked across eight different kiwifruit rootstocks. A Canonical Variate Analysis (CVA) was performed each season. Canonical correlations, eigenvalues, percentages of variance explained by eigenvalue, and likelihood test are also shown.

Response Variables	1988-89				1989-90				1990-91[x]	
	CV 1	CV 1	CV 2	CV 2	CV 1	CV 1	CV 2	CV 2	CV 1	CV 1
	r	SCC	r	SCC	r	SCC	r	SCC	r	SCC
% Bud Burst	-0.15 (NS)	-0.32	0.08 (NS)	-0.26	-0.19 (*)	-0.04	0.41 (***)	0.07	-0.33 (NS)	-0.33
% Floral Bud Burst	-0.18 (NS)	-0.11	0.39 (**)	-0.00	-0.17 (*)	-0.09	0.18 (*)	0.10	-0.04 (NS)	-0.37
Number of Flowers per Shoot	-0.31 (**)	-0.46	0.50 (**)	0.00	-0.17 (*)	-0.38	0.84 (***)	0.59	0.53 (**)	0.59
Trunk Diam. (mm)	-0.22 (*)	-0.32	0.77 (**)	0.50	0.39 (**)	0.34	0.80 (***)	0.60	---	---
Yield (Kg/Vine)	0.17 (NS)	0.46	0.85 (***)	0.74	0.35 (**)	0.43	0.60 (***)	-0.06	0.52 (**)	0.71
Mean Fruit Weight (g)	0.78 (***)	0.79	-0.34 (**)	-0.73	0.83 (***)	0.88	-0.19 (*)	-0.10	0.45 (*)	0.87
Canonical Correleation Value	0.42		0.31		0.45		26		0.59	
Eigenvalue	0.22		0.10		0.26		0.07		0.55	
% Variance Explained by Eigenvalue	65.00		32.00		75.00		20.00		100.00	
Likelihood P ≥ F for CVs	***		NS		***		NS		NS	

[x]CVA on five response variables of two different 'Hayward' selections across two rootstocks.
[NS, *, **, ***]Non-significant or significant at P ≤ 0.05, 0.01, or 0.001, respectively.

Table 2 - 9. Canonical variate (CV) score means of the measured response variates for four 'Hayward' selections topworked across eight different kiwifruit rootstocks. A Canonical Variate Analysis was performed each season. In the last season, two 'Hayward' selections across two different rootstocks were analysed.

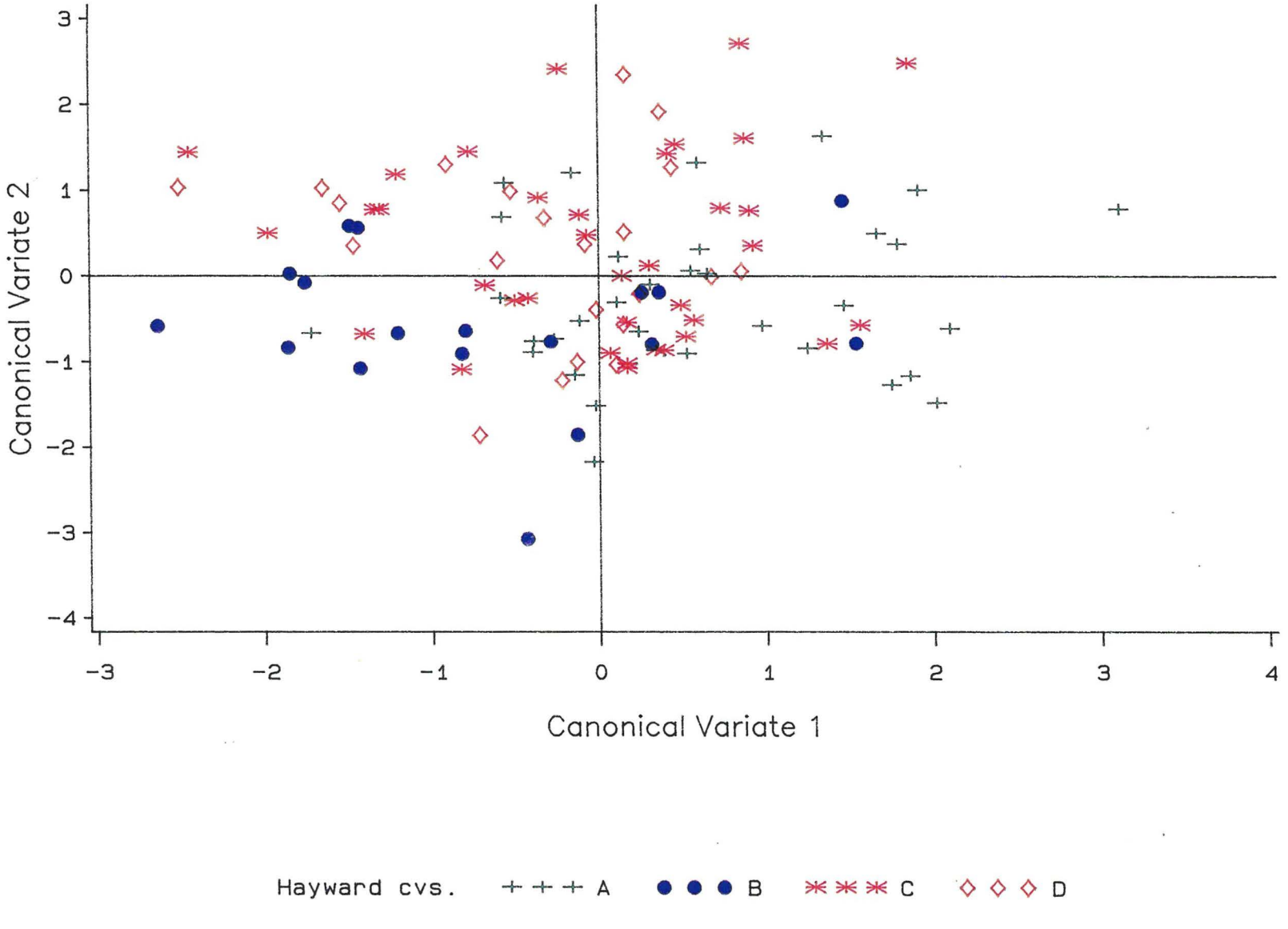
'Hayward' selections	1988-89			1989-90			1990-91	
	N[z]	CV 1[x]	CV 2[x]	N[z]	CV 1[x]	CV 2[x]	N[z]	CV 1[y]
A	33	0.63 a	-0.19 b	46	0.47 a	-0.03 b	11	0.71 a
B	21	-0.61 c	-0.50 c	45	-0.85 c	-0.04 b		
C	36	0.02 b	0.28 a	43	0.13 b	0.42 a		
D	22	-0.32 b	0.30 a	46	0.23 b	-0.31 b	12	-0.71 b

[x]Least square means in each column with the same subscript are not significantly different, at 5 % level.

[y]Means with the same subscript in each column are not significantly different, by Duncan's multiple range test 5 % level.

[z]Number of individuals.

Figure 2 - 4 Plot of the canonical scores of the first two canonical variates for field performance of vines of four 'Hayward' selections across eight kiwifruit root systems. 1988-89 Season.


Canonical Variate 2
Canonical Variate 1
3
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3
4
Hayward cvs.
A
B
C
D

In the second CV, the standardized canonical coefficients showed a large influence of high yield of smaller fruit and large trunk diameter (Table 2 - 8). 'Hayward' scions C and D had the highest canonical score mean value, whereas 'Hayward' B the lowest (Table 2 - 9). 'Haywards' C and D had larger fruit number than 'Hayward' B ($P \leq 0.03$) (Table 2 - 7).

4.2.2. 1989-90 Season.

The independent ANOVAs indicated significant differences among the four different scions regarding the number of flowers per shoot, trunk diameter, fruit number, yield, and mean fruit weight (Table 2 - 10).

CV 1 accounted for 75 % of the variation between scions. The standardized canonical coefficients showed it was mainly influenced by scions having low number of flowers per shoot, large trunk diameter, and high yield of large fruit size (Table 2 - 8). Vines topworked with scion 'A' reached the highest canonical coefficient mean score, and were significantly different from the vines topworked with scions 'B', 'C', and 'D'. 'Hayward' B vines had the lowest CV 1 score, and were mainly characterised by small trunk diameter, and low yield of smaller fruit (Table 2 - 9).

The second CV accounted for 20 % of the variation between the different 'Hayward' selections. The canonical standardized structure was determined dominantly by number of flowers per shoot, and trunk diameter (Table 2 - 8). 'Hayward' C had the highest canonical coefficients, and 'Hayward' D the lowest (Table 2 - 9).

Table 2 - 10. Least square means (± standard error of the least square means), and analysis of variance (ANOVA) for the measured response variates of four 'Hayward' selections topworked across eight different kiwifruit root systems. 1989-90 season.

'Hayward' selections	N[3]	% Bud burst	% Floral bud burst	Number of flowers per shoot	Trunk diam. (mm)	Yield (Kg/vine)	Fruit number	Mean fruit weight (g)
A[1]	46	57.7 (1.0)	91.1 (1.2)	3.5 (0.1)	33.9 (0.7)	49.0 (2.6)	501 (25)	99.8 (1.2)
B[1]	45	59.0 (1.4)	92.7 (1.1)	3.6 (0.1)	31.3 (0.8)	40.6 (2.2)	453 (26)	90.5 (1.3)
C[2]	43	58.7 (1.2)	92.5 (0.9)	3.8 (0.1)	35.3 (0.6)	48.4 (2.2)	507 (26)	97.1 (1.4)
D[2]	46	55.9 (1.2)	91.4 (1.2)	3.4 (0.1)	32.4 (0.9)	41.5 (2.4)	426 (26)	99.4 (1.3)
ANOVA significance								
'Hayward' selections		NS	NS	**	**	**	*	**

NS, *, **Non-significant or significant at $P \leq 0.05$ or 0.01, respectively.
[1]'Hayward' derived from 'good' vines which produced high yield of large fruit.
[2]'Hayward' derived from 'poor' vines which produced low yield of small fruit.
[3]Number of individuals.

The nature of the separation among the 'Hayward' selections is illustrated in Figure 2 - 5. Although there is some overlapping 'Hayward' A is separated from 'B' along the first CV direction. In this CV, low number of flowers per shoot, large trunk diameter, and high yield of large fruit influenced the discrimination between those two 'Hayward' selections across eight root systems.

4.3. 'Hayward' selection effects on individual root systems.

Only root systems having a significant likelihood test, and a relatively large percentage of the degree of separation between the scions are shown in two seasons.

4.3.1. 1988-89 Season.

Own rooted vines.

The ANOVAs showed significant differences among the four own rooted 'Hayward' selections on percentage bud burst, trunk diameter, fruit number, yield, and mean fruit weight (Table 2 - 11). Vines of 'Hayward' B on their own roots achieved the highest least square means for bud burst, number of flowers, trunk diameter, fruit number, and yield (Table 2 - 11).

The first two CVs accounted for 93 % of the total variation among the rooted vines. The standardized canonical coefficients of CV 1 accounted for 72 % of the variation and indicate that vines of 'Hayward' B on its own roots were strongly characterised by large

Figure 2 - 5 Plot of the canonical scores of the first two canonical variates for field performance of vines of four 'Hayward' selections across eight kiwifruit root systems. 1989-90 Season.

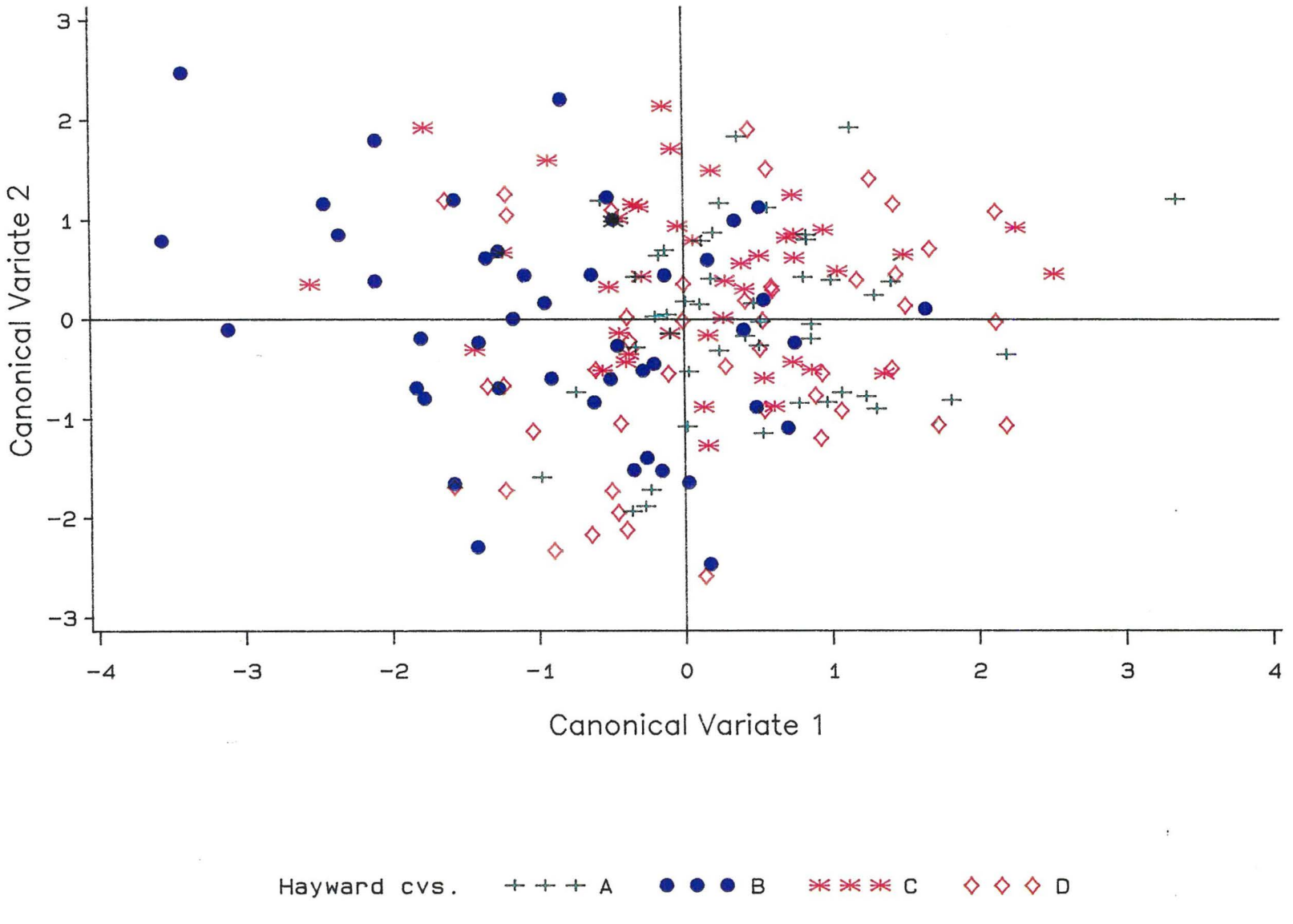

Canonical Variate 2
3
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3
4
Canonical Variate 1
Hayward cvs.
A
B
C
D

Table 2 - 11. Least square means (± standard error of the least square means) on each of three root systems, and analysis of variance (ANOVA) for the measured response variates of diferent root systems among four 'Hayward' selections. 1988-89 season.

Root systems	'Hayward selections	N[z]	% Bud burst	% Floral bud burst	Number of flowers per shoot	Trunk diameter (mm)	Yield (Kg/vine)	Fruit number	Mean fruit weight (g)
Own Roots	A	5	50.1 (2.6)	88.7 (4.5)	2.8 (0.2)	24.7 (0.9)	30.6 (5.0)	241 (51)	128.2 (2.3)
	B	3	63.9 (3.7)	91.2 (6.4)	3.7 (0.3)	31.9 (1.3)	59.2 (7.0)	514 (65)	118.0 (3.2)
	C	5	56.3 (2.6)	90.3 (4.5)	3.3 (0.2)	28.0 (0.9)	34.6 (5.0)	291 (51)	120.3 (2.3)
	D	5	51.5 (2.6)	79.9 (4.5)	3.2 (0.2)	26.9 (0.9)	35.4 (5.0)	311 (51)	116.2 (2.3)
ANOVA significance	df								
Own roots	3		*	NS	NS	**	*	*	**
6	A	5	56.1 (3.0)	88.0 (5.4)	3.2 (0.3)	24.2 (1.6)	37.3 (5.3)	299 (48)	124.9 (5.0)
	B	3	54.4 (2.3)	89.0 (4.2)	3.4 (0.3)	23.2 (1.2)	18.9 (3.8)	169 (37)	112.6 (4.1)
	C	6	58.4 (2.3)	93.0 (4.2)	3.2 (0.3)	25.7 (1.2)	36.9 (3.8)	315 (37)	118.5 (4.1)
	D	3	60.3 (3.0)	83.0 (5.4)	3.4 (0.4)	23.0 (1.7)	29.5 (4.9)	282 (53)	108.3 (5.0)
ANOVA significance	df								
'Hayward' Selections	3		NS	NS	NS	NS	*	*	NS
9[x]	A	6	55.5 (3.1)	78.3 (4.9)	2.7 (0.2)	25.6 (1.0)	22.4 (3.3)	187 (33)	118.9 (2.9)
	B	3	48.1 (4.4)	84.9 (7.0)	3.1 (0.2)	25.2 (1.5)	11.4 (4.7)	100 (47)	112.7 (4.2)
	C	5	52.8 (3.4)	88.3 (5.4)	3.2 (0.2)	25.7 (1.1)	26.0 (3.6)	261 (37)	106.2 (3.2)
ANOVA significance	df								
'Hayward' Selections	2		NS	NS	NS	NS	NS	*	*

[NS, *, **]Non-significant or significant at $P \leq 0.05$, or 0.01, respectively.
[x]'Hayward' D was not included in the analysis due to lack of replications.
[z]Number of individuals.

trunk diameter and high yield (Table 2 - 12). On this CV, these vines were significantly different from the other 'Hayward' selections each on their own roots (Table 2 - 13). CV 2 was mostly influenced by percentage floral bud burst, and mean fruit weight (Table 2 - 12). Own roots 'A' scored high and was significantly different from the other vines (Table 2 - 13).

Root system 6.

The first CV accounted for 75 % of the variation between the 'Hayward' selections topworked on this root system (Table 2 - 12). CV 1 revealed differences among the 'Hayward' selections on the basis of low percentage of bud burst, high percentage of floral bud burst, low number of flowers per shoot, large trunk diameter, and high yield of large fruit size (Table 2 - 12). 'Haywards' A, and C achieved the highest canonical score means and were significantly superior to 'Haywards' B, and D (Table 2 - 13). Scion 'Hayward' B had low ability to size fruit in comparison to 'Hayward' A, as reflected by its low yield of 19 Kg of fruit per vine (Table 2 - 11). This may indicate fewer fruiting canes in the 'Hayward' B vines topworked on root system 6.

Root system 9.

Data for 'Haywards' A, B, and C were used in the CVA. 'Hayward' B was significantly different from A. 'Hayward' B was primarily characterised by having higher floral bud burst, larger number of flowers per shoot, and lower yield of small fruit. In comparison to 'Hayward' A (Tables 2 - 12, 2 - 13). 'Hayward' B had low fruit

Table 2 - 12. Standardized canonical coefficients (SCC), and correlation coefficients (significance) between the canonical variates (CVs) and the measured variates of four 'Hayward' selections topworked on each of three root systems. Percentage of variance explained by eigenvalues, and significance of the likelihood test are also shown. 1988-89 season.

Response variates	Own roots	Own roots	Own roots	Own roots	R 6	R 6	R 6	R 6	R 9[x]	R 9[x]	R 9[x]	R 9[x]
	CV 1	CV 1	CV 2	CV 2	CV 1	CV 1	CV 2	CV 2	CV 1	CV 1	CV 2	CV 2
	r	SCC	r	SCC	r	SCC	r	SCC	r	SCC	r	SCC
% Bud burst	0.74 (**)	-0.03	0.03 (NS)	0.07	-0.05 (NS)	-0.91	0.54 (*)	1.04	-0.25 (NS)	-0.49	0.18 (NS)	-0.83
% Floral bud burst	0.39 (NS)	0.27	0.40 (NS)	0.92	0.34 (NS)	1.90	-0.10 (NS)	-0.50	0.43 (NS)	1.02	0.16 (NS)	0.55
Number of flowers per shoot	0.66 (**)	-0.00	-0.31 (NS)	-0.30	-0.18 (NS)	-1.05	0.02 (NS)	-0.88	0.51 (*)	1.02	0.12 (NS)	-2.63
Trunk diam. (mm)	0.86 (**)	1.61	0.24 (NS)	0.56	0.37 (NS)	0.80	0.24 (NS)	-0.10	0.03 (NS)	-0.52	0.08 (NS)	-0.36
Yield (Kg/Vine)	0.80 (**)	1.09	-0.15 (NS)	-0.05	0.52 (*)	0.82	0.65 (*)	1.38	-0.07 (NS)	-1.18	0.50 (*)	2.59
Mean fruit weight (g)	-0.48 (*)	0.60	0.73 (*)	1.36	0.57 (*)	1.27	-0.01 (NS)	-1.05	-0.63 (*)	-1.08	-0.40 (NS)	-1.74
% Variance explained by eigenvalue	72.00		21.00		75.00		22.00		60.00		40.00	
Likelihood P > F for CVs	*		NS		*		NS		*		NS	

[NS, *, **]Non-significant or significant at $P \leq 0.05$, or 0.001, respectively.
[x]CVA performed among 'Hayward' selections A, B, and C.

Table 2 - 13. Canonical variate (CV) score means of the measured response variates of the four 'Hayward' selections topworked on each of three root systems. 1988-89 season.

'Hayward' selections		Own roots	Own roots		R 6	R 6		R 9[x]	R 9[x]
	N[y]	CV 1	CV 2	N[y]	CV 1	CV 2	N[y]	CV 1	CV 2
A	5	-1.44 c	1.12 a	5	1.86 a	-0.09 b	6	-1.76 b	-0.24 b
B	3	3.77 a	0.10 b	3	-1.15 b	-1.53 c	3	1.76 a	-1.94 c
C	5	0.12 b	0.25 b	6	2.03 a	0.68 a	5	1.06 ab	1.45 a
D	5	-0.94 c	-1.44 c	3	-3.34 c	1.51 a		-	-

[x]CVA performed among three 'Hayward' selections.
[y]Number of individuals.
Least square means with the same subscript in each column are not significantly different at $P \leq 0.05$.
'Hayward' D vines on root system 9 were not analysed for lack of replications.

number with respect to the other scions (Table 2 - 11). This may show that scion 'Hayward' B had a lower number of fruiting canes per vine when topworked onto root system 9.

4.3.2. 1989-90 Season.

Root system 3.

There was a significant effect of 'Hayward' selection on mean fruit weight when topworked on this root system (Table 2 - 14).

On the basis of six measured variates, CVA revealed significant differences among the 'Hayward' scions topworked on this root system. The characters trunk diameter and fruit size had a strong effect in characterising and distinguishing the scion groups. This was reflected in their high correlation with the CV, and their high standardized canonical coefficients (Table 2 - 15). 'Hayward' C achieved the highest canonical mean values, and was statistically similar to 'Hayward' A, but different from 'B' and 'D' (Table 2 - 16). The crop load was similar for all scions (Table 2 - 14). Therefore, the fruit sizing ability of 'Haywards' A and C was superior to the other scions. Scion 'Hayward' B which was a 'poor' scion across eight root systems achieved high yield when topworked on root system 3 (Table 2 - 14) may be as a reflection of a high crop load due to a large cane number.

Table 2 - 14. Means (± standard error of the means), and analysis of variance (ANOVA) for the measured response variates on each of three root systems among four 'Hayward' selections. 1989-90 season.

Root Systems	'Hayward' selections	N[x]	% Bud Burst	% Floral Bud Burst	Number of Flowers per Shoot	Trunk Diam. (mm)	Yield (Kg/vine)	Fruit number	Mean Fruit Weight (g)
3	A	6	60.7 (2.3)	88.3 (4.0)	3.6 (0.1)	35.2 (1.9)	47.6 (5.4)	481 (58)	96.8 (1.5)
	B	6	61.8 (4.4)	89.3 (4.0)	3.6 (0.3)	32.2 (1.9)	53.2 ((6.9)	583 (85)	92.4 (2.8)
	C	6	56.7 (2.9)	95.2 (2.7)	3.7 (0.1)	36.3 (1.6)	49.6 (2.8)	521 (38)	96.9 (3.0)
	D	6	59.7 (2.8)	89.7 (3.1)	3.6 (0.2)	31.1 (3.2)	41.1 (5.3)	473 (77)	86.6 (4.0)
ANOVA significance			NS	NS	NS	NS	NS	NS	*
7	A	6	58.3 (3.7)	91.7 (2.5)	3.8 (0.2)	32.5 (2.0)	47.7 (4.5)	476 (41)	103.6 (1.8)
	B	6	61.7 (3.9)	94.0 (3.8)	3.5 (0.2)	25.5 (2.3)	26.9 (4.0)	309 (43)	87.5 (4.6)
	C	6	61.2 (2.6)	95.3 (1.6)	3.9 (0.2)	31.6 (1.9)	47.4 (3.2)	459 (49)	95.9 (2.9)
	D	6	55.2 (3.5)	93.3 (2.2)	3.4 (0.2)	28.6 (1.9)	32.8 (5.6)	326 (56)	101.4 (1.4)
ANOVA significance			NS	NS	NS	*	**	*	**
9	A	6	55.7 (3.8)	85.8 (4.5)	3.4 (0.2)	35.0 (0.7)	51.3 (5.5)	530 (64)	99.0 (4.0)
	B	6	54.2 (4.9)	93.0 (3.7)	3.4 (0.2)	30.6 (1.5)	31.4 (4.1)	349 (48)	88.7 (3.4)
	C	6	54.3 (4.0)	90.7 (2.9)	3.6 (0.3)	34.4 (1.1)	43.6 (4.5)	505 (61)	92.7 (2.8)
	D	6	54.3 (1.8)	97.2 (1.8)	3.5 (0.0)	28.5 (1.1)	43.5 (3.9)	453 (40)	98.6 (3.0)
ANOVA significance			NS	NS	NS	**	**	NS	NS

NS, *, **Non-significant or significant at $P \leq 0.05$, or 0.01, respectively.
[x]Number of individuals.

Table 2 - 15. Standardized canonical coefficients (SCC), and correlation coefficients (significance) between the canonical variates (CVs) and the measured variates of four 'Hayward' selections topworked on each of three root systems. Percentage of variance explained by eigenvalues, and significance of the likelihood test are also shown. 1989-90 season.

Response variates	R 3	R 3	R 3	R 3	R 7	R 7	R 7	R 7	R 9	R 9	R 9	R 9
	CV 1	CV 1	CV 2	CV 2	CV 1	CV 1	CV 2	CV 2	CV 1	CV 1	CV 2	CV 2
	r	SCC	r	SCC	r	SCC	r	SCC	r	SCC	r	SCC
% Bud burst	-0.14 (NS)	-0.28	0.33 (NS)	0.47	-0.14 (NS)	0.31	0.49 (*)	-0.00	-0.01 (NS)	0.86	0.07 (NS)	0.10
% Floral bud burst	0.20 (NS)	0.08	-0.30 (NS)	-0.80	-0.11 (NS)	-0.59	0.17 (NS)	-0.31	0.39 (*)	0.90	-0.37 (NS)	-0.25
Number of flowers per shoot	0.02 (NS)	0.01	-0.00 (NS)	-1.03	0.30 (NS)	-0.24	0.62 (*)	0.43	-0.01 (NS)	-0.00	0.06 (NS)	0.03
Trunk diam. (mm)	0.48 (*)	0.92	-0.14 (NS)	-0.84	0.62 (**)	0.70	0.27 (NS)	-0.42	-0.64 (***)	-1.61	0.56 (**)	0.54
Yield (Kg/Vine)	0.25 (NS)	0.30	0.35 (NS)	1.91	0.74 (***)	0.79	0.47 (*)	1.09	0.09 (NS)	1.02	0.69 (***)	1.01
Mean fruit weight (g)	0.68 (***)	1.31	0.10 (NS)	0.24	0.73 (***)	0.85	-0.55 (*)	-0.96	0.34 (NS)	0.97	0.49 (*)	1.06
% Variance explained by eigenvalue	65.00		31.00		78.00		20.00		57.00		42.00	
Likelihood P ≥ F for CVs	*		NS		*		NS		**		*	

NS, *, **, ***Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively

Table 2 - 16. Canonical variate (CV) score means of the response variates of four 'Hayward' selections topworked on each of three root systems. 1989-90 season.

'Hayward' selections		R 3	R 3		R 7	R 7		R 9	R 9
	N[x]	CV 1	CV 2	N[x]	CV 1	CV 2	N[x]	CV 1	CV 2
A	6	0.78 ab	0.30 ab	6	1.57 a	0.01 ab	6	-0.53 b	1.82 a
B	6	-0.34 b	1.14 a	6	-1.99 c	0.26 a	6	-0.83 b	-1.88 c
C	6	1.24 a	-0.77 b	6	0.51 b	0.76 a	6	-1.24 b	0.20 b
D	6	-1.68 c	-0.66 b	6	-0.09 b	-1.04 b	6	2.61 a	-0.13 b

[x]Number of individuals.
Least square means with the same subscript in each column are not significantly different at 5 % level.

Root system 7.

From the ANOVAs performed on the four 'Haywards' topworked on this root system, trunk diameter, fruit number, yield, and mean fruit weight showed significant differences. 'Hayward' A achieved the highest trunk diameter, fruit number, yield, and fruit size (Table 2 - 14).

On the basis of the CVA, 'Hayward' A was distinguished significantly from the other selections by its large trunk diameter, and high yield of large fruit. 'Hayward' B had the 'poorest' performance on those response variates (Tables 2 - 15, 2 - 16).

Root system 9.

The standardized canonical coefficients for CV 1 were highly influenced by small trunk diameter, and high yield of large fruit (Table 2 - 15). 'Hayward' D reached the highest mean canonical score, whereas 'Hayward' C the lowest (Table 2 - 16).

The variates which made the highest contribution to CV 2 were high yield, and large fruit size (Table 2 - 15). 'Hayward' A had the highest canonical coefficient score mean, and B the lowest (Table 2 - 16).

4.4. Root system effects on individual 'Hayward' selections.

Only 'Hayward' selections having a significant likelihood test, and a relatively large percentage of the degree of separation between the root systems are shown in two seasons.

4.4.1 1988-89 Season.

'Hayward' A.

The independent ANOVAs for nine root systems with 'Hayward' A scion showed significant differences in number of flowers per current season shoot, and mean fruit weight (Table 2 - 17).

In CV 1, 'Hayward' A own rooted and on root systems 4, 5, and 7 were significantly distinguished mainly for having the largest mean fruit weight. In contrast root system 8 resulted in vines with the smallest fruit size (Tables 2 - 17, 2 - 18, 2 - 19).

CV 2 was primarily characterised by a large number of flowers per shoot. 'Hayward' A on root system 7 obtained the highest mean score, and own rooted 'Hayward' A the lowest (Table 2 - 18).

Table 2 - 17. Least square means (± standard error of square means), and analysis of variance (ANOVA) significance of the measured response variates for each of three 'Hayward' selections own rooted, and topworked on eight root systems. 1988-89 season.

'Hayward selections	Root systems	N[x]	% Bud burst	% Floral bud burst	Number of flowers per shoot	Trunk diam. (mm)	Yield (Kg/vine)	Fruit number	Mean fruit weight (g)
A	1 Own rooted	5	50.5 (3.8)	88.4 (5.5)	2.8 (0.2)	24.6 (1.2)	31.0 (4.1)	240 (38)	129.9 (3.6)
	2 'Bruno' seedlings	4	57.2 (4.4)	81.7 (6.2)	3.2 (0.2)	23.1 (1.3)	28.2 (4.7)	240 (43)	121.9 (4.1)
	3	5	57.1 (3.8)	91.6 (5.5)	3.2 (0.2)	22.1 (1.2)	29.8 (4.1)	260 (38)	114.4 (3.6)
	4 (male)	2	59.0 (6.3)	70.9 (8.9)	2.4 (0.3)	23.7 (1.9)	15.8 (6.7)	105 (62)	142.1 (5.9)
	5	3	47.8 (4.1)	76.9 (7.0)	2.8 (0.2)	23.2 (1.5)	19.9 (5.3)	151 (49)	130.8 (4.7)
	6	3	55.7 (4.1)	86.9 (7.0)	3.1 (0.2)	24.4 (1.5)	34.6 (5.3)	279 (49)	123.8 (4.7)
	7	4	50.2 (4.4)	90.5 (6.2)	3.8 (0.2)	21.3 (1.3)	29.7 (4.7)	227 (43)	128.1 (4.1)
	8	6	55.7 (3.5)	84.0 (4.1)	3.3 (0.2)	26.3 (1.1)	30.6 (3.8)	272 (35)	113.9 (3.3)
	9	6	55.5 (3.5)	78.3 (4.1)	2.7 (0.2)	25.6 (1.1)	22.5 (3.8)	187 (35)	118.1 (3.3)
ANOVA significance			NS	NS	**	NS	NS	NS	***
B[x]	1 Own rooted	3	66.0 (3.8)	88.8 (4.1)	3.6 (0.4)	31.2 (1.5)	62.7 (5.5)	543 (46)	113.6 (4.2)
	3	3	67.4 (3.5)	81.9 (3.7)	3.2 (0.4)	21.9 (1.4)	29.1 (5.2)	240 (43)	120.1 (3.9)
	4 (male)	2	55.2 (4.2)	85.5 (4.6)	2.9 (0.5)	28.6 (1.7)	24.9 (6.3)	219 (52)	114.4 (4.7)
	5	5	58.3 (2.7)	82.6 (2.9)	3.2 (0.3)	23.8 (1.1)	20.3 (3.1)	187 (33)	112.6 (3.0)
	6	5	54.9 (2.7)	87.6 (2.9)	3.3 (0.3)	23.2 (1.1)	18.6 (3.1)	162 (33)	113.8 (3.0)
	9	3	50.6 (3.5)	84.7 (3.8)	3.2 (0.4)	25.3 (1.4)	13.5 (5.2)	118 (43)	113.9 (3.9)
ANOVA significance	df		*	NS	NS	**	**	***	NS

D[y]	Own Rooted	5	51.3 (3.1)	80.4 (5.5)	3.2 (0.2)	26.8 (1.4)	35.7 (5.3)	313 (52)	116.4 (3.0)
	2 'Bruno' seedlings	3	54.1 (4.3)	91.6 (7.7)	3.4 (0.3)	28.2 (1.1)	30.9 (7.4)	295 (73)	106.9 (4.3)
	3	3	54.1 (4.3)	86.6 (7.7)	3.7 (0.3)	25.5 (1.7)	27.4 (7.4)	255 (73)	111.4 (4.3)
	4 (male)	4	57.5 (3.4)	93.5 (6.1)	2.9 (0.3)	27.6 (1.5)	22.1 (5.9)	190 (58)	121.5 (3.4)
	5	4	56.0 (3.4)	91.0 (6.1)	3.7 (0.3)	24.6 (1.5)	32.2 (5.9)	264 (58)	122.2 (3.4)
	6	3	60.1 (4.3)	81.2 (7.7)	3.4 (0.3)	22.9 (1.7)	25.3 (7.4)	226 (73)	113.7 (4.3)
	7	2	51.5 (4.8)	72.5 (8.6)	3.9 (0.4)	21.7 (2.2)	23.1 (8.3)	206 (81)	115.1 (4.8)
	8	3	59.8 (4.3)	86.9 (7.7)	3.3 (0.3)	27.3 (1.7)	33.4 (7.4)	355 (73)	108.9 (4.3)
ANOVA significance			NS	NS	NS	NS	NS	NS	NS

[x]Number of individuals.
Root systems [x]5, [x]7, [x]8, and [y]9 were excluded from the analysis for lack of replications.
[NS, **, ***]Non-significant or significant at P = 0.05, 0.01, or 0.001, respectively.

