LEAF-FRUIT RELATIONSHIP IN KIWIFRUIT

(Actinidia deliciosa (A. Chev.)

C.F. Liang et A.R. Ferguson)

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ABSTRACT

Net photosynthetic rates of kiwifruit (Actinidia deliciosa (A. Chev.) C.F. Liang et A.R. Ferguson) leaves were lowered by as much as 50 $^0/_0$ of light saturated rates when the vines were shaded to half the light saturating level (280 uE m^{-2} s^{-1}). The photosynthetic response also showed a broad temperature optimum around 20 C. Vines which were grown in 10 or 30 C conditions acclimatised rapidly when they were transferred to a 20 C growth temperature, and adjusted their photosynthetic rates within 24 days.

Fruit growth in the kiwifruit was dependent on current photosynthates. Only negligible amounts of ^{14}C-label, which accumulated in the stems and roots of the vines from the previous season, were remobilized to support fruit growth. Kiwifruit leaves exported ^{14}C-assimilate when they were 60 $^0/_0$ of full expansion, or 40 days from emergence. The principal source leaves which supplied the fruits were the leaves which subtended the fruits. On an intact shoot system, each subtending leaf supplied as much as 62 $^0/_0$ of their total ^{14}C-assimilate exclusively to its own fruit. The fruit also received smaller amounts of ^{14}C-assimilate from some distal leaves via vascular connections which linked at

least, the n, n+5, and n+8 nodes. However, this pattern of ^{14}C translocation was altered when the fruiting shoot was pruned. Each fruit then received supplies of ^{14}C-assimilate from every distal leaf, plus an increased amount (78 $^0/_0$ of total leaf ^{14}C) from its subtending leaf.

The minimum leaf-fruit ratio to support normal fruit growth lies between 0.83:1 (86 cm^2) and 1.7:1 (173 cm^2). A shortfall in the supply of assimilate within a fruiting shoot below this ratio was readily met by surplus ^{14}C-assimilate from source leaves on adjacent fruiting or non-fruiting shoots, up to 8 nodes distance away. It was probably because of this flexibility in the translocation of assimilate that kiwifruit leaves did not show any photosynthetic response to increased fruit demand for carbohydrate. Both fruiting and non-fruiting shoots had similar maximum photosynthetic rates of about 657 $ugCO_2$ m^{-2} s^{-1}.

The fruit growth of a kiwifruit, as determined by fruit volume or fresh weight, followed a double sigmoid pattern. Increases in fruit dry weight however were linear throughout the growth period. Final fruit sizes were partly determined by pre-anthesis factors, although vine management practices and pollination also had a significant influence on fruit growth.

Fruits which developed from early flowers were as much as 31g larger than those from late flowers. The early

flowers had bigger ovaries and were found on strong, vigorous shoots, which were mostly long shoots. It was also found that fruits produced on long shoots contained more viable seeds so that they carried larger fruits than those on short shoots, even though both developed from flowers with the same day of anthesis.

The early stage of fruit growth on a fruiting shoot was inhibited by large leaf numbers greater than 8 distal leaves, but this effect was diminished on vines older than 5 years. However, there was no effect of fruit number on fruit size within a fruiting shoot. Fruits with similar numbers of seeds developed in synchrony with each other, whereas fruits with lower seed numbers were inhibited by those with higher seed numbers at adjacent positions.

Pollination had an important effect on fruit size as fruits with high seed numbers were able to overcome the leaf inhibitory effects on fruit growth. It was also found that at equal seed numbers, fruit sizes on some vines were consistently smaller than other vines within the same orchard block. Thus there was an overall effect of vine vigour, possibly related to the rootstock, which limited the growth of the fruits on a kiwifruit vine.

ACKNOWLEDGEMENTS

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GENERAL INTRODUCTION

In its natural habitat, the kiwifruit (<u>Actinidia</u> <u>deliciosa</u> (A. Chev.) C.F. Liang et A.R. Ferguson) vine has a vigorous, climbing growth habit of a liane (Ferguson, 1984). A current problem in the commercial kiwifruit orchard is the need to manage the scrambling vegetative growth, and to direct the flow of assimilate into economic yield. To achieve this, it is important to understand the basic physiology of the vine, so that appropriate pruning and training systems can be designed.

Crop yield depends on an adequate production of photoassimilate from the 'source' parts of a plant, and an adequate capacity of the 'sinks' to accept the products of photosynthesis (Zelitch, 1982). The factors relating to the establishment of a leaf canopy in a plant are important in determining its photosynthetic capacity. For the kiwifruit vine, these include the effects of temperature and light on early spring growth (e.g. Morgan, Warrington, and Halligan, 1985; Snelgar, 1986). The optimisation of light distribution within the established vine canopy for maximum photosynthesis is also an important consideration.

The sink capacity of a kiwifruit vine depends on its

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total crop load, as well as the sink strength of the individual fruit. Overcropping is undesirable, as this encourages biennial bearing (Davison and Sutton, 1984), with all its disadvantages, including the production of undersized fruits. Fruit sizing is important in the commercial production of kiwifruit in New Zealand because fruits below 70g fresh weight do not meet export standards.

According to Warren-Wilson (1972), sink strength equals sink size x sink activity. In this concept, 'sink activity' is simply the relative growth rate, whereas Wareing and Patrick (1975) have pointed out that the concept of 'mobilizing ability' or 'competitive ability', rather than 'sink activity' may be more useful. The mobilizing activity of a fruit correlates closely with the number of seeds it contains. Thus, pollination is an important activity in the kiwifruit orchard because the ability of a kiwifruit to mobilize assimilate for fruit growth depends largely on the fruit seed number (Hopping, 1976). However, large variations in the relationship between fruit size and seed numbers indicate that other factors may be important in affecting the sink strength (Pyke and Alspach, 1986). These may include the effects of the environment, such as shading (Grant and Ryugo, 1984a). Different vine management strategies in training, pruning, and fruit thinning, are also likely to alter the interactions between the fruit and the other parts

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of the vine.

The objective of this study was to investigate some of the above aspects of source and sink capacity in the kiwifruit vine. The effect of the relationship between the leaves and fruits on the partitioning of assimilates towards fruit growth was also investigated.

CHAPTER ONE

GENERAL MATERIALS AND METHODS

1.1 Plant Materials

Plant Variety

The experimental vines used in this study were mainly of
the 'Hayward' ~~variety~~ *cultivar*. 'Monty' and 'Bruno' were the other
female ~~varieties~~ *cultivars* which were used, while male vines included
the 'Matua' and 'Tomuri' ~~varieties~~ *cultivars*.

Nomenclature of Vine Structure

In this study, a nomenclature of vine structure, similar
to that described by Sale and Lyford (1987) was adopted.
This is shown in figure 1.1. The kiwifruit vine is grown as
a main trunk from the ground. Permanent leaders are then
branched off at the top of the structure. The vine canopy is
formed from a system of canes which are developed from the
leaders. In the orchard, the canes are trained in different
ways, the most common of which are the 'T-bar' and 'pergola'

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Figure 1.1.   Nomenclature of kiwifruit vine
structure.

subtending leaves

distal leaves

cane

fruit

determinate
(short) lateral,
shoot

cane

fruiting lateral
(shoot)

indeterminate
(long) lateral,
shoot

trunk

non-fruiting,
vegetative,
leafy lateral
(shoot)

roots

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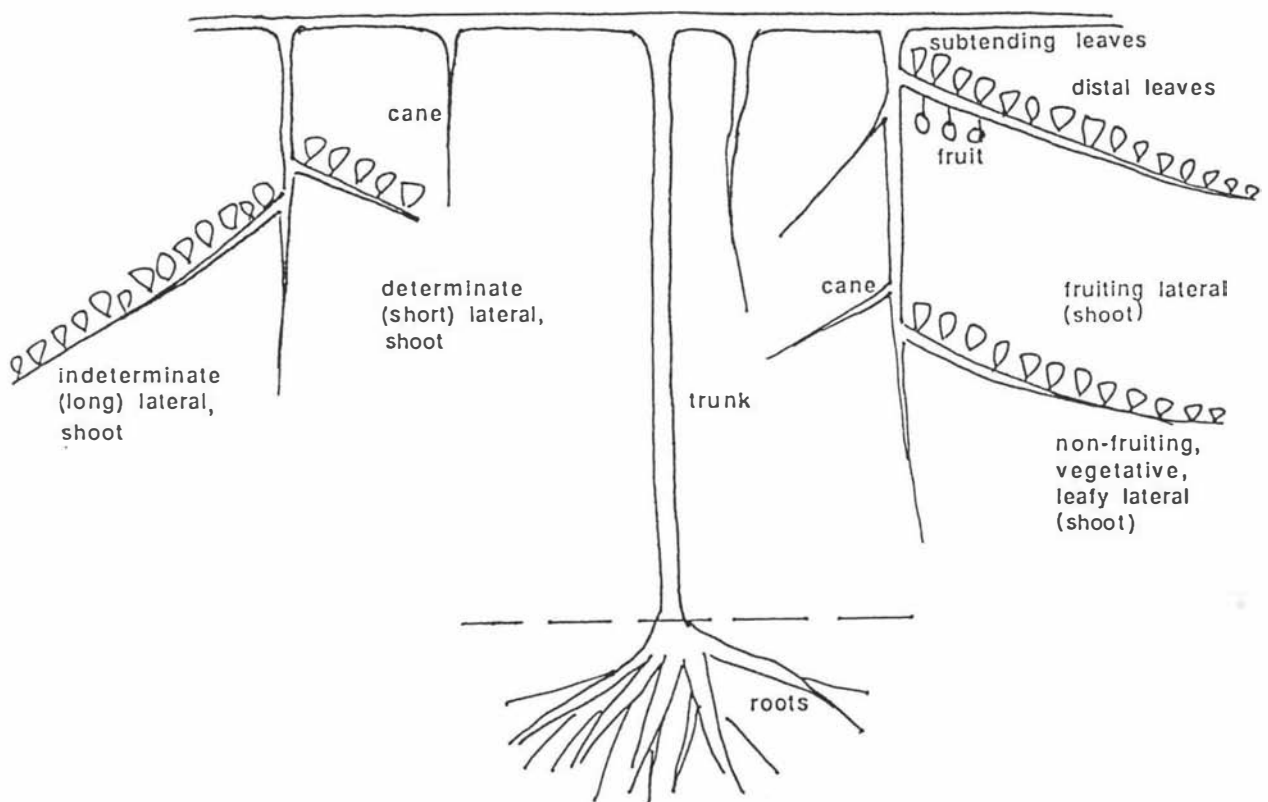
trellis systems (Sale and Lyford, 1987).

Vegetative buds develop from the canes during spring to become the current season's wood called laterals. A fruiting shoot is a lateral which carries fruits whereas a non-fruiting, or leafy shoot refers to laterals which remained vegetative.

Within a fruiting shoot, the leaves which subtend fruits are denoted as 'subtending leaves', whereas leaves beyond the last fruit are 'distal leaves'.

Fruiting and non-fruiting laterals can be either indeterminate (*i.e.* non-terminating, long) or determinate (*i.e.* self-terminating, short) shoots.

1.2 Plant Growth Environment and Cultural Conditions

Field Trials

Field experiments were mainly conducted at a commercial kiwifruit orchard (Summerland Orchard) near Levin. The vines were trained on pergola trellises and planted at a 3.5m x 5m spacing.

Experiments were also carried out at the Massey University orchard, Palmerston North. The vines in this

orchard were grown on T-bars and planted 3.5m apart with 4.5m
between rows.

In both the above orchards, sprays and irrigation were
applied to the vines according to commercial cultural
practices.

Glasshouse Experiments

The plants which were used in the glasshouse experiments
were either grown from cuttings or they were lifted from the
field just before bud burst. These plants were bagged in
perforated polyethylene bags containing a soilless mix of
50:50 (v/v) peat-sand and a standard nutrient mix (see New
Zealand Nursery Research Centre Annual Report, 1984). A
trickle irrigation system supplied each plant with water
twice a day.

The ventilated glasshouse was maintained at minimum day
and night temperatures of 21 and 15 C respectively. In some
experiments the photoperiod was extended to 16 hours by
artificial lighting using incandescent lamps.

Growth-room Experiments

Experiments were also carried out in
controlled-environment rooms at the DSIR climate laboratory,

Palmerston North (Anon., 1981). The plants which were moved
into these rooms just before bud break were grown in 4.5
litre pots containing a medium of 50:30 (v/v) Opiki loam:sand
and incorporated fertiliser [0.4 kg MagAmp (7 $^0/_0$ N, 14 $^0/_0$ P,
5 $^0/_0$ K, 13 $^0/_0$ Mg), 0.3 kg dolomite, and 25g fritted
trace elements per m^3]. Further nutrients were added as a
half-strength modified Hoagland's A solution (Brooking,
1976). This was supplied via the automated irrigation
system.

The CO_2 concentration in the rooms was monitored with an
infrared gas analyser, and was 330 $\pm$ 20 ppm. The
photosynthetic photon flux density (PPFD; 400-700 nm
waveband) was measured with a LiCor LI-185 meter and LI-190S
quantum sensor, at 1m from the ground, and averaged 650 uE
m^{-2} s^{-1}.

1.3 Collection of Leaf Data

Leaf Area

The leaf areas of harvested leaves were measured by a
LiCor LI-3100 meter. Leaf areas which were calculated from
the product of the length and width of a mature leaf were

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highly correlated with the measured leaf areas by a factor of 0.805 (r^2=0.98). This method was used to estimate the areas of intact, mature leaves.

The leaf areas of intact leaves were also estimated by cutting the trace of a leaf on paper and measuring the area with a LiCor LI-3100 meter.

Leaf Dry Weight

Harvested leaf were dried to a constant weight in a vacuum oven set at 2 mm Hg pressure and 40 C (Haslemore et.al., 1980).

Photosynthesis

A closed system incorporating a BINOS infra-red gas-analyser, described by McPherson et al. (1983) was used to measure net leaf photosynthesis. The system was modified by interfacing with an Epson HX-20 computer. (see plate 1).

Stomatal Resistance

A LiCor LI-700 autoporometer was used to measure leaf stomatal resistance. The four quadrants of each leaf were measured to give a mean value for the leaf.

Plate 1.1   Portable infra-red gas analyser for
measuring kiwifruit leaf photosynthesis.

Plate 1.2   Apparatus for the application of $^{14}CO_2$
to kiwifruit vines.

Leaf Chlorophyll

Leaf chlorophyll on intact leaves was measured using a portable photometer which was calibrated for kiwifruit (Hardacre et.al., 1984).

1.4 Collection of Fruit Data

Fruit Size

Fruit volume was measured by water displacement in a measuring cylinder. Calipers were used to measure fruit length while the circumference of the mid-section of the fruit was measured with a piece of string and ruler.

Fruit fresh weights were obtained immediately after harvest so as to avoid shrinkages from respiratory and transpiration losses. Fruits were sliced in 3-4 parts and dried for 3-4 days in a vacuum oven at 2mm Hg and 40 C before their dry weights were recorded.

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Fruit Tissue

Fruits were cut at the mid-section and the number of locules *was* ~~were~~ counted. The thickness of the central core, inner and outer pericarp was measured with calipers.

Soluble Solids

Fruit soluble solids were determined by using a hand refractometer. Each fruit was cut at 1.5 cm from the stem and *distal* ~~blossom~~ end so that the juice from both ends of the fruit was measured (see New Zealand Ministry of Agriculture and Fisheries AgLink HPP 213).

Seed Numbers and Seed Weights

Fruits were softened either by over-ripening the fruits or by soaking slices of fruit tissue in a solution containing a pectolytic enzyme for 3-4 days. The seeds from each fruit were extracted by separating them from the pulp with an electric juice extractor (Braun model 4154) and by repeated washing in a sieve under a running tap.

Fruit seed numbers were counted and dry weights were obtained after drying them in a vacuum oven set at 2mm Hg and 40 C.

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1.5 [14]C Method

Administration of $^{14}CO_2$

Potted vines were labelled with ^{14}C by a method which was modified from Hale and Weaver (1962). An assimilation chamber was made by enclosing a single leaf in a 'Mylar' (polyethylene terephtalates) bag. The bag was initially inflated to a 5-litre volume and tied around a plasticine seal at the leaf petiole with rubber bands. A closed-loop assembly of plastic tubes connected the bag with a diaphragm pump and a 25 cm^3 conical flask which contained an aliquot of $Na_2^{14}CO_3$ (specific activity 2.17 GBq per mmol). Excess 70 $^0/_0$ lactic acid was dripped into the flask from a syringe and the generated $^{14}CO_2$ was circulated through the bag (see plate 2).

The system was air-tight and no leakage of ^{14}C-activity was detected in tests in which bags were sealed around petioles with leaves excised (fig. 1.2). An exposure period of 3 hours was chosen although leaves assimilated up to 92 $^0/_0$ of the $^{14}CO_2$ within 30 minutes (fig. 1.2). The air in the bags was passed through NaOH solution before they were vented outside the glasshouse.

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Figure 1.2. Time course of depletion of ^{14}C activity (dpm per cm^3 of air) in assimilation chamber. $\times$, without leaf; $\triangle$, with leaf.
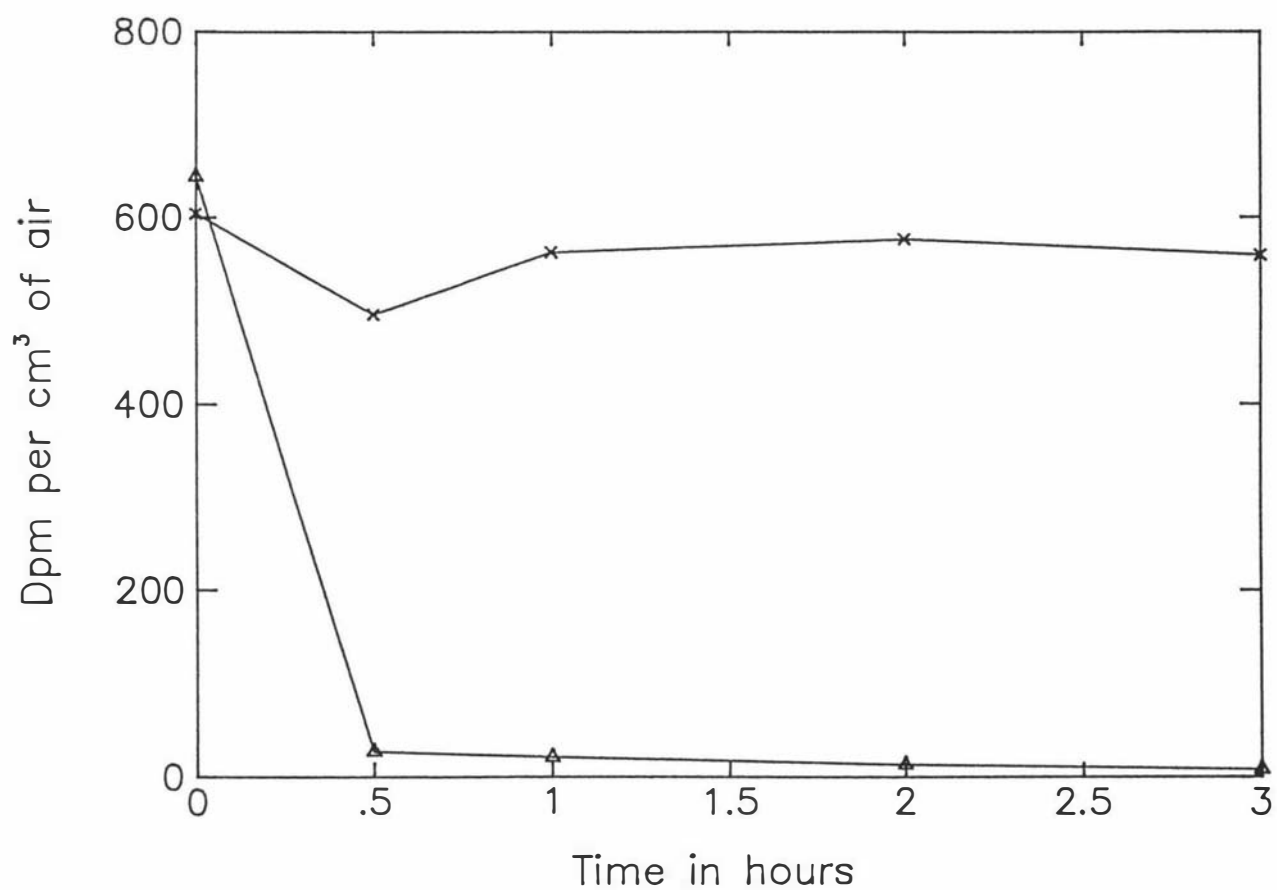
Plant Harvest

Plants were harvested 6 days after they were labelled.
This was determined from an experiment in which the
^{14}C-activity of ethanolic extracts from repeated samples of
punched leaf discs were measured each day after the leaf was
labelled. Figure 1.3 shows that the depletion in
^{14}C-activity came to an equilibrium after 6 days. After the
soluble carbohydrates were extracted, residual ^{14}C-activity
was also determined. This was found to be very low (9 dpm
per mg DW) and consistent from day 0 to day 6. Similar
results were reported by Hansen (1967b) for apple leaves.

Assay for ^{14}C-Activity

A 'wet' digestion technique, similar to that described
by Shimshi (1969) was employed for ^{14}C determination. Stem,
leaf, or root samples of the harvested plant were dried and
ground to pass through 1mm sieve before they were assayed.
Each 50 mg sample of the ground tissue was then placed at the
bottom of a 250 cm^3 screw-topped jar. A 2 cm^3 aliquot of CO_2
absorbent (10 $^0/_0$ ethanolamine and 10 $^0/_0$ ethanol in water)
was placed in a 20 cm^3 scintillation vial and suspended
inside the jar, from the rim at the top of the jar. The jars
were sealed immediately after 20 cm^3 of cold chromic acid was

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Figure 1.3. Depletion of ^{14}C-activity (dpm per mg
dry weight) in the kiwifruit cv. Hayward leaf
after 37 kBq of ^{14}CO$_2$ was applied. Daily
estimates ^{14}C-activity from ethanol soluble (△)
and residual (×) fractions of punched leaf discs
were plotted.
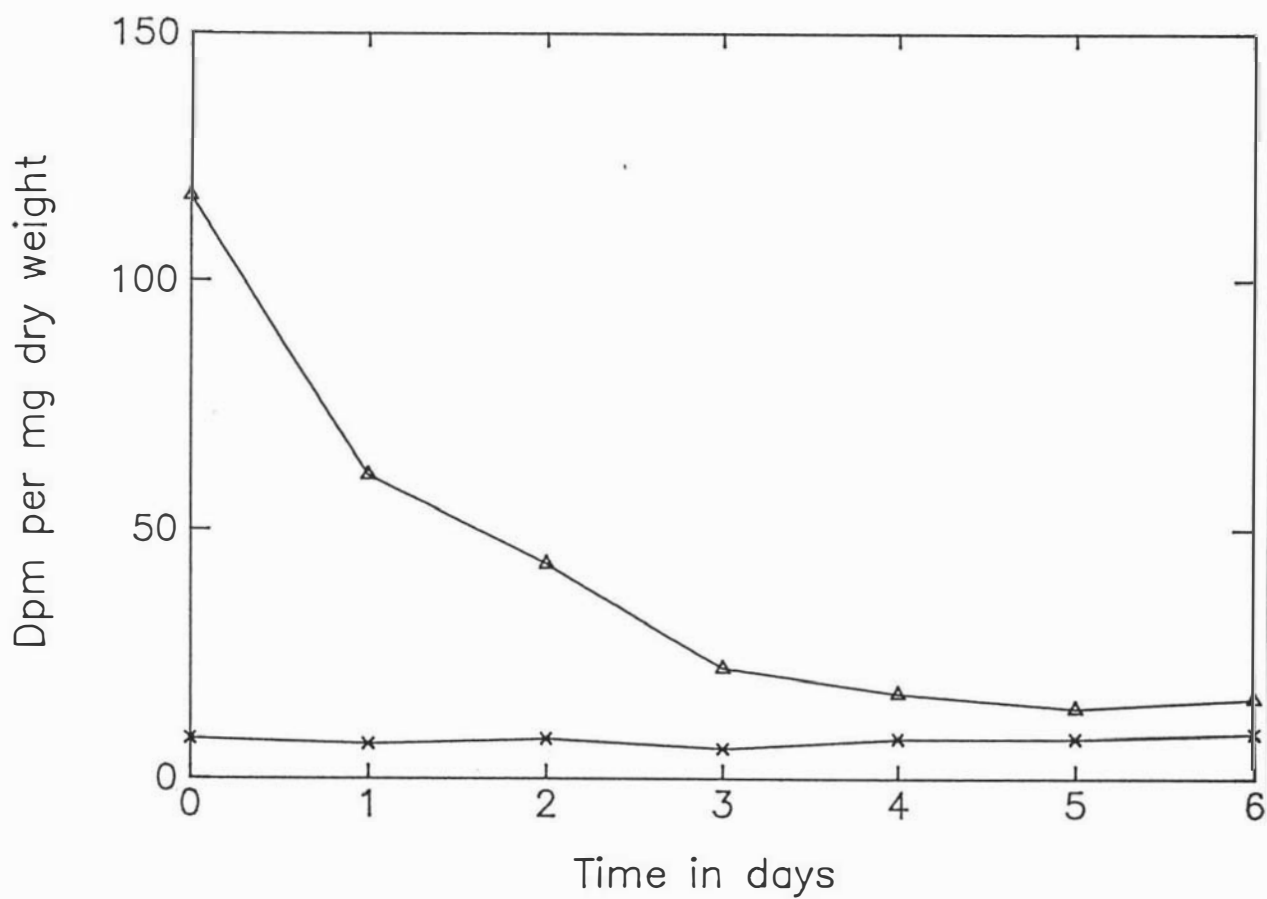
added to the plant sample. Care was taken that the plant
sample was evenly dispersed on the surface to ensure complete
digestion.

After a trial was carried out, it was decided that the
best proportion of materials for acid digestion was 50 mg
plant sample, 2 cm^3 absorbent, and 20 cm^3 chromic acid (table
1.1). A period of 3-hour digestion in a 40 C water bath was
also shown to be sufficient (table 1.2). After the digestion
was completed, 10 cm^3 of a cocktail containing 2 parts of
toluene scintillation solution (0.4 $^0/_0$ PPO) and 1 part of
triton-X-100 detergent (Patterson and Greene, 1965) was added
to the CO_2 absorbent in the vials. 1 cm^3 of distilled water
was added to each vial to obtain a stable emulsion for liquid
scintillation (LS) counting. The effect of an unstable
emulsion, which breaks down into 2-phases, was to alter the
Compton response during LS counting, and give inaccurate
results (Beckman LS 3801 Liquid Scintillation System
Operating Manual).

Liquid Scintillation (LS) Counting

A Beckman (LS 3801) LS counter was used to measure the
^{14}C-activity of the sample vials. No evidence of any
photoluminescence or chemiluminescence was detected when the
samples were counted within 24 hours from preparation. The

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Table 1.1. Results of an experiment to determine the optimum proportion of plant sample (50, 100 mg), chromic acid (20, 40 cm^3), and CO_2 absorbent (1, 2, 5 cm^3) for ^{14}C assay. (LSD_2 (0.05)=17926; n=5).

Total Dpm Recovered

Plant sample:	50 mg		100mg	
Chromic acid:	20 cm^3	40 cm^3	20 cm^3	40 cm^3
CO_2 absorbent:				
1 cm^3	124606	126648	128774	140498
2 cm^3	169788	160424	204408	216104
5 cm^3	159820	145980	234080	234250

Table 1.2. Results of an experiment to determine the optimum bath temperature (30, 35, 40 and 45 C), and period of 'wet' digestion (1-5 hours) for ^{14}C assay. (LSD (0.05)= 12863; n=5).

Total Dpm Recovered

temperature:	30 C	35 C	40 C	45 C
period :				
1 hour	60679	74320	73341	99093
2 hour	85764	87689	137425	138228
3 hour	117574	113643	183754	175784
4 hour	132244	137548	185604	179306
5 hour	173753	176803	185048	177261

LS counter was set to an open channel to accommodate the full
^{14}C-spectrum. The samples had a constant quench and counting
efficiencies were estimated as 89 to 93 $^0/_0$. Background
radiation, obtained by counting blank samples, ~~were~~ *was* deducted
and the final results for each radioactive sample were
expressed as disintegrations per minute (dpm).

1.6 Data Analysis

All statistical analyses were carried out on a Prime
9955 computer at Massey University, Palmerston North.
Statistical packages which were used included the Minitab,
SPSS, and BMDP software.

CHAPTER TWO

KIWIFRUIT LEAF PHYSIOLOGY

2.1 Introduction

Leaf Growth and Development

Like most plants, the growth of the kiwifruit leaf, as measured by the expansion of the leaf area, can be described as being typically sigmoid (Brundell, 1975a).

An expanding leaf becomes a net exporter of carbohydrate only after its photosynthetic activity is sufficiently high to produce an excess of carbohydrate over what it needed for its own growth. For most plants export starts when a leaf is only about 30 $^0/_0$ full size and reaches a maximum when the leaf has unfolded by 70 $^0/_0$ (Dale and Milthorpe, 1983).

In the kiwifruit, vine leaf production rate increases as the temperature increases to 20 or 30 C. Once formed, the growth of individual leaves is also most rapid in that temperature range (Morgan, Warrington, and Halligan, 1985). Significant changes in the morphology and anatomy of leaves are produced by a decrease in temperature. Morgan,

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Warrington, and Halligan (1985) found that kiwifruit plants which were grown in a constant 10 C and high irradiance environment showed distorted leaf growth and a loss of chlorophyll.

Temperature and Leaf Photosynthesis

The influence of temperature alone on photosynthesis is difficult to evaluate because it is greatly modified by light intensity, CO_2 availability, water stress, and ontogenetic factors. Generally, a C_3 plant under saturating light and ambient CO_2 is relatively insensitive to leaf temperature over the range of between 10 and 30 C (Biscoe and Gallagher, 1977).

The optimum temperature for leaf photosynthesis for most fruit crops lie between 20 and 30 C (eg. Barden, 1971; Crews et.al., 1975; Kriedemann and Canterford, 1971; Kriedemann and Smart, 1971; Seeley and Kammereck, 1977a). Laing (1985) investigated the short term photosynthesis response of kiwifruit leaves to temperature and found 20 C to be the optimum. Increasing either the $p(CO_2)$ or irradiance from low levels will cause an increase in the optimum temperature (Berry and Bjorkmann, 1980). Both will also cause the temperature response to become sharper (eg. Seeley and Kammereck, 1977b).

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The optimum temperature for citrus leaf photosynthesis is between 15 and 20 C in dry air (Kriedemann, 1968b). This is surprisingly low, considering that citrus thrives in hot dry environments under irrigation. Obviously, the enviromental factors which promoted maximum leaf photosynthesis in fruit crops need not necessarily favour the production of high quality fruits.

Acclimation to Temperature

Acclimation occurs when plants are grown at different temperatures. Plants occupying thermally contrasting environments generally exhibit photosynthetic and respiratory characteristics that reflect acclimation to the temperature regimes of their respective environments (Berry and Bjorkmann, 1980).

The potential for acclimation appears to depend on the natural habitat from which the plant originated; thus plants coming from habitats with large seasonal contrasts of temperature tend to acclimatise to new environments better than plants coming from habitats with relatively stable temperatures.

During the process of acclimation there is a threshold temperature at which electron transport became irreversibly inhibited which appears to be a function of growth

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temperature (Farquhar and Kirschbaum, 1985). It was shown by
Armond et.al. (1978) that high growth temperatures conferred
higher thermostability at high temperature while low growth
temperatures resulted in improved performance at temperatures
below the optimum.

Acclimation to Irradiance

Leaves acclimatise to the light environment in which they are
grown (Singh et.al., 1974), and have profoundly different
structure and function which affects their photosynthetic
rates (Patteron, 1980).

The light level within the canopy of kiwifruit vines can
be very low, and interior leaves which grow under these
conditions function slightly above the light compensation
point during most of the day (Grant and Ryugo, 1984b).

Lower rates of leaf photosynthesis of sun plants which
have developed in low PPFD can be explained by the lower cell
volume and cell surface area per unit leaf area of the
thinner shade leaves compared with sun leaves
(Charles-Edwards and Ludwig, 1975; Nobel, 1980; Patterson,
1980). Consequently there is a higher resistance to CO_2
uptake by, and transport within, mesophyll tissues and ~~less~~ fewer
photochemical and biochemical components per unit leaf area.
This then gives rise to a lower light saturation point and

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lower light-saturated rate of photosynthesis (Bjorkman
et.al., 1974). Hence Laing (1985) found that lower
photosynthetic rates were found on shaded (280 uE m^{-2} s^{-1})
kiwifruit vines as compared with non-shaded (650 uE m^{-2} s^{-1})
vines, and the photosynthetic rates of shaded vines also
saturated at lower PPFD.

Effect of Fruit Sink on Photosynthesis

Avery (1975) reviewed the literature and reported that
the majority of photosynthesis measurements have shown that
the rate of CO_2 assimilation by apple leaves associated with
fruits was 45 to 60 percent greater than leaves without
fruits. However, the presence of alternative sinks, such as
stem tissues, have often made it difficult to demonstrate a
clear response of leaf photosynthesis to any localised fruit
demand for carbohydrate.

Wardlaw (1985) believed that it was important to
consider the storage capacity of the plant organs,
particularly leaves, which were capable of acting as a
carbohydrate buffer between periods of high and low sink
demand. One other important consideration to be taken into
account, when making observations on source-sink
correlations, is the possibility of vascular constraints
between the source and sink. This was discussed by Watson

and Casper(1985), who pointed out that sometimes vascular linkages between specific source and sink parts could isolate distinct physiological units within a plant translocation system.

It was thought that the presence or absence of fruits affected the assimilate level in the leaf, which controlled photosynthesis by end-product inhibition. This popular hypothesis was thoroughly reviewed by Neales and Incoll (1968) and Sharkey (1985) discussed a possible mechanism based on the limitation of triose-phosphate utilization.

There were also suggestions that growth regulators were involved (eg. Gifford and Evans, 1981; Lenz, 1979; Wardlaw, 1985). It is highly probable that growth regulators, or other signals emanating from the sink are directed to the organs producing assimilates, and affecting leaf photosynthesis.

2.2 Experiment 2A

2.2.1 Introduction

It is known in other fruit crops that leaf growth may
be co-ordinated with the stages of fruit development
(Lakso, 1984; Nitsch, 1970). This experiment was
designed to investigate the growth of kiwifruit leaves
from emergence until maturity. Simple measurements of
leaf growth were monitored to determine growth curves.

2.2.2 Materials and Methods

Thirty 3-year-old 'Hayward' plants, grown in a
glasshouse, were used.

After bud burst, about 3 indeterminate vegetative
shoots on each plant were selected for treatment. A
single, recently unfolded leaf at about node position 10
on each shoot was tagged. Beginning from 8 Nov 1984, 5 of
these tagged leaves were harvested at random, every 5 to
10 days, and their leaf area and dry weights were
obtained.

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The experiment was concluded on 24 Mar 1985 after leaf growth had stopped. In the course of the experimental period, significant plant developmental events which may affect the partitioning of dry matter in the vine were noted. Full bloom occurred from 10 Nov 1984 for about 2 weeks, with subsequent fruit set and development on fruiting shoots. These fruiting shoots were used for another experiment (experiment 5C) and they were harvested between 2 and 5 Jan 1985. A further developmental change was the appearance of shoot regrowth from axillary buds from about 2 Feb 1985.

Growth curves were fitted to the leaf data using a constrained B-spline curve fitting program (Spriggs, 1986).

2.2.3 Results

Figure 2.1a shows that the kiwifruit leaf lamina expanded rapidly for 80 days, from leaf emergence until full expansion. The maximum growth rate occurred on day 19, at about 5 cm^2 per day (fig. 2.1b). The rate of leaf expansion declined rapidly after day 20. By day 55, about 90 $^0/_0$ of the mean final leaf area was attained. The mean final leaf size was about 202 cm^2.

Figure 2.1. Time course of a kiwifruit cv. Hayward
leaf expansion in a glasshouse environment. The leaf
lamina at the 10th node of indeterminate shoots was
measured (bars indicate s.e.). (a) leaf area
expansion (b) rate of leaf expansion.
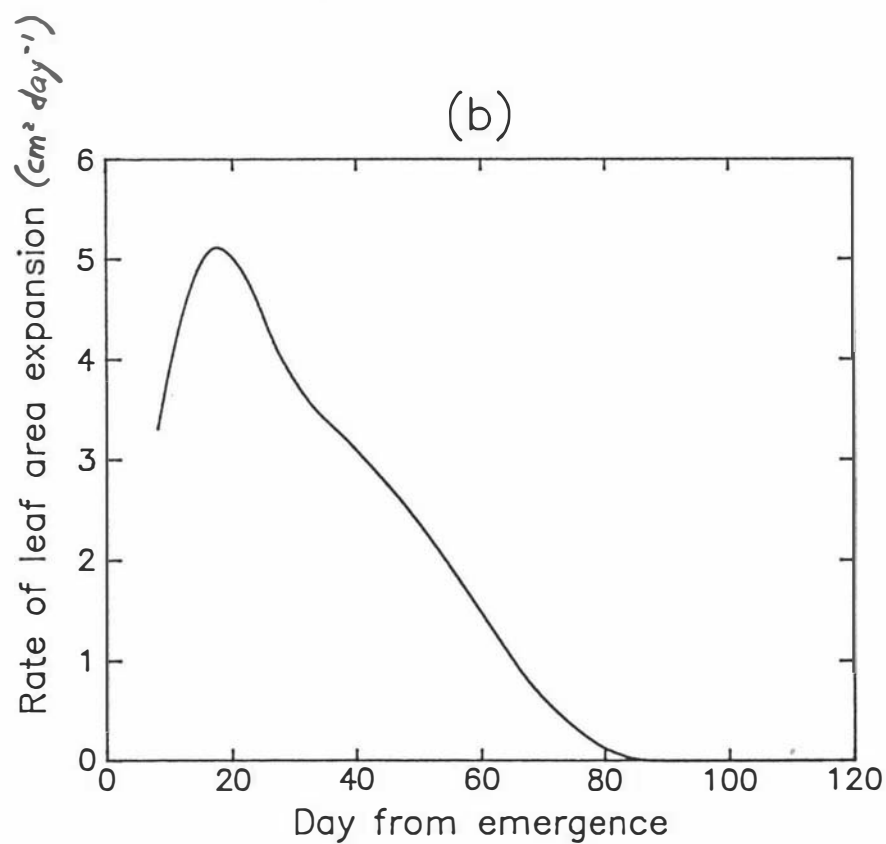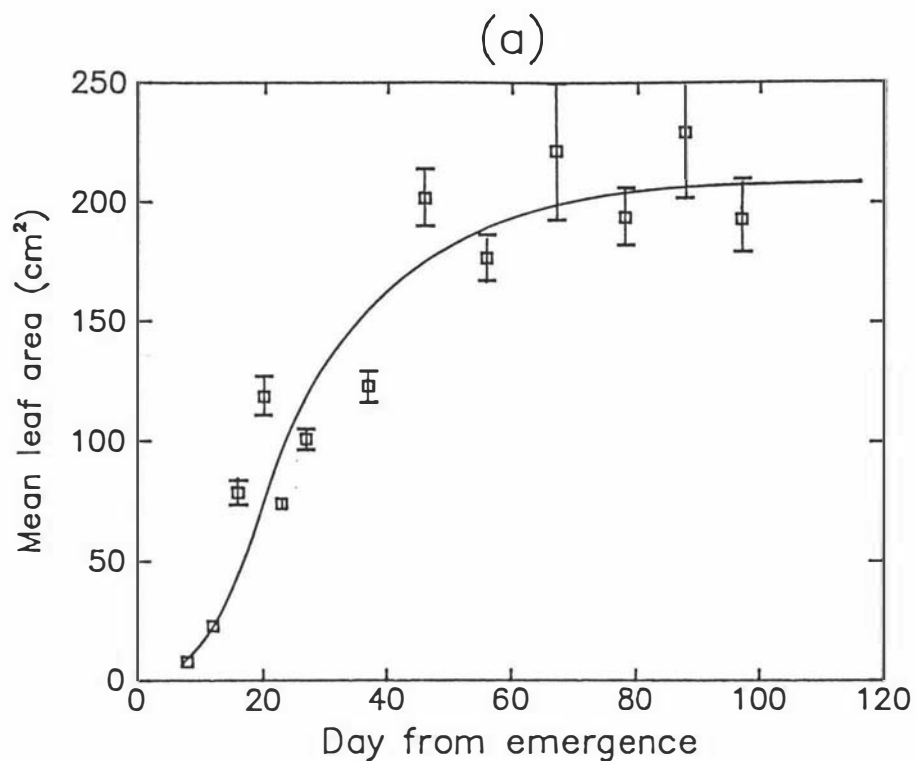
The pattern of leaf dry matter accumulation was irregular (fig. 2.2). Leaf dry weight increased rapidly to about 1.84g on day 46 when the mean leaf size was 154 cm^2. Following that, there was a loss of carbon from the leaf for the next 16 days which was significant ($p < 0.05$). From day 62 onwards however, the leaf was able to recover the carbon it lost and dry weight rose again to about 2g after full expansion.

Figure 2.3 shows that initially, specific leaf weight dropped because leaf area was expanding very rapidly (fig. 2.1b). A minimum of 4.5 mg cm^{-2} on day 17 was observed. The specific leaf weight then increased rapidly until day 40. From that time until day 68, the loss in leaf dry weight caused it to decline again. The mean leaf area at day 40 was 120 cm^2. After the leaf regained its dry weight on day 62 (fig. 2.2), its specific leaf weight also recovered, and reached a steady value of about 9.9 mg cm^{-2} at full leaf expansion.

Figure 2.2. Time course of changes in the dry
weight of a kiwifruit cv. Hayward leaf grown in a
glasshouse environment. The leaf lamina at the
10th node of indeterminate shoots was measured.
Bars indicate s.e.
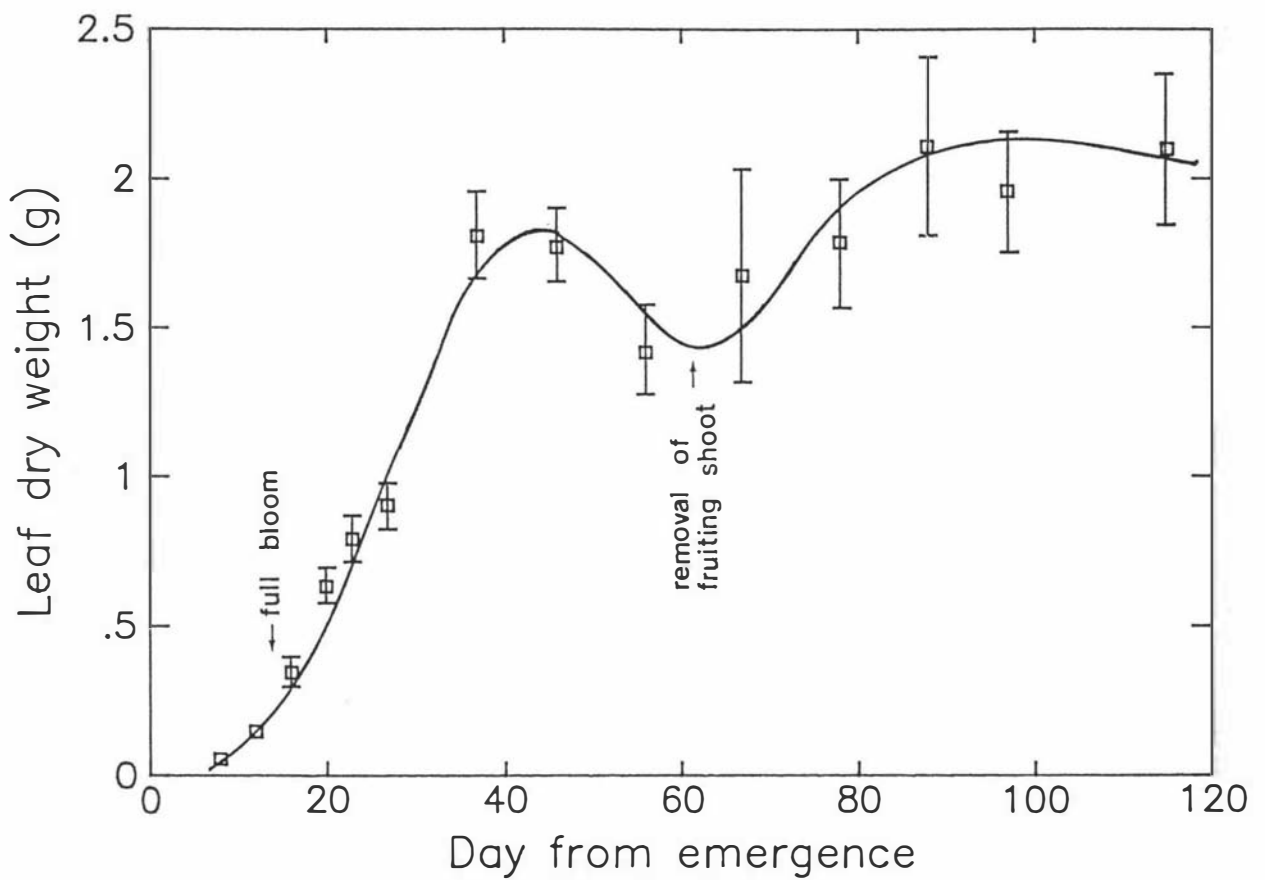
Figure 2.3. Time course of changes in the specific
leaf weight of a kiwifruit cv. Hayward leaf in a
glasshouse environment. The leaf lamina at the
10th node of indeterminate shoots was measured.
Bars indicate s.e.
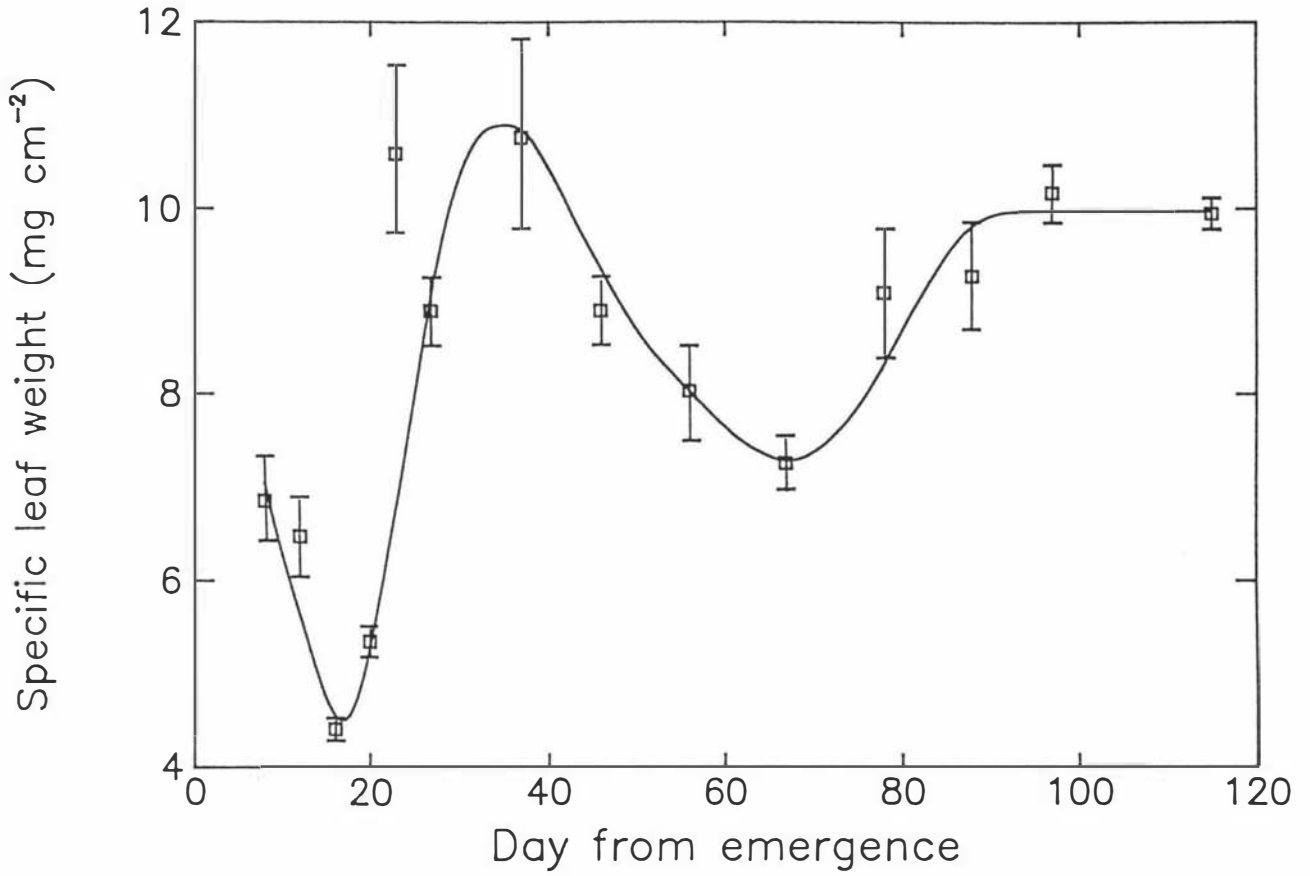
2.3 Experiment 2B

2.3.1 Introduction

In a kiwifruit orchard, climatic fluctuations cause temperature variations which affect vine growth. Light levels however, are altered by orchard management practices such as in the use of natural or artificial shelters (Sale and Lyford, 1987; Snelgar, 1986); and in the amount of within-canopy shading associated with support structures and pruning methods.

Morgan, Warrington, and Halligan (1985) reported significant growth responses in the kiwifruit vine to shade and temperature variables.

In this experiment, the effect of shade and temperature on the photosynthesis of kiwifruit vines was studied. Photosynthetic responses to temperature acclimation were also investigated.

2.3.2 Materials and Method

Trial 1

Five-year-old 'Matua' and 'Hayward' vines were used
in this trial. They were grown in 2 controlled-
environment rooms at either 21/11 C or 17/7 C, day and
night temperatures. Bud burst occurred on 23 Jul 1984,
and the new shoots were trained on horizontal supports so
that every leaf on a shoot received equal irradiance.

Leaf photosynthesis measurements were recorded during
the petal fall growth stage, on 1 Nov 1984 and 11 Nov
1984.

Trial 2

Rooted cuttings of 'Hayward' and 'Tomuri' were used.
A low light treatment was imposed on half the plants by
shading with a neutral density shade cloth. The average
PPFD for this treatment was 280 uE m^{-2} s^{-1}.

The plants were grown in 5 growth rooms, each
maintained at a constant day and night temperature of 10,
15, 20, 25, and 30 $\pm$ 0.5 C. Male plants were grown in
all but the 15 C growth temperatures, and only in a high

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PPFD environment. Vapour pressure deficit in the growth

rooms was maintained at a constant 0.8 kPa for all the

rooms, which gave relative   humidities of 35, 53, 66, 75

and 81 ($\pm$ 5) $^0/_0$ respectively. A 14 hour photoperiod was

imposed throughout the period of the experiment.

Each plant was pinched to one bud so that a single

lateral was trained vertically on to stakes. To avoid

positional effects, the plants in each room were rotated

periodically (see Morgan, Warrington, and Halligan, 1985).

The plants were also lowered in the room to maintain the

PPFD at mid plant height.