Table 2 - 18. Standardized canonical coefficients (SCC), and correlation coefficients (Significance) between the canonical variates (CVs) and the measured variates of each three different 'Hayward' selections among nine different kiwifruit root systems. Percentage of variance explained by eigenvalues, and the likelihood significance test are also shown. 1988-89 season.

Response variates	'Hayward' A	'Hayward' A	'Hayward' A	'Hayward' A	'Hayward' B[x]	'Hayward' B[x]	'Hayward' B[x]	'Hayward' B[x]	'Hayward' D[y]	'Hayward' D[y]	'Hayward' D[y]	'Hayward' D[y]
	CV 1	CV 1	CV 2	CV 2	CV 1	CV 1	CV 2	CV 2	CV 1	CV 1	CV 2	CV 2
	r	SCC	r	SCC	r	SCC	r	SCC	r	SCC	r	SCC
% Bud burst	-0.19 (NS)	-0.22	-0.08 (NS)	-0.05	0.62 (**)	0.85	-0.39 (NS)	-0.23	0.21 (NS)	0.95	-0.09 (NS)	0.12
% Floral bud burst	-0.09 (NS)	0.38	-0.00 (NS)	-0.59	0.19 (NS)	-0.34	0.34 (NS)	-0.21	0.43 (*)	1.34	-0.08 (NS)	0.21
Number of flowers per shoot	-0.22 (NS)	-0.58	0.67 (*)	1.59	0.26 (NS)	-0.57	0.10 (NS)	-0.54	-0.49 (*)	0.69	0.07 (NS)	0.69
Trunk diam. (mm)	-0.33 (*)	-0.42	-0.51 (*)	-0.05	0.47 (*)	-0.88	0.82 (**)	2.27	0.42 (*)	1.35	-0.45 (NS)	-0.34
Yield (Kg/Vine)	-0.10 (NS)	0.26	-0.03 (NS)	-0.68	0.89 (**)	3.47	0.31 (**)	-0.73	-0.14 (NS)	-0.88	-0.33 (NS)	-0.00
Mean fruit weight (g)	0.91 (**)	1.22	-0.03 (NS)	0.22	0.16	-0.63	-0.26 (NS)		0.24 (NS)	0.73	0.83 (**)	1.55
% Variance explained by eigenvalue	47.00		24.00		74.00		22.00		66.00		21.00	
Likelihood P ≥ F for CVs	*		NS		**		NS		**		NS	

Root systems [x]2, [x]7, [y]8, and [y]9 were excluded from the CVA because of the lack of replications.
[NS, *, **]Non-significant or significant at P ≤ 0.05, or 0.01, respectively.

Table 2 - 19. Canonical variate (CV) score means for the measured response variates of each of three different 'Hayward' selections among nine different kiwifruit root systems. 1988-89 season.

Root Systems		'Hayward' A	'Hayward' A		'Hayward' B^x	'Hayward' B^x		'Hayward' D^y	'Hayward' D^y
	N^x	CV 1	CV 2	N^x	CV 1	CV 2	N^x	CV 1	CV 2
Own roots	5	1.18 ab	-1.08 c	3	5.55 a	1.52 a	5	-0.74 b	-0.08 bc
2 'Bruno' seedlings	4	-0.12 bcd	0.68 ab	---	---	---	3	0.38 b	-1.75 c
3	5	-0.74 cd	-0.36 bc	3	2.00 b	-2.61 c	3	-1.18 b	-0.60 bc
4 (Male)	2	2.40 a	0.16 abc	2	-1.08 c	2.43 a	4	4.24 a	0.60 ab
5	3	1.10 ab	0.46 abc	5	-0.66 c	-0.27 b	4	-0.01 b	1.99 a
6	3	0.30 bc	-0.33 bc	5	-1.49 c	-0.68 b	3	-1.07 b	-0.29 bc
7	4	0.46 bc	1.53 a	---	---	---	2	-4.20 c	1.22 ab
8	6	-1.50 d	0.16 abc	---	---	---	3	0.28 b	-1.48 c
9	6	-0.61 cd	-0.56 bc	3	-3.42 d	1.06 ab	---	---	---

[x]Number of individuals.

Least square means with different subscript in each column are significantly different, 5 % level.

Root systems [x]2, [x]7, [x]8, and [y]9 were not analysed because of the lack of replications.

'Hayward' B.

ANOVA showed significant differences in: bud burst, trunk diameter, and yield (Table 2 - 17). 'Hayward' B on six different root systems reached the highest values on those horticultural parameters.

The first two CVs accounted for 96 % of the total variation among the nine root systems. CV 1 was predominantly influenced by high yield (Table 2 - 18). 'Hayward' B own rooted, achieved the highest canonical score mean value. In contrast, root system 9 had the lowest (Table 2 - 19).

In CV 2, trunk diameter had the highest canonical coefficient value (Table 2 - 18). Vines on root system 4 (male) achieved the highest canonical mean score value (Table 2 - 19).

'Hayward' D.

According to the standardized canonical coefficient values for CV 1, a high score was influenced by high floral and non-floral bud burst, low number of flowers, trunk diameter, and low yield of large fruit size (Table 2 - 18). 'Hayward' on root system 4 obtained the highest canonical coefficient mean values, and root system 7 the lowest (Table 2 - 19).

4.4.2. 1989-90 Season.

'Hayward' B.

The root systems had significant effects on scion trunk diameter, yield, and fruit number according to the ANOVAs. 'Hayward' B own rooted vines were distinguished from the topworked 'Hayward' B scions by a large trunk diameter. This scion when own rooted or topworked on root system 3 achieved a yield of about 53 Kg/vine, which was the highest in comparison to 'Hayward' B scions topworked on other root systems (Table 2 - 20).

CV 1 was primarily influenced by large trunk diameter, low flower bud burst and number of flowers, as reflected in their standardized coefficients (Table 2 - 21). 'Hayward' B own rooted reached the highest mean score values, and was significantly different from the other root systems topworked with that scion (Table 2 - 22).

The second CV was characterised by high bud burst, and yield of large fruit size on the standardized canonical values (Table 2 - 21). Root system 3 achieved the highest score mean value, and was significantly different from root system 7, 4, and 9 which had the lowest value (Table 2 - 22).

'Hayward' C.

ANOVA showed significant root system effects on number of flowers per current shoot, and fruit size of 'Hayward' C (Table 2 - 20).

Table 2 - 20. Least square means (± standard error of square means), and analysis of variance (ANOVA) significance for the measured response variates of each of three different 'Hayward' selections own rooted, and topworked on eight root systems. 1989-90 season.

'Hayward selections	Root systems	N°	% Bud burst	% Floral bud burst	Number of flowers per shoot	Trunk diam. (mm)	Yield (Kg/vine)	Fruit number	Mean fruit weight (g)
B	Own Rooted	6	54.1 (2.1)	85.0 (3.5)	3.5 (0.2)	39.2 (1.7)	52.4 (5.2)	532 (62)	96.4 (3.4)
	2 'Bruno' Seedlings	5	59.2 (2.1)	92.8 (3.5)	3.6 (0.2)	28.1 (1.7)	43.2 (5.2)	454 (62)	97.3 (3.4)
	3	4	61.8 (2.1)	89.3 (3.5)	3.7 (0.2)	32.2 (1.7)	53.2 (5.2)	583 (61)	92.4 (3.4)
	4 (male)	6	58.3 (3.3)	95.1 (3.9)	3.7 (0.2)	37.7 (1.9)	42.5 (5.7)	462 (68)	88.5 (3.7)
	5	6	58.0 (2.3)	96.5 (3.5)	3.9 (0.2)	32.3 (1.7)	41.8 (5.2)	492 (63)	89.1 (3.4)
	6	6	58.7 (2.1)	91.8 (3.5)	3.9 (0.2)	33.1 (1.7)	43.7 (5.2)	452 (62)	92.1 (3.4)
	7	6	61.7 (2.1)	94.0 (3.5)	3.5 (0.2)	25.5 (1.7)	26.9 (5.2)	309 (62)	87.5 (3.4)
	8	6	62.8 (3.6)	87.7 (4.3)	3.3 (0.2)	30.4 (2.1)	44.7 (6.4)	572 (76)	84.6 (4.2)
	9	6	54.2 (2.1)	93.0 (3.5)	3.4 (0.2)	30.6 (1.7)	31.3 (5.2)	349 (62)	88.6 (3.4)
ANOVA significance			NS	NS	NS	***	**	*	NS
C	Own Rooted	6	53.7 (3.4)	94.5 (2.3)	3.5 (0.2)	38.8 (1.5)	47.1 (5.3)	470 (59)	97.6 (3.3)
	2 'Bruno' seedlings	6	57.7 (3.4)	93.5 (2.3)	3.7 (0.2)	35.7 (1.5)	36.1 (5.3)	371 (59)	99.8 (3.3)
	3	6	56.7 (3.4)	95.2 (2.3)	3.7 (0.2)	36.3 (1.5)	49.6 (5.3)	521 (59)	96.9 (3.3)
	4 (male)	3	58.2 (4.9)	92.9 (3.3)	3.4 (0.2)	40.6 (2.1)	68.5 (7.5)	653 (85)	105.4 (4.7)
	5	5	60.5 (3.8)	92.6 (2.5)	3.7 (0.2)	33.1 (1.6)	52.9 (5.8)	569 (65)	97.8 (3.6)
	6	6	60.0 (3.4)	91.2 (2.3)	3.7 (0.2)	34.7 (1.5)	50.3 (5.3)	503 (59)	103.2 (3.3)
	7	6	61.2 (3.4)	95.3 (2.3)	3.9 (0.2)	32.6 (1.5)	47.7 (5.3)	459 (60)	95.8 (3.3)
	8	5	59.7 (3.8)	87.2 (2.5)	3.9 (0.2)	37.3 (1.7)	48.6 (5.8)	553 (65)	88.5 (3.6)
	9	6	54.3 (3.4)	90.7 (2.3)	3.6 (0.2)	34.4 (1.4)	43.5 (5.3)	505 (59)	92.6 (3.3)
ANOVA significance			NS	NS	*	NS	NS	NS	*

D	Own Rooted	6	60.2 (3.3)	87.5 (3.4)	3.8 (0.2)	36.9 (2.0)	40.7 (5.3)	438 (58)	93.2 (3.2)
	2 'Bruno' seedlings	5	52.6 (3.7)	88.8 (3.7)	3.0 (0.2)	32.7 (2.2)	31.7 (5.8)	351 (63)	94.7 (3.5)
	3	6	59.7 (3.3)	89.7 (3.4)	3.6 (0.2)	31.1 (2.0)	41.1 (5.3)	473 (57)	86.5 (3.2)
	4	6	52.8 (3.3)	92.5 (3.4)	3.5 (0.2)	37.2 (2.0)	49.3 (5.3)	493 (57)	103.1 (3.2)
	5	5	58.7 (3.6)	93.3 (3.7)	3.5 (0.2)	34.1 (2.2)	43.5 (5.8)	416 (63)	107.0 (3.5)
	6	6	58.8 (3.3)	91.3 (3.4)	3.5 (0.2)	33.1 (2.0)	52.8 (5.3)	516 (57)	107.0 (3.2)
	7	6	55.2 (3.3)	93.3 (3.4)	3.4 (0.2)	28.6 (2.0)	32.8 (5.3)	326 (57)	101.4 (3.2)
	8	6	54.0 (3.3)	84.7 (3.4)	3.3 (0.2)	31.1 (2.0)	32.7 (5.3)	333 (58)	97.5 (3.2)
	9	6	54.3 (3.3)	97.2 (3.4)	3.5 (0.2)	28.5 (2.0)	43.5 (5.3)	453 (57)	98.6 (3.2)
Source of Variation			NS	NS	NS	*	NS	NS	***

[a]Number of individuals.
[b]NS, *, **, ***Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 2 - 21. Standardized canonical coefficients (SCC), and correlation coefficients (Significance) between the canonical variates (CVs) and the measured variates of each of three different 'Hayward' selections among nine different kiwifruit root systems. Percentage of variance explained by eigenvalues, and the likelihood test are also shown. 1989-90 season.

Response Variates	'Hayward' B	'Hayward' B	'Hayward' B	'Hayward' B	'Hayward' C	'Hayward' C	'Hayward' C	'Hayward' C	'Hayward' D	'Hayward' D	'Hayward' D	'Hayward' D
	CV 1	CV 1	CV 2	CV 2	CV 1	CV 1	CV 2	CV 2	CV 1	CV 1	CV 2	CV 2
	r	SCC	r	SCC	r	SCC	r	SCC	r	SCC	r	SCC
% Bud Burst	-0.24 (NS)	0.46	0.21 (NS)	0.64	-0.02 (NS)	0.12	0.32 (*)	0.23	-0.00 (NS)	0.39	-0.16 (NS)	-0.48
% Floral Bud Burst	-0.30 (*)	-0.54	-0.27 (NS)	0.23	0.28 (*)	0.42	0.23 (NS)	0.43	0.40 (**)	0.37	-0.21 (NS)	-0.14
Number of Flowers per Shoot	-0.05 (NS)	-0.57	0.15 (NS)	-0.05	-0.30 (*)	-0.59	0.27 (NS)	0.31	0.03 (NS)	-0.20	-0.15 (NS)	-0.47
Trunk Diam. (mm)	0.84 (***)	1.33	0.04 (NS)	-0.52	0.35 (*)	0.25	-0.73 (***)	-1.15	-0.08 (NS)	-0.83	0.58 (***)	1.45
Yield (Kg/Vine)	0.48 (***)	0.12	0.66 (***)	1.08	0.46 (**)	0.62	0.06 (NS)	0.46	0.35 (**)	0.98	0.09 (NS)	-0.41
Mean Fruit Weight (g)	0.17 (NS)	-0.23	0.44 (***)	0.84	0.65 (***)	0.92	0.18 (NS)	0.26	0.76 (***)	1.08	0.46 (***)	0.44
% Variance Explained by Eigenvalue	56.00		20.00		45.00		31.00		54.00		28.00	
Likelihood P > F for CVs	*		NS		*		NS		*		NS	

NS, *Non-significant or significant at $P \leq 0.05$, respectively.

Table 2 - 22. Canonical variate (CV) score means of the measured response variates of three different 'Hayward' selections among nine different kiwifruit root systems. 1989-90 season.

Root Systems		'Hayward' B	'Hayward' B		'Hayward' C	'Hayward' C		'Hayward' D	'Hayward' D
	N[x]	CV 1	CV 2	N[x]	CV 1	CV 2	N[x]	CV 1	CV 2
Own roots	6	2.34 a	0.23 ab	6	0.53 b	-0.99 d	6	-1.28 c	0.22 abc
2 'Bruno' seedlings	5	-0.96 d	0.98 a	6	-0.19 bc	-0.26 bcd	5	-1.10 c	0.68 ab
3	4	-0.04 bc	1.03 a	6	0.22 b	0.04 abcd	6	-1.12 c	-1.25 d
4 (Male)	6	1.05 b	-0.68 b	3	2.46 a	-0.56 cd	6	0.32 b	1.14 a
5	6	-0.45 c	-0.15 ab	5	0.08 b	0.98 ab	5	1.14 a	0.43 ab
6	6	0.04 bc	0.08 ab	6	0.60 b	0.47 abc	6	1.59 a	0.12 abc
7	6	-1.79 d	-0.51 b	6	-0.44 bc	1.24 a	6	0.42 b	-0.53 cd
8	6	0.05 bc	-0.03 ab	5	-1.50 c	-0.89 cd	6	-0.85 bc	0.38 ab
9	6	-0.04 bc	-1.07 b	6	-0.77 bc	-0.29 bcd	6	0.88 a	-1.03 cd

[x]Number of individuals.
Least square means with different subscript in each column are significantly different, 5 % level.
Root systems [x]2, [x]7, [x]8, and [y]9 were not analysed because the lack of replications.

CV 1 was structured mainly by high yield, and large fruit size (Table 2 - 21). Root system 4 (male) was significantly superior to the other root systems. Root system 8 had the lowest performance on this CV (Table 2 - 22).

CV 2 was mostly influenced by small trunk diameter. Root system 7 had the highest mean score (Tables 2 - 21, 2 - 22).

'Hayward' D.

Root system effects on this scion were significant for trunk diameter, and mean fruit weight. Root systems 5 and 6 achieved the largest fruit size (Table 2 - 20).

The standardized canonical coefficients of CV 1 mainly characterised vines with high yield of large fruit (Table 2 - 21). Root systems 5, 6 and 9 attained the highest canonical score means, and were significantly different from the other vines. In contrast, own rooted 'Hayward' D had the lowest performance in yield and fruit weight (Table 2 - 22).

Root system 4 (male) was predominantly distinguished in CV 2 by a large trunk diameter and large fruit (Table 2 - 21). This root system was significantly different from root systems 3, 7 and 9 (Table 2 - 22).

5. Discussion

5.1. Root system effects across four different 'Hayward' selections.

The MANOVA revealed significant differences among the vines on the different root systems, in each of the three seasons studied (Table 2 - 1). There were significant interactions between root systems and scions in the first season. In the second season the interaction was significant at 10 % level ($P \leq 0.09$) (Table 2 - 1). According to Mead *et al.* (1993), when the interaction is smaller than the corresponding main effects the interpretation of the significant main effects may be investigated. Therefore, CVA was used to characterize the field performance of superior root systems. This multivariate analysis generated independent and composite 'new variates' that summarised the relationships between the measured variates. The structure of the CVs was useful in comparing the root systems across a range of important distinguishing characteristics.

In the first season of the experiments, vines on root system 4 (male) scored the highest in CV 1, and hence according to the standardized coefficients were characterised by large trunk diameter, low flower number, and large fruit size (Tables 2 - 3, 2 - 4). Although CVA showed that flower number was an important variate to consider for discriminating among root systems, in practical terms the differences for this variate on the various root systems were low (Table 2 - 2). In two consecutive seasons, vines on root system 4 had a large trunk diameter which was associated with large fruit. In orchard experiments with apple and peach, fruit yield has been

positively correlated with trunk diameter (Westwood, 1978). Rootstocks can influence the size of the vessel elements of the trunk (Vasconcellos and Castle, 1994). Thus, an increase in trunk diameter in the scion may indicate more vascular tissue to transport water, minerals, and plant growth regulators to the shoot to support growth, and particularly fruit development. This view is supported by results of Woolley *et al.* (1992) who associated large vascular tissues in the pedicel (fruit stalk) with large kiwifruit. A large trunk diameter may be also associated with an efficient capacity of the vine to store carbohydrates to be used in the growth of the vine.

Vines on root system 4, in the second and third seasons were associated with high floral bud burst, and heavy yield of large fruit (Table 2 - 3). Root system effects of a selection of *A. hemsleyana* on improving floral bud burst, yield, and fruit size attributes of 'Hayward' have been reported by Lowe *et al.,* (1992). They found that starch concentrations in the roots were reduced in spring in comparison with other root systems, and mucilage was a major carbohydrate component in the root bark of only that root system. It is unknown if there is any relationship between root carbohydrate content and fruit productivity of root system 4.

In apple, root systems differ in their influence on partitioning of photosynthetically produced dry matter between fruit and wood in the scion (Forshey and Elfving, 1989). In this species, the total yield/scion weight ratio has been used to assess assimilate partitioning by estimating the proportion of fixed dry weight incorporated into crop vs. tree structure. The dwarfing M.9 rootstock

has one of the highest ratios of crop to scion weight while more vigorous rootstocks have lower ratios (Preston, 1978; Stutte *et al.*, 1994). However, vigour is not always inversely related to the ratio of crop-to-scion weight. For example, the rootstock MM.106 had a higher crop-to-scion weight relationship than its tree size might suggest (Parry, 1977). This indicates that factors other than tree size influence 'productivity'. Studies regarding root morphology, anatomy, and carbon partitioning of contrasting vines on specific root systems showing high and low yielding ability, could reveal the mechanisms of root system effects in kiwifruit development.

Rootstocks can also influence the root hydraulic conductivity of the tree. Vigorous rootstocks tend to have greater root conductivity than less vigorous rootstocks. The vigorous apple MM106 and rough lemon rootstocks present greater root conductivity than the less vigorous rootstocks M9 (Olien and Lakso, 1984) and Carrigo Citrange (Syversten, 1981), respectively. Studies on the root conductivity of contrasting 'poor' and 'good' root systems investigated in this work may show root system effects on the water consumption and vigour of the vines.

Hopping *et al.* (1991), proposed another explanation for root system effects on kiwifruit. They propagated root systems from roots taken from high producing vines growing in established kiwifruit orchards, and reported root system effects of increased cane number which resulted in high yield of the cv. Brodie. The vines with the higher cropping performance had lower root:shoot ratios in comparison to the low yield ones. Their results suggest early vigour enhanced canopy development which increased vine yield in young

plantations. The evaluation of root:shoot ratios was not carried out in this work. However, Lawes, Woolley, Zhu and Cruz (1990), found in the first year after propagation, the male root system 4 made stronger vegetative growth than the other root systems. In the present work, the large trunk diameter found in vines on root system 4 suggest these vines may have had a larger canopy because trunk diameter is an indicator of tree size (Westwood, 1978). Thus, our results also suggest that vine vigour in the nursery may indicate potential rootstocks to be used in the orchard.

Loreti *et al.* (1991), showed root system effects on 'Hayward' total leaf area. Topworked vines had 25 % greater leaf area than vines from cuttings. Fruit productivity of kiwifruit vines is affected by leaf area, for example, low leaf to fruit ratios reduced yield and fruit size (Lai, 1987; Snelgar and Thorp, 1988; Buwalda and Smith, 1990; Cooper and Marshall 1989, 1990 a, 1990 b, 1991, and see Chapter 6). In other tree fruit species, like peach, rootstocks can increase total scion leaf area (Baroni *et al.*, 1990). In apples, rootstock can modify the number of scion spur leaves. Scions with a large number of spur leaves generally show large fruit fresh weights (Schechter *et al.*, 1991). Root system effects on scion leaf to fruit ratios were not investigated in this trial but in future investigations of rootstock effects, the annual rate of leaf and canopy development should be monitored.

The improvement in yield of 'Hayward' vines on male 'Bruno' seedlings in comparison to female seedlings was recognised by Weet (1978). In this trial, 'Hayward' vines on the male clonal root system

4 were superior in two seasons to vines on a range of female root systems in terms of floral bud burst, yield, and fruit size. The physiological basis of the improvement in kiwifruit scion productivity (yield and fruit size) by male or female root systems is unknown. . Unfortunately only one male root system was evaluated in this work, but it is possible there are advantages in using vigorous male plants. In the nursery they could give strong early growth and, by increasing early orchard canopy development, they appear promising new root systems for 'Hayward' vines. There are few published data comparing male and female root systems influencing field performance of 'Hayward'. Loreti *et al.* (1991), and Monastra and Testoni (1991), demonstrated the superiority in field performance of 'Hayward' vines on a male root system, in comparison with own rooted vines and vines on 'Bruno' seedlings. Loreti *et al.*, (1991) showed that vines on a male root system had a high number of leaves on more vigorous shoots.

Woolley *et al.* (1991), suggested that kiwifruit size is probably limited by cytokinin levels. In grape, the root is a major site of cytokinin synthesis (Skene, 1970). Kato and Lou (1989) found that levels of cytokinins, gibberellin-like substances and indole acetic acid were the highest in the xylem sap of eggplants grafted on a selected rootstock which promoted the highest scion yield. In grape, Skene and Antcliff (1972) suggested that the reduced fruit yield of 'Sultana' topworked on 1613 rootstock, compared with 'Sultana' on 'Salt Creek' rootstock was related to a reduced capacity of 1613 rootstock for cytokinin synthesis. Similar rootstock effects have been reported in sweet cherry (Stevens and Westwood, 1984). It is unknown if kiwifruit vines with high productivity have a large capacity

for root synthesis and/or transport of auxins, gibberellins, and cytokinins to the top that can influence fruit sizing. Studies evaluating hormone levels in the xylem sap of 'Hayward' vines topworked on the male root system 4, Kaimai, and on 'poor' female field performing root systems may indicate root system mechanisms on fruit sizing.

Own rooted vines scored the highest for CV 2 in the 1988-89 season, around four years after being grafted (Table 2 - 4). These vines were distinguished from the other eight root systems on the basis of low bud burst, and high yield of large fruit (Table 2 - 3). In the second season (1989-90), own rooted vines presented high yield (Table 2 - 5). Thus, own rooted vines showed high precocity in the first two seasons. The ability of the root system to meet transpirational demands of the shoot is determined by root hydraulic conductance (Markhart and Smit, 1990). Thus, it is possible to speculate that young own rooted 'Hayward' vines were more precocious than vines on different root systems because they were more efficient in transporting water, nutrients, and growth regulators to the shoot. In grape, the stem dry weight has been found to be higher in own rooted vines than in grafted vines aged two years (Zelleke, and Kliewer, 1979). Perhaps in the first two years grafted vines had lower root conductance due to a slow establishment of all the vascular functions between the scion and the root system. The yield advantage of some own rooted vines in relation to topworked vines was not sustained in the third season (1990-91) (Table 2 - 6). However, in 'Muscat Gordo Blanco' grape, the cumulative yields over a period of 7 years on several rootstocks were similar to own rooted

vines (Sarooshi *et al.*, 1982). Thus, studies comparing the fruit productivity of own rooted vines with grafted vines for a longer period than in this work is important.

Vines on the female root systems 5 and 6 had similar field performance to the male root system 4 mainly in floral bud burst, yield, and fruit size, as was reflected by the correlations in CV 2 for the second season (Table 2 - 4). Vines on 'Bruno' seedlings had inferior field performance in number of flowers per shoot, trunk diameter, and mean fruit weight in relation to own rooted vines, as shown by the first season CV 1, and the scores (Tables 2 - 3, 2 - 4). They also had a significantly lower CV 2 score than vines on root system 4 (male) in the second season (Table 2 - 4). The variability in field performance of vines topworked on 'Bruno' seedlings was in general similar to that of vines on their own roots, or topworked on the clonal root systems, as reflected in the scattering along CV 1 and CV 2, in two seasons (Figures 2 - 1, 2 - 2). This may be influenced by the small sample size of vines evaluated in this investigation. Thus, it was demonstrated that specific young clonal root systems can have a superior fruit productivity (yield and fruit size) compared to vines on 'Bruno' seedlings. This indicates that an adequate selection of a root system is necessary to achieve 'good' fruit productivity. Vines on root system 7 and 9 were associated with low field performance mainly in yield and fruit size, in the second and third seasons, respectively (Tables 2 - 3, 2 - 4).

CVA provided an indication of the relative overall vine performance across four 'Hayward' scions topworked onto a range of root systems. CVA examined the relationships between several

variates and determined independent linear functions that differentiated the root systems under study on the basis of these multiple characteristics. For example, vines on root system 4 during two seasons showed consistently high floral bud burst, and high yield of large fruit size (Tables 2 - 3, 2 - 4); own rooted vines were not inherently 'poor'; and the root systems 7 and 9 were characterised by low yield of small fruit size (Tables 2 - 3, 2 - 4). The accounted for variation among vines topworked on several different root systems in the CVA suggest that future comparisons need only focus on measurements of floral bud burst, trunk diameter, fruit yield, and fruit weight. The work described here, and in Cruz-Castillo *et al.* (1992; 1994) is probably the only reported use of CVA in rootstock research. It has demonstrated that this technique has applicability and potential for wider use in rootstock research because it gives a holistic approach to the analysis and interpretation/evaluation of field performance of vines topworked on selected root systems.

With the use of specific clonal root systems for 'Hayward' it is more likely to achieve fruit weight in preferred market sizes, for example, in the first, second and third seasons of experiments, vines on root system 4 had on average, 27 % , 58 %, and 72 % of the fruit in the counts 36 - 33 (New Zealand KMB, 1991), respectively. In contrast, vines on root system 9 had 21 %, 37 %, and 25 % of the fruit in those counts, in each of those seasons studied, respectively. When fruit in count 30 or larger was evaluated, vines on root system 7 had 9 % and 5 % more fruit in that commercial size than vines on root system 9 in the first and second seasons, respectively.

In most instances the original 'good' and 'poor' orchard vine performance on which the original root systems were selected, was correlated with their relative performance in the trial. When a field vine had cropped well, it was found that usually the use of its root material as a root system resulted in superior cropping performance. Thus root systems 4 and 6 were derived from 'good' vines, and root systems 7 and 9 from 'poor' ones. This suggests that it is worthwhile to investigate vines with better fruit productivity in an orchard, because there is a 'good' chance that the root systems are inherently superior, and will produce more productive vines at other sites. This is supported by the fact that in Israel in avocado (Ben-Ya'acov *et al.*, 1992) and rose (Raviv *et al.*, 1993) the selection of root systems of highly productive plants from commercial and experimental orchards has proved to be useful in substantially improving these industries through increased yields when they have been used in the propagation of planting rootstock.

Thus, it has been demonstrated that two rootstock selections positively influenced aspects of vine performance, that 'Hayward' on its own roots was not inherently 'poor', and that at least two clonal, and one seedling root system was associated with 'poor' vine performance in vines four, five, and six years after being grafted or own rooted. The effect of rootstock on mature vines remains to be determined. This study was an example that root system selection to improve kiwifruit productivity can work.

5.2. 'Hayward' scion effects across eight root systems.

In the fourth and fifth seasons after grafting, 'Hayward' A as a scion achieved the best fruit productivity in comparison to the three other selections of 'Hayward' used as scions. In an analysis of vine performance on eight root systems 'Hayward' A was distinguished by a slightly lower flower number, and high yield of large fruit size (Tables 2 - 8, 2 - 9). In the second season, large trunk diameter was associated with those variates in characterising that scion (Table 2 - 8). The consistent low number of flowers measured on current shoots in 'Hayward' A may not be of great commercial importance considering the small differences in number of flowers among the 'Hayward' scions (see Tables 2 - 7, 2 - 10). The fruit sizing capacity of 'Hayward' A was not influenced by the crop load in each of the two seasons in comparison to 'Hayward' B. In the first two seasons, 'Hayward' A had a similar crop load to 'Hayward' B (first and second season, $P \leq 0.30$ and 0.19, respectively), and its fruit size was larger (Tables 2 - 7, 2 - 10).

Scions 'C' and 'D' tended to have vines of large trunk and high yield in the first season, as indicated by CV 2 (Tables 2 - 8, 2 - 9). They had a larger fruit number than 'Hayward' B. This result, and the large trunk diameter may indicate a larger number of canes per vine on 'Haywards' C and D in comparison to 'Hayward' B. In two seasons, the lowest fruit productivity was shown by 'Hayward' B. These vines had a large number of flowers, and low yield of small fruit. Likewise, in the second season, small trunk diameter together with those variates was important in distinguishing this scion from the

others (Tables 2 - 8, 2 - 9). The possible lack of vigour represented by a low trunk diameter in 'Hayward' B may be the result of reduced root development influenced by this 'Hayward' selection. In 'Delicious' apple, strains may decrease the root development of the rootstock, and then reduce the vigour of the tree (Barritt, 1988). Further studies in this area, probably using kiwifruit plants in the nursery may show the influence of the different 'Haywards' on the root development of particular root systems.

'Haywards' A and B were originally considered 'good' vines, whereas C and D were 'poor'. 'Haywards' A and B when grafted were associated with a 'good' and 'poor' performance, respectively, in this trial. Although the roots of 'Hayward' B were not selected to be investigated in this trial, it is possible the root system topworked with this scion influenced its productivity.

The work described here may be the only reported use of CVA in scion research. In 'Delicious' apple (Warrington *et al* ., 1990; Fallahi *et al.*, 1993) and 'Cabernet Sauvignon' grape (Cirami *et al.*, 1993), clonal selection has resulted in several strains with high fruit productivity but in kiwifruit there are no reports comparing the effects of different 'Hayward' strains on field performance of the vines. Lawes *et al.* (1986), and Woolley *et al.* (1988) pointed out that there was considerable variation in the ability of individual 'Hayward' vines of similar appearance within an orchard to size their fruit. Some vines consistently produced fruit which was larger than average, while others produced consistently smaller fruit. They suggested that one of the causes of this variability could be related to 'Hayward' scion effects. In this trial, with a range of root systems it was

demonstrated that the 'Hayward' scion influenced fruit productivity of the kiwifruit vines. The effects of 'Hayward' strains as the vines mature remains to be determined. The results suggest that in establishing new orchards the selection of the 'Hayward' scion is important. The choice of an 'Hayward' selection of known superior performance could bring a number of benefits. In this study, the superior 'Hayward' A resulted in increases in yield and large fruit size in two seasons of experiments. On average, in the first season, 76 % of the fruit was located in the counts 30 or larger. In contrast, 'Hayward' B had only 33 % of the fruit in those counts (New Zealand KMB, 1991). In the second season studied, 'Hayward' A had 31 % more fruit between the counts 33 and 36 than 'Hayward' B.

It could be worthwhile to promote the use of specific 'Hayward' strains with superior performance in orchards, but first, studies should be carried out to identify the better ones. This is the first work showing significant 'Hayward' scion effects on vine performance.

5.3. The field performance of 'Hayward' selections topworked on different root systems.

'Hayward' A on root systems 6 (Table 2 - 13), and 7 (Table 2 - 16) achieved the highest field performance as described by CV 1 in one of the two experimental seasons. These vines were generally characterised by larger trunk diameter, higher yield, and larger fruit size (Tables 2 - 12, 2 - 15) compared with 'Hayward' B on root systems 6 and 7 (Tables 2 - 13, 2 - 16). The low crop load of

'Hayward' B on root system 6 may indicate less cane number (Table 2 - 11).