Photosynthesis measurements were taken when there

were 10, 16, 22, and 28 emerged leaves. As growth rates

in each temperature treatment differed, the day number for

the final measurements, that is when 28 leaves had

emerged, in the 10, 15, 20, 25 and 30 C environments was

82, 57, 40, 41, and 41 days respectively.

On each plant, photosynthesis measurements were taken

from every alternate leaf. A replicate of 4 plants in the

high PPFD (650 uE m^{-2} s^{-1}) and 4 plants in the low PPFD

(280 uE m^{-2} s^{-1}) were measured in each growth room.

Trial 3

The plant materials and growth environments in this

experiment were similar to trial 2, except that only the 10, 20 and 30 C climate rooms were used. On 11 Oct 1983, four plants from the high PPFD (650 uE m^{-2} s^{-1}) environment, and four plants from the low PPFD (280 uE m^{-2} s^{-1}) environment, in the 30 C room, were transferred to 20 C growth rooms in the same respective light regime. These plants were denoted as '30-20 C' treatments. A similar transfer of plants from 10 C growth temperature to 20 C took place one month later, on 11 Nov 1983. These plants were denoted as '10-20 C' treatments. All the plants had 28 emerged leaves at the time of shifting. In each of the 10, 20 and 30 C rooms, an equal number of plants which were not transferred was used as 'controls'. These plants were denoted as 10, 20, and 30 C treatments, respectively.

Photosynthesis measurements were carried out at 5 time intervals for both the plants which remained in the same growth temperatures, as well as those which were transferred. The 5 time intervals were day number 0, 3, 8, 15, and 24 from the beginning of plant acclimation.

Stomatal resistance of the leaves was monitored at day 24 from shifting the plants. At the conclusion of the experiment, the leaves of each plant were harvested. Leaf chlorophyll, leaf area, and specific leaf weight were determined.

2.3.3 Results

Photosynthesis Model

Multiple regression analysis of the data from horizontally trained shoots (trial 1) provided partial regression coefficients which related the independent effect of leaf position (leafno) and net photosynthesis (PS) by the equation:

$$PS \text{ (leaf effect)} = 3.09317 \times leafno - 2.13791 \times leafno^2$$

From this, the proportion of total photosynthesis which was attributed to leaf position was obtained for each node, and a function which corrected for the effect of leaf position on photosynthesis was derived:

$$Y = 119.09032 - 24.4684 \times leafno + 1.18797 \times leafno^2$$

where Y= percentage correction of photosynthesis at each leaf node position.

This function was then applied to the photosynthesis data of trial 2 so as to remove the confounding effects of light attenuation and leaf position on the vertically trained shoots.

Consequently, a simple photosynthesis model was derived from multiple regression analysis (r^2=38.4). Thus:

$$r^2 \text{ change}$$

Net leaf PS = 166 ($\pm$ 75)

+0.55334 ($\pm$ 0.04863) x light   29.48

+0.98931 ($\pm$ 0.10112) x leaf area   8.62

−1.42980 ($\pm$ 0.84597) x leaf age   0.23

−1.32008 ($\pm$ 2.00653) x temperature 0.03

+14.2333 ($\pm$ 28.2787) x shade   0.02

Light was the single most important determinant of kiwifruit leaf photosynthesis in the set of environmental conditions experimented, accounting for up to 77 $^0/_0$ of the variance.

Leaf area and leaf age were relatively more important than the other environmental conditions such as growth temperature, and shade.

Male and Female Vine Photosynthesis

Multiple regression analysis, using the sex of the
plants as a dummy variable, showed that horizontally
trained 'Matua' shoots had significantly higher
photosynthetic rates ($p < 0.05$) than 'Hayward' shoots in
trial 1. At 17 C, the photosynthetic rate of 'Matua' was
452 $ugCO_2$ m^{-2} s^{-1}, compared with 392 $ugCO_2$ m^{-2} s^{-1} for
'Hayward'. At 21 C, they were 444 and 319 $ugCO_2$ m^{-2} s^{-1},
respectively.

Multiple regression models of male and female vine
photosynthesis in trial 2, at day 40, were also compared.
The results showed that they were not significantly
different ($F_{2,171} = 3.07$; $p > 0.05$). The mean net
photosynthesis of 'Tomuri' plants at day 40 was 692 $ugCO_2$
m^{-2} s^{-1}, while that of 'Hayward' plants was 759 $ugCO_2$
m^{-2} s^{-1}.

Effect of Shade on Photosynthesis

Quadratic regressions were fitted to the relationship
between net leaf photosynthesis and leaf position for
shaded (low PPFD) and non shaded (high PPFD) plants, at
each growth temperature in trial 2. A comparison of the
relationships is shown in figure 2.4. Maximum

Figure 2.4. Comparison of fitted regressions of leaf photosynthesis of kiwifruit cv. Hayward, grown at 10, 15, 20, 25, and 30 C, and at either low PPFD (———, 280 uE m^{-2} s^{-1}) or high PPFD (-----, 650 uE m^{-2} s^{-1}).

40
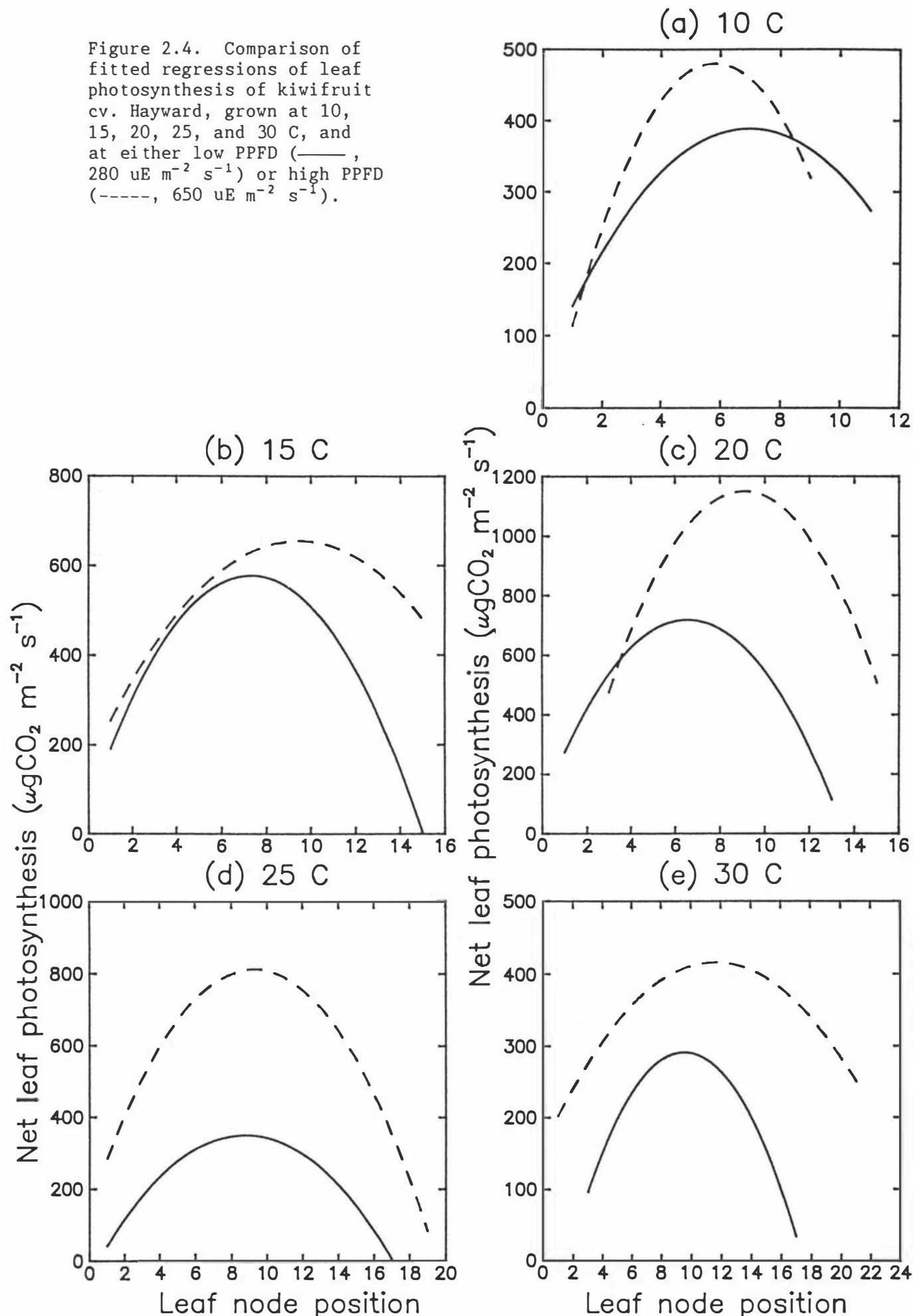
photosynthetic values (P_{max}) for each shade and
temperature treatment (table 2.1) showed that non-shaded
plants had higher photosynthetic rates than shaded plants.
The difference was more significant ($p < 0.05$) at the higher
temperatures, and could be as much as 50 $^0/_0$.

Photosynthetic Response to Temperature

Table 2.1 shows clearly that the optimum temperature
for kiwifruit photosynthesis is 20 C. The response of
non-shaded plants to temperature was sharp, as compared
with shaded plants (fig. 2.5).

Quadratic regressions between the total net
photosynthesis per plant and day number were fitted for
each temperature and shade treatment. From these, the
cumulative net photosynthesis after 40 days of growth was
calculated. As can be seen from table 2.2, the results
indicate that there was an even greater contrast in the
effect of growth temperature on the total net CO_2
assimilation. At day 40, the total net CO_2 assimilation
at 10 C was very low (5.76 and 7.89 g for low and high
PPFD, respectively). This increased by large amounts with
increasing temperature until the maximum at 20 C (97.93
and 162.63 g, respectively). It then declined so that at
30 C, the total net photosynthesis decreased by half the

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Table 2.1. Estimated P_{max} values ($ugCO_2$ m^{-2} s^{-1}) of kiwifruit cv. Hayward leaf, grown under 10, 15, 20, 25, and 30 C, at either low PPFD (280 uE m^{-2} s^{-1}) or high PPFD (650 uE m^{-2} s^{-1}) conditions. S.E. in parenthesis.

| | Temperature (deg C) | | | | |
	10	15	20	25	30
High PPFD	431(49)	656(90)	1123(93)	763(120)	419(41)
Low PPFD	369(34)	572(59)	667(77)	358(72)	245(65)
	p=0.31	0.45	0.00	0.01	0.04

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Figure 2.5. Temperature response curve of kiwifruit
cv. Hayward leaf photosynthesis (P_{max}) under
low PPFD ($\square$, 280 uE m^{-2} s^{-1}) and high PPFD ($\triangle$, 650
uE m^{-2} s^{-1}) conditions.

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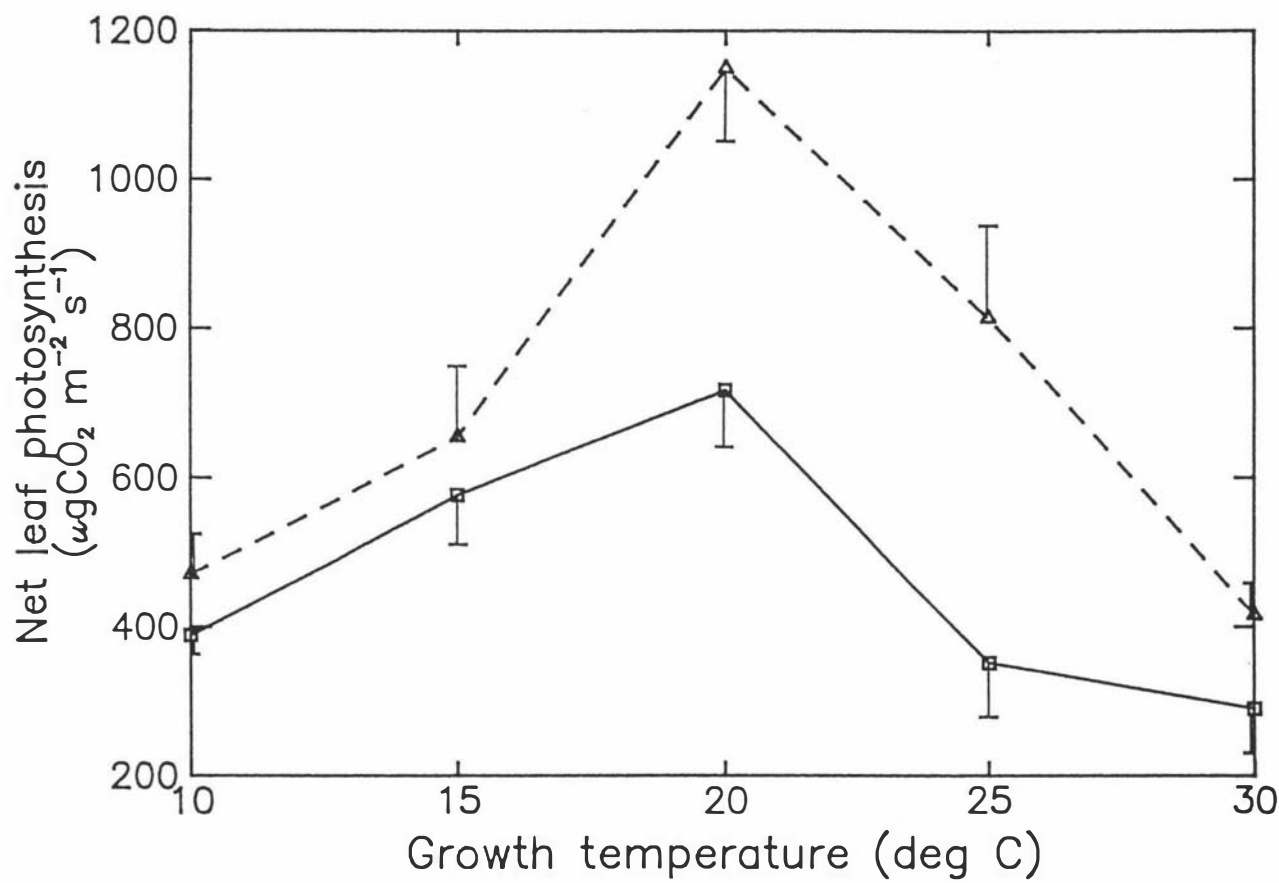
Table 2.2. Estimates of cumulative photosynthesis for kiwifruit cv. Hayward grown for 40 days under constant temperatures of 10, 15, 20, 25, and 30 C, and at either low PPFD (280 uE m^{-2} s^{-1}) or high PPFD (650 uE m^{-2} s^{-1}) conditions. * Data for total dry weight accumulation per plant from Morgan et.al.(1985).

		Temperature (deg C)				
		10	15	20	25	30
Total net CO_2 assimilation	High PPFD	7.89	44.89	162.63	–	86.04
per plant (g)	Low PPFD	5.76	36.61	97.93	82.01	47.07
Total dry weight accumulation per	High PPFD	1.5	15.0	33.3	–	19.2
plant (g) *	Low PPFD	1.0	6.2	18.4	22.0	12.6

amount at 20 C. The effect of low PPFD was a significant reduction in the total net CO_2 assimilation at each temperature.

Comparison of Photosynthesis of Transfer Plants

At each time period where photosynthesis measurements were recorded in trial 3, multiple regression analysis on the effect of irradiance, temperature, and leaf node position on net photosynthesis was carried out. The effect of plant transfer was also included in the analysis as a dummy variable, so that the statistical significance of its reduction in the residuals of the regression models could be used as an indication of the adaptation of a transfer plant to its new growth environment. Each of these comparisons was recorded in the form shown in table 2.3.

The photosynthesis of transfer plants in 10-20 C treatments was significantly different from those in 10 C treatments after 8 days from transfer, in shaded conditions. In non-shaded conditions, this took only 3 days.

When plants from the 10-20 C treatment were compared with those in the 20 C treatment, it can be seen that in a shaded environment the transfer plants were able to very

Table 2.3. Summary of the statistical significance of multiple regression comparisons between the photosynthesis of transfer (ie. 10-20 C and 30-20 C treatments; see text) and control (ie. 10, 20, 30 C treatments) kiwifruit cv. Hayward plants at 0, 3, 8, 15, or 24 days from transfer, under low (280 uE m^{-2} s^{-1}) or high (650 uE m^{-2} s^{-1}) PPFD conditions. (ns, not significant; *, 0.05 > p > 0.01; ** p < 0.01).

		Temperature Comparisons			
		10-20 C vs 10 C	10-20 C vs 20 C	30-20 C vs 30 C	30-20 C vs 20 C
	Day from transfer				
	0	*	**	–	–
LOW	3	ns	ns	**	**
	8	**	ns	**	ns
PPFD	15	**	ns	**	*
	24	**	ns	**	ns

....

	Day from transfer				
	0	ns	**	–	–
HIGH	3	**	**	ns	ns
	8	**	**	**	**
PPFD	15	**	**	**	*
	24	**	ns	**	ns

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quickly acclimatise to the new growth temperature. They
took only 3 days, whereas under high PPFD, the same
acclimation took 24 days.

The acclimation of the 30-20 C transfer plants to the
20 C growth temperature was not so clear. However, it
appeared that under a low PPFD environment, the
photosynthesis of a 30-20 C transfer plant became markedly
different from its original 30 C environment only 3 days
after transfer. On the other hand, it took about 8 days
for the photosynthesis of transfer plants to be similar to
that of plants which were continuously grown in 20 C
environment.

In the non-shaded treatments, it took 8 days for the
30-20 C transfer plants to be significantly distinct from
their original 30 C environment. On the other hand, 24
days was needed before the photosynthesis characteristics
of transfer plants were similar to the 20 C treatments.

Change in P_{max} with acclimation

Plots of net photosynthesis with leaf insertion
gradients were carried out for every set of data collected
in trial 3. Quadratic equations were then fitted to the
data and estimations of P_{max} at the prevailing irradiance
were subsequently computed from the maximas of the fitted

curves. All the estimated P_{max} values are presented in table 2.4.

Changes in the maximum photosynthesis rate in a transfer plant could also be used to indicate the photosynthetic acclimation of plants to new growth temperatures. It appeared that under a low PPFD environment, the P_{max} value of plants in the 10-20 C transfer treatment were similar to control plants in 10 C and 20 C treatments. Their P_{max} values were in the range of 200 to 480 $ugCO_2$ m^{-2} s^{-1}. A plant in the 30 C treatment has a P_{max} value between 200 to 370 $ugCO_2$ m^{-2} s^{-1}, but upon transferring to a 20 C environment (ie. 30-20 C treatment), its P_{max} value was able to exceed 400 $ugCO_2$ m^{-2} s^{-1} after 3 days.

Changes in P_{max} with temperature acclimation were more distinct under non-shaded conditions. Table 2.4 shows that the range of P_{max} values in the 10 and 30 C control treatments were below 600 $ugCO_2$ m^{-2} s^{-1} whereas at 20 C, P_{max} exceeded 600 $ugCO_2$ m^{-2} s^{-1}. When plants were transferred from 10 C to 20 C growth temperatures (ie. 10-20 C treatments), their P_{max} value increased within 3 days, from 459 to 869 $ugCO_2$ m^{-2} s^{-1}. A similar acclimation was observed for the 30-20 C transfer plants, and they took 15 days before P_{max} increased from 460 to 805 $ugCO_2$ m^{-2} s^{-1}.

Table 2.4. P_{max} values ($ugCO_2$ m^{-2} s^{-1}) of transfer (ie. 10-20 C and 30-20 C treatments; see text) and control (ie. 10, 20, 30 C treatments) kiwifruit cv. Hayward plants, at 0, 3, 8, 15, and 24 days from transfer, under low (280 uE m^{-2} s^{-1}) and high (650 uE m^{-2} s^{-1}) PPFD conditions.

		Treatment				
		10 C	10-20 C (transfer)	20 C	30-20 C (transfer)	30 C
	Day from transfer					
	0	422	461	406	281	281
LOW	3	472	401	216	476	370
	8	298	453	321	286	206
PPFD	15	342	452	408	290	309
	24	392	410	439	473	309
	Day from transfer					
	0	389	459	651	460	460
HIGH	3	497	869	481	476	429
	8	220	590	716	425	323
PPFD	15	456	784	796	805	521
	24	475	688	645	563	343

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Changes in Other Leaf Characteristics

Differences between kiwifruit leaves which developed in shaded and non-shaded environments in trial 3 are shown in table 2.5.

Shading increased the stomatal resistance to CO_2 uptake, although this was not significant (p=0.25). Lower stomatal resistance values were observed at 20 C in both low and high PPFD environments (7.4 and 9.5 s cm^{-1}, respectively).

The effect of shading did not alter the chlorophyll content of kiwifruit leaves (p=0.19). A similar insensitivity to temperature was also apparent at low PPFD environments. In high PPFD environments low temperature caused visual signs of leaf chlorosis which was reflected in the low leaf chlorophyll content in those leaves (35 ugChl per cm^2).

The leaves of 10 C plants in low PPFD environment was visually thicker, hence its specific leaf weight was also highest (9.02 mg cm^{-2}). Otherwise, in both high and low PPFD conditions, the highest specific leaf weights were observed for the plants in the 20 C growth temperature.

Leaf expansion in the shaded environment appeared to be rather insensitive to temperature (p=0.77). By

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Table 2.5. Leaf characteristics of transfer (10-20 C and 30-20 C treatments; see text) and control (10, 20 and 30 C treatments) kiwifruit cv. Hayward plants grown under low (280 uE m^{-2} s^{-1}) and high (650 uE m^{-2} s^{-1}) conditions. S.E. in parenthesis.

LOW PPFD

	Growth temperatures			transfer	
	10 C	20 C	30 C	10-20 C	30-20 C
rs (s cm^{-1})	11.9(0.7)	7.4(0.2)	11.3(0.6)	8.7(0.2)	11.0(0.6)
Mean leaf area (cm^2)	218(18)	229(12)	195(14)	212(19)	220(25)
SLW (mg cm^{-2})	9.02(.97)	6.31(.66)	5.01(.13)	7.05(.35)	6.41(.48)
Chlorophyll (ugChl cm^{-2})	45.2(.4)	55.4(.2)	41.9(.7)	48.7(.3)	43.2(.8)

HIGH PPFD

	10 C	20 C	30 C	10-20 C	30-20 C
rs (s cm^{-1})	10.9(0.8)	9.5(0.5)	10.0(0.2)	7.9(0.2)	9.8(0.5)
Mean leaf area (cm^2)	147(17)	195(6)	246(5)	207(17)	246(5)
SLW (mg cm^{-2})	7.71(.46)	8.39(.12)	7.25(.29)	8.99(.53)	7.96(.67)
Chlorophyll (ugChl cm^{-2})	35.7(.4)	53.8(.1)	53.0(.1)	52.9(.2)	55.8(.9)

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contrast, the mean leaf size at high irradiance varied from 147 cm^2 at 10 C to 246 cm^2 at 30 C (table 2.5).

Plants which were stressed by the low, 10 C temperature, and high irradiance treatments suffered not only a reduction in leaf expansion and loss of chlorophyll but also had reduced specific leaf weight (7.71 mg cm^{-2}). However, after 24 days of acclimation to 20 C, these stressed plants increased their leaf chlorophyll to 52.9 ug Chl cm^{-2}, which was similar to that found in 20 C treatments (53.8 ug Chl cm^{-2}). The stressed leaves also regained their full photosynthetic potential quite early so that further leaf expansion (from 147 cm^2 to 207 cm^2) and accumulation of dry matter (from 7.71 to 8.99 mg cm^{-2}) occurred.

Transfer plants from 30–20 C treatments also showed signs of acclimation to the new 20 C growth temperature. Their stomatal resistance, mean leaf size, specific leaf weight, and leaf chlorophyll content were mostly intermediate between the values for 20 and 30 C.

2.4 Experiment 2C

2.4.1 Introduction

Differences between the leaves of fruiting and non-fruiting shoots in the accumulation of dry matter were reported by Smith et.al. (1986). This experiment was designed to investigate if there was also a leaf photosynthetic response to the presence of fruits on a kiwifruit shoot.

2.4.2 Materials and Methods

Plant Materials

A 7-year-old 'Hayward' vine, in a commercial orchard block at Levin was used in this experiment. Four fruiting and 4 non-fruiting, indeterminate shoots in well exposed positions were selected. Each shoot had about 5 to 7 leaves and each fruiting shoot carried 3 fruits. At the time of photosynthesis measurement, fruit sizes were about 85 cm^3, probably at about stage III of fruit growth

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(experiment 3A).

Data Collection

Photosynthesis measurements were taken between 2 and 4 pm on 16 Mar 1985. The prevailing weather conditions at that time were a cloudless sky, negligible wind, and 20 C leaf temperature.

2.4.3 Results

Quadratic regressions were fitted to the data of net leaf photosynthesis with incident PPFD for fruiting and non-fruiting shoots (fig. 2.6). The two curves were not significantly different (F 1,85 = 6.81; p>0.05). The maximum photosynthesis rate for Hayward kiwifruit leaves was about 657 ugCO$_2$ m^{-2} s^{-1}.

Figure 2.6. Comparison of regression curves fitted
to leaf photosynthesis measurements of fruiting and
non-fruiting shoots of kiwifruit cv. Hayward at
different PPFDs and 20 C leaf temperature.
△ ,-------, non-fruiting shoot; □ , ———— ,
fruiting shoot.
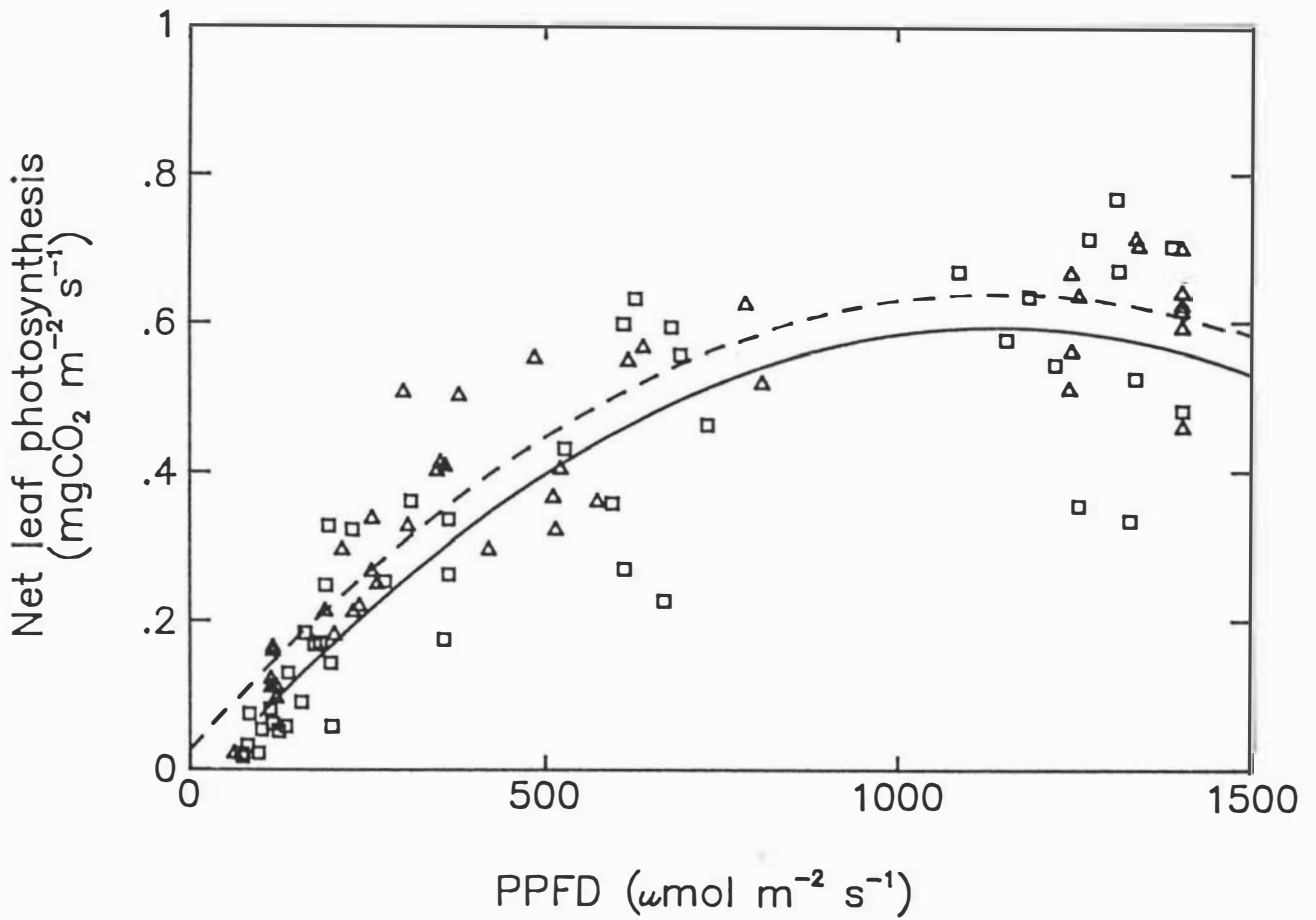
2.5 Discussion

2.5.1 Kiwifruit Leaf Growth

The growth of the kiwifruit leaf was sigmoid (fig. 2.1a). Leaves expanded rapidly for 80 days. Similarly, Smith et.al. (1986) observed that the fastest rate of leaf growth occurred for 70 days, from emergence to fruit set.

The irregularity in leaf dry weight and specific leaf weight from about day 40 to 90 was significant. There was no evidence of any anomaly in the weather records to suggest that the plants were stressed, although it was possible for the glasshouse vents or the automatic irrigation supply to malfunction. During that period, leaf expansion was still progressing at a rate of about 3.1 cm^2 per day (fig. 2.1b). The effect was therefore unlikely to be that of water stress, which primarily causes a reduction in leaf expansion through a decrease in leaf turgor pressure (Terry et.al., 1983).

Plant development is an integration of phases of vegetative and reproductive growth (Goodwin, 1978; Wareing, 1978). Growth rates of the vegetative parts of a

plant may be inhibited during active fruit development (Nitsch, 1970). For example, Lakso (1984) reported a dramatic decline in the daily leaf area increment of apple trees at the onset of full bloom. The loss of carbon from the kiwifruit leaves from about day 40 appeared to correspond with the initial stage of fruit growth when absolute growth rates were very high (experiment 3A). The recovery in leaf dry matter from about day 65 also coincided with the removal of several fruit sinks and shoot meristems when entire fruiting shoots were harvested (experiment 5C). It therefore appears that carbon was exported out of the leaf in response to the fruit demand for growth. Since the mean leaf area at day 40 was 120 cm^2, it can be suggested that the kiwifruit leaf became a net exporter of carbon when it reached about 60 $^0/_0$ full size.

Smith et.al.(1986) worked with 13-15 years old vines grown in the field and reported differences in the growth of leaves from fruiting and non-fruiting shoot after fruit set. Closer examination of their data indicated a very slight decrease in leaf dry weight, on both fruiting and non-fruiting shoots, for 2-3 weeks immediately after fruit set. The response in experiment 2A could be similar, given that the age of the vines, the environmental conditions, and node positions of the measured leaf were

different.

2.5.2 Light Responses and Shade Effects

Wareing (1979) stated that, in many temperate crops, photosynthesis was relatively insensitive to temperature over the optimum range of 20 to 30 C so that the yield of temperate C_3 plants was limited mainly by the availability of light. This study found that light was the single factor that accounted for the greatest proportion (77 $^0/_0$) of the variance in kiwifruit leaf photosynthesis. It was also shown that a reduction in the mean PPFD from 650 to 280 uE m^{-2} s^{-1} reduced the net photosynthesis rate of kiwifruit significantly, particularly at the optimum temperature (fig. 2.5). The leaf stomatal resistance of shaded vines was also higher than non-shaded vines (table 2.5).

It is frequently reported for other crops that shading decreases the chlorophyll content of leaves (eg. Ghosh, 1973; Terry et.al., 1983). Although the reduction in photosynthesis between shaded and non-shaded leaves was as much as 50 $^0/_0$ (table 2.1), this was not related to the amount of chlorophyll in the leaf. Table 2.5 shows that shaded and non-shaded kiwifruit leaves had similar amounts

of chlorophyll per unit area. The results of Grant and
Ryugo (1984b) agree with this observation.

Barden (1977) pointed out that whereas leaf
chlorophyll and leaf photosynthesis were usually poorly
correlated in the apple tree, specific leaf weight was a
good index of photosynthetic potential. Similarly, in the
kiwifruit vine, there was no relationship between the
chlorophyll content of kiwifruit leaves and the effect of
shading on their photosynthesis, but the specific leaf
weight of leaves which were acclimatised to shaded
environments was significantly lower (table 2.5).

Under shaded conditions, the kiwifruit vine showed
lower relative growth rates and reduced dry matter
accumulation (Morgan, Warrington, and Halligan, 1985).
Zelitch (1982) reported that the total net photosynthesis
and dry matter accumulation of a plant were closely
related. This can be seen in the correlation between
total net photosynthesis of a kiwifruit vine, and its
total dry weight at high and low PPFD (table 2.2).

Table 2.5 shows that the specific leaf weight of
leaves acclimatised to shaded environments was
significantly lower ($p < 0.05$) than non-shaded leaves.
Barden (1974,1977) showed that specific leaf weight of a
fully expanded apple leaf could alter when it is exposed
to changing light levels. Similarly, kiwifruit leaves

responded to their light environment by changing their specific leaf weights.

Excessive shade conditions in the orchard, such as caused by wind breaks, are therefore likely to limit the potential dry matter production of the kiwifruit vine. This is unusual when one considers that in its natural habitat the kiwifruit vine thrived in gullies, under tree canopies, or on the edge of forest where they were shaded for much of the day (Ferguson, 1984).

The pattern of dry matter production and distribution can also be affected significantly by the manner in which the vine canopy is managed. Training and pruning systems have to be aimed at the removal of excessive within-canopy shading.

2.5.3 Temperature Responses

The response of kiwifruit leaf photosynthesis to temperature (fig. 2.5) is typical of most temperate fruit crops, for example: grape (Possingham, 1970); apple (Lakso and Seeley, 1978; Watson et.al., 1978); pear (Kriedemann and Canterford, 1971); and peach (Crews et.al., 1975). Maximum photosynthesis was observed at the growth temperature of 20 C. This agreed with the optimum

short-term response temperature reported by Laing (1985).

He also observed a large degree of plasticity in the

temperature response curve of kiwifruit leaves, whereby

the temperature optimum shifted by 0.58 degrees per degree

shift in growth temperature.

It can be seen from table 2.5 that significant

differences in the stomatal resistance of kiwifruit leaves

were clearly in response to growth temperatures.

Corresponding to the highest photosynthetic rates at 20 C

was the lowest leaf stomatal resistance (7.4 and

9.5 s cm^{-1} for low and high PPFD conditions, respectively).

Grant and Ryugo (1984b) also reported a similar

correlation between net photosynthesis and stomatal

resistance.

The optimum temperature for kiwifruit growth and

total photosynthesis was similar (table 2.2). This

appeared to be different from most plants where growth

processes like leaf initiation and leaf growth generally

show higher temperature minima and higher temperature

optimum than photosynthesis (Monteith and Elston, 1971).

It also meant that the kiwifruit vine had the advantage of

early canopy establishment in the spring since unlike most

crops, its crop growth rate was not limited by the rate at

which assimilates can be utilised in growth. In other

words, dry matter production of the kiwifruit during

spring was not 'sink limited'.

The balance between total net photosynthesis and respiration was highest at 20 to 25 C (table 2.2). Total net photosynthesis at 10 C was minimal, and the total dry weight at day 40 had only just recovered from respiratory losses associated with initial shoot growth (Morgan, Warrington, and Halligan, 1985). According to Zelitch (1982) instantaneous photosynthesis measurements on a single leaf may not correlate positively with dry matter accumulation. This study however showed that the temperature response of both instantaneous photosynthesis (table 2.1) and total net photosynthesis (table 2.2) of the kiwifruit vine were quite similar, and closely related to total dry matter accumulation.

2.5.4 **Light and Temperature** Interactions

It was found in the apple tree that the optimum temperature for photosynthesis increased with irradiance (Seeley and Kammereck, 1977b). This study however, showed that although the temperature response of kiwifruit leaves showed a broad optimum when shaded (fig. 2.5), maximum photosynthesis occurred at 20 C regardless of whether the vines were grown under low (280 uE m^{-2} s^{-1}) or high (650

uE m^{-2} s^{-1}) PPFD conditions (table 2.1).

In a non-shaded environment, the highest specific leaf weight was observed at the optimum for growth, ie. 20 C (table 2.5). Shaded vines however, showed the highest specific leaf weight when they were grown in 10 C conditions (9.02 mg cm^{-2}). This anomaly may be caused by the accumulation of soluble carbohydrates and reduced translocation rates which is likely to happen at low temperatures (Evans et.al., 1964).

Kiwifruit leaf growth and leaf chlorophyll content were insensitive to growth temperatures under shaded conditions (table 2.5). However, under a high PPFD environment, stress symptoms were evident at 10 C. The leaf area (147 cm^2) was the smallest, and leaf chlorophyll content was significantly lower (35.7 ug Chl cm^{-2}) than other treatments. Morgan, Warrington, and Halligan (1985) attributed the condition of the leaves to chilling injury, although it is also likely to have been the result of prolonged photoinhibition (Greer et.al. 1987).

2.5.5 Acclimation to Temperature

Kiwifruit vines grown at 10 or 30 C acclimate to a
20 C growth environment within 3 to 24 days (table 2.3).
Shaded plants acclimate quicker (3 to 8 days), probably
because of the broad temperature optimum for
photosynthesis at low irradiances (fig. 2.5). Other
plant species also take a few days to acclimatise to new
growth temperatures. For example, Nerium oleander
required one to two days to acclimatise from 20 to 45 C
(Osmond et.al., 1980), and photosynthetic changes in
tropical grass and legume leaves which developed at 20 C
were completed after 15 hours overnight in a new
temperature of 30 C (Ludlow and Wilson, 1971). The
rapidity of these photosynthetic adjustments suggested
that biochemical processes were likely to be involved. A
plant is acclimatised to a certain temperature by changing
its ratio of carboxylase activity and electron transport
capacity to a fine balance so that there was an
enhancement of their thermal stability (Farquhar and
Kirschbaum, 1985).

The time period for plants to acclimatise to 20 C
from either 10 or 30 C was more gradual (up to 24 days)
when comparisons of multiple regression analysis were used
(table 2.3). This compared with the shorter time periods

(3 to 8 days) when changes in P_{max} values were used (table 2.4). The regression analysis, unlike changes in P_{max}, would have included components of plant variability in the leaf structure which required longer periods for change. P_{max} as a measure of photosynthetic acclimation to temperature in mature leaves was unlikely to have been greatly dependent on changes in leaf structure. For example, vines which were transferred from the stress conditions of high PPFD and 10 C, showed an immediate improvement (3 days) in adjusting its P_{max} value (table 2.4). However, at the end of the acclimation period (24 days), the leaf area on these vines expanded from 147 to 207 cm^2; specific leaf weight increased from 7.71 to 8.99 mg cm^{-2}; and leaf chlorophyll increased from 35.7 to 52.9 ug Chl cm^{-2} (table 2.5).

Table 2.5 also shows that the mean leaf size, specific leaf weight, and chlorophyll content for all the other transfer plants approached values which were close to those in the 20 C treatment. Some changes in stomatal resistance were also evident although according to Ludlow and Wilson (1971) and Williams (1974), stomata only played a minor role in determining the photosynthetic acclimation to low and high temperatures. The residual resistance was considered to be more important.

Ferguson (1984) reported that in their natural

habitat, kiwifruit plants are subjected to large day and night variations of up to 15 C difference, and summer and winter maxima and minima of up to 50 C difference. It is therefore not surprising that the results of this study confirmed that the kiwifruit vine has a high potential for temperature acclimation.

2.5.6 Male and Female Photosynthesis

Field observations suggested that the male kiwifruit vines had more vigour than female vines (Davison, 1987; Sale, 1980). This may be because unlike female vines, male plants do not have to partition substantial amounts of dry matter towards fruit growth and development. The data of Morgan, Warrington, and Halligan (1985) on one-year-old cuttings of male and female plants showed significantly higher growth rates for male plants. In this study, 'Matua' showed higher photosynthetic rates than 'Hayward'. However, no significant difference between 'Tomuri' and 'Hayward' was found.

2.5.7 Effect of Fruit Sinks on Leaf Photosynthesis

Evidence for the effects of fruit demand on photosynthesis has been equivocal. It probably depends on different factors such as: the starch levels of the leaf (Wardlaw, 1985); stage of fruit development during the season (Hansen, 1970b); the type of shoots from which leaf photosynthesis is monitored (Watson et.al., 1978); or the presence of constrained vascular linkages between leaves and fruits (Watson and Casper, 1984). It is perhaps because of these reasons, and the difficulty in isolating the leaf-fruit system from the presence of other alternative sinks, that the comparisons of photosynthesis data in this (fig. 2.6), and other experimental work (eg. experiments 8A, 8B) have invariably failed to distinguish any effect of assimilate demand on kiwifruit leaf photosynthesis.

The maximum rate of photosynthesis in this study was 657 ugCO$_2$ m^{-2} s^{-1}. Grant and Ryugo (1984b) reported P$_{max}$ values of about 530 ugCO$_2$ m^{-2} s^{-1} (12 umol m^{-2} s^{-1}). Correlations between fruit development and net photosynthesis rate have often been reported (eg. Chalmers et.al.,1975; Crews et.al., 1975; Lenz, 1979). In the work of Grant and Ryugo (1984b), measurements were taken in late August, probably during a stage of fruit

growth which was different from this study.

When DeJong et.al.(1984) studied the effects of nitrogen on kiwifruit leaf photosynthesis they found differences of as much as 100 $^0/_0$ in P_{max}. It was therefore possible that the discrepancies in P_{max} values was due to variations in leaf mineral nutrition or other environmental differences.

CHAPTER THREE

FRUIT DEVELOPMENT

3.1 Introduction

Fruits are important determinants in the partitioning of
dry matter (Gifford and Evans, 1981). It is therefore useful
to know the fruit growth pattern of the kiwifruit.

Fruit Growth Pattern

Fruit development is a complex growth process which is
slow and variable. Several reviews have been written on the
subject, eg: Bollard (1970), Coombe (1976), Crane (1964),
and Nitsch (1970,1971).

Two types of fruit growth curves are commonly described.
Fruit crops with the single sigmoid curve include apples
(Denne, 1960,1963); pear (Griggs and Iwakari, 1956);
'Clementine' mandarin (Garcia-Papi and Garcia-Martinez,
1984); mango (Prakash and Ram, 1984); tomato, date,
pineapple, banana, avocado, strawberry, orange, and melon
(cited in Bollard, 1970). Those exhibiting a double sigmoid

pattern include: peach (Chalmers and Van Den Ende, 1977); apricot (Jackson and Coombe, 1966); Japanese pear (Nii, 1980); fig, blackcurrant, raspberry, blueberry, grape, and olive (cited in Bollard, 1970).

The growth pattern of kiwifruit was described as a double sigmoid (Hopping, 1976), although Pratt and Reid (1974) decided it was a unique triple sigmoid. In the double sigmoid pattern, three fruit growth phases in the kiwifruit can be distinguished. They correspond to the different rates at which cell division and enlargement occur in the different fruit tissues (Hopping, 1976). As endogenous growth hormones are produced in large quantities in the seeds, seed growth also has an important role in regulating fruit development (Crane, 1964, 1969). In contrast to the cyclic nature of the curves for increases in fruit fresh weights, linear increases in dry weights are commonly observed for many fruits (Bollard, 1970). This indicates that the intake of water into different tissues during fruit development is likely to have been variable.

The moisture content of fruits is usually very high. Apples and pears for instance consisted of up to 85 $^0/_0$ water (Bollard, 1970). Reduced rates of fruit growth occurred when plants were water-stressed during dry weather because of high transpiration rates. Diurnal growth patterns were frequently observed. For example, Kozlowski (1968) observed that the

rate of volume increase of sour cherry was several times higher in the night than in the day. Shrinkage of fruits also occurs in the middle part of the day (Bollard, 1970).

Large variations in the growth period of different fruits have been reported. Strawberries required only 25 days from anthesis before they were ripened for harvest (Nitsch, 1950) whereas the 'Valencia' orange needed a lengthy 413 days (Bain, 1958).

The kiwifruit ripens after harvesting. In New Zealand, export kiwifruits are not harvested until they have attained a maturity index of 6.2 $^0/_0$ soluble solids (Harman, 1981). Seasonal and site effects are known to delay maturity by at least 4 weeks (pers.com., McPherson H.G., Plant Physiology Division, DSIR, Palmerston North). The period of fruit development from anthesis to harvest is also likely to be highly variable.

Fruit Growth Measurements

The growth of most fruits had been followed by measuring fruit attributes such as diameter, length, volume, fresh weight, and dry weight. The choice of attributes depended on whether the individual fruits were measured in situ, or were harvested at time intervals. Intact fruits were measured by recording their length or diameter, or by water displacement

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to find their volumes. However, the use of a linear
dimension to estimate fruit size was not precise, although
formulae could be used to convert diameter or length
measurements to equivalent volumes (eg. Pratt and Reid,
1974).

Accurate estimation of fruit growth from fresh and dry
weights could be obtained from samples of fruits which were
sequentially harvested. In this instance, Coombe(1976)
indicated the importance of taking samples from a selected
population of fruits whose development were synchronous.

3.2 Experiment 3A

3.2.1 Introduction

The fruit growth of the kiwifruit was described by a double sigmoid (Hopping, 1976) or triple sigmoid pattern (Pratt and Reid, 1974).

In this experiment, kiwifruit growth was followed by sequential measurements of fruit volume, fruit fresh and dry weight, fruit circumference, and fruit length. Fruit volumes were also estimated from the linear dimensions and compared with measured volumes.

3.2.2 Materials and Methods

Experimental

Five uniform, eight-year-old 'Hayward' vines were used in this experiment. They were located at a commercial orchard block at Levin. Fruits on each vine were selected from a population whose development were as

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synchronous as possible. Therefore only short shoots were tagged, and each shoot carried 3 flowers; all of which had the same day of anthesis (1 Dec 1983).

Hopping (1976) noted that his sampling interval was probably too long to detect small changes in fruit size. In this experiment a sequential harvest of one shoot per vine was made at short, regular intervals of about 10 days, throughout the season. The removal of a total of ~~45~~ *51* fruits from an average crop load of 1000 fruits was not expected to affect the vines significantly. The last harvest was made 178 days after anthesis on 26 May 1984. This was several days after the completion of the commercial harvest in the region (10 May 1984).

At each harvest, the following fruit growth attributes were measured: volume, fresh weight, length, circumference, and dry weight.

Data Analysis

A constrained B-spline curve-fitting program (Spriggs, 1986) was used to fit the data collected. Derivatives from the fitted curves were obtained, and subsequent plots of absolute and relative growth rate were derived. Fruit volumes were also estimated from the linear measurements of fruit length and circumference, on

the assumption that the fruits had a uniform shape which could be described by a cylinder and two halves of a sphere.

3.3 Results

The cumulative growth of fruit fresh weight followed a double sigmoid pattern (fig. 3.1a). Absolute growth rate was maximal (1.44 g per day) at 34 days after anthesis (fig. 3.1b). Growth then declined into the stage II phase and reached a minimum of 0.4 g per day at day 95. It then rose to a second peak at 0.69 g per day at day 133. The relative growth rate increased rapidly within a period of 16 days to a maxima of 0.16 g per g per day (fig. 3.1c). From day 16 to day 75 it fell off quickly to a low rate. Stage III growth is reflected by only a very slight hump in the relative growth rate graph.

The growth pattern for measured fruit volume (fig. 3.2) was very similar to fruit fresh weight. However, there were changes in fruit density during the growth period. Minimum fruit density (0.75 g per cm^3) was observed from the beginning of fruit growth on day 11 (fig. 3.3). During the early period of fruit development until about day 65, fruit density was less than 1 g per cm^3. Fruit fresh weight increased faster than fruit volume and reached a maximum density of 1.04 g per cm^3 during harvest.

Figure 3.1. Time course of fruit development of kiwifruit cv. Hayward, as measured by fresh weight. (a) Change in fresh weight; (b) absolute growth rate; (c) relative growth rate. Bars indicate s.e.
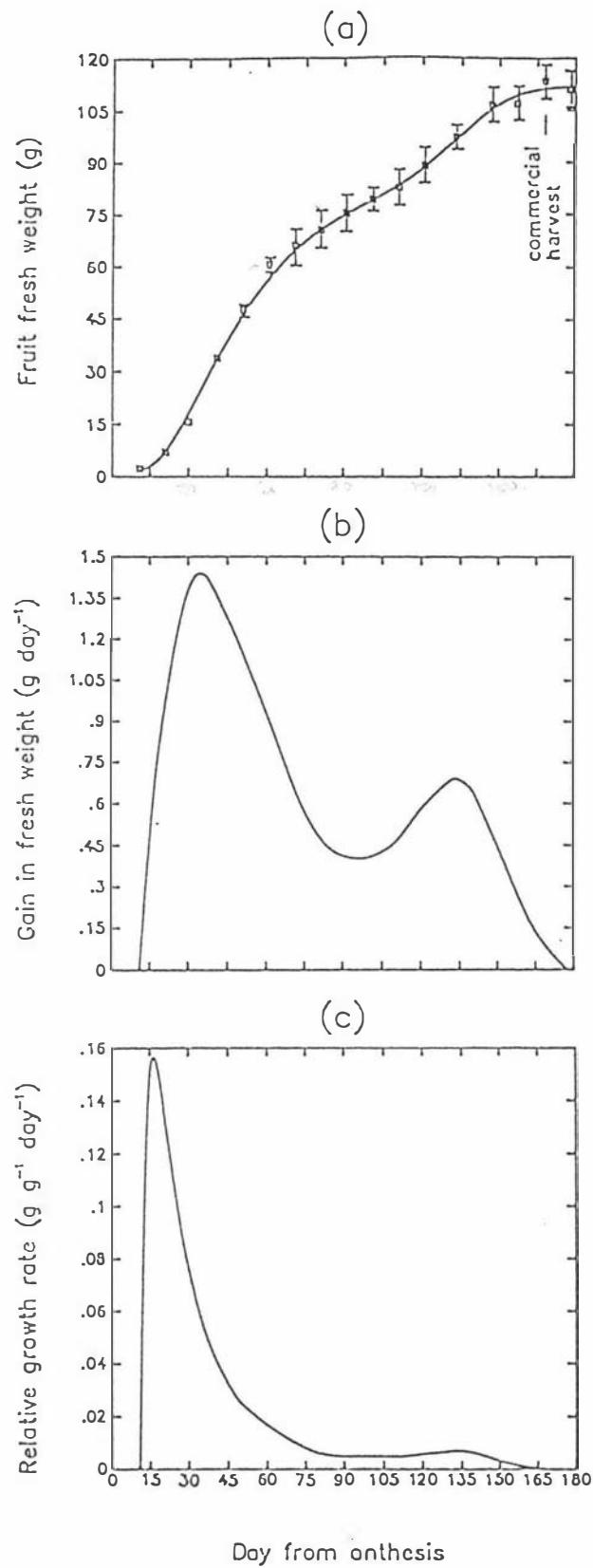
Figure 3.2. Time course of fruit development of kiwifruit cv. Hayward, as measured by volume. (a) Change in fruit volume; (b) absolute growth rate; (c) relative growth rate. Bars indicate s.e.

Day from anthesis
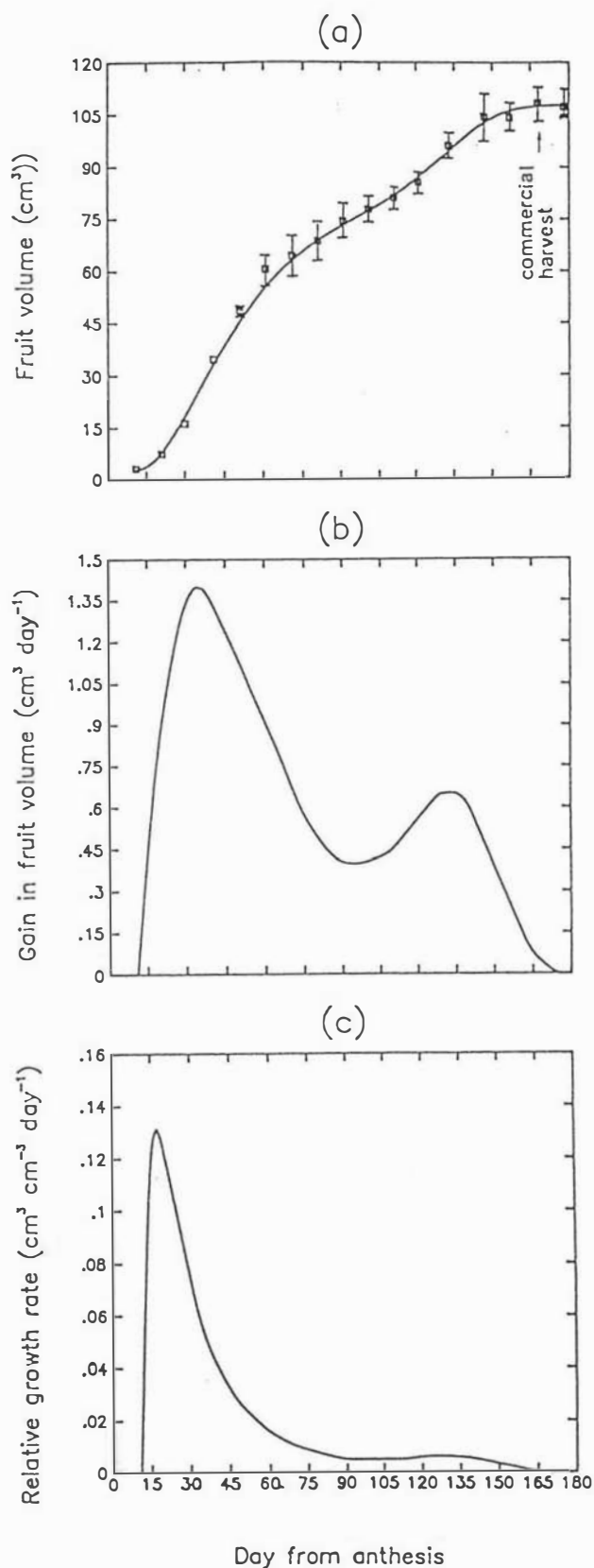
Figure 3.3. Change in fruit density of kiwifruit cv. Hayward during fruit development. Data was derived from figures 3.1 and 3.2. Bars indicate s.e.
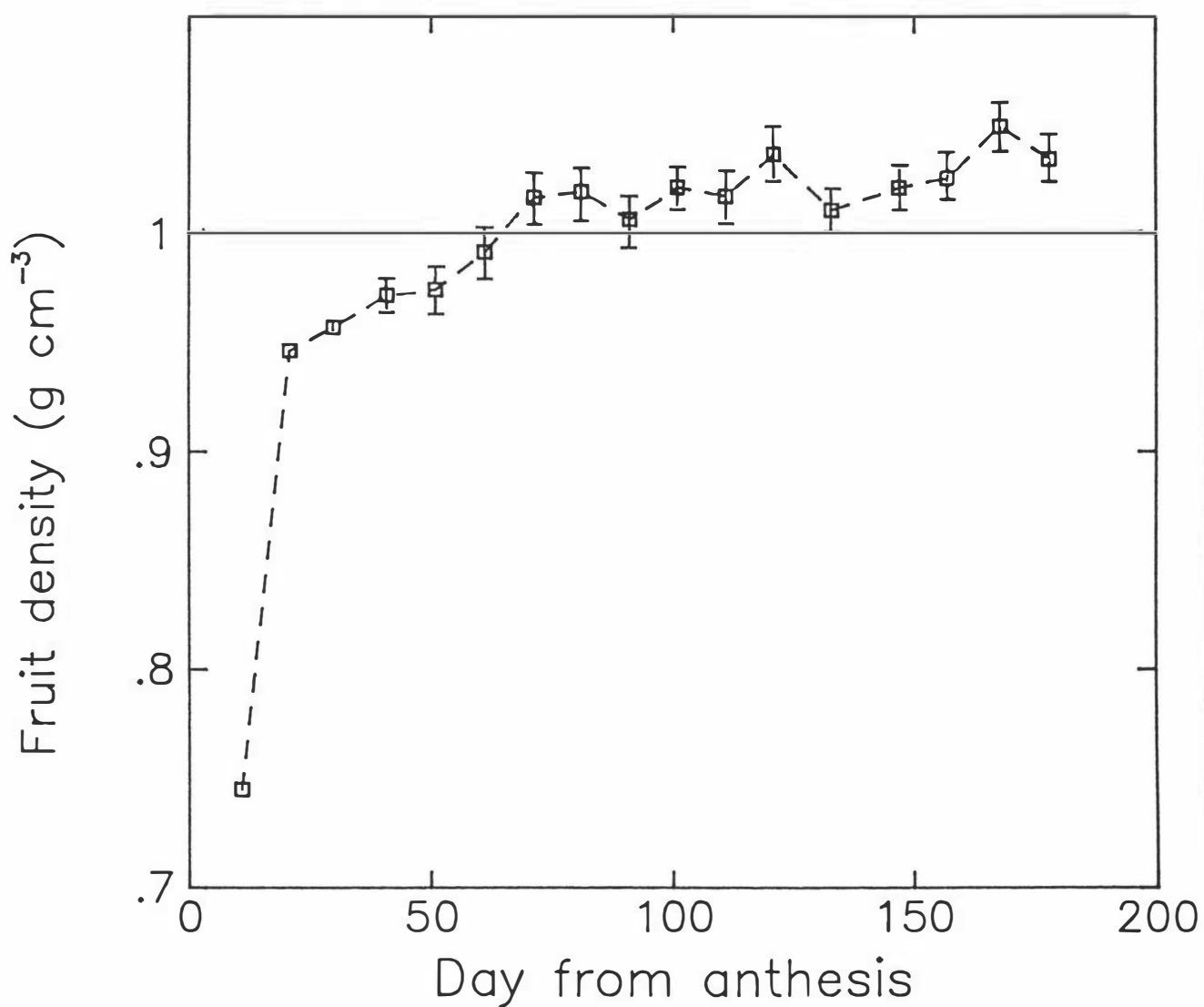
The rates of increase in fruit length and fruit circumference are shown in figures 3.4 and 3.5. Fruit volumes which were estimated from these linear measurements were highly correlated with measured fruit volumes (r^2=99.8), but the shape of their growth curves were slightly different (fig. 3.6). A noticeable deviation occured between day 91 and day 101 where estimated fruit volume increased significantly by 6.7 cm^3 (p=0.02). Measured fruit volume increased by only 2.7 cm^3 (p=0.29) during the same period.

The dry weight increment of the kiwifruit throughout the season was almost linear (fig. 3.7a). A plot of its derivative shows that the growth rate increased up to 0.123 g day^{-1} in the first 36 days from anthesis, after which a plateau of growth was maintained until day 150 when growth began to decline. A slight rise in absolute growth rate after day 90 (fig. 3.7b) coincided with the second growth stage of the fruit fresh weight curves. Relative growth rate increased to a maximum of 0.1g per g dry weight per day at day 18 after which it declined (fig. 3.7c).

Figure 3.4. Time course of fruit development in kiwifruit cv. Hayward as measured by fruit length. Bars indicate s.e.
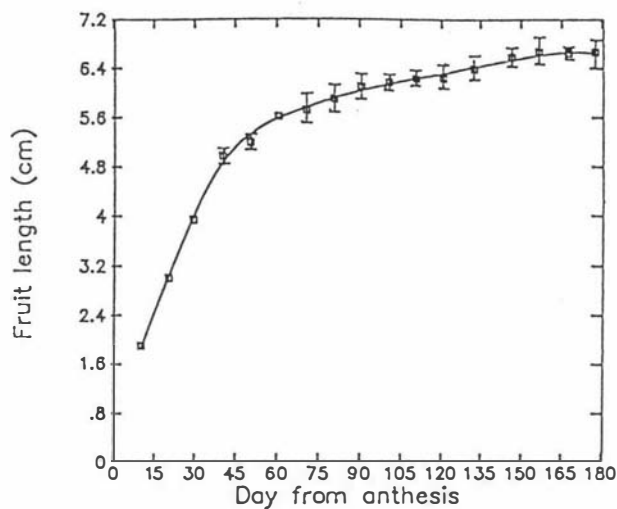
Figure 3.5. Time course of fruit development in kiwifruit cv. Hayward as measured by fruit circumference. Bars indicate s.e.
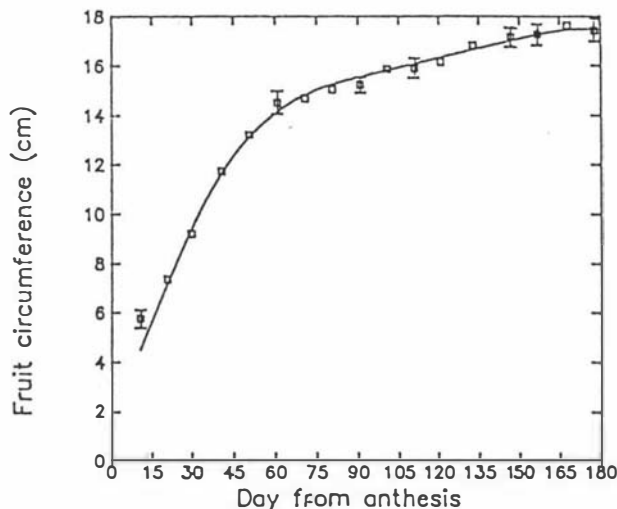
Figure 3.6. Comparison of fruit growth curves of kiwifruit cv. Hayward. △ , measured fruit volumes; □ , fruit volumes estimated from linear measurements of fruit length (fig. 3.4) and circumference (fig. 3.5). Bars indicate s.e.
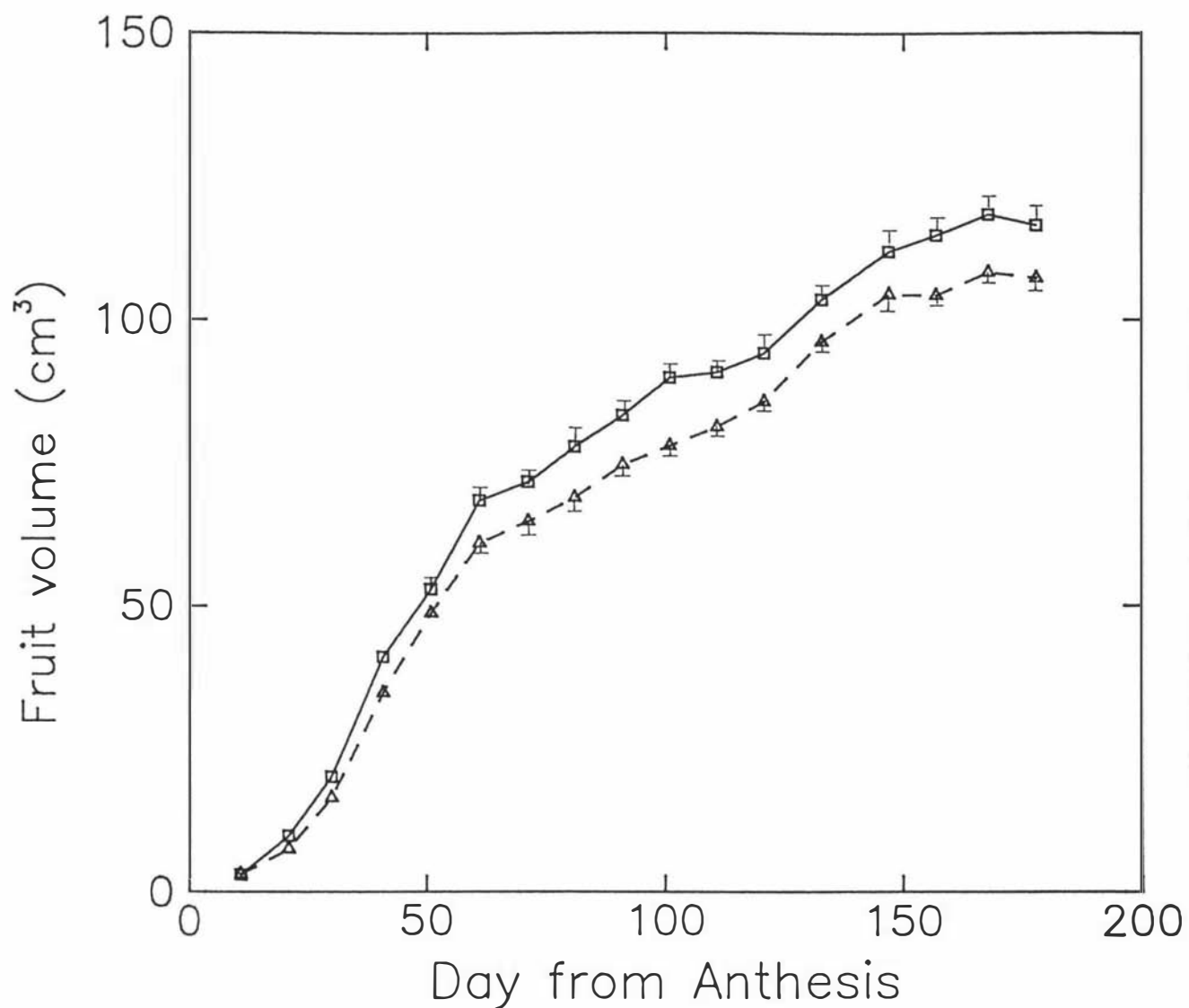
Figure 3.7. Time course of fruit development of kiwifruit cv. Hayward as measured by dry weight. (a) Change in dry weight; (b) absolute growth rate; (c) relative growth rate. Bars indicate s.e.

Day from anthesis
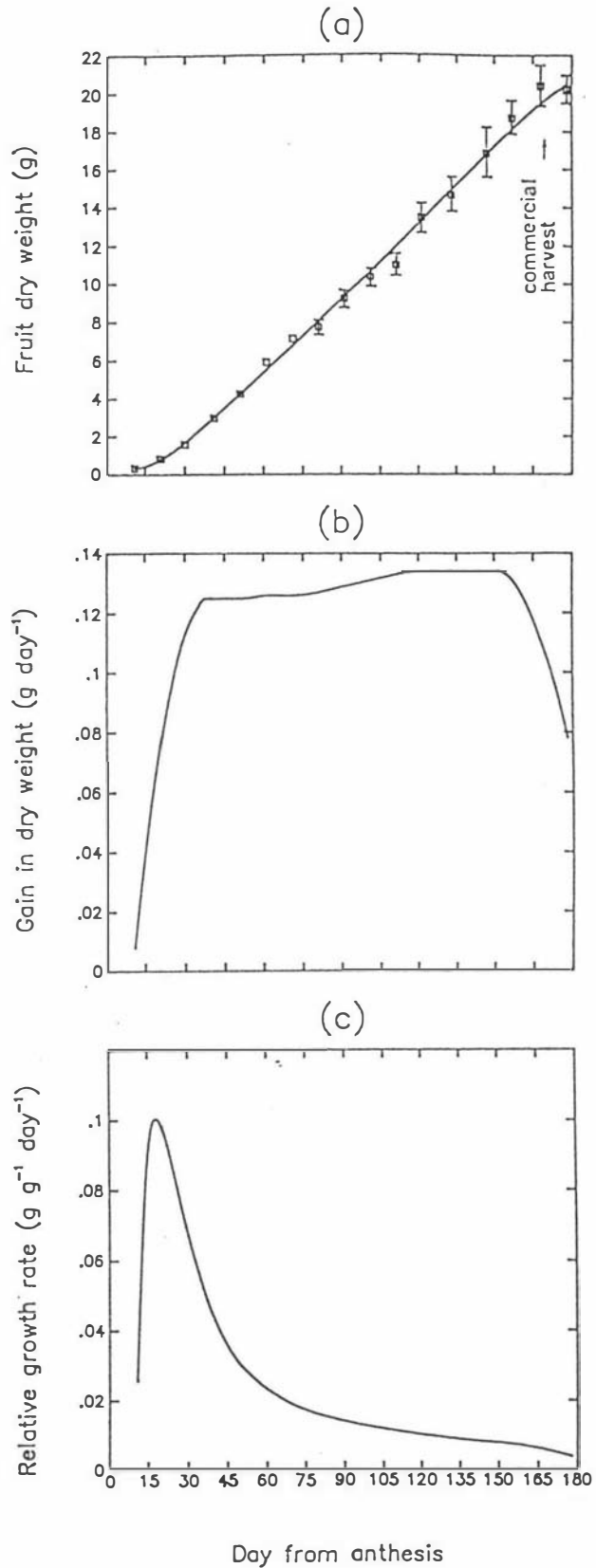
3.4 Discussion

3.4.1 Kiwifruit Growth Pattern

The results of the experiment indicated that an adequate
description of fruit growth can be obtained by the sequential
harvest of kiwifruits. Griggs and Iwakiri(1956) had shown
that there was a close correspondence between the growth
curves of 'Bartlett' pears which were obtained by measuring
the diameters of either the same fruit through the season, or
samples of fruit picked at regular intervals.

In the kiwifruit, the changes in fruit growth as
measured by fruit fresh weight and fruit volume were similar
(figs. 3.1 and 3.2). However, there was a rapid increase in
fruit density during the early growth stage so that by day
65, fruit density exceeded unity (fig. 3.3). There was only
a very slight increase in fruit density from day 65 until
harvest.

Fruit growth of the kiwifruit was clearly double sigmoid
(figs. 3.1 and 3.2). Hopping (1976) reasoned that he was
not able to observe the triple sigmoid growth pattern
reported by Pratt and Reid (1974) because the time intervals

between his data points were too great to detect the growth inflexions peculiar to a triple sigmoid. The sample period in this experiment was shorter (10 days), and the results shown in figures 3.1 and 3.2 do not support a triple sigmoid growth curve.

Chalmers and Van Den Ende (1975b) reported that the pattern of growth of peach fruits can differ between varieties. The triple sigmoid curve for kiwifruit reported by Pratt and Reid (1974) was probably unique to the 'Bruno' variety, whereas Hopping (1976) described the growth curve for 'Monty' fruits.

Pratt and Reid's fruit volume data were not true measurements of fruit size but were calculated estimates from fruit length and diameter measurements. This may have contributed to the discrepancy. Figure 3.6 shows that the fruit growth curves of measured and estimated fruit volumes were different. The significant deviation in estimated fruit volume at day 101 provided some evidence that the curve could be interpreted as a triple sigmoid growth curve.

3.4.2 Fruit Growth Stages

The duration of the fruit growth stages found in this study appears to be different from the work of Hopping (1976). He described for 'Monty' the following stages: stage I, from 0 to 58 days after flowering; stage II, from 58 to 76 days after flowering; and stage III, from 76 to 160 days after flowering. In the 'Hayward' the stages appeared to last from day 0 to 58 (stage I); day 58 to 90 (stage II); and day 90 to 178 (stage III). However, as Coombe (1976) has commented, the three-stage system of describing a double sigmoid growth pattern is arbitrary and there is no indication of the precise position of the boundaries between the stages.

3.4.3 Fruit Dry Weight

This study agreed with the work of Hopping (1976) that dry weight increment in the kiwifruit was a linear function. This increase is similar to drupes (Bollard, 1970), and many other plants (Biscoe and Gallagher, 1977). The displacement in time between fresh weight and dry weight indicated that assimilates were incorporated into the fruit with different amounts of water (Chalmers and Wilson, 1978).

Pratt and Reid (1974) reported that the Bruno fruit matured at about 161 days after anthesis. This study indicated that 'Hayward' fruits were still accumulating dry matter 180 days after anthesis. Similar results were reported by Lees (1982) who observed that the fruit growth of kiwifruit could be as long as 210 days. The fruits had reached the minimum 6.2 $^0/_0$ soluble solids level long before 210 days, but further increases in yield could obviously be achieved if growers harvested later in the season.

CHAPTER FOUR

FACTORS AFFECTING FRUIT SINK STRENGTH

4.1 Introduction

Early Fruit Development

Differences in the supply of carbohydrate during the early
ontogeny of reproductive structures are important.

The potential of tomato fruit
development is determined before fruit growth began, and is
(see Ho et al., 1984)
closely related to the number of cells in the ovary. In many
fruit species cell division in the flesh is usually limited to
an initial period of a few weeks after anthesis (Bollard, 1970).

Coombe (1973) estimated that in grapes, 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 as compared to 4.5
doublings after (Pearson and Robertson, 1953). Clearly, the
variations in final fruit sizes were very much dependent on

early cell division and the factors affecting it.

Weather conditions which result in high dry matter production during the plant developmental periods are known to be particularly favorable to high fruit yield (Biscoe and Gallagher, 1977). The rate of apricot fruit growth during the initial period after anthesis was shown by Jackson and Coombe (1966) to increase as the average air temperature became warmer.

Differences in access to carbohydrate reserves in the stem, particularly when fruits are competing with active shoot meristems or developing leaves, can also have large effects on final fruit sizes. It was thought that the amount of reserves stored in woody tissue during the previous season may have a controlling influence on the amount of cell division in apple fruit (Martin et.al., 1964). In addition, Jackson and Coombe (1966) found that apricot fruits from early flowers were larger at ripeness because of a greater number of cells and mesocarp volume. They considered the differences between fruits from early and late flowers to have arisen from the different amounts of cell division within the ovaries before anthesis.

Effect of Seeds on Fruit Development

In the tomato, it was found that the number of cells in the ovary did not increase after anthesis (Dempsey and Boynton, 1965). Subsequent increase in fruit size was due to cell

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expansion and it was established that the presence of more seeds

gave bigger fruits, presumably because of the attraction of

metabolites towards ~~fruit with~~ larger amounts of growth hormones associated

with the seeds (Nitsch, 1950). Similar correlations between

seed numbers and fruit size have been observed in other crops

(eg. Abbott, 1960; Darron and Schander, 1941; Lavee, 1960;

Luckwill, 1939; Mann, 1943; Nitsch, 1950; Olmo, 1946;

Simmonds, 1953), as well as in the kiwifruit (eg. Grant and

Ryugo, 1984a; Hopping, 1976; Hopping and Hacking, 1983;

McAneney et.al., 1984; McKay, 1976).

A kiwifruit contains up to 1861 seeds (Pyke and Alspach,

1986) and fruit size can be manipulated by controlling seed

number after applying different pollination treatments (Hopping,

1976). Although Hopping and Hacking (1983) reported that 700 to

1400 seeds were needed to produce an export size kiwifruit (ie.

70 g), other studies have shown that as little as 200 seeds were

sufficient (Pyke and Alspach, 1986). Therefore there appeared

to be large variation in the relationship between fruit size and

seed number in the kiwifruit.

Lee (1984) reported that the intensity of pollination was

important in stimulating the ovary to act as a larger sink for

assimilates. Thus in Cassia fasciculata, fruits initiated with

untreated pollen had significantly greater growth rates than

those initiated with dilute pollen, even when the number of

developing seeds per fruit was similar in both treatments (Lee

and Bazzaz, 1982).

Sastry and Muir (1963) demonstrated that in the tomato, pollen grains contained gibberellin that caused the production of growth-stimulating auxins in the ovary. Therefore, when pollination is intense, a surge in the level of growth hormones in the ovary could make the difference in increasing its sink strength and competitive ability.

Seed abortion, *owing* ~~due~~ to the lack of carbohydrate at the critical period of fruit and seed development, is also an important factor affecting fruit growth. Abbott (1960) found that in the apple fruit, seed number was correlated with the availability of stored reserves. After anthesis, peach seed and fruit development occurred simultaneously and although the seed and pericarp competed for assimilates the seed was often the weaker sink (Chalmers and Van Den Ende, 1977). Seed growth did not inhibit sink strength of the peach fruit. Instead, it created a high nutrient demand in response to a stimulus from the seed.

Fruit Competition

The occurrence of fruit competition for assimilates can also affect the growth of fruits which are developing at the same time. Wyatt (1982) observed that the physical location of a flower within an inflorescence of Asclepias tuberosa affected

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its chances of maturing into a fruit. Similar observations were made by Stephenson (1981) when he reviewed the causes of fruit abortion in several plant species. An example can be found in the study of seed production in <u>Rumex</u> <u>crispus</u> where larger seeds were produced in flowers which were located closest to the plant axis or to the leaves receiving more resources (Maun and Cavers, 1971). Ho et.al.(1982) reported that there was a reduction in tomato fruit size on passing down the truss from the main axis. Apparently the first fruit to set commenced growth and, although the other fruits may be fertilised in quick succession, it appeared that the first fruit monopolised the available nutrients to the extent that the remaining fruits grew less quickly.

Ho et.al.(1982) also discovered that the proximal fruits, which accumulated dry matter most rapidly during early development, generally had least ABA. Subsequent experiments with fruit thinning demonstrated changes in ABA and IAA contents in proximal or distal fruits but the evidence was insufficient to demonstrate any causal relationship.

The reduction of fruit competition by thinning could also be explained by the greater availability of carbohydrate resources during the early development of fruits. Thus when Denne (1960,1963) and Havis (1962) observed that early thinning of apple trees was more effective in increasing fruit size than late thinning, it was thought that this could be accounted for

by the differences in the amount of cell division in the flesh
of the fruits.

4.2 Experiment 4A

4.2.1 Introduction

The final size of a kiwifruit is primarily dependent on the number of seeds it contains (Pyke and Alspach, 1986). Under conditions of limited carbohydrate supply, such as a high fruit load, fruits with fewer seeds may be at a competitive disadvantage as compared to those with high seed numbers.

Apart from seeds, the growth of a kiwifruit may also be dependent on the vigour and type of fruiting shoot (McKay, 1976), and whether they developed from early or late flowers (Davison and Sutton, 1984).

This experiment was designed to investigate the influence of the above factors on the growth of the kiwifruit.

4.2.2 Materials and Methods

Experimental

This trial was carried out at the Massey University orchard during the 1982-83 season. Four 12-year-old 'Hayward' vines were used.

The treatments were imposed on two shoot types: long (indeterminate) shoots, and short (determinate) shoots. Two replicates of each treatment were randomly allocated to each vine. Only shoots in well-exposed positions were tagged prior to blossom, and treatments were applied during the period of anthesis, ie. 29 Nov to 10 Dec 1982.

During anthesis, styles of flowers were excised so that fruits of different sizes were obtained. Six types of style treatments were made:

1. 5 styles

2. 10 styles

3. 20 styles

4. 30 styles

5. intact flowers - ie. approximately 40 styles

6. hand-pollinated flowers

Style excision was carried out before bee pollination could take place, when the flowers were just opened.

Two types of interfruit competition were made by the selective excision of the styles on the 3 flowers of each experimental unit. Type A competition consisted of giving the same style treatment to all the 3 fruits, so that each shoot carried fruits of a similar sink size. In type B competition, only the middle fruit on a shoot was treated while the proximal and distal fruits were left intact.

Data Collection

The dates of anthesis of flowers were recorded. Fruit volume was measured at the following times during the season:

Days After Anthesis	Date
Day 15	23 Dec
Day 27	4 Jan
Day 34	11 Jan
Day 40	17 Jan
Day 48	25 Jan
Day 55	1 Feb
Day 65	11 Feb
Day 75	21 Feb
Day 82	28 Feb

Day 89   7 Mar

Day 96   14 Mar

Day 103   21 Mar

Day 110   28 Mar

Day 120   7 Apr

Day 129   16 Apr

Day 141   28 Apr

Day 150   7 May

Anthesis was assumed to happen on 8 Dec 1983, when 70 $^{0}/_{0}$ blossom had occurred (fig. 4.1).

The fruits were harvested at maturity on 7 May 1983 (day 150) and their fresh weights were recorded. Fruit seed numbers and seed weight were subsequently obtained.

Analysis of Data

The mean value of the data of the 3 treated fruits from type A competition was used for all the statistical analyses. In type B competition, only the middle, treated fruit was measured, and the data of the single fruit was used for statistical comparisons with other treatments.

Figure 4.1. Cumulative percentage of anthesis in kiwifruit cv. Hayward vines.
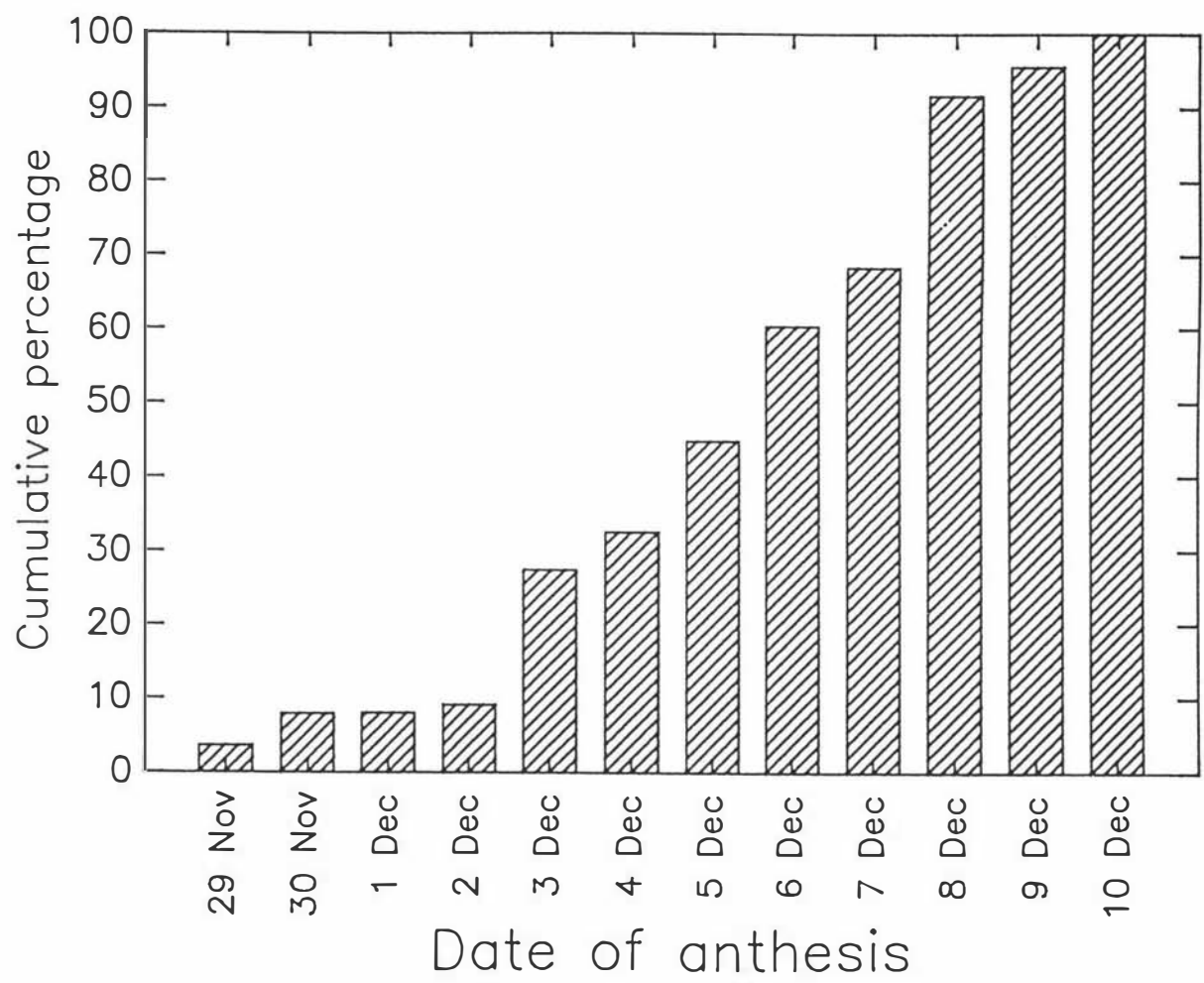
4.2.3 Results

Fruit Size Treatments

Manipulation of fruit sizes by style excision was effective. Five classes of fruit size treatments were made from the following ranges of fruit seed weight:

<div>

seed weight per fruit

1	$\leq$ 750 mg
2	751 _ 1000 mg
3	1001 _ 1250 mg
4	1251 _ 1500 mg
5	$\geq$ 1501 mg

</div>

The mean fruit size of each class of treatment is shown in table 4.1.

Effect of Day of Anthesis

A decrease in average fruit size *at harvest* of about 2 cm^3 was observed for each day of delay in anthesis (fig. 4.2). Figure 4.3 shows that the difference in fruit sizes between each day of anthesis was bigger when seed numbers were low.

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Table 4.1. The effect of Type A and B fruit competition on mean fruit volume (cm^3), fruit seed number, and mean seed size (ug) of kiwifruit cv. Hayward. S.E. in parenthesis. (See text for explanation on fruit seed weight classes).

	Fruit seed weight class	Type A	Type B	
Fruit volume (cm^3) (27 days after anthesis)	1	7.8(0.8)	7.3(0.8)	p=0.68
	2	10.2(0.9)	8.0(0.9)	0.12
	3	10.5(0.7)	9.8(0.6)	0.42
	4	10.8(0.6)	11.5(0.9)	0.56
	5	11.0(0.9)	12.9(0.6)	0.11
Fruit Volume (cm^3) (at harvest – 150 days after anthesis)	1	52.5(2.9)	44.7(4.1)	0.14
	2	66.7(3.5)	56.1(2.7)	0.03
	3	68.7(1.9)	60.5(4.3)	0.13
	4	74.5(2.7)	74.2(3.1)	0.94
	5	81.9(2.3)	85.6(3.0)	0.34
Mean Fruit Volume(cm^3)		68.4(1.7)	66.5(2.5)	0.51
Fruit Seed Number		1062(45)	1092(57)	0.67
Mean Seed Size (ug)		1069(12)	996(43)	0.08

Figure 4.2. Relationship between the mean fruit volumes (cm^3) of kiwifruit cv. Hayward and the day of flower anthesis (R^2=56.5). Bars indicate s.e.
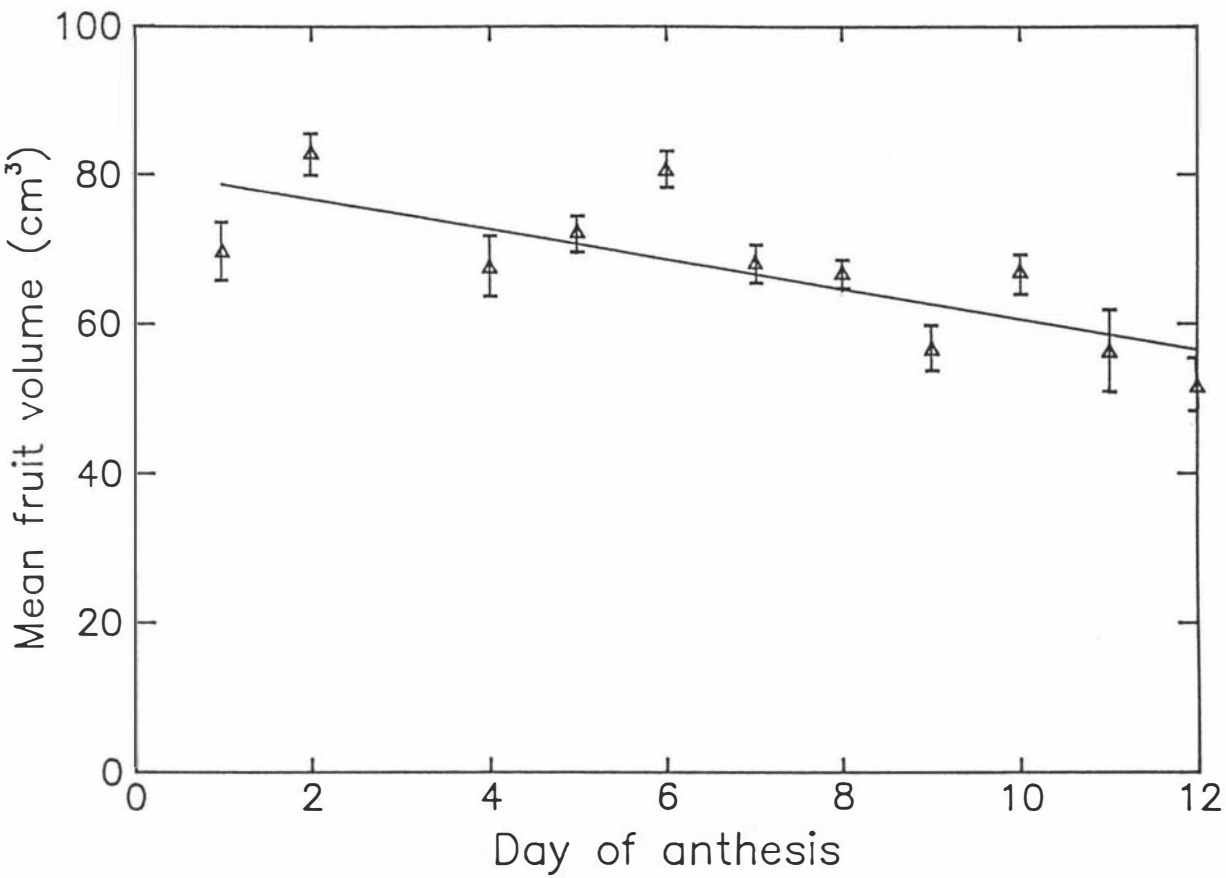
Figure 4.3. Comparison of regression curves of fruit fresh weight per seed (mg) versus fruit seed number in kiwifruit cv. Hayward, for fruits which developed from flowers at different days (1 to 12) of anthesis.
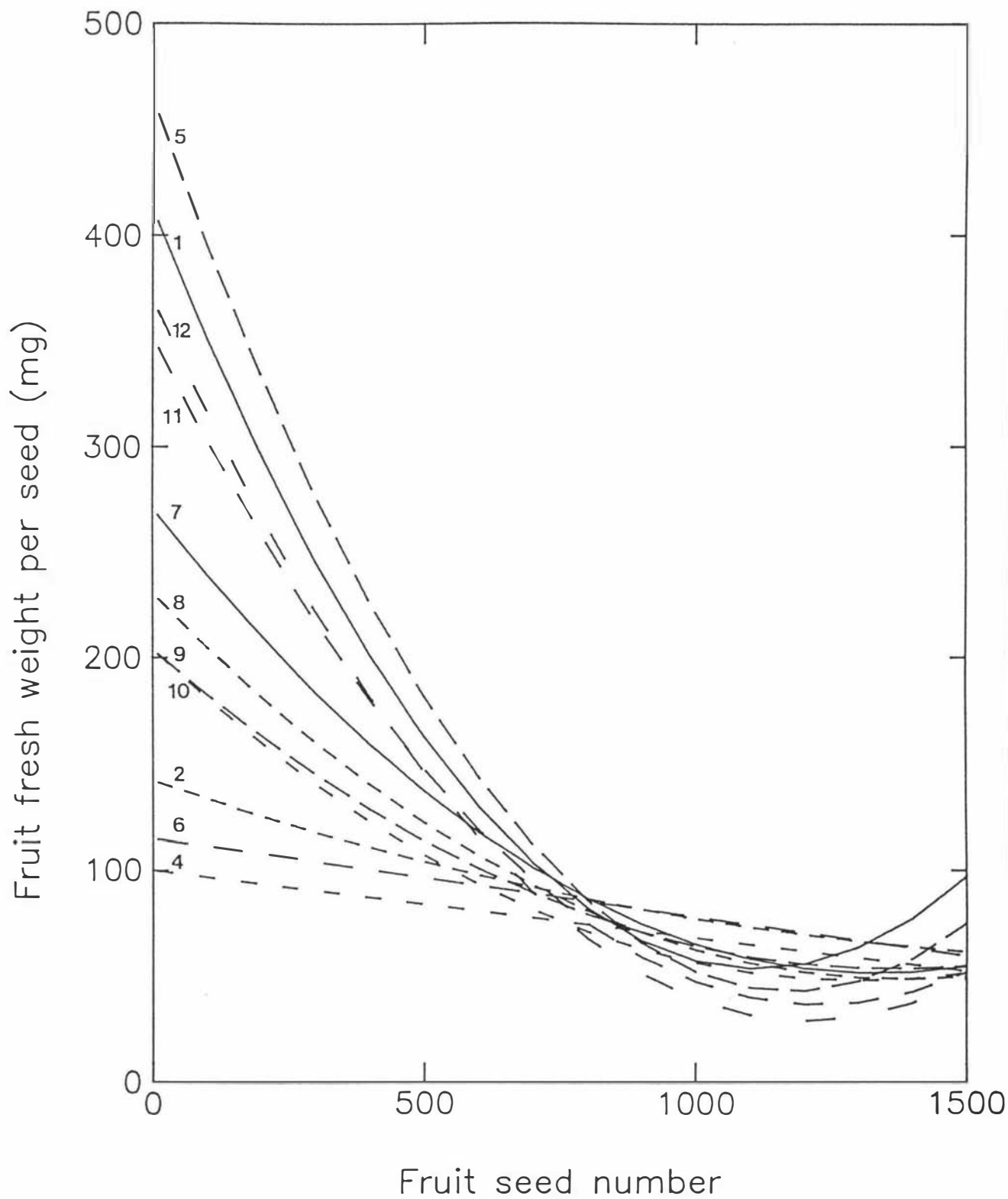
From the regression curves in figure 4.3, fruit sizes at
an equal fruit seed number (1000) _were_ estimated. The result
was plotted in figure 4.4 which shows that there was a
decrease in fruit size, even at the same fruit seed number,
when anthesis was delayed.

The mean fruit size for each day of anthesis correlated
positively with fruit seed numbers (r^2=0.594), and fruit seed
weight (r^2=0.721; table 4.2).

Effects of Fruit Competition

When fruit seed weights were low, fruits from type A
competition tended to be bigger than those from type B
competition (table 4.1). The mean fruit size at harvest for
fruits with less than 750 mg seed weight, was 52.5 cm^3 for
Type A as compared with 44.7 cm^3 for Type B (p=0.14). The
observed effect was evident from as early as Day 27. Over
the entire range of fruit seed weight classes however, the
difference between the mean fruit size of type A and type B
treatments was reduced; the means at harvest (Day 150) were
68.4 and 66.5 cm^3 respectively (p=0.51). There was also no
significant difference (p>0.05) in the fruit seed number and
seed size between the two types of fruit competition (table
4.1).

```
Derivation of fig.4.4
=====================

Quadratic equations from fig. 4.3 were:

Day 1 : Y = 416 - 0.64 X + 0.00029 X2
    2 : Y = 142 - 0.08 X + 0.000022 X2
    4 : Y = 100 - 0.03 X
    5 : Y = 464 - 0.72 X + 0.000305 X2
    6 : Y = 114 - 0.03 X
    7 : Y = 271 - 0.32 X + 0.000123 X2
    8 : Y = 230 - 0.26 X + 0.000094 X2
    9 : Y = 204 - 0.23 X + 0.000091 X2
   10 : Y = 202 - 0.22 X + 0.000807 X2
   11 : Y = 352 - 0.51 X + 0.000208 X2
   12 : Y = 370 - 0.56 X + 0.000233 X2


where Y = fruit fresh weight per seed (mg)
      X = seed number

At 1000 seeds, this translates to:

Day 1 : Y = 60
    2 : Y = 77
    4 : Y = 68
    5 : Y = 52
    6 : Y = 77
    7 : Y = 65
    8 : Y = 62
    9 : Y = 56
   10 : Y = 64
   11 : Y = 47
   12 : Y = 39

where Y = fruit fresh weight per seed (mg)
        or fruit fresh weight (g), as plotted in fig. 4.4
```

Figure 4.4. Relationship between the size (cm^3) of
kiwifruit cv. Hayward fruits which contained 1000
seeds, and different days of anthesis. Fruit sizes
were estimated from the regression curves in figure
4.3. $(R^2 = 52.3)$.
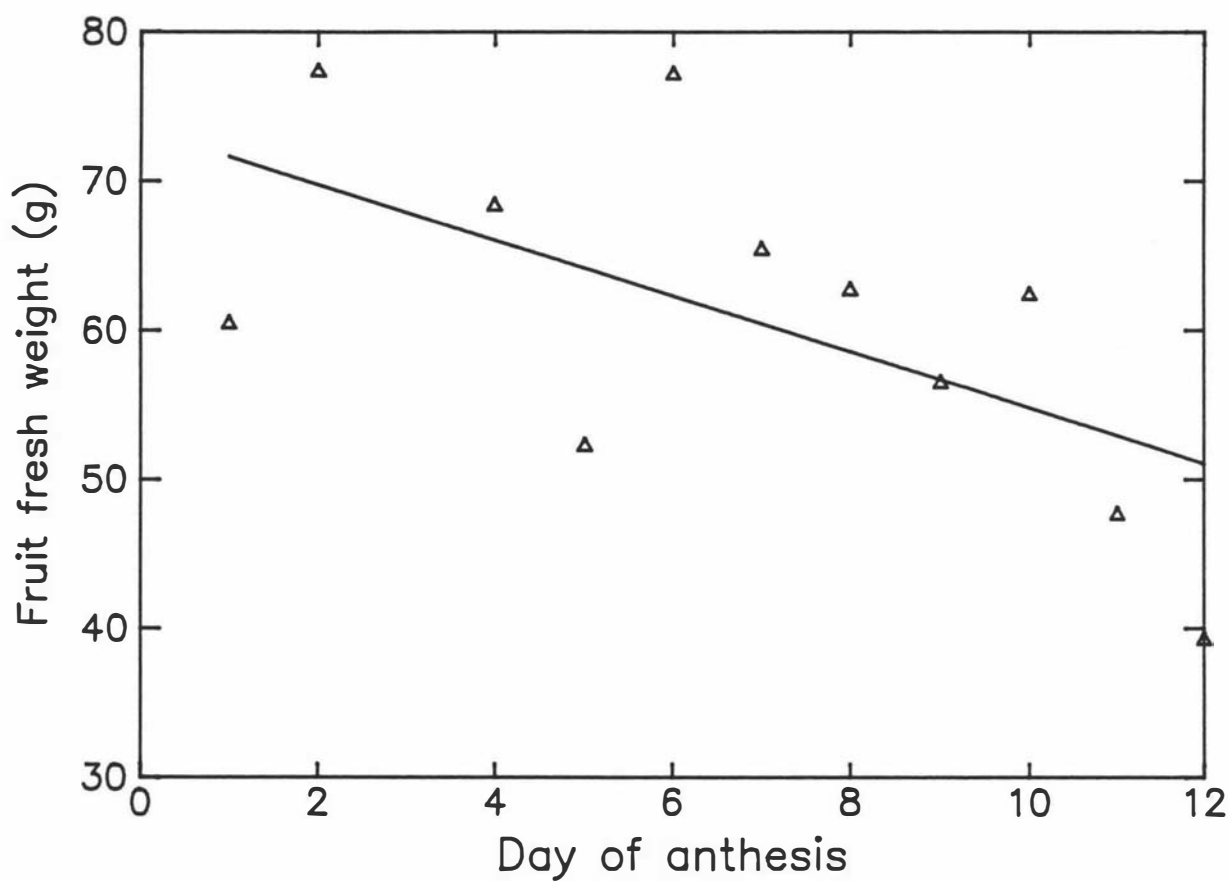
Table 4.2. Mean fruit seed data for each day of anthesis on kiwifruit cv. Hayward vines. S.E. in parenthesis

	Final Fruit Volume(cm^3)	Fruit Seed Number	Fruit Seed Weight(g)	Mean Seed Size (ug)
Day of Anthesis				
1	69(4)	688(183)	754(206)	1114(49)
2	83(3)	1232(90)	1321(108)	1066(18)
4	67(4)	1096(65)	1023(100)	930(47)
5	72(2)	1038(59)	1053(57)	1028(14)
6	80(2)	1310(67)	1377(68)	1055(20)
7	56(2)	945(91)	967(89)	1043(14)
8	67(2)	1122(72)	1109(69)	999(15)
9	56(6)	861(80)	867(79)	1003(23)
10	67(2)	1145(60)	1155(60)	1017(14)
11	56(6)	924(186)	977(194)	1099(50)
12	51(6)	735(187)	710(167)	1052(39)
	p=0.00	0.00	0.00	0.02

Shoot Type Effects

Long shoots carried bigger fruits than short shoots and this happened from about Day 48 (table 4.3). Quadratic curves were fitted to the data of fruit fresh weight per seed for equivalent seed number (fig. 4.5) and it was found that there was no significant difference between long and short shoots ($p > 0.05$).

Table 4.3. Mean fruit volumes (cm^3) on long and short fruiting shoots of kiwifruit cv Hayward, at different day number from anthesis. S.E. in parenthesis.

	Day 40	Day 48	Day 150
Short Shoot	22.6(0.7)	29.1(0.8)	65.7(1.8)
Long Shoot	22.5(0.9)	29.8(1.1)	69.7(2.2)
	p=0.95	0.55	0.04

Figure 4.5. The effect of long and short shoots of
kiwifruit cv. Hayward on the relationship between
fruit fresh weight per seed and fruit seed number
(p > 0.05). (————, long shoot; ------, short
shoot).
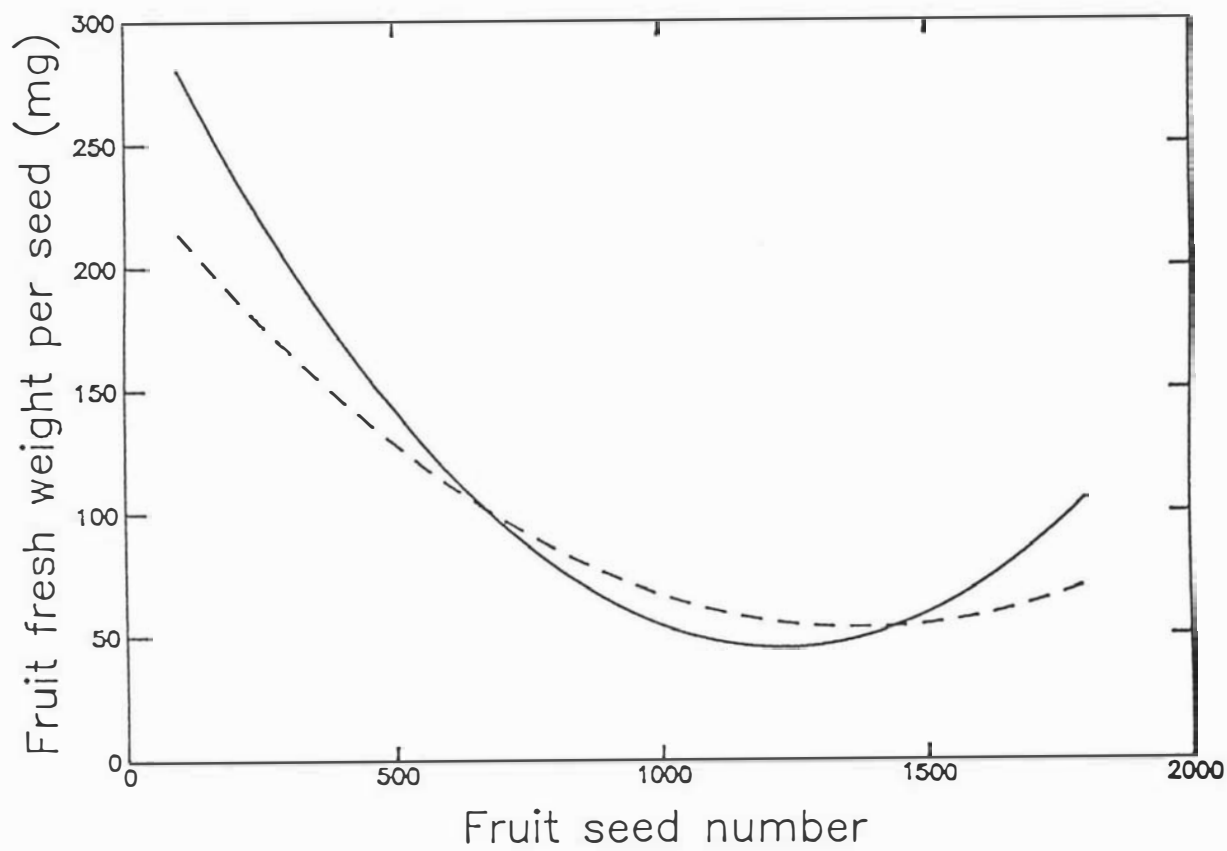
4.3 Experiment 4B

4.3.1 Introduction

The results of the previous experiment (4A) indicated a clear response of fruit size which was dependent on the earliness or lateness of kiwifruit flowers (fig. 4.2). A relationship between the time of blossom and the vigour of the fruiting shoot may exist (Davison and Sutton, 1984; McKay, 1976).