Multivariate analysis showed the four 'Hayward' selections on root system 9 differed significantly in field performance in two seasons (Tables 2 - 13, 2 - 16). This result indicated a significant interaction between scions and rootstocks. 'Hayward' A was distinguished from the three other 'Hayward' scions by slightly lower floral bud burst, large trunk diameter, and high yield of large fruit, in two seasons, according to the CVs 1 and 2, in the first and second seasons, respectively (Tables 2 - 12, 2 - 13, 2 - 15, 2 - 16). In the second season, 'Hayward' D on root system 9 was different from the three other scions on the basis of small trunk diameter, and high yield of large fruit (CV 1 Tables 2 - 15, 2 - 16). This shows that large trunk diameter was not always associated with large fruit size. These results contrast with the observation that stock 9 was a 'poor' root system in this trial (Tables 2 - 12, 2 - 13, 2 - 15, 2 - 16), and in its orchard of origin. Thus, the effects of a root system on field performance were not always the same with different 'Hayward' strains, and the differences between 'Haywards' sometimes seems to depend on a particular root system-scion interaction. Therefore, in addition to individually 'good' rootstocks or scions, the propagation of known high productive rootstock-scion combinations may be also considered for commercial purposes.

The CVA carried out for own rooted vines data showed significant differences in the first season. Own rooted 'Hayward' B was significantly different from the three other rooted selections on the basis of large trunk diameter and high yield (Tables 2 - 12, 2 -

13). Although it was intended to winter prune all the vines to similar cane number, the large fruit number of these vines may indicate a greater cane number was retained (Table 2 - 11). This is supported by the observation that a larger fruit number was found in own rooted 'Hayward' B and flower density was statistically unaltered (Tables 2 - 2, 2 - 5). It is interesting to note this 'Hayward' selection had a 'poor' field performance when topworked on a range of eight different root systems (Tables 2 - 7, 2 - 9). Therefore, it is evident that a number of root systems reduced the fruit yielding potential of this scion. CV 2 differentiated 'Hayward' A on its own roots by high floral bud burst, and large mean fruit weight (Tables 2 - 12, 2 - 13). In contrast, own roots 'Hayward' D had the 'poorest' field performance on those variates (Tables 2 - 12, 2 - 13). Although in their place of original selection, 'A' and 'B' were considered 'good' vines, and 'C' and 'D' were 'poor', field selection of vines can be difficult because potentially 'good' vines can show a 'poor' field performance because of the root system.

In this trial, own rooted 'Haywards' A and B had superior performance in large trunk size and high yield, and high floral bud burst and yield, respectively, in relation to 'Haywards' C and D. Only selected 'Hayward' strains known to perform superiorly on their own roots such as 'Hayward' B should be propagated for field planting on their own roots. The evaluation of the field performance of own rooted vines beyond six years from orchard planting remains to be determined.

5.4. The effect of the root systems on the performance of different 'Hayward' selections.

Significant root system effects on scion 'Hayward' A were found in the first season. Mainly large fruit size characterised the CV 1 (Table 2 - 18) of this scion. The CV 1 scores were highest when 'Hayward' A was own rooted and topworked on root systems 4 and 5 (Table 2 -19). However, the large fruit size achieved by vines on root systems 4 and 5 may be influenced by their low fruit number (Table 2 -17).

In general, the fruit sizing capacity of 'Hayward' A was higher than that observed on the vines topworked with the strains 'B' and 'D' (Table 2 - 17). Further studies are required to investigate the physiological basis of the large fruit weight response of the vines topworked with 'Hayward' A. For example, investigations on flower quality (Chapter 4), and leafiness of the vines (Chapter 6) may show aspects of the fruit sizing capacity of 'Hayward' A.

'Hayward' B was influenced significantly by the root systems in two successive seasons of experiments. In the first season, own roots 'B' was mainly characterised by having high yield. In contrast, vines of this scion on root system 9 had the 'poorest' yield performance (Tables 2 - 18, 2 - 19). For the second season, own roots 'B' had high bud burst, and high yield of large fruit size (CV 2), and they were significantly different from vines on root system 7 and 9 (Tables 2 - 21, 2 - 22). According to the large fruit number, and the large trunk diameter in the two seasons studied (Tables 2 - 17, 2 - 20), possibly own rooted 'Hayward' B had larger cane number or

longer canes in comparison with most of the root systems topworked with scion 'B'. Thus, the early vine vigour of these vines may have had a significant effect in ensuring superior early cropping performance. The results suggest that if a superior vine is identified in the field, it may be worthwhile to evaluate its field performance on its own roots. It appears possible the 'productivity' potential of a scion may be limited when it is grown on a different root system. This can only be determined by observation as at present there is no other test for identifying the rootstock or rootstock/scion combination that will maximise or limit vine performance.

Root systems effects on 'Hayward' D were recorded in two seasons. Vines of this scion on root system 4 were mainly discriminated by their high floral bud burst, and large trunk diameter in the first season (CV 1) (Tables 2 - 18, 2 - 19). Vines on root systems 5 and 6 achieved a 'good' performance in yield and fruit size in the second season (Tables 2 - 21, 2 - 22). There was non-significant difference in fruit number across all the root systems topworked with 'Hayward' D in the two seasons (Table 2 - 20). Therefore, the fruit sizing ability of root systems 5 and 6 was not affected by the crop load, and it is evident that the fruit sizing of 'Hayward' can be affected by 'Hayward' scion and root system interactions. This study indicated that if a superior vine is identified root system effects should be considered because the improved performance may be due either to a universally superior root system, or to the favourable interaction of an unique rootstock/scion combination.

Kiwifruit producers in New Zealand have traditionally not recognised that root systems or 'Hayward' scion selections confer any particular advantage such as in yield and fruit size (Lawes, 1990; Lowe *et al.*, 1992). In the present work it has been demonstrated that in kiwifruit, root system selection can influence aspects of vine performance of different 'Hayward' selections. Thus, the careful choice of all propagation material is important for increasing early cropping in kiwifruit orchards. While the costs of converting established orchards to a new root system is prohibitive, in the future kiwifruit rootstock choice will be part of the interrelated management considerations prior to planting the orchard. In contrast to other fruit species like apple (Martinez-Rodriguez, 1993), avocado (Ben-Ya'acov, 1993), or grape (Morton and Jackson, 1988) where several clonal rootstocks are available, in kiwifruit only 'Kaimai' (Lowe *et al.*, 1992), and 'D 1' (Viti *et al.*, 1990) have been identified to be potentially useful rootstocks. In this work, 'Hayward' B on its own roots in two seasons, and vines on the male root system 4 in three seasons had high 'productivity', in comparison with other clonal root systems. Future studies are advocated to compare the field performance of 'Hayward' on the root systems 'Kaimai', male root system 4, and 'Hayward' B on its own roots because they significantly increase 'Hayward' fruit productivity. Economic return studies comparing these root systems should be considered because 'Kaimai' may have the disadvantage of producing a relatively high percentage of misshapen and lateral 'Hayward' fruit (Lowe *et al.*, 1992; Wang *et al.*, 1994 b). Vines topworked with 'Hayward' A as scion achieved the best fruit productivity across a range of root systems in two seasons in comparison with the three other selections of 'Hayward' used as scions. This is the first report showing significant effects of different

'Hayward' scions on field performance of kiwifruit vines. A significant interaction was observed when 'Haywards' A and D topworked on root system 9 had high and low fruit productivity in two seasons, respectively.

The fact that the material studied in this work was selected from commercial orchards indicate that part of the variation in field performance observed within and between orchards can be related to the different root system genotypes, 'Hayward' strains, and/or the interactions between them.

CHAPTER 3.

THE INFLUENCE OF ROOTSTOCK AND 'HAYWARD' SCION SELECTION ON FRUIT FIRMNESS AND SOLUBLE SOLIDS.

1. Introduction.

Kiwifruit (*Actinidia deliciosa*) was New Zealand's sixth largest export earner in 1991 (New Zealand KMB, 1991). In that year the crop earned $NZ 621.5 million with a further $NZ 64 million in sales being lost due to postharvest fruit losses (New Zealand KMB, 1991) mainly caused by soft fruit (Banks *et al.*, 1992). The fruit firmness until about 24 weeks after harvest should be above 1.2 kg (11.8 Newtons (N)) to avoid repacking and discarding fruit of inadequate firmness (New Zealand KMB, 1992). There are orchard factors such as vine mineral nutrition influencing the storage quality of kiwifruit (Prasad and Spiers, 1991). Based on work with other fruit crops (Barden and Marini, 1992; Fallahi *et al.*, 1993). The selection of rootstocks and 'Hayward' strains may influence the maturity of fruit at harvest, and its capacity to withstand long storage, and so the consumer acceptance of kiwifruit. The aim of this work was to evaluate the effects of 'Hayward' selections both own rooted, and topworked on different rootstocks on harvest maturity and cold storage of kiwifruit, and determine if such effects were correlated with vines of high fruit productivity.

Chapter three

2. Literature Review.

In fruit trees like grapefruit and orange (Wutscher, 1979) some rootstocks have increased the TSS of the fruit after harvest. In apple, fruit maturity at harvest was advanced (Yadava and Doud, 1989; Barden and Marini, 1992), and fruit firmness after storage increased (Autio, 1991; Drake *et al.*, 1988) with the use of specific rootstocks. In kiwifruit, the effect of rootstock on postharvest fruit quality of the cv. Brodie was studied by Hopping *et al.* (1991), who found no rootstock effects on TSS content at harvest, and fruit softening during storage was not affected. Loreti *et al.* (1991), did not find differences in fruit TSS, and flesh firmness at harvest from 3 and 4 years old kiwifruit vines propagated by either micropropagation, cuttings, or grafting onto the micropropagated rootstock 'D1'. Monastra and Testoni (1991) found that fruit from 'Hayward' vines grafted on 'D1' stored longer than from vines on their own roots, or topworked on 'Bruno' seedlings. The poorest storage performance was shown for fruits of 'Hayward' vines grafted onto 'Bruno' seedlings. Cruz-Castillo *et al.* (1991), showed that different clonal kiwifruit rootstocks significantly influenced 'Hayward' fruit TSS at harvest. Lowe *et al.* (1992), demonstrated that 'Hayward' fruit from vines topworked on the 'Kaimai' rootstock reached 6.2 °Brix a few days before fruit from vines on 'Bruno' seedlings. In coolstorage, fruit from vines on 'Kaimai' softened more rapidly than fruit on 'Bruno' seedlings during the initial storage period, but after 85 days in storage fruit from vines on each rootstock had similar flesh firmness. In apple, the strain of 'Delicious' influenced the TSS of the fruit at harvest (Fallahi *et al.*,

1993). However, there are no reports in the literature on the effects of 'Hayward' strains on the postharvest life of kiwifruit.

3. Material and Methods.

For details about methodology of the selection, propagation, and orchard plantation of the scions and rootstocks studied in this experiment see Materials and Methods in Chapter 2. From several rootstock-scion combinations growing at Massey University the scions and rootstocks investigated in these experiments were selected randomly on the basis of vines showing contrasting fruit productivity (fruit yield and mean fruit fresh weight). Fruit from three 'Hayward' selections each topworked on three different rootstocks, and one 'Hayward' selection own rooted and topworked on eight rootstocks were studied during 1988-89 and 1989-90. Fruit firmness and juice percentage TSS were evaluated at harvest, and after storage at 0 ± 0.5 °C for 12, and 15 weeks in each of those seasons. The dates were selected because fruit firmness was close to 1.2 Kg (11.8 N) which is the minimum firmness allowable for export (New Zealand KMB, 1992).

Flesh firmness of the fruit was tested with an Effe-gi (8 mm tip) pressure tester with the fruit held against a hard static surface. The penetrometer was calibrated at the start of each recording date with an electronic balance. Two readings were taken on opposite sides of each fruit (the readings were taken in Kg and converted into N; $N = Kg \times 9.81\ m.s^{-2}$) after removing 1-2 mm thickness of fruit skin with a sharp blade. The juice TSS was determined with a hand

refractometer promptly after harvest and at room temperature. Usually, juice from the two ends of a fruit is recorded (Sale, 1990 a) but in this work juice from only the proximal end of each fruit was evaluated. Fruit were cut transversely 1.5 cm from the proximal end and juice squeezed onto the refractometer prism. The refractometer was zeroed with distilled water at the beginning and at half-hourly intervals during use.

The experimental fruit were 36 and 39 count (New Zealand KMB, 1991) with a mean weight of about 90 g. Fruit were harvested within 0.50 m of the trunk on the horizontal part of the T bar canopy. From each stock/scion treatment a total of 60 fruit were harvested from the six vines located randomly on the orchard. Half the fruit were analysed immediately. The other fruit were packed in poly-lined single layer export trays and stored at 0 ± 0.5 °C. After coolstorage for either 12 or 15 weeks, the fruit were held at room temperature for 15 hours, and then evaluated. Trays of fruit with all the treatments were treated as blocks in a random design. The data were analysed using the procedure ANOVA of SAS (SAS Institute, 1989).

In the 1988-89 season all fruit over 50 g were harvested from each vine at commercial maturity, counted and weighed individually on an electronic balance connected to an Epson HX20 computer. In the following season 1989-90, the total crop of each vine was weighed in the field using a Salter 236 thermoscale, and the mean fruit weight determined by randomly subsampling 60 fruit on two non-terminating canes of visually similar size situated in each

side of the vine. The data were analysed using the procedure GLM of SAS for unbalanced designs (SAS Institute, 1989).

Throughout the experiments vines were winter and summer pruned as in commercial orchards. Lateral and flat fruit were removed and the vines thinned to about 35 - 40 fruit/m^2 on canopies of each 8.5 m^2 for the first and second seasons, respectively.

4. Results.

1988-89 Season.

Significant scion and rootstock effects were recorded for fruit firmness at harvest. 'Hayward' selections B and C had the highest fruit firmness, and 'A' the lowest (Table 3 - 1). Vines on rootstock 3 had the highest fruit firmness and were significantly different from 7 (Table 3 - 1). There was a significant interaction between rootstocks and scions for fruit firmness after twelve weeks in storage at 0 ± 0.5 °C. Fruit firmness was highest in the scion/rootstock combinations 'A'/3, 'B'/4, 'B'/7, 'C'/7, and lowest in 'A'/7 (Table 3 - 2).

At harvest the percentage of fruit soluble solids was influenced significantly by scion and the rootstock, and was highest for scions 'A' and 'B', and rootstock 7 (Table 3 - 3). After twelve weeks in storage fruit TSS for scions 'A' and 'B' depended on the rootstock used (Table 3 - 4). For scion 'A', rootstock 3 was significantly higher than 7. Conversely, for scion 'B', rootstock 7

Table 3 - 1 Fruit firmness (N) at harvest for three 'Hayward' selections topworked on three different kiwifruit rootstocks. 1988-89 Season.

Blocks	NS
Rootstocks	*
3[1]	110.0 a
4 (male)[1]	106.1 ab
7[2]	102.1 b
Scions	**
'A'[1]	97.3 b
'B'[1]	109.6 a
'C'[2]	111.2 a
Rootstocks*Scions	NS

NS,*,**Non-significant or significant at $P \leq 0.05$ or 0.01, respectively. Means separation by Duncan's multiple range test at $P \leq 0.05$.

[1]Rootstock or scion derived from 'good' vines which produced high yield of large fruit.

[2]Rootstock or scion derived from 'poor' vines which produced low yield of small fruit.

Table 3 - 2 Fruit firmness (N) after twelve weeks in storage at 0 ± 0.5 C for three 'Hayward' selections topworked on three different kiwifruit rootstocks. 1988-89 Season.

Blocks	NS
Rootstocks	NS
Scions	NS
Rootstock*Scion	**

'Hayward' scions	Rootstocks	Fruit firmness
'A'[1]	3[1]	22.9 a
'A'[1]	4[1]	16.7 cd
'A'[1]	7[2]	16.2 d
'B'[1]	3[1]	18.8 bcd
'B'[1]	4[1]	20.4 abc
'B'[1]	7[2]	19.7 abcd
'C'[2]	3[1]	17.1 bcd
'C'[2]	4[1]	17.8 bcd
'C'[2]	7[2]	20.7 ab

NS,**Non-significant or significant at $P \leq 0.01$, respectively. Means separation by Duncan's multiple range test at $P \leq 0.05$.

[1]Rootstock or scion derived from 'good' vines which produced high yield of large fruit.

[2]Rootstock or scion derived from 'poor' vines which produced low yield of small fruit.

Table 3 - 3 Fruit % soluble solids at harvest for three 'Hayward' selections topworked on three different kiwifruit rootstocks. 1988-89 Season.

Blocks	NS
Rootstocks	**
3[1]	7.8 b
4 (male)[1]	7.8 b
7[2]	8.4 a
Scions	**
'A'[1]	8.2 a
'B'[1]	8.3 a
'C'[2]	7.6 b
Rootstocks*Scions	NS

NS,** Non-significant or significant at $P \leq 0.01$, respectively. Means separation by Duncan's multiple range test at $P \leq 0.05$.

[1]Rootstock or scion derived from 'good' vines which produced high yield of large fruit.

[2]Rootstock or scion derived from 'good' vines which produced low yield of small fruit.

Table 3 - 4 Fruit % soluble solids after twelve weeks in storage at 0 ± 0.5 C for three 'Hayward' selections topworked on three different kiwifruit rootstocks. 1988-89 Season.

Blocks	NS
Rootstocks	**
Scions	NS
Rootstock*Scion	**

'Hayward' scions	Rootstocks	% Soluble solids
'A'[1]	3[1]	14.5 b
'A'[1]	4[1]	14.1 bc
'A'[1]	7[2]	13.3 c
'B'[1]	3[1]	14.2 b
'B'[1]	4[1]	13.7 bc
'B'[1]	7[2]	15.4 a
'C'[2]	3[1]	14.5 b
'C'[2]	4[1]	14.5 b
'C'[2]	7[2]	14.3 b

NS,** Non-significant or significant at $P \leq 0.01$, respectively. Means separation by Duncan's multiple range test at $P \leq 0.05$.

[1]Rootstock or scion derived from 'good' vines which produced high yield of large fruit.

[2]Rootstock or scion derived from 'good' vines which produced low yield of small fruit.

was significantly higher than rootstock 3. There were non-significant differences when the rootstocks were topworked with scion 'C' (Table 3 - 4). Yield, and fruit number per vine were not statistically different for these combinations (Table 3 - 5). However, there was a significant interaction between rootstocks and scions for mean fruit weight per vine (Table 3 - 5). Typically as usual found in the first season of cropping mean fruit weight per vine was high.

1989-90 Season.

'Hayward' C was investigated in this season because it tended to have high yield in the 1988-89 season (Table 3 - 5). There were significant rootstock effects on fruit firmness and percentage soluble solids at harvest, and after 15 weeks in storage for 'Hayward' C (Table 3 - 6). Fruit on rootstocks 8 and 9 had the lowest firmness at harvest but were the firmest after storage. 'C'/8 scion/rootstock combination had the highest fruit percentage soluble solids at harvest (Table 3 - 6). Own rooted 'Hayward' C had lower fruit percentage soluble solids at harvest and after storage compared with fruit on rootstocks 5 and 9 (Table 3 - 6). There were no rootstock effects on yield and vine fruit number. In contrast, fruit weight was significantly influenced by the rootstocks (Table 3 - 6).

Table 3 - 5 Yield, fruit number, and fruit size of scion/rootstock combinations studied for kiwifruit quality at harvest, and after storage. 1988-89 Season.

Scion/Rootstock combinations	Yield (Kg/vine	Fruit number	Mean fruit size per vine (g)
'A'[1]/3[1]	28.4 a	250 a	113.8 b
'A'[1]/4 (male)[1]	23.0 a	157 a	146.3 a
'A'[1]/7[2]	26.1 a	202 a	126.5 ab
'B'[2]/3[1]	28.5 a	231 a	122.7 b
'B'[1]/4 (male)[1]	24.9 a	219 a	114.4 b
'B'[1]/7[2]	25.1 a	342 a	73.4 c
'C'[2]/3[1]	34.6 a	306 a	113.8 b
'C'[2]/4 (male)[1]	31.5 a	369 a	117.9 b
'C'[2]/7[2]	26.9 a	259 a	115.6 b
ANOVA significance			
Rootstock	NS	NS	*
Scion	NS	NS	**
Interaction	NS	NS	**

[NS]Non-significant or significant at $P \leq 0.05$, respectively. Means with different subscript are significantly different, by Duncan's multiple range test at $P \leq 0.05$.

[1]Rootstock or scion derived from 'good' vines which produced high yield of large fruit.

[2]Rootstock or scion derived from 'poor' vines which produced low yield of small fruit.

Table 3 - 6 Fruit firmness (N) and percentage total soluble solids at harvest, and after fifteen weeks in storage at 0 C for 'Hayward' C own rooted, and topworked on 8 different kiwifruit rootstocks. Scion 'Hayward' C was derived from 'poor' vines which produced low yield of small fruit. Crop load, and fruit size data are also shown. 1989-90 Season.

Root Systems	Fruit firmness at harvest	Fruit firmness after storage	Fruit % total soluble solids at harvest	Fruit % total soluble solids after storage	Yield (kg/vine)	Fruit number	Mean fruit size (g)
Own roots	90.7 ab	15.8 cd	8.5 cd	12.2 c	47.1 a	470 a	97.6 abc
'Bruno' seedlings	98.4 a	14.1 d	8.8 bcd	13.1 b	36.1 a	371 a	99.8 ab
3[1]	93.2 ab	13.0 d	7.7 e	12.4 bc	49.6 a	521 a	96.9 abc
4[1]	92.3 ab	15.8 cd	9.0 bcd	12.9 bc	68.5 a	653 a	105.4 a
5[1]	91.0 ab	18.7 bc	9.6 b	14.1 a	52.9 a	569 a	97.8 abc
6[2]	94.1 ab	17.0 cd	8.3 de	13.0 bc	50.3 a	503 a	103.2 a
7[2]	89.4 bc	21.7 ab	8.3 de	12.7 bc	47.7 a	459 a	95.8 abc
8[2]	82.7 cd	23.0 a	10.5 a	12.9 bc	48.6 a	553 a	88.5 c
9[2]	76.6 d	23.8 a	9.2 b	13.1 b	43.5 a	505 a	92.6 bc
ANOVA significance	**	**	**	**	NS	NS	*

NS,*,**Non-significant or significant at $P \leq 0.05$ or 0.01, respectively.
Means with different subscript in each column are significantly different, by Duncan's multiple range test at $P \leq 0.05$.
[1]Rootstocks derived from 'good' vines which produced high yield of large fruit.
[2]Rootstocks derived from 'poor' vines which produced low yield of small fruit.

5. Discussion

In the first season of experiments the selected 'Hayward' vines topworked on different kiwifruit rootstocks showed significant independent rootstock and scion effects on fruit firmness at harvest (Table 3 - 1). After three months of fruit cold storage a significant interaction of rootstock and scion on fruit firmness was observed (Table 3 -2). These different effects on fruit firmness at harvest and after cold storage suggests a more detailed evaluation in long kiwifruit storage would be justified. The effects shown were not related to fruit yield and fruit number differences between the vines as these variables showed non-significant differences for the scions and rootstocks studied (Table 3 - 5). While mean vine fruit weight was influenced by rootstock or scion, fruit weight did not influence the storage results because all fruit were of similar size (counts 36 and 39).

The association of lower flesh firmness at harvest with some scions ('A') and rootstocks (7) in the first year was supported by significant rootstock differences in the following year. In the second season of experiments, the combinations 'C'/7, 'C'/8, and 'C'/9 (Table 3 - 6) had low fruit firmness at harvest (less than 89.4 N) but were the firmest after 15 weeks in storage. This type of relationship between the time of harvest and storage potential was not achieved for fruit with firmness at harvest higher than 92.0 N. These results support those of Hopkirk and Clark (1990) and Mitchell *et al.* (1991) who found that kiwifruit with lesser firmness at harvest are generally firmer after cold storage.

'C'/ 'Bruno' seedlings showed poor fruit firmness after storage (Table 3 - 6). Similar results have been reported in Italy with fruit from 'Hayward' vines topworked on 'Bruno' seedlings (Monastra and Testoni, 1991). Therefore, it is suggested that when 'Hayward' is grown on 'Bruno' seedling rootstocks the interaction between rootstock and scion may account for some of the differences in fruit firmness seen at harvest and after storage.

The mean fruit weight from the rootstock-scion combinations with highest fruit firmness after cold storage were statistically similar to fruit on other topworked vines with less storage potential (Table 3 - 6). Thus, fruit size did not appear to be a dominant factor affecting storage potential. In New Zealand (Seagar *et al.*, 1991) and in Italy (Tombesi *et al.*, 1993) there is considerable interest in identifying factors most responsible for influencing fruit firmness in cold storage. This study indicates that when young vines of different 'Hayward' selections are topworked or grown on their own roots, there may be significant differences in fruit firmness at harvest, and after storage. The fruit cold storage periods (12 and 15 weeks) used in this work represents fruit marketed or shipment 3 or 4 months after harvest. However, firmness values determined at 12 and 15 weeks may well be of value in predicting long term storage since Hopkirk and Clark (1990) found that relative differences in firmness between fruit were maintained for at least 20 weeks.

Additional research is required to define the physiological explanation of these orchard effects. For example, it is not known if rootstocks and scions act individually, or it is an interaction that

influences fruit firmness by alteration of vine growth pattern. Vine leaf canopy density is reported to affect kiwifruit firmness in cold storage (Smith, Gravett and Curtis, 1992). The leafiness of the vine may also influence the mineral content of the fruit (Ferree and Palmer, 1982). Nitrogen (Prasad and Spiers, 1991) and calcium (Prasad and Spiers, 1991; Mowatt and Banks, 1992; Gu *et al.*, 1994) composition of the kiwifruit have been found to be important in relation to firmness in cold storage. In apple, the use of specific rootstocks can influence the calcium content of the fruit (Drake *et al.*, 1988) and this is know to alter fruit quality in postharvest (Volz, 1991). Kiwifruit rootstocks effects on fruit firmness in storage may be related to the nutritional status of the scion (Viti *et al*, 1990) and the fruit (Prasad and Spiers, 1991; Mowatt and Banks, 1992; Gu *et al.*, 1994), by affecting the leafiness of the vine (Loreti *et al.*, 1991). Further studies should consider the interaction between vine leaf area, and mineral content of fruit on both own rooted and topworked vines to identify possible effects with fruit firmness in storage.

The fruit of the scion-rootstock combination 'B'/7 achieved the highest percentage of soluble solids after twelve weeks in storage (Table 3 - 4). This result may have been influenced by the higher total soluble solids at harvest of this rootstock-scion combination in comparison with other combinations (Table 3 - 3). In the second season of experiments, 'Hayward' C own roots had significantly lower fruit percentage soluble solids at harvest and after storage than fruit on rootstocks 5 and 9 (Table 3 - 6). Cruz-Castillo *et al.* (1991), showed that fruit from vines of four own rooted 'Hayward' selections had low TSS at harvest in comparison to a range of topworked vines. In grape, the TSS of the fruit at harvest

was also significantly higher for specific topworked vines compared to own rooted plants (Sarooshi *et al.*, 1982; Whiting, 1988). This indicates that the use of specific rootstock-scion combinations may influence fruit maturity, and probably the date of commercial harvest (6.2 °Brix (New Zealand KMB, 1992)) in a greater degree than other rootstock-scion combinations.

Significant scion and rootstock differences in fruit percentage soluble solids at harvest and after storage were found for some scions, rootstocks, and particular scion/rootstock combinations in two seasons (Tables 3 - 3, 3 - 4, 3 - 6). To confirm such effects, comparisons should be done storing fruit with the same harvest percentage soluble solids for all the scion/rootstock combinations. This is because the maturity of the fruit at harvest affects its storage potential (Hopkirk, 1990; Mitchell *et al.*, 1991). When kiwifruit are harvested with low percentage soluble solids, the fruit become unacceptably soft (Snelgar *et al.*, 1993). However, in this work fruit percentage soluble solids had little relationship with fruit firmness at harvest and storage (Tables 3 - 2, 3 - 3, 3 - 6). Similar results were found by Seager *et al.* (1991). Emphasis must be on frequent monitoring of fruit firmness during storage. Fruit firmness curves were not calculated in this work because long term fruit storage was not investigated. Future work should consider juice evaluation from the two ends of the fruit to obtain comparisons on a kiwifruit industry basis.

Starch content and hydrolysis in kiwifruit growth and development accounts for some of the increase of TSS in the fruit

(Okuse and Ryugo, 1981). However, some of the rapid increases in TSS that occurs during the late stages of fruit development is due to incoming photosynthate and not just to starch degradation within the fruit (MacRae and Redgwell, 1990). Leaf:fruit ratios on the different rootstock-scion combinations were not measured in this investigation. However, a high leaf:fruit ratio may increase the concentration of soluble solids of kiwifruit in storage (Smith, Gravett, and Curtis, 1992; Seager, 1993). Kiwifruit with high total soluble solids at harvest can have the greatest potential for long term storage potential (Seager, 1993). In grape, a defoliation close to harvest reduce the TSS of the fruit (Kataoka *et al.*, 1982), and large leaf:fruit ratios related positively with fruit °Brix (Jackson, 1986). Kiwifruit rootstocks can modify the leaf area of 'Hayward' (Loreti *et al.*, 1991). Thus, rootstock-scion effects regulating leaf area may influence the TSS concentration in kiwifruit.

CHAPTER 4.

THE INFLUENCE OF THE TIME OF ANTHESIS AND THE APPLICATION OF GROWTH REGULATORS ON THE GROWTH OF KIWIFRUIT.

1. Introduction.

It has been shown that fruits of apricot (Jackson and Coombe, 1966), apple (Marguery and Sangwan, 1993), citrus (Praloran *et al.*, 1981), peach (Scorza *et al.*, 1991), grape (Coombe, 1973), persimmon (Hasegawa and Nakajima, 1990), and strawberry (Cheng and Breen, 1992) from early opening flowers are larger at maturity than those from later blooms. Therefore, the potential final size in some fruits may be determined before anthesis. Lai (1987) found that kiwifruit from early flowers are larger than fruit from late flowers. In contrast, Patterson *et al.* (1991) did not find any significant size differences between kiwifruit from early and late flowers. In the present work, the effect of flowering date within kiwifruit vines on fruit size for flowers opening early or late was evaluated during three seasons with the purpose of confirming Lai (1987) results. The effect of time of anthesis on final fruit shape, seed number, seed weight, ovary shape, ovary dry weight, ovary cell size, ovary cell number, and final fruit cell number and cell size, was also investigated.

Chapter four

In Chapter 2 of this thesis it was hypothesized that the rootstock influence on fruit productivity may be partly mediated by root produced growth regulators influencing internal regulation of fruit tissue development. Therefore, studies of plant growth regulators on fruit growth are relevant. Iwahori *et al.* (1988), showed that the synthetic cytokinin-active substance CPPU (N-(2-chloro-4-pyridyl)-N-phenylurea) increased the size of kiwifruit, and a similar effect was described by Lawes and Woolley (1990). The application of CPPU has also significantly increased fruit size in apple (Greene, 1993), and grape (Nickell, 1986). Hopping (1976 b) found that auxins, gibberellins, and cytokinins when applied alone on kiwifruit did not stimulate fruit growth. However, the application of a hormone mixture of those plant growth regulators increased fruit weight, but only slightly.

In this study, five aspects were investigated: 1) The effect of different plant growth regulator combinations on the fruit weight of 'Hayward' and 'Kramer Hayward ' kiwifruit; 2) The effect of a hormone mixture on the amount of different kiwifruit tissues; 3) Interactions between CPPU and hormone mixture on sizing of 'Hayward' fruit with low and high seed number; 4) The effect of flowering date and CPPU application on final fruit size; and 5) The uptake, distribution and residues at harvest of ^{14}C-CPPU in different tissues of 'Hayward' fruit following the application of ^{14}C-CPPU alone and in combination with GA_3 + 2,4-D.

2. Literature Review.

2.1. Time of anthesis and fruit size.

Cell numbers of mature fleshy fruits depend on the number of cell divisions that occur before (and often after) anthesis (Coombe, 1976; Bohner and Bangerth, 1988 b). In kiwifruit, Lai *et al.* (1990) found the final size of the fruit was partly determined by pre-anthesis factors. Differences in mean fruit size at harvest between fruit developing from early or late flowers on uniform, short laterals were as much as 31 g. The difference was independent of fruit seed number. Significant differences between early and late flowers were present at the time of anthesis. Smith, Gravett, and Curtis (1992), found kiwifruit from early flowers on pergola trellis were larger at harvest than those from late flowers. In contrast, Patterson *et al.*, (1991) did not find any relationship between timing of kiwifruit flower opening and fruit weight at harvest.

In other plant species it has been found that the potential for fruit development can be determined before fruit growth begins. In tomato, final fruit size is closely related to the number of cells in the flower ovary (Ho *et al.*, 1984). Bohner and Bangerth (1988a) showed that fruit size differences between proximal and distal fruits in a tomato truss at maturity, were due to differences in cell number of unpollinated ovaries at anthesis. Jackson and Coombe (1966) found apricot fruits from early flowers were larger at ripeness because of a greater number of cells. They considered the differences between fruits from early and late flowers to have arisen from the different

number of cell divisions within the ovaries before anthesis.

The importance of the initial cell number at anthesis in relation to final fruit size in grapes was reported by Coombe (1973). He estimated that 17 doublings were required to attain 0.2 million cells in the ovary at anthesis, whereas only 1.5 doublings occurred after anthesis. Similarly in apples, although there were 2 million cells in the ovary at anthesis, and 40 million cells at harvest, this represented 21 doublings of cell division before anthesis, compared with 4.5 doublings after anthesis (Pearson and Robertson, 1953). In several strawberry cultivars, the genotypic variation in the size of mature fruit was not the result of large differences in either duration of cell division after anthesis or mean cell volume, but rather was primarily due to differences in the number of receptacle cells established by anthesis (Cheng and Breen, 1992). Thus, the total number of fruit cells produced postanthesis was a function of the number of cells present at anthesis (Cheng and Breen, 1992). In peach, the differences in fruit size between large- and small-fruited cultivars were evident before anthesis. The basis of that difference in fruit size was in mesocarp cell number and not cell size (Scorza *et al.*, 1991).

2.2. Effects of field applied PGRs on kiwifruit growth.

PGRs are used in fruit crops as a means of meeting the needs of modern commercial production. For example, PGR fruit thinning practices are well developed for apples (Williams and Edgerton, 1981). British Columbia's black sweet cherries intended

for export are treated with GA_3 to improve fruit size, fruit appearance, and to reduce the incidence of bruising-related storage disorders (Looney and Lidster, 1980).