The objective of this experiment was to study the effect of the above factors on the fruit growth of the kiwifruit. The role of seed numbers, and the extent to which the size of the flower ovary predetermined fruit size was also investigated.

4.3.2 Materials and Methods

Plant Materials

This experiment was carried out at a commercial

kiwifruit orchard block at Levin. Six-year-old 'Hayward' vines were used.

Trial 1

In this trial only short shoots, each carrying 3 fruits were selected for treatment. The treatments consisted of grouping these shoots into 3 days of anthesis:

1. early – on 21 Nov 1984
2. mid   – on 28 Nov 1984
3. late   – on 5 Dec 1984

Two replicates of the treatments were allocated to each of 5 vines. Fruit growth was followed throughout the season by measuring fruit volumes. After harvest on 28 Apr 1985, fruit fresh weights were recorded. Fruit locule numbers were also counted, and fruit seed numbers and seed weight were subsequently obtained.

The stem diameters of the fruiting shoots, measured at 5 cm from the base; and fruit pedicel diameters, measured at 1 cm from the fruits, were also recorded.

Trial 2

This trial consisted of tagging random shoots, both long and short, according to the day of anthesis. Only shoots which had all their flowers opening on the same day were selected.

During harvest on 28 Apr 1985, fruit fresh weights were measured. The stem diameter of the fruiting shoot was also recorded.

Trial 3

Flowers on short shoots were harvested on each day of anthesis between 25 Nov to 5 Dec 1985. Three flowers were picked from each of 5 vines, so that a total of 15 flowers per day were collected for measurements. The diameter of each ovary was measured using calipers. Fresh weights and dry weights of the flowers were also measured.

4.3.3 Results

Early and Late Fruits

Table 4.4 shows that the mean final fruit fresh weight
in trial 2 decreased as anthesis was delayed. Differences
between early and late fruits varied by as much as 31 g.
Fruit locule numbers were also smaller for late fruits as
compared with early fruits (38 cf. 41; table 4.5).

Fruits from late flowers had ~~less~~ *fewer* seeds per fruit (908
cf. 1039 and 1152), and their seeds were also smaller (1.059
mg cf. 1.145 and 1.142 mg). The scattergram of seed size
versus fruit seed numbers (fig. 4.6) shows that at the same
fruit seed number, seeds of 'early' and 'mid' fruits were
larger than those from 'late' fruits. It can also be seen
from table 4.6 that at the same seed size, early fruits were
significantly bigger than late fruits ($p < 0.05$). A
scattergram of the relationship between fruit size and fruit
seed number shows that early fruits were clearly scattered
above late fruits at the same seed numbers (fig. 4.7). A
comparison of the quadratic regressions between fruit fresh
weight per seed and fruit seed number in figure 4.8 showed
that early fruits were significantly bigger than late fruits
at fruit seed numbers below 800 seeds ($p < 0.05$).

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Table 4.4. Fruit fresh weight, stem diameter, and the percentage of short shoots in kiwifruit cv. Hayward for (a) each day of anthesis (1-15), and (b) each period (early, mid, late), of anthesis. S.E. in parenthesis.

	Fruit Fresh Weight (g)	Stem Diameter(mm)	Percentage of Short Shoot
(a) Day of Anthesis			
1	111(4)	7.9(1.2)	18.2
2	111(3)	8.7(0.7)	9.1
3	116(3)	9.0(0.5)	16.7
4	117(2)	9.3(0.5)	4.5
5	112(2)	9.8(0.4)	24.4
6	116(2)	8.6(0.3)	40.0
7	114(2)	8.4(0.3)	44.4
8	110(2)	8.1(0.3)	50.6
9	98(2)	7.2(0.2)	39.6
10	99(2)	8.0(0.3)	76.2
11	96(2)	7.2(0.3)	56.0
12	94(3)	7.1(0.3)	66.7
13	92(3)	7.2(0.3)	63.2
14	87(2)	6.8(0.3)	85.7
15	86(2)	6.4(0.4)	100.0

....

(b) Period of Anthesis			
Early (Day 1 - 5)	115(1)	9.0(0.2)	14.6(3.5)
Mid (Day 6 - 10)	104(1)	7.8(0.1)	50.1(6.8)
Late (Day 11 - 15)	91(1)	7.0(0.2)	74.3(8.1)
	$p=0.00$	0.00	0.00

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Table 4.5. Fruit, seed, stem, and leaf data of kiwifruit cv. Hayward from either the early (day 1-5), mid (day 6-10), or late (11-15) period of anthesis. Only short shoots were used. S.E. in parenthesis. (Common letter within columns denotes groups not significantly different, LSD (0.05)).

	Fruit volume (cm^3)	Fruit fresh weight(g)	Fruit seed number	Fruit seed weight(mg)	Seed size (ug)
Early	108(3)a	117(4)a	1039(115)a	1181(26)a	1145(13)a
Mid	101(2)a	110(2)a	1152(61)a	1304(48)a	1142(23)a
Late	83(4)	89(4)	908(82)	960(90)	1059(28)a
	p=.00	.00	.09	.03	.03

	Locule number per fruit	Fresh wt per seed (mg)	Seed no. per locule (g)	Fresh wt per locule (~~mm~~) *mg*
Early	41(1)a	127(15)a	25(3)a	2.8(0.1)a
Mid	41(1)a	98(7)	28(1)a	2.7(0.1)a
Late	38(1)	104(8)a	24(2)a	2.3(0.1)
	p=.02	.04	.24	.00

	Stem diameter (mm)	Pedicel diameter (mm)	Leaf area per fruit (cm^2)	Leaf area per g FW (cm^2)
Early	8.3(0.2)a	3.0(0.8)a	268(13)a	2.3(.1)a
Mid	7.4(0.3)a	2.9(0.5)a	245(20)a	2.2(.2)a
Late	6.7(0.3)	2.6(0.5)	189(19)	2.2(.3)a
	.00	.00	.03	.92

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Figure 4.6. Relationship between seed size and fruit seed number of kiwifruit cv. Hayward. Fruits developed from early (△ , day 1-5), mid (× , day 6-10), or late (□ , day 11-15) periods of anthesis.
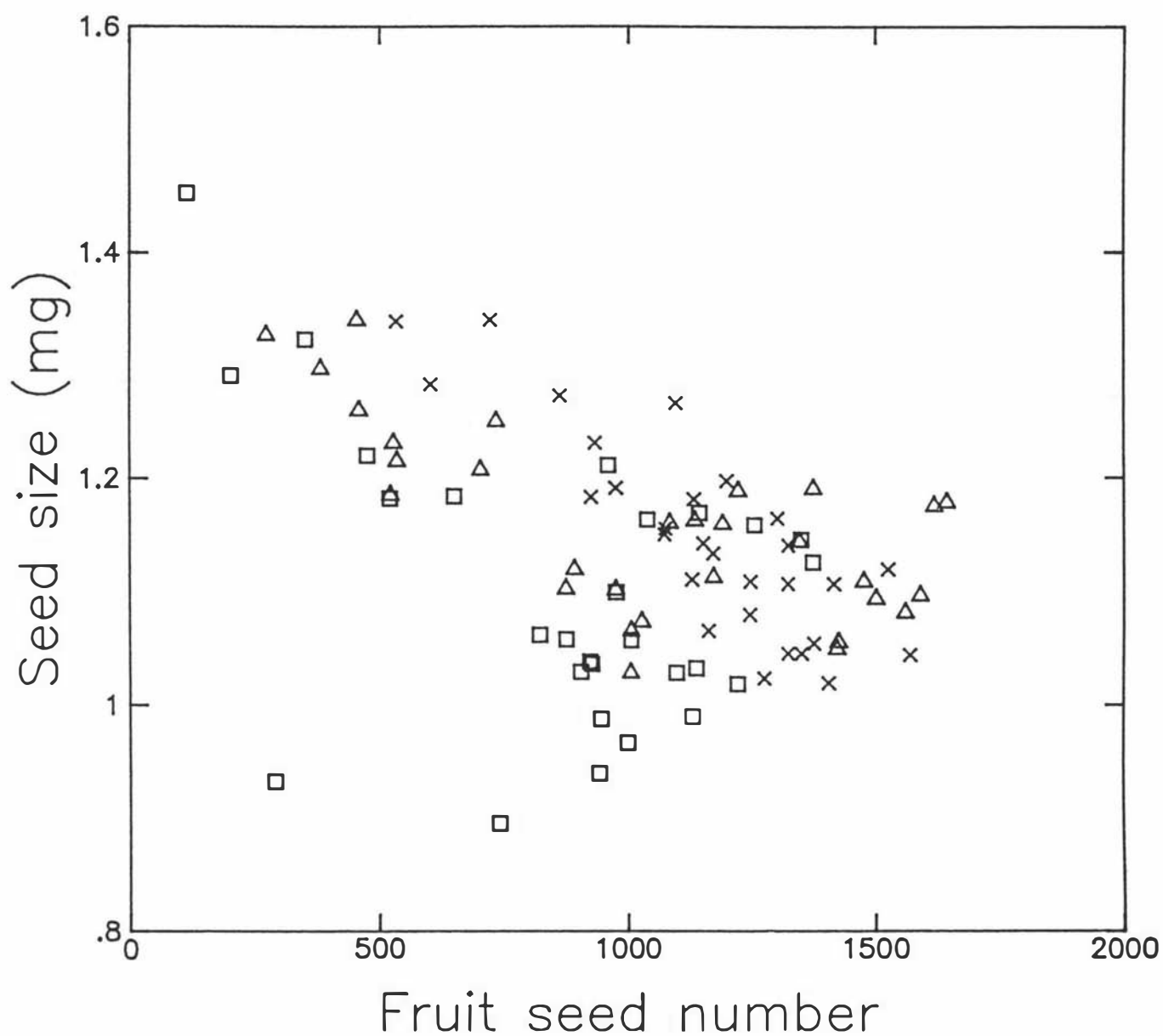
Table 4.6. Fruit fresh weight (g) of kiwifruit cv.
Hayward, at equivalent seed sizes (mg) from early
(day 1–5), mid (6–10), and late (11–15) periods of
anthesis. S.E. in parenthesis.

	Fruit Fresh Weight (g)			
Seed Size (mg)	early	mid	late	
1.0 – 1.1	124(4)	104(3)	94(3)	p=0.00
1.1 – 1.2	119(5)	113(3)	100(4)	0.03
1.2 – 1.3	111(2)	113(3)	84(12)	0.01

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Figure 4.7. Scattergram of the relationship between fruit fresh weight of kiwifruit cv. Hayward with fruit seed number. Fruits developed from early (△ , day 1–5), mid (× , day 6–10), or late (□ , day 11–15) periods of anthesis. Curve fitted by a constrained b-spline program (Spriggs, 1986).
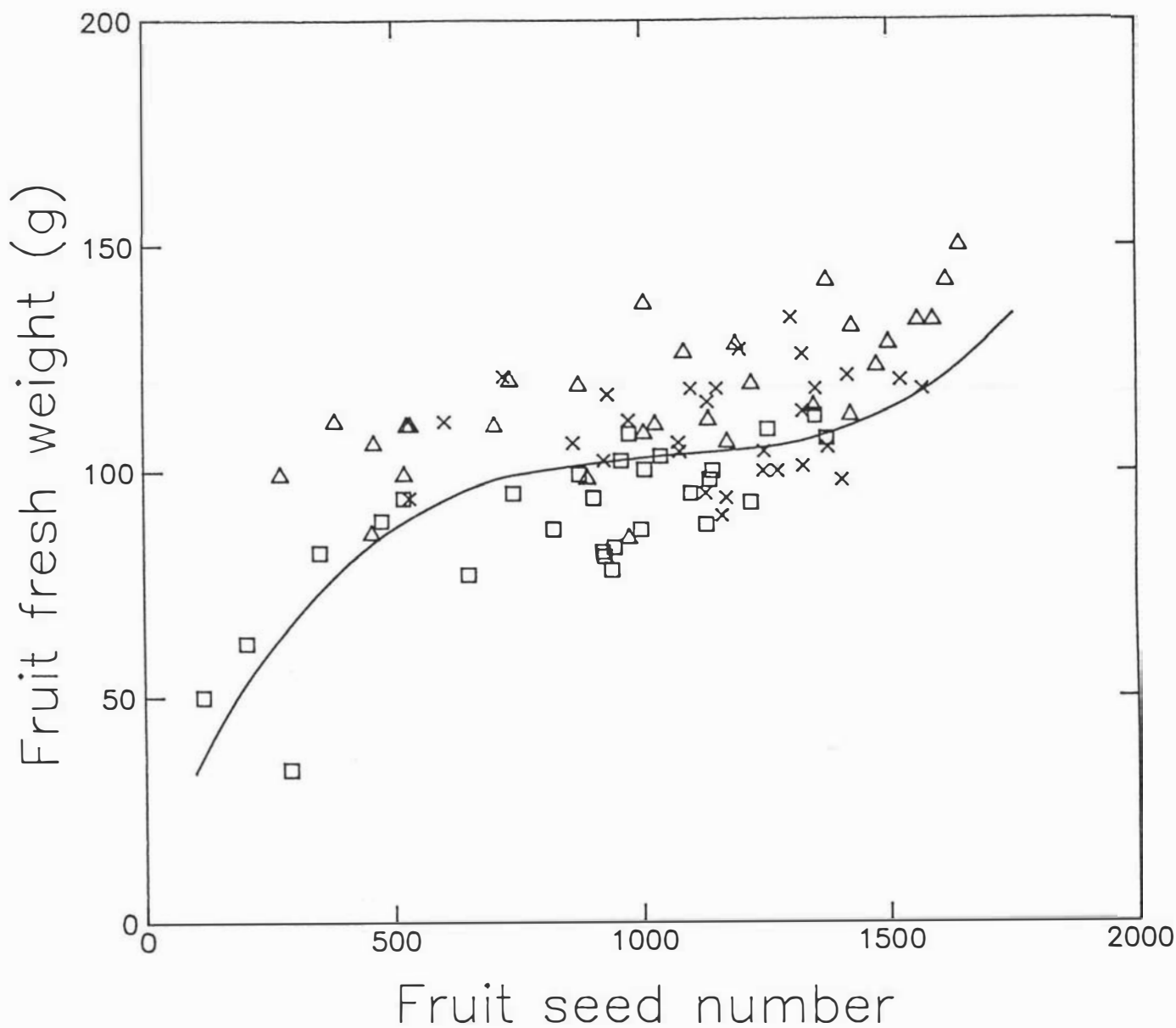
Figure 4.8. Comparison of the relationship between fruit fresh weight per seed and fruit seed number for fruits which developed from early (△ , day 1-5) and late (□ , day 11-15) periods of anthesis. The difference between the regression lines fitted to data with < 800 seeds was significant ($p < 0.05$).
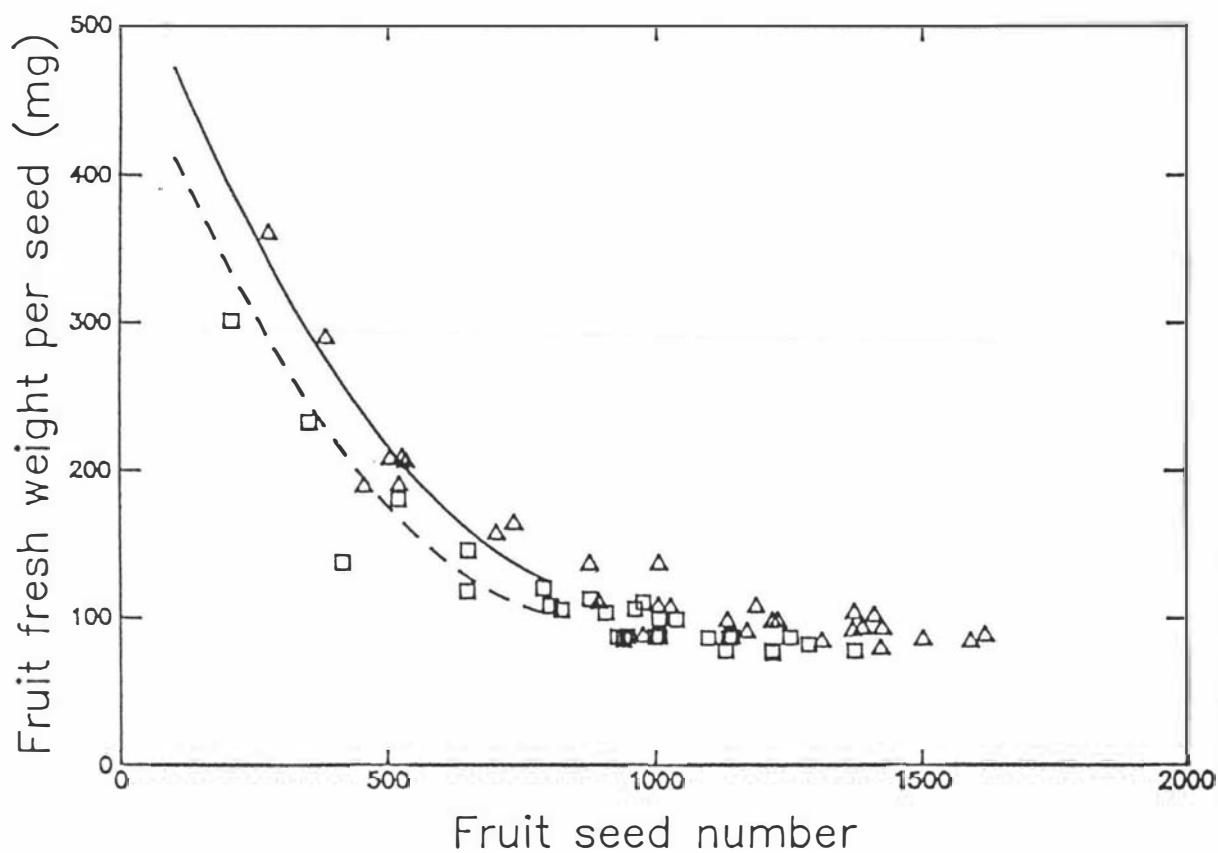
Early and Late Flowers

The results of trial 3 (table 4.7) indicated that the difference in fruit size actually began from differences in the size of the flowers. Early flowers had bigger sized ovaries with a maximum diameter of 9.80 mm as compared with a minimum diameter of 8.43 mm for late flowers. Differences in the dry weight of early and late flowers of about 0.13 g ($p<0.01$) were observed.

Stem and Fruit Pedicel Diameter

There was a clear correlation between the day of anthesis and the mean diameter of the fruiting shoot (table 4.4). When the treatments were grouped into early, mid, and late categories, it can be seen that the differences in stem diameter ranged significantly from 9.0 to 7.8 to 7.0 mm respectively ($p=0.00$). The results also indicated that 74.3 $^0/_0$ of late flowers were found on short shoots as compared to 14.6 $^0/_0$ for early flowers (table 4.4). Fruit pedicel diameter correlated with sink size in trial 1 ($r^2=0.72$; figure 4.9). This varied from 3.0 mm for the largest fruits, to 2.6 mm for the smallest (table 4.5).

The total leaf area per fruit also appeared to correlate

Table 4.7. Mean flower data of kiwifruit cv. Hayward for each day of anthesis. S.E. in parenthesis.

Day of anthesis	Mean ovary diameter(mm)	Mean flower fresh weight(g)	Mean flower dry weight(mg)
1	9.35(.13)	2.8(0.1)	362(37)
2	9.59(.19)	2.7(0.1)	358(64)
3	9.80(.16)	3.2(0.1)	396(72)
4	9.72(.12)	3.5(0.1)	357(42)
5	9.49(.10)	3.0(0.1)	347(31)
6	9.52(.16)	2.9(0.1)	345(39)
7	8.99(.16)	2.7(0.1)	313(27)
8	9.10(.14)	2.5(0.1)	324(38)
9	9.12(.21)	2.5(0.1)	275(43)
10	8.99(.13)	2.3(0.1)	283(30)
11	8.43(.12)	2.1(0.1)	267(21)
	$p=0.00$	0.00	0.00

Figure 4.9. The relationship between fruit size (g) and fruit pedicel diameter (mm) in kiwifruit cv. Hayward. The fruits developed from early (△ , day 1-5), mid (× , day 6-10), and late (□ , day 11-15) periods of anthesis.
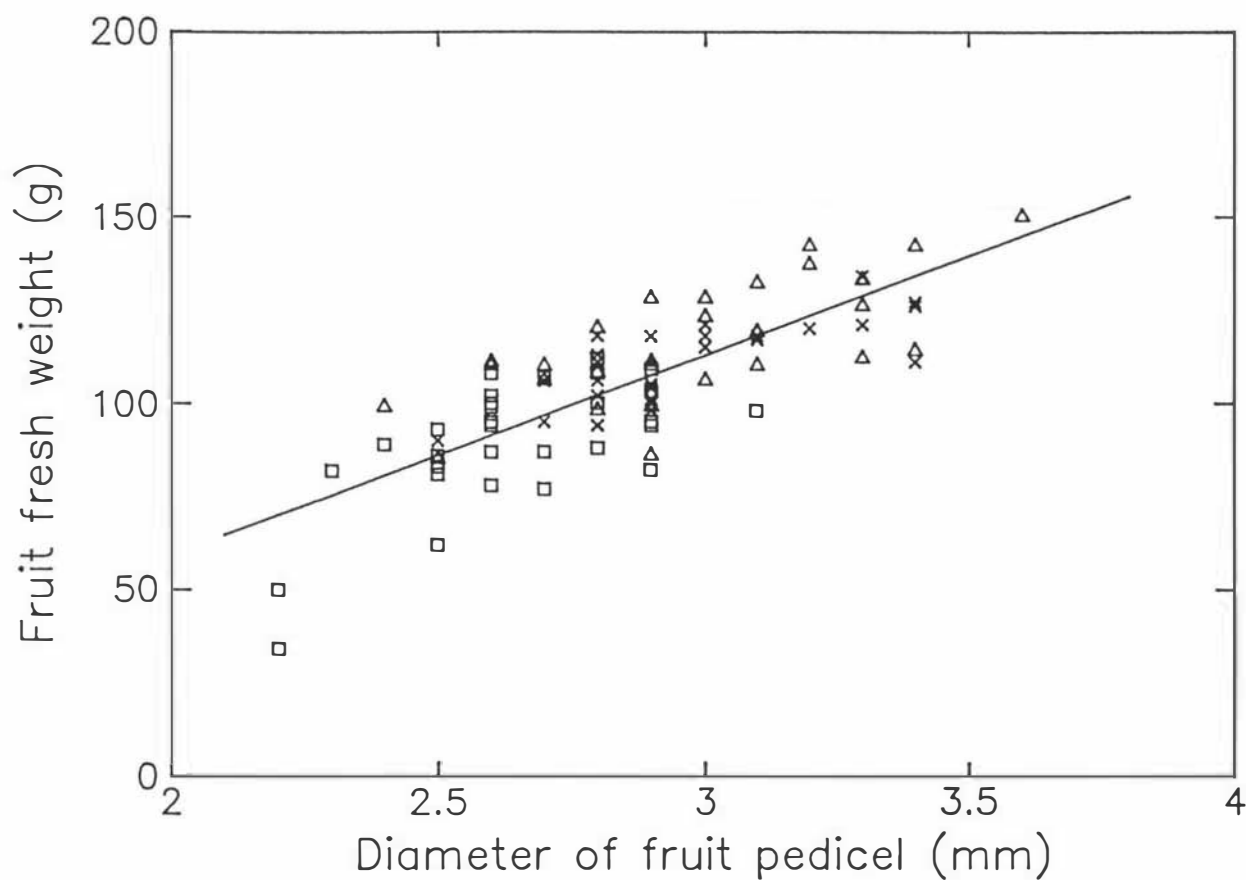
with stem diameter. In Trial 1, as stem diameters of short shoots decreased from 8.3 to 7.4 to 6.7 mm for early to mid to late treatments (table 4.5), leaf area per fruit differed by 79 cm^2, declining from 268 to 245 and 189 cm^2, respectively (p<0.05). However, the actual amount of leaf area per g of fruit fresh weight was consistent over all treatments (p=0.92); an average of 2.2 cm^2 per g of fruit fresh weight was observed (table 4.5).

4.4 Experiment 4C

4.4.1 Introduction

It was observed in experiment 4A (table 4.3) that long indeterminate shoots produced bigger fruits than short shoots. McKay (1976) reported a similar observation, and related the smaller fruits on short shoots with low seed numbers because they developed from late flowers on shaded locations of the vine. In this experiment, shade and flower variables were removed, and the effect of the type of fruiting shoot on fruit growth was investigated.

4.4.2 Materials and Methods

The experiment was carried out in a commercial orchard block at Levin, using 6-year-old 'Hayward' vines. Three types of fruiting shoots were selected:

      1. short ie. determinate shoots with about 5-6 leaves,

      2. medium ie. long, indeterminate shoots which

were pruned to 8 distal leaves one week after petal fall

     3. long ie. indeterminate shoots which were left intact

Each fruiting shoot carried 3 fruits. They were selected from well exposed parts of the vine canopy. The vines were trained on pergola trellises so that all the shoots were equally disposed for pollination. Only those shoots with the same 2 consecutive days of anthesis, on 24 and 25 Nov 1984, were selected.

The styles of flowers were excised at blossom so that a range of fruit sizes containing different seed numbers was produced. Three classes of fruit size were made by either excising flowers to 5 or 20 styles, or leaving them intact (40 styles).

Harvest was carried out on 27 Apr 1985, and fruit volume and fruit fresh weight were measured. Fruit locule numbers and tissue thickness were also recorded, and seeds were subsequently extracted to obtain fruit seed numbers and seed weight.

Fruit pedicel and stem diameters were also measured during harvest. The total leaf area on each treated shoot was determined after stripping off the leaves.

4.4.3 Results

Fruit Size Treatments

A range of fruit sizes was satisfactorily obtained by
the excision of flower styles at anthesis. Mean fruit sizes
for the 5, 20, and 40 styles treatments were 93, 105, and 114 g
respectively (table 4.8). This correlated with the mean
seed numbers of 668, 982, and 1184 respectively.

Effect of Shoot Type

The mean final fresh weight of fruits from all sizes on
short, medium, and long shoots were 97, 106, and 109 g
respectively (table 4.9). The mean fruit seed number of
fruits on long shoots was higher than for short shoots (1052
cf 819). Seed sizes however, was similar for all shoot types
(1176, 1187, 1183 ug; p=0.88). Figure 4.10 shows that at
the same fruit seed number there was no difference in the
fruit size between the different type of shoots (p>0.05).

Thicker fruit pedicel diameters (2.98 mm), and stem
diameters (11.8 mm) were found on long shoots as compared
with short shoots (2.66 and 7.0 mm, respectively). The total
leaf area of a long shoot was about 4 times that of a short

Table 4.8. Mean fruit data of kiwifruit cv. Hayward
for fruits which developed from flowers with 5, 20,
and 40 styles. S.E. in parenthesis.

Treatment	Fruit volume (cm^3)	Fruit fresh weight(g)	Fruit seed number	Fruit locule number
5 styles	86(4)	93(5)	668(82)	41(1)
20 styles	97(4)	105(5)	982(82)	41(1)
40 styles	105(4)	114(5)	1184(78)	41(1)
	p=.00	.00	.00	.98

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Table 4.9.   Mean fruit, stem and leaf data for long, medium, and short shoots of kiwifruit cv Hayward. S.E. in parenthesis. (Common letter within columns denotes groups not signicantly different, LSD (0.05)).

	Fruit Fresh Wt(g)	Fruit Volume (cm^3)	Fruit Seed Number	Mean Seed Size(ug)	Fruit Locule Number
Shoot Type:					
Short	97(6)	89(6)	819(97) b	1176(20)a	41(1)a
Medium	106(4)a	99(4)a	963(81)ab	1187(16)a	41(1)a
Long	109(5)a	101(5)a	1052(90)a	1183(22)a	41(1)a
p =	.14	.06	.07	.88	.98

	Pedicel Diameter (mm)	Stem Diameter (mm)	Leaf Area Per Shoot (cm^2)	Specific Leaf Wt (mg cm^{-2})
Shoot Type:				
Short	2.66(0.7)	7.0(.2)	823(51)	14.3(3.5)a
Medium	2.92(0.7)a	10.8(.3)a	1622(81)	13.3(0.8)a
Long	2.98(0.8)a	11.8(.3)a	3346(207)	13.5(0.4)a
	.00	.00	.00	.94

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Figure 4.10. Comparison of the relationship between fruit fresh weight per seed and fruit seed number for fruits from short (———), medium (— —), and long (-----) shoots. (p > 0.05).

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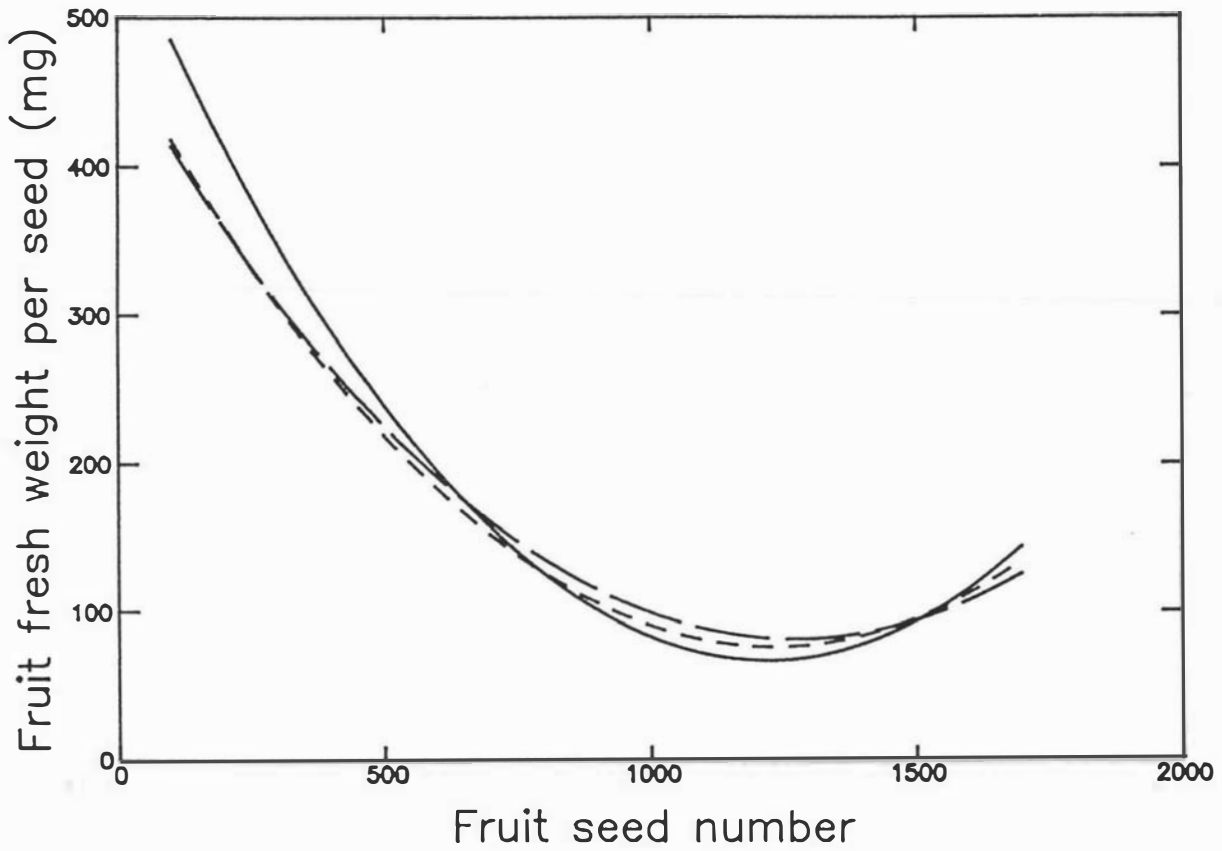
shoot (table 4.9).

Although fruit locule numbers were similar (table 4.9), some differences in the thickness of the inner pericarp and central core were observed (table 4.10). The mean tissue thickness of the inner pericarp was 12.08 mm for fruits from long shoots, as compared to 11.40 mm for short shoots (p=0.06). The thickness of the central core tissues were 5.45 and 5.20 mm respectively (p=0.20).

Table 4.10. Thickness of fruit tissue (mm) of kiwifruit
cv. Hayward. S.E. in parenthesis.

	Outer Pericarp	Inner Pericarp	Central Core
Short Shoot	6.61(.13)	11.40(.29)	5.20(.16)
Long Shoot	6.50(.12)	12.08(.23)	5.45(.15)
	p=.49	.06	.20

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4.5 Discussion

4.5.1 Interfruit Competition

Type A treatments in experiment 4A lacked interfruit competition because each of the 3 fruits on a shoot were of the same sink strength. The middle fruit in type B treatments however, had to compete with the large proximal and distal fruits. The results indicated that the presence of interfruit competition (type B) had reduced the size of fruits with less than 750 mg of seeds from their potential 52.5 g (type A) to 44.7 g (table 4.1).

Fruit competition effects on fruit size have been reported for cucumbers (Schapendonk and Brouwer, 1984). Older cucumbers were dominant in acquiring their own assimilates for growth such that depending on the availability of carbohydrate in the plant, young fruits abscised. The kind of fruit competition observed in this study however, could not be attributed to the competitive advantage given to an older fruit since all the fruits in experiment 4A had synchronous development.

In the tomato, individual fruits within a truss developed at the same time but the proximal fruits were

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always bigger (Walker and Ho, 1977a,b). Ho et.al. (1982) attributed this to the effects of hormones in the fruits. They suggested that under conditions of reduced assimilate supply, ABA moved from the proximal fruits to the distal fruits, so that the accumulation of high levels of ABA in the distal fruits reduced their capacity to import assimilates. In addition, it is also thought that the greater capacity of the proximal fruits to receive assimilates was related to the large amounts of IAA found in these fruits as compared to distal fruits.

The fruit competition effects in the kiwifruit observed in experiment 4A may also be due to the effects of hormones. It is unlikely that the growth of the middle fruit in type B treatment was reduced because the supply of assimilates was limiting. Since equivalent fruit size treatments had the same number of seeds and the same seed size (table 4.1), the amount of growth promoting hormones associated with the seeds would be expected to be similar. Therefore, it is probable that inhibitory substances have moved across, from the large adjacent fruits, to reduce the capacity of the middle fruit to acquire as much assimilates as those fruits with equivalent seed numbers in type A treatments. This inhibitory influence is apparently reduced as the seed numbers in the middle fruit increased, so that at some point between 1250 to 1500 seeds (class 3 in table 4.1), fruit

fresh weights were comparable with type A treatment. Mann (1943) found that in Cucumis melo about 180 seeds were needed to ensure fruit set, while normal fruit development could only be attained when a fruit contained more than 400 seeds. It was likely that in a similar way, a threshold level of seeds was required, above which the kiwifruit was not affected by the inhibitory effects of fruit competition.

Differences in fruit size between apple trees which were either thinned early or late in the season could be partly explained by the differences in cell division in the flesh of the fruits (Denne, 1960,1963; Havis, 1962). The effect of fruit competition in the kiwifruit was first evident from the data set collected at Day 27 (table 4.1). Since fruit cell division in the kiwifruit occurs for a period of up to 33 days after anthesis in the outer pericarp (Hopping, 1976), it was probable that interfruit competition inhibited fruit size by affecting cell division.

4.5.2 **Long and Short Shoots**

On T-bar trellises such as in experiment 4A, long shoots were commonly observed on higher and more exposed parts of the canopy whereas short shoots were more likely to occur at the distal, vertical drop of the canes. It was thought that

since long shoots in exposed positions were better disposed for pollination, an inevitable bias in sampling was introduced in the experiment, so that bigger fruits were found on long shoots (table 4.3), probably because of the presence of more seeds.

A pergola trellis was used the following season, in experiment 4C, so that long and short shoots were equally disposed for pollination. The results indicated clearly that the mean fruit size of long shoots was significantly bigger than that of short shoots (109 g cf. 97 g; table 4.9). The fruits on long shoots also contained more seeds (1052) than short shoots (819) and the seed sizes were similar (1183 cf. 1176 ug; p>0.05). Figures 4.5 and 4.10 further show that at equivalent fruit seed number, fruit fresh weight per seed was independent of the type of fruiting shoot. This then implies that the effect of long and short shoots on fruit growth was simply the effects of different seed numbers on fruit growth.

All the above observations agree with the work of McKay (1976). The suggestion that long shoots carried bigger fruits because the shoots were located in vine positions which were better predisposed for bee pollination may be over-simplified. Although McKay (1976) pointed out that shoot vigour may have a direct effect on fruit size, this study shows that there was probably a factor, inherent in the vigour of long shoots, which was responsible for the

production of larger numbers of viable seeds per fruit. It had been suggested by Possingham (1970) that the carbohydrate nutrition of the grape inflorescence was the limiting factor in fruit set. Similarly, Stephenson (1981) indicated that fruit seed numbers were matched by the available resources to develop seeds. From the stem diameter and total leaf area data in table 4.9 it can then be suggested that long shoots had a greater carbohydrate resource which was important initially, for the development of more seeds per fruit, and subsequently to meet the greater assimilate demand for more fruit growth.

Cell enlargement during stage II of kiwifruit growth was confined mainly to the inner pericarp and central core (Hopping, 1976). Table 4.10 shows that differences between long and short shoots were found in these two fruit tissues, indicating that cell expansion may be affected in the treatments. In addition, it was also shown that the difference in fruit size were not evident till about 48 days after anthesis (table 4.3), when most fruit cell division would have declined.

4.5.3 Fruit Pedicel Diameter

In both experiments 4B and 4C bigger fruits from early flowers, or long shoots were highly correlated with the fruit pedicel diameter (fig. 4.9, table 4.9). It was unlikely that the size of a kiwifruit was limited by the fruit pedicel diameter. Jahn (1978) for instance, found that fruiting in the orange and grapefruit tree was associated with an increase in the diameter of the fruit twig. He suggested that fruit development produced hormones which directed the differentiation of the vascular tissues and orientated it towards the fruit so as to facilitate translocation. In the kiwifruit, bigger pedicel diameters in large fruits could perhaps be due to responses to higher sink demands and greater translocation load.

4.5.4 Effect of Time of Flower Anthesis

Fruits from early flowers have been shown to be larger than fruits from late flowers in apples (Denne, 1963) and apricots (Jackson and Coombe, 1966). Similar observations were found in the kiwifruit (table 4.2 and 4.4).

It was shown in chapter 3 that the fruit growth of a kiwifruit approached an equilibrium at maturity. The

difference in final fruit size, as a result of 12-14 days delay in anthesis, and assuming that early and late fruits have similar growth patterns, is only 1 g. However table 4.2 shows that the differences in mean final fruit size at harvest was as much as 31 g. This represented a reduction in fruit size of about 2 g per day as anthesis was delayed (fig. 4.2).

Early flowers had a bigger ovary size than late flowers (table 4.7). Thus, differences in fruit size from early and late flowers were evident from the beginning of fruit development, even before fruit set.

Jackson and Coombe (1966) postulated that any factor that affected apricot fruit growth by modifying cell size could be operative at any stage of growth whereas a factor which was operative only before, or during the first few weeks after anthesis, was likely to affect fruit growth by its effect upon cell division. The effect of flowering dates on the growth of the kiwifruit was already significant during blossom (table 4.7). It was therefore likely that cell division was affected. Table 4.5 also show that early fruits have a mean of 41 locules as compared with 38 locules in late fruits. Clearly then, cell division at the early, pre-anthesis stage must have been affected by the factor that caused early or late anthesis of kiwifruit flowers.

Experiment 4B showed that early fruits had higher fruit

seed numbers and larger seeds (table 4.5; fig. 4.6). Table
4.6 shows that early fruits were bigger than late fruits
irrespective of seed size. Thus the effect of seed numbers
is a more important influence on the fruits of early or late
fruits. Kiwifruit pollen from male vines was viable for only
the first 2 to 3 days after male flowers were opened (Sale,
1981). Anthesis of male plants was earlier than the blossom
period of 'Hayward' (Ford, 1971) and it has been suggested
that during the anthesis of late female flowers, there was
less viable pollen available so that smaller fruits,
containing less seeds, were produced (McKay, 1976). This may
be an over-simplified explanation.

Although it was discussed earlier that the effect of
long and short shoots on fruit size may be correlated with
seed numbers, it is likely that early and late flowers
affected fruit growth directly. Even before pollination had
occurred, it was observed that early flowers had bigger
ovaries (table 4.7), and therefore the greater potential for
developing into bigger fruits. Figures 4.3 and 4.8 also show
that the fruit fresh weight per seed of early fruits was
distinctly greater than late fruits, especially at low fruit
seed numbers. This can also be seen clearly in figures 4.4
and 4.7 where there was a reduction in fruit size, as
anthesis was delayed, which was independent of fruit seed
number. However, it appeared that the presence of high fruit

seed number in late fruits may compensate for the initial
set-back in their fruit size (fig. 4.8).

The initial carbon resource which was available to a
flower bud probably determined the earliness or lateness of a
flower. Fruits from early apricot flowers had a greater
number of cells and bigger mesocarp volume because of the
greater availability of carbohydrate which promoted cell
division in the ovaries before anthesis (Jackson and Coombe,
1966).

In the kiwifruit vine, there was a predominance of long
shoots during early anthesis (table 4.4). It was also shown
in table 4.5 that the stem diameters of short shoots which
carried early fruits were bigger than those with late
flowers. This suggests that early kiwifruit flowers were
found on shoots which had greater carbohydrate resources.
Interestingly, these bigger shoots also had larger leaf
areas. The shoots which carried early fruits had 79 cm^2 more
leaf area per fruit than shoots which carried late flowers
(table 4.5). However, the leaf areas were proportional to
fruit size (2.2 cm^2 per g) for early or late fruits. This
may suggest that the growth of late fruits was limited by the
leaf area on its shoot but the results of other experiments
in chapters 6, 7, and 8 clearly indicated a flexibility in
the translocation of assimilate from outside a fruiting shoot
to support fruit growth. The production of bigger fruits was

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therefore largely decided during the early development of the flower ovary, when the supply of assimilates was more critical then during later stages of fruit growth.

Stem reserves may be important, not only during flower development, but also in the production of viable and large seeds.

CHAPTER FIVE

ASSIMILATE SUPPLY FROM SOURCE LEAVES ON A FRUITING SHOOT

5.1 Introduction

General Pattern of Assimilate Supply

Assimilate supply to fruits comes mainly from leaf photosynthesis, or stored substrates. In most species, fruit photosynthesis makes a negligible contribution to fruit growth (Chauhan and Pandey, 1984; Hansen, 1970b; Kriedemann, 1968a,c)

On a stem, the leaves which supply the fruits can be situated either above or below them (Hale and Weaver, 1962; Hansen, 1969). There is also a marked tendency for fruits to obtain their supply of assimilates from adjacent leaves (Khan and Sagar, 1969; Mooney, 1972).

The Source Leaf

During development a leaf passes from a stage during which it imports photosynthates, through a phase of simultaneous export and import, to a stage where export is predominant

(Thrower, 1962). The leaf however is not homogenous with regard to these processes. Larson and Dickson (1973) have shown that during leaf expansion the leaf contains cells of different developmental age. Even in the early stages of leaf development, some of the leaf cells will be able to export surplus photosynthate, despite the fact that the leaf as a whole may have a negative carbohydrate balance.

The source leaf must be sufficiently developed to the stage where the phloem through which export occurs is competent, both structurally and functionally (Dale and Milthorpe, 1983). Several studies have documented that developing leaves begin to export photosynthate before they have achieved their maximum size.

The stage of leaf development at which export begins varies. Generally, net export of carbon commences when a leaf has reached between one-third to half its final area (Wardlaw, 1968). According to Dale and Milthorpe (1983), this is the period when net photosynthesis reaches its maximum, and cell division has ceased in the palisade at the base of the blade.

Translocation from Source Leaf

Different levels of export from source leaves which were labelled with ^{14}C have been documented. In apple trees, Hansen (1970a) reported the major part of the ^{14}C absorbed in fully

developed leaves disappeared within the following 4 to 5 days.
In muskmelon plants, 68 $^0/_0$ of ^{14}C-label was exported in 2 hours
(Hughes et.al., 1983), while in cucumber leaves, it was found
that 80 $^0/_0$ of the total ^{14}C activity was incorporated into the
developing fruit within 24 hours (Barrett and Amling, 1978).

The rate of export of assimilates is not only controlled by
the rate of fruit growth (Hansen and Ryugo, 1979), but is also
affected by the leaf position and age. Thus, Hansen (1967b)
found that up to 80 $^0/_0$ of the ^{14}C-assimilates was retained in
the younger leaves of apple shoots, while larger and older
leaves exported as much as 80 $^0/_0$ of the labelled assimilates
during the same period.

Vascular Connections as Constraints to Assimilate Distribution

An important factor which determines the pattern of
assimilate supply from source leaves to fruit sinks is the
presence of vascular connections. Murray et.al. (1982)
suggested the possibility that photosynthates take the path of
least resistance by moving from sources to sinks which are
restricted to the same vascular pathway, or orthostichy. Hence
patterns of assimilate supply may be very specific. For
instance, Blomquist and Kust (1971) reported that in the soybean
plant, developing pods were supplied by leaves which were in
direct vertical alignment only, even though there were pods on

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the opposite side of the stem which were nearer to the same leaves. In the chickpea plant, assimilates cannot be translocated from one branch to the fruit produced on another (Singh and Pandey, 1980). Koch (1984) reported that only a certain source leaf will supply a particular fruit segment in the citrus fruit.

An interesting observation was made on tomato and pepper plants, when Bible (1976) discovered that higher yields were obtained from those plants which exhibited right-handed rather than left-handed phyllotaxy.

In a stem, a relation between the vascular system and leaf phyllotaxy is often implied. The definition of 'phyllotaxy' strictly applies to the arrangement of leaves as they develop at the stem apex (Richards, 1948). The helical arrangement of leaves on the stem is described by fractions from the Fibonacci series, such as 3/8 or 5/13, in which the 8th or 13th leaf above the one from which counting is started is reached after 3 or 5 revolutions round the axis, and falls more or less vertically in line with the starting leaf (Roach, 1939).

'Parastichy' refers to the ranks of arrangements of leaves (Erickson, 1983). Thus a stem with 3/8 phyllotaxy exhibits a 3-parastichy and 8-parastichy arrangement. Leaves that lie directly above one another form vertical ranks called 'orthostichies'. The number of orthostichies bears a simple relationship to the number of main vascular strands in the stem

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(Larson, 1983). It is also equivalent to the denominator of the fraction in a given phyllotactic ratio. The term 'vascular phyllotaxy', such as used by Larson (1977), describes the arrangement of vascular traces in the stem.

Alterations in Translocation Patterns

Changes in the relative strength of sinks can alter the predominant pathways of translocation. For example, in young tomato plants, all leaves were capable of supplying fruits on all trusses, but as the number of trusses increased, particular groups of leaves became the principal suppliers of particular trusses (Khan and Sagar, 1966).

In the cucumber plant, a source leaf exports to a particular fruit according to a pattern of assimilate distribution related to phyllotaxy. Schapendonk and Brouwer (1984) observed that this was only temporary; the removal of one sink led to an altered path along which leaf export proceeded to another sink.

Similarly in bean plants, a flexibility in translocation existed, such that photosynthates crossed orthostichies when partial defoliation and depodding placed the foliage in one orthostichy, and the pods in another (Nooden et.al., 1978).

Larson (1980) reported from his work on the cottonwood plant that the order of phyllotaxy increased as the plant

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increased in size and age. It was also suggested that the ontogenetic stages at which the phyllotactic transitions occurred were predictable, and were probably programmed in the plant's development. Thus the cottonwood plant progressed from a 1/2 phyllotaxy in the cotyledon stage, through the phyllotactic orders of 1/3, 2/5, 3/8, until it finally arrived at a stable order of 5/13.

5.2 Experiment 5A

5.2.1 Introduction

This experiment was designed as a preliminary study on the distribution of ^{14}C-photosynthate after a mature leaf on an indeterminate kiwifruit shoot was labelled with $^{14}CO_2$. The shoot was girdled at two positions below the labelled leaf to see if the girdling positions affected the pattern of assimilate distribution.

5.2.2 Materials and Methods

Four 1-year-old potted 'Hayward' vines were used. These plants were grown as a single shoot in a ventilated glasshouse environment. ^{14}C-label was applied on 27 July 1983 when the plants were at the 28th emerged leaf stage. A single, fully expanded leaf at node 15 on each plant was exposed to 37 kBq of $^{14}CO_2$. Just before the ^{14}C-label was applied, the plants were girdled at either 4 or 8 nodes below the labelled leaf.

5.2.3 Results

^{14}C-assimilate was transported acropetally (fig. 5.1) even though the labelled leaf retained 34 dpm mg^{-1} of activity. This is approximately 10 percent of the total activity in the plant. The stem tissues were the main sinks for the ^{14}C-assimilate. Young, developing leaves at the distal end of the shoot were also strong sinks. ^{14}C distribution in the two girdling treatments did not differ from each other.

Figure 5.1. The distribution of ^{14}C (dpm mg^{-1}) from a labelled leaf at the 15th node of a single-stem kiwifruit cv. Hayward vine. The vines were girdled at either 4 (node 11) or 8 (node 7) nodes below the labelled leaf.

Position of Stem Girdle

node position	node 7		node 11	
	stem	leaf	stem	leaf
28	5	17	8	11
27	8	4	10	5
26	7	4	9	6
25	7	4	8	4
24	5	2	8	5
23	3	9	7	2
22	3	0	5	1
21	4	0	4	1
20	4	0	4	1
19	5	0	7	0
18	3	0	5	0
17	4	0	5	0
16	5	0	7	1
15	7	34	8	33
14	11	0	10	1
13	0	0	0	0
12	0	0	0	0
11	0	0	0	0
10	0	0	girdle -	
9	0	0		
8	0	0		
7	0	0		
6	girdle -			
5				
4				
3				
2				
1				
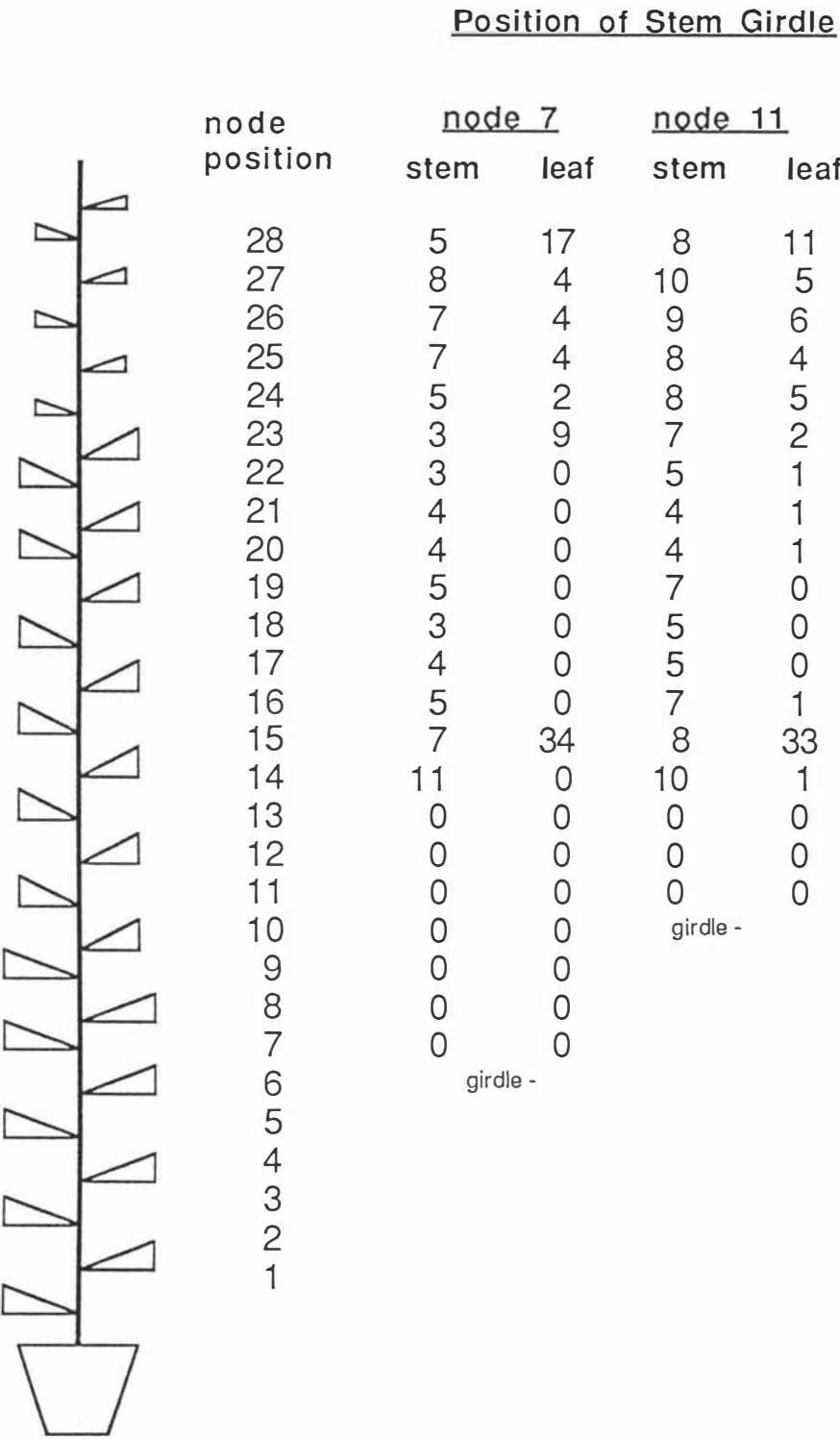
5.3 Experiment 5B

5.3.1 Introduction

The growth of a kiwifruit vine is sustained in the
winter by the use of reserve substrates (Davison, 1987).
During the first 30 days of spring growth, it was estimated
that only 20 to 40 $^0/_0$ of leaves on a mature vine could be
supported by the nutrient reserves in 1-year-old canes (Smith
et.al., 1986). In order to achieve a positive carbon budget
early in spring, it is important that young kiwifruit leaves
become net exporters in the shortest time after emergence.

In this experiment, young kiwifruit leaves were fed with
^{14}C-label to determine the stage of development when leaves
begin to export photoassimilates.

5.3.2 Materials and Methods

Eight 1-year-old potted 'Hayward' vines, grown as a
single stem in a glasshouse, were used. ^{14}C-label was
applied on 3 Aug 1983 when the plants were at the 25th
emerged leaf stage. Only a single leaf per plant was

labelled with 37 kBq of $^{14}CO_2$. The labelled leaf was at either the 13, 15, 17, or 19th node. Every plant was girdled at 4 nodes below the labelled leaf, just before the treatments were applied.

By using 8 'control' plants of the same age as treated plants, it was found that the areas of the leaves on the 13, 15, 17, and 19th node at the time when label was applied, were 87, 87, 64, and 49 $^0/_0$ of full leaf expansion, respectively.

5.3.3 Results

The results presented in figure 5.2 show that the young expanding leaf at the 19th node did not export ^{14}C-assimilate. Export began from the next older leaf, ie. at the 17th node, when they were at about 64 $^0/_0$ of full leaf area expansion. The export was acropetal, with the stem tissues making up the major sinks. Younger leaves above the labelled leaf also attracted the ^{14}C-photosynthate. In particular, the 3rd, 5th, and 8th leaf above the labelled leaf tended to be strong sinks, as compared with other leaves.

Position of Labelled Leaf

node position	leaf 13 stem	leaf	leaf 15 stem	leaf	leaf 17 stem	leaf	leaf 19 stem	leaf
25	31	4	43	5	43	15	1	0
24	19	16	31	4	35	2	1	0
23	16	15	68	31	31	5	1	0
22	19	1	36	3	29	25	1	0
21	14	7	24	3	26	3	1	0
20	27	1	30	64	24	10	0	0
19	12	0	37	1	32	2	2	311
18	21	1	22	1	21	2	0	0
17	20	1	19	1	15	344	0	0
16	13	1	33	0	58	1	0	0
15	20	0	33	235	1	0	0	0
14	36	1	44	3	1	0	girdle-	
13	44	266	1	0	1	0		
12	33	1	0	0	girdle-			
11	0	0	0	0				
10	0	0	girdle-					
9	0	0						
8	girdle-							
7								
6								
5								
4								
3								
2								
1								

5.4 Experiment 5C

5.4.1 Introduction

Smith et.al. (1986) reported that the main suppliers of assimilate to early fruit growth are the leaves in close proximity. Since summer pruning involves the removal of a large number of leaves on a long fruiting shoot, it is useful to know the relative importance of each leaf on every node of the shoot.

The previous experiments (5A and 5B) showed that ^{14}C was exported acropetally from a source leaf to the growing shoot tip of a long, non-fruiting shoot. This experiment was designed to determine the effect of fruits on the translocation of ^{14}C-assimilate from source leaves at different node positions along the fruiting shoot. The effect on the translocation patterns after pruning the shoots to different numbers of leaves was also investigated.

5.4.2 Materials and Methods

Thirty 3-year-old potted 'Hayward' vines grown in a glasshouse were used. Indeterminate shoots, carrying 2 fruits each, were selected and tagged for treatment. About 5 to 8 shoots were tagged on each vine, and the shoots were allocated to 3 treatment groups as follow:

1. Group A: Ten tagged shoots, each from a separate plant, were selected at random as a control to determine the total amount of ^{14}C activity which could be recovered immediately after labelling a fully mature leaf at the 8th node with 37 kBq of $^{14}CO_2$. Five shoots were girdled at the base, while the remainder were left intact.

2. Group B: This group consisted of a set of 11 treatments which were replicated 4 times. Each treatment was randomly assigned to one of the previously tagged shoots. The first treatment was to apply the ^{14}C-label to the leaf subtending the first fruit (denoted as leaf S1, see fig. 5.3a). The second treatment was to apply the ^{14}C-label to the leaf subtending the second fruit (denoted as leaf S2). Treatments 3 to 10 consisted of labelling leaves on the next 8 consecutive nodes (ie. leaf D3 to D10). The last treatment was made by labelling the first leaf proximal to

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Figure 5.3. Diagrammatic representation of the notation used in group B and C treatments: X-1, leaf proximal to fruit; S1 - S2, leaves subtending fruits; D3 - D10, distal leaves. (a) example of group B treatments, (b) example of group C treatments.

(Experiment 5c)

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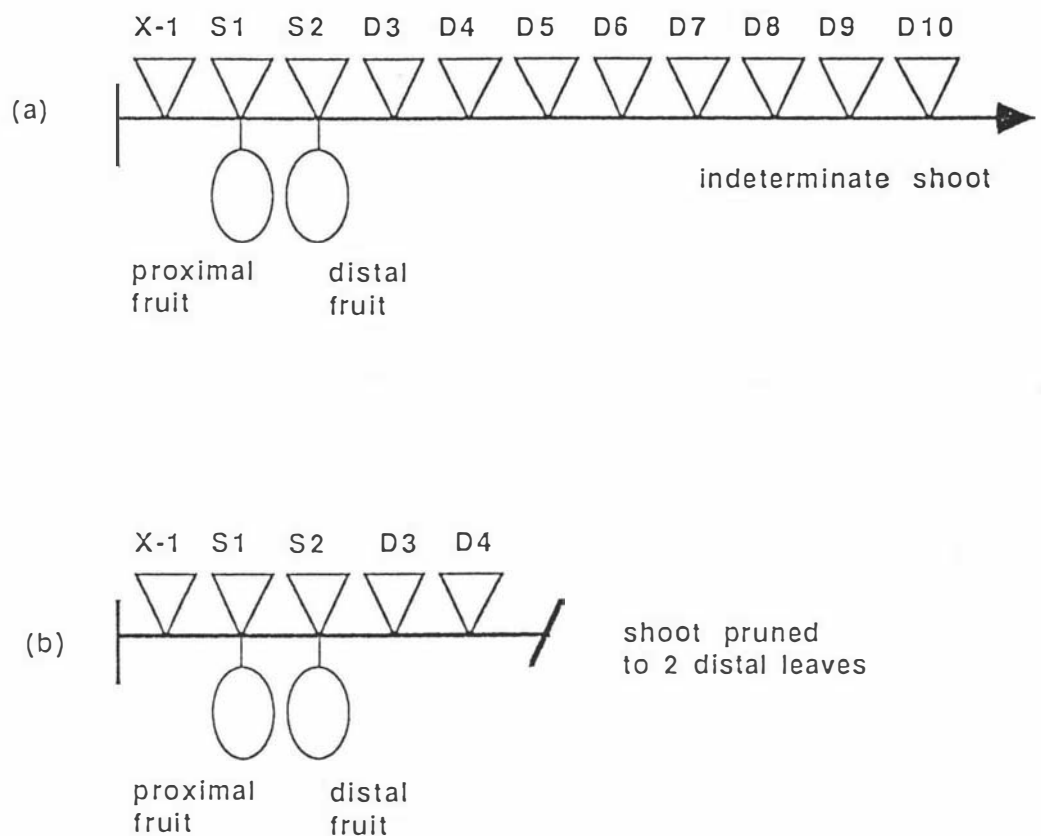
the first fruit (denoted as leaf X–1).

3. <u>Group C</u>: Shoots were pruned one week before
^{14}C–label was applied to compare the pattern of translocation
with treatments on intact shoots in group B. Twelve shoots
were pruned back to only the subtending leaves and ^{14}C–label
was applied to leaf X–1, S1, or S2. Another 12 shoots were
pruned to 2, 4, or 8 distal leaves and label was applied to
the last leaf, ie. leaf D4, D6, and D10 respectively (see
fig. 5.3b).

^{14}C–label was applied to all the above treatments
between 26 and 29 Dec 1984. The fruits were growing at an
absolute growth rate of 0.9 g per day and the average fruit
size was about 33 cm^{3}. The shoot apex was still active and
each shoot had between 22 and 34 nodes. Harvest was carried
out between 2 and 5 Jan 1985 and the plant materials were
subsequently prepared for ^{14}C assay.

5.4.3 Results

Translocation of ^{14}C

The results of the group A treatment presented in figure 5.4 indicate that transport of photoassimilate from the source leaf to sites of demand occurred within the 3 hour period of $^{14}CO_2$ application. Translocation was blocked when the phloem transport system was severed in a girdled stem. Up to 98.6 $^0/_0$ (790 dmp mg^{-1}) of the total ^{14}C recovered was retained in the labelled leaf.

Constraints of Vascular Connections in Translocation

Table 5.1 shows clearly that the transport of ^{14}C assimilate in an indeterminate shoot with 2 fruits was compartmentalised. The movement of ^{14}C assimilate was restricted by vascular connections between the 5th and 8th leaf above a labelled leaf. Thus, the proximal fruit (node 1) received its main supply of assimilate from its subtending leaf, plus further supplies from node 1+5 and node 1+8 (table 5.1). Similarly, the distal fruit (node 2) was linked to its source leaves at nodes 2, 2+5, and 2+8. The extent to which leaves beyond leaf D9 and leaf D10 supplied the fruits was

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Figure 5.4. Distribution of ^{14}C activity (dpm mg^{-1}) in a kiwifruit cv. Hayward fruiting shoot 3 hours after ^{14}C-label was applied to the leaf at node 8. Total ^{14}C recovered per shoot equals 1.98 x 10^{6} dpm. Shoots were either girdled or left intact. Percentage of total ^{14}C in parenthesis.
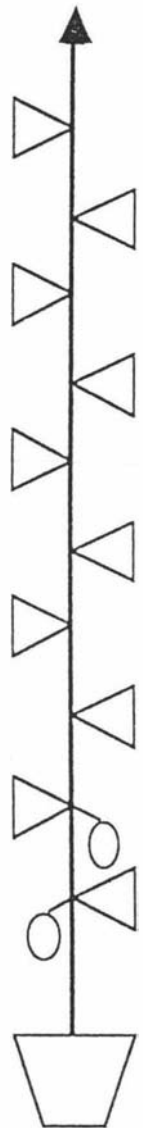
node position	girdled stem	girdled leaf	non-girdled stem	non-girdled leaf
10	0	0	0	0
9	0	0	0	0
8	13 (1.2)	790 (98.6)	7 (1.9)	556 (94.4)
7	2 (0.2)	0	6 (1.3)	0
6	0	0	4 (0.9)	0
5	0	0	4 (0.8)	0
4	0	0	3 (0.5)	0
3	0	0	1 (0.2)	0
2	0	0	0	0
1	0	0	0	0

fruits

	girdled	non-girdled
proximal	0	0
distal	0	0

Table 5.1. Recovery of ^{14}C-activity (dpm mg^{-1}) in the proximal and distal fruits of an indeterminate kiwifruit cv. Hayward shoot carrying 2 fruits. ^{14}C-label (37 kBq) was applied to leaves at different node positions. Figures in parenthesis represent the amount of ^{14}C-activity recovered in the fruit as a percentage of the total ^{14}C fixed per shoot. No activity was recovered from the distal end of the shoot.

Node position of labelled leaf	Proximal fruit	Distal fruit
D10	0	84(37)
D9	111(35)	0
D8	0	0
D7	0	74(35)
D6	85(43)	0
D5	0	0
D4	0	0
D3	0	0
S2	0	163(57)
S1	136(62)	0
X-1	0	0

not investigated.

The movement of ^{14}C assimilate out of the labelled leaves was directional. Leaves which did not supply fruits in experiment 5C were too distant from the shoot apex. They exported basipetally towards the main cane (fig. 5.4).

Alteration in Translocation Pattern

When a fruiting shoot was pruned to fewer leaves (group C), the pattern of assimilate distribution was altered. This is shown in table 5.2.

In group B, the contribution of leaf X-1 in an intact shoot system was not important. By contrast, leaf X-1 on a pruned shoot system was rather significant in supplying assimilates to both the proximal (14 $^{0}/_{0}$) and distal (21 $^{0}/_{0}$) fruits.

In the pruned shoot system, leaf S1 and S2 continued to feed their subtending fruit almost exclusively by 78 and 74 $^{0}/_{0}$ of the total label, respectively. This represented further increases of 16 and 17 $^{0}/_{0}$ when compared with intact shoots (62 and 57 $^{0}/_{0}$, respectively; table 5.1).

After the shoot was pruned, leaf D6 and D10 still supplied the fruits at node 6-5 (ie. proximal) and 10-8 (ie. distal), respectively. However, unlike intact shoots, some ^{14}C activity was also recovered in the other fruit on either

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Table 5.2. Recovery of ^{14}C-activity (dpm mg^{-1}) in the proximal and distal fruits of kiwifruit cv. Hayward shoots carrying 2 fruits. The shoots were pruned to 0, 2, 4, or 8 distal leaves and ^{14}C-label was applied to a leaf at different node positions. Figures in parenthesis represent the amount of activity recovered in the fruits as a percentage of the total ^{14}C fixed per shoot (1.98 x 10^6 dpm).

Number of distal leaves	Node position of labelled leaf	Proximal fruit	Distal fruit
8	D10	11(6)	63(26)
4	D6	175(55)	17(5)
2	D4	54(21)	87(39)
0	S2	0	236(74)
0	S1	250(78)	0
0	X-1	18(14)	34(21)

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treatments.

Like leaf X-1, leaf D4 on a pruned shoot system also became a source leaf. The distal fruit attracted 39 $^{0}/_{0}$ of the ^{14}C-photosynthate from this leaf, while the proximal fruit imported 21 $^{0}/_{0}$.

5.5 Discussion

5.5.1 The Source Leaf

Leaves of most plants become net exporters from between one-third to half their full final size (Watson and Casper, 1984). It was indicated in chapter 2 that a net loss of dry matter from kiwifruit leaves occurred when they were about 60 $\%$ full size. The results of experiment 5B (fig. 5.2) showed that the kiwifruit leaf began to export assimilates from between 49 to 64 $\%$ full expansion.

The amount of ^{14}C activity retained in leaves varies according to sink demand. For instance, apple leaves were reported to retain 45 $\%$ or more of the ^{14}C absorbed during the period of full bloom, but this dropped to about 20 to 30 $\%$ after full bloom (Hansen, 1967a). As much as 40 to 50 $\%$ of the total ^{14}C absorbed by apple leaves was respired (Hansen, 1967 b, c). In the kiwifruit leaf, only 10 $\%$ of ^{14}C was retained in the leaf of a non-fruiting shoot after a period of a week (fig. 5.1). It was also shown previously (chapter 1) that the major part of ^{14}C absorbed by the leaf was exported within 6 days (fig. 1.3).

The effect of girdling in experiment 5C (group A) was to

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delay the translocation of ^{14}C-assimilate out of the source leaf. Thus, figure 5.4 shows that during the 3-hour feeding period, 98 $^0/_0$ of the ^{14}C was still retained in the labelled leaf on a girdled shoot, whereas 5.6 $^0/_0$ had started to move out from the leaf into an intact shoot.

5.5.2 Direction of Assimilate Translocation

The export of ^{14}C-photosynthate from the mature kiwifruit leaf was directional. Younger leaves in experiments 5A and 5B exported mainly acropetally to the stem, growing shoot apex, and newly emerged leaves (figs. 5.1 and 5.2). The positions of the stem girdles did not affect the acropetal transport. Older leaves exported basipetally to supply fruit growth (fig. 5.4). Thus like most fruit crops such as grape (Hale and Weaver, 1962), apple (Quinlan and Preston, 1971), and mango (Chauhan and Pandey, 1984), the kiwifruit vine also has a flexibility in the direction of assimilate translocation.

5.5.3 Sectorised Transport in the Fruiting Lateral

The results of experiment 5C show that vascular connections were an important factor which determined the distribution of assimilates in the kiwifruit shoot. Table 5.1 indicates distinct orthostichies which linked the n, n+5, and n+8 nodes. Thus the proximal fruit (node 1) was supplied by leaves S1, D6, and D9, while the distal fruit (node 2) imported assimilates from leaves S2, D7, and D10. The remaining leaves which did not supply either fruit exported ^{14}C out of the fruiting lateral. There was also some indication in figure 5.2 that younger leaves on the 3rd, 5th, and 8th node above a labelled leaf attracted more ^{14}C.

Although the kiwifruit has been described as exhibiting a 2/5 phyllotaxy (Ferguson, 1984), the above results suggest that other phyllotactic orders existed. Transitions of phyllotaxis within the vascular system of plants are known to occur before they were expressed at the shoot apex (Larson, 1975). This may not be detected in the external morphology of the shoot. Apparently, the pressure to reorganise the vascular system was related to the vigour of the plant. Thus the work of Larson (1975,1979) indicated that low orders of phyllotaxy in the cottonwood plant could not sustain a high level of leaf production when growth was vigorous.

Pulawska (1965) studied the relationship between

phyllotaxis and vascular organisation in Actinidia arguta and reported that during the ontogeny of long shoots the plant changed the organisation of its vascular system. The Actinidia arguta shoot went through the phyllotatic order which linked the leaf traces n and n+8, followed by n and n+13, and later n and n+21. This study indicated that similar vascular transitions may have occurred in the kiwifruit shoot.

5.5.4 Effects of Pruning on Assimilate Distribution

The fruits on an intact shoot could only obtain their supply of ^{14}C-assimilate from leaves which were in the same orthostichy (table 5.1). However, when the fruiting shoot was pruned, all the leaves could become source leaves. Table 5.2 shows that subtending leaves still supplied exclusively to the fruit on the same node. In fact, in the absence of any distal leaves past the fruit, leaf S1 and S2 exported 16 and 17 $^0/_0$ more ^{14}C assimilate to the proximal and distal fruit respectively.

Leaf D4, which did not supply either fruits on an intact shoot, became a source leaf as a result of pruning the shoot. It then supplied 21 and 39 $^0/_0$ of the total ^{14}C per shoot to the proximal and distal fruit, respectively.

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Similarly leaf X-1, which lies in a position proximal to the fruits, became an important source leaf to both the fruits after the shoot was pruned.

In an intact shoot system, leaf D6 supplied only the fruit in node 6-5 (ie. the proximal fruit), while leaf D10 supplied only the fruit in node 10-8 (ie. the distal fruit). This pattern of translocation was altered after the shoot was pruned. Some ^{14}C-assimilate from leaf D6 was then found in the distal fruit, while the proximal fruit also imported ^{14}C from leaf D10 (table 5.2).

Pate and Farrington (1981) found that with the development of secondary growth in the lupin plant, assimilates began to move laterally between orthostichies. The shoots in experiment 5C were pruned a week before ^{14}C-label was applied, and it is possible that vascular connections between orthostichies were developed de novo, in response to the need for rerouting assimilates to relative sink demands. The obvious advantage to the kiwifruit vine is that fruits are ensured of a carbohydrate supply from alternative source leaves, not only in pruning situations, but also when the original source leaves are destroyed by disease or other natural disasters.

CHAPTER SIX

SOURCES OF ASSIMILATE SUPPLY OUTSIDE THE FRUITING SHOOT

6.1 Introduction

Studies on the assimilate supply and translocation patterns in several crops indicated an autonomy in the use of carbon within a fruiting shoot during the growing season. It has been shown in peach (Schneider, 1977), pecans (Davis and Sparks, 1974), and apples (Hansen, 1967a) that leaves on the same shoot supply much of the carbohydrate requirements for the development of the fruits. Assimilate produced by mature leaves which is not utilised in fruit development, generally supplies sites of vegetative growth or is used to build up the reserve substrates in the roots (Kriedemann, 1969b; Hansen, 1967c).

Supply of Assimilates to Fruits from Distant Leaves

When the assimilate demand of a fruit is not met by its nearby leaves, carbohydrate can be drawn from the leaves in adjacent shoots. Thus in apple trees, translocation from extension shoots occurred after the fruits had exhausted the

carbohydrate supply from their own spur leaves (Hansen, 1969).

For most fruit trees, there is some flexibility in the movement of carbohydrate from one branch to another. For example, Quinlan and Weaver (1970) investigated the extent of phloem translocation between adjacent shoots of the grape vine, and reported significant movements of assimilate from adjacent grape shoots after treatments which included gibberellins, shading, or defoliation.

The relative demand for assimilates from distant leaves is correlated with the leaf-fruit ratio of the fruiting shoot. Thus, Hansen and Christensen (1974) found that during the early period of apple fruit growth, when only a small leaf area was necessary to support the growth of one fruit, little ^{14}C was translocated from the leaves on adjacent shoots. However, during the later stages of rapid increases in fruit size, the proportion of ^{14}C-photosynthate transferred from non-fruiting adjacent shoots was nearly as great as the proportion translocated from leaves to fruits on the same spur.

Utilisation of Reserve Substrates

Reserve material accumulates in fruit trees mainly during the last 5 to 7 weeks before leaf-fall, and the greater part of it is stored in the roots (eg. Hansen and Grauslund, 1973). Starch is a common component of the reserve carbohydrate (Meir

and Reid, 1982), although in the kiwifruit vine, Redgewell (1983) showed that there can be a considerable amount of mucilage polysaccharides.

Early in spring, the major part of the reserves in the apple tree was assumed to be used for respiration, in connection with the development of leaves, flowers, and shoots (Hansen, 1967c,1971). The dependence on reserves was short, so that most of the materials for growth in spring came from the current production of assimilates by the leaves (Hansen,1971a).

Some reports indicated that fruits can mobilize reserve substrates (Ho, 1979a,b; Kozlowski and Keller, 1966; Rawson and Evans, 1971). For example, Ho (1979b) showed that tomato fruit growth was supplied by reserve carbohydrate, after treatments that either reduced concurrent photosynthesis, or increased sink strength.

6.2 Experiment 6A

6.2.1 Introduction

In the kiwifruit vine, the percentage of 1-year-old
laterals that remained vegetative ranged from 20 to 65 $^0/_0$
(Brundell, 1975c; Mulligan, 1986; Snowball, 1986). The
maintenance of a minimum vine leaf to fruit ratio can be
achieved by a balance between the removal of vegetative
shoots and pruning fruiting shoots to appropriate leaf
numbers. Little is known about the extent to which
vegetative shoots contribute to fruit growth, and the
objective of this experiment was to investigate this further.

6.2.2 Materials and Methods

Plant Materials

Eight 8-year-old 'Hayward' vines in a commercial orchard
block at Levin were used. Four of these vines were thinned
by removing flower buds from every alternate shoot along a

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second-year cane. The remaining 4 vines were left intact.

Thus light cropping vines had about 500 fruits, whereas

intact vines had a crop load of 1000 fruits.

Application of Treatments

Fruiting and vegetative shoots at the distal ends of

2-year-old canes were selectively removed to obtain one of

the three basic shoot arrangements shown diagrammatically in

figure 6.1.

Two other factors were also imposed over the shoot

treatments:

> 1. leaving a vegetative shoot (5 leaves) at
> the distal end of the 2-year-old cane, as a further
> source of photoassimilates.
> 2. girdling the 2-year-old cane to isolate
> the shoot arrangement from the rest of the vine.

The total of 16 treatments (4 shoot treatments x 2 leafy

shoot x 2 girdling) was replicated over 4 'light' cropping

and 4 'high' cropping vines so as to give an overall

'split-plot' experimental design.

The treatments were applied on 21 Dec 1983, and the

treated shoots were exposed by the removal of any surrounding

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Figure 6.1. Diagrammatic representation of shoot treatments 1-4 in experiment 6A. Shoot treatments 1 and 2 corresponded with shoot arrangements A and B respectively. Shoot treatments 3 and 4 lie adjacent to each other in shoot arrangement C. Each shoot arrangement was located at the distal end of a 2-year-old cane, and were either girdled to isolate from the rest of the cane, or left intact. A leafy shoot was also either present or absent at the distal end of each shoot arrangement. The mean leaf area of the fruiting shoot was 520 ± 28 cm².

Shoot Arrangement A

± girdle

Shoot Treatment 1

3 fruit : 5 leaf

± leafy shoot

pruned

Shoot Arrangement B

± girdle

Shoot Treatment 2

3 fruit : 0 leaf

± leafy shoot

pruned

Shoot Arrangement C

± girdle

Shoot Treatment 3

3 fruit : 5 leaf

Shoot Treatment 4

3 fruit : 0 leaf

± leafy shoot

pruned

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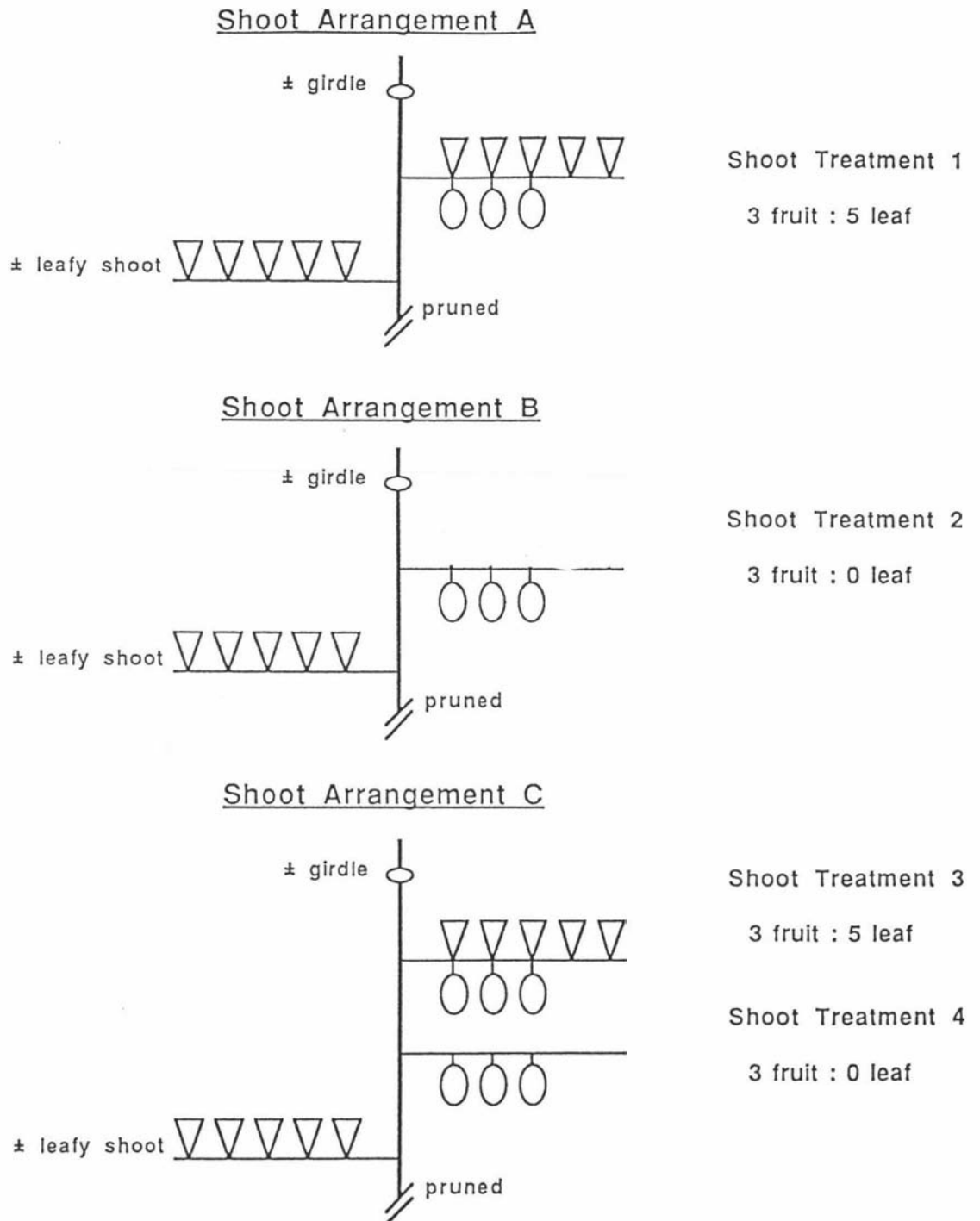
shading shoots. Shoot regrowths were also removed when they appeared. Girdled canes were also checked periodically to ensure that any callus which had formed over the girdle was removed.

Data Collection

Fruit volumes and fresh weights were obtained after harvest on 10 May 1984. The number of fruits and shoots, on the part of the 2-year-old cane proximal to the treated laterals, was recorded. The fruit load on each cane was then expressed as a factor given by the total number of fruits divided by the total number of shoots.

There was a considerable loss of fruits and leaf damage, either through treatment effects (treatment 2), or vine conditions. Consequently, statistical analysis was carried out on an uneven number of replicates in each treatment.

6.2.3 Results

Main Effects

The effect of the shoot treatments on fruit size was

significant (p<0.05; table 6.1). Table 6.2 shows that shoot treatments 1 and 2 had higher mean fruit volumes (100 and 98 cm^3, respectively) than treatments 3 and 4 (92 and 86 cm^3, respectively).

The overall effect of girdling was a significant reduction in fruit size from 96 to 91 cm^3 (p<0.05). Leafy shoots contributed to an increase in mean fruit size from 92 to 96 cm^3 although this was not statistically significant (p>0.05).

High and low cropping vines however, did not show any difference in fruit size (p=0.93).

Interactions

The interactions between crop load and each of the other factors were not significant (table 6.1). The appropriate test for the effect of high and low cropping vines was to compare only the non-girdled treatments. Table 6.3 shows the table of means for the interaction between crop load and girdling. The mean fruit size of non-girdled treatments on high cropping vines (96 cm^3) was similar to low cropping vines (96 cm^3; p=0.98). For this reason, vine loads were combined so as to give greater degrees of freedom in the statistical analysis of the effects of other factors.

A significant interaction was observed between girdling

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Table 6.1. Summary of the significance of
F values from an unbalanced split-plot ANOVA
in experiment 6A.

Main Effects:

Crop Load	P=0.926
Shoot Treatment	.022
Leafy Shoot	.135
Girdle	.021

Interactions:

Load x Shoot Treatment	.998
Load x Leafy Shoot	.720
Load x Girdle	.903
Shoot Treatment x Leafy Shoot	.593
Shoot Treatment x Girdle	.109
Leafy Shoot x Girdle	.013

Table 6.2. Table of means of final fruit volume (cm^3) for main effects in experiment 6A. S.E. in parenthesis.
(Common letter denotes groups not significantly different at LSD (0.05)).

	N	Final Fruit Volume (cm^3)
High Crop Load	53	94(18)
Low Crop Load	44	95(16)
		p=.93
Non-girdled	52	96(14)
Girdled	45	91(19)
		p=.02
− Leafy Shoot	45	92(17)
+ Leafy Shoot	52	96(16)
		p=.14
Shoot Treatment		
1	28	100(13)a
2	18	98(14)a
3	27	92(14)b
4	24	86(21)b
		p=.02

Table 6.3. Influence of high and low cropping vines, and girdling on the fruit volume (cm^3) of kiwifruit cv. Hayward. S.E. in parenthesis.

	High Crop Load	Low Crop Load	
Non-girdled	96(13)	96(15)	p=0.98
Girdled	91(13)	93(17)	0.82
	p=0.23	0.48	

and the presence or absence of leafy shoots ($p < 0.05$). In the presence of leafy shoots, the mean fruit size on girdled (97 cm^3) and ungirdled (95 cm^3) treatments were not significantly different ($p = 0.46$; table 6.4a). However, in the absence of a leafy shoot, girdling reduced fruit growth from 98 cm^3 to 85 cm^3 ($p < 0.01$).

It can also be seen from table 6.4a that in non-girdled treatments, fruit sizes were reduced when a leafy shoot was present. This was more pronounced in shoot treatments 3 and 4 where fruit sizes were inhibited by up to 9 cm^3. The fruit load factors on the rest of the 2-year-old cane were also smaller for those treatments with leafy shoots (table 6.4b).

An opposite effect was observed on girdled treatments. The result of the presence of a leafy shoot was to increase fruit size by an average of 12 cm^3 ($p < 0.01$; table 6.4a). In shoot treatment 1, the difference in fruit size was 16 cm^3 ($p < 0.01$). Fruits did not set in shoot treatment 2 when there was no leafy shoot. However, the presence of a leafy shoot was able to restore fruit growth on the completely defoliated shoots to 95 cm^3. Fruit growth on pruning treatment 3 was similar, regardless of the presence or absence of leafy shoots ($p = 0.85$). Fruit set occurred on the completely defoliated shoot of pruning treatment 4, even in the absence of an adjacent leafy shoot. The fruit size however, was significantly smaller (71 cm^3) than those fruits where an

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Table 6.4. (a) The effect of girdling and leafy shoots on the fruit size (cm^3) of kiwifruit cv Hayward in different shoot treatments (see fig. 6.1). (b) Fruit load factor (ie. total number of fruits divided by total number of shoots on the rest of the 2-year-old cane) corresponding to the non-girdled treatments. S.E. in parenthesis. Common letter within columns denotes groups not significantly different at LSD(0.05).

(a) Fruit volume (cm^3)

	Non-Girdled			Girdled		
	-Leafy Shoot	+Leafy Shoot		-Leafy Shoot	+Leafy Shoot	
Shoot Treatments						
1	100(3)a	97(2)b	p=0.49	94(4)a	110(3)b	p=0.00
2	100(4)a	102(3)b	0.61	0	95(4)a	−
3	97(3)a	88(3)a	0.04	90(3)a	91(4)a	0.85
4	97(3)a	89(5)a	0.18	71(4)b	88(5)a	0.01
	p=0.87	0.00		0.00	0.00	
mean	98(2)	95(2)		85(3)	97(2)	
		p=.17	.00	.46	.00	

....

(b) Load Factor on non-girdled canes

	-Leafy Shoot	+Leafy Shoot	
Shoot Treatments			
1	1.5(0.3)	1.4(0.2)	p=0.88
2	1.3(0.2)	1.7(0.2)	0.12
3	1.8(0.1)	1.5(0.1)	0.01
4	1.8(0.1)	1.6(0.1)	0.22
	p=0.23	p=0.39	
mean	1.7	1.6	

p=0.41

adjacent leafy shoot was present (88 cm^3; p=0.01).

6.3 Experiment 6B

6.3.1 Introduction

It was shown in the last experiment (6A) that the carbohydrate requirements for fruit growth in the kiwifruit can be met from sources outside the fruiting shoot. Fruit growth benefitted from excess photosynthate exported from adjacent fruiting or non-fruiting shoots.

Experiments 5A and 5B showed that within a kiwifruit lateral the transport of ^{14}C-assimilate was directional. However, it was not known whether the translocation of assimilate from one lateral to another was preferentially acropetal or basipetal, and whether this was influenced by different sink strengths.

A clear indication that vascular connections constrained the movement of photosynthates within a fruiting lateral was shown in experiment 5C. However, it was also not known as to whether these constraints persisted in the transport of assimilates in 2-year-old cane.

This experiment consisted of several treatments which were designed to use ^{14}C-tracer to investigate the above aspects of assimilate translocation in the kiwifruit vine.

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6.3.2 Materials and Methods

All the vines in this experiment were potted, 3-4 years old plants grown in a ventilated glasshouse environment at Massey University. Each vine was labelled with 185 kBq of $^{14}CO_2$. All the vines were girdled, just before the label was applied, by removing a 5mm strip of the bark at the base of the stem.

Treatment 1 (6 Dec 1983)

Five 'Hayward' and four 'Bruno' vines were pruned to the basic shoot arrangement shown in figure 6.2. $^{14}CO_2$ was applied to a single, fully expanded leaf on the lowest non-fruiting lateral. Each of the fruiting shoots above were pruned to 2 fruits and 4 leaves. During harvest, the mean fruit size on the 'Hayward' and 'Bruno' vines was 46 and 36 cm^3 respectively.

Treatment 2 (3 Jan 1984)

The vines used in this treatment were pruned to 4 types of shoot arrangements as shown in figure 6.3. Three

Figure 6.2. Percentage distribution of ^{14}C in
4-year-old (a) 'Hayward', (b) 'Bruno' vines. Each
fruiting shoot was pruned to 2 fruits and 4 leaves.
$^{14}CO_2$ (185 kBq) was applied to a mature leaf
(hatched) on a leafy shoot.

(a) Hayward   (b) Bruno

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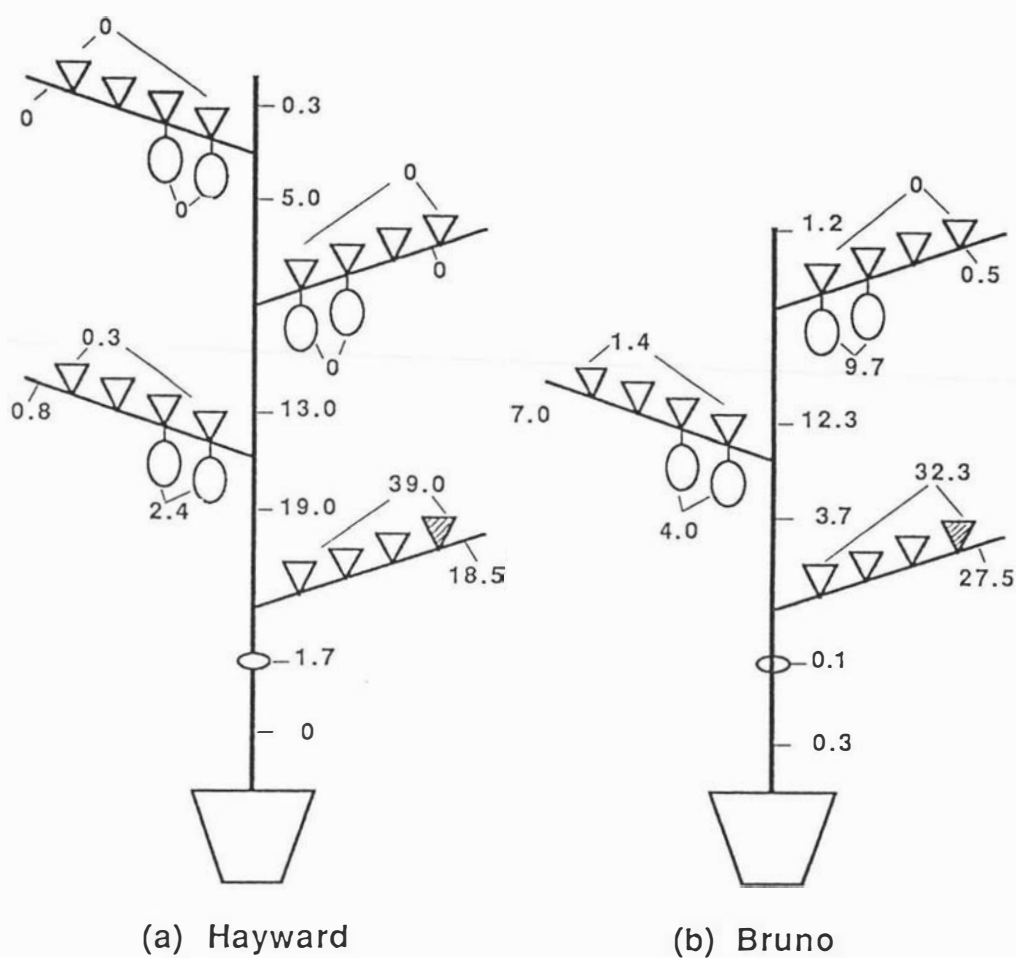
Figure 6.3. Percentage distribution of ^{14}C in 3-year-old potted 'Monty' vines. Each vine was pruned to 3 fruiting shoots and a basal leafy shoot. The top fruiting shoot and basal leafy shoot were pruned to 4 leaves. The other fruiting shoots were either pruned to 8-10 leaves or 2 leaves. ^{14}C-label was applied to a fully expanded leaf on either the top fruiting shoot (type C and D) or basal leafy shoot (type A and B).

(a) Type A

(b) Type B

(c) Type C

(d) Type D
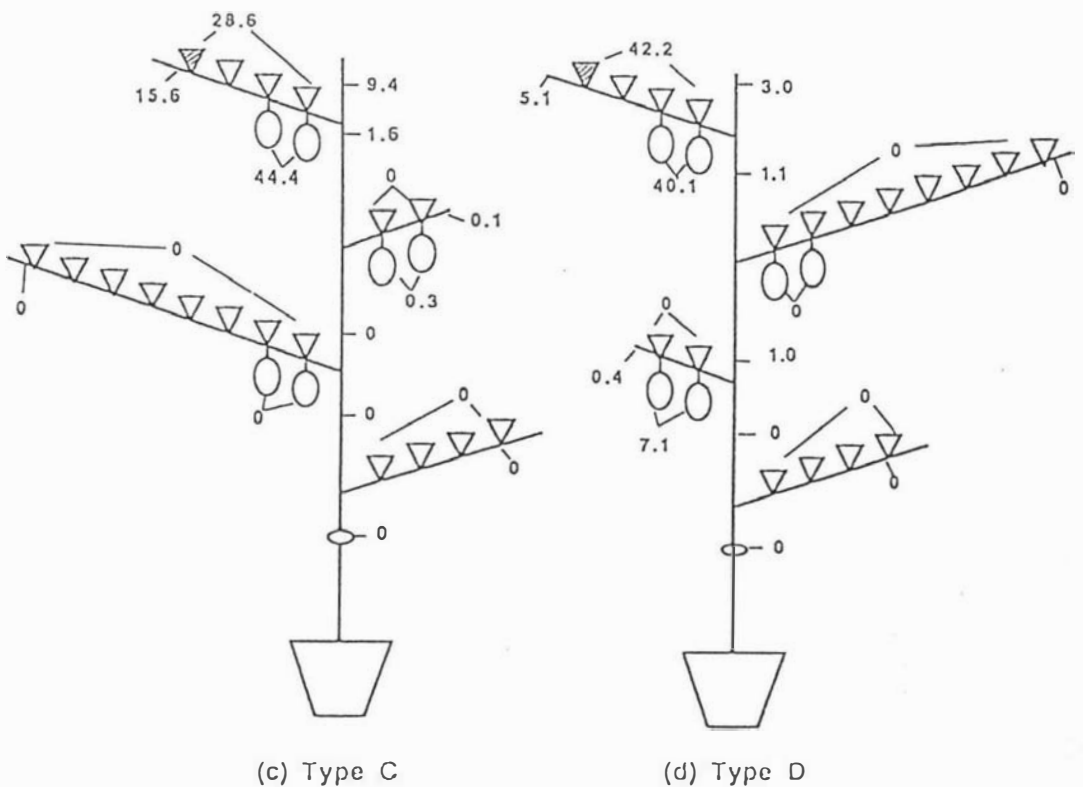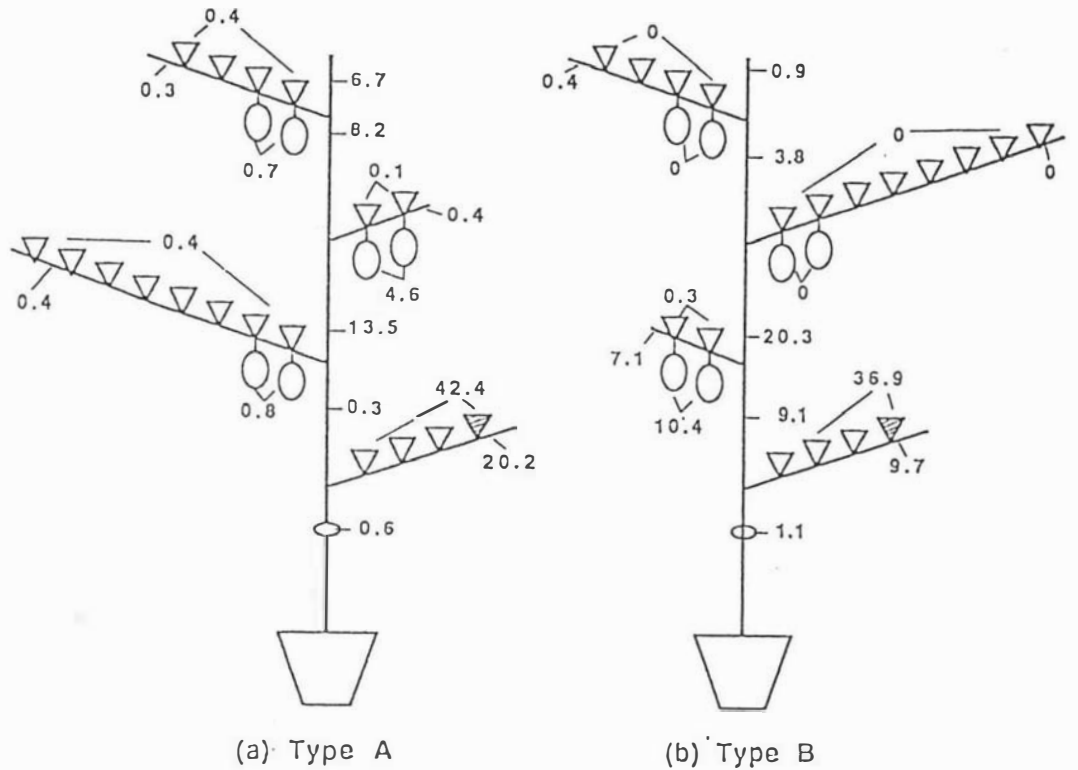
replicates of potted 'Monty' vines were allocated to each pruning type. ^{14}C-label was applied to a fully expanded leaf on either a fruiting or leafy shoot. High or low local demands for assimilates were made by either pruning fruiting shoots to 2 leaves or 8-10 leaves. The average fruit size during harvest was about 50-60g.

Treatment 3 (22 Dec 1984)

In this treatment, 4 'Hayward' vines were used. They were pruned to 2 types of shoot arrangements consisting of a top leafy shoot and two fruiting shoots, each carrying 2 fruits (fig. 6.4). One of the fruiting shoots was pruned to 8-10 leaves while the other was pruned to 2 leaves. ^{14}C-label was applied to the entire leafy shoot, which was pruned to 4 leaves, when the mean fruit size was 35 cm^3.

Treatment 4 (22 Dec 1984)

Each of 2 potted 'Bruno' vines were pruned to a shoot arrangement which consisted of a top leafy shoot of 4 leaves, and fruiting shoots below with 6 leaves (fig. 6.5). ^{14}C-label was applied to the entire leafy shoot when the mean fruit size was 34 cm^3.

Figure 6.4. Percentage distribution of ^{14}C in 4-year-old kiwifruit cv. Hayward after feeding $^{14}CO_2$ to the top leafy shoot. The fruiting shoot immediately adjacent to the leafy shoot was pruned to either (a) 8-10 leaves (type A), or (b) 2 leaves (type B).