The distribution of photosynthates within a plant is regulated by assimilate supply (from source leaves), and demand by developing regions (sinks). On fruiting trees, growing fruits become the major sinks for assimilates (Avery *et al.*, 1979). The relative sink strength may be the main factor influencing assimilate distribution. Sink strength was defined by Ho (1988) as the ability of a sink organ to import assimilate. Sink strength has been considered as a product of sink size and sink activity. Sink size is defined as the physical constraint (e.g. fruit cell number), and sink activity as the physiological constraint (e.g. metabolic activity of the fruit during development) upon a sink organ's assimilate import. Ho (1988) pointed out that PGRs are involved in all aspects of growth, and therefore they may play a key role in sink strength. The exact mechanism(s) by which hormones regulate assimilate partitioning and transport remains unknown (Patrick, 1988). Patrick (1982) proposed two possible models for such control at the whole plant level. In the 'sink' hypothesis, control is mediated solely by assimilate transport within the sink, and changes in assimilate pool size provide the signal to coordinate supply to the sink. The assimilate pool at the sink may be considered a 'barometer' reflecting the balance between assimilate supply and utilization as well as possibly determining rates of these processes. In the 'supply sink' hypothesis, sink produced hormones integrate the assimilate supply with utilization by controlling both processes. 'Sink' control could be an adequate strategy when assimilate concentrations in the vascular tissues or in

the photosynthetic apparatus are not limiting. Under conditions of limited assimilate concentration, the 'supply-sink' strategy could ensure greater flow of assimilates to the sink region than that generated by 'sink' control. In this case, sink produced hormones would also mediate regulation of supply processes (Patrick, 1982).

The control of assimilate distribution to developing fruit is complex, and it appears PGRs interact with many aspects of fruit growth and development, such as cell division and/or expansion (Woolley *et al*, 1991); regulation of assimilate partitioning into fruit tissues (Patrick and Wareing, 1976); or regulation of turgor pressure within the phloem (Lang, 1983).

In kiwifruit, PGRs have been applied experimentally in attempts to increase fruit size and quality, and to improve the understanding of factors controlling the growth and development of the fruit (Lawes, Woolley and Lai, 1990). Hopping (1976 b) applied combinations of growth regulators to kiwifruit and observed their influence on fruit growth. He found that auxins, gibberellins, and cytokinins when applied alone did not stimulate fruit development; nor did combinations of auxin + gibberellin, and gibberellin + cytokinin. However, auxin (2,4-D or 2,4,5-T) + 6-benzylamino-purine, and auxin + cytokinin + gibberellin stimulated fruit growth, although only slightly.

Iwahori *et al.* (1988) induced parthenocarpic fruit development by spraying the cytokinin CPPU on unpollinated flowers of 'Hayward' kiwifruit. Flowers treated 3 days before anthesis

developed small and completely seedless fruit. Flowers treated at anthesis developed large fruits with many small seeds which consisted of seed coat only without any indication of the development of embryo and endosperm. Post-bloom application of CPPU strongly stimulated fruit growth, with application about 3 weeks after anthesis being more effective than that just after anthesis. These fruit were larger than untreated open-pollinated control fruit and ripened earlier, as shown by softening of the flesh and a decrease in titratable acidity.

Kurosaki and Mochizuki (1990) accelerated the fruit weight increase of 'Monty' kiwifruit with CPPU treatment at 35-42 days after bloom, but some deformity in fruit shape was attributed to this treatment. Analysis of fruit carbohydrates at maturity revealed that the treated fruit were 1.2 times higher than the control in the concentrations of fructose, glucose and sucrose, and total sugar concentration. The chlorophyll concentration of the fruit was also increased by CPPU treatment.

'Hayward' kiwifruit is composed of three distinct tissues: outer pericarp, inner pericarp, and core (Ferguson, 1984). Kurosaki and Mochizuki (1990) found no change in cell size with the CPPU treatment, suggesting that fruit enlargement was caused by increased cell number. Then, Woolley *et al.* (1991) found that in CPPU treated fruit the percentage of outer pericarp increased, while inner pericarp decreased and the core remained constant. They also showed an increased cell number in the outer pericarp of treated fruit.

Costa *et al.* (1990), and Lötter (1991) showed that application of CPPU to kiwifruit about three weeks after anthesis increased the size of the fruit. This response was associated with a faster sugar build-up, and a more rapid decrease in flesh firmness.

Lawes *et al.* (1991), evaluated timing and concentrations of CPPU on kiwifruit fresh weight in vines with different crop loads. They found that treating fruit 21-38 days after full bloom increased fruit size by about 60 g, but when this application was repeated one month later the increase was 73 g. CPPU applications resulted in a higher proportion of the crop being in the larger size grades, and there was no loss of response as vine crop load increased. They pointed out that the fruit process of size response to CPPU could occur in two phases. a) In the initial meristematic stage when fruit cell division is limited by photoassimilate supply ; and b) in the fruit expansion phase, increasing sink metabolic activity with an associated improved (sink-demand regulated) translocation. With regards to fruit quality they found that the treated fruit had darker colour, a small reduction in flesh firmness and an increase in soluble solids, and some changes to fruit appearance as stylar tissues enlarged.

Kiwifruit weight at harvest is related to seed number per fruit. Hopping (1976 b) found a 29 g response to PGRs on fruit fresh weight in kiwifruit containing over 200 seeds. However, he did not present information about the interaction between seed number and PGRs on the growth of kiwifruit. In CPPU treated fruit, there was not a significant interaction between seed number and CPPU, on fruit

fresh weight. Thus, the increase in fruit fresh weight was similar at both high (1140) and very low (350) seed per fruit (Woolley *et al.*, 1991).

The effect on kiwifruit dry weight after a CPPU application was reported by Woolley *et al.* (1991), and Biasi *et al.*, (1991). They showed that the dry weight:fresh weight ratios were slightly lower in CPPU treated fruit at harvest. Woolley *et al.* (1991), suggested that CPPU increased the ability of treated fruit to compete with the rest of the vine for carbohydrate (increased sink activity) but increased demand for carbohydrate and/or increased cell number and cell size appeared to slightly decrease the percentage dry matter.

Despite the kiwifruit growth promotion by CPPU little has been published about its uptake and translocation inside the fruit, and the concentration of residues at harvest. Studies with labelled CPPU as a technique are important to understand the fruit translocation and utilization/metabolism of that PGR, and its residues at harvest. Biasi *et al.* (1993), showed that the ^{14}C-CPPU movement from the skin to inside the fruit was very limited. Neri *et al.* (1993), applied ^{14}C-CPPU to kiwifruit leaves on fruiting shoots and the radioactivity recovered in the fruit was negligible.

Because of the strong kiwifruit response to CPPU, studies on uptake, metabolism and responses to CPPU would be helpful. Determining the relation of this PGR to fruit cell activity, seed number, exogenous and endogenous hormones, and fruit quality could improve the understanding of physiological mechanisms controlling growth and development of kiwifruit.

Ethylene, and abscisic acid (ABA) were also tested in this work with the purpose of increasing kiwifruit size, and quality. Crane (1969), promoted growth in fig with application of ethylene. Dann and Chalmers (1978) supported the idea that fresh and dry weight growth of peach fruit are separate processes with separate controls. They found that after commencement of the final major growth stage FW III (fresh weight stage III) ethephon stimulated fruit growth. Growth could be stimulated with ethephon during periods when the rate of fresh weight growth was rising but not when it was falling. Thus endogenous ethylene appeared to limit growth of peach fruit during the stages of rapid increase in fresh weight. In kiwifruit, when Bowen *et al.* (1988) applied ethephon at 4.8% soluble solids (about 5 months after anthesis) there was no significant increase in fruit fresh weight. Ethephon effects on kiwifruit growth from earlier applications have not been published.

Correlations between ABA concentrations and sugar import in apple fruit (Beruter, 1984), soybean embryo explants (Ackerson, 1984), and strawberry fruit cortex explants (Archbold, 1988) have implicated this hormone in the control of assimilate partitioning. However, the effects of ABA on sugar transport are often contradictory. Transport of assimilates is sometimes stimulated by ABA treatment (Archbold, 1988), or inhibited (Lucas and Madore, 1988). There is no published information about ABA effects on the growth of kiwifruit in the field.

3. Materials and Methods.

3.1. Effects of time of anthesis on fruit growth.

Experiments were carried out on 4-6 year old T-Bar trained 'Hayward' vines at Massey University, over three seasons.

1988-89 Season.

During the flowering period both early (day 2), and late opening (day 8) flowers were selected on each of 20 vines in the same orchard block. The vines were selected on the basis of the number of flowers found at anthesis in each of the dates investigated. Flowers with an early and late anthesis were selected on vines at the beginning and end of bloom, respectively. These floral anthesis dates were similar on all the selected vines. Within each of these periods five well exposed flowers per vine were tagged, and their final fruit size subsequently recorded.

Flower fresh weight, ovary fresh weight (minus the stigmas), and ovary diameter at the maximum width were determined on 27 early and late flowers at full bloom spread over 9 of those vines. Fruit seed number and weight were recorded from a random 20 fruit subsample for each of the two treatments, from the 200 fruit tagged. For seed extraction, whole fruit were cut into slices and soaked in a solution of 1 % ammonium oxalate for 3 or 5 days. The seeds from each fruit were extracted by separating them from the pulp with an electric juice extractor, and by repeated washing in a sieve under a running tap. The seeds were dried at room

temperature. The total seed number and mean seed weight were calculated from the total seed weight based on the weight of a sample of 150 seeds for each fruit. The data were analyzed using the procedure TTEST of SAS for independent samples (SAS Institute, 1989).

1989-90 Season.

Fruit growth was evaluated for fruit from two periods of anthesis on each of 20 vines. The vines investigated were selected as in the 1988-89 season. For each of early (day 2) and late flowers (days 11-12) shoots approximately 30 cm length with 3 fruit and a leaf:fruit ratio of 3:1 were tagged and their fruit subsequently measured. There were six replicates of each treatment on each vine. Fruit length was measured with a digital calliper at intervals of about 10 days from anthesis until harvest. These measurements were converted to volume using the formula of Green *et al.*, (1990). Flower ovary length, diameter (maximum, and minimum), fresh and dry weight (including stigma tissue) were recorded on 50 early and 50 late flowers at anthesis. At harvest, fruit weight, length, diameter (maximum, and minimum) were recorded on 120 fruit each from early, and late flowers spread over the orchard. A subsample of 50 fruit from each of the two treatments were cut into quarters transversely, and the seed number counted on the six surfaces. The data were analyzed using the procedure TTEST of SAS for independent samples (SAS Institute, 1989).

1990-91 Season.

In an orchard block, two hundred early (day 2), and late (day 11) flowers were tagged on 20 vines now aged 6 years having similar floral anthesis dates. All the flowers were rub pollinated manually. Ovary fresh and dry weight, and percentage ovary dry matter (Woolley *et al.*, 1991) were recorded at anthesis on 12 flowers for each of the two treatments. A t-test for independent samples using the TTEST procedure of SAS was carried out on each of the variates measured on those flowers. CPPU (15 ppm) was applied as a 5 seconds fruit dip 23 days after anthesis to a total of 120 fruit from early and late flowers. The four resulting treatments were: fruit from two periods of anthesis each with or without CPPU. To evaluate fruit growth, five fruit from each of the four treatments were harvested at 2-4 week intervals. At each harvest fruit fresh weight, dry weight, and percentage dry matter were recorded. Final fruit fresh weight, fruit surface seed number, and fruit shape were determined for 60 fruit per treatment. Data were analyzed as a randomized complete factorial design using the procedure ANOVA of SAS (SAS Institute, 1989).

Cell number and size was investigated on ovaries at anthesis, and for fruit at harvest. At anthesis twelve early and late ovaries were selected randomly, and at harvest six fruit from each of the four treatments were used. Transverse sections of ovary, and fruit were fixed in formalin : acetic acid : ethyl alcohol (60 %), (1:1:20) (see Hopping, 1976 a). Previous experiences in the laboratory indicated this formula did not significantly influence the shrinkage of the tissues. After fixation, the ovary and 3 mm thick

fruit sections were processed in labelled embedding cassettes in a Shandon Hypercenter tissue processor. The full cycle of the tissue embedding processing took about 14 hours, and was carried out as follows:

70 % alcohol	1 hour
95 % alcohol	1 hour
100 % alcohol	1 hour
100 % alcohol	1 hour
100 % alcohol	2 hours
100 % alcohol	2 hours
Xylene	45 minutes
Xylene	45 minutes
Xylene	45 minutes
Wax	2 hours
Wax	2 hours

Prior to wax embedding the tissue was evacuated at 1.72 bars for 4-5 hours to remove all air bubbles in the cells. The wax used was Paraplast (Medium) melting point 56 °C. The two wax baths were under a vacuum of 1.03 bars. Then the tissues were embedded in moulds in a Shandon Hypercenter tissue processor. A Heitz 1512 microtome was used to cut ovary and fruit transverse sections of 8 μm thickness which were dried overnight in an oven at 60 °C.

The process of staining was as follows:

Dewax sections in xylene (2 x 5 minutes)
Hydrate through alcohol 70 % to water
Stain in Gills haematoxylin (3 minutes)
Wash in tap water (30 seconds)
Wash in Scotts tapwater (30 seconds)
Wash in tap water (60 seconds)
Dehydrate through alcohol 95 %
Clear in Xylene
Mount in DPX (BDH).

The cell numbers were counted across the outer pericarp, inner pericarp between the locules, and right across the narrowest transverse core using a Reichert microscope equipped with Nomarski differential interference optics. Cells counts represented number of cells in a straight line across the outer pericarp and inner pericarp on one side of the fruit but the total number across the whole core. The SAS procedures TTEST and ANOVA, at anthesis and harvest, respectively, were used (SAS Institute, 1989). A completely random design model, and Duncan's multiple range test were employed for the separation of treatment means on the variates at harvest.

Chapter four

3.2. Effects of field applied plant growth regulators on kiwifruit growth.

1988-89 Season.

In January 1989, fruit on 'Hayward' T-bar trellis in Palmerston North aged 6 years, were treated 56 days after full bloom (DAFB) to investigate effects in late fruit growth. The treatments were: 1. Control (undipped); 2. CPPU (20 ppm); 3. CPPU (20 ppm) + 2,4-D (25 ppm) + GA_3 (50 ppm); 4. ABA (50 ppm); 5. ABA (50 ppm); 6. Ethrel (10 ppm); 7. Ethrel (10 ppm) + ABA (50 ppm applied fifteen days later). The chemical applications were made as 5-10 seconds dip to the fruitlet and peduncle base. A wetting agent was not added to the preparation of each of the plant growth regulator treatments. On each of three vines on the same row 15 shoots each with three fruit were selected for each treatment in a randomised complete block design, each vine being a block. The fruit were harvested at commercial maturity (about 6.2 % total soluble solids), and weighed. A subsample of 15 fruits per treatment was taken for counting seed number, and total seed weight. The data were analyzed using the procedures ANOVA or GLM of SAS (SAS Institute, 1989).

1989-90 Season.

Fruit on 'Hayward' vines in Levin, and 'Kramer Hayward' vines at Massey University aged 5-8 years, and trained on a Pergola and T-bar trellis respectively, were chemically treated 21 DAFB in

1989. The treatments for each different cultivar were: 1. Control; 2. CPPU (10 ppm); 3. CPPU (10 ppm) + 2,4-D (2.5 ppm) + GA_3 (5 ppm); 4. CPPU (10 ppm) + 2,4-D (25 ppm) + GA_3 (50 ppm); 5. CPPU (20 ppm) + Promalin (GA_{4+7} + BA) (5 ppm). Chemical applications were made as in 1988-89. On each of three vines (blocks) per cultivar seven shoots each with three fruit were selected for every treatment. In both experiments treatments were arranged in a randomised complete block design. The fruit were harvested in April-May, and weighed. A subsample of 30 fruit per treatment of size typical of the vine were taken for measuring locule number, surface seed number (visible after the fruit were cut longitudinally and then into thirds transversely), fruit shape (fruit length/maximum width (L/W_1), and fruit minimum width/maximum width (W_2/W_1)); firmness (Effe-gi pressure tester 8 mm tip), total soluble solids (hand refractometer); fruit colour lightness (L), and Hue angle of the skin using a Minolta chromameter (Singha *et al.*, 1991; Watkins *et al.*, 1991; Dixon, 1993). Data were analyzed using the SAS procedures ANOVA, or GLM (SAS Institute, 1989).

In a parallel experiment using Massey T-bar trained 'Hayward' vines, fruiting laterals with three similarly sized fruit and a 3:1 leaf to fruit ratio per lateral were treated as follows: 1) Control; 2) CPPU (10 ppm); 3) CPPU (10 ppm) + 2,4-D (25 ppm) + GA_3 (50 ppm). The chemical treatments were applied 33 days after anthesis as described. On each treatment, 3 laterals were harvested 45, 124, and 130 days (commercial fruit harvest in the orchard) after application. The fruit diameter, and thickness of the outer pericarp, inner pericarp, and minimum diameter of the core on a transverse cut at the middle of the fruit were determined with digital callipers. The

relative width of each tissue was expressed as a percentage of the transverse section. These data were not transformed because the Bartlett's test showed homogeneity of variances among the treatments in each harvest date (Little, 1985). Data were analyzed using the procedure ANOVA of SAS (SAS Institute, 1989).

1990-91 Season.

To produce fruit with low seed number, flowers on 7 year 'Hayward' vines growing on a T-bar trellis were partially destyled just before anthesis to leave 5 styles. Other flowers were left intact to produce high seeded fruit. Fruit were treated 31 days after full bloom as follows; 1. Control; 2. CPPU (20 ppm); 3. CPPU (20 ppm) + 2,4-D (2.5 ppm) + GA_3 (5 ppm). Chemical dip applications were as previously described. On each of four vines situated in the same row, nine shoots located on different well exposed shoots were selected for each treatment. The treatments were assigned to a randomized complete block factorial design, each vine being a block. The fruit were harvested at normal commercial harvest, and fruit fresh weight and seed number was recorded. The seeds were extracted with an electric juice extractor, after soaking the fruit in 1 % ammonium oxalate for seven days. Data were analyzed using the procedure GLM of SAS (SAS Institute, 1989).

3.3 Uptake of ^{14}C-CPPU by 'Hayward' kiwifruit, and the distribution of radioactivity in fruit tissues.

In December 1989 well exposed uniform fruiting laterals each with three similarly sized fruit and a 3:1 leaf fruit ratio on a 'Hayward' T-bar trellis were selected. The treatments were: control, and fruit treated with either ^{14}C-CPPU or ^{14}C-CPPU + 2,4-D + GA_3. The specific activity of the phenyl ring labelled ^{14}C-CPPU was 22, but it was diluted 1:1 with cold CPPU, resulting in a final specific activity of 11 μci/μmol. The concentrations were: CPPU 10 ppm, 2,4-D 25 ppm, and GA_3 50 ppm. The two treatments were applied as a 10-15 seconds dip, 33 days after anthesis.

Three laterals of fruit per treatment were harvested at 6 and 48 hours, and 21, 105 and 145 days (commercial harvest) from chemical application. The fruit from the first three harvests were divided transversely to give the stem, middle, and blossom (stylar) end sections. The middle zone was further divided into outer pericarp (including skin) inner pericarp and core. Fruit from the last four harvest dates were divided into skin, outer pericarp, inner pericarp, and core. The distribution of the ^{14}C label in the fruit tissues were followed by liquid scintillation counting of extracts using a Beckman LS800 instrument and a scintillation cocktail of 6 g of 2-5-Diphenyloxazole (PPO) in 1 l of toluene and 0.5 l of triton-X-100 detergent. Fractions were prepared for counting as follows:

a) At harvest the fruit surface was washed with 100 ml 50 % ethanol. -Wash fraction.

b) After division each tissue sample was ground, and extracted in 100 ml acetone. -The acetone soluble fraction.

To 200 μl of each of the wash and acetone soluble fractions were added in 15 ml of scintillation cocktail, and then sample extracts counted.

c) The acetone insoluble residues were dried and stored. - The acetone insoluble fraction.

The ^{14}C was released from a weighed sample of about 10 mg of the acetone insoluble residue by combustion using a biological oxidizer OX600 (R.J. Harvey Instrument Corporation) and trapped in a 13 ml cocktail containing 5.5 g of PPO/l in 10:7:1 parts of toluene, 2-ethoxyethanol, and ethanol amine, respectively, and then counted.

No evidence of any photoluminescence or chemiluminescence was detected when samples were stored in darkness and counted 24 hours after preparation. The ^{14}C counting efficiency was estimated by the channels ratio method (Williams and Wilson, 1981). Background radiation, obtained by counting blank samples was subtracted and the activity of each radioactive sample was expressed as disintegrations per minute (DPM) per fruit.

In each harvest period the data were analyzed by t-test (Steel and Torrie, 1980) using the procedure TTEST of SAS for independent samples (SAS Institute, 1989). A total ^{14}C decay model

for all tissues was not determined because different type of fruit tissues were investigated in the beginning and end of the experiment.

4. Results.

4.1. Effects of time of anthesis on fruit growth.

1988-89 Season.

The flower fresh weight at anthesis showed significant differences between early and late flowers (Table 4 - 1). There were non-significant differences for ovary fresh weight and diameter between the two types of flower (Table 4 -1). Fruit fresh weight, and fruit seed number at harvest were significantly higher for fruit from early flowers (Table 4 - 1). The individual fruit seed weight was similar in the two treatments (Table 4 - 1).

1989-90 Season.

At anthesis, the ovaries from the early flowers were significantly greater in length, diameter, fresh weight, and dry weight (Table 4 - 2). There was a non-significant difference in ovary percentage dry matter for the two types of flowers (Table 4 - 2). The shape of the ovaries determined by L/W_1, and W_2/W_1 were similar for both types of flowers (Table 4 - 2). The increase in fruit volume (Figure 4 - 1) was a double sigmoid curve as also found by Lai (1987). The fruit grew rapidly, reaching a first plateau of near zero daily growth at about 60 days from anthesis for the early flowers,

Table 4 - 1. Flower and fruit size for fruit from early and late flowers. 1988-89 Season.

Flower type	Flower fresh weight at anthesis (g)	Ovary fresh weight at anthesis (g)[x]	Ovary diam. at anthesis (mm)	Fruit fresh weight (g)	Fruit seed number	Individual fruit seed weight (mg)
Early	2.86 a	0.385 a	9.13 a	121.0 a	1386 a	1.22 a
Late	2.50 b	0.364 a	9.09 a	109.2 b	1183 b	1.20 a

[x]Ovaries without stigmas.
Numbers in the same column with different letters significantly different by t-test, at $P \leq 0.05$.

Table 4 - 2. Ovary and fruit size for fruit from early and late flowers. 1989-90 Season.

Flower type	Ovary length at anthesis (mm)	Ovary diam. at anthesis (mm)	Ovary L/W_1[x] at anthesis	Ovary W_2/W_1 at anthesis	Ovary fresh weight at anthesis (g)[z]	Ovary dry weight at anthesis (g)[z]	Ovary % dry matter at anthesis	Fruit fresh weight (g)	Fruit surface seed number	Fruit L/W_1[x]	Fruit W_2/W_1[x]
Early	8.62 a	8.04 a	1.07 a	0.93 a	0.531 a	0.075 a	14.1 a	100.0 a	204 a	1.15 a	0.92 a
Late	7.39 b	7.08 b	1.08 a	0.92 a	0.459 b	0.066 b	14.4 a	86.8 b	202 a	1.13 a	0.90 a

[x]Length/maximum width or minimum width/maximum width.
[y]Minimum width/maximum width.
[z]Ovaries with stigmas.
Numbers in the same column with different letters significantly different by t-test, at $P \leq 0.05$.

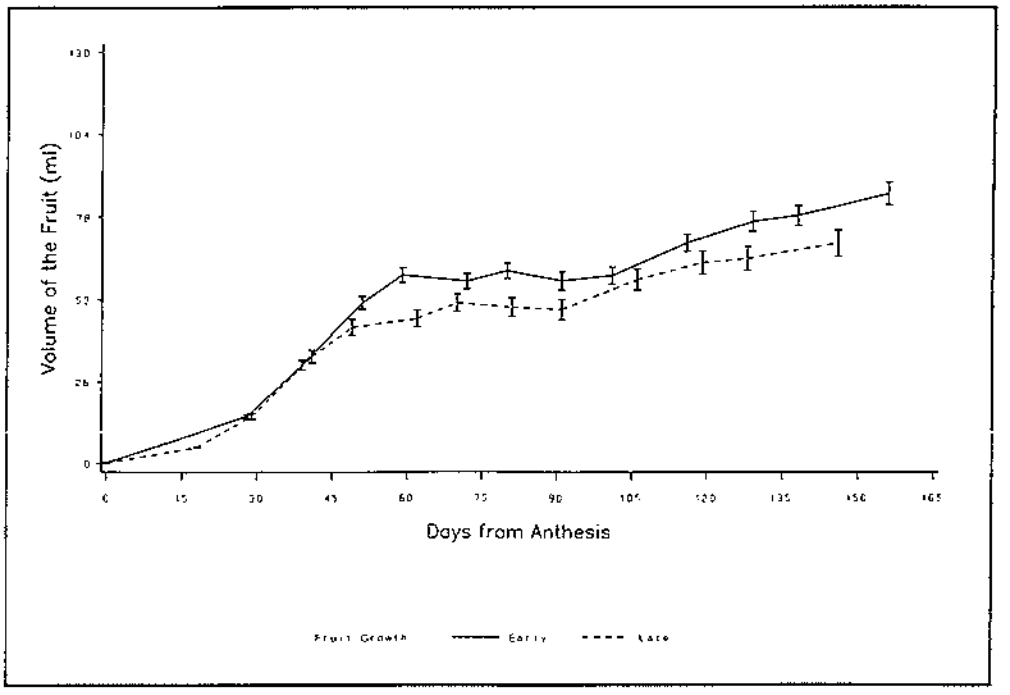


Figure 4 - 1. Change in fruit volume (ml) of kiwifruit cv 'Hayward' for fruit from early and late flowers. Standard errors of the mean are shown. 1989-90 Season.

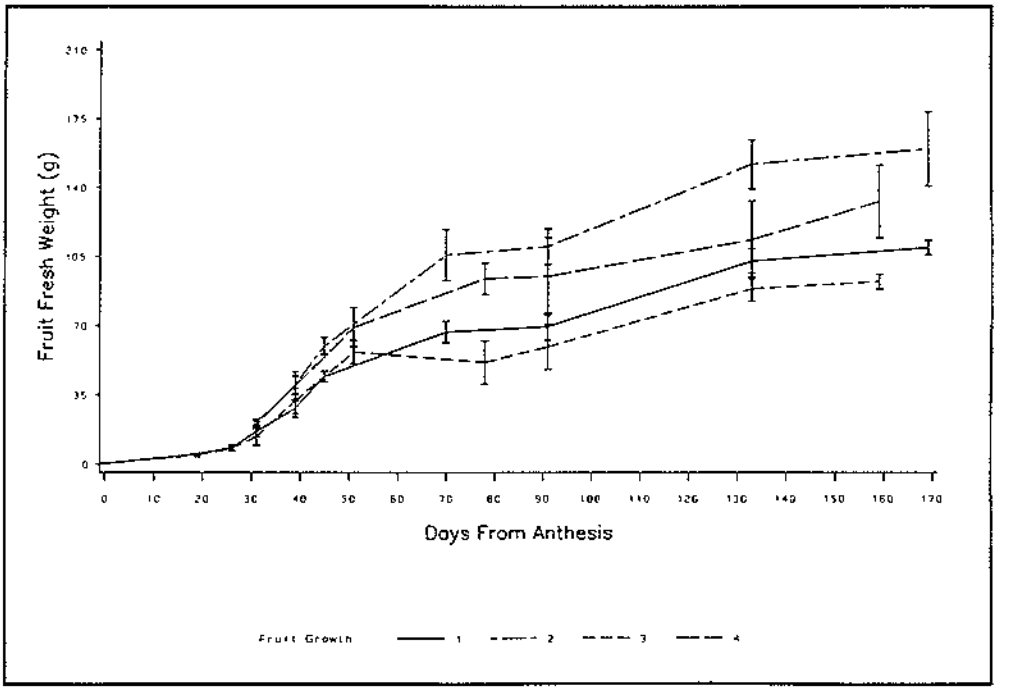


Figure 4 - 2. Change in fruit fresh weight of 'Hayward' kiwifruit for CPPU treated and untreated fruit from early and late flowers. Treatments: 1 = Fruit from early flowers. 2 = CPPU treated fruit from early flowers. 3 = Fruit from late flowers. 4 = CPPU treated fruit from late flowers. Standard errors of the means are shown. 1990-91 Season.

and 54 days for the late flowers. At harvest, fruit from early flowers had significantly greater fresh weight (Table 4 - 2). The fruit surface seed number, and fruit elongation (L/W_1), and symmetry (W_2/W_1) were not affected significantly by the time of anthesis (Table 4 - 2).

1990-91 Season.

The ovary fresh weight at anthesis was significantly higher for the early flowers (Table 4 - 3). In contrast, there were non-significant differences in ovary dry weight, and percentage dry matter, for the two treatments. There was a significant interaction between the time of anthesis and the CPPU application on final fruit fresh weight. The highest fruit fresh weight was achieved by fruit from early flowers treated with CPPU. Untreated fruit from late flowers had the lowest fresh weight (Table 4 - 3). All treatments had similar fruit surface seed number, and fruit W_2/W_1 ratios (Table 4 - 3). Fruit from early flowers were the most elongate, and CPPU late fruit the most square (Table 4 - 3).

Cell number, and cell size in the outer, and inner pericarp of the ovary at anthesis were similar for early and late fruit (Table 4 - 4). The core cell number was significantly higher for ovaries from early flowers. There were non-significant differences in core cell size between the two different ovary types (Table 4 - 4). At harvest, the CPPU treated fruit from early and late flowers achieved the highest cell number in the outer pericarp (Table 4 - 5). However, there were non-significant differences among treatments for cell number in the inner pericarp, and core. The cell size in the outer pericarp, and core

Table 4 - 3. The effect of bloom date and CPPU on flower and kiwifruit characteristics. 1990-91 Season.

Flower type	Ovary fresh weight at anthesis (g)[x]	Ovary dry weight at anthesis (g)[x]	% Ovary dry matter at anthesis[x]	Fruit fresh weight (g)[y]	Fruit surface seed number[y]	Fruit L/W_1[yz]	Fruit W_2/W_1[yz]
Early	0.384 a	0.051 a	13.4 a	100.8 c	228.6 a	1.20 a	0.84 a
Early + CPPU	-	-	-	152.6 a	221.2 a	1.17 ab	0.80 a
Late	0.362 b	0.048 a	13.5 a	91.7 d	221.7 a	1.16 ab	0.79 a
Late + CPPU	-	-	-	126.0 b	218.5 a	1.13 b	0.78 a

[x]Numbers in the same column with different letters significantly different by t-test, at $P \leq 0.05$.
[y]Numbers in the same column with different letters significantly different by Duncan's multiple range test, at $P \leq 0.05$.
[z]Length/maximum width or minimum width/maximum width.

Table 4 - 4. Cell number, and cell size (μ) of the outer pericarp (OP), inner pericarp (IP), and core (C) of ovaries from early and late flowers at anthesis. 1990-91 Season.

Flower type	Cell number OP	Cell size OP	Cell number IP	Cell size IP	Cell number C	Cell size C
Early	35.9 a	24.0 a	21.7 a	48.2 a	90.7 a	27.0 a
Late	38.3 a	23.6 a	24.0 a	44.7 a	76.1 b	25.7 a

Numbers in the same column with different letters significantly different by t-test, at $P \leq 0.05$.

Table 4 - 5. Cell number and size (μ) in the outer pericarp (OP), inner pericarp (IP), and core (C) of commercially harvested fruit as influenced by bloom date and CPPU. 1990-91 Season.

Flower type	Cell number OP	Cell size OP	Cell number IP	Cell size IP	Cell number C	Cell size C
Early	69.0 b	106.0 a	57.0 a	204.1 a	115.0 a	71.9 a
Early + CPPU	78.0 a	96.3 a	59.0 a	176.3 b	132.0 a	66.9 a
Late	60.0 c	99.6 a	52.1 a	220.0 a	105.0 a	76.0 a
Late + CPPU	75.0 ab	100.0 a	49.3 a	175.0 b	122.0 a	73.0 a

Numbers in the same column with different letters significantly different by Duncan's multiple range test, at $P \leq 0.05$.

were not affected significantly by the treatments. In contrast, the cell size of the inner pericarp was significantly reduced for the chemically treated fruit (Table 4 - 5).

The fresh and dry weight gain was greatly stimulated by CPPU between 8 (31 DAFB) and about 50 days after application, respectively, in both type of fruit (Figures 4 - 2, 4 - 3). Treated fruit from early flowers showed the highest gain in fresh and dry weight, in comparison to untreated fruit from late flowers (Figures 4 - 2, 4 - 3). The fruit percentage dry matter decreased during the 40 days following anthesis in all four treatments. At final harvest, the gain in percentage dry matter was greater by 2 % on average for the early and late untreated fruit (Figure 4 - 4).

4.2. Effects of field applied plant growth regulators on kiwifruit growth.

1988-89 Season.

When PGRs were applied 56 DAFB, the hormone mixture resulted in fresh fruit weight significantly higher than all other treatments (Table 4 - 6). A skin blistering was observed on some fruit treated with this mixture. CPPU alone was significantly superior to the control. Non-significant fresh weight effects for ABA, Ethrel, and ABA and Ethrel were observed (Table 4 - 6). The fruit seed number, and total seed weight were similar for all the treatments (Table 4 - 6).