(a) Type A

(b) Type B
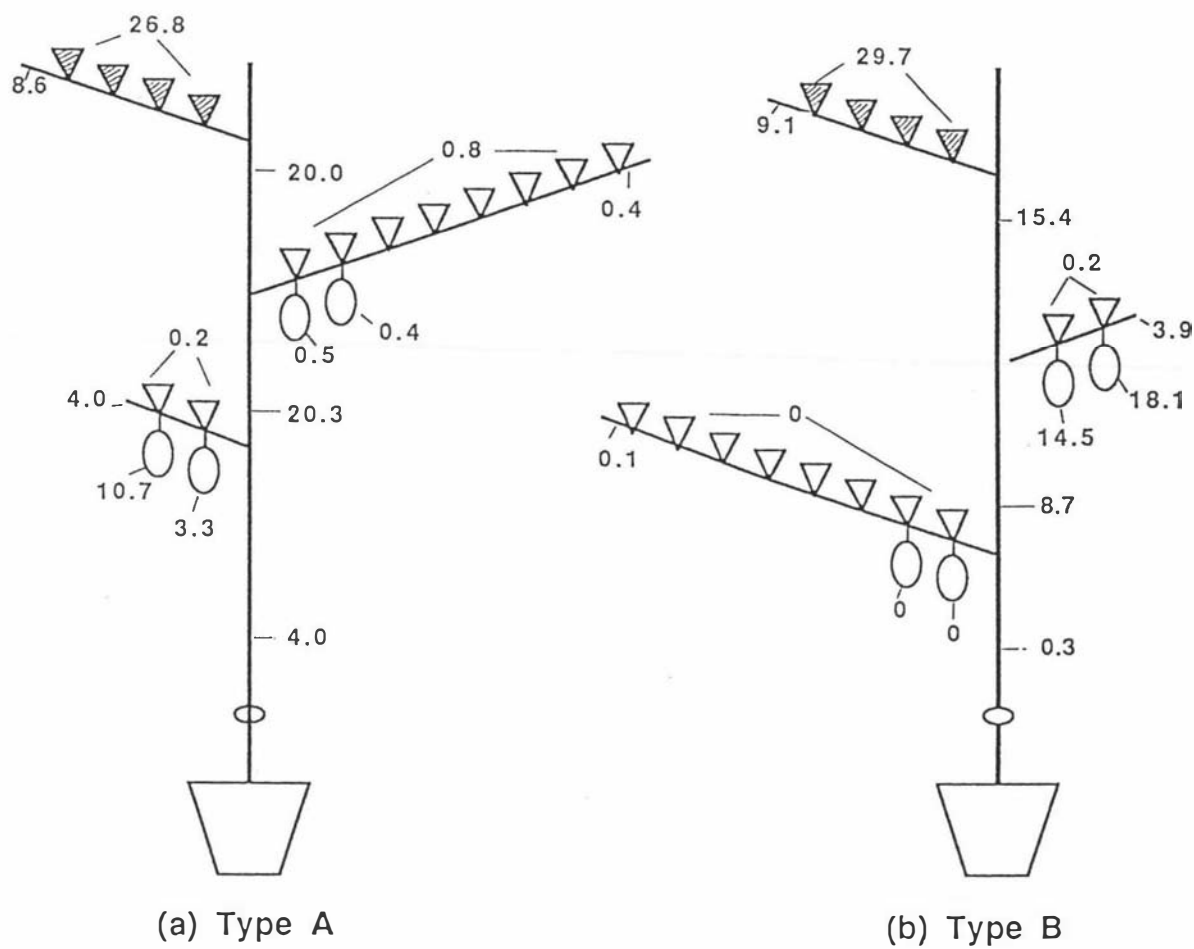
Figure 6.5. Percentage distribution of ^{14}C in kiwifruit cv. Bruno after feeding a top vegetative lateral with $^{14}CO_2$. The fruiting shoot below the labelled shoot was pruned to 6 leaves.

Replicate A

Replicate B
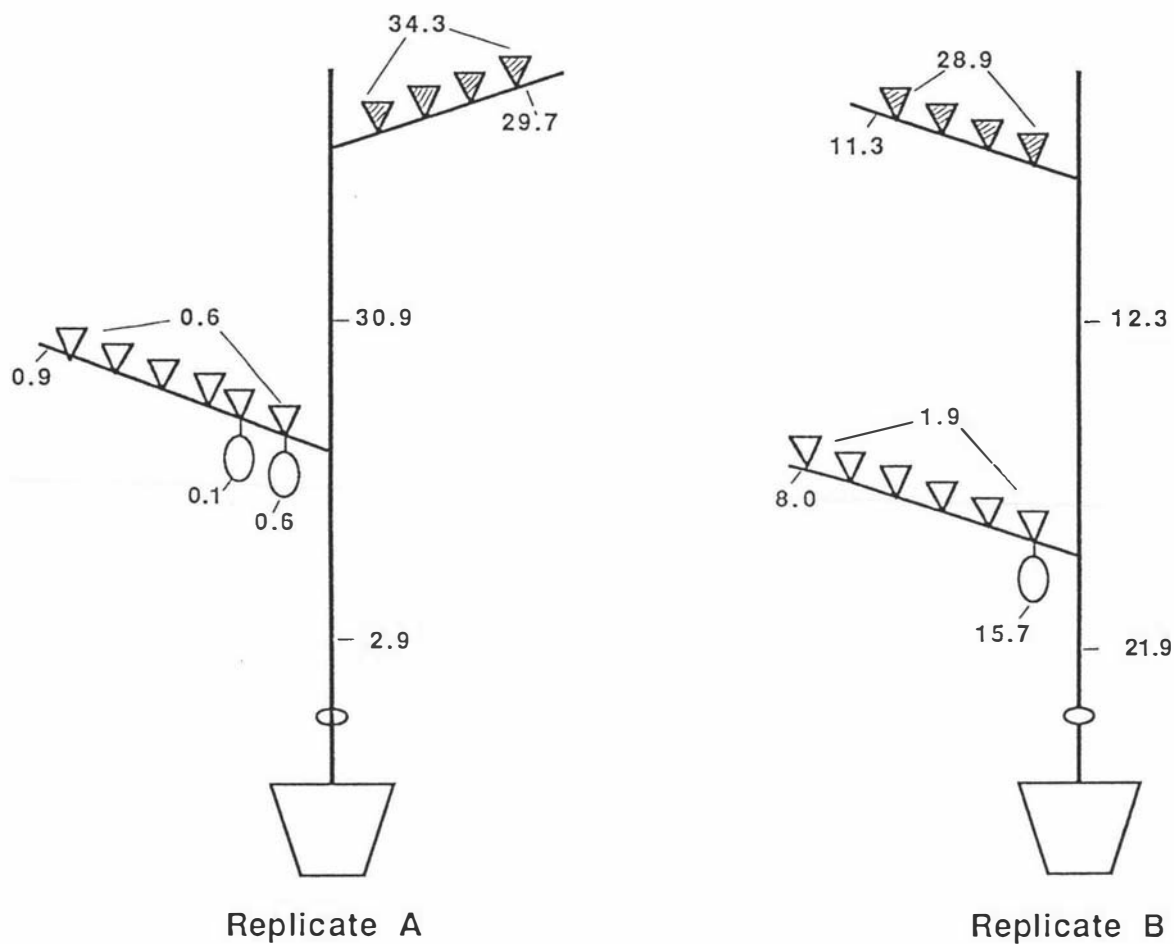
Treatment 5 (23 Dec 1984)

Fourteen potted 'Hayward' vines were used in this treatment. Each vine consisted of one second-year cane with more than 8 nodes. The 1-year-old lateral at the top node was a fruiting shoot which was pruned to a 1:1 leaf-fruit ratio. Vegetative laterals were located at varying node positions below the top node. They were cut back to 4-6 leaves (fig.6.6). For each of 2 replicate of 'Hayward' plants, ^{14}C-label was applied to an entire vegetative shoot at a different position from node 1 to 7 below the top fruiting shoot.

6.3.3 Results

Treatment 1

Most of the ^{14}C remained in the treated shoot (fig. 6.2). About 40 $^0/_0$ was translocated into the main cane. The direction of ^{14}C-assimilate transfer was mainly acropetal since little ^{14}C-activity was found at the stem girdle.

Fruits on 'Bruno' vines were stronger sinks for the ^{14}C-assimilates as compared with 'Hayward'. The 'Bruno'

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Figure 6.6. Distribution of ^{14}C (dpm mg^{-1}) in a single-stem kiwifruit cv. Hayward vine, after applying $^{14}CO_2$ to leafy shoots located 1 to 7 nodes below a fruiting shoot.

	node position of labelled shoot from the fruiting shoot						
	1	2	3	4	5	6	7
fruit	311	94	87	110	44	2	51
stem	231	75	31	88	55	5	2
leaf	12	4	4	8	2	11	12
stem	498	5	15	0	5	3	16
leaf	437	2	3	0	2	2	11
stem	0	374	15	12	0	0	3
leaf	0	395	4	5	0	0	1
stem	105	0	205	0	0	0	0
leaf	4	0	304	0	0	0	0
stem	2	5	5	527	2	0	6
leaf	0	0	2	452	2	0	2
stem	0	18	0	0	601	0	0
leaf	0	3	0	0	472	0	0
stem	0	0	0	0	0	927	0
leaf	0	0	0	0	0	782	0
stem	0	0	0	3	13	0	347
leaf	0	0	0	3	2	0	420

girdle

fruits were able to draw substantial amounts of ^{14}C-assimilates (9.7 $^0/_0$) even in the presence of other fruits which were closer to the source leaves.

Treatment 2

Figure 6.3 shows that the fruits on a shoot with 1:1 leaf-fruit ratio were strong sinks. In type A, 4.6 $^0/_0$ of the ^{14}C-assimilate was transported out of the leafy shoot to these strong sinks, even though they were not in adjacent positions. The fruits on the other fruiting shoots attracted negligible amounts of ^{14}C-assimilate.

More ^{14}C-activity (10.4 $^0/_0$) was accumulated in the fruits on shoots with 1:1 leaf-fruit ratio when they were in close proximity to the labelled leafy shoot (Type B).

Where the ^{14}C-label was applied to a fruiting shoot (Type C and D), most of the ^{14}C-assimilate (40 to 44 $^0/_0$), was taken up by the fruit sinks on the same lateral. Fruits on shoots with 1:1 leaf-fruit ratio also received some ^{14}C-label, in spite of all the alternative sinks in between.

Treatment 3

It can be seen from figure 6.4 that ^{14}C-assimilate was transported basipetally from the labelled shoot to the fruits

on lower laterals. In type A, high ^{14}C-activity (10.7 and 3.3 $^0/_0$) was found in the fruits with a high sink demand (1:1 leaf-fruit ratio), even though they were not immediately adjacent to the labelled leafy shoot. Only trace amounts of ^{14}C (0.9 $^0/_0$) was discovered in the shoots with low sink demand. However, when the fruits with a high sink demand were located in closer proximity to the labelled shoot, as in Type B, they drew greater quantities of ^{14}C-assimilates (14.5 and 18.1 $^0/_0$)

Treatment 4

Figure 6.5 shows that in one of the 'Bruno' vines, large amounts of ^{14}C (15.7 $^0/_0$) was translocated into the fruit in spite of the high leaf-fruit ratio.

Treatment 5

The distribution of ^{14}C within each plant is shown in figure 6.6. The movement of ^{14}C-assimilate in the 2-year-old cane was directional. ^{14}C-activity was recovered at node positions above and below the treated shoot. Basipetal transport towards the girdle was weaker than acropetal transport towards the fruits. Fruits at the top of each vine were able to import ^{14}C-assimilate from labelled shoots at

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every node, up to 7 nodes away.

6.4 Experiment 6C

6.4.1 Introduction

During spring, bud break and growth in the kiwifruit
vine is dependent on the mobilization and use of reserve
materials (Davison, 1987; Ferguson and Turner, 1981; Smith
et.al., 1986). However, little is known about the
contribution of stored versus current assimilates for fruit
growth. The objective of this experiment was to study the
storage and remobilization of ^{14}C-assimilate in the kiwifruit
vine.

6.4.2 Materials and Methods

Six 3-year-old potted 'Hayward' plants grafted on 'Bruno'
rootstocks were used. Each vine was pruned to a single
lateral, and each of 5 leaves at the mid-section of the
lateral was labelled with 740 kBq of ^{14}CO$_2$. The label was
applied on 20 Apr 1983.

Three harvests, each consisting of 2 plants, were
carried out. Harvest 1 was made 6 weeks after treatment, on

2 Jun 1983. Harvest 2 was made after bud ~~movement~~ *break* in the

following spring on 26 Oct 1983, and harvest 3 was carried

out on 12 Feb 1984 when the average fruit size was 25 g.

The labelled leaves of vines in harvest 2 and 3 were

also harvested prior to leaf-fall so that the amount of

^{14}C-activity retained in them were determined.

6.4.3 Results

Figure 6.7 shows the distribution of ^{14}C six weeks after

the plants were treated (harvest 1). The labelled leaves

retained a high percentage of the total recovered

radioactivity (24.6 $^0/_0$). Although some ^{14}C-label was

recovered from the top section of the vine, its transport was

mainly basipetal, towards the root system. More than half

the total recovered ^{14}C-activity (56.6 $^0/_0$) was found in the

roots. Both the > 2mm and < 2mm sized roots were active in

accumulating ^{14}C-assimilate.

At harvest 2 (fig. 6.8) new shoot growth throughout the

vine contained some ^{14}C-activity. A high level of the

^{14}C-assimilate (69.1 $^0/_0$) remained in the roots.

Fruit size at harvest 3 was about 25g, indicating that

they were in an active growth stage (chapter 3). However,

the amount of ^{14}C-activity found in the fruits was almost

Figure 6.7. Distribution of ^{14}C (dpm mg^{-1}) in a kiwifruit cv. Hayward vine, 6 weeks after labelling 5 leaves at the mid-section of the lateral with a total of 740 kBq of $^{14}CO_2$. Percentage distribution in parenthesis.

top section	stem	leaf
	30 (0.1)	23 (0.1)

mid section	stem	leaf
	1085(11.2))	2081(24.6)

bottom section	stem	leaf
	474 (5.2)	26 (0.5)

graft   172 (1.7)

thick roots (> 2mm)   558 (28.1)

fine roots   (< 2mm)   407 (28.5)
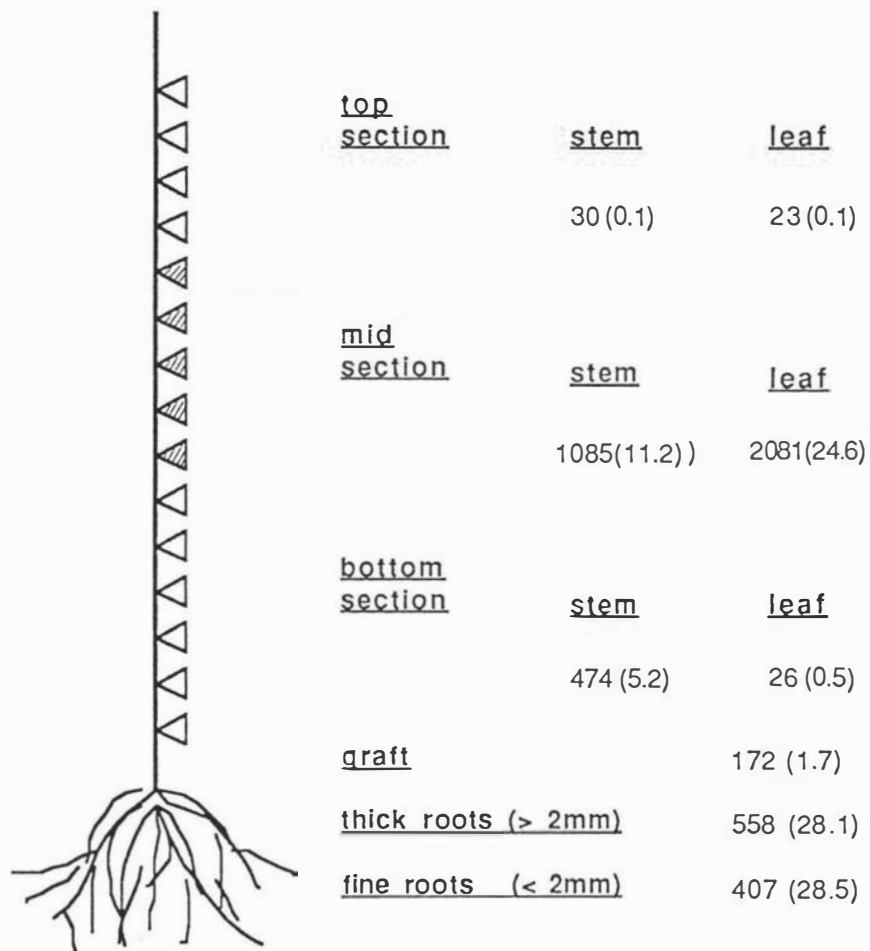
Figure 6.8. Distribution of ^{14}C (dpm mg^{-1}) in a kiwifruit cv Hayward vine 6 weeks after bud burst, following the application of $^{14}CO_2$ label (740 kBq) to the mid section of the main cane just before leaf fall in the previous season. Percentage distribution in parenthesis.

	stem	leaf
top section		
new growth	184(0.7)	98(0.7)
2-year-old cane	40(0.1)	
mid section	**stem**	**leaf**
new growth	277(2.0)	147(2.0)
2-year-old cane	115(0.6)	
bottom section	**stem**	**leaf**
new growth	128(2.0)	99(0.6)
2-year-old cane	110(2.0)	
graft	118 (1.5)	
thick roots (> 2mm)	1179 (37.2)	
fine roots (< 2mm)	1103 (31.9)	
leaf-fall	2687 (18.7)	
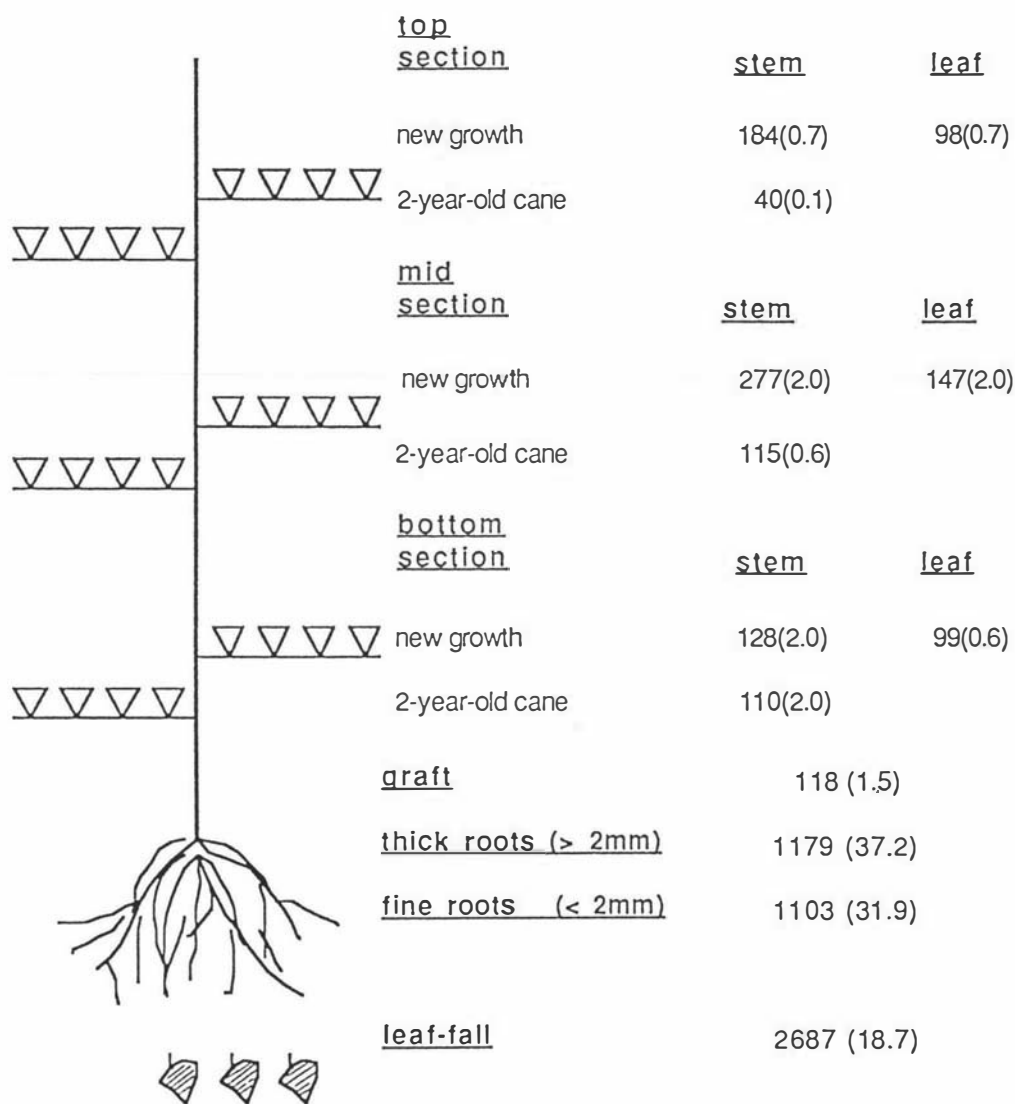
negligible (fig. 6.9). ^{14}C-activity in the roots was reduced to 31.1 $^0/_0$ at harvest 3.

Figure 6.9. Distribution of ^{14}C (dpm mg^{-1}) in a kiwifruit cv Hayward vine during early fruit growth, following the application of $^{14}CO_2$ label (740 kBq) to the mid section of the main cane just before leaf fall in the previous season. Percentage distribution in parenthesis.

top section	stem	leaf	fruit
new growth	29 (0.4)	23 (1.7)	2 (0.2)
2-year-old cane	17 (3.2)		

mid section	stem	leaf	fruit
new growth	45 (0.7)	32 (1.4)	2 (0.3)
2-year-old cane	211 (8.4)		

bottom section	stem	leaf	fruit
new growth	12 (1.8)	22 (5.6)	1 (0.1)
2-year-old cane	39 (9.9)		

graft   18 (2.2)

thick roots (> 2mm)   58 (14.6)

fine roots (< 2mm)   65 (16.5)

leaf-fall   1355 (32.5)
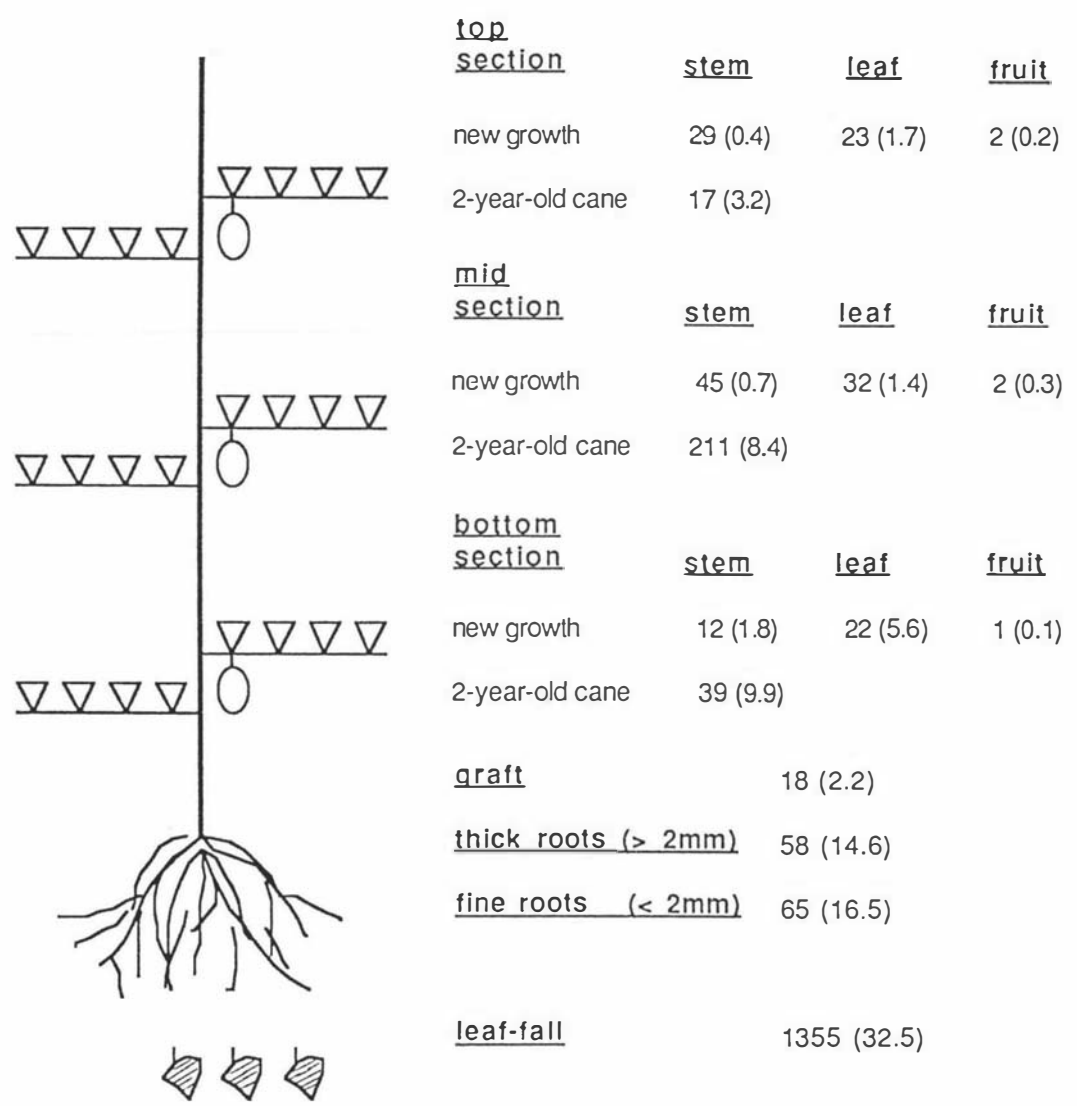
6.5 Discussion

6.5.1 Effect of Vegetative Shoots

Kiwifruit flowers borne on completely defoliated shoots
(shoot treatment 2) which were also girdled, could not
develop into fruits (table 6.4). Reserve substrates in the
stem were probably not available. However, when a source of
current photosynthates from an adjacent shoot was available,
the fruits on the defoliated shoots grew to a final fruit
size (95 cm^3) similar to those fruits which grew on shoots
which were not defoliated (94 cm^3; table 6.4).

The fruits on a completely defoliated shoot, when the
cane was girdled (pruning treatment 4, table 6.4a), also
benefitted from the presence of an adjacent leafy shoot.
Their mean fruit size increased significantly from 71 to 88
cm^3 (p=0.01).

While it is obvious that adjacent leafy shoots were
important in supplying the assimilate demands from nearby
fruits, the presence of these shoots *may*
depress fruit growth. This can be seen from the non-girdled
treatments in experiment 6A (table 6.4). In shoot treatments
3 and 4, fruit sizes were reduced by up to 9 cm^3 (p=0.04)

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when an adjacent leafy shoot was present. A comparison of the fruit load on the rest of the 2-year-old cane showed that there was actually a lighter fruit load on those treatments with a leafy shoot. This does not help to explain the smaller fruit size, since there was more leaf area for assimilate production. It is probable that the large number of leaves had an inhibitory effect on fruit growth and this will be discussed further in chapter 7.

The effect of girdling treatments in experiment 6A was to annul the inhibitory effects of adjacent leafy shoots. Thus in treatment 1, fruits actually benefitted from the presence of a leafy shoot by an increase in size from 94 to 110 cm^3 ($p < 0.01$; table 6.4). Although this may be caused by the accumulation of carbohydrate above a girdle (Priestley, 1976b), there are also possibilities for the involvement of plant growth substances. This will be discussed in chapter 10.

6.5.2 Leaf-Fruit Ratios

Gifford and Evans (1981) suggested that assimilate partitioning in plants is largely determined by sink demands for carbohydrate. The ability of apple fruits to draw assimilates from distant sources of supply depended on

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whether they were strong or weak sinks (Hansen, 1977; Cook and Evans, 1978). Hansen (1969) noted that translocation from adjacent leafy spurs and extension shoots in the apple tree varied according to the local leaf-fruit ratio.

Some indication of a minimum leaf-fruit ratio for a kiwifruit shoot, below which the carbohydrate demand of the fruits is not met, is observed in experiment 6A. This can be seen in the girdled treatments in table 6.4. In the absence of an adjacent leafy shoot, fruits in shoot treatment 4 were able to make some growth (71 cm^3), even though the fruiting shoot was completely defoliated. This suggests that the fruits must have drawn their supply of carbohydrate from the 5 leaves on the adjacent treatment 3 shoot. However, since the 5 leaves were not sufficient to fully supply the growth of 6 fruits, it implies that the minimum leaf-fruit ratio has to be greater than 5:6 (ie. 0.83, or approximately 87 cm^2 per fruit).

In spite of the export of carbohydrate in treatment 4, the fruits on a treatment 3 shoot had a similar size (90 cm^3) as fruits in treatment 1 (94 cm^3). As both treatments 1 and 3 had the same number of leaves and fruits, it also implies that the minimum leaf-fruit ratio of a kiwifruit shoot is likely to be less than 5:3 (ie. 1.7, or approximately 173 cm^2 per fruit).

6.5.3 Effect of Sink Strength on Assimilate Translocation

'Hayward' fruits on fruiting laterals with a leaf-fruit ratio greater than 1.7:1 did not attract ^{14}C-assimilate from outside the shoot. These fruits were probably supplied by the leaves on the same lateral. 'Bruno' fruits however, imported ^{14}C-assimilate from adjacent shoots, even when the leaf-fruit ratio was greater then 1.7:1 (figs. 6.2, 6.5). The difference is not likely to be due to differences in the growth stages between 'Hayward' and 'Bruno' fruits at the time of the experiments, since the dry weight gain (at least in 'Hayward' fruits) was linear (fig. 3.7).

Fruits on shoots which were pruned to 1:1 leaf-fruit ratio, were strong sinks for ^{14}C-assimilate from the leaves on other shoots (figs. 6.2, 6.3).

Depending on the location of the sinks, the direction of translocation can either be acropetal (fig. 6.2) or basipetal (fig. 6.4). The ability to draw ^{14}C from adjacent leafy shoots was reduced when other fruits were located in between (compare type A and type B treatments in figure 6.3, and in figure 6.4).

A high fruit demand for assimilate can be met from every adjacent shoot located as far as 7 nodes distance (fig. 6.6). Unlike the definite patterns of assimilate translocation between the nodes in 1-year-old laterals (table

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5.1), there is no clear indication from figure 6.6
that the transport of ^{14}C-assimilate in 2-year-old canes
was restricted by vascular phyllotaxy. It is likely that
secondary thickening in the kiwifruit, like the grape vine
(Esau, 1948), caused changes in the stem vascularization so
that ^{14}C was translocated freely between fruiting and
vegetative shoots at any node positions.

6.5.4 Dependence on Current Photosynthesis

The kiwifruit vine accumulated considerable quantities
of ^{14}C in the root system before leaf-fall (fig. 6.7). Up
to 56 $^0/_0$ of the ^{14}C-photosynthate was imported into both the
fine (< 2mm) and thick (> 2mm) roots. The stem also retained
some of the ^{14}C-photosynthate.

In the following spring, the roots still retained a high
proportion (69.1 $^0/_0$) of the ^{14}C, and very little was
remobilized during bud-break (fig. 6.8).

There was still no increase in ^{14}C in the new shoot
growth at harvest 3 (fig. 6.9). Negligible amounts of
radioactivity was found in the fruits, and it is likely that
fruit development in the kiwifruit vine was mainly dependent
on current photosynthesis. The amount of ^{14}C in the roots
had also declined, probably as a result of root respiration.

CHAPTER SEVEN

LEAF EFFECTS ON FRUIT GROWTH

7.1 Introduction

Fruit and Shoot competition

Fruit growth is strongly affected by the partitioning of
assimilates between competing meristems within the shoot system.
This is well documented for several fruit crops (eg. Abbott,
1960; Hansen, 1977; Hilgerman et.al., 1967; Kriedemann,
1968a; Loomis, 1949; Quinlan and Preston, 1971; Saur, 1954;
Skene, 1969)

For example, in the apple tree, a delicate balance exists
between the fruit and vegetative shoot during early fruit
development. The apple fruitlets are weak sinks (Quinlan and
Preston, 1971), and are likely to abscise when they have to
compete with shoot growth (Abbott, 1960). Removing the
competition effects by cutting off the tips of vigorous shoots,
or by partial defoliation, favoured fruit growth (Quinlan and
Preston, 1971). The total removal of the spur leaves however,
depressed fruit set (Llewelyn, 1968). This is because the

greater part of early fruit development is dependent on current leaf photosynthesis (Hansen, 1971). The retention of sufficient leaf area was found to be beneficial in supplying carbohydrate to fruits at a later stage (Quinlan and Preston, 1971).

Involvement of Plant Hormones

The regions of meristematic activity within the shoot are also the sites of high concentration of plant hormones. These hormones are able to mobilize nutrients (Seth and Wareing, 1964), and it has been suggested that the internal competition for resources between the growth centres in a shoot is likely to be related to the action of plant hormones rather then limitations in carbohydrate supply (Avery et.al., 1979).

A major role for hormone directed transport in the competition between shoots and fruits has often been postulated (eg. Abbott, 1960; Luckwill, 1970). The principal hormones involved are auxins and cytokinins. Abbott (1960) discussed the possibility of supra-optimal level of auxin, or some inhibitor produced in distal apple leaves, as the cause for the inhibition of fruit growth. Luckwill (1970) suggested that shoots control the translocation of carbohydrates by the movement of auxin downwards from the shoot tip. Fruits however, work against this competition from the shoot by attracting assimilates to the

centres of hormone production in the seeds. It is believed that the relative strength of the hormonal stimuli from the shoot tip and seeds will determine the general direction in which carbohydrates will move. Implications for the involvement of gibberellin (Kurashi and Muir, 1962; Seth and Wareing, 1964), cytokinin (Luckwill, 1968), and ABA (Eagles and Wareing, 1964; Goldsmidt, 1984; Setter et.al., 1980) suggested the existence of some overall hormonal regulating mechanism which maintained a balance between fruit and leaf growth.

7.2 Experiment 7A

7.2.1 Introduction

Although flowering in the kiwifruit vine occurs about 2 months after bud burst, shoot growth is still active, and growth competition between fruits and shoots are significant (Davison, 1987). The effect of summer pruning a fruiting shoot is to remove the competing sink in the shoot apex so that stronger gradients of assimilate transfer to the fruits are established.

A minimum leaf to fruit ratio in the vine can be achieved by pruning a fruiting shoot to different leaf numbers. However, experiment 6A (chapter 6) indicated that large leaf numbers may inhibit fruit growth (table 6.4).

In this experiment, shoot apices were removed after pruning fruiting shoots to different distal leaf numbers, and the effect of these mature leaves on fruit growth was investigated. The influence of the time of pruning, as well as the interactions with the number of fruits on a shoot, and fruit seed number, were also studied.

7.2.2 Materials and Methods

Plant Materials

The experiment was carried out in a commercial orchard block near Levin. Eight uniform 4-year-old vines were selected during the 1982-83 season for treatment. The layout of these vines in the orchard block is shown in figure 7.1. Trials were repeated on the same vines during the 1983-84 and 1984-85 seasons. The vines were winter-pruned to uniform cane lengths each year.

Experimental Unit

The experimental unit was an indeterminate fruiting lateral which was pruned back to a desired number of distal leaves. Later removal of shoot regrowths kept the correct number of leaves for each treatment throughout the season. Treated shoots were exposed in the canopy by the removal of any surrounding shading shoots.

Each vine was taken as an experimental block and the replicate of each treatment was randomly allocated to the experimental units within each block.

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Figure 7.1. Layout of experimental kiwifruit cv. Hayward vines (a to h) in an orchard block at Summerland Orchard, Levin. 'm' denotes male ~~pollinator~~.
pollinizer.
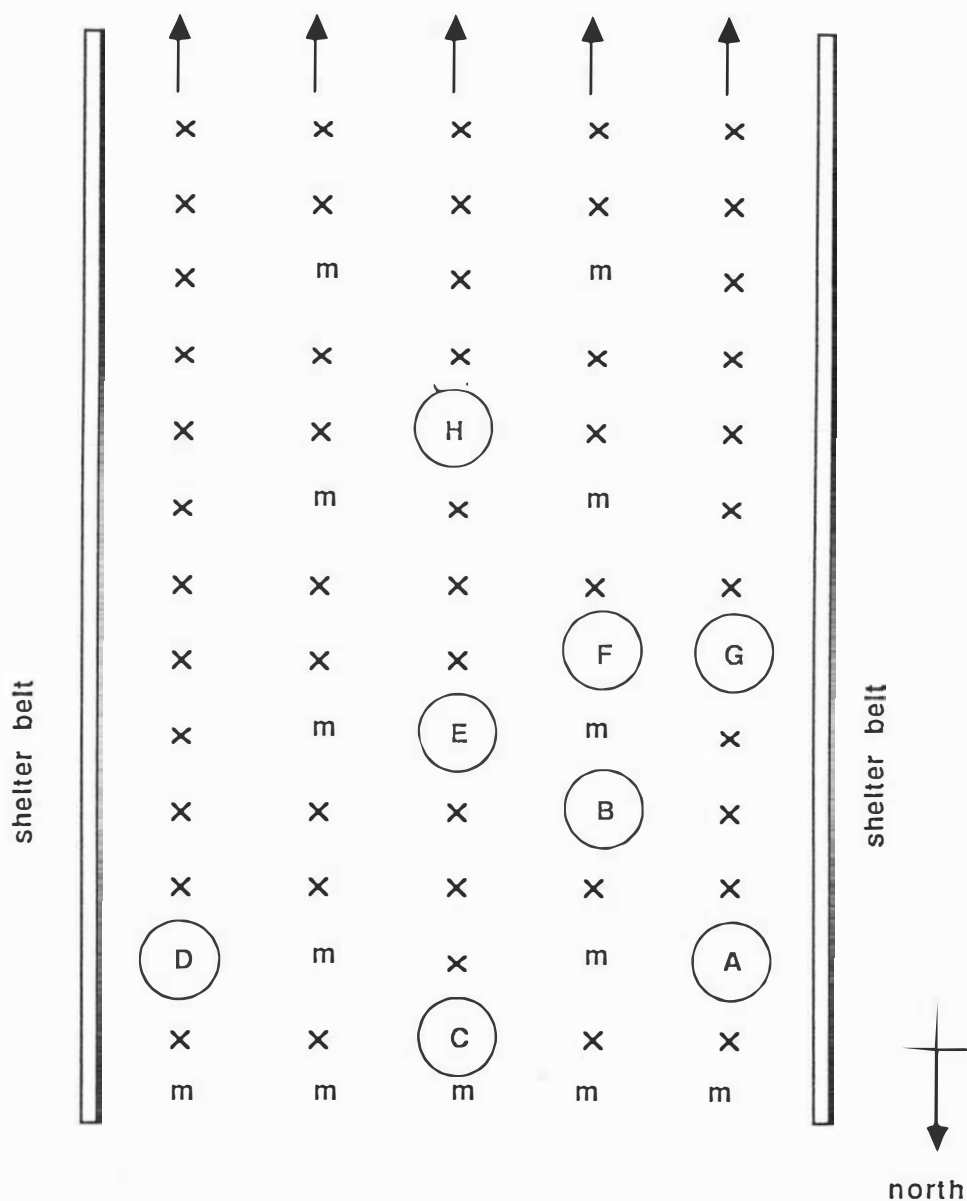
Experimental Designs

1982-83 trial

During the 1982-83 trial, 5 levels of fruit (ie. 1 to 5 fruits per lateral) were varied with 5 levels of leaf (ie. 0, 2, 4, 8, or 12 distal leaves). The experimental design was therefore a 5 x 5 factorial, giving a total of 25 treatments. A drawing of 3 treatments is illustrated is figure 7.2.

The pruning treatments were applied on 22 Dec 1982, approximately 3 weeks after anthesis (70 $^{0}/_{0}$ flowering). Fruit harvest was carried out on 13 May 1983.

1983-84 trial

Only shoots which carried 3 fruits each were used in this trial. Three pruning treatments, ie. 0, 2, and 8 distal leaves were applied over six time intervals around the period of flowering and fruit set. The six times of pruning were:

(i)   17 Nov 83 - (T1) preblossom stage

(ii)   28 Nov 83 - (T2) full bloom stage

Figure 7.2. Schematic drawing of selected
treatments in experiment 7A.
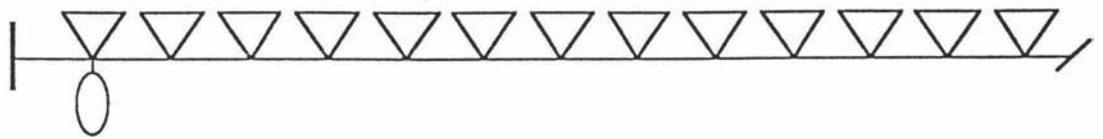
1 fruit - 12 distal leaves
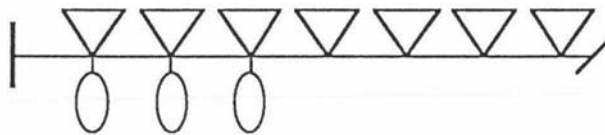
3 fruits - 4 distal leaves
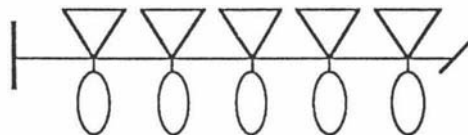
5 fruits - 0 distal leaf

(iii)   10 Dec 83 - (T3) petal fall stage

        (iv)   24 Dec 83 - (T4) 2 weeks after petal fall

        (v)   7 Jan 83 - (T5) 4 weeks after petal fall

        (vi)   21 Jan 83 - (T6) 6 weeks after petal fall

The experimental design was therefore a 3 x 6 factorial. One further treatment was also included; it consisted of removing all the leaves from a fruiting shoot at preblossom time (T1).

Fruit harvest on 11 May 1984 included picking 20 control fruits at random from non-treated shoots on each vine.

1984-85 trial

Fruiting shoots, each carrying 3 fruits, were pruned to either 2 or 8 distal leaves. The pruning treatments were applied in 3 time intervals: 1, 4, and 8 weeks after petal fall (ie. 1 Dec 1984). In addition, 3 levels of fruit size were made by excising the styles of each of the 3 flowers on a shoot to either 5 or 20 styles, or leaving the flower intact (ie. 40 styles). Thus the experimental design was a 3 x 2 x 3 factorial. The fruits were harvested on 29 Apr 1985. A random selection of 20 control fruits were also picked from non-treated shoots on each vine.

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7.2.3 Results

Differences in Vine Performance

During each season, the mean fruit sizes were highly variable among the 8 experimental vines. However, the vine differences were largely consistent over the 3 seasons. Table 7.1 shows that 'poor' performing vines, such as vines d and g, consistently produced smaller fruits whereas 'good' performing vines, such as vines a and e, always carried larger fruits.

Vine performance was not related to trunk girth or crop load (table 7.1). The leaf-fruit ratio for each vine appeared to be correlated with the mean fruit size during the 1983-84 season. Thus 'good' vines (eg. vines a and e) had higher leaf-fruit ratios (443 and 401 cm^2 per fruit, respectively) than the 'poor' vines (306 and 252 cm^2 per fruit for vines d and g, respectively). However, this trend was not observed in the next season. For instance, during the 1984-85 trial, vine e had a low leaf-fruit ratio of 399 cm^2 per fruit, yet its mean fruit size of 129 g was the highest.

Differences in mean final fruit sizes between vines were not related to the mean fruit seed numbers during the 1983-84

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Table 7.1. Comparison of the performance of vines
used in experiment 7A during the (a)1982-83,
(b)1983-84, and (c)1984-85 seasons. (* Data from
20 control fruits harvested from random shoots on
each vine). S.E. in parenthesis.

(a) 1982-83 trial.

Vine	Fruit Fresh Weight(g)	Crop Load	Stem Girth 1m above ground(cm)	Percent Soluble Solids
a	92(3)	239	10.0	7.6(0.1)
b	93(4)	252	10.3	8.0(0.1)
c	94(3)	442	11.8	7.7(0.1)
d	73(5)	465	12.1	7.7(0.1)
e	99(4)	469	11.5	7.6(0.1)
f	80(3)	394	10.0	7.9(0.1)
g	62(2)	305	9.2	9.0(0.1)
h	92(4)	418	12.0	7.5(0.1)
	p=0.00			0.00

Table 7.1 (contd.)

(b)1983-84 trial.

Vine	Fruit Fresh Weight(g)	Crop Load	Fruit Seed Number	Leaf Area Per Vine (m^2)	Vine Leaf-Fruit Ratio	Seed Size (mg)
a	105(3)	427	1255(51)	18.9	443	1.275(.030)
b	96(1)	525	1346(19)	-	-	1.198(.019)
c	108(2)	607	1353(47)	-	-	1.138(.019)
d	97(3)	581	1250(29)	-	-	1.167(.020)
e	126(3)	593	1397(37)	23.8	401	1.264(.021)
f	87(1)	584	1450(30)	17.9	306	0.963(.011)
g	80(2)	654	1156(76)	16.5	252	1.235(.018)
h	111(3)	450	1105(51)	-	-	1.342(.044)
	p=0.00		0.00			0.00

*'Control' Fruits

Vine	Fruit Fresh Weight(g)	Fruit Seed Number
a	109(2)	1272(22)
b	97(2)	1349(45)
c	115(3)	1369(35)
d	106(1)	1318(53)
e	129(2)	1437(38)
f	89(1)	1441(34)
g	85(3)	1204(12)
h	109(2)	1228(22)
	p=0.00	0.00

Table 7.1 (contd.)

(b) 1984-85 trial.

Vine	Fruit Fresh Weight(g)	Crop Load	Fruit Seed Number	Leaf Area Per Vine (m^2)	Vine Leaf-Fruit Ratio	Seed Size (mg)
a	108(6)	267	1003(117)	29.7	1112	1.213(.015)
b	116(3)	567	1239(64)	–	–	1.160(.023)
c	111(5)	541	993(110)	–	–	1.201(.014)
d	86(5)	634	725(115)	–	–	1.169(.023)
e	129(5)	674	1223(82)	26.9	399	1.153(.019)
f	118(4)	522	1217(69)	28.3	542	1.134(.014)
g	95(5)	397	852(109)	21.7	546	1.160(.074)
h	99(5)	852	718(75)	–	–	1.242(.022)
	p=0.00		0.00			0.23

*'Control' Fruits

Vine	Fruit Fresh Weight(g)	Fruit Seed Number
a	128(3)	1350(39)
b	115(2)	1352(23)
c	120(4)	1373(26)
d	107(3)	1261(81)
e	124(3)	1302(40)
f	113(3)	1350(58)
g	100(1)	1032(43)
h	107(2)	1181(19)
	p=0.00	0.00

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trial (table 7.1). However, the following year showed that 'poor' vines such as vines d and g had significantly lower mean fruit seed numbers (725 and 852 respectively), as compared with 'good' vines like b and e (1239 and 1223, respectively). Similar correlations were found from the results obtained from control fruits harvested at random from non-treated shoots (table 7.1).

The relationship between fruit size and seed numbers was different for 'good' and 'poor' vines. Figure 7.3 shows that fruits from a 'good' vine, such as vine a, attained 100g fresh weight when the fruit seed number was about 580. By contrast, fruit growth in a 'poor' vine such as vine d was suppressed; more than 1000 seeds were needed before fruits were able to grow to a final size of 100g fresh weight. Seed size for both 'good' and 'poor' vines were similar ($p > 0.05$; table 7.1; 1984-85 trial).

Effect of Fruit Number on a Fruiting Shoot

There was no effect of fruit load on fruit size within a fruiting lateral ($p = 0.80$; table 7.2). Figure 7.4 shows that fruit size was similar, regardless of the number of fruits the fruiting shoots carried. A plot of the growth curves of the proximal (no. 1) and distal (no. 5) fruits in figure 7.5 shows that they were similar.

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Figure 7.3. Relationship between fruit size and
fruit seed number on a 'good' (× , ———— , vine a)
and a 'poor' (△ , – – – – , vine d) vine. Curves
were fitted by a constrained b-spline technique
(Spriggs, 1986).
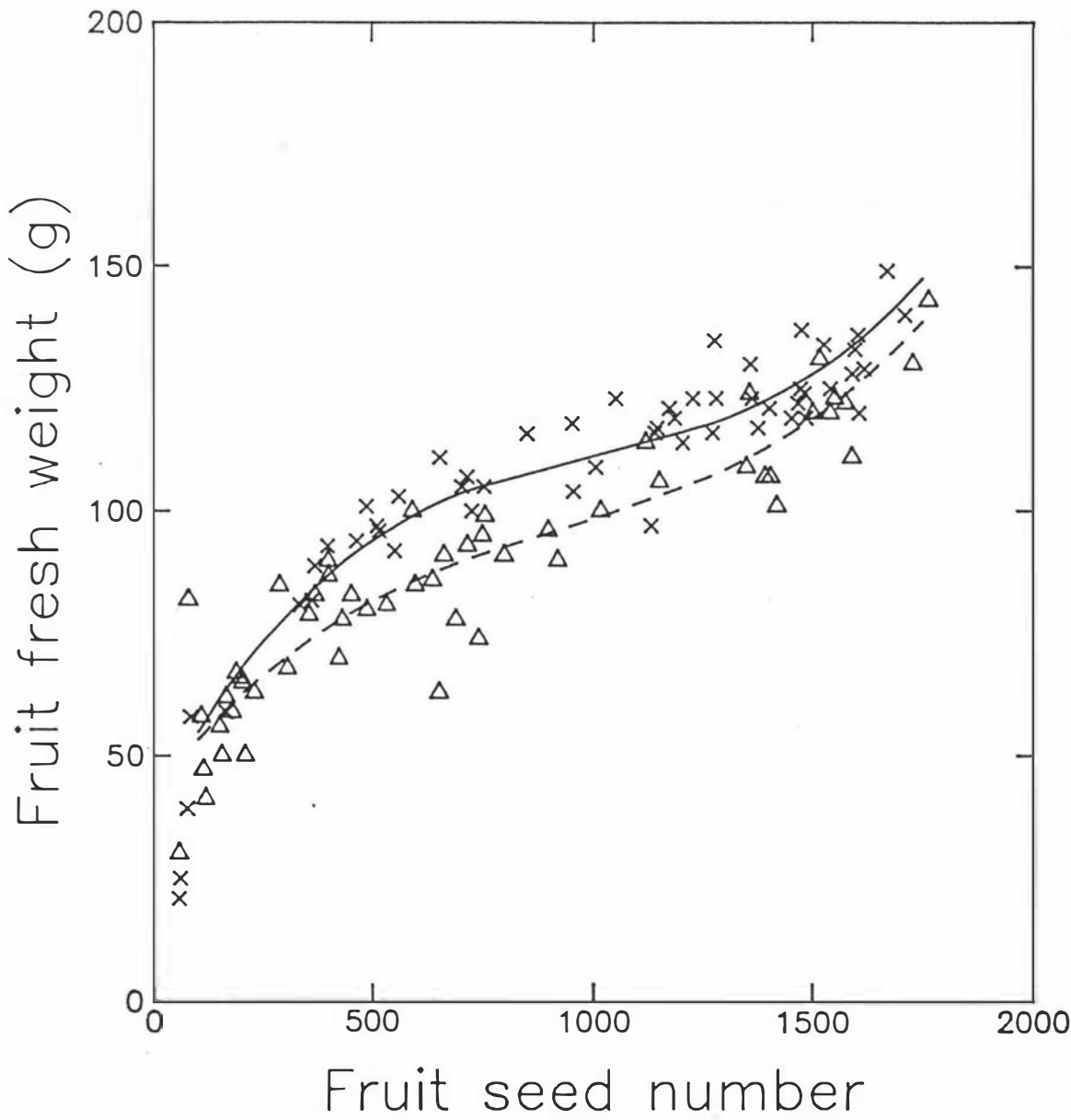
Table 7.2. Effect of leaf number and fruit
number on the fruit growth of kiwifruit cv Hayward.
Summary of ANOVA. Data from 'good' (a, b, c, e,
and h) vines only.

Significance of F value

| | Fruit volume (cm^3) | | | Fresh |
	7 Jan	4 Apr	8 May	weight(g)
Leaf	.001	.022	.031	.019
Fruit	.630	.941	.802	.944
Leaf x fruit	.372	.706	.479	.522

Figure 7.4. Mean fruit size (cm^3) of different
fruit load on fruiting shoots. S.E. in parenthesis.

1 fruit

95
(5)

2 fruit
(p=0.35)

94
(5)

99
(4)

3 fruit
(p=0.65)

91
(3)

93
(2)

88
(5)

4 fruit
(p=0.88)

92
(3)

96
(5)

94
(4)

93
(3)

5 fruit
(p=0.99)

87
(5)

94
(4)

92
(6)

89
(6)

88
(6)
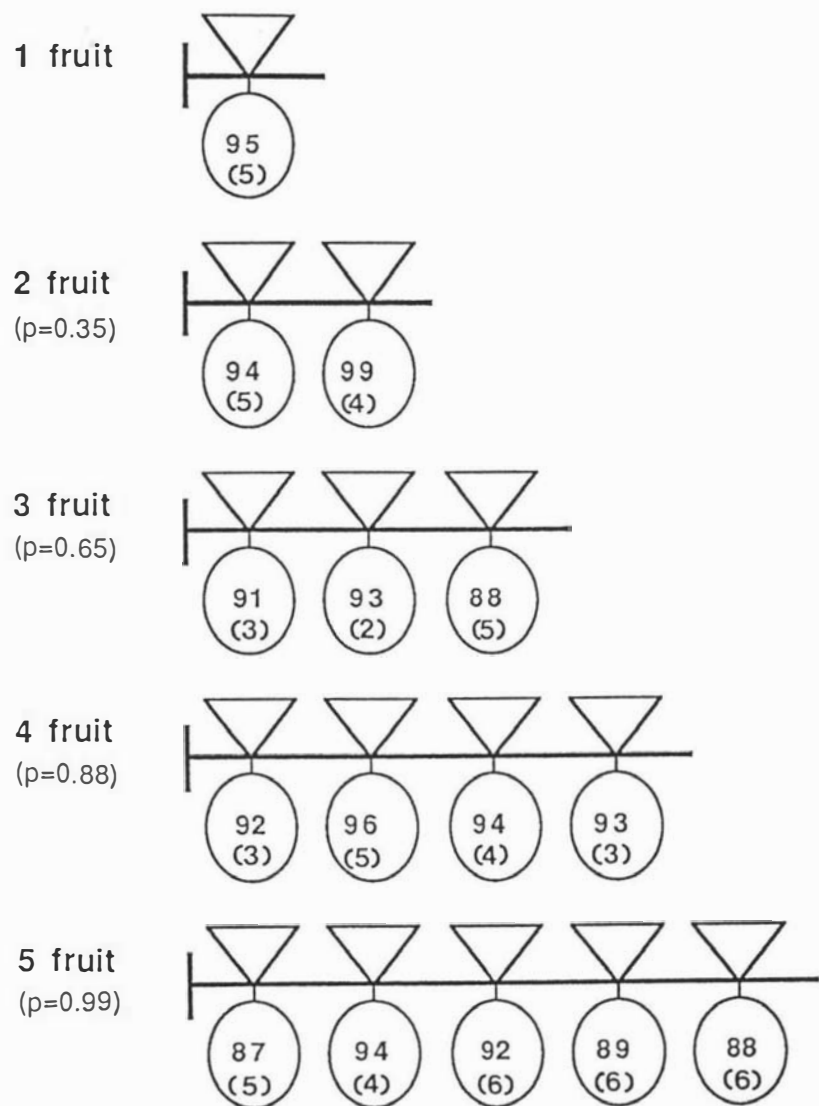
Figure 7.5. Time course of fruit development of the first (o , proximal) and fifth (□ ,distal) fruit on a kiwifruit cv Hayward fruiting shoot carrying 5 fruits. Bars indicate s.e.
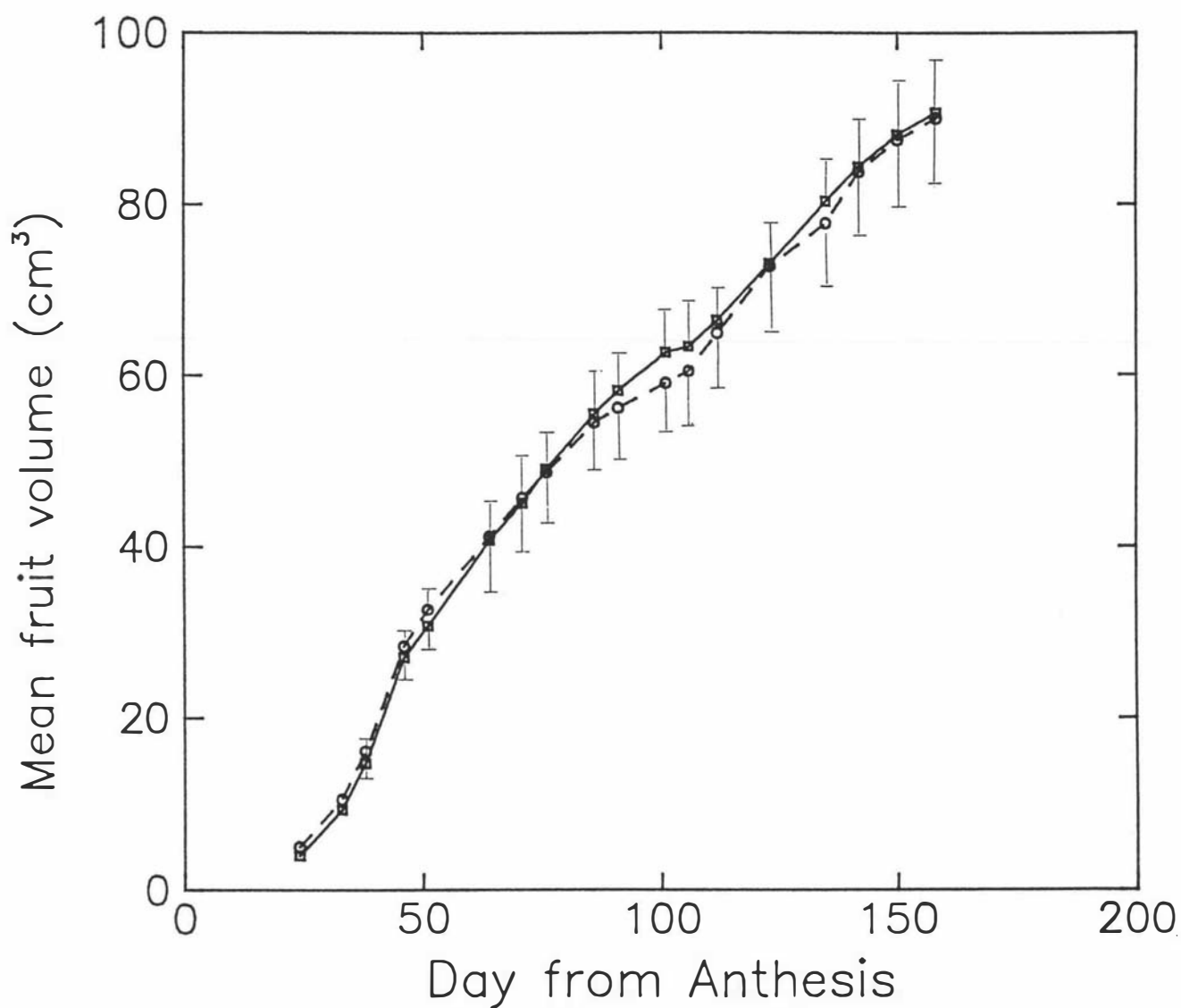
Effect of Shoot Leaf Number

A highly significant effect of leaf numbers on fruit size was observed during the 1982-83 trial (table 7.2). Leaf number and fruit number interaction was absent.

Two populations of fruits were distinguished. Fruits from the 0, 2, and 4- distal leaf treatments were significantly bigger than those from the 8 and 12-distal leaf treatments (table 7.3). The growth curves of fruits in each category of leaf treatment was plotted for a 'poor' and 'good' vine (fig. 7.6). The difference in mean final fruit size between small and large leaf number treatments for all the 'good' vines was 14.1 cm^3 (p<0.01). This difference was reduced to 1.9 cm^3 for 'poor' vines (p=0.58).

The growth curves were further resolved into groups whereby the fruits were either initially small (ie. below the mean fruit size of 12 cm^3 on 7 Jan 1983), or initially big (ie. greater than 12 cm^3). It then became evident that on a 'good' vine, leaf numbers only affected the growth of fruits which were initially small (fig. 7.7).

Table 7.4 also shows that during harvest, above average sized fruits (> 80 cm^3) were found mostly in the 0, 2, 4-distal leaf treatments as compared with the 8, 12-distal leaf treatments. The large fruits in the 0, 2, 4-distal leaf

Table 7.3. Effect of small (0, 2, 4) and large
(8, 12) distal leaf numbers on fruit size of
kiwifruit cv Hayward. Pruning was carried out on
22 Dec 1982, ie.. 1 week after petal fall.
S.E. in parenthesis.

Mean fruit volume (cm^3)

	0, 2, 4-leaf	8, 12-leaf	
24 Dec	4.7(0.3)	4.3(0.3)	p=.410
3 Jan	9.9(0.5)	7.3(0.7)	.014
7 Jan	14.5(0.5)	11.1(0.6)	.000
4 Apr	81.7(1.5)	72.2(2.7)	.003
8 May	98.2(1.7)	88.4(3.1)	.008

Figure 7.6. Fruit growth curve of small (△ , 0, 2, 4) and large (□ , 8, 12) distal leaf number treatments on a (a) poor (vine f), and (b) good (vine h). 1982-83 trial. Bars indicate s.e.
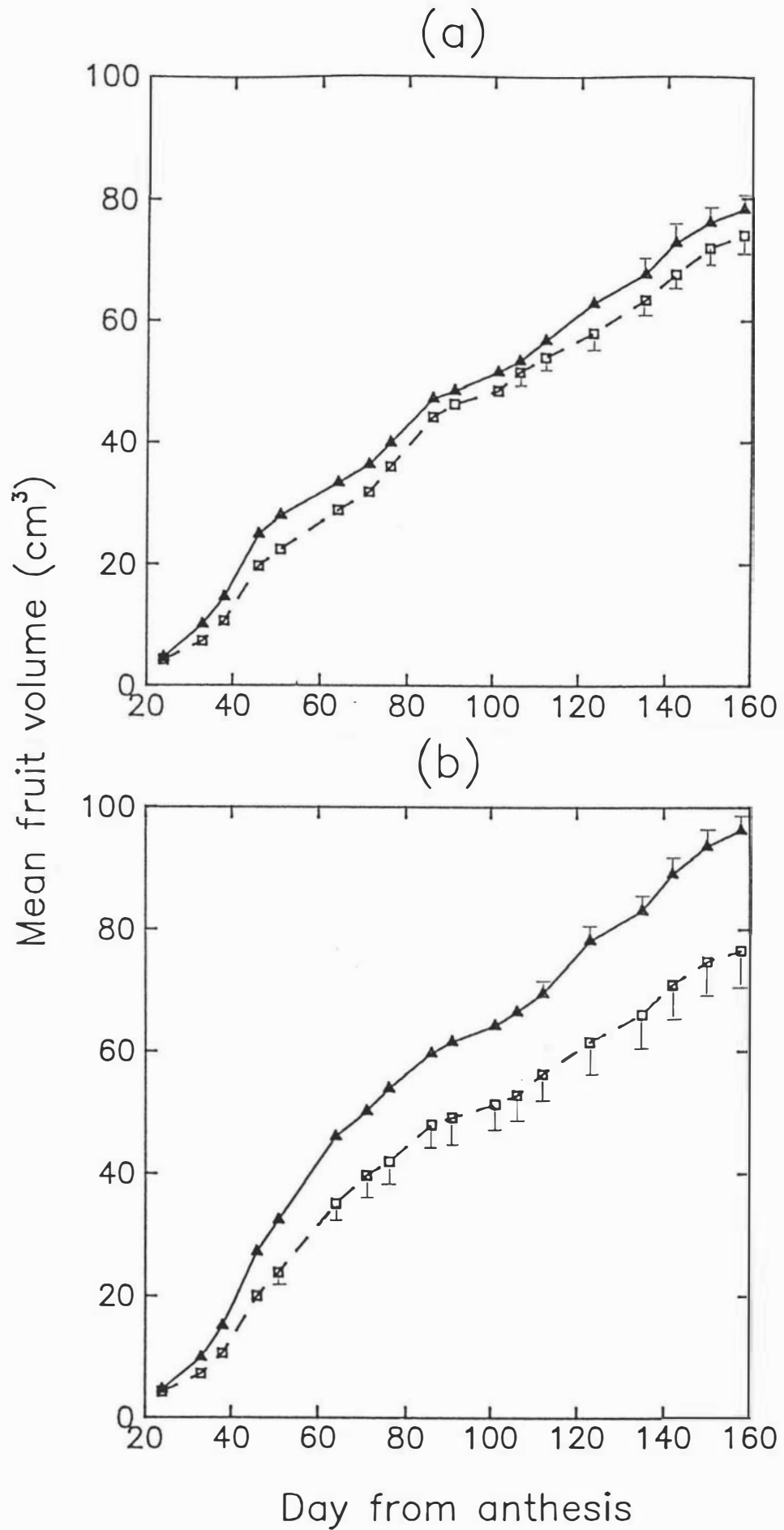
Figure 7.7. Effect of small (0, 2, 4) and large (8, 12) distal leaf number treatments on the growth of initially small (<12 cm^3 on day 38) or large ($\geq$12 cm^3) fruits of kiwifruit cv. Hayward. (a) 'poor' vine (b) 'good' vine. (✳ , 0,2,4 leaf;small fruit. × , 0,2,4 leaf;big fruit. □ , 8,12 leaf;small fruit. ● , 8,12 leaf;big fruit). Bars indicate s.e.

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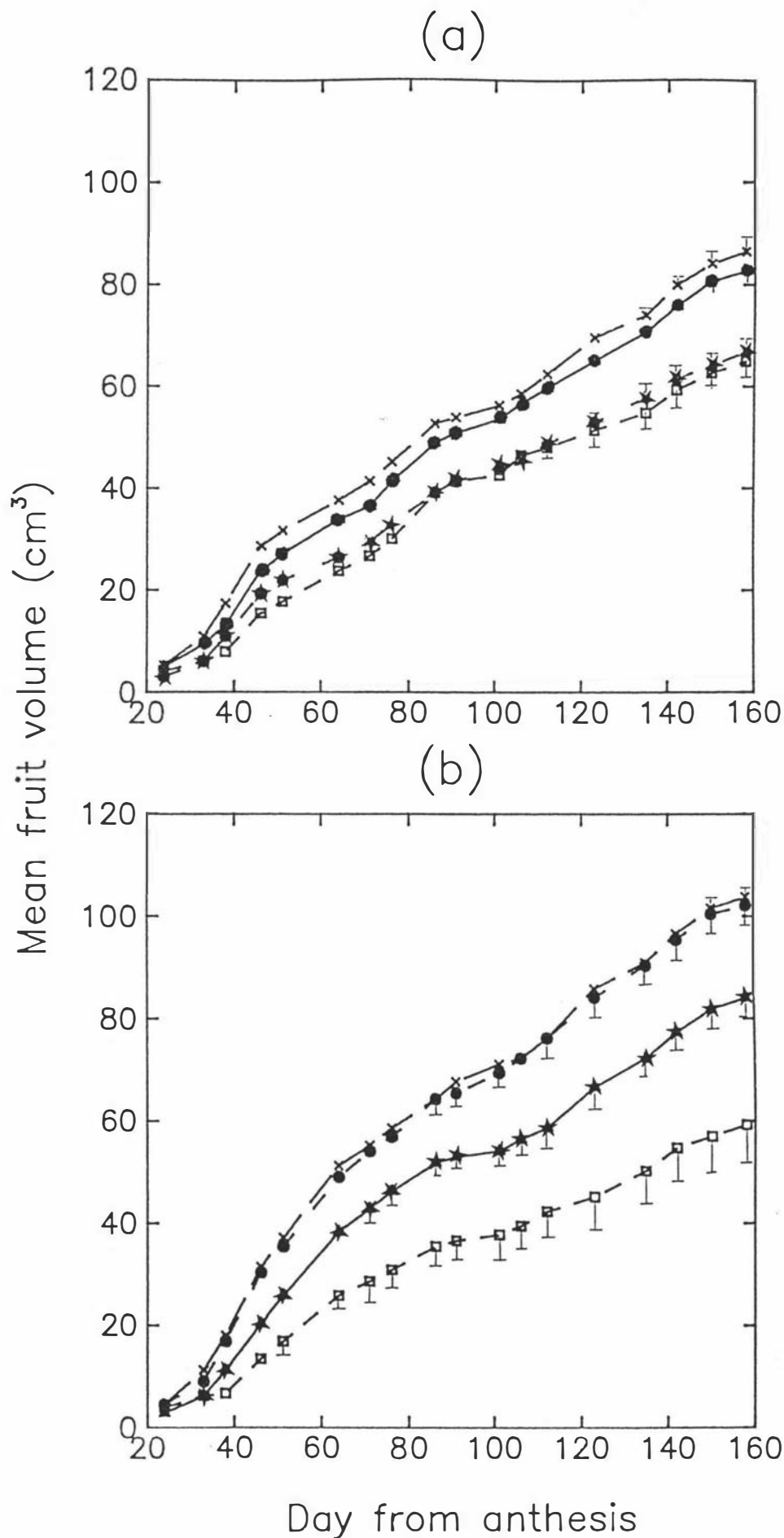
Table 7.4. Distribution of the number of treatments with above average final fruit sizes (> 80 cm^3) which were initially small (< 12 cm^3 on 3 Jan 1983) or large ($\geq$ 12 cm^3) fruits. (Data from vines a,b,c,e, and h).

Number of Treated Shoots

Leaf Treatment (no. of distal leaves)	Initially small fruit (< 12 cm^3)	Initially big fruit ($\geq$ 12 cm^3)	Total
0	6	17	23
2	6	19	25
4	5	21	26
8	12	6	18
12	11	8	19

treatments were mostly greater then 12 cm^3 during the initial stage of fruit growth. In the 8, 12-distal leaf treatments however, most of the large fruits were initially small fruits. It can also be seen from table 7.5 that large leaf numbers affected small fruits because of their low seed numbers. Fruits which contained more than 1200 seeds, were not affected by leaf numbers.

On a 'poor' vine, leaf numbers had no effect on final fruit size, regardless of whether they were initially small or big fruits (fig. 7.7).

Leaf numbers had no effect on fruit size (p>0.05) during the next season (ie. 1983-84; table 7.6). There was also no interaction between leaf number and time of pruning. The result of using initial fruit volume data at each pruning time as covariates, also did not show any significant effect of leaf number on final fruit size (table 7.7). When only those fruits with less than 1200 seeds were separated out for analysis, there was a slight indication (p=0.24), that fruit size was reduced in 8-distal leaf treatments (table 7.8). However there was only a small number of fruits in this category.

During the 1984-85 season, there was again no effect of leaf numbers on fruit size (p=0.51; table 7.9). No differences between leaf number treatments within classes of fruit seed weight were observed (table 7.10). There was

Table 7.5. Effect of the interaction between seed number and leaf number on fruit size of kiwifruit cv. Hayward. S.E. in parenthesis. (Data from vines a, b, c, e, and h only).

Mean fruit volume (cm^3)

Fruit Seed Number	0, 2, 4–distal leaves	8, 12–distal leaves	
401 – 800	77(4)	68(3)	p= 0.051
801 – 1200	104(3)	93(3)	0.027
> 1200	108(3)	104(8)	0.595

Table 7.6. Effect of time of pruning and leaf numbers on kiwifruit cv. Hayward fruit size. S.E. in parenthesis. (Data from vines a,c,e, and h only; Seed data for T2, T4 and T6 was not collected).

	Fruit fresh weight (g)	Fruit seed number	Fruit seed weight (mg)
Pruning Time			
T1	112(14)	1266(156)	1598(181)
T2	114(10)	-	-
T3	114(15)	1270(208)	1591(192)
T4	114(17)	-	-
T5	113(14)	1289(175)	1588(169)
T6	109(16)	-	-
Leaf Treatment			
0-distal leaf	112(13)	1257(139)	1564(174)
2-distal leaf	111(15)	1256(185)	1570(96)
8-distal leaf	115(15)	1317(206)	1647(237)

....

Significance of F Value:			
Time	.90	.93	.97
Leaf	.66	.45	.33
Leaf x Time	.92	.60	.12

Table 7.7. Effect of interaction of leaf number and pruning time on final fruit size (cm^3) of kiwifruit cv. Hayward. Significance of F value were obtained using initial fruit volumes at each pruning time as covariates. (Data from vines a, c, e and h only). S.E. in parenthesis.

Pruning Time:	T1	T2	T3	T4	T5	T6
Leaf Treatment:						
0-distal leaf	101(6)	99(5)	103(5)	100(6)	96(5)	92(5)
2-distal leaf	95(3)	95(5)	102(3)	92(7)	99(6)	98(6)
8-distal leaf	103(6)	106(3)	97(9)	100(1)	101(6)	93(7)
	p=.56	.26	.52	.56	.08	.58

Table 7.8. Effect of leaf number treatment on
the size of fruits which contained less than
1200 seeds. S.E. in parenthesis.

Leaf Treatment	Final Fruit Volume (cm^3)
0–distal leaf	93 (8)
2–distal leaf	97 (4)
8–distal leaf	86 (11)
	p= 0.24

Table 7.9. Effect of time of pruning and leaf
number treatment on fruit size, stem diameter,
and specific leaf weight of kiwifruit cv. Hayward.
S.E. in parenthesis.

Time of Pruning (weeks from petal fall)	Fruit Fresh Weight(g)	Specific Leaf Wt. (mg cm^{-2})	Stem Diameter (mm)
1	107(3)	15.3(2.0)	10.6(0.2)
4	107(4)	13.9(1.8)	10.7(0.2)
8	107(4)	12.5(0.6)	11.2(0.2)
No. of distal leaves:			
2	106(3)	13.0(1.5)	10.5(0.2)
8	108(3)	14.8(1.2)	11.1(0.2)
Significance of F value:			
Time	.99	.47	.09
Leaf	.51	.33	.02
Time x Leaf	.27	.17	.38

Table 7.10. Effect of the number of distal leaves on the final fruit size of kiwifruit cv. Hayward. in different fruit seed weight classes. S.E. in parenthesis.

Fruit seed weight classes:	Fruit fresh weight (g)		
	2-distal leaf	8-distal leaf	
< 400 mg	59(4)	57(3)	p=.31
401 - 600	80(2)	78(2)	.32
601 - 800	91(2)	90(3)	.14
801 - 1000	99(2)	103(2)	.95
1001 - 1200	107(2)	108(2)	.00
1201 - 1400	115(2)	117(2)	.85
1401 - 1600	123(2)	123(1)	.14
1601 - 1800	127(1)	128(1)	.04
> 1801	143(4)	145(3)	.60

however, a slight indication that at fruit seed weights of less than 800mg, fruits from 2-distal leaf treatments were more consistently bigger than the fruits from 8-distal leaf treatments.

Table 7.11 shows that the presence of large numbers of distal leafs did not affect the growth of those leaves which subtended fruits. The leaf area, specific leaf weight, and chlorophyll content of subtending leaves in either 0 or 12-distal leaf treatments were similar (p>0.05). However, the mean stem diameter of 8-distal leaf treatments were significantly bigger (p=0.02) than a 2-distal leaf treatment (table 7.9).

Effect of Time of Pruning

Table 7.3 shows that during the 1982-83 trial, the effect of leaf numbers on fruit size was evident from as early as 3 Jan 1983, ie. 12 days after the pruning treatments were applied (or about 3 weeks after petal fall). In the following season (1983-84), no significant effect on fruit size was observed when the fruiting shoots were pruned at different times (p=0.90; table 7.6). Similar results were found in the 1984-85 season, where the mean fruit fresh weight remained at 107g for each of the 3 times of pruning (p=0.99; table 7.9). However, the mean stem diameters of

Table 7.11. Comparison of leaf data between 0, and 12-distal leaf treatments (averaged over all fruit numbers). Only the data from leaves which subtended fruits were included. S.E. in parenthesis.

	Treatments		
	0-distal leaf	12-distal leaf	
Final leaf area (cm^2)	93(5)	83(5)	p=0.12
Increase in leaf area during experimental period (cm^2)	6(1)	5(1)	0.51
Specific Leaf Weight ($mg\ cm^{-2}$)	11.7(0.3)	11.1(0.4)	0.14
Chlorophyll ($mgChl\ cm^{-2}$)	46.9(3.6)	46.2(4.0)	0.90

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shoots which were late pruned were bigger (11.2 cm) than those of early pruning treatments (10.6 cm).

Effect of Complete Defoliation

Fruits from a completely defoliated shoot were not reduced in fruit size. Table 7.12 shows that the mean final fruit size of these shoots were 115g, which is similar to those on shoots with different number of leaves on them ($p=0.63$).

Table 7.12. Effect of leaf number treatments on fruit
size of kiwifruit cv. Hayward. (Data from vines a, c,
e, and h only). S.E. in parenthesis.

Treatment	Fruit fresh weight (g)	Fruit seed number	Fruit seed weight (mg)
completely defoliated	115.0(21.0)	1211(132)	1575(209)
0-distal leaf	106.0(6.8)	1255(173)	1534(64)
2-distal leaf	115.3(13.7)	1332(178)	1684(237)
8-distal leaf	105.0(7.2)	1167(116)	1407(171)
	p=.63	.55	.31

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7.3 Experiment 7B

7.3.1 Introduction

The previous experiment (7A) showed a highly significant
leaf effect on fruit growth which diminished in the next 2
seasons as the vines grew older. This experiment
investigated the influence of vine age on the relationship
between leaf numbers and fruit size in a fruiting lateral.

7.3.2 Materials and Methods

Four 3-year-old and four 7-year-old 'Hayward' vines were
selected for this experiment. They were located within the
same orchard block at Massey University.

Sixteen fruiting laterals, each carrying 3 fruits, were
selected from each vine for treatments. They were pruned to
either 2 or 8 distal leaves on 14 Dec 1985, about 2 weeks
after anthesis. A range of fruit sizes was obtained by
excising the flower styles during anthesis. Shoot regrowths
occurred in mid January and were left intact as a separate
treatment.

Fruit harvest was carried out on 22 May 1986.

7.3.3 Results

Leaf Inhibitory Effect

Table 7.13 shows that on the older vine, fruit growth was not affected by either 2 or 8-distal leaf treatments (98 cf 95 cm^3; p=0.56). On a young vine however, it was clear that the 8-distal leaf treatment inhibited fruit growth by 17g (102 cf. 85 cm^3; p=0.03). A comparison between the young and old vines shows that fruit sizes on the 2-distal leaf treatment was similar (p=0.61), whereas the 8-distal leaf treatments reduced the fruit size on young vines by 10 g (p=0.06). None of the above differences in fruit size were correlated with the fruit seed numbers or seed weights.

Effect of Shoot Regrowth

The influence of shoot regrowth on fruit size is shown in table 7.14. In a young vine, fruit sizes were similar

Table 7.13. Comparison of the effect of 2 and 8-distal leaf treatments between young (3-year-old) and old (7-year-old) kiwifruit cv. Hayward vines. S.E. in parenthesis.

	3-year-old vines			7-year-old vines		
	2-distal leaf	8-distal leaf		2-distal leaf	8-distal leaf	
Fruit fresh weight (g)	102(6)	85(4)	p=.03	98(4)	95(3)	p=.56
Fruit seed number	732(64)	793(63)	.50	846(46)	999(36)	.01
Fruit seed weight (mg)	912(78)	1007(84)	.41	1049(56)	1209(58)	.05

Table 7.14. Effect of shoot regrowths from fruiting shoots of kiwifruit cv. Hayward after they were pruned to 2 or 8-distal leaves, on young (3-year-old) and old (7-year-old) vines. S.E. in parenthesis.

3-year-old vines

	2-distal leaf			8-distal leaf		
	- regrowth	+ regrowth		- regrowth	+ regrowth	
Fruit fresh weight(g)	102(8)	102(9)	p=.99	86(5)	80(9)	p=.58
Fruit seed number	777(73)	596(133)	.26	815(65)	698(192)	.58
Fruit seed weight(mg)	963(89)	758(162)	.29	1045(88)	841(242)	.46

7-year-old vines

	2-distal leaf			8-distal leaf		
	- regrowth	+ regrowth		- regrowth	+ regrowth	
Fruit fresh weight(g)	96(4)	106(13)	p=.49	94(3)	121(0)	p=.00
Fruit seed number	879(50)	748(105)	.29	1017(33)	454(0)	.00
Fruit seed weight(mg)	1078(66)	963(111)	.39	1230(56)	547(0)	.00

(102g) on 2-distal leaf treatments, with or without regrowths. On 8-distal leaf treatments however, the presence of regrowths inhibited fruit size by a further 6g (p=0.58).

The effect was different on older vines. Both 2 and 8-distal leaf treatments had bigger fruit sizes (106 and 121g, respectively) as compared with the treatments where shoot regrowths were not present (96 and 94g, respectively).

Differences in fruit seed number and seed weights were not correlated with the fruit size differences observed in the above treatments.

7.4 Discussion

7.4.1 Vine Performance

The results of experiment 7A indicated that over a
period of 3 consecutive seasons, some vines (eg. vines d and
g) consistently produced smaller fruits while others (eg.
vines a and e), consistently carried larger fruits.

Although Burge (1986) had shown that fruit sizes on
older kiwifruit vines were correlated with crop load, table
7.1 shows that the differences in fruit size between 'good'
and 'poor' vines were not related to the crop load. These
vines were young and light cropping, so it was unlikely that
the carbohydrate resource to supply fruit growth was
limiting.

Vine leaf-fruit ratios did not show a consistent
relationship with vine performance (table 7.1). Therefore
the differences in fruit size between vines is not likely to
be attributable to this factor.

Grant and Ryugo (1984a) showed that smaller fruits were
produced on shaded canes. However, the selected vines in
experiment 7A were located in random positions (fig. 7.1).
For instance, both 'good' (vine a) and 'poor' (vine g) vines

were located on the same row next to a shelter belt. Thus
the production of smaller fruits on vine g could not be
caused by shading effects.

The proximity of every 'Hayward' vine to a male
pollinator was also random (fig. 7.1). This also removed
the possibility that differences in pollination could account
for the differences between vines. However, during the
1984-85 trial, there was a clear indication that 'poor' vines
(eg. vines d and g) had the lowest fruit seed number (725
and 852 respectively; table 7.1). Fruit seed abortion is
known to increase during apple fruit set when the supply of
carbohydrate to the fruits is limiting (Abbott, 1960). If
this was the cause of low seed numbers in the 'poor' vines,
then it was likely that some mechanism was inhibiting the
supply of carbohydrate to support fruit growth as well. Thus
figure 7.3 shows that at equivalent fruit seed numbers, fruit
sizes of 'poor' vines were much smaller than those on 'good'
vines.

Root growth has an important effect on the maintenance
and balance of the growth of the whole plant (Wareing, 1970).
Growth hormones inter-relations between roots and shoots have
a major role in the partitioning of assimilates (Wareing,
1978). It is probable that the differences in vine
performance observed in this study were linked to genetic
differences in the rootstock.

7.4.2 Leaf Inhibitory Effect

The results of experiments 7A and 7B showed that fruit growth on a young vine (3-4 years) was inhibited by the presence of more than 8 distal leaves on the same shoot (tables 7.3, 7.13). The results shown in table 7.4 suggests that the large leaf number treatments inhibited fruit growth only during the initial stage of fruit development. A greater proportion of initially small fruits (< 12 cm^3) in the large leaf number treatments became large fruits (> 80 cm^3) at harvest, presumably because of the compensatory effect of a bigger leaf area during the later stages of fruit growth.

The period of early fruit development coincided with the stage when vegetative growth in the kiwifruit vine was still active (Davison, 1987). In this study, apical meristems were removed in all the pruning treatments so that the effect of leaf numbers in reducing the growth of fruitlets was not due to the competition for assimilates between the fruit and apical sinks. The data of Smith et.al. (1986) also showed that leaves on fruiting shoot stopped accumulating dry matter after fruit set. There was some evidence however, that the stem cambium was an active sink during the brief period around fruit set (table 7.9).

Growth inhibitors are known to accumulate in mature

leaves (eg. Eagles and Wareing, 1964; Edwards, 1985; Goldsmidt, 1984; Setter et.al., 1980). The results of this study suggest the possibility of the involvement of a growth inhibitor originating from the leaves that suppressed early fruit growth. Then the effect of pruning a fruiting shoot to less than 8 distal leaves was to reduce the supply of the inhibitor, and free the uptake of assimilates in the fruits.

There was a clear indication (table 7.5) that fruits with seed numbers greater than 1200 were not affected by the leaf inhibitory effect. This suggest that a threshold level of growth substances associated with seeds was required, above which fruits were able to overcome the inhibitory effects from the leaves.

Leaf effects on fruit growth was influenced by vine age. Thus while fruit growth was significantly inhibited by large leaf numbers in 1982-83 when the vines were 4-year-old, the effect was less evident in the trials of the subsequent 2 seasons, on the same vines. During the 1983-84 season, good pollination resulted in high fruit seed numbers (table 7.1). Some fruits from that trial which contained less than 1200 seeds indicated a reduction in fruit size in the 8-distal leaf treatments (table 7.8). Although a range of fruit seed numbers were obtained in the 1984-85 trial, table 7.10 shows that the inhibitory effect of large leaf numbers, on the fruit size of these 6-year-old vines, were diminished. Only

a slight trend was observed in fruits with low seed numbers.

Evidence that a significant leaf effect is observed only on young vines became clearer from the results of experiment 7B. 8-distal leaf treatments on 3-year-old vines reduced fruit growth by 17g (p=0.03), whereas no inhibitory effects were observed on 7-year-old vines (p=0.56; table 7.13).

Chalmers and Van Den Ende (1975a) found that in the peach tree, the proportion of the annual increment of dry weight going to the root system decreased from 20 $^0/_0$ in a young tree (4-5 years) to 1 $^0/_0$ in a mature tree (8-10 years). Corresponding values for percentages of dry weight production directed into fruit growth were 30 and 70 $^0/_0$, respectively. This transition in the physiological condition of a tree is described as an aging process (Hackett, 1985). It is also indicated by a loss of apical dominance as the branch system increased in size and complexity (Wareing, 1970). It was thought that a factor associated with the growth activity of the peach root system may limit vegetative growth in mature trees, thus making an increased supply of assimilate available for fruit growth (Chalmers and Van Den Ende, 1975a).

The influence of kiwifruit vine age on the effect of leaf inhibition of fruit growth may be explained by a similar mechanism. Like the peach tree, the young kiwifruit vine also goes through similar changes in assimilate partitioning,

whereby the proportion of dry matter shifted from the roots to fruits, as the vine matured (Buwalda, 1986). The young vine probably responded to a strong factor, coming from the roots, to activate a leaf inhibitor which prevented assimilate uptake in the fruit sinks. This favours the partitioning of assimilates towards vegetative growth. As the root activity decined with aging, the shoots may have received a weaker signal, so that the effect of the leaf inhibitor was diminished.

Although the leaf number treatments did not affect fruit growth in a 'poor' vine (fig. 7.7), the mean fruit size was small (table 7.1). This may be due to the effect of a poor root system, which not only produced a weak signal, but also limited the supply of nutrients to support top growth.

7.4.3 **Time of Pruning**

In the kiwifruit vine, the time of summer pruning may be critical in the achievement of maximum fruit growth. Lay Yee and Pringle (in Davison, 1987) found that early fruit growth rates were increased when fruiting shoots were tipped shortly after flowering. The results of the 1983-84 (table 7.6) and 1984-85 (table 7.9) trials show that fruit size was not affected when fruiting shoots were pruned during the period

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from blossom to 8 weeks after petal fall. There was also no interaction with the pruning treatments in these trials. However, where the pruning treatments were significant for the young vines in the 1982-83 trial, the results also show that pruning may have to be carried out not later than a week after petal fall (table 7.3).

7.4.4 Effect of Shoot Regrowth

Edwards (1985) reported that the pruning of apple shoots was in effect the removal of a source of ABA which inhibited axillary buds from expanding. The reduction in the supply of inhibitors then allowed the content of gibberellins in the apical tissues to rise so that bud burst followed.

The occurrence of shoot regrowths in the kiwifruit vine introduced further growth centres which may compete with fruit growth. Shoot regrowths on 2-distal leaf treatments on a young (3-year-old) vine did not affect fruit size, in spite of the large total number of leaves (p=0.99; table 7.14). This may be because the bud break occurred after the period of early fruit development.

8-distal leaf treatments inhibited fruit growth on a young vine by about 17 g (table 7.13), and fruit size was further reduced by about 6 g where shoot regrowths had taken

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place (table 7.14).

Although leaf inhibitory effects were not present on older (7-year-old) vines (table 7.13), fruit growth on both the 2 and 8-distal leaf treatments benefitted from the presence of extra leaf area from shoot regrowths (table 7.14).

7.4.5 Shoot Fruit Numbers and Fruit Size

In some crops, fruit size depended on its position relative to other fruits on the same fruiting lateral (Ho et.al., 1982; Maun and Cavers, 1971; Stephenson, 1981; Wyatt, 1982). However, this does not apply to the kiwifruit where it was found that every fruit on the same fruiting shoot developed in synchrony. Fig 7.5 shows that the growth patterns of both the proximal and distal fruits on a fruiting shoot with 5 fruits were similar. Thus there was no interfruit competition, and final fruit sizes were not affected by the fruit load on a single shoot (p=0.94, table 7.2, fig. 7.4).

As there was also no leaf-fruit interaction (p=0.52; table 7.2), it implies that either fruits in the 0-distal leaf treatments had all their carbohydrate needs met by the subtending leaves, or assimilates were drawn from outside the

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fruiting lateral. Evidence that large amounts of carbohydrate were translocated to support fruit growth was seen in the normal development of completely defoliated treatment (table 7.12). It was also shown in chapter 6 that fruits imported ^{14}C-assimilates from adjacent shoots.

Table 7.11 shows that there was a lack of leaf response to fruit load. The leaf area, specific leaf weight, and chlorophyll content of leaves which subtended fruits in 0-distal leaf treatments were similar to those on treatments with 12-distal leaves. This could be explained by the ease with which carbohydrate were transported around the vine to meet fruit demands (chapter 6). It can also be suggested that under the conditions where carbohydrate did not appear to be limiting, the potential for kiwifruit fruit growth depended largely on factors of sink strength, such as the presence of sufficient seeds to attract metabolites, and the lack of inhibitory factors.

CHAPTER EIGHT

LEAF-FRUIT RATIO AND FRUIT GROWTH

8.1 Introduction

The kiwifruit vine is known for its vigorous vegetative growth (Ferguson, 1984) and winter and summer pruning practices are important factors in achieving optimum leaf to fruit ratios for increased yield. Several reports from other crops have indicated the beneficial effect of increasing leaf-fruit ratio on fruit growth. This included apples (Denne, 1963; Haller and Magness, 1925), peach (Weinberger, 1931; Weinberger and Cullinan, 1932) and tomatoes (Gustafson and Stoldt, 1936; Gustafson and Houghtaling, 1939).

Attempts to establish the minimum leaf-fruit ratio to saturate apple fruit growth have been made (Hansen, 1969, Magness 1928, Magness and Overley, 1929), but this is known to vary with the time of season.

In the kiwifruit vine, the traditional summer practice is to leave 2 leaves after the last fruit. Lees (1982) reported that this is sufficient for fruit growth provided the fruiting shoot is exposed to good lighting conditions. Since there is

considerable flexibility in the translocation of assimilates from distant sources outside the fruiting shoot (chapter 6), the overall leaf to fruit ratio of a vine, rather than the individual shoot, may be more important.

8.2 Experiment 8A

8.2.1 Introduction

Although the growth of the entire vine depends on the overall leaf-fruit ratio, it is useful to know the minimum leaf-fruit ratio to support fruit growth. The results from experiment 6A have indicated that this ratio may lie between 0.83:1 and 1.7:1.

The objective of this experiment was to determine if a 2:1 leaf-fruit ratio is adequate to supply the growth of up to 5 fruits on a fruiting shoot.

8.2.2 Materials and Methods

This experiment was carried out during the 1983-84 season at Levin. Single, indeterminate fruiting shoots carrying either 1, 3, or 5 fruits on 5-year-old 'Hayward' vines were used. Treatments were applied on 17 Dec 1983 (ie. 1 week after petal fall) by pruning the shoots to leaf-fruit ratios of 1:1 or 2:1. This was maintained by removing any shoot regrowths as they appeared. Half the treatments were

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girdled, while the other half were left intact. Throughout the experimental period, the girdles were recut periodically to prevent reconnection of the phloem. Leaf areas were measured initially on 16 Dec 1983 and again on 10 May 1984 to determine any changes in leaf area during the period of treatment. Net leaf photosynthesis and stomatal resistance measurements were taken on 10 May 1984 and leaf dry weight was also measured at harvest, to obtain specific leaf weights. Fruit harvest was carried out on 10 May 1984.

8.2.3 Results

Main Effects

Girdling and leaf-fruit ratio had highly significant effects on fruit size (table 8.1). On average, fruits from girdled treatments were 10 cm^3 smaller than intact treatments (table 8.2; p=0.03).

Fruits from shoots with 2:1 leaf-fruit ratios have a mean fruit size 15 cm^3 bigger than those from 1:1 leaf-fruit ratio (p<0.01). The average leaf area per fruit was 242 and 99 cm^2, respectively (table 8.3; p<0.01)

The effect of leaf-fruit ratio was significant from as

Table 8.1. Effect of girdling, fruit number, and leaf-fruit ratio on kiwifruit cv. Hayward. Summary of ANOVA - significance of F values.
(*, 0.05>p>0.01; **, p<0.01; -, p>0.05).

	# Fruit Volumes					FW
	16 Dec	14 Jan	27 Feb	3 Apr	28 Apr	
Girdle	-	-	-	*	**	*
Fruit	-	-	-	-	-	-
Ratio	-	*	**	**	**	**
Girdle x Fruit	-	-	-	-	-	-
Girdle x Ratio	-	*	**	**	**	**
Fruit x Ratio	-	-	-	-	-	-
Gir-Fr-Ratio	-	-	-	-	-	-

● ●

	SNO	SWT	MSWT	TOTAL LAREA	LAREA /FRUIT	LAREA /FW
Girdle	-	-	-	-	-	-
Fruit	-	-	-	**	*	*
Ratio	-	-	-	**	**	**
Girdle x Fruit	-	-	-	-	-	-
Girdle x Ratio	-	*	**	-	-	*
Fruit x Ratio	-	-	-	**	-	-
Gir-Fr-Ratio	-	-	-	-	-	-

\# Fruit volumes taken on 16 Dec 1983;14 Jan 1984;
      27 Feb 1984;3 Apr 1984;28 Apr 1984
FW - fruit fresh weight
SNO - fruit seed numbers
SWT - fruit seed weight (mg)
MSWT - mean seed weight per 1000 seeds ie. SWT/SNO * 1000 (mg)
TOTAL LAREA - mean total leaf area per shoot (cm^2)
LAREA/FRUIT - mean total leaf area per fruit (cm^2)
LAREA/FW - mean total leaf area per fruit fresh weight ($cm^2\ mg^{-1}$)

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Table 8.2. Effect of girdling and leaf-fruit ratio on fruit size (cm^3) of kiwifruit cv. Hayward. S.E. in parenthesis.

Leaf-fruit ratio	1:1	2:1		mean
non-girdled	106(10)	104(9)	p=.58	105(9)
girdled	78(16)	110(10)	.00	95(21) p=.03
mean	92(19)	107(8)	.00	

Table 8.3. Effect of girdling, leaf-fruit ratio, and fruit number on the leaf area per fruit (cm^2) of kiwifruit cv. Hayward. S.E. in parenthesis.

	Leaf-fruit ratio			
	1:1	2:1		mean
girdled shoots:				177(18)
1 fruit	82(11)	184(49)	p=.13	
3 fruit	98(2)	265(22)	.00	
5 fruit	105(12)	267(32)	.07	
non-girdled shoots:				171(18)
				p=.80
1 fruit	107(15)	212(33)	.04	
3 fruit	101(25)	235(13)	.01	
5 fruit	99(7)	287(18)	.00	
mean	99(5)	242(12)	.00	

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early as 14 Jan 1984 (ie. 5 weeks after petal fall) whereas girdling effects were not significant until 3 Apr 1984 (table 8.1).

There was no significant difference between the mean fruit sizes of the 1, 3, or 5 fruit treatments (p=0.70; table 8.4).

Interaction between Girdling and Leaf-Fruit Ratio

A highly significant interaction between girdling and leaf-fruit ratio was observed ($p < 0.01$; table 8.1). The fruit sizes between the two leaf-fruit ratios in non-girdled treatments were similar (106 cf 104 cm^3; p=0.58). The mean fruit size on girdled, 1:1 and 2:1 ratio treatments were 78 and 110 cm^3, respectively ($p < 0.01$; table 8.2).

Figure 8.1 shows a scattergram of fruit fresh weight versus fruit seed number. It can be seen clearly that at the same seed number, fruits from girdled, 2:1 leaf-fruit ratio treatments were bigger than those from girdled, 1:1 leaf-fruit ratio treatments. Data for non-girdled treatments clustered between the girdled treatments.

A highly significant interaction between girdling and leaf-fruit ratio was also observed for total fruit seed weight ($p < 0.05$), and weight per seed ($p < 0.01$; table 8.1).

Seed growth was affected by a girdled, 1:1 leaf-fruit

Table 8.4. Effect of girdling and leaf-fruit ratio on fruit size (cm^3) of fruiting shoots carrying 1, 3, or 5 fruits. S.E. in parenthesis.

	Fruit number		
	1 fruit	3 fruit	5 fruit
girdled shoots:			
ratio 1:1	80(10)	78(10)	77(4)
2:1	103(8)	114(2)	112(1)
	p=.13	.04	.01
non-girdled shoots:			
ratio 1:1	117(3)	102(5)	108(2)
2:1	107(5)	108(3)	98(3)
	p=.17	.31	.12
mean	102(5)	101(4)	97(4) p=0.70

Figure 8.1. Relationship between seed number and fruit fresh weight of kiwifruit cv. Hayward. △ , non-girdled treatments. × , girdled, 2:1 leaf-fruit ratio treatments; □ , girdled, 1:1 leaf-fruit ratio treatments.
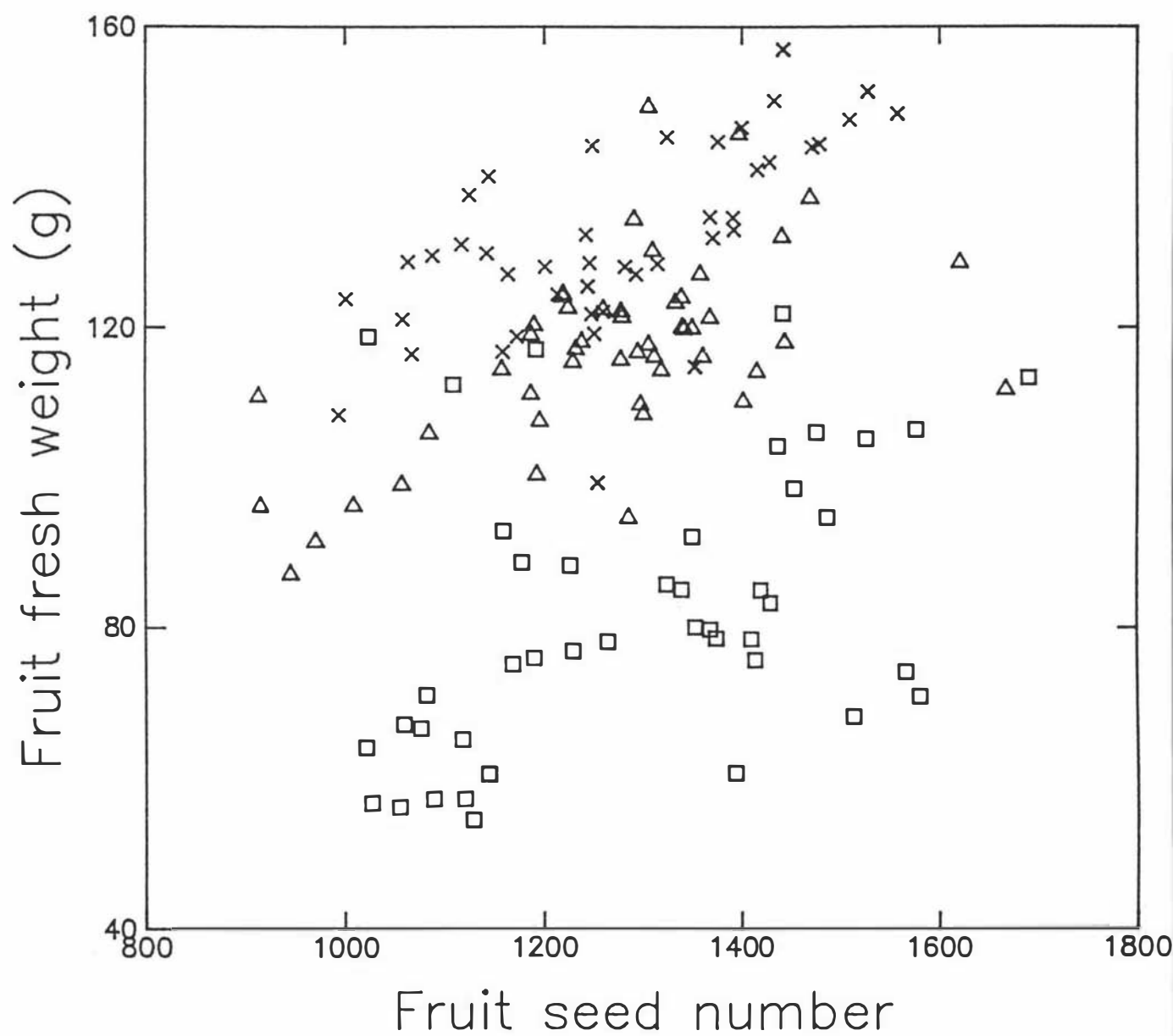
ratio treatment. Table 8.5 shows that this treatment had similar fruit seed number as the other treatments (1285 cf. 1251, 1332, 1287), but its fruit seed weight was more than 100mg lower (1485 cf. 1634, 1616, 1668).

Interaction between Girdling and Shoot Fruit Number

Both girdled and non-girdled treatments had similar leaf areas per fruit (177 and 171 cm^2 respectively; p=0.80; table 8.3). The leaf areas on a kiwifruit shoot are usually smaller at the first few node positions. Thus for a 2:1 leaf-fruit ratio treatment, leaf area per fruit increased as the number of fruits per shoot increased (table 8.3).

Table 8.4 shows that in a non-girdled, 2:1 ratio treatment, mean fruit sizes decreased from 107 and 108 cm^3 to 98 cm^3 as the number of fruits increased from 1 to 3 to 5 fruits. The reverse was observed in girdled, 2:1 ratio treatments, where mean fruit size increased from 103 to 114 and 112 cm^3, respectively.

Figure 8.2 shows the mean fruit size of each fruit along a fruiting shoot which carried 5 fruits. There was no evidence of any interfruit competition for the girdling or leaf-fruit ratio treatments.

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Table 8.5. Effect of girdling and leaf-fruit ratio interactions on fruit seed number and seed weight. S.E. in parenthesis.