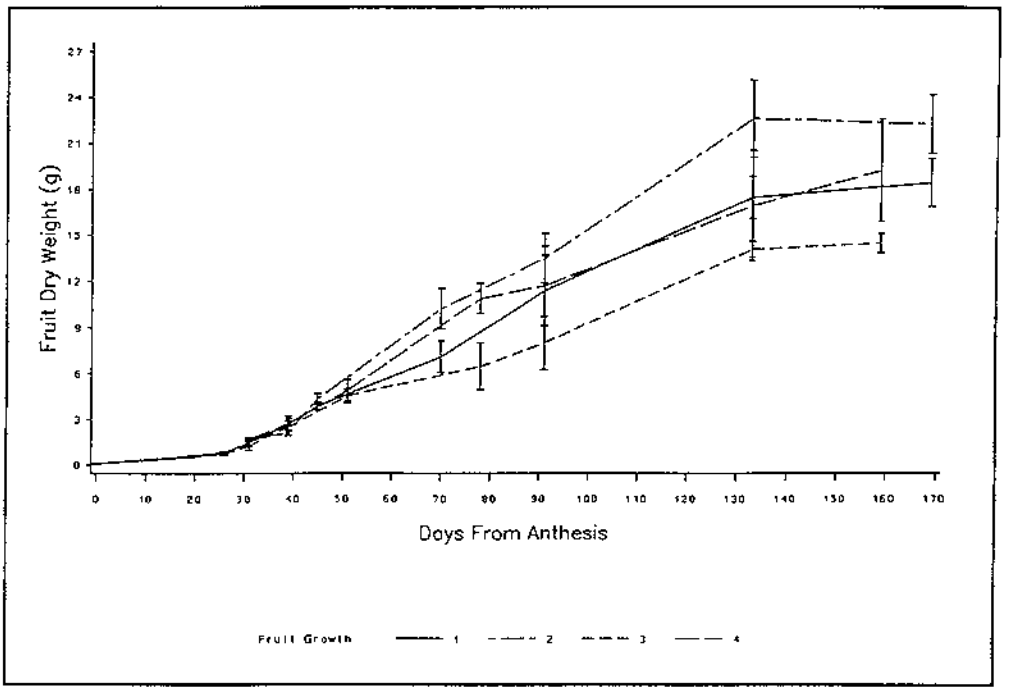


Figure 4 - 3. Change in dry weight of 'Hayward' kiwifruit for CPPU treated and untreated fruit from early and late flowers. Treatments: 1 = fruit from early flowers. 2 = CPPU treated fruit from early flowers. 3 = fruit from late flowers. 4 = CPPU treated fruit from late flowers. Standard errors of the mean are shown. 1990-91 Season.

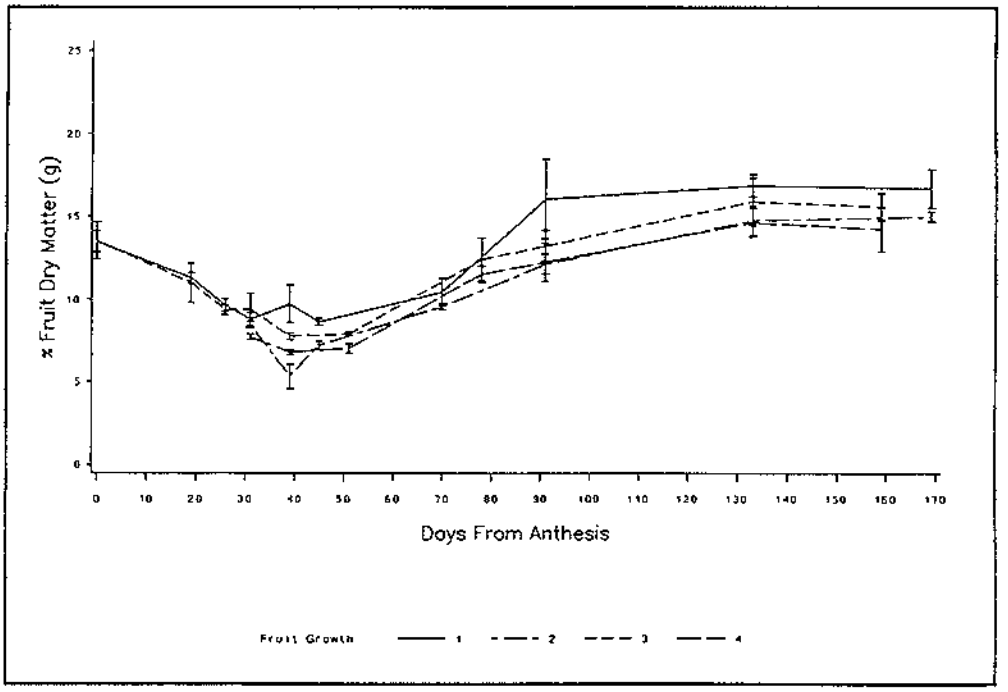


Figure 4 - 4. Change in percentage of dry matter of 'Hayward' kiwifruit for CPPU treated and untreated fruit from early and late flowers. Treatments: 1 = fruit from early flowers. 2 = CPPU treated fruit from early flowers. 3 = fruit from late flowers. 4 = CPPU treated fruit from late flowers. Standard error bars are shown. 1990-91 Season.

Table 4 - 6. Effects of a late application (56 days after full bloom) of growth regulators on kiwifruit fresh weight at harvest. 1988-89 Season.

Treatment	Fresh fruit weight (g)	Seed number	Total seed weight (g)
1. Control	105.7 c	1383 a	1.853 a
2. CPPU	120.8 b	1277 a	1.795 a
3. CPPU + 2,4-D + GA_3	128.1 a	1429 a	1.830 a
4. ABA (Low)	107.0 c	1400 a	1.801 a
5. ABA (High)	106.0 c	1457 a	1.770 a
6. Ethrel	107.6 c	1399 a	1.823 a
7. Ethrel + ABA	108.0 c	1371 a	1.799 a

Numbers in the same column with different letters are significantly different at $P \leq 0.05$ by Duncan's multiple range test.

1989-90 Season.

All the chemical treatments increased the fruit weight of the kiwifruit at harvest (Tables 4 - 7, 4 - 8). CPPU with high concentrations of 2,4-D and GA_3 resulted in the largest fruit size with a mean size of 168.1 and 173.1 g for 'Hayward' and 'Kramer Hayward', respectively (Tables 4 - 7, 4 -8). This treatment caused some skin blistering in both cultivars. The fruit fresh weight response of the hormone mixture with the low concentrations of 2,4-D and GA_3 was different for the cv Hayward and the strain 'Kramer'. Whereas the addition of Promalin or low concentration hormone mix increased the response of 'Kramer Hayward' to CPPU, in 'Hayward' they did not enhance the effect of CPPU (Tables 4 - 7, 4 - 8). The number of fruit locules, surface seed number, shape (L/W_1), and skin Hue angle ('colour') were not significantly different for any treatment (Tables 4 - 7, 4 - 8). A significantly lower fruit firmness was observed on fruit chemically treated (Tables 4 - 7, 4 - 8). In 'Hayward' fruit, similar total soluble solids were found for all treatments. In contrast, in 'Kramer Hayward' fruit, CPPU + Promalin had significantly lower total soluble solids at harvest with respect to CPPU + 2,4-D + GA_3 (high) (Tables 4 - 7, 4 - 8). Chromaticity measurements showed treated fruit had significantly lower skin L values. This indicates the fruit skin appearance of fruit treated with CPPU was darker than the untreated control (Tables 4 - 7, 4 - 8).

Fruit dipped in CPPU alone, or in combination with a high concentration of 2,4-D + GA_3 had the greatest diameter 124 and 130 days after application (Table 4 - 9). These differences were

Table 4 - 7. Growth regulator effects on 'Hayward' kiwifruit fresh weight and quality at harvest. Treatments applied 21 days after anthesis. 1989-90 Season.

Treatment	Fresh fruit weight (g)[1]	Number of fruit locules[2]	Seed count[2]	L/W_1[2,3]	W_2/W_1[2,4]	Fruit firmness (Newtons)[2]	Total Soluble Solids (%)[2]	Lightness (L)[2]	Colour (Hue)[2]
1. Control	106.3 c	40.0 a	190.0 a	1.0 a	0.88 a	105.8 a	8.5 a	45.9 a	145.6 a
2. CPPU	154.1 b	41.0 a	211.0 a	1.0 a	0.86 a	96.9 b	9.2 a	44.4 b	147.3 a
3. CPPU + 2,4-D + GA_3 (Low)	157.0 b	41.0 a	207.0 a	1.0 a	0.85 a	93.7 b	9.2 a	44.2 b	150.5 a
4. CPPU + 2,4-D + GA_3 (High)	168.1 a	40.0 a	182.0 a	1.0 a	0.85 a	95.3 b	8.5 a	43.5 c	150.5 a
5. CPPU + Promalin	153.0 b	42.0 a	180.0 a	1.0 a	0.86 a	94.8 b	8.9 a	44.4 b	143.5 a

[1]Least square means.
[2]Numbers in the same column with different letters are significantly different at $P \leq 0.05$ by Duncan's multiple range test.
[3]Fruit length/maximum width.
[4]Minimum width/maximum width.

Table 4 - 8. Growth regulator effects on 'Kramer Hayward' kiwifruit fresh weight, and quality at harvest. Treatments applied 25 days after anthesis. 1989-90 Season.

Treatment	Fruit fresh weight (g)[1]	Number of fruit locules[2]	Seed count[2]	L/W_1[2,3]	W_2/W_1[2,4]	Fruit firmness (Newtons)[2]	Total Soluble Solids (%)[2]	Lightness (L)[2]	Colour (Hue)[2]
1. Control	99.2 d	39.0 a	220.0 a	1.1 a	0.90 a	105.3 a	7.6 b	47.5 a	173.6 a
2. CPPU	132.5 c	38.0 a	236.0 a	1.1 a	0.91 a	95.1 b	7.8 b	43.6 b	171.4 a
3. CPPU + 2,4-D + GA_3 (Low)	152.4 b	37.0 a	217.0 a	1.1 a	0.89 a	92.9 bc	8.5 ab	43.9 b	167.5 a
4. CPPU + 2,4-D + GA_3 (High)	173.9 a	39.0 a	222.0 a	1.1 a	0.90 a	94.2 b	8.7 a	41.1 c	175.1 a
5. CPPU + Promalin	151.4 b	38.0 a	230.0 a	1.1 a	0.90 a	85.6 c	7.3 b	44.4 b	171.2 a

[1]Least square means.
[2]Numbers in the same column with different letters are significantly different at $P \leq 0.05$ by Duncan's multiple range test.
[3]Fruit length/maximum width.
[4]Fruit minimum width/maximum width.

Table 4 - 9. Fruit diameter, and % thickness of outer and inner pericarp, and core of 'Hayward' kiwifruit treated with CPPU, and CPPU + 2,4-D + GA_3. 1989-90 Season.

Days after application	Treatments	Fruit diam. (mm)	% thickness of tissues		
			Outer pericarp	Inner pericarp	Core
45	Control	40.9 a	33.8 b	50.2 a	16.0 a
	CPPU	45.6 a	42.4 a	42.7 b	14.8 a
	CPPU + 2, 4-D + GA_3	46.7 a	39.4 a	45.2 b	15.3 a
124	Control	43.3 c	33.9 b	50.0 a	16.1 a
	CPPU	46.0 b	41.2 a	43.6 b	15.2 a
	CPPU + 2, 4-D + GA_3	49.6 a	40.7 a	42.4 b	16.8 a
130	Control	45.7 b	39.4 b	45.3 a	15.3 a
	CPPU	49.6 a	43.7 a	39.5 b	16.8 a
	CPPU + 2, 4-D + GA_3	53.0 c	43.2 a	41.0 b	15.8 a

Numbers in each column per time of application with the same subscript are not significantly different by Duncan's multiple range test, 5% level.

present 45 days after application. The percentage of core remained similar for all treatments on the three harvest dates (Table 4 - 9).

1990-91 Season.

There was no significant interaction between hormones and seeds on fruit fresh weight. Both PGR treatments significantly increased fruit fresh weight at both low and high seed number (Table 4 - 10). The increased fruit size response to CPPU was enhanced significantly when applied in combination with 2,4-D and GA_3 to fruit with low (272) and high (901) seed number. Low and high seeded fruit treated with the hormone mixture were significantly superior to the respective untreated fruit controls by 55 and 46 g (Table 4 - 10). The mean fruit weights for CPPU alone of 81 and 120 g, were increased by 21 and 16 g, respectively by the addition of the hormone mix (Table 4 -10). Analysis of covariance for each group of fruit with high, and low seed number, respectively, including seed number as a covariate and fruit weight as a variate indicated the same differences among treatments as shown in Table 4 - 10. For performing the analysis of covariance the procedure GLM of SAS (SAS Institute, 1989) was used (analysis not shown).

4.3. Uptake of ^{14}C-CPPU by 'Hayward' kiwifruit, and the distribution of radioactivity in fruit tissues.

The fresh weight of fruit treated with ^{14}C-CPPU + 2,4-D + GA_3 was higher than for ^{14}CPPU alone after 21, 105, and 145 days of application (Table 4 - 11). A high activity was present within the fruit 6 hrs after application, and in the first 48 hours the highest

Table 4 - 10. Fruit fresh weight and seed number of 'Hayward' kiwifruit treated with CPPU and a growth regulator mixture. 1990-91 Season.

Treatments	High Seed		Low Seed	
	Fruit Weight (g)	Seed Number	Fruit Weight (g)	Seed Number
Control	90 cd	957 a	47 e	184 b
CPPU	120 b	820 a	81 d	267 b
CPPU + 2,4-D + GA_3 (low)	136 a	901 a	102 c	272 b

Means for either fruit weight or seed number, with different letters, are significantly different at $P \leq 0.05$ by Duncan's multiple range test.

Table 4 - 11. Fruit fresh weight of 'Hayward' kiwifruit at intervals after an application of ^{14}C-CPPU and ^{14}C-CPPU + 2,4-D + GA_3 (CPPU + H).

Time after application	Treatments	Fruit Weight (g)
6 hours	Control	11.7 a
	^{14}C-CPPU	10.7 a
	^{14}C-CPPU + $_H$	10.0 a
48 hours	Control	10.7 a
	^{14}C-CPPU	10.4 a
	^{14}C-CPPU + $_H$	11.4 a
21 days	Control	43.6 b
	^{14}C-CPPU	54.5 a
	^{14}C-CPPU + H	58.7 a
105 days	Control	96.2 c
	^{14}C-CPPU	138.2 b
	^{14}C-CPPU + $_H$	176.1 a
145 days	Control	98.0 b
	^{14}C-CPPU	141.4 b
	^{14}C-CPPU + H	176.3 a

Numbers in each column per time of application with the same subscript are not significantly different by Duncan's multiple range test, 5% level.
Nine fruit per treatment in each period were used for the analysis of variance.

counts were recorded in the blossom end, and the lowest in the inner pericarp and core (Tables 4 - 12, 4 - 14). From 21 days after application until commercial harvest the skin had the highest radioactivity (up to 80 % of the total) followed by the outer pericarp. The lowest radioactivity was found in the inner pericarp and core (Tables 4 - 13, 4 - 15). The radioactivity found in the skin washing declined regularly during fruit growth (Tables 4 - 12, 4 - 13). The application of 2,4-D + GA_3 significantly increased ^{14}CPPU counts for the acetone soluble fraction in the blossom end after 6 hours (Table 4 - 12), in the skin washing after 48 hours (Table 4 - 12), and in the skin, and outer pericarp after 21 days (Table 4 - 13). The radioactivity residues from the recovery acetone insoluble residues following application of ^{14}C-CPPU hormone mixture was also significantly higher ($P \leq 0.05$) than from ^{14}C-CPPU alone in the skin and outer pericarp after 48 hours (Table 4 - 14), and in the outer pericarp after 21 days (Table 4 - 15).

At commercial harvest there were non-significant differences of concentrations of radioactive residues derived from ^{14}C-CPPU, and ^{14}C-CPPU + 2,4-D + GA_3 in the acetone soluble and insoluble fractions (Tables 4 - 13, 4 - 15). Concentrations of radio-active metabolites of CPPU for both treatments, expressed as parts per billion CPPU equivalents, were on average 6.2 and 4.8 ppb (fresh weight basis) for soluble and insoluble acetone fractions, respectively (Table 4 - 16). Of this activity, 90 % was present in the skin and 10 % in the flesh.

Table 4 - 12 Acetone-soluble ^{14}C-residues (DPM/ml acetone) in wash and 'Hayward' fruit tissue at intervals after an application of ^{14}C-CPPU, and ^{14}C-CPPU + 2,4-D + GA_3 (^{14}C-CPPU + H). The standard errors are shown below the means.

Fruit tissues	Treatments	6 hrs	48 hrs
Stem end	^{14}CPPU	52780 5600	38290 4763
	^{14}CPPU + H	53000 2314	43980 5630
Blossom end	^{14}CPPU	167050 15000	186120 34000
	^{14}CPPU + H	276850* 19050	234130 26000
Skin and outer pericarp	^{14}CPPU	96080 3183	77320 7728
	^{14}CPPU + H	85720 5735	67220 9240
Inner pericarp	^{14}CPPU	5310 982	2360 1069
	^{14}CPPU + H	4070 700	2130 800
Core	^{14}CPPU	470 137	450 260
	^{14}CPPU + H	630 206	670 200
Skin wash fractions	^{14}CPPU	345900 14100	147000 8748
	^{14}CPPU + H	372500 20000	200500* 10000
Total radioactivity	^{14}CPPU	667590	451540
	^{14}CPPU + H	792770	548630

Fruit divided transversely into thirds to give: stem end, middle, and blossom (stylar) end sections. The middle section was separated into outer pericarp with skin, and inner pericarp and core.

*Significance in each column within different tissues at 5 % level, by t-test.

Table 4 - 13 Acetone-soluble ^{14}C residues (DPM/g dry weight) in wash and 'Hayward' fruit tissue by date after an application of ^{14}C-CPPU, and ^{14}C-CPPU + 2,4-D + GA_3 (^{14}C-CPPU + H). The standard errors are shown below the means.

Tissue	Treatments	21 days	105 days	145 days
Skin	^{14}CPPU	173700	119900	79200
		46000	18001	24050
	^{14}CPPU + H	268500*	100001	41700
		44332	23621	32000
Outer pericarp	^{14}CPPU	19220	2500	2200
		1723	800	1100
	^{14}CPPU + H	30675*	2000	2350
		1632	520	936
Inner pericarp and core	^{14}CPPU	10200	1000	800
		1527	400	600
	^{14}CPPU + H	11700	790	650
		3000	510	241
Wash of the Skin	^{14}CPPU	106500	37000	15450
		6922	2718	2850
	^{14}CPPU + H	92200	31200	19100
		7800	5220	3137
Total radioactivity	^{14}CPPU	309620	160400	97650
	^{14}CPPU + H	403075	133991	63800

*Significance in each column within different tissues at 5 % level, by t-test.

Table 4 - 14. Acetone-insoluble ^{14}C-residues (DPM/ml acetone) in 'Hayward' fruit tissues at intervals after an application of ^{14}C-CPPU, and ^{14}C-CPPU + 2,4-D + GA_3 (^{14}C-CPPU + H). The standard errors are shown below the means.

Tissue	Treatments	6 hrs	48 hrs
Stem end	^{14}CPPU	1249 371	1219 222
	^{14}CPPU + H	1292 255	1774 354
Blossom end	^{14}CPPU	7537 670	6786 1241
	^{14}CPPU + H	7424 861	7027 700
Skin and outer pericarp	^{14}CPPU	1802 433	2216 776
	^{14}CPPU + H	2619 460	4180* 500
Inner pericarp	^{14}CPPU	46 20	20 11
	^{14}CPPU + H	26 10	8 5
Core	^{14}CPPU	8 2	8 3
	^{14}CPPU + H	6 1	5 1
Total Radioactivity	^{14}CPPU	10642	10249
	^{14}CPPU + H	11367	12994

Fruit divided transversely into thirds to give: stem end, middle, and blossom (stylar) end sections. The middle section was divided into outer pericarp with skin, inner pericarp, and core.
*Significance in each column within different tissues at 5 % level, by t-test.

Table 4 - 15 Acetone-insoluble ^{14}C-residues (DPM/g dry weight) in 'Hayward' kiwifruit tissue by date after an application of ^{14}C-CPPU, and ^{14}C-CPPU + 2,4-D + GA_3 (^{14}C-CPPU + H). Standard error below the means.

Tissue	Treatments	21 days	105 days	145 days
Skin	^{14}CPPU	80000	78686	70859
		14600	4246	6029
	^{14}CPPU + H	61963	66499	83012
		20000	8020	7300
Outer pericarp	^{14}CPPU	2382	2499	2846
		412	399	300
	^{14}CPPU + H	4191*	3654	2450
		630	1000	773
Inner pericarp and core	^{14}CPPU	251	20	35
		150	10	12
	^{14}CPPU + H	363	15	32
		63	5	14
Total radioactivity	^{14}CPPU	82745	81205	73740
	^{14}CPPU + H	66517	70168	85494

*Significance in each column within different tissues at 5 % level, by t-test.

Table 4 - 16. Concentration (standard error of the mean) in parts per billon (ppb) of acetone-soluble and insoluble ^{14}C-residues in 'Hayward' kiwifruit commercially harvested[1]. The ^{14}C-CPPU, and ^{14}C-CPPU + 2,4-D + GA_3 (CPPU + H) were applied 33 days after anthesis.

Fruit fraction	Treatments	ppb[3]
Soluble in acetone[2]	^{14}C-CPPU	6.9 (1.5)
	^{14}C-CPPU + H	4.6 (1.3)
Insoluble in acetone	^{14}CPPU	5.4 (1.1)
	^{14}C-CPPU + H	4.9 (0.9)

[1]Fruit having about 7.2 % total soluble solids.
[2]Including the wash of the skin with 50 % ethanol.
[3]Calculations on the basis of mean fresh fruit weights of 141.4g, and 176.4g, for ^{14}C-CPPU and ^{14}C-CPPU + 2,4-D + GA_3, respectively.

5. Discussion.

5.1 Effects of time of anthesis on fruit growth.

The fresh weight of fruit from early flowers at harvest was significantly higher than fruit from late flowers by 12 g (Table 4 - 1), 13 g (Table 4 - 2) and 9 g (Table 4 - 3) in each of the three seasons, respectively. In two of those seasons, the size increase was independent of seed number (Tables 4 - 1, 4 - 2, 4 - 3). In contrast Patterson *et al.* (1991), and Gould *et al.* (1992) did not find any relationship between timing of kiwifruit flower opening and fruit weight at harvest. They presented no data on fruit seed number, and the lack of an effect may have been due to high variability of fruit seed number, or fruit location on the vine, or variability between vines. The difference in size increase of the fruit from early and late flowers occurred from about 47 (1989) and 57 days (1990) after anthesis (Figures 4 - 1, 4 - 2), which corresponded with the start of the lag growth phase stage II, and about the end of cell division (Woolley *et al.*, 1991). Fruit from early flowers had larger diameter at anthesis than fruit from late flowers (Table 4 - 2). Thus, the initial differences in ovary diameter at anthesis may account for the differences in fruit growth when phase stage I ceased earlier in late fruit. This suggests that fruit with a growth phase I of long duration may have high commercial value.

Volume, and fresh weight increases in kiwifruit from early and late flowers (Figures 4 - 1, 4 - 2) showed the double sigmoid curve described by Lai (1987), Woolley *et al.* (1991), and Smith *et al.* (1992). Conversely, Cooper and Marshall (1990b), and Patterson

et al. (1993) determined a single sigmoid curve for 'Hayward'. This discrepancy may be related to water stress in vines which would otherwise present a double sigmoid fruit growth curve (Clothier, B. 1993. Personal Communication. The Horticultural and Food Research Institute. Palmerston North, New Zealand), or to the use of simple mathematical forms in the interpretation of fruit growth (Coombe, 1976; DeJong and Goudriaan, 1989). For example, the use of constrained splines improved the curve fitting of kiwifruit growth data, and two cycles of kiwifruit growth were determined (Lai, 1987; Cruz-Castillo *et al.*, 1991). The significance of a double sigmoid curve in 'Hayward' may be also related to the differential growth capability of the various kiwifruit tissues.

In all three seasons, flowers or ovaries of early flowers had higher fresh weight than flowers with a late anthesis (Tables 4 - 1, 4 - 2, 4 - 3). Early flowers had higher ovary core cell number at anthesis than late flowers (Table 4 - 4). This suggests that flowers with an early anthesis may have greater metabolic activity in the preceding season and/or before bud break. Thus, flowering date and hence the timing of flower bud development, influenced flower size and quality at anthesis. Fruit from early flowers at harvest showed significantly higher cell numbers in the outer pericarp than in fruit from late flowers although mean cell size was the same (Table 4 - 5). Fruit cell counts were carried out in one dimension only. Cell counting per area of tissue would bring higher accuracy to the data. Thus, this work has demonstrated that the superior characteristics of flowers with an early anthesis were related to enhanced fruit growth and fruit size apparently by increasing final cell number. Further

research is required to elucidate how a large number of cells in the core of the ovaries with early anthesis may translate into large final fruit size.

The importance of pre-anthesis factors in the growth of 'Hayward' kiwifruit outlined by Lai *et al.* (1990), has been suggested by this work. In two of the three seasons studied seed number was similar between early and late flowers but fruit from early flowers was significantly larger. In apple it was found that early opening flowers had a greater subtending expanded leaf area than later opening flowers (Denne, 1963). Spurs with less leaf area seem to require significant import of photosynthesis from other parts of the branch to maintain apple fruit development 3 weeks after bloom (Grappadelli *et al.*, 1994). Therefore, in addition to pre-anthesis factors (eg. large ovary cell number or more developed vascular tissue (Lai, 1987)) early flowers may have a larger supply of resources with respect to late opening flowers. In this work no data on vine leaf area was recorded.

Although it has been suggested that the carbon resources available to a flower bud probably determine the time of anthesis of a flower (Lai *et al.*, 1990), further research is required to elucidate the relative importance of factors that influence flower development such as the timing of cane growth, time and severity of pruning, and cane angle. According to this trial, environmental conditions or practices improving floral bud conditions before anthesis could be effective in increasing fruit size through improved flower quality.

Lai (1987) demonstrated that when the spread of vine flowering was small so that flowers at full bloom were only 6-12 days apart the differences in final fruit size for fruit from early and late flowers were not significant. The larger fruit size of fruit from early flowers in comparison to late fruit (Tables 4 - 1, 4 - 2, 4 - 3) suggests a short bloom period may result in an increased number of larger sized export fruit, or at least a more uniform fruit size range. Spraying vines with hydrogen cyanamide, or late spring tipping of canes contracts the blooming period and promotes large fruit size (Snelgar and Manson, 1992). More attention to other vine management practices that may reduce the duration of the period of blooming such as the use of specific rootstocks (Wang *et al.*, 1994 b) is required because of the potential to significantly improve the return to growers.

Lai *et al.* (1990) found larger pedicel diameter on fruit from early flowers. Antognozzi *et al.* (1991), also linked large pedicel diameter with large fruit size. Therefore, a large pedicel size may be associated with high loading of photoassimilates and nutrients into the fruit from early flowers. Thus, early flowers at anthesis and set, with high core cell number and active cell division would develop a high sink strength. Enhanced development of vascular tissue in the peduncle would assist more rapid fruit growth by faciliting imports to meet the growth demand.

Significantly larger cell number was observed in the outer pericarp of early fruit treated with CPPU in relation to non CPPU fruit treatments (Table 4 - 5). The cell size in the outer pericarp, and core

were not significantly affected, but the cell size of the inner pericarp was significantly reduced (Table 4 - 5), maybe as a reflect of the larger cell number in the outer pericarp. Kurosaki and Mochizuki (1990) concluded that in CPPU treated 'Monty' kiwifruit there was no change in the cell size, and the fruit size increase was due to a raised cell number. In contrast, Patterson *et al.* (1993) found that CPPU stimulates only cell expansion in kiwifruit. Woolley *et al.* (1991), studying the outer pericarp of treated fruit found increases in both cell number, and cell expansion. In this work CPPU increased only cell number. However, future studies may consider cell counting per area of fruit tissue to improve the accuracy of the data, and evaluate if there are any changes in cell expansion in treated fruit. Cell counts in a straight line across the tissue in only one dimension do not consider the variation in size, and shape of the cells. Thus, some errors in the calculation of cell number and cell size may occur.

The final fruit size response to CPPU was 17 g higher in fruit from early flowers than in fruit from late flowers with respect to untreated fruit for each time of anthesis. This fresh weight increase was independent of their seed number (Table 4 - 3). Thus, the response to CPPU was more effective on fruit showing a higher number of cells at anthesis with an early period of growth. The increase in fruit dry weight (Figure 4 - 3) was similar in broad detail to that found by Hopping (1976 a), and Lai (1987) using 'Monty' and 'Hayward', respectively. Treated fruit from early flowers accumulated the highest dry weight during the season, while untreated fruit from late flowers the lowest (Figure 4 - 3). The higher fruit dry weight achieved by the CPPU fruit from early flowers (Figure

4 - 3) suggest that the carbohydrate and nutrient supply from the vine to the fruit was increased.

The fruit percentage dry matter declined rapidly until approximately 45 days after anthesis, and subsequently increased up to harvest (Figure 4 - 4). The end of this first period of fruit growth coincided with about the end of kiwifruit cell division (Hopping, 1976 a; Woolley *et al.*, 1991). Water potential differences within plants influence translocation flow, with regions at lower potentials attracting large shares of assimilate (Lang and Thorpe, 1986). Water movement into the fruit can vary with the stage of fruit development, as well as the rate of fruit transpiration (Boyer, 1985). Transpiration losses are higher during early fruit growth than in later stages in kiwifruit (Clark and Smith, 1988) and citrus fruit (Huang *et al.*, 1992). Walton and De Jong (1990) showed that high levels of osmotica were present in the early stage of kiwifruit growth. These studies may suggest that the initial decline of percentage dry matter in the fruitlet (Figure 4 - 4) was due to water accumulation promoted by high fruit transpiration and high levels of osmotica. Fruit treated with CPPU tended to have lower percentage dry matter during growth in comparison to control fruit (Figure 4 - 4). This significant accumulation of water into the chemically treated fruit may be associated with higher metabolism rate influenced by a high concentration of cytokinins.

In this work, the size of fruit from early flowers was greater than late fruit, but the early and late fruitlets appeared to be below their potential. This was shown by the fact that they responded to

CPPU application with increased size. The CPPU effect of increasing cell division in the outer pericarp, supports the idea that maximum cell number in the fruitlet at the earliest stages of its development is desirable for ensuring large final fruit size. Thus, it was demonstrated that CPPU treated fruit from early flowers had higher sink strength than early, late, and CPPU treated late fruit caused at least in part by a significant increase in sink size (cell number) at anthesis and during fruit expansion.

5.2. The effect of field application of plant growth regulators on kiwifruit growth.

In the 1988-89 season late CPPU treated 'Hayward' fruit (56 days after full bloom) were significantly larger than the control by 15 g (Table 4 - 6). This response was smaller than the mean increase of 48 g obtained by an earlier application (21 days after full bloom) (Table 4 - 7). The greatest response to CPPU occurred when it was applied during the major period of fruit cell division (Woolley *et al.*, 1992) which occurs in a period of 6-8 weeks after anthesis (Hopping, 1976 a; Woolley *et al.*, 1991). This suggests there was a variation in tissue sensitivity to exogenous cytokinin -active substances as the kiwifruit grew (see Trewavas and Allan, 1987).

The increase in fruit fresh weight promoted by the hormone mixture of CPPU with high concentrations of 2,4-D and GA_3 was significantly superior to CPPU alone in all three seasons tested (Tables 4 - 6, 4 - 7, 4 - 8, 4 - 10). In grapes a mixture of GA_3 and CPPU was also more effective, increasing berry size more than CPPU alone (Diaz and Maldonado, 1991). The fruit fresh weight response

to the hormone mixture with the low concentration of 2,4-D and GA_3 was influenced by the kiwifruit selection. In 'Kramer Hayward', fruit dipped in this mixture were significantly larger than fruit treated with CPPU alone (Table 4 - 8). In contrast, the size of 'Hayward' fruit was similar when treated with each of those treatments (Table 4 -7). In grape, the fruit growth responsiveness to GA_3 (Hagiwara *et al.*, 1980; Halbrooks and Mortensen, 1988), and other PGRs (Considine, 1983) has also varied among different selections. Further studies are required to elucidate if any anatomical and/or physiological fruit differences between those selections influence the action of the hormone mixture on those fruit. In treated 'Hayward' fruit, the thickness of the outer pericarp as a proportion of fruit diameter was increased, while the inner pericarp decreased and the core remained constant (Table 4 - 9). Similar results using CPPU were found by Woolley *et al.*, (1991).

For both selections, CPPU significantly decreased flesh firmness at harvest (Tables 4 - 7, 4 - 8) as reported by Iwahori *et al.* (1988), and Lawes *et al.*, (1991). 'Kramer Hayward' fruit treated with CPPU + Promalin had the lowest total soluble solids (Table 4 - 8). The control, and fruit treated with CPPU had similar total soluble solids (Table 4 - 9). 'Hayward' fruit had similar total soluble solids in all the treatments (Table 4 - 7). These findings are different from the results obtained by several workers (Iwahori *et al.* 1988; Lawes *et al.* 1991; and Biasi *et al.* 1991) who found higher total soluble solids in 'Hayward' fruit treated with CPPU. This discrepancy may be related to the different concentrations of CPPU used in the experiments, and/or to vine factors that influence fruit maturity such

as rootstocks (Cruz-Castillo *et al.*, 1991 b; Chapter 3), 'Hayward' strains (Chapter 3), or leaf:fruit ratios (Smith *et al.*, 1992).

The fruit skin L value was significantly reduced by the treatments including CPPU in each of the 'Hayward' selections. This indicates that treated fruit had a skin with a darker colour in comparison to control fruit (Tables 4 - 7, 4 - 8). The application of CPPU has stimulated chlorophyll synthesis in cucumber cotyledons (Karanov *et al.*, 1992). Lawes *et al.* (1991) reported that CPPU promoted a dark green appearance in 'Hayward' kiwifruit. Patterson *et al.* (1993) suggested the changes in colour may be associated with high chlorophyll production and a high level deposition of tannins in the skin of kiwifruit. In this work, the application of CPPU promoted a darker appearance in the skin of the fruit. This effect was enhanced when CPPU was applied with 2,4-D + GA_3 (High) in 'Hayward' and 'Kramer Hayward' fruit (Tables 4- 7, 4 - 8). The results show that the visual appearance of fruit from these cultivars may be influenced by the application of CPPU alone or mixed with other PGRs.

The hormone mixture was significantly more effective than CPPU alone in increasing size of both high and low-seeded fruit (Table 4 - 10). Woolley *et al.* (1991) indicated that the response to CPPU was additive to that of seed number. In this work, there was not a significant interaction between hormones and seeds, and an additive effect between seeds and PGRs was found. For example, low and high seeded fruit respectively treated with the hormone mixture had a mean fresh weight of 102 and 136 g, compared with 47 and 90 g for the control fruit (Table 4 - 10). Thus, in each case

CPPU added about 50 g to the weight of a fruit which complemented rather than substituted for the effect of seeds. This suggests that hormones produced in the seeds and in the vine may be necessary to maximise fruit growth. Woolley *et al.* (1991) suggested that seeds which are known to produce plant hormones (Moore, 1989) and CPPU may act through the same mechanism increasing fruit size. They also indicated that the growth of high and low seeded 'Hayward' may be limited by a low concentration of auxins, gibberellins, and cytokinins. Because the seeds played a key role in maximising sizing of chemically treated fruit, the hormone mixture and CPPU should be considered as an complement to pollination not as an alternative. Lawes *et al.* (1991), pointed out that the process of kiwifruit size response to CPPU could occur in two phases: in the initial meristematic stage when fruit cell division is limited by photoassimilate supply by influencing potential sink size; in the fruit expansion phase, by influencing sink metabolic activity. In this work, most of the fresh weight response to CPPU occurred in the fruit cell expansion stage up to about 50 days after anthesis (Figure 4 - 2).