	Ratio	Fruit Seed Number	Fruit Seed Weight (mg)
non-girdled			
	1:1	1251(30)	1634(47)
	2:1	1332(38)	1616(42)
	p=.12		.78
girdled	1:1	1285(52)	1485(62)
	2:1	1287(36)	1668(42)
	p=.98		.02

Figure 8.2. Effect of girdling and leaf-fruit
ratio on the mean final fruit size of each fruit on
a. fruiting shoot carrying 5 fruits. S.E. in
parenthesis.

non - girdled 5 fruit : 5 leaf	93 109 105 101 98 (5) (4) (2) (3) (5)				p=0.10
non - girdled 5 fruit : 10 leaf	94 103 101 92 98 (3) (1) (2) (11) (4)				p=0.62
girdled 5 fruit : 5 leaf	73 73 76 71 71 (7) (7) (9) (8) (7)				p=0.99
girdled 5 fruit : 10 leaf	107 111 113 112 109 (5) (2) (1) (3) (3)				p=0.63
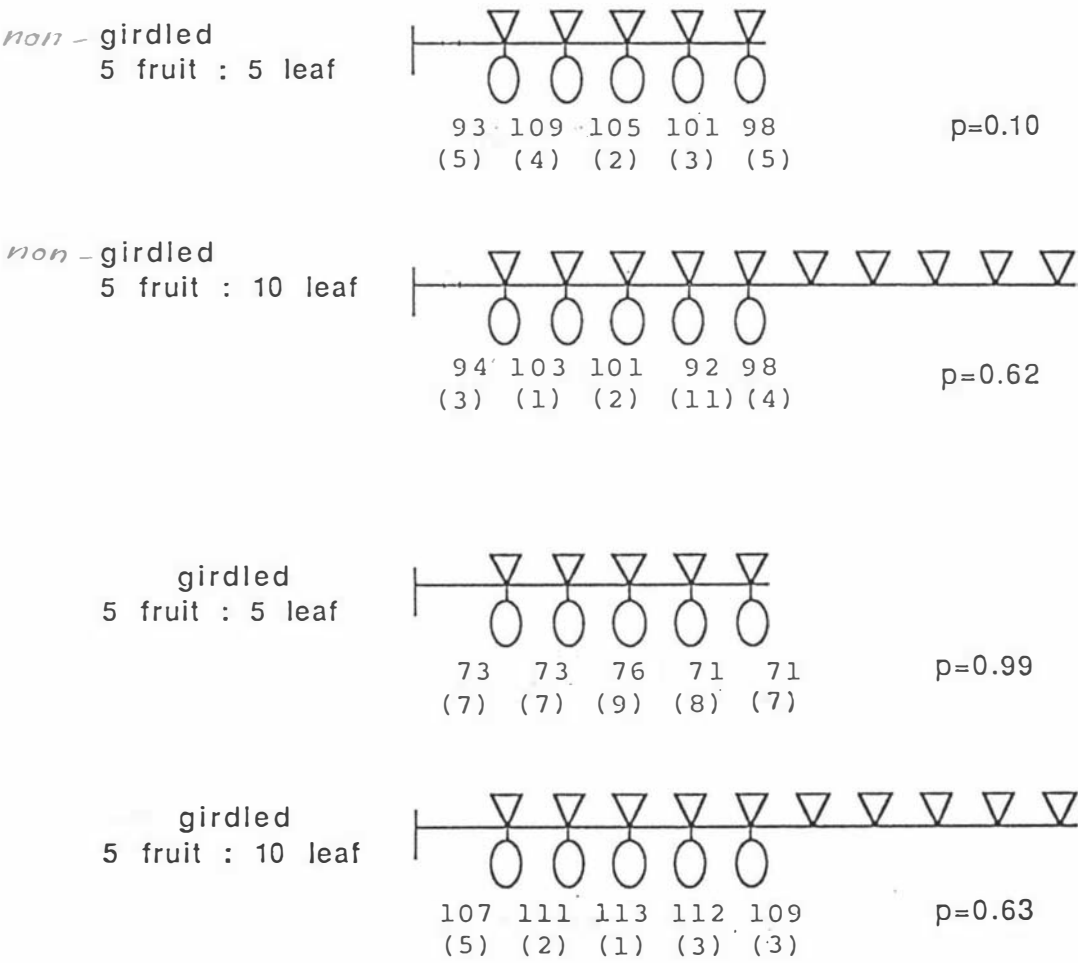
Comparison of Leaf Characteristics

Table 8.6 shows that subtending leaves (leaf groups 1 and 2) expanded by 8.3 and 10.0 $^0/_0$, while the distal leaves (leaf-group 3) only expanded by 6.9 $^0/_0$ during the period of the experiment. No differences were observed in the specific leaf weights. Photosynthetic rates and stomatal resistance were similar in all treatments for both subtending and distal leaves.

Table 8.6. Leaf data for girdled and non-girdled treatments. Leaf groups: 1, leaves subtending fruits in 1:1 leaf-fruit ratio; 2, leaves subtending fruits in 2:1 leaf-fruit ratio; and 3, distal leaves in 2:1 leaf-fruit ratio treatments. S.E. in parenthesis.

	Final Leaf Area (cm^2)	Percent Increase in Leaf Area	Specific Leaf Weight ($mg\ cm^{-2}$)	#Net Leaf Photosynthesis ($ugCO_2\,m^{-2}s^{-1}$)	*Mean PPFD ($uE\ m^{-2}s^{-1}$)	Stomatal Resistance ($s\ cm^{-1}$)
non-girdled	122(4)	8.2(0.5)	20.4(0.5)	537(22)	497(27)	3.8(0.2)
girdled	123(4)	8.6(0.6)	21.3(0.8)	558(22)	378(27)	3.6(0.2)
	p=0.76	0.55	0.28	0.51	0.61	0.43
leaf-group						
1	103(4)	8.3(0.7)	20.0(0.6)	552(27)	507(33)	3.6(0.2)
2	106(6)	10.0(1.1)	20.8(1.3)	539(37)	377(49)	3.8(0.4)
3	158(7)	6.9(1.3)	22.2(0.9)	557(38)	530(43)	3.6(0.4)
	p=0.00	0.60	0.25	0.80	0.91	0.54
non-girdled: leaf-group						
1	101(4)	8.0(0.8)	18.9(0.8)	566(36)	501(45)	3.4(0.3)
2	103(5)	9.8(0.9)	20.8(2.1)	518(36)	510(73)	4.2(0.3)
3	163(5)	6.8(0.7)	21.7(0.9)	521(41)	452(80)	3.9(0.5)
	p=0.00	0.46	0.23	0.54	0.72	0.16
girdled: leaf-group						
1	106(7)	8.6(1.2)	21.3(0.9)	540(40)	513(48)	3.8(0.4)
2	109(5)	10.2(0.8)	20.4(1.5)	560(27)	475(63)	3.5(0.4)
3	153(6)	7.0(1.0)	22.2(1.6)	590(53)	604(33)	3.3(0.6)
	p=0.02	0.94	0.05	0.55	0.65	0.57

\# Net leaf photosynthesis and stomatal resistance measurements were taken on 15 Dec 1983. Leaf temperature was 20 C.

* PPFD data was recorded for each leaf corresponding to the photosynthesis measurements.

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8.3 Experiment 8B

8.3.1 Introduction

Previous experiments (6A, 6B, 8A) showed that with girdled shoots, the minimum leaf-fruit ratio for fruit growth was greater than 1:1. In this experiment, ^{14}C-label was used to investigate the minimum leaf-fruit ratio at which carbohydrate was no longer supplied from outside the fruiting lateral.

8.3.2 Materials and Methods

Four 3-year-old potted 'Hayward' plants, grown in a glasshouse, were used in this experiment. The experimental unit consisted of an indeterminate shoot carrying 3 fruits, and an adjacent vegetative shoot below it. The fruiting shoot was pruned to leaf-fruit ratios of either 1:1, 2:1, 3:1, or 4:1 on 10 Dec 1984. Each pruning treatment had 4 replicates. 74 kBq of ^{14}CO$_2$ was applied to the entire vegetative shoot below each fruiting shoot 2 weeks after the shoots were pruned. Leaf photosynthesis and leaf area

measurements were taken after the ^{14}C was applied and harvest was carried out on 3 Jan 1985.

8.3.3 Results

The distribution of ^{14}C-activity in the fruiting shoot is shown in figure 8.3. The results confirmed that the fruits on shoots with a 1:1 leaf-fruit ratio can attract large amounts of carbohydrate from outside the shoot (eg. experiments 6A, 6B, 7A).

As the leaf area per fruit increased from 86 cm^2 to 697 cm^2 the amount of ^{14}C-photosynthate declined to negligible counts. The proximal fruit on each fruiting shoot attracted the highest percentage of ^{14}C-activity. On the 3 leaf:3 fruit treatment for instance, the proximal fruit had 116 dpm of ^{14}C per mg dry weight, while the middle and distal fruit had 38 and 30 dpm per mg respectively. This corresponded with leaf areas of 68,92, and 97 cm^2 respectively (table 8.7).

Trace amounts of ^{14}C-activity was also observed in the stem and leaf segments past the fruits. Table 8.7 shows that leaf photosynthesis did not respond to the fruit demand for ^{14}C-assimilate. As the leaf-fruit ratio increased from 1:1 to 2:1, 3:1, and 4:1, the total supply of photosynthate to each shoot was 114, 417, 690, and 1710 mg Carbon per hour,

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Figure 8.3. Distribution of ^{14}C (dpm mg^{-1}) imported into fruiting shoots of kiwifruit cv. Hayward, pruned to 3 fruits and different leaf numbers.
 + , proximal fruit; o , middle fruit;
 □ , distal fruit; × , the rest of the fruiting shoot.
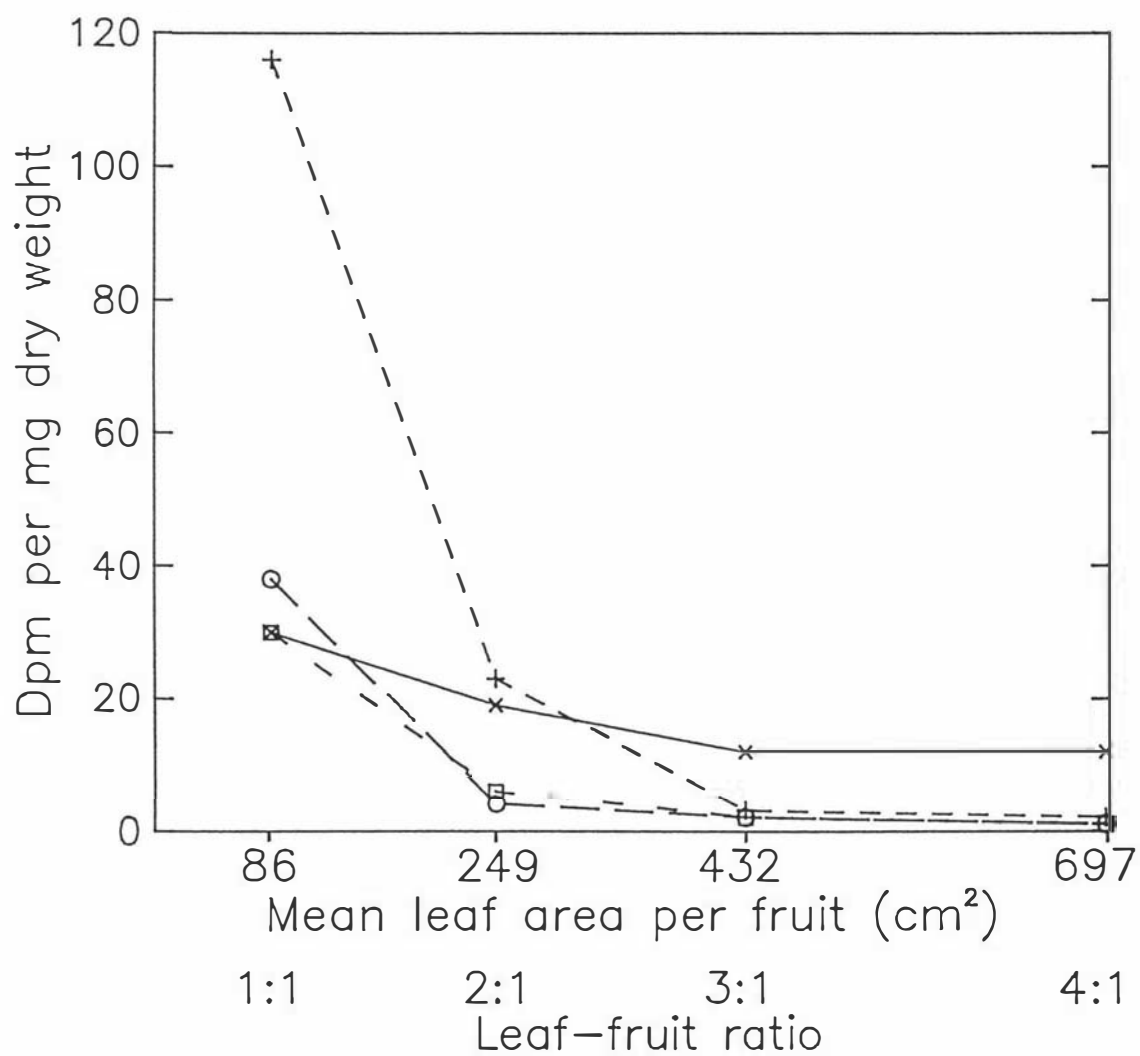
Table 8.7. Effect of different leaf-fruit ratios on net leaf photosynthetic rate ($ugCO_2$ m^{-2} s^{-1}) measured at saturating light conditions (PPFD > 600 uÉ m^{-2} s^{-1}).# Mean leaf areas (cm^2) in parenthesis.

leaf node position	3F3L	3F6L	3F9L	3F12L	
	#				
1	320(68)	271(96)	403(102)	545(142)	p=0.83
2	354(92)	499(101)	384(120)	437(143)	0.15
3	545(97)	453(107)	475(134)	662(147)	0.97
4		501(144)	516(138)	544(163)	0.65
5		634(156)	575(141)	700(205)	0.73
6		671(162)	589(162)	552(201)	0.15
7			442(175)	717(214)	0.06
8			486(171)	947(220)	0.29
9			579(194)	849(242)	0.08
10				845(240)	
11				671(235)	
12				775(211)	

....

Total Photosynthesis Per Shoot (mg Carbon per hour).	114	417	690	1710

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respectively.

Table 8.8 shows that the specific leaf weights of leaves on non-fruiting shoots were significantly lower (P<0.05) than those on fruiting shoots. Leaves which subtended fruits (leaf number 1 to 3) however, had similar specific leaf weights regardless of the number of distal leaves on the fruiting shoot. It can also be seen from table 8.8 that specific leaf weight increased as the leaf number on a fruiting or non-fruiting shoot increased.

Table 8.8. Effect of leaf-fruit ratio on the specific leaf weight of kiwifruit cv Hayward plants grown in a glasshouse environment. (Common letter within columns denotes groups not significantly different at LSD (0.05)). S.E. in parenthesis.

	Leaf nodes				
leaf-fruit ratios:	1-3	4-6	7-9	10-12	
3F3L	11.21(.29)a	-	-	-	p=0.00
3F6L	11.29(.35)a	13.08(.24)a	-	-	0.01
3F9L	10.85(.32)a	12.54(.43)a	13.07(.63)a	-	0.02
3F12L	10.86(.37)a	12.69(.24)a	14.50(.46)a	14.95(.34)a	0.00
....					
non -fruiting shoot	8.15(.33)b	10.57(.36)b	10.57(.30)b	13.04(.41)a	
	p=0.03	0.01	0.01	0.08	

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8.4 Discussion

8.4.1 Effect of Girdling

The girdling of the trunk or branch of a fruit tree is a technique which is used to increase fruit set and fruit size (Priestley, 1967a,b). Davison (1980) reported increases of kiwifruit yield of more than 60 $^0/_0$ on girdled vines as a result of heavier fruiting.

Table 8.2 shows that the overall effect of the girdling treatment was to reduce fruit size by 10 cm^3 (p=0.03). However, a significant interaction with leaf-fruit ratio was present (p<0.01). The real effect of girdling was a severe reduction in fruit size from 106 to 78 cm^3 when the carbohydrate supply is limiting (ie. 1:1 leaf-fruit ratio), or an increase in fruit size from 104 to 110 cm^3 when carbohydrate is not limiting (ie. 2:1 leaf-fruit ratio). Similar observations were reported previously in experiment 6A.

The above fruit responses to girdling treatments were not related to any changes in the leaf characteristics. Table 8.6 shows that the specific leaf weight, net photosynthesis, and stomatal resistance between the girdled

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and control treatments were similar.

In 2:1 leaf-fruit ratio treatments, there was a corresponding reduction in fruit growth on non-girdled shoots as leaf areas increased with fruit number (table 8.3, 8.4). This may be due to increasing levels of an inhibitor associated with the leaves, which caused a reduction in the uptake of assimilate in the fruits. Similar observations were found and discussed in chapter 7.

On girdled shoots however, fruit size increased with increasing leaf area per fruit when the leaf-fruit ratio was 2:1 (table 8.3, 8.4). It would seem that a substance need to be imported or exported, via the phloem of the lateral, for the inhibitory effect to be manifested.

Plant growth substances are known to accumulate above a girdle (Chalmers, 1985; Skene, 1972), and the result of a diminished supply of the growth substances to the roots is a reduction in root activity (Dann et.al., 1984). However, as only an insignificant fraction of the 1-year-old laterals on each vine were girdled in experiment 8A, the removal of leaf inhibitory effects in girdled shoots was not likely to be due to root-produced factors. The accumulation of growth substances, or even supraoptimal levels of the leaf inhibitor, may have a direct effect on fruit growth. The view that carbohydrate accumulates above a girdle is widely held and supported experimentally (Noel, 1970). This

probably explains the increase in fruit size on girdled shoots as the leaf area per fruit increased.

8.4.2 Leaf-Fruit Ratios

It was shown previously (chapter 6) that the minimum leaf-fruit ratio of a kiwifruit fruiting shoot lie between 0.83:1 and 1.7:1. The results of experiment 8A and 8B established that practically, 2 leaves were needed to support the the growth of each fruit on a fruiting shoot. Thus table 8.2 shows that on girdled treatments, a 1:1 ratio (or 99 cm^2 per fruit) was insufficient to support fruit growth (78 cm^3), whereas a 2:1 ratio (or 242 cm^2 per fruit) was sufficient (110 cm^3). This represented an increase of 32 g in fruit size from an additional leaf per fruit. Snelgar et.al. (1986) reported very similar results, and also confirmed that the minimum leaf-fruit ratio is 2:1.

Under the conditions of experiment 8B, fruiting shoots with a 1:1 and 2:1 leaf-fruit ratio assimilated 114 and 417 mg of carbon per hour. Therefore, each fruit needed between 38 and 139 mg carbon per hour, at daily photoperiods of 15-16 hours, for growth.

Although the fruit sizes between the two leaf-fruit ratios were significantly different ($p < 0.01$), their fruit

seed numbers were similar (1285 cf 1287; p=0.98; table 8.5). Fruit seed weight however, was reduced by 183mg on girdled, 1:1 leaf-fruit ratio treatments (table 8.5). Thus although seed abortion did not occur under conditions of limiting carbohydrate supply, seed growth was significantly affected.

A fruiting shoot with 1:1 leaf-fruit ratio imported carbohydrate from outside to meet all its requirements for fruit growth. Thus in the non-girdled treatments (table 8.2) fruit sizes between the different leaf-fruit ratio treatments were similar (p=0.58). It was also clearly demonstrated in experiment 8B that the fruits on a 1:1 leaf-fruit ratio treatment imported significantly greater amounts of ^{14}C-assimilate from outside the shoot, as compared with the other leaf-fruit ratio treatments. Similar observations were found in chapter 6.

There were some indications from experiment 8A that in response to fruit growth, leaves which subtended fruits expanded more than distal leaves (table 8.6). However, net leaf photosynthesis and stomatal resistance were similar for all leaves in all the treatments. The results of experiment 8B (table 8.7) also show that kiwifruit leaves did not respond to a high demand for carbohydrate by increasing their photosynthesis, even in a 1:1 leaf-fruit ratio situation.

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8.4.3 Interfruit Competition

It was shown in figure 8.3 that a significantly larger quantity of ^{14}C-assimilate was imported into the proximal fruit on a fruiting shoot. Although this may suggest that the proximal fruit received more photosynthates for growth than the other fruits, figure 8.2 shows that the fruit sizes of each fruit on a fruiting shoot were similar (p>0.05). It was also observed that on a girdled shoot, the distal fruit was of the same size as the other fruits. Experiments in chapter 7 had also indicated an absence of interfruit competition, even on a completely defoliated shoot (table 7.12). It was shown in chapter 7 that the growth patterns of both the proximal and distal fruit along a shoot were similar (fig. 7.5). Thus the higher concentration of ^{14}C in the proximal fruit could not be due to asynchronous fruit development along a fruiting shoot.

Fruits obtained a large proportion of their assimilates from their subtending leaves (chapter 5). The leaf area corresponding to the proximal, middle, and distal fruits on the 1:1 ratio shoot in figure 8.3 was 68, 92, and 97 cm^2, respectively (table 8.7). It is therefore likely that the proximal fruit attracted more ^{14}C-assimilates from outside the shoot because the leaf area of its subtending leaf was smaller. This suggest that within the fruiting shoot, leaves

do not respond to increased fruit demand for carbohydrate because of the flexibility in which assimilates were drawn from other parts of the vine.

CHAPTER NINE

GENERAL DISCUSSION

9.1 Canopy Establishment and Photosynthesis

This study shows that the kiwifruit leaf grew rapidly (expt
2A) and became exporter of carbon at 60 $^0/_0$ full size, after 40
days from emergence (fig. 2.2; 5.2). Morgan, Warrington, and
Halligan (1985) reported shoot elongation rates of up to 6.7 cm
per day under optimal conditions in controlled environments.
They also observed leaf appearance rates as high as 0.6 leaf per
day. In addition, the optimum temperature for kiwifruit growth
and total photosynthesis were similar (table 2.2). This is
unlike most crops, where growth processes generally show higher
temperature optimum than does photosynthesis (Monteith and
Elston, 1971), so that crop growth rate is frequently limited by the
rate at which assimilates can be utilised in growth, rather than
by the rate of assimilate production in photosynthesis.

Fruit growth in the kiwifruit vine is dependent on current
photosynthates (experiment 6C). The above observations suggest
that the vine is able to establish a canopy rapidly after bud
burst in late September. By the time fruit development begins
in early December, the vine leaf-fruit ratio would have been

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greater than 2:1, so that a positive carbon budget is available (experiment 8B). Evidence from experiment 7B, which shows that shoot regrowth did not compete with early fruit development, also suggest that the growth of fruits with adequate seed numbers was not limited by the amount of carbon available in the vine early in the season.

The maximum photosynthetic rate of a crop sets the limits of its maximum biological and economic productivity (Leopold and Kriedemann, 1975). This study found that the maximum net leaf photosynthetic rate in the kiwifruit vine was 657 ug m^{-2} s^{-1}. This is comparable to those reported for most fruit crops in the field (eg. Crews et.al., 1975; Kriedemann, 1968b; Kriedemann and Canterford, 1971; Kriedemann and Smart, 1971). Kiwifruit leaves are also known to have a long duration in the orchard (Taylor and Woodfield, 1986). Net leaf photosynthetic rates of up to 250 ugCO$_2$ m^{-2} s^{-1} in July have been observed on vines which were protected from frost and wind (pers. comm., Greer, D.H. and Laing, W.A., Plant Physiology Division, DSIR, Palmerston North). It therefore appears that the kiwifruit vine has a large potential for dry matter production, so that assimilate partitioning within the vine is not likely to be source limited.

9.2 Shade and Temperature Effects on Photosynthesis

Differences in the shade and temperature environment of a kiwifruit vine have a direct effect on its photosynthetic response, as well as several important residual effects relating to bud break, flowering, and fruit development (eg. Grant and Ryugo, 1984a; Morgan, Stanley, and Warrington 1985; Snelgar, 1986; Warrington and Stanley, 1986).

Shading to reduce light levels below the saturation levels between 500 to 700 uE m^{-2} s^{-1} (Grant and Ryugo, 1984b; Laing, 1985) had a significant reduction in photosynthetic rates at all temperatures (fig. 2.5). Thus in the orchard, careful considerations have to be given to the use of the various types of wind shelters available. However, the effect of within-canopy shading is more important. Grant and Ryugo (1984b) reported that the light levels falling on shade leaves did not exceed 12 uE m^{-2} s^{-1} and they functioned only slightly above the light compensation point during most of the day. Appropriate training and pruning methods, aimed at the removal of within-canopy shading, are therefore needed. Perhaps the feasibility of using aluminium reflectors on the orchard floor, which was reported to increase apple yield (Moreshet et.al., 1975) should be considered.

The optimum temperature for kiwifruit photosynthesis is 20 C (fig. 2.5). Unlike irradiance, temperature fluctuations in

the orchard are not likely to be controlled by management practices. However, it may be important to leave summer pruning to days of warmer temperatures. Shaded parts of the canopy, which are suddenly exposed to high irradiance after pruning, are more photoinhibited at low temperatures (Greer et.al. 1987). Greer and Laing (1987) showed that the rate of recovery of photoinhibition was also temperature dependent. Thus, depending on the light and temperature conditions, the photosynthesis of a vine could be severely affected immediately after pruning, not only through a loss of photosynthetic surface, but also through the photoinhibition effects on the newly-exposed parts of the canopy.

9.3 Effects of the Presence of Fruits on Photosynthesis

This study could not demonstrate any photosynthetic response of kiwifruit leaves to the presence of fruits on a fruiting shoot (experiment 2C, 8B). This may be due to the presence of alternative sinks, such as the stem cambium.

It was shown in experiment 8B that considerable quantities of ^{14}C-assimilate was imported into the fruiting shoot with a 1:1 leaf-fruit ratio when the fruit demand for carbohydrate was not met by its own leaves (fig. 8.3). Each fruit appeared to import an amount of assimilate from outside the shoot, which is

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inversely proportional to the area of its subtending leaf. It was also found in experiment 5C that the subtending leaf supplied only its own fruit, rather than other adjacent fruits.

All the above evidence seems to indicate that while the kiwifruit leaves did not respond to fruit demand by increasing their photosynthetic rates, they may initially adjust by losing dry weight. The subsequent response was an import of carbohydrate from outside the fruiting shoot which balanced the deficit in the local supply of photosynthate to each individual fruit.

9.4 Sources of Assimilate Supply to Fruits

The main sources of assimilate supply to the fruits can be classified into 3 groups in their order of priority:

1. leaves which subtend fruits,

2. leaves which are distal to fruits on the same fruiting shoot, and

3. leaves from adjacent fruiting or non-fruiting shoots.

Experiment 5C demonstrated that subtending leaves on intact shoots supplied as much as 62 $^0/_0$ of their assimilate to their own fruits. This increased to 78 $^0/_0$ when the shoot was pruned to 0 distal leaves.

In an intact shoot system, fruits also received smaller supplies of assimilate from distal leaves which were linked by the same vascular connections (table 5.1). Distal leaves which were not linked to any fruits exported out of the fruiting shoot to other growth centres. However, after the fruiting shoots were pruned, all the distal leaves contributed to the growth of the fruits on the same shoot (table 5.2).

Distal leaves on shoot regrowths also supplied the fruits on the same shoot. It was shown in experiment 7B that the fruit size on girdled shoots were significantly bigger when shoot regrowths were present (table 7.14).

A high local demand for assimilates which was not met by the leaves on the fruiting shoot resulted in the import of assimilates from source leaves on adjacent fruiting or non-fruiting shoots (experiments 6A, 6B, 8B). This was most clearly demonstrated on a completely defoliated fruiting shoot (experiments 6A, 7A), where normal fruit development occurred when there was an adjacent supply of surplus assimilate from adjacent shoots.

9.5 Flexibility in Assimilate Translocation

A flexibility in the translocation of assimilate within a kiwifruit vine was already implied in the above discussion. Within an intact fruiting shoot, assimilates flowed along pathways of least resistance which linked the fruit on the nth node with its subtending leaf, and at least, the leaves on the n+5 and n+8 nodes (table 5.1). However, after the shoot was pruned, rerouting of the translocates occurred, so that all the distal leaves supplied every fruit (table 5.2).

Assimilates were also translocated freely between laterals. It was shown in experiment 6B that translocation occurred either in a basipetal or acropetal direction, depending on the relative positions of the regions of carbohydrate surplus and shortage. The movement of assimilates between laterals was not restricted by vascular phyllotaxy in the 2-year-old cane (experiment 6B), presumably because of the development of interconnections with secondary thickening. Fruits were also found to have drawn ^{14}C-assimilate from source leaves on laterals up to 7 node distance away (fig. 6.6). A greater distance of up to 2m was reported by Snelgar et.al. (1986). Such a flexibility in the movement of assimilates in the kiwifruit vine is an important consideration in the design of training and pruning systems, whereby fruiting shoots can be separated from other source leaves in another part of the canopy.

9.6 Fruit Development and Seed Number

With a leaf-fruit ratio of greater than 2:1, fruit growth does not seem to be limited by source strength or vascular connections, but may be limited by factors affecting sink strength. For example, the results of experiment 7A (table 7.1) illustrated a sink limited condition whereby the fruits on certain vines could not size up even though the leaf to fruit ratio for the vines were relatively high. Therefore, yield increases in the kiwifruit vine depended on increasing the sink activity of the fruits so that assimilates were partitioned in favour of fruit growth.

Although it is known that the fruit size of a kiwifruit correlates with its seed number (Hopping, 1976), large variations in the relationship were reported. For example, the number of seeds required for a fruit to attain the minimum export size of 70 g ranged from 200 (Pyke and Alspach, 1986) to 1400 (Hopping and Hacking, 1983). The differences were often attributed to varying crop loads (Hopping and Hacking, 1983), or weather (Clinch, 1984) and shade (Grant and Ryugo, 1984a) conditions.

The results of this study show that apart from the presence of sufficient fruit seed numbers, factors relating to the pre-anthesis condition of the vine (chapter 4), and current vine management practices (chapters 7, 8), also had significant

influence on fruit development.

9.7 Effects of Pre-Anthesis Factors on Fruit Size

Larger fruits were developed from early flowers which were mostly carried on vigorous shoots (experiment 4A, 4B). The difference between early and late fruits was independent of fruit seed number (fig. 4.3, 4.7, 4.8). This was because significant differences between the size of the ovary of early and late flowers were already present at the beginning of fruit development (table 4.7).

The relationship between fruit size and fruit seed number often show a peculiar increase in fruit size when the seed number exceeded 1000 (eg. figures 4.5, 4.10; Hopping, 1976; McKay, 1976). It is likely that this was caused by the distribution of early fruits which not only contained higher seed numbers, but also had higher fruit weight per seed (fig. 4.7).

Fruits on long shoots were also larger than those on short shoots because of undefined factors associated with the vigour of the long shoot, which produced more viable seeds (experiment 4A, 4C). Such a relationship between fruit size and shoot vigour was also observed by McKay (1976). It suggests that the potential size of a fruit was already determined before

anthesis.

An understanding of the factors that control flowering and
the production of vigorous shoots within a vine is therefore
important. This may be related to the level of carbohydrate
resources on each cane which was available for growth during bud
break. For instance, shaded parts of a canopy carried smaller
fruits which developed from late flowers on weak, short shoots
(Grant and Ryugo, 1984a; McKay, 1976). Because of their low
photosynthetic production (Grant and Ryugo, 1984b), fruit growth
of shaded shoots must be supplied by considerable amounts of
assimilate translocated from exposed portions of the canopy.
Experiment 6B indicated that ^{14}C-assimilate can be transported
to fruits over considerable distances. However, in spite of the
available photosynthate shaded fruits often remained small. It
is therefore likely that the growth of shaded fruits was limited
to what was predetermined before anthesis.

Grant and Ryugo (1982) have shown that buds which break
earlier inhibited the flowering potential of later buds. The
probability that a bud may develop into a vigorous shoot, which
carried early flowers, may therefore depend on its ability to
compete with the other buds for growth.

In the orchard, it may be important to use appropriate
training and pruning techniques which enhance the production of
strong fruiting shoots. It may be possible to use plant growth
regulators to control vine growth. For instance, Henzell and

Briscoe (1986) reported recent investigations into the use of hydrogen cyanamide to advance bud break and compress the flowering period to 3-4 days, and showed that fruit yield was increased as a result of increases in floral bud break. They also pointed out that early shoot growth, as a consequence of advanced bud break, reduced vine vigour. This may then adversely affect renewal cane production and result in a decreasing proportion of vigorous fruiting shoots on a vine.

9.8 Leaf-Fruit Ratios

Carbohydrate reserves in the stem, which influenced bud break and floral initiation during spring growth, is assumed to depend on the leaf to fruit ratio of the kiwifruit vine in the previous season. A correct balance between the size of the leaf canopy and the crop load will not only ensure sufficient supplies of photosynthate for fruit growth, but also an adequate build up of reserves.

The minimum leaf to fruit ratio required to support only the growth of fruits lies between 0.83:1 (86 cm^2) to 1.7:1 (173 cm^2) (experiment 6A). However, Snelgar et.al. (1986) found that fruit size on girdled shoots can be saturated by increases of 30 g fresh weight for every unit increment of leaf-fruit ratio from 1:1 to 3:1. This again indicates that in some

situations there is a sink limited condition in the kiwifruit vine. It also means that fruits on normal, intact shoots can be significantly increased to their potential size, provided that there are ways to increase sink strength similar to that observed on girdled shoots.

For the entire vine, the minimum required leaf-fruit ratio is likely to exceed 1.7:1 since the growth of the other parts of the vine needs to be accounted for. It may also vary according to vine age and vigour, and environmental conditions such as shade. Snelgar et.al. (1986) observed a linear increase in fruit weight of 6.9 g for each unit increase in vine leaf-fruit ratio up to 5.5:1.

The usefulness of non-fruiting shoots as a source of assimilate was shown in chapter 6. It was also found that fruit growth was not likely to be limited by the translocation of assimilates between regions of carbohydrate surplus and demand, even at a distance. This then allows a degree of flexibility in summer pruning to suit different trellis designs, so that the overall leaf-fruit ratio of a vine can be maintained above the optimum level required to support fruit growth.

9.9 Leaf Inhibitory Effects on Fruit Growth

The removal of competing apical meristems on a fruiting shoot during summer pruning enhances fruit growth (Lay Yee and Pringle, in Davison, 1987). This study shows that at least on young vines, summer pruning should be aimed at reducing the level of a putative inhibitor which it is postulated, accumulates in the remaining leaves and moves down the fruiting shoot to suppress fruit growth (experiment 7A). Inhibitory effects of large leaf numbers from nearby vegetative shoots (experiment 6A) or shoot regrowths (experiment 8A) may also be important.

The leaf inhibitory effect was effective only during the early stage of fruit development and it was shown that a large leaf area may compensate for the initial reduction in fruit growth, provided fruits contained a large number of seeds (table 7.4). A balance between the level of the putative leaf inhibitor and growth hormones associated with seeds in the fruits probably existed. Thus small leaf numbers did not reduce fruit growth because of a reduction in the supply of the inhibitory substance, whereas fruits with large seed numbers have exceeded a threshold level of growth substances to overcome the leaf inhibitor.

Leaf inhibitory effects was also annulled by girdling treatments (experiment 8A). Again, this may be linked to the

interaction with hormones such as auxins, which probably accumulated above the girdle to promote fruit growth.

Chalmers and Van Den Ende (1975a) have postulated that signals from the root system of peach trees may limit vegetative growth. It was shown in chapter 7 that the strong leaf inhibitory effects which were observed in young kiwifruit vines (< 4 years) diminished on older vines (5-7 years). Perhaps stronger signals were transmitted to the leaves from the more vigorous roots on young vines. There is a possibility that in the orchard, significant leaf inhibitory effects may be present on older vines which have a renewed vigour for growth after they were severely winter pruned. Summer pruning may then have to be adjusted for these vines to reduce the inhibitory effect of large leaf numbers on fruit growth.

9.10 Interfruit Competition

The result of overcropping a kiwifruit vine has the immediate effect of producing undersized fruits because of increased competition for available nutrients (Burge, 1986; Davison and Sutton, 1984). In addition, high crop loads lead to the problem of alternate bearing (Davison, 1987). Hopping and Martyn (1986) reported that no amount of pollination will correct for the fruit size of vines with excessive loads. As

fruit drop does not normally occur in the kiwifruit, fruit numbers need to be thinned down to 1500 to 1600 per vine (Davison and Sutton, 1984; Hopping and Martyn, 1986).

The desired crop load of a vine may have to be adjusted according to the vine performance. The results of experiment 7A show that vines with poor performance consistently cropped smaller fruits. Figure 7.3 shows that differences in vine performance may also account for the wide discrepancies in the relationship between seed number and fruit size reported by different workers (Pyke and Alspach, 1986). Thus a poor vine in experiment 7A required more than 1000 seeds before fruits attained 100 g fresh weight, whereas only 580 seeds were needed on good vines. This was thought to be related to the root system which probably limited the supply of nutrients to supply top growth. Fruit size on these poor vines could perhaps be increased by reducing their crop loads to appropriate levels below the optimum for good vines.

This study shows that interfruit competition is not present when fruits on the same shoots have equal seed numbers, or sink activity. Each fruit developed in synchrony with the others (fig. 7.5), and final fruit sizes were similar (fig. 7.4). However, a fruit with lower seed number than adjacent fruits, had a reduced ability to compete for assimilates (experiment 4A). These fruits could perhaps be removed first when thinning is required.

Fruitlets that are unlikely to develop into export-sized fruits may also be removed. They included those from late flowers or weak, short shoots found in shaded parts of the vine (experiments 4B and 4C), as well as lateral fruits on doubles and triplets (Henzell and Briscoe, 1986). It is also desirable to thin out 'flats' and 'fans' as these fruits do not meet export standards.

CONCLUSION

This study shows that the kiwifruit vine had a high
potential for dry matter production. The strategy in the
orchard is to maximise vine photosynthesis so that crop yield
can be increased by directing photoassimilates towards fruit
growth. The important factors affecting photosynthesis included
temperature and light conditions such as imposed by windshelters
over the whole vine, or by different types of training systems
over different parts of the vine canopy.

It is desirable that the kiwifruit vine carry a maximum
crop load, appropriate to the size of the total photosynthetic
surface, such that sufficient supplies of assimilates are
available for fruit sizing and reserves. Under a sink-limited
condition, fruit sizing in the kiwifruit is not only dependent
on pollination, but also pre-anthesis effects, and the current
vine management practices.

The potential size of an individual fruit is partly
determined before anthesis. This may be linked to the
carbohydrate resource of the fruiting cane. Thus it was found
that fruiting shoots of strong vigour, which were mostly long
shoots, carried early flowers with bigger ovaries which
developed into bigger fruits. It may therefore be desirable to
have a higher proportion of vigorous fruiting shoots on the

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vine. This may be attained by laying down sufficient reserves from the previous season. Training systems which allow replacement canes to be positioned in exposed light conditions may also be advantageous. However, it is not known as to whether the problems associated with uneven bud-break have any influence on subsequent shoot development. Until there is a better understanding of the factors which cause buds to develop into shoots of different type and vigour, the control of pre-anthesis effects on fruit size by orchard management may be limited.

The effect of summer pruning is to alter the light levels within the vine canopy. The removal of shoot competition for assimilates, and the allowance of sufficient leaf area for fruit growth and reserves are also important. Although pruning systems are constrained by the different ways the vines are trained to different support structures, maximum use should be made of the flexibility in which assimilate can be translocated around the vine. A logical approach is to prune the fruiting shoot back to twice the number of leaves as fruits. This leaf-fruit ratio will ensure sufficient supplies of carbohydrate for the fruits, provided the leaves are not shaded. Leafy shoots can then be used to supply the balance of carbon which is required for vine growth and reserves. The amount of leafy shoots to be removed may have to be adjusted according to the carbohydrate demands for vine growth which changes with vine age

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and vigour. In addition, leaf inhibitory effects on fruit growth also decreased as a vine ages, but this may again be significant when vine vigour is renewed after incidences of severe winter pruning.

The need for efficient pollination remains the single, most important factor in fruit sizing. This study shows that fruits with high seed numbers are not likely to be limited by inhibitory effects on fruit growth. In this regard, important considerations should be given to the provision of an open canopy for either bee or artificial pollination in the design of training and pruning systems.

Finally, no amount of pollination can increase fruit size if a vine carries an excessive crop load. To correct for this condition, fruit numbers have to be reduced, and it may be important to thin during early fruit development, so that maximum growth in the remaining fruits on the vine can be achieved. However, skilled management of the vines will also allow heavy loads to be carried, as the reduction in fruit size of potentially large fruits need not decrease their size below the export standard of 70g.

BIBLIOGRAPHY

Abbott, D.L. (1960).
The bourse shoot as a factor in the growth of apple fruits.
Annals of Applied Biology 48(2):434-438.

Anon. (1981).
The DSIR Climate Laboratory. Alpha No. 14, DSIR Extension
Information, Science Information Division, DSIR, Wellington,
New Zealand. 4 p.

Armond, P.A., Schreiber U. and Björkmann O. (1978).
Photosynthetic acclimation to temperature in the desert shrub,
Larrea divaricata. II.Light·harvesting efficiency and
electron transport. Plant Physiology 61:411-415.

Avery, D.J. (1977).
Maximum photosynthetic rate - a case study in apple. New
Phytologist 78:55-63.

Avery, D.J., Priestley, C.A. and Treharne, K.J. (1979).
Integration of assimilation and carbohydrate utilization in
apple. In Photosynthesis and plant development. p.221-231.
Edited by Marcelle, R., Clijsters, H. and Van Poucke, M.
The Hague, Junk. 379p.

Bain, J.M. (1958).
Morphological, anatomical, and physiological changes in the
developing fruit of the Valencia orange,Citrus sinensis (L.)
Osbeck. Australian Journal of Botany 6:1-24. + 4 plates

Barden, J.A. (1971).
Factors affecting the determination of net photosynthesis of
apple leaves. HortScience 6(5):448-451.

Barden, J.A. (1974).
Net photosynthesis, dark respiration, specific leaf weight,
and growth of young apple trees as influenced by light
regime. Journal of the American Society for Horticultural
Science 99(6):547-551.

Barden, J.A. (1977).
Apple tree growth, net photosynthesis, dark respiration, and
specific leaf weight as affected by continuous and
intermittent shade. Journal of the American Society for
Horticultural Science 102(4):391-394.

Barrett, J.E. and Amling, H.J. (1978).
Effects of developing fruits on production and translocation of ^{14}C-labelled assimilates in cucumber. HortScience 13:545-547.

Berry, J. and Björkmann, O. (1980).
Photosynthetic response and adaptation to temperature in higher plants. Annual Review of Plant Physiology 31:491-543.

Bible, B.B. (1976).
Non-equivalence of left-handed and right-handed phyllotaxy in tomato and pepper. HortScience 11(6):601-602.

Biscoe, P.V. and Gallagher, J.N. (1977).
Weather, dry matter production and yield. In Environmental effects on crop physiology. p.75-100. Edited by Landsberg, J.J. and Cutting, C.V. London, Academic Press. 388p.

Björkmann, O. et al. (1974). see Addendum pg. 321.

Blomquist, R.V and Kust, C.A. (1971).
Translocation pattern of soybeans as affected by growth substances and maturity. Crop Science 11:390-393

Bollard, E.G. (1970).
The physiology and nutrition of developing fruits. In The biochemistry of fruits and their products. Volume 1. p.387-425. Edited by Hulme, A.C. London, Academic Press. 620p.

Brundell, D.J. (1975a).
Effect of defoliation, shading, and tipping of shoots on flower bud development and vegetative growth of Chinese gooseberry (Actinidia chinensis Planch.). New Zealand Journal of Agricultural Research 18:365-370.

Brundell, D.J. (1975b).
Quantitative aspects of flowering in the Chinese gooseberry (Actinidia chinensis Planch.). New Zealand Journal of Agricultural Research 18:371-374.

Brundell, D.J. (1975c).
Flower development of the Chinese gooseberry (Actinidia chinensis Planch.). II.Development of the flower bud. New Zealand Journal of Botany 13:485-496.

Brooking, I.R. (1976).
Soilless potting media for controlled-environment facilities. New Zealand Journal of Experimental Agriculture 4:203-208.

Burge, G.K. (1986).
   And more fruit, but not too many. New Zealand Kiwifruit.
   February 1986. p.29

Buwalda, J.G. (1986).
   And the big MAF carve-up. New Zealand Kiwifruit. March
   1986. p.26

Chalmers, D.J. (1985).
   Position as a factor in growth and development effects. In
   Hormonal regulation of development. III.Role of
   environmental factors. p.169-192. Edited by Pharis, R.P.
   and Reid, D.M. Encyclopedia of Plant Physiology. New
   Series. Volume 11. Springer-Verlag, Berlin. 887p.

Chalmers, D.J., Canterford, R.L., Jerie, P.H., Jones, T.R.
   and Ugalde, T.D. (1975).
   Photosynthesis in relation to growth and distribution of
   fruit in peach trees. Australian Journal of Plant Physiology
   2:635-645.

Chalmers, D.J. and van den Ende, B. (1975a).
   Productivity of peach trees: factors affecting dry-weight
   distribution during tree growth. Annals of Botany
   39:423-432.

Chalmers, D.J. and van den Ende, B. (1975b).
   A reappraisal of the growth and development of peach fruit.
   Australian Journal of Plant Physiology 2:623-634.

Chalmers, D.J. and van den Ende, B. (1977).
   The relation between seed and fruit development in the peach
   (Prunus persica L.). Annals of Botany 41:707-714. + / plate

Chalmers, D.J. and Wilson, I.B. (1978).
   Productivity of peach trees: tree growth and water stress in
   relation to fruit growth and assimilate demand. Annals of
   Botany 42:285-294.

Charles-Edwards, D.A. and Ludwig, L.J. (1975).
   The basis of expression of leaf photosynthetic activities.
   In Environmental and biological control of photosynthesis.
   p.37-44. Edited by Marcelle, R. The Hague, Junk. 408p.

Chauhan, P.S. and Pandey, R.M. (1984).
   Relative $^{14}CO_2$ fixation by leaves and fruits, and
   translocation of ^{14}C-sucrose in mango. Scientia
   Horticulturae 22:121-128.

Clinch, P.G. (1984).
  Kiwifruit pollination by honey bees. 1.Tauranga
  observations, 1978-81. New Zealand Journal of Experimental
  Agriculture 12:29-38.

Cook, M.G. and Evans, L.T. (1978).
  Effect of relative size and distance of competing sinks on
  the distribution of photosynthetic assimilates in wheat.
  Australian Journal of Plant Physiology 5:495-509.

Coombe, B.G. (1973).
  The regulation of set and development of the grape berry.
  Acta Horticulturae 34:261-273.

Coombe, B.G. (1976).
  The development of fleshy fruits. Annual Review of Plant
  Physiology 27:207-228.

Crane, J.C. (1964).
  Growth substances in fruit setting and development. Annual
  Review of Plant Physiology 15:303-326.

Crane, J.C. (1969).
  The role of hormones in fruit set and development HortScience
  4(2):108-111.

Crews, C.E., Williams, S.L. and Vines, H.M. (1975).
  Characteristics of photosynthesis in peach leaves. Planta
  126:97-104.

Dale, J.E. and Milthorpe, F.L. (1983).
  General features of the production and growth of leaves. In
  The growth and function of leaves. p.151-178. Edited by
Dale, J.E. and Milthorpe, F.L. Cambridge, University Press.
  540p.

Dann, I.R., Wildes, R.A. and Chalmers, D.J. (1984).
  Effects of limb girdling on growth and development of
  competing fruit and vegetative tissues of peach trees.
  Australian Journal of Plant Physiology 11:49-58.

Darron, G.M, and Schander (1941). see Addendum pg. 321.

Davis, J.T. and Sparks, D. (1974).
Assimilation and translocation patterns of carbon-14 in the shoot of fruiting pecan trees, Carya illinoensis Koch. Journal of the American Society for Horticultural Science 99:468-480.

Davison, R.M. (1980).
Girdling of young kiwifruit vines to increase cropping. The Orchardist of New Zealand. February 1980.(53)p:5,7.

Davison, R.M. (1987).
Physiology of the kiwifruit. In Kiwifruit: science, management and marketing. Edited by Weston, G.C. and Warrington, I.J. New Zealand Society for Horticultural Science. (In Press).

Davison, R.M. and Sutton, P.G. (1984).
Research shows thinning increases crops. New Zealand Kiwifruit. December 1984. p.15-16.

DeJong, T.M., Tombesi, A. and Ryugo, K. (1984).
Photosynthetic efficiency of Kiwi (Actinidia chinensis Planch.) in response to nitrogen deficiency. Photosynthetica 18(1):139-145.

Dempsey, W.H. and Boynton, J.E. (1965).
Effect of seed number on tomato fruit size and maturity. *Proceeding*Journal of the American Society for Horticultural Science 86:575-581.

Denne, M.P. (1960).
The growth of apple fruitlets, and the effect of early thinning on fruit development. Annals of Botany 24:397-406.

Denne, M.P. (1963).
Fruit development and some tree factors affecting it. New Zealand Journal of Botany 1:265-294.

Eagles, C.F. and Wareing, P.F. (1964).
The role of growth substances in the regulation of bud dormancy. Physiologia Plantarum 17:697-709.

Edwards, G.R. (1985).
Changes in endogenous hormones in apple during bud burst induced by defoliation. Acta Horticulturae 158:203-210.

Erickson, R.O. (1983).
   The geometry of phyllotaxis. In The growth and function of
   leaves. p.53-88. Edited by Dale, J.E. and Milthorpe, F.L.
   Cambridge, University Press. 540p.

Esau K. (1948).
   Phloem structure in the grapevine, and its seasonal changes.
   Hilgardia 18(5):217-296.

Evans, L.T., Wardlaw, I.F. and Williams, C.N. (1964).
   Environmental control of growth. In Grasses and grasslands.
   p.102-125. Edited by Barnard, C. MacMillan, London. 269p.

Farquhar, G.D. and Kirschbaum, M.U.F. (1985).
   Environmental constraints on carbon assimilation. In
   Regulation of sources and sinks in crop plants. p.87-97.
   British Plant Growth Regulator Group, monograph 12.

Ferguson, A.R. (1984).
   Kiwifruit: a botanical review. Horticultural Reviews
   6:1-64.

Ferguson, I.B. and Turner, N.A. (1981).
   Mobilization of macro-nutrients in cuttings of kiwifruit
   (Actinidia chinensis Planch.). Annals of Botany 47:229-237.

Ford, I. (1971).
   Chinese gooseberry pollination. New Zealand Journal of
   Agriculture 122(2):34-35.

Garcia-Papi, M.A. and Garcia-Martinez, J.L. (1984). Fruit
   set and development in seeded and seedless Clementine
   mandarin. Scientia Horticulturae 22:113-119.

Ghosh, S.P. (1973).
   Internal structure and photosynthetic activity of different
   leaves of apple. Journal of Horticultural Science 48:1-9.

Gifford, R.M. and Evans, L.T. (1981).
   Photosynthesis, carbon partitioning, and yield. Annual
   Review of Plant Physiology 32:485-509.

Goldschmidt, E.E. (1984).
   Endogenous abscisic acid and 2-trans-abscisic acid in
   alternate bearing 'Wilking' mandarin trees. Plant Growth
   Regulation 2:9-13.

304

Goodwin, P.B. (1978).
   Phytohormones and fruit growth. In Phytohormones and related
   compounds - a comprehensive treatise. Volume 2. p.175-214
   Edited by Letham, D.S., Goodwin, P.B. and Higgins, T.J.V.
   Elsevier/North-Holland, Biomedical Press. 648p.

Grant, J.A. and Ryugo, K. (1982).
   Influence of developing shoots on flowering potential of
   dormant buds of Actinidia chinensis. HortScience
   17(6):977-978.

Grant, J.A. and Ryugo, K. (1984a).
   Influence of within-canopy shading on fruit size, shoot
   growth, and return bloom in kiwifruit. Journal of the
   American Society for Horticultural Science 109(6):799-802.

Grant, J.A. and Ryugo, K. (1984b).
   Influence of within-canopy shading on net photosynthetic
   rate, stomatal