Trewavas (1991) stated: 'the hypothesis that growth substances are major controlling elements in development can be maintained but at the expense of admitting that other processes contributed substantially.' Several factors have been proposed to be involved in kiwifruit sizing, for example timing and severity of summer pruning (Volz *et al.*, 1991), organic acids (Walton and De Jong, 1990), seed number (Woolley *et al.*, 1991), unknown factors released by the seeds (Hopping, 1976 b; Trustrum, 1983; and Chapter 5), flower quality (Woolley *et al.*, 1992; and this work),

rootstocks (Lowe *et al.*, 1992; and Cruz-Castillo *et al.*, 1991 a, b); leaf:fruit ratios (Woolley *et al.*, 1988); shoot girdling (Woolley *et al*, 1988); nutrients (Buwalda and Smith, 1990), 'Hayward' strains (In this work), and PGRs (Lawes, Woolley and Lai, 1990; and this work). CPPU significantly increased kiwifruit size, but the fact that low 'Hayward' kiwifruit size responses to CPPU have been recorded on vines with a 'poor' field performance irrespective of pollination (data not shown) may indicate that the concurrence of a whole system is required for maximum kiwifruit sizing. Therefore, studies with an integrative approach observing several events, and exploring factors that might influence them could improve our understanding of the interactions between exogenous PGRs and another factors influencing fruit growth.

CPPU is already being used in Japan (Lawes and Woolley, 1990). In New Zealand, the practical significance of CPPU as a fruit size enhancer is important to the kiwifruit industry because allows growers to maintain high load and still get preferred larger sizes, and then maximum income. Investigations have indicated that with the use of CPPU it may be possible to obtain large fruit (eg. 112 g), even at heavy crop loads of 50 fruit/m^2 canopy (Woolley *et al.*, 1992). However, overcropping can result in a lowering of return bloom in the following season (Cooper and Marshall, 1990). Therefore, research may be conduced to study the sustainability of vines treated with CPPU.

In New Zealand there is a reluctance to allow the use of this plant growth regulator due to the risk to residue free image, and beyond that too, its use (even with no residues) indicates getting

away from the desirable system of growing fruit trees in a pure natural environment, an ecological-conservation issue.

5.3. Uptake of ^{14}C-CPPU by 'Hayward' kiwifruit, and the distribution of radioactivity in fruit tissues.

The final fruit size response to CPPU application was increased about 20 % when applied together with 2,4-D + GA_3 (Table 4 - 11). The percentage of total flesh counts presented in the acetone-soluble fractions of ^{14}C-CPPU and ^{14}C-CPPU + 2,4-D + GA_3 treated fruit fell about 89 % on average at commercial harvest. In contrast, the acetone-insoluble fractions of the two chemical treatments increased about six times on average at final harvest (calculations assuming 100 % radioactivity at 6 hours after chemical application). This may indicate that CPPU compounds were metabolized in growth and development because they were incorporated into plant dry matter.

Woolley *et al.* (1991) and Biasi *et al.* (1993), found low CPPU translocation from a kiwifruit following a dip application. Similar results have been found in apple (Tartarini *et al.*, 1993). Hence, the reduction (about 90 %) in total fruit radioactivity during growth may be related mainly to losses by respiration rather than translocation into the vine. In the first 48 hrs, the greatest amount of radioactivity was found in the blossom end (Tables 4 - 13, 4 - 15). This may be associated with ^{14}C-CPPU runoff to the lower point of the fruit, and may cause the excessive enlargement and protruded stylar tissues found in kiwifruit treated with CPPU (Lawes *et al.*,

1991). When different fruit tissues were individually analyzed, most of the radioactivity was in the skin. Generally the outer pericarp had higher radioactivity than the inner pericarp in most of the harvests (Tables 4 - 13, 4 - 15). The high accumulation of radioactivity found in the outer pericarp may be explain the greater cell division response of this tissue to CPPU. Woolley *et al.* (1991) found that the increase in cell number and size promoted by CPPU occurred mainly in the outer pericarp. 'Hayward' inner pericarp tissue cultured in vitro has been found to respond to CPPU (0.5 ppm) by producing callus (Cruz-Castillo unpub.). The low capacity of CPPU for reaching the inner pericarp at the stages of fruit cell division and expansion (Tables 4 - 12, 4 - 13, 4 - 14, 4 -15) may limit its potential for growth promotion of this tissue. The low translocation of CPPU into different kiwifruit tissues has been described by others workers (Biasi *et al.*, 1993; and Neri *et al.*, 1993).

Substrate use in plants can be divided into that incorporated into new structures and that consumed in growth and maintenance respiration (Walton and Fowke, 1992). Walton and De Jong (1990) found a substantial increase in organic acids and sugars in kiwifruit about the period of CPPU application in this trial. They associated those compounds with the cell growth. In tomato, organic acids has been also associated with fruit growth but its physiological role in fruit development is unknown (Knee and Finger, 1992). Perhaps some sugars and organic acids are associated with the mechanism of action of CPPU as in meeting the energy needs of active cell division stimulated by this PGR, and then causing their expansion.

In this work, no data was obtained to show whether all the counts at harvest were still CPPU. It is also unknown whether the increased fruit size was brought about by CPPU or a metabolite. Future studies using chromatographic and mass spectrometric techniques may elucidate the radioactive metabolites of CPPU in kiwifruit tissues, and their involvement in the fruit growth response.

The radioactive residues in the acetone soluble, and insoluble fractions of fruit following treatment with the ^{14}C-CPPU hormone mixture were significantly greater than from ^{14}C-CPPU alone in the outer pericarp after 21 days (Tables 4 - 13, 4 -15). It implies that 2,4-D, and GA_3 increased the retention of CPPU residue compounds in those tissues. The lowest radioactivity was found in fruit at commercial harvest, and most of it was found in the skin (90 %) rather than in the flesh. If the skin was removed as is usual in the normal consumption of kiwifruit, the flesh levels of radio-active metabolites following application of ^{14}C-CPPU and ^{14}C-CPPU + 2,4-D + GA_3 could be of 0.48 and 0.62 ppb for the average of the sum of soluble and insoluble acetone fractions, respectively (Table 4 - 16). Nickell (1987) indicated that CPPU is not very toxic to higher animals. However, if CPPU were certified for commercial use in New Zealand, national and international kiwifruit markets would react negatively to buy chemically treated fruit.

CHAPTER 5.

THE EFFECTS OF PLANT GROWTH REGULATORS (PGRs) AND SEEDS ON THE GROWTH OF 'HAYWARD' INNER PERICARP TISSUE CULTURED *IN VITRO*.

1. Introduction.

Although seeds are recognized as a source of PGRs in many plants (Moore, 1989) several issues concerning their activity in fruit development are unresolved. The culture of *Actinidia deliciosa* kiwifruit tissue *in vitro* may provide a suitable system for the observation of fruit tissue responses to seed-produced factors, provided the cultured cells are physiologically and biochemically comparable with the original fruit cells. In this study, the effect of seeds and growth regulators on the callus growth of kiwifruit inner pericarp cultured *in vitro* were compared.

2. Literature Review.

2.1. The relationship between seed number and kiwifruit weight.

Kiwifruit flowers must be pollinated in order to set fruit. Pollination is often a factor limiting regular cropping, as yields are reduced due to small fruit size when inadequate pollen transfer has occurred. 'Hayward' fruit must normally contain around 850 seeds

for development to an acceptable export size of 80-90 g or higher (Hopping, 1976 b). This contrasts with the usual situation for other crops such as apple, in which a low percentage set and lower seed numbers are adequate for economic yields (Ferguson, 1984).

The high fruit set and pollination requirements are complicated by several factors. Firstly the crop is dioecious, thus requiring the transfer of pollen between vines during the flowering period. At present, commercial pollination is accomplished by introducing honey bees into orchards. Due to the lack of nectar provided by the flowers, the crop is relatively unattractive to these insects, thus making pollen transfer difficult (Palmer-Jones and Clinch, 1974). Cool, wet, and windy weather has been shown to adversely affect bee activity (Way, 1961), thus presenting growers with difficulties in pollination assurance during flowering. There are a number of pollination devices currently available for kiwifruit pollination. These include airflow pollinator, rollon pollinator, pollenaid, turbo bee, and polli. Most of the devices are used by orchardists to supplement honey bee pollination in orchards with average pollination (Goodwin, 1992).

The relationship between fruit size and seed number in kiwifruit was first described by Hopping (1976 b). The data presented suggested a curvilinear relationship, with large incremental gains in fresh weight/seed at less than 200 seeds and at greater than 1000 seeds. Unfortunately sample size was small enough to cause concern about the true relationship. Subsequent studies have presented conflicting results. Hopping and Hacking (1983) proposed a linear relationship for seed numbers greater than 850. Grant and

Ryugo (1984) confirmed this model for seed numbers between 50 and 1000. Sneigar *et al.* (1991), found a linear relationship to fresh weight for fruit with more than 300 seeds. In contrast, McKay (1976), Trustrum (1983), Pyke and Alspach (1986), and Lai (1987) have supported the original model presented by Hopping (1976 b). These divergences suggest that the relationship between seed number and fresh weight is complex, and may be influenced by vine factors such as leaf:fruit ratios and inter-fruit competition (Woolley *et al.*, 1988; Lawes, Woolley and Lai, 1990).

2.2. Fruit seeds as a source of growth regulators.

Although it has been demonstrated that plant seeds are a source of auxins, gibberellins (GAs), cytokinins, and abscisic acid (ABA) (Moore, 1989), the influence on fruit development of those growth regulators released by the seeds is not clearly understood.

Auxins.

Nitsch (1950) provided evidence that the achenes of strawberry fruit supplied the auxin required for receptacle growth. Achenes were required for at least 20 days after pollination (Nitsch, 1965). Archbold and Dennis (1984) found that free IAA levels in achenes of strawberry peaked at 14 days after anthesis. Veluthambi *et al* (1985) presented evidence for the possible involvement of an auxin-repressed polypeptide in cessation of strawberry growth. Subsequently, Reddy and Poovaiah (1990), isolated, characterized and sequenced a cDNA clone (λSAR5) to an auxin-repressed mRNA from flesh tissue. They also presented evidence indicating a positive correlation between repression of mRNA corresponding to λSAR5 and

strawberry fruit growth. For example, when achenes were removed from fruit 7 days after pollination, the fruit did not grow and the auxin-repressed mRNA level increased. However, when auxins were supplied to de-achened fruits, the fruit grew, and repression of *λ*SAR5 mRNA was observed. Then they demonstrated the importance of the achenes as auxin producers in the early development of strawberry fruit. This evidence that the achenes of strawberry fruit supplied auxins for receptacle growth may be a special case since botanically the achenes are the fruit.

Gustafson (1939 b), showed that the auxin concentration in tomato was much higher in the seeds than in the placenta. Verkerk (1957) found that *Lycopersicum peruvianum* pollen had a similar effect on fruit growth as tomato pollen, although no seeds were formed. Varga and Bruinsma (1976) concluded that an enhanced sink activity of a tomato fruit is due to high auxin production by developing seeds. However, Sjut and Bangerth (1982) pointed out that parthenocarpic fruit may have similar fruit size to seeded fruit, and therefore the auxin produced in the seed is most likely not the limiting factor for pericarp growth after fruit set. Therefore, in tomato, auxins produced in the seed do not limit early fruit growth. In grape, parthenocarpic cultivars are found to have a higher auxin content at anthesis than do seeded cultivars (Gustafson, 1939 a), thus, auxins produced in the seed appear not to limit grape berry growth.

Luckwill (1953) identified two major peaks of auxin content in apple seeds. These peaks were coincident with the period of: a) endosperm development and the spherical embryo stage and b) the

beginning of seed maturation. In fig seeds, auxins also exhibit a peak during endosperm cytokinensis (Crane, 1964). Coombe (1960) and Nitsch *et al.* (1960), in several varieties of seeded grapes, found correlations between auxin level and meristematic activity in the seeds. Randey and Singh (1989) evaluated the endogenous level of auxins in developing grape seeds, and showed high levels of auxins during the third and fourth weeks after anthesis (fruit growth stage I). The content of auxin fell during the following two weeks, but increased again during the seventh or eight weeks. There was no clear relationship between the growth rate of the grape and the auxin seed content. Miller *et al.* (1987), and Miller and Walsh (1990) measured IAA concentration and content in ovules and mesocarp of peaches. They found that IAA was high in the ovule when cytokinesis in the endosperm occurred (fruit growth stage I), but in this period, the concentration of IAA in the mesocarp decreased. Thus, they could not demonstrate a significant positive correlation of IAA content in the seed and the mesocarp of peach fruit.

Gibberellins (GAs).

Immature seeds of many species of angiosperms contain maximal amounts of extractable GAs when the seeds are half their maximum fresh weight (Moore, 1989). In an study of changes in GA-like substances during development of peach fruits (Jackson, 1968) no GA was found in the ovary before bloom. However, immediately after full bloom GA activity was found first in the seed and later in the mesocarp and endocarp. Jackson and Coombe (1966) compared growth rates of seed, endocarp, and mesocarp of apricot between anthesis and fruit maturity with the concentrations of GA-like substances extracted from those tissues. A strong

correlation was shown between the concentration of GA-like substances in all three tissues and their respective growth rate for the first 60 days after anthesis. Coombe (1971) concluded that GA_{32} is the apricot pericarp cell-elongation hormone and seed is its source. Iwahori *et al* (1968) found more GA-like activity in seeded than in seedless *Vitis* berries, indicating that grape seeds may be a rich source of GA-like substances. This is supported by the larger fruit size response of seedless grapes to GA_3 with respect to fruit seeded cultivars (Coombe, 1973; Weaver, 1976), and by experiments with de-seeded grape where exogenous GA_3 substituted the flesh growth effects of the seeds (Coombe, 1973). In contrast, non-significant differences in fruit concentration of GAs during the period of fruit set were observed for seeded and parthenocarpic cultivars of orange (Talón *et al.*, 1990). Therefore, it is possible GAs produced in the seeds do not limit fruit growth in parthenocarpic oranges. Groot *et al* (1987) used the homozygous GA-deficient ga-1 mutant of tomato cv Moneymaker to study the role of GAs in seed and fruit development. Dwarf ga-1 plants produced no normal flowers, but initiated flower buds, which did not develop further, but parthenocarpic fruit development was observed occasionally on the dwarf plants. A single application of GA_{4+7} restored normal flower development and seed set following pollination. Endogenous GAs were not found in seeds and the fruit. Thus they demonstrated that tomato fruit and seed could develop in the absence of endogenous GAs. Likewise, Ram and Pal (1979) suggested that the gibberellins synthesized in mango seeds does not play any major role in the rapid growth of the epicarp.

Cytokinins.

Powell (1964) isolated cytokinins from the embryo and endosperm of peach fruits. The relative abundance of cytokinins in apple seed has been reported by Letham (1969). In maize (Miller, 1967) and wheat seed (Wheeler, 1972) cytokinins levels peaked 11 days after pollination and declined almost to base level during the next 10 days. Takagi *et al.* (1989) analyzed free-base, riboside, ribotide and glucoside cytokinins in rice seed at various stages of development. The highest level/activity of cytokinins was recorded at the time of anthesis. *Cis* isomers of zeatin derivatives were always present during the period of seed growth, suggesting that type of cytokinins may play important roles in the development of grain. An interesting correlation has been found in field pea (*Pisum arvense*) during seed development where one major and two minor cytokinin peaks coincided with the maximum volume of the endosperm and with the two periods of rapid growth of the whole seed and embryo (Burrows and Carr, 1970). Blumenfeld and Gazit (1970) monitored cytokinin activity in avocado seeds, and showed that cotyledonous callus was competent to synthesize cytokinins (Blumenfeld and Gazit, 1971). Cutting *et al.* (1986) indicated that the cytokinin isopentyladenine probably played a prominent role in the early fruit and seed development of avocado. They developed a radioimmunoassay to validate the presence of that substance. Their results supported the idea that seeds control early fruit growth by synthesizing or attracting PGRs, which then become available to stimulate fruit fresh weight gain.

Lewis *et al.* (1992), in a preliminary experiment showed that when the seed number of kiwifruit was reduced from 935 to 399,

cytokinin content per fruit also decreased. This was reflected in reduced final fruit size. Their results were on the basis of whole fruit, so the fruit tissue was not isolated from seed tissue. In contrast, Woolley (Woolley, D. J. 1993. Personal communication. Department of Plant Science, Massey University. Palmerston North, New Zealand) found no significant differences in cytokinin content in the outer pericarp of commercially harvested kiwifruit that were either high or low seeded.

Fruit tissue may be capable of synthesize cytokinins (Nitsch, 1970) that interact with unknown seed factors in the promotion of fruit growth. Probably the core is a source of cytokinins to the fruit because it stills cell divide when the outer and inner pericarp have only cell elongation (Hopping, 1976 a). Endogenous cytokinins are associated with water uptake in citrus (Erner, 1989). Thus, cytokinins produced in the core may play a role in kiwifruit expansion.

Abscisic acid (ABA).

Seeds are a source of ABA (Brenner, 1987; Hein *et al.*, 1984). Studies involving isolated embryos from a number of species (Zeevart and Creelman, 1988), and with ABA mutants (Koorneef *et al.*, 1989), have indicated that ABA has an important role in seed development. On a whole tissue basis, the greatest quantity of ABA is generally found in the prime storage tissue of seeds such as cotyledons of soybeans (Schussler *et al.*, 1984). Compared with expressing hormone levels as the content in a tissue, the activity on a concentration basis is presumably a measure of greater

physiological significance. ABA is also found in high concentrations in the seed coats of soybean (Schussler *et al.*, 1984). In wheat, ABA accumulates during grain development and is present at high levels during starch accumulation (Radley, 1976). Dewdney and McWha (1978) suggested that the increasing level of ABA during the period of dry matter accumulation is due to biosynthesis within the grain. Marx *et al.* (1988), observed changes in the quantity of ABA in embryos of walnut during the development of these organs. The highest concentrations of ABA were found 4 to 5 weeks before fruit abscission and lowest amounts were measured at the end of the ripening period. In avocado fruit, ABA was found at equally high levels in fruit flesh and in the seed embryo throughout most of the growth and development of the fruit. The levels of ABA found in the fruit flesh exceeded those in the seed in the last few weeks of fruit development (Cutting *et al.*, 1986).

As indicated above, some workers have shown a relationship between seed content of growth regulators and fruit development (Nitsch, 1950; Luckwill, 1953; Jackson and Coombe, 1966, Jackson, 1968; and Cutting *et al.*, 1986) which suggests the importance of the seeds in this process. Results showing a non-significant correlation between growth regulators in the seed and fruit development (Hopping and Bukovac, 1975; Cawthon and Morris, 1982) do not necessarily negate the significant role of the seeds. They may reflect the requirement for sensitive (Wareing, 1986) and accurate physico-chemical methods of quantification of the hormones in specific target tissues together with research focusing on mutants with different fruit growth rates or variation in abilities to complete normal seed development (Miller, 1990). The time of plant growth analysis during fruit growth may be also important because in

'Golden Delicious' apple the fruit only require seeds to grow for about six weeks after full bloom (Gucci *et al.*, 1991). In contrast, according to Trewavas and Allan (1987) the sensitivity of plant tissues to the growth substance may be the primary controlling factor in growth rather than the level of endogenous growth substances.

Trustrum (1983) using *in vitro* techniques found an interaction between exogenous PGRs and seed factor (s) on the production of kiwifruit callus. These suggests that non-seeded produced PGRs are also important in fruit development, and that they may interact with seed produced factor (s) in the regulation of fruit growth. Evidences *in vitro* have shown fruit tissue may have an autonomous mechanism for synthesize PGRs (Browning, 1989). Avocado (Schroeder, 1955), and citron (Schroeder and Spector, 1957) fruit tissue have the ability to cell divide and produce cytokinins. Other researchers have pointed out that PGRs produced in the roots are also important in fruit sizing (Niimi and Torikata, 1978; Cutting and Lyne, 1993). Stevens and Westwood (1984) found a high concentration of cytokinins in the xylem sap of cherry trees at early stage of fruit growth. They indicate that the root system may play an important role in the control of fruit size as a producer of PGRs. The leafiness of the plant may also influence the PGRs content of the fruit. Citrus fruit grown on a leafy inflorescence may have high cytokinin content (Erner, 1989). Therefore, in addition to PGRs produced in the seeds or fruit flesh, other organs from the plant may supply PGRs to regulate fruit sizing.

2.3. *In vitro* fruit tissue culture studies.

Nitsch (1967) pointed out that the technique of *in vitro* fruit culture would be widely applicable to physiological studies of fruit development, but this has not been utilized widely by many researchers.

Schroeder (1955) proliferated *in vitro* mature avocado pericarp tissue, and mesocarp pieces of a mature citron (Schroeder and Spector, 1957). Their results suggested that tissue responded to a range of gibberellins in the presence of exogenous indoleacetic acid.

Blumenfeld and Gazit (1971) investigated the dependence of avocado fruit tissues on the supply of cytokinins. Their results showed that cytokinins in the nutrient media were vital for the growth of mesocarp callus but not for the growth of cotyledonous callus. Thus they concluded cotyledonous callus synthesized cytokinins.

Asahira and Hosoki (1977) used *in vitro* fruit culture to evaluate tomato puffiness as influenced by exogenous PGRs. 2,4-D supplements increased fruit weight and degree of puffiness. GA_3 induced puffiness and retarded locule development, while CCC (chlorocholine chloride), SADH (succinic acid 2,2-dimethylhydrazide) and TIBA (2,3,5-triiodobenzoic acid), which lower auxin level decreased fruit puffiness. Although BA slightly promoted fruit growth, the effect on puffiness remained unclear. In other studies, Varga and Bruinsma (1983) indicated that a combination of PGRs was able to produce normal tomato fruit development *in vitro.*

Other researchers have successfully utilised this technique to study fruit ripening and senescence (Lieberman *et al.*, 1979; Latché and Pech, 1983), and fruit storage (Ferguson and Lurie, 1992). Hence studies using this technique can provide insights into fruit physiology and maturation.

Hirsch *et al.*, (1977) used kiwifruit tissue culture to study the effect of *in vitro* culture conditions on metabolism of free amino acids. They cultured fruit tissue in Murashige and Skoog's medium containing glucose, 2,4-D, and coconut milk. The addition of gibberellic acid to the medium increased the growth of newly formed tissues. Mature kiwifruit pericarp tissue could not be induced to form callus. Trustrum (1983), cultivated kiwifruit inner pericarp tissue to study seed and growth regulator interactions. Callus formed when seeded tissue was cultured with a PGR cocktail NAA + BAP + GA_3. No additional callus growth response occurred when zeatin was added to the medium. It was suggested the presence of both seeds and growth regulators were required for inner pericarp callus formation.

While fruit tissue culture studies *in vitro* have advantages when investigating some physiological aspects of the growth and development of the fruit, it is clear that the experimental environment where the fruit, or the pieces of fruit tissue are growing, is completely artificial and could produce results that can not be corroborated *in vivo*. Krikorian and Stewars (1969) noted 'it is difficult to cause cultured tissues and free cells to recapitulate in isolation the metabolism and biochemistry which they exhibit in the environment of the intact plant'. Pech *et al.* (1979), described the

possible alterations in the activity and expression of amylase isozymes induced by the *in vitro* culture of 'Passe Crassane' pears. Fruit tissues grown *in vitro* showed a typical juvenile amylase pattern, caused by 2,4-D in the medium. Similarly, Wallner (1977) found that the textural characteristics of apple fruits at different periods of development were not maintained after *in vitro* culture. Therefore caution needs to be exercised in extrapolating from *in vitro* fruit tissue culture to *in vivo*.

3. Materials and Methods.

Preparation of the fruit tissue.

Tissue was obtained from the inner pericarp of immature 'Hayward' kiwifruit harvested in February (100 days after full bloom) and March 1990 (124 and 126 days after full bloom), and in March 1991 (90 and 95 days after full bloom) from T-bar vines aged 5 and 6 years, respectively. In each experiment the fruit were visually of similar size, and were harvested within an area of 1.0 m from the trunk along each top permanent leader. The pedicel and any floral remnants were removed from freshly harvested fruit before surface sterilization by dipping in 95 % ethanol, and flaming. Long forceps were used to hold the flaming fruit, which was rotated to distribute the flame over the surface for 15 to 20 seconds. A 25 % v/v solution of Janola® (2-3 % sodium hypochlorite) was prepared with 1 or 2 drops of Tween 20. The fruit was immersed in this solution for 15 minutes and then rinsed twice in sterile water. The proximal and distal stem ends from the sterilized fruit were cut and discarded. A number of four or five transverse slices of 5 mm thickness were

cut from the fruit, and 8 mm cores cut from the inner pericarp of each slice. Seeds were removed aseptically from some inner pericarp cores to obtain unseeded tissue. Three fruits per experiment were used. The cores from those fruit were mixed in a petri dish containing sterilized water before establishing the treatments.

Preparation of culture media.

Murashige and Skoog (1962) medium was prepared using analytical grade chemicals. All components of the media were weighed and dissolved separately. Concentrated stock solutions of all chemicals were stored in glass bottles at 4 ± 1 °C in the dark.

Agar (Bacteriological grade Dri-Form) and sucrose were weighed and dissolved separately in water at 45 °C. After mixing together, they were made to volume, with final concentrations of agar and sucrose of 0.85 %, and 3 %, respectively.

Quantities of macronutrients, micronutrients, iron, vitamins, and growth regulator solutions were added to the agar and sucrose solution/mixture. The pH of the medium was adjusted to 5.5 with NaOH or HCl. After autoclaving for 15 minutes at 121 °C, 18 ml was pipetted into petri dishes.

PGRs used in culture media.

PGR stock solutions were stored in a refrigerator at 4 ± 1 °C in the dark. They were prepared by dissolution in a small quantity of 1 M NH_4OH except BAP which was dissolved in hot deionised

water. Growth regulators were incorporated in the media to give final concentrations of: 2,4-D (5 μM), GA_3 (40 μM), ABA (1 or 10 μM), and BAP (20 μM). The treatments for five experiments are shown in Table 5 - 1.

Conditions of the experiment and data analysis.

Three or four pieces of tissue were put in each plastic petri dish on the solid agar medium, and they were treated as an individual treatment. Three or four replicates of each treatment were maintained in a seed germination cabinet at 27 °C in low intensity light (9.4 μmol m^{-2} s^{-1}) from warm white fluorescent tubes. After 75 days incubation final callus fresh weight was recorded on an electronic balance (accurate ± 0.1 mg). The petri dishes were arranged in a randomized complete block factorial design. Seeded and unseeded tissues, and PGRs were the two main effects. Data were analysed using the general linear models procedure of SAS (SAS Institute, 1989) for unbalanced designs because of missing values.

4. Results.

Experiment 1.

A significant interaction between seeds and 2,4-D + GA_3 + BAP on callus fresh weight was found (Table 5 - 2). No visible callus growth was observed on tissue cultured in the absence of 2,4-D + GA_3 + BAP, irrespective of the presence of seeds. The growth

Table 5 - 1 Treatments used to study the effects of plant growth regulators and seeds on the growth of 'Hayward' kiwifruit inner pericarp tissue cultured *in vitro*. Five experiments are shown.

Treatments	Expt. 1***	Expt. 2*	Expt. 3**	Expt. 4**	Expt. 5***
1	Seeded tissue	Seeded tissue	Seeded tissue	Seeded tissue	Seeded tissue
2	Seeded tissue + 2,4-D + GA_3 + BAP	Seeded tissue + ABA	Seeded tissue + ABA	Seeded tissue + ABA	Seeded tissue + 2,4-D
3	Seedless tissue	Seeded tissue + 2,4-D + GA_3 + ABA	Seeded tissue + 2,4-D + GA_3 + ABA	Seeded tissue + 2,4-D + GA_3 + ABA	Seeded tissue + GA_3
4	Seedless tissue + 2,4-D + GA_3 + BAP	Seedless tissue	Seeded tissue + 2,4-D + GA_3 + ABA + BAP	Seeded tissue + 2,4-D + GA_3 + ABA + BAP	Seeded tissue + BAP
5		Seedless tissue + ABA		Seedless tissue	Seeded tissue + 2,4-D + GA_3
6		Seedless tissue + 2,4-D + GA_3 + ABA		Seedless tissue + ABA	Seeded tissue + 2,4-D + BAP
7				Seedless tissue + 2,4-D + GA_3 + ABA	Seeded tissue GA_3 + BAP
8				Seedless tissue + 2,4-D + GA_3 + ABA + BAP	Seedless tissue
9					Seedless tissue + 2,4-D
10					Seedless tissue + GA_3
11					Seedless tissue + BAP
12					Seedless tissue + 2,4-D + GA_3
13					Seedless tissue 2,4-D + BAP
14					Seedless tissue + GA_3 + BAP

*Established in February 1990 at 100 days after full bloom (expt. 2).

**Established in March 1990 at 124 (expt. 4) and 126 (expt. 3) days after full bloom.

***Established in March 1991 at 90 (expt. 1) and 95 (expt. 5) days after full bloom.

Table 5 - 2 ANOVA for fresh weight (g) of 'Hayward' kiwifruit inner pericarp cultured *in vitro*. Least square means and one contrast are included. Fruit collected 90 days after full bloom in March 1991.

Source of Variation	df	F Value	Pr > F
Blocks	3	4.4	*
Plant Growth Regulators (PGRs)	1	202.4	***
Seeds (seeded and seedless tissues)	1	27.8	**
PGRs*Seeds	1	18.5	**
Error	54		

Callus Fresh Weight

Treatments	Seeds Present	Seeds Absent
No PGRs	0.519	0.439
2,4-D + GA_3 + BAP	1.868	1.170

Contrast	Pr. > F
Seeded tissue + 2,4-D + GA_3 + BAP vs Seedless tissue + 2,4-D + GA_3 + BAP	***

*, **, ***Significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

regulator mixture with seeds gave the greatest stimulation of callus growth (Table 5 - 2).

Experiment 2.

A significant interaction between seeds and PGRs on callus fresh weight was found in February 1990 (Table 5 - 3). No visible callus formation was produced by the tissues cultured *in vitro* in the absence of both 2,4-D + GA_3 even in the presence of seeds (Table 5 - 3). ABA at 10 μM alone in the media produced signs of phytotoxicity after two weeks; the tissue turned a pallid green colour, later changing to a dark grey, and produced the lowest final fresh weight. Incorporating GA_3 + 2,4-D in the medium overcame the inhibitory effect of ABA. The presence of seeds together with 2,4-D + GA_3 provided the greatest stimulation of callus growth (Table 5 - 3).

Experiment 3.

Similarly, in fruit harvested in March, significant differences in callus growth were found (Table 5 - 4). The inhibitory effect of ABA (1 μM) was overcome by the inclusion of 2,4-D + GA_3, and ameliorated further by adding BAP to the medium. This treatment produced the greatest stimulation of callus growth (Table 5 - 4). No visible callus growth occurred in the explants cultured without added PGRs (Table 5 - 4).

Table 5 - 3 ANOVA for fresh weight (g) of 'Hayward' kiwifruit inner pericarp cultured *in vitro*. Least square means and three contrast are included. Fruit collected 100 days after full bloom in February 1990.

Source of Variation	df	F Value	Pr > F
Blocks	2	3.2	*
Plant Growth Regulators (PGRs)	2	48.0	***
Seeds (seeded and seedless tissue)	1	1.0	NS
PGRs*Seeds	2	5.2	**
Error	65		

Mean Callus Fresh Weight		
Treatments	Seeds Present	Seeds Absent
No PGRs	0.441	0.543
ABA[1]	0.387	0.408
2,4-D + GA_3 + ABA[1]	1.785	1.228

Contrast	Pr > F
Seeded tissue + 2,4-D + GA_3 + ABA vs Seedless tissue + 2,4-D + GA_3 + ABA	***
Seeded tissue vs Seedless tissue	NS
Seeded tissue + ABA vs Seedless tissue + ABA	NS

[1]Concentration in the media of 10 μM for ABA alone, or in combination with the hormones.

NS,*,**,***Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 5 - 4 ANOVA for fresh weight (g) of 'Hayward' kiwifruit inner pericarp in the presence of seeds cultured *in vitro*. Means and two contrasts are included. Fruit collected 126 days after full bloom in March 1990.

Source of Variation	df	F Value	Pr > F
Blocks	2	2.2	NS
Plant Growth Regulators (PGRs)	3	29.4	*
Error	45		

Callus Fresh Weight

Treatments	Callus Fresh Weight
No PGRs	0.600
ABA[1]	0.355
2,4-D + GA_3 + ABA[1]	1.135
2,4-D + GA_3 + ABA[1] + BAP	1.518

Contrast	Pr > F
ABA vs 2,4-D + GA_3 + ABA	*
2,4-D + GA_3 + ABA vs 2,4-D + GA_3 + ABA + BAP	*

[1]Concentration in the media of 1 μM for ABA alone, or in combination with the hormones.

NS, *Non-significant or significant at $P \leq 0.01$, respectively.

Experiment 4.

There was a significant increase in callus growth in the presence of growth regulator mixture and seeds, and a significant interaction between them (Table 5 - 5). No visible callus growth was produced by the seedless inner pericarp cultured in the absence of 2,4-D + GA_3 + BAP in the media. ABA (10 μM) alone resulted in signs of phytotoxicity. The inclusion of 2,4-D + GA_3 in the media, especially in the presence of BAP, overcame the inhibitory effect of ABA. The presence of the seeds together with the hormone mixes gave the greatest stimulation of callus growth. (Table 5 - 5).

Experiment 5.

Significant independent effects on final callus fresh weight for the PGRs and the seeds were found in tissues cultured in the next season (Table 5 - 6). 2,4-D alone across the seeded and seedless tissue promoted the highest callus fresh weight, and was significantly different from the other treatments. The callus fresh weight of seeded tissue growing on media with 2,4-D, and 2,4-D + GA_3 were significantly higher than for the corresponding seedless treatments, as was shown by orthogonal comparisons (Table 5 - 6). Least square means of the treatments are shown in Table 5 - 7. GA_3 significantly increased the growth of a distinct bright green callus after three weeks in culture. No callus growth was recorded for BAP alone, and the tissues changed from a pale green to white suggesting possible phytotoxicity. The addition of 2,4-D to the medium in the presence of GA_3 or BAP significantly promoted callus growth. In contrast, no callus growth was recorded for tissue cultured on media supplemented with GA_3 + BAP (Table 5 - 6). Seeds significantly

Table 5 - 5 ANOVA for fresh weight (g) of 'Hayward' kiwifruit inner pericarp cultured *in vitro*. Least square means and contrast are also included. Fruit collected 124 days after full bloom in March 1990.

Source of Variation	df	F Value	Pr > F
Blocks	2	1.8	NS
Plant Growth Regulators (PGRs)	3	65.9	*
Seeds (seeded and seedless tissues)	1	19.2	*
PGRs*Seeds	3	6.3	*
Error	92		

Callus Fresh Weight

Treatments	Seeds Present	Seeds Absent
No PGRs	0.791	0.774
ABA[1]	0.526	0.460
2,4-D + GA_3 + ABA[1]	1.352	0.712
2,4-D + GA_3 + ABA[1] + BAP	1.848	1.468

Contrast	Pr > F
Seeded tissue + 2,4-D + GA_3 + ABA vs Seedless tissue + 2,4-D + GA_3 + ABA	*
Seeded tissue + 2,4-D + GA_3 + ABA + BAP vs Seedless tissue + 2,4-D + GA_3 + ABA + BAP	*

[1]Concentration in the media of 10 μM for ABA alone, or in combination with the hormones.

NS, *Non-significant or significant at $P \leq 0.01$, respectively.

Table 5 - 6 ANOVA for fresh weight (g) of 'Hayward' kiwifruit inner pericarp cultured *in vitro*. Means and four contrasts are included. Fruit collected 95 days after full bloom in March 1991.

Source of Variation	df	F Value	Pr > F
Blocks	2	5.8	**
Plant Growth Regulators (PGRs)	6	137.6	**
Seeds (seeded and no seeded tissues)	1	4.0	*
PGRs*Seeds	6	1.4	NS
Error	153		

PGRs across seeds	Callus Fresh Weight
No PGRs	0.469
2,4-D	2.824
GA_3	1.394
BAP	0.542
2,4-D + GA_3	1.948
2,4-D + BAP	1.623
GA_3 + BAP	0.635
Seeds across PGRs	
Absent	1.286
Present	1.409

Contrast	Pr > F
2,4-D vs Others	**
GA_3 vs GA_3 + 2,4-D	**
BAP vs BAP + 2,4-D	**
Seeded tissue + 2,4-D vs Seedless tissue + 2,4-D	*
Seeded tissue + 2,4-D + GA_3 vs Seedless tissue + 2,4-D + GA_3	*
BAP + GA_3 vs No PGRs	NS

NS, *, **Non-significant or significant at $P \leq 0.05$ or 0.01, respectively.

Table 5 - 7. Least square means (± standard error of the least square means) of 'Hayward' inner pericarp cultured *in vitro*. Fruit collected 95 days after full bloom in March 1991.

Treatment	Seed present	Seed absent
No Plant Growth Regulators	0.497 (0.146)	0.436 (0.125)
2,4-D	2.990 (0.089)	2.658 (0.090)
GA_3	1.397 (0.146)	1.391 (0.118)
BAP	0.560 (0.118)	0.523 (0.112)
2,4-D + GA_3	2.154 (0.102)	1.742 (0.112)
2,4-D + BAP	1.661 (0.103)	1.586 (0.111)
GA_3 + BAP	0.604 (0.099)	0.666 (0.119)

increased final fresh callus weight in the plant growth regulator treatments (Table 5 -6).

5. Discussion.

Inner pericarp tissue from fruit in later stages of development (90-124 days after full bloom) had no visible callus growth *in vitro* in the absence of exogenous PGRs even when the seeds were present. A significant interaction between seeds and growth regulators on callus growth was found (Tables 5 - 2, 5 - 3, 5 - 5). The response to a hormone mixture was enhanced significantly in the presence of seeds (Tables 5 - 2, 5 - 3, 5 - 5). Thus, in addition to the PGR mixture, some unknown seed factor(s) released by the seeds, or by the seeded inner pericarp tissue may have contributed in the stimulation of callus growth *in vitro*. Hopping (1976 b) and Trustrum (1983) using *in vivo*, and *in vitro* experiments, respectively, concluded that unknown factor(s) released by the seeds could be responsible for stimulating the growth and development of kiwifruit. The lack of callus growth response of the tissues *in vitro* in the absence of PGRs may also suggest that the isolation of the tissues from other parts of the vine limited the interaction of natural growth regulators with unknown substances produced from the seed or seedless tissue. This view is supported by findings of Woolley *et al.* (1991) and the results in chapter 4 showing additive effects between fruit seed number and exogenous PGRs on final fresh weight of 'Hayward' fruit. Therefore, hormones synthesized in fruit tissue and/or transported to the fruit from other parts of the vine may act together with seed and/or seeded tissue produced factors to

maximize fruit growth. Fruit tissue is capable of producing hormones (Nitsch, 1970; Browning, 1989) but the root system may also be a major supplier of hormones influencing fruit size (Niimi and Torikata, 1978; Stevens and Westwood, 1984; Cutting and Lyne, 1993). The leaves may also supply the fruit with hormones (Erner, 1989).

This work confirms effects found by Trustrum (1983) related to *in vitro* interactions between seeds and PGRs on inner pericarp callus growth of explants containing fully-sized seeds (fruit harvested in later stages of development). In our investigation and in Trustrum's (1983) work, the callus growth involved cell division which would actually represent de-differentiated tissue more representative of young fruit in cell division phase than the older fruit from which it was derived. However, it would seem that even old seeds attached to the inner pericarp tissue can still provide a factor (s) that stimulates cell activity in fruit tissue. Although seeds end their growth about 80 days from anthesis the embryo continues growing until about 120 days from anthesis (Hopping, 1976 a). Thus, seeds may provide a factor (s) released from the embryo which would interact with PGRs in the fruit tissue for the production of callus growth. No experiments were attempted on the effect of PGRs on kiwifruit inner pericarp cultured *in vitro* from fruit in early development due to the difficulty in the experimental management of removing the small seeds from that fruit tissue. Experiments using kiwifruit at the growth stage of cell division would be of interest because seeds often play a major role in fruit growth during early fruit development (Dennis, 1986; Cutting *et al.*, 1986; Gucci *et al.*, 1991).

Although independent comparisons indicated seeded tissue cultured on a medium with 2,4-D, and 2,4-D + GA_3 had a significantly higher growth rate than seedless tissue in a PGR media, the non-significant interaction between seeds and PGRs in the last experiment (Table 5 - 6) revealed the complexity of the system under study. The 2,4-D treatment irrespective of the presence or absence of seeds achieved the highest callus fresh weight (Table 5 - 6) suggesting auxin may be the most required PGR for callus growth in this experiment. This study corroborates work on Satsuma mandarin, when 2,4,5-T, and GA_3 alone promoted endocarp growth *in vitro* (Guardiola *et al.*, 1992). Similarly, using tuber explants of *Helianthus tuberosus*, 2,4-D induced rapid cell proliferation on a simple medium of mineral salts, and sucrose (Aitchinson *et al.*, 1977). According to Rashid (1988), generally auxin is an essential requirement for cell multiplication; whereas a cytokinin is beneficial, but not essential. However, for some tissues, such as tobacco pith, inclusion of a cytokinin is especially beneficial (Hansen *et al.*, 1987). Okuse and Ryugo (1981) shown kiwifruit was a rich source of cytokinins during most of its growth. Therefore, it may be hypothesised that 2,4-D or GA_3 alone are only indirectly regulating the formation of callus, whereas a complex interaction between the external supply of auxin, gibberellin, and the endogenous level of cytokinin is playing an important role in cell division of *in vitro* cultured kiwifruit inner pericarp and probably in fruit growth.

Unlike 2,4-D, GA_3 actively promoted chlorophyll formation in callus. Exogenous gibberellins have also induced regreening in the peel of citrus (Goldschmidt, 1976). Gibberellins may be associated with delaying the onset of chloroplast senescence in kiwifruit. With

regard to BAP, callus did not grow on media with this PGR alone, or mixed with GA_3 (Table 5 - 6). Explants growing on media containing BAP showed signs of chlorophyll degradation and possible phytotoxicity, although the BAP concentration (20 μM) was similar to that active in other bioassays (Matsubara, 1990). The level of cytokinin related inhibition of chlorophyll in senescence may be a specific response of kiwifruit. However, BAP together with 2,4-D induced callus growth with no evidence of phytotoxicity. This suggests 2,4-D influenced uptake and /or metabolism of BAP, as noted by Zhang *et al.* (1987) when 2,4-D inhibited BAP metabolism in soybean leaves. Indole-3-acetic acid modified BAP metabolism in *Solanum andigena* stem cuttings (Woolley and Wareing, 1972). Furthermore, the stability of zeatin riboside supplied to excised tobacco pith explants was inversely related to NAA concentration in an incubation medium (Palni *et al*, 1988). Interactions between PGRs, such as cytokinin and auxin are important in determining plant tissue growth and development. Complex growth regulator effects were also found with BAP in the PGR mixture which significantly reduced the inhibitory callus growth influence of ABA (Table 5 - 3).

Both ABA concentrations (1 or 10 μM) examined (Tables 5 - 3, 5 - 4, 5 - 5) inhibited callus formation in the absence of other growth regulators. 2,4-D + GA_3, especially in presence of seeds significantly reduced the inhibitory effect of ABA on callus growth (Table 5 - 3). The addition of BAP to the hormone mixture in the presence of seeds significantly enhanced this effect (Tables 5 - 4, 5 - 5). Cytokinins have antagonistic effects with ABA with respect to metabolic events in plants (Chaloupková and Smart, 1994). For example, Cowan and Railton (1987) showed that several cytokinins inhibited ABA biosynthesis in *Persea gratissima* mesocarp. Although

little is known about the endogenous effects of ABA in fruit sizing (Weaver, 1972; Beruter, 1983; Klages and Smith, 1993), it is possible to speculate that cytokinins limit the inhibitory activity of ABA permitting changes in metabolism that influence fruit growth.

Using a typical *in vitro* tissue culture assay, this study demonstrated the interaction between seed factor(s), and growth regulators using fruit tissue from later stages of fruit development but which nevertheless retained the capability to divide and form callus tissue. Unknown factors released by the seeds or by the seeded inner pericarp acted with a range of known PGRs in promoting growth (Tables 5 - 2, 5 - 3, 5 - 5). The inhibitory effect of ABA was overcome with the inclusion of seeds + 2,4-D + GA_3 in the medium (Tables 5 - 2, 5 - 3). The inclusion of BAP in the medium enhanced this effect (Table 5 - 4). The observation that 2,4-D and GA_3 were both effective in promoting callus growth (Table 5 - 6) may indicate that auxins and gibberellins may influence kiwifruit growth and development. Although the field application of CPPU + 2,4-D + GA_3 to the fruit is effective in increasing fruit weight (Chapter 4), field applications of 2,4,5-T and GA_3 individually and as a mixture did not significantly increase kiwifruit size (Hopping, 1976 b) suggesting environmental and physiological interactions more complex *in vivo* than *in vitro*. Field application of growth regulators may not be promoting kiwifruit growth because endogenous supply from the vine to the fruit may be adequate. Studies concerning fruit uptake and translocation of 2,4-D and GA_3 in kiwifruit were not found in the literature.

The relationship between seed number and kiwifruit size is not well understood (Woolley *et al.*, 1988; Lawes, Woolley and Lai, 1990). Comparatively large fruit are occasionally found with very low seed number (Pyke and Alspach, 1986; Woolley *et al.*, 1988). This suggests that low seed number may only limit fruit development severely when high competition between fruit exists. Vine conditions such as fruit number per unit of vine cane length may influence the response of kiwifruit to seeds. Future experimentation *in vitro* may consider using fruit from vines under different conditions of inter-fruit competition to identify any relationship of crop load with seed effects in the growth of kiwifruit.

The PGRs used in this investigation are not registered to be used in the commercial production of kiwifruit. This study may be useful for researchers investigating manipulation of endogenous and exogenous PGRs in kiwifruit sizing, or investigating further the unknown seed factor (s).

CHAPTER 6.

EFFECTS OF PARTIAL DEFOLIATION ON FRUIT SIZE, RETURN BLOOM, AND CARBOHYDRATE CONTENT OF 'HAYWARD' KIWIFRUIT VINES.

1. Introduction

The accumulation and storage of reserves during a growing season may be an important determinant of kiwifruit vine growth the following season. Starch is the main storage reserve, and factors affecting leaf area, such as defoliation, directly influence the ability of the vine to produce and built up food reserves (Davison, 1990). Smith, Clark, and Boldingh (1992), studied the accumulation of starch for various components of kiwifruit vines. They found peak concentrations in leaves and shoots at fruit set and fruit harvest, and pointed out the importance of this carbohydrate in the growth of kiwifruit vines.

Studies on photoassimilates and carbohydrate reserves in kiwifruit vines by decreasing source (leaf) to sink (fruit) ratios can provide information on demand and allocation within the vine. This data may assist in planning management practices (Cooper and Marshall, 1989), and contribute to an overall understanding of the nature of specific physiological events in fruit trees. For example, the strength of the various carbon sinks within fruit trees can be assessed from the results of defoliation studies (Buttrose, 1966;

Brundell, 1975; Buwalda and Smith, 1990; Tombesi *et al.*, 1993). Buwalda and Smith (1990), and Tombesi *et al.* (1993) described the effects of partial defoliation at various stages of the growing season on fruit yield, root growth, and return bloom for kiwifruit. However, little is known about the carbohydrate costs to the different organs when a reduced leaf fruit:ratio is established. For example, a) there is no information regarding the effect of a reduced leaf:fruit ratio on the carbohydrate reserves in the trunk and roots; and b) it is unknown what level of vine leafiness in the 'replacement cane zone' (the 1.5 m wide horizontal area between the trellis support wires) is required to maintain fruit growth. Therefore, the purpose of this study was to evaluate the effects of a partial defoliation on fruit yield, vegetative growth, reproductive development, changes in the seasonal content of starch, reducing sugars (glucose, and fructose), and sucrose in several parts of kiwifruit vines.

2. Literature Review.

Carbohydrates formed by photosynthesis are used in many ways in the kiwifruit vine. They form the organic constituents of cell walls produced in new growth, are consumed in the respiratory energy-releasing process and are primary chemicals for the formation of fats and proteins. Carbohydrates not used in these processes accumulate as reserves within the vine. Storage carbohydrates are continually being transformed and recycled within the plant (Davison, 1990). The kiwifruit vine is a woody vine which, because of its physical bulk, can have considerable regions of the stems and roots

available as sites for storage of reserves. These reserves must sustain the vine during winter, and provide for the intense growth activity in the spring which occurs before any contribution of carbohydrate can be made from the current photosynthetic activity of new leaves. Thus the extent of accumulation and storage of reserves during a growing season may be an important determinant of kiwifruit vine growth the following season. Starch is the main storage reserve, and factors affecting leaf area such as defoliation, directly influence the ability of the vine to produce and built up food reserves (Davison, 1990).

The relative strengths of the various carbon sinks within the vine appear to be related to the respective relative growth rates of the component organs. Buwalda and Hutton (1988) showed that, during the growing season, there is a clear progression in peak relative growth rates, from shoots immediately after bud burst, to fruit immediately after flowering, and finally roots during late summer. The growth analysis of Buwalda and Hutton (1988) suggested that carbon partitioning would be strongly in favour of the shoots in early spring, the fruit in late spring and early summer, and the roots only in late summer.

The strength of the various carbon sinks within fruit trees can be assessed from the results of defoliation studies. Buwalda and Smith (1990) described the effects of partial defoliation at various stages of the growing season on fruit yield, root growth, and return bloom for kiwifruit. They made an arbitrary distinction between shoots arising from the 'replacement zone' , the 1.5 m wide horizontal area between the trellis support wires, and shoots arising

from the 'fruiting zone', the remaining area of the vines. On the normally pruned vines, the total fruit yield in the first season was 3.8 Kg m^{-2}, with an overall leaf to fruit ratio of 4.8:1. The replacement cane zone included 60 % of the total leaf area but only 30 % of the fruit yield. The average fruit weight was about 8 % lower within the replacement zone than within the fruiting zone. Spring defoliation of all shoots within the fruiting zone reduced fruit numbers and average fruit weights in that zone, decreasing fruit yield there by up to 44 %, but had no effect on fruit yields elsewhere in the vine. This treatment had very little effect on root growth. Defoliation within the replacement cane zone had no effect on fruit numbers but reduced average fruit weight by up to 45 % in the replacement and by 15 % in the fruiting zone. The effect of this treatment on root growth was greater than that on fruit yields, while flowering in the following season was significantly reduced except where this defoliation was imposed very late in the growing season. Buwalda and Smith (1990) concluded that: a). The effects of the treatments on the growth of various component organs of the kiwifruit vine were consistent with a ranking of competitive strengths of the assimilate sinks as (in descending order), shoots, fruit, roots, return bloom. b). The overall sensitivity of the vines to partial defoliation suggested that kiwifruit production was limited by a tight carbohydrate budget.

3. Materials and Methods.

In the 1988/89 season the effects on fruit yield, return bloom, and the carbohydrate content of 'Hayward' kiwifruit topworked on 'Bruno' seedlings after a partial defoliation were determined. The eight year old vines were trained on a pergola trellis on a commercial orchard in Levin. An arbitrary distinction was made between shoots arising from the 'replacement cane zone' (RCZ), the horizontal area 0.5 m on other side of the vine leader, and the fruiting zone (FZ), comprising all growth arising outside the above area (Buwalda and Smith, 1990). The treatments imposed on nine vines arranged in three blocks were 0, 50, and 75 % defoliation of all the shoots within the RCZ. In the FZ a leaf to fruit ratio of 2:1 was established on all vines. Treatments were applied 5 days after full bloom in 1988. In sweet corn a defoliation at full bloom has a larger effect on grain size than defoliation later in the season (Mack, 1965). The defoliated shoots were maintained through the whole growing season by removing any shoot regrowth as it appeared. All vines were pruned in summer without affecting the treatments, and in the following winter according to standard commercial practice. A crop load of 550 fruit per vine was established.

Fruit from each of the two zones of each vine were harvested at commercial maturity (6.2 % soluble solids) in 1989, and fruit number and final fruit fresh weights recorded. Fruit seed number and seed dry weights were determined for 20 fruit randomly selected from each of the two vine zones of the three vines receiving the 0 and 75 % defoliation treatments. From a total of 80 fruits the seeds were extracted by soaking fruit slices in a solution of 1 %

ammonium oxalate for 3-5 days. The seeds were separated from the pulp with an electric juice extractor and repeated washing in a sieve under running tap water, and dried at room temperature. The total seed number and mean seed dry weight for each fruit were calculated from a sample of 150 seeds for each fruit.

In October 1989 percentage budburst, number of flowers per shoot, percentage floral budburst, and percentage of flowers with a compound dichasium ('triples') were recorded for each vine on five non-terminating one year old canes situated randomly on each side of the vine.

At five harvest dates from December 1988 to October 1989 (13-December-88; 18-January-89; 8-March-89; 6-July-89; and 24-October-89) fructose, glucose, sucrose and starch content of shoots, and stem bark was determined. Only starch was evaluated in the roots. Non-defoliated vines, and vines 75 % defoliated were sampled. Two or four replications per vine were analyzed on each date. Current season root samples per vine were collected at 20 cm below the surface, and at 50 cm from the trunk. At each sampling two shoots per vine were taken from current season non-terminating canes in the RCZ. Two bark tissue discs 1 cm diameter per vine were taken on the main trunk at 1.30 m above the ground. Samples were immediately frozen in a chilly bin of dry ice. The tissues were later freeze dried, ground, and stored at -16 °C.

Carbohydrates were extracted by a modification of the method of Haslemore and Roughan (1976). Glucose, fructose, and

sucrose were extracted from tissue samples in 80 % ethanol at 55 °C for 45 minutes. Samples were centrifuged, the supernatant reduced to aqueous phase and Polyclar (0.3 to 1 g) added. Extracts were centrifuged, and the supernatant partitioned with chloroform. The aqueous phase was filtered and 5 μl of sample was analyzed by HPLC using an Optilab 5922 refractive index detector. The column was a Bio-Rad 300 mm x 4.7 mm Aminex, HPX-87C column, and sugar eluted with water at 85 °C and a flow rate of 0.6 ml/min.

After mono- and disaccharide extraction starch was analyzed in the residues by gelling in boiling water and followed by hydrolysis by amyloglucosidase. The glucose released was determined colorimetrically using glucose oxidase and o-dianisidine hydrochloride and compared with glucose standards and starch controls.

4. Results

Effect of partial vine defoliation on fruit yield, seed number and fruit weight.

No fruit drop was caused by defoliation and at harvest all vines had similar fruit number. Non-significant differences in mean fruit sizes were found between the fruiting and replacement cane zones on the control vines (Table 6 - 1). Each level of defoliation of the RCZ significantly reduced mean fruit size in both canopy zones. The vines with 75 % defoliation in the RCZ had a significant reduction in mean fruit size of 13 and 7 g in the RCZ and in the FZ, respectively, compared with the control vines (Table 6 - 1). A 50 %

Table 6 - 1 Yield performance in the replacement cane zone (RCZ) and fruiting zone (FZ) of vines after different levels of defoliation in the RCZ in the 1988-89 season (harvested in June 1989).

% Defoliation	Canopy Zone	Fruit Number	Mean Fruit Weight (g)	Fruit Seed Number	Fruit Seed Dry Weight (g)
0	RCZ	263.0 a	121.1 a	1261.0 a	1.694 a
	FZ	276.0 a	118.9 a	1327.0 a	1.787 a
50	RCZ	267.0 a	112.1 c	-	-
	FZ	279.0 a	115.6 b	-	-
75	RCZ	232.0 a	108.1 d	1287.0 a	1.728 a
	FZ	313.0 a	112.3 c	1336.0 a	1.718 a

Means with the same subscript in each column are not significantly different, by Duncan's multiple range test, 5 % level.

Data for seed number and weight, only for 0 and 75 % defoliation in the RCZ, and their respective FZs.

defoliation of the RCZ resulted in a smaller, but still significant ($P \leq 0.05$) reduction (Table 6 - 1). After partial (50 or 75 %) defoliation of the RCZ the reduction in fruit size was significantly greater in that zone than in the FZ (Table 6 - 1). Fruit seed number and seed weight were not significantly different between treatments or canopy zones (Table 6 - 1).

Seasonal changes of glucose, fructose, sucrose, and starch in shoots, bark, and roots.

The concentration of glucose, and fructose in the current season shoots was significantly ($P \leq 0.05$) higher in December (when the treatments were established) than at other dates sampled, according to orthogonal contrast (not shown). Those carbohydrate concentrations declined to similarly low values from January to July (Tables 6 - 2, 6 - 3). In the stem bark, the concentration of glucose was significantly higher ($P \leq 0.05$) in July, and low in March in comparison to the concentrations determined at other dates (orthogonal contrast not shown in tables 6 - 2, 6 - 3). Shoot and bark sucrose were not significantly influenced at any time by the defoliation (Table 6 - 4). Shoot sucrose concentration was highest in July, and lowest in March with less variation in the bark samples (Table 6 - 4). The defoliation treatment significantly reduced the starch content of the shoots in March, and of the bark in January, and March. The treatments did not significantly alter the root starch content over the five dates sampled (Table 6 - 5). For the shoots on the control vines, starch was high in March and July, and low in December (Table 6 - 5). In the stem bark, high starch concentrations

Table 6 - 2 Concentration of glucose (mg/g dry weight) in shoots from current season canes in the replacement cane zone, and stem bark of vines partially defoliated in the replacement cane zone in December 1988.

Month	% Defoliation	Shoot	Bark
December	0	16.6	5.9
	75	16.1	6.3
January	0	8.2	5.5
	75	6.4	5.3
March	0	7.2	4.6
	75	5.0	4.1
July	0	6.3	8.9
	75	7.5*	7.8

*Significant differences per month between treatments in each individual part of the vine, by a t-test, 5 % level.

Table 6 - 3 Concentration of fructose (mg/g dry weight) in shoots from current season canes in the replacement cane zone, and stem bark of vines partially defoliated in the replacement cane zone in December 1988.

Month	% Defoliation	Shoot	Bark
December	0	13.0	8.4
	75	13.7	10.8*
January	0	9.6	7.6
	75	8.3	6.2
March	0	8.8	5.9
	75	6.5	5.4
July	0	5.8	8.5
	75	7.0*	7.1

*Significant differences per month between treatments in each individual part of the vine by t-test, 5 % level.

Table 6 - 4 Concentration of sucrose (mg/g dry weight) in shoots from current season canes in the replacement cane zone, and stem bark of vines partially defoliated in the replacement cane zone. Defoliation in December 1988.

Month	% Defoliation	Shoot	Bark
December	0	20.5	34.7
	75	17.6	33.9
January	0	21.3	30.6
	75	21.4	35.3
March	0	16.8	34.8
	75	14.7	31.1
July	0	41.4	34.1
	75	43.3	25.8

Non-significant differences per month between treatments in each individual part of the vine by t-test.

were high in January, and March, and lowest in December. The roots showed a clear increase in starch in October (Table 6 -5).

Effect of partial vine defoliation on vegetative and bloom return.

The vegetative and return bloom characteristics of percentage budburst, number of flowers per shoot, percentage floral budburst, and percentage flowers with 'triples' were significantly reduced by defoliation. The 75 % defoliation had the greatest effect on all four parameters (Table 6 - 6). Vines with 50 % defoliation showed a significant reduction in the number of flowers per shoot, and the percentage of flowers with 'triples' (Table 6 - 6).

5. Discussion

On the current season shoots of the control vines, high glucose and fructose, and low starch were observed in December when the shoots were at full bloom (Tables 6 - 2, 6 - 3, 6 - 5) and floral evocation may occur (Snowball and Walton, 1992). Glucose, and fructose in the stem bark, and sucrose in the shoots were high in winter (Tables 6 - 2, 6 - 3, 6 - 4). This may indicate a possible role of those carbohydrates in preventing frost damage at certain low temperatures. Similar speculations about that function have been reported in apple (Yoshioka *et al.*, 1988), and pecan (Wood, 1986). An accumulation of starch in the roots was noticed in October (Table 6 - 5) when the period of root growth commences (Davison, 1990). Smith *et al.* (1992 a), subsequently showed that the maximum starch

Table 6 - 5 Concentration of starch (mg/g dry weight) in shoots from current season canes in the replacement cane zone, stem bark, and roots of vines partially defoliated in the replacement cane zone. Defoliation in December 1987.

Month	% Defoliation	Shoot	Bark	Root
December	0	5.2	7.5	4.2
	75	5.0	4.8	3.7
January	0	11.1	15.3**	4.8
	75	9.3	4.7	3.3
March	0	22.8**	21.5*	4.2
	75	14.8	16.5	4.1
July	0	23.0	8.2	5.8
	75	21.3	8.0	5.7
October	0	13.5	9.0	15.1
	75	12.7	6.0	13.3

Significance per month between treatments in each individual part of the vine determined by t-test, 5 (*) and 1 % (**) levels.

Table 6 - 6 Return bloom in 1989 of vines partially defoliated in the replacement cane zone in December 1988.

% Defoliation	% Budburst	Number of flowers per shoot	% Floral budburst	% Flowers with 'triples'
0	59.3 a	4.9 a	100.0 a	34.6 a
50	52.6 ab	4.2 b	97.9 a	22.7 b
75	49.4 b	3.3 c	84.2 b	9.8 c

Means with the same subscript in each column are not significantly different, by Duncan's multiple range test, 5 % level.

content in perennial and annual tissues of kiwifruit vines occurred between fruit harvest and bud break. In this work, a comparable starch concentration trend was observed in shoots analysed in July and October (Table 6 - 5).

On non-defoliated vines the mean fruit size recorded in the RCZ was statistically similar to the fruit size of the FZ (Table 6 - 1). Buwalda and Smith (1990) found that the mean fruit size from the RCZ was larger (by 8 g) than within the FZ, on non-defoliated vines. In their experiment 70 % of the total fruit number was localized within the FZ. In this work a similar crop load was imposed on each zone of the vines. Although the leaf:fruit ratio in the RCZ was not recorded, it was probably much greater than in the FZ. The severe partial defoliation of 75 % of the RCZ caused a significant reduction of 13, and 7 g in fruit with similar seed number and seed weight in the RCZ and FZ respectively (Table 6 - 1). The defoliation had a greater effect on mean fruit weight in the RCZs than in the FZs. This vine zone effect was also recorded by Buwalda and Smith (1990) who defoliated all the shoots within the RCZ, and obtained a mean fruit size reduction of 43 % there. In several plants like tomato (Tanaka and Fujita, 1974), strawberry (Kerkhoff *et al.*, 1988), and grape (Hofäcker, 1978; Kliewer, 1982) when source-sink ratios of whole plants are lowered experimentally, the net photosynthesis of the remaining leaves increases. In cucumber an increase in the level of defoliation caused an increase in accumulation of dry weight in the remaining leaves, and a decrease in the dry weight of the fruit (Ramirez *et al.*, 1988). Therefore, the inhibitory effect of defoliation on kiwifruit growth may impose a self regulatory mechanism by

decreasing the demand for photoassimilates from the fruit (sink). This speculation is supported by a study of Lai (1987) where a transitory decline in leaf dry weight coincided with the period of rapid kiwifruit growth. Thus, for normal kiwifruit development a large leaf:fruit ratio is a major determinant of fruit size.

Snelgar *et al* (1986) presented results that implied that only the overall ratio of fruit to leaves, rather than the proximity of individual fruit and leaves affect fruit size in kiwifruit. Those results are supported by the similar mean fruit size values found on our control vines in spite of a possible difference in leaf:fruit ratio between vine zones. Studies by Lai *et al.* (1989) demonstrated that fruit size in the kiwifruit vine was not affected by different leaf:fruit ratios within the fruiting lateral, even with complete defoliation. This was explained by the ease with which carbohydrates were imported from other parts of the vine. Our results on a whole vine basis, indicate that under a severe partial defoliation carried out in the RCZ at full bloom and maintained until commercial fruit harvest, the leaves close to the fruit had priority in supporting their 'own' fruit, and there was no carbohydrate surplus to export to the fruiting zone.

Partial defoliation had no significant effect on glucose, fructose, and sucrose in the shoots, bark, and roots or on root-starch content at any sampling date (Tables 6 - 2, 6 - 3, 6 - 4, 6 - 5). Kozlowski and Keller (1966) pointed out that carbohydrate depletion begins nearest the site of utilization. Thus, the shoot starch was significantly reduced by 16 % in March; and the stem bark showed significant starch reductions of 69 and 23 % in January and March, respectively. These depletions may indicate that the shoots and the

bark have a role in keeping the supply and demand balance in carbohydrates by degradation of the starch in the cells when a severe partial defoliation occurs. Thus, the starch depletion in those tissues, and the reduction in final fruit size may suggest that the vine carbohydrates synthesis is not enough to support large fruit sizing and maximum storage in the vine framework after a severe partial defoliation. In grapevine (Marangoni *et al.*, 1980) and pecan (Worley, 1979) a reduction in starch by a defoliation was also observed in the framework of these fruit trees. The effect of a reduction in vine carbohydrate reserves in relation to fruit sizing is supported by the results of Snelgar and Hopkirk (1988) who showed that individual kiwifruit on heavily shaded vines weighed, on average, 14 g less than fruit on unshaded vines. However, it is not clear what is the specific relationship between a depletion of starch in bark and shoots, and kiwifruit growth. Although the role of other carbohydrates cannot be discounted, for example sugar alcohols (sorbitol or mannitol) or other soluble carbohydrates (inositol or xylose), it is likely that other factors affected by the defoliation may also influence fruit size, for example, concentrations of nutrients, plant growth regulators, aminoacids, and polyamines in the fruit.

While not contributing to biomass gain, partitioning of root-assimilate mineral ions influence crop productivity (Patrick, 1988). For example, potassium governs photoassimilate partitioning controlling membrane transport (Geiger and Fondy, 1980), or cell expansion can be limited by low concentration of nitrogen compounds in the cell wall (Boyer, 1988). Much of the nitrogen and potassium transported in the phloem is able to be supplied from

leaves on kiwifruit laterals, where significant remobilization commences about 8 weeks after pollination (Clark and Smith, 1988). Kiwifruit size from nitrogen-deficient vines may be reduced (Smith, Asher, and Clark, 1987), and small fruit number per vine may be related to potassium deficient vines (Smith, Clark, and Buwalda, 1987). Thus, the partial defoliation could affect negatively the normal active leaf transport of minerals to the fruit, or indirectly by limiting the mineral supply by a reduction in vine transpiration (Boyer, 1988).

Bohner and Bangerth (1988) found that defoliation carried out two days after pollination reduced cell division and cytokinin levels in tomato fruit, resulting in a high loss in final fruit fresh weight. Lee *et al* (1989) showed that the final grain size of wheat was severely reduced when detached ears were cultured in the absence of sucrose, and an increase in ABA concentration was observed on those grains. They pointed out that there is a possible negative relationship between ABA concentration and grain size. Kiwifruit growth and final size depend on the number of cells present at fruit set, the number of cell divisions that occur subsequently and the extent to which these cells expand. Cell division and expansion is under hormonal control and early growth is normally influenced by a triple interaction between the three major groups of natural growth promoters, auxins, gibberellins and cytokinins (Woolley *et al.*, 1992). Kato and Lou (1989) reported that roots are a source of cytokinins, gibberellins, and auxin synthesis, and that these hormones move upward by the process of transpiration. Since the leaves are the most important organs for transpiration and ascent of sap (Lakso *et al.*, 1989), their removal probably reduces hormonal transport from

the roots to other plant organs, including developing fruit. In this manner the process of phloem loading (Daie, 1991), long distance translocation (Patrick and Wareing, 1976), and uptake of assimilates (Patrick, 1988) may be disturbed causing a reduction in fruit growth. Reduction in leaf area also reduces the growth of roots (Buttrose, 1966), which itself may decrease the availability of hormones for kiwifruit growth.

In grape, apparently GA_3 can substitute for the loss in leaf area with regard to berry weight (Sidahmed and Kliewer, 1980). Lockhart (1957) proposed that if the response normally elicited by an organ could be reproduced by application of a pure hormone following excision of the organ, the presumption is strong that the organ removed normally supplies to the plant comparable substance (s). Thus, further investigations applying plant growth regulators after a partial defoliation in kiwifruit vines would indicate empiric effects of hormones that may be supplied from the leaves to the fruit for the promotion of growth.

A significant decrease in return bloom was caused by the 75 % defoliation (Table 6 - 6). In kiwifruit, buds develop the capacity to flower during the summer but the timing of flower evocation is unknown. It is considered to occur during the previous summer (Davison, 1974) in December and January (Snelgar and Warrington, 1990) at which time future potential flowering sites are present. Any extra stress on the vine at this time is likely to reduce the flowering potential of the vine (Snelgar and Warrington, 1990). Non-significant effects of defoliation on glucose, fructose, and sucrose in shoots

were recorded in December, and January (Tables 6 - 2, 6 - 3, 6 - 4). However, defoliation reduced stem and shoot starch in January and March (Table 6 - 5) which is indicative of a carbohydrate deficit within the vine. Defoliation (Buwalda and Smith, 1990), and shading of the vines (Snelgar and Warrington, 1990) during mid summer reduced kiwifruit return bloom. The reduction in starch concentration may have been associated with the low return bloom. In pecan a carbohydrate depletion has also been associated with a decrease in return bloom (Smith *et al.*, 1986). Evidence suggests that an early high carbohydrate concentration at the apical bud is critical for flower initiation but that is not sufficient alone to trigger initiation (Bodson and Bernier, 1985). Hydrogen cyanamide when sprayed on kiwifruit vines stimulated synthesis of proline before bud break (Walton *et al.*, 1991), but it is unknown if it also directly stimulated starch breakdown. In grape, root stored amino acids may influence bud burst. The root system contains large concentrations of stored amino acids, and they reach a maximum level prior to bud burst (Kliewer, 1967). Kliewer (1967) suggested that the changes in the root reserves of amino acids may reflect the requirements of the growing organs and the export of material from leaves before abscission. Therefore, a defoliation may reduce the pool of root reserve amino acids, negatively affecting bud burst. Thus, it is evident that photoassimilates are essential for return bloom and bud burst, but they are only part of a complex controlling system which is poorly understood (Davison, 1990).

Endogenous cytokinins synthesized in the roots may play an important role in controlling floral initiation in mango (Chen, 1987), apple (Luckwill, 1970), grape (Srinivasan and Mullins, 1981), and

lychee (Chen, 1990). The main contribution of the leaves could be promoting an active transpiration stream to ensure a supply of cytokinin to the bud to be evocated. Other compounds such as substrates (Bodson and Bernier, 1985), polyamines (Evans and Malmberg, 1989) oligosaccharides (Ryan and Farmer, 1991), and non-hormonal regulators (Kefeli and Dashek, 1984; Hilderbrand and Grayburn, 1991) have also been reported to be involved in floral induction and differentiation, and defoliation may negatively influence the synthesis, and/or transport of these compounds from the root to the top and vice versa.

In this work it has been demonstrated that kiwifruit responded to a severe defoliation by reducing the starch content of current season shoots and bark of the main stem. The effect on starch was associated with a reduction in mean fruit size, and return bloom of the vines. Thus, obtaining and retaining as much *productive* leaf area as possible in kiwifruit vines appears prudent. This is supported by results of Cooper and Marshall (1989, 1990 a, 1990 b, 1991). A high number of leaves to fruit on a whole vine basis may contribute to increase yield and fruit size. For example, in grapevine the traditional pruning may limit production, conversely, minimal pruned vines resulted in high yield (Clingeleffer, 1984). A severe partial defoliation reduced fruit size, bud burst, and return bloom, but it had no significant effect on glucose, fructose, and sucrose in the current season shoots, bark, and roots or on root-starch concentration. The specific effects of a starch reduction in stem bark and shoots at early and middle season, respectively, are unknown and require attention to improve the understanding of the

effects of carbohydrates on vital physiological vine processes like fruit sizing and return bloom.

CHAPTER 7.

GENERAL DISCUSSION.

7.1. Effects of kiwifruit vine management on fruit size and fruit storage potential.

7.1.1. Fruit size.

Increasing production costs and decreasing returns for kiwifruit in recent years have highlighted the need to study vine factors that can improve vine fruit yield and fruit size. In 1990-91, the New Zealand Kiwifruit Marketing Board introduced a differential payment system favouring large fruit size counts (New Zealand KMB, 1991), thus giving clear signals to growers that small fruit were less desired in overseas markets.

Kiwifruit yield and fruit sizing is controlled by the interaction between the genetic potential of the vine and the production environment, including climate and cultural practices. These factors influence physiological processes and in the end regulate fruit productivity. The regulation of the processes connected with kiwifruit sizing has become an important area of investigation for plant science researchers in recent years (Woolley *et al.*, 1988; Lawes and Woolley, 1990; Buwalda and Smith, 1990; Costa *et al.*, 1990; Cooper and Marshall, 1990 b; Biasi *et al.*, 1991; Loreti *et al.*, 1991).

It has been proposed that several physiological factors and horticultural practices are involved in kiwifruit sizing (Woolley *et al.*, 1988). In the current study, we investigated several horticultural aspects that could influence final weight of 'Hayward' fruit, such as: root system genotype, 'Hayward' strains, plant growth regulators, flower quality (timing of flowering opening), vine leafiness, concentration of vine carbohydrate reserves, fruit seed number, and fruit seed activity. These factors are associated with fruit sizing according to the model presented in Figure 7 - 1, and they are part of a whole system influencing fruit production in kiwifruit vines. The model developed for kiwifruit production assumed adequate weed and pest control, and that fertilization and irrigation were not limiting high fruit productivity. In practice it is also very important for orchard managers to control these factors.

Kiwifruit growers in New Zealand have traditionally not recognised that root systems (Lawes, 1990; Lowe *et al.*, 1992) or 'Hayward' scion selections confer any particular advantage in yield and fruit size. This investigation has demonstrated that the male root system 4, significantly increased the fruit productivity of 'Hayward' with respect to other root systems four, five and six years after being grafted. This suggests that research on kiwifruit clonal rootstock selection is desirable to improve early vine productivity. In addition, when the scion selection 'Hayward' B was grown on its own roots it was also highly productive. Thus, for some 'Hayward' selections the practice of grafting may be unnecessary.

The strain 'Hayward' A when topworked across a range of root systems showed high fruit productivity. Thus, specific

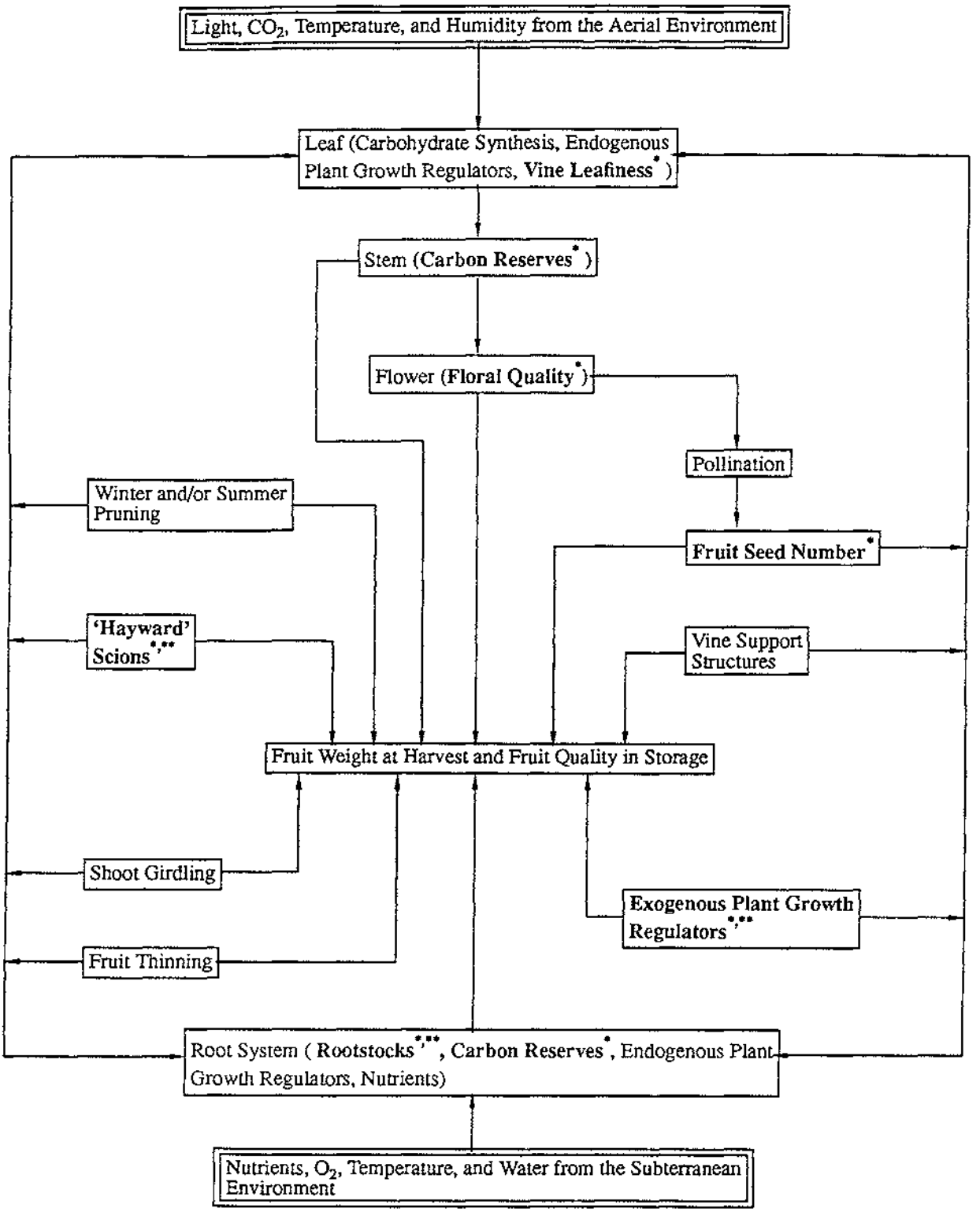


Figure 7 - 1. Diagramatical representation of endogenous and exogenous factors influencing fruit growth and fruit cold storage potential of 'Hayward' kiwifruit. Factors influencing **fruit size*** , and **fruit quality**** studied in this thesis.

'Hayward' scions have the potential to increase the fruit productivity in orchards. 'Hayward' scions could be further characterised and selected to improve yield and quality fruit production. Following propagation of kiwifruit, it is recommended the commercial nurseries only sell highly productive clones of 'Hayward'.

There was an interaction between rootstocks and scions on fruit productivity. Therefore, in addition to individually 'good' rootstocks or scions, the propagation of known high productive rootstock-scion combinations may be also considered for commercial purposes. For commercial orchards it is increasingly important that only plants selected on the basis of high productivity should be grown. As returns for kiwifruit in the world market diminish, it becomes increasingly important for orchardist to maximise productivity. This study has shown that there is potential in selection of high fruit productivity rootstocks, scions or rootstock-scion combinations for new plantings.

It maybe the first time the multivariate statistical method Canonical Variate Analysis has been used in rootstock and scion research. About six response variates were measured on the vines in each of three seasons (Chapter 2, table 2 - 3). The Canonical Variate Analyses generated independent and composite 'new variates' that detected vines with superior field productivity. Although the analyses of each individual response variate was of interest, they may be of limited value. The analyses of variance did not show how different rootstocks and scions compared with respect to all variates considered together, and how those variates may be interrelated. Thus, in this work it was demonstrated that Canonical Variate Analysis in rootstock and scion research has potential to be used

because it reduced the dimensionality of the data sets, and facilitates the interpretation of the results.

In this study conducted over three growing seasons the application of the synthetic cytokinin compound CPPU (Woolley *et al.*, 1991) to a small proportion of fruit per vine increased fresh weight of 'Hayward' by 36 g on average with respect to chemically untreated fruit (Chapter 4). About similar fruit size response was obtained when CPPU was applied to whole vines (Lawes *et al.*, 1991). The mechanisms of action of CPPU in kiwifruit sizing are not well known (Lewis *et al.*, 1994). However, CPPU may be metabolised to cytokinin active compounds that increase the level of cytokinin in kiwifruit tissue (Lennard, S. 1994. Personal communication. Department of Plant Science. Massey University. Palmerston North, New Zealand) and citokinins added exogenously may transiently enhance levels of some endogenous cytokinins (Lewis, unpublished data, Woolley, unpublished data). This is supported by studies of Feito *et al.* (1994) who found a similar relationship between the exogenous application of BA and endogenous cytokinin levels in kiwifruit shoots *in vitro*. Therefore, endogenous cytokinins in the fruit may be an important limiting factor with respect to source strength and fruit growth.

In grape, low fruit production in vines has been related to reduced cytokinin production in the root system (Skene and Antcliff (1972). Higher concentrations of cytokinin-like substances have been found in the xylem sap of high-yielding sweet cherry trees topworked on specific rootstocks (Stevens and Westwood, 1984). Lawes (1979) found cytokinin activity in the xylem sap of kiwifruit vines

using a bioassay. Therefore, the kiwifruit root system as in other plants (Lee, 1994; Cutting and Lyne, 1993) may be a major source of cytokinins that move into the canopy where they may influence a range of physiological processes such as fruit production.

Cytokinins from the root may not act alone in the process of kiwifruit sizing. The application of a mixture of auxins, gibberellin, and cytokinin to fruit tissue in the field (Chapter 4) and *in vitro* (Chapter 5) significantly promoted 'Hayward' fruit growth over three seasons. Rootstocks may influence the plant growth regulators content in xylem sap of apple scions (Jones, 1984). In eggplants topworked on selected root systems the concentration of plant hormones in the xylem of the scion was root- system dependent, and the fruit yield was positively associated with the concentration of auxin, gibberellin, and cytokinin in the xylem sap. In this work, the root system influenced the final mean fruit size of all four 'Hayward' strains used as scions (Chapter 2). The innate physiological competence of each rootstock to produce and/or transport plant growth regulators may be an important factor affecting fruit size in kiwifruit vines.

Stevens and Westwood (1984) found the highest concentration of cytokinins in the xylem sap of sweet cherry trees in the period of fruit set. In the present work, the largest final fruit weight response to CPPU and CPPU + 2,4-D + GA_3 occurred when the plant growth regulators were applied in early fruit growth when fruit cell division was most active (Chapter 4). Basic work is required to show if concentrations of plant growth regulators in the xylem sap at fruit set are related to final fruit size, because monitoring them may

be a useful method to estimate the fruit sizing capacity of potential kiwifruit rootstocks.

A partial defoliation at bloom reduced the kiwifruit weight by 12 g (Chapter 6). Reductions in kiwifruit weight caused by a vine partial defoliation has also been reported by Cooper and Marshall (1989, 1991) and Buwalda and Smith (1990). The availability of hormones in the fruit for attracting assimilates for growth may be interrupted after the defoliation. Citrus fruitlets grown on leafy inflorescences may have greater cytokinin content (Erner, 1989). In grape, Sidahmed and Kliewer (1980) found GA_3 can substitute for the loss in leaf area with regard to the loss in final berry weight. In kiwifruit, the application of CPPU to the fruit has consistently shown increases in fruit weight (Chapter 4). Thus, the application of this plant growth regulator to the fruit may substitute for a sub-optimal leaf area and hence negate the effect of a low leaf:fruit ratio in reducing final kiwifruit weight as was observed in Chapter 6. The sustainability of this effects would depend on the extent to which stored reserves and return bloom are affected.

The effects of plant growth regulators in kiwifruit sizing may be indirectly related to the total leaf area of the kiwifruit vines. High transpiration streams caused by large leaf area may be associated with high hormone content in the canopy of fruit trees (Lakso *et al.*, 1989). Loreti *et al.* (1991) showed the root system can increase the total leaf area of 'Hayward' vines. Strains of the apple cultivar 'Delicious' can also influence the leaf area in apple which may translate into high fruit yields (Warrington *et al.*, 1990). In the present work, leaf area was not evaluated in the rootstock-scion

experiments (Chapter 2). However, root systems and/or 'Hayward' strains may influence leaf:fruit ratios of kiwifruit vines. Thus, a large leaf:fruit ratio in the vine may contribute in promoting high transpiration streams that ensure a large supply of cytokinins from the root to the top and then transported to the fruit for increasing weight, in addition to a straight carbohydrate supply.

Lawes, Woolley, Zhu and Cruz-Castillo (1990) found in the first year after propagation, the male root system 4 made stronger vegetative growth than the other root systems. Despite only one male root system being evaluated in this work (Chapter 2), it is possible there are advantages in using vigorous plants. In the nursery they could give strong early growth and by increasing early orchard canopy development they appear promising new rootstocks for 'Hayward' vines.

Vine defoliation as investigated in Chapter 6 may have reduced the growth of the root system because a major limitation in the production of photoassimilates reduce the normal growth and development of the vine. The root is known to be a poor competitor for carbon with respect to other parts of the vine such as the fruit, and shoot (Buwalda and Smith, 1990). Low productivity kiwifruit vines may have roots demanding higher carbon resources for subterranean growth, while highly productive vines may have a better strategy for increasing carbon allocation to the shoots for producing a large number of leaves and/or large sized leaves to more efficiently supply the fruit with carbohydrates. Studies on the carbohydrate balance between the root and the top may shown rootstock effects on fruit productivity.

In the rootstock-scion experiments generally, vines with a large trunk diameter had larger mean fruit size (Chapter 2). A large trunk diameter in the vine may indicate high carbon reserves to support vine growth. In this work, partial defoliation limited final kiwifruit size (Chapter 6), and also reduced the concentration of starch in the trunk bark suggesting a limitation or reduction of photoassimilates relative to demand by the vine for normal growth. Therefore, vines with larger trunk diameter may be more efficient in maintaining the supply and demand balance of starch for vine and fruit growth. Kiwifruit rootstock-scion effect on the vine trunk diameter may also influence the number and/or the size of the vascular tissue that transport water, minerals, and plant growth regulators from the roots to the top, and particularly to the fruit. This is supported by findings of Wang *et al.* (1994 a) who reported large cross-sectional areas of xylem vessels in a kiwifruit rootstock promoting a large number of flowers in the scion. Measurements of scion trunk diameter in young vines could be a useful early indicator of productive vines.

In kiwifruit, root growth rates are specially low during the flowering period and early fruit growth (Buwalda, 1993). Both root systems and 'Hayward' scions may influence early kiwifruit vegetative growth reducing the competition between the root and the shoot for vine assimilate resources in the period of fruit cell division. Therefore, vines with rapid vegetative growth rate in the period of fruit cell division may reduce the partitioning of carbohydrates to the fruitlets. Cultural practices at fruit set that increase vine vegetative growth such as soil nitrogen application or shoot tipping may reduce

fruit size by increasing competition of other vine sinks such as young growing leaves.

The percentage dry matter in fruit declined sharply for 45 days after anthesis as a result of the rapid increase in water uptake by the fruit (Figure 4 - 4). Yang and Glenn (1994) found that the magnitude of the osmotic potential may reflect the metabolic activity of a sink. The high water attraction of the kiwifruit in the period of cell division may be caused by a low osmotic potential related to a high fruitlet metabolic activity. Fruit with low water potential at fruit set may require of an efficient vascular system to transport organic and inorganic compounds from the soil to the fruit. Fruit with high water uptake at fruit set tended to have large fruit size (Chapter 4, figure 4 - 4). Vines producing large fruit size may have higher root conductivity at early fruit growth than vines producing small fruit. Studies on kiwifruit root conductivity at fruit set may discriminate vines with different potential for fruit sizing.

Palmer (1993) pointed out more basic work could be done on the relation of flower quality (cell number) with final fruit size. In the present work, results showed that final fruit size was increased by a large number of cells in the ovary at anthesis (Chapter 4). It would be of great interest to learn how and when cell number in these fruitlets is determined. If this is known then growers may be able to perform cultural practices to increase the production of fruit in large sizes, and then the economic losses due to small fruit can be reduced. With the use of specific rootstocks flower quality may be improved. For example, rootstocks may influence ovary cell number indirectly by affecting flower bud diameter in apple (Rom *et al.*, 1990) or flower

bud development in peach (Durner, 1991; Durner and Goffreda, 1992). However, in kiwifruit there is no information in this regard.

Flowers with an earlier anthesis (days 0-2) had 9 % higher ovary fresh weight (Chapter 4, tables 4 - 2, 4 - 3) and 16 % more cells in the core than flowers with a late anthesis (days 10-12), had an increase in final fruit size of 10 g (Chapter 4, tables 4 - 2, 4 - 3). This suggests that on the same vine, a delay of 8 - 10 days in bloom represents 10 g smaller fruit at commercial harvest. Spraying vines with hydrogen cyanamide, or late spring tipping of canes contracts the blooming period and increase fruit size (Snelgar and Manson, 1992). Other vine management practices that may reduce the duration of the period of kiwifruit blooming such as the use of specific rootstocks (Wang *et al.*, 1994 b) may promote large final fruit size.

In a field experiment there was an additive effect between seeds and exogenous plant growth regulators (Chapter 4). Fruit with low and high seed numbers when treated with CPPU + 2,4-D + GA_3 had a mean fresh weight of 102 and 136 g, respectively, while the untreated fruit were 47 and 90 g. It is clear from this experiment that exogenous plant growth regulators and seed producer factor (s) act in concert in the regulation of fruit size, and that the effect of seeds in kiwifruit growth can not be substituted with an exogenous application of plant growth regulators. This contrasts with results in strawberry (Nitsch, 1950; 1965; 1970) and grape berry (Coombe, 1973) where exogenous plant growth regulators substitute the effect of the achenes and seeds in fruit growth, respectively. These may be special cases since in strawberry the achenes are botanically the fruit (Coombe, 1976), and in grapevine in addition to its unique capacity

to produce parthenocarpic fruit naturally, it has from 0 to 4 seeds only (Weaver, 1976).

In an *in vitro* experiment fruit tissue was induced to undergo cell division and callus formation. There was a significant interaction between seeded inner pericarp tissue and exogenous plant growth regulators on callus fresh weight (Chapter 5). This suggests that seeds in the inner pericarp which was isolated *in vitro* from vine sources of plant growth regulators, such as the root system (Skene, 1970), modulated the activity of the exogenous hormones. Therefore, to maximize fruit growth, growers require information on how seed produced factor (s) or seeded pericarp together with the plant growth regulators transported from the vine to the fruit, may be important determinants of large fruit size. While scientists may seek to understand these processes, growers need to interpret this information and apply it as part of their vine management programme to maximise fruit size.

Kiwifruit seeds may also regulate the competition for assimilates between adjacent kiwifruit. A higher number of seeds per fruit can alleviate the dominating effect of earlier developing squash fruits (Stephenson *et al.*, 1988). In a related study Bangerth *et al.* (1989) found that tomato fruit with higher seed number have greater IAA export out of the fruit, and this hormone may inhibit adjacent fruit development (Bangerth, 1989, 1993). In kiwifruit, fruit with low seed counts were particularly small when the fruit adjacent to them had a greater seed content (Lawes, Woolley and Lai, 1990). There is no published information about inter-kiwifruit dominance involving hormonal signals such as IAA. If the internal regulation of kiwifruit in the early stages of development is considered as a simple

competition with other sinks for available resources, seeds may play an important role in fruit development regulating adjacent fruit dominance. Cultural practices aimed at high fruit seed number in all fruit, and contracting the bloom period may reduce inter-fruit competition that may translate into greater fruit sizes.

In developing a more complete understanding of the role of plant growth regulators in kiwifruit growth it may be particularly useful to focus on the importance of the kiwifruit vine as a producer of natural plant growth regulators, and especially cytokinins that influence fruit sizing. Work on rootstocks, scions, fruit seeds, and fruit fresh tissues as producers of endogenous plant growth regulators to increase fruit size should be encouraged.

7.1.2. Fruit storage.

Deterioration of kiwifruit in storage is a major economic problem. In 1991 fruit losses following harvest mainly caused by soft fruit (Banks *et al.*, 1992) were worth $NZ 64 million (New Zealand KMB, 1991). As there is considerable variation between orchards, there is considerable interest in identifying orchard factors that most have influence on cold storage potential of 'Hayward' fruit (Hopkirk and Clark, 1992).

In this study, different young 'Hayward' selections on their own roots or topworked on different selected root systems varied significantly in percentage soluble solids in fruit, and fruit firmness at both harvest and after cold storage. For example, 'Hayward' C on

'Bruno' seedlings showed a poor performance for fruit firmness after cold storage with respect to other clonal rootstock-scion combinations (Chapter 3). Future rootstock and scion kiwifruit research work should concentrate on physiological causes that affect fruit quality in cold storage. It is known that the density of the leaf canopy in the vine may affect percentage soluble solids and flesh firmness in kiwifruit cold storage (Smith, Gravett, and Curtis, 1992; Seager, 1993), and that kiwifruit rootstocks (Loreti *et al.*, 1991) and strains of 'Delicious' apple (Warrington *et al.*, 1990) influence leaf:fruit ratios. Therefore, vines with large leaf:fruit ratios may have long fruit storage potential because of the high carbohydrate content in its fruit. This is supported by studies in grape, where defoliation reduced the total soluble solids of the fruit and high carbohydrate fruit stored better (Kataoka *et al.*, 1982). Thus, rootstock-scion effects determining a large leaf:fruit ratio in the vine would positively influence fruit quality (fruit firmness and fruit total soluble solids) in long periods of cold storage.

Apple fruit quality at harvest is influenced by the leafiness of the tree which may be correlated with the calcium content of the fruit (Ferree and Palmer, 1982; Volz, 1991). Kiwifruit with high calcium content tend to be firmer at cold storage (Mowatt and Banks, 1992; Gu *et al.*, 1994). In this crop, rootstocks can modify the nutritional status of the scion (Viti *et al.*, 1991) and may influence the mineral content of the fruit by indirectly affecting the leafiness of the vine. Kiwifruit rootstock-scion combinations with high leaf:fruit ratios may have a higher transpiration rate that increase the scion availability of minerals for fruit growth. Future research may consider these factors (leafiness of the vine and fruit calcium content) to understand

possible kiwifruit rootstock-scion effects in 'Hayward' fruit quality after storage.

In apple, a low seed number may decrease the calcium content of the fruit (Bramlage *et al.*, 1990; Brookfield et al., 1993). This could have financial consequences as low calcium concentration in the fruit is related to postharvest disorders in apple (Bramlage *et al.*, 1990), and low fruit firmness after cold storage in kiwifruit (Prasad and Spiers, 1991; Gu *et al.*, 1994). Acropetal calcium transport into tomato (Banuelos et al., 1987), avocado (Cutting and Bower, 1989), and nectarine (Wand *et al.*, 1991) fruits is affected by polar basipetal auxin transport. Seeds are a source of auxins during early fruit growth (see Literature Review in Chapter 5). Therefore, auxins produced in the seeds may influence the transport of calcium into the fruit during early fruit growth, and fruit calcium content at harvest may be reduced. In this work, the effect of seeds on fruit growth *in vitro* (Chapter 5) and in the field (Chapter 4) were evaluated, and seeds influenced fruit growth. However, seed effects on postharvest quality of kiwifruit are unknown, and information in this regard is required to evaluate whether kiwifruit seed number and/or seed factor (s) such as auxins are physiological causes influencing fruit firmness after cold storage.

Dry matter is a measure of the total weight of solid material in kiwifruit and is related to total carbohydrate concentration in the fruit (Hopkirk, 1991). Thus, the higher fruit dry weight achieved by the fruit from early flowers compared with late fruit (Chapter 4, figure 4 - 3), suggests that the supply of organic and inorganic substances such as starch and minerals from the vine to the fruit was higher for

early fruit. Therefore, fruit from early flowers may present better storage potential than fruit from late flowers. This view is supported by results of Volz (Volz, R. K. 1994. Personal communication. HortResearch. Havelock North. New Zealand) who found that apple fruit from early flowers tend to have higher calcium content than fruit from late flowers. Future research should consider the postharvest quality of kiwifruit from flowers that open successively over the spring period.

The application of the plant growth regulators CPPU, and CPPU + GA_3 + 2,4-D decreased flesh firmness at harvest (Chapter 4). The kiwifruit size response to CPPU was also characterised by an increase in fruit dry weight (Chapter 4, figure 4 - 3), and a small reduction in percentage fruit dry matter (Chapter 4, figure 4 - 4). Similar results were found by Woolley *et al.* (1991), Biasi *et al.* (1991), and Antognozzi *et al* (1993). Fruit treated with CPPU had a larger cell number in the outer pericarp than chemically untreated fruit (Chapter 4, table 4 - 4), resulting in a larger outer pericarp thickness (Chapter 4, table 4 - 9). Fruit with a large cell number in the outer pericarp apparently imported greater amounts of water for cell expansion leading to reduced percentage of dry matter at commercial harvest (Chapter 4, figure 4 - 4). The lower flesh firmness at harvest in treated fruit could reflect the cells of the outer pericarp having higher water content and possibly thinner cell walls (Chapter 4, tables 4 - 7, 4 - 8). Thus, fruit treated with CPPU may have a shorter postharvest life than untreated fruit.

While the plant growth regulators CPPU, 2,4-D, and GA_3 are not registered to be used in the production of kiwifruit in New Zealand, this study sought to use these materials to advance our

understanding in fruit development with no suggestion that these materials should be applied to commercial orchards without testing for harmful residues and formal approval given for those plant growth regulators in New Zealand. The commercial use of these plant growth regulators as enhancers of kiwifruit size should be use with caution as they have the potential to damage the reputation of clean green environmental conditions for the production of the horticultural commodities in New Zealand.

The horticultural factors studied in this thesis (Chapter 7, figure 7 - 1) demonstrated the concurrence of a whole system influencing productivity of 'Hayward' kiwifruit vines. This study showed that root systems, 'Hayward' scions, vine leafiness, plant growth regulators, fruit seeds, and ovary size at anthesis may play an important role in fruit sizing, and fruit quality in cold storage.

CHAPTER 8.

FUTURE DIRECTIONS FOR RESEARCH.

The current study revealed some further areas for examination of kiwifruit growth and developmental physiology.

8.1. Rootstock and scion studies.

Having found differences in field performance by using selected root systems and/or different clonal 'Hayward' material, it is appropriate to seek the physiological causes of the 'Hayward' yield and fruit sizing improvement.

Loreti *et al.*, (1991) showed that kiwifruit vines on a male root system had a higher number of leaves than own rooted vines. Lai (1987), and Buwalda and Smith (1990), have also emphasised the importance of the leaf area in kiwifruit productivity. Leaf growth and development should be included in future evaluations of kiwifruit root system-scion combinations to study physiological causes of yield improvement.

In kiwifruit, root growth rates are especially low during bloom and early fruit growth (Buwalda, 1993). Final kiwifruit size is strongly influenced by the ovary cell number at anthesis (Chapter 4). It is possible to speculate that 'good' root systems may influence early kiwifruit vegetative growth reducing its competitive ability for vine assimilate resources in the period of fruit cell division. 'Good' and

'poor' vines detected in this work could be an appropriate material to study probable effects of root growth in sizing kiwifruit.

Woolley *et al.* (1991), suggested that kiwifruit size probably is limited by cytokinin levels. Citokinins have been extracted from root tissue of grapevines (Skene, 1970). It is unknown if kiwifruit vines with high productivity have a large capacity for synthesis of cytokinins. Studies evaluating hormone levels in the root apex of 'Hayward' vines topworked on the male root system 4 and/or 'Kaimai', and on 'poor' field performing root systems may indicate root system effects on fruit sizing.

The influence of site on performance of root systems and 'Hayward' selections should be evaluated to determine their field performance under other environmental conditions, for example different soil conditions and higher temperatures.

Root distribution and root density can be influenced by rootstocks (Southey, 1992), and these parameter may affect fruit productivity in grapevines (Swanepoel and Southey, 1989). Therefore, root studies of kiwifruit vines topworked on different rootstocks would be useful to understand root growth effects on vine productivity.

There is considerable interest in identifying factors most responsible for influencing fruit quality (total soluble solids and fruit firmness in storage) (see Hopkirk and Clark, 1992). Young 'Hayward' vines own rooted, and topworked on several selected kiwifruit root

systems showed significant effects on fruit firmness at harvest, and after storage during two seasons (Chapter 3). Further research is required to define physiological causes of these effects. In several fruits including kiwifruit the nutrient composition of the fruit has been found to be important in relation to storage quality (Prasad and Spiers, 1992; and Mowatt *et al.*, 1992). Kiwifruit root systems can modify the nutritional status of the scion (Vity *et al.*, 1990). Scion and/or rootstock effects on fruit shape could also be considered.

8.2. Time of anthesis and plant growth regulators.

Practices aimed at improving preanthesis kiwifruit flower quality should be studied. For example, timing of cane growth, time and severity of pruning, and cane angle, shoot girdling, and flower thinning in the current year should be tested. Studies about this will facilitate the development of vine management practices to manipulate vine performance more fully.

Fruit from early opening flowers are larger than late fruit (Lai, 1987; Chapter 4). Bangerth (1989) proposed a model of dominance among fruit-sinks. He pointed out that polar basipetal transport of auxin may be a signal regulating dominance between fruit sinks in trees. It is unknown if early set kiwifruit inhibit growth of late fruit. Information about inter-fruit dominance involving hormonal signals such as IAA (Bangerth, 1989), and its role in early kiwifruit growth would be required.

In apple CPPU inhibits return bloom (Greene, 1989; Curry and Greene, 1993). In a preliminary work it was found that CPPU

treatments did not affect 'Hayward' return bloom at least during the first two seasons (Woolley, D. J. 1993. Personal Communication. Department of Plant Science. Massey University. Palmerston North, New Zealand). Studies about sustainable bloom productivity effects of CPPU and the hormone mixture are required.

Woolley *et al.* (1991), suggested that kiwifruit size may be limited by cytokinins. Studies on application of the hormone mixture, and CPPU on fruitlets with higher final size potential (possibly less limited by cytokinins), may require reduced PGR dosage to reach a large fruit size. For example a lower concentration of PGR application may be required for fruit from early flowers and/or fruit on girdled shoots having high leaf to fruit ratios, than for fruit with a low potential for achieving large final fruit size.

Other plant growth regulators such as BAP could also be mixed with CPPU, and evaluated for field fruit sizing responses. In grape, thidiazuron (cytokinin) (N-phenyl-N-1,2,3-thiadiazol-5-ylurea) has effectively enlarged grape clusters (Reynolds *et al.*, 1992). This PGR alone or mixture with CPPU may be worth testing in relation to kiwifruit sizing.

Work on the metabolism of ^{14}CPPU residues ± 2,4-D and GA_3, and fruit plant growth regulator levels (auxins, gibberellins, cytokinins, and ABA) will assist in understanding the hormonal control of fruit growth.

Several auxins and GA_3 were applied independently and together in the field by Hopping (1976), and no increased fruit size was registered. However, when they were used in fruit tissue cultured *in vitro* callus growth was recorded. Studies with radioactively labelled 2,4-D and/or GA_3 would be valuable to understand the fruit growth response differences in field, and *in vitro*. Further research on seed and growth regulator interactions in fruit tissue cultured *in vitro* at early fruit growth stages when cell division is occurring may improve the understanding of how hormonal substances influence fruit size.

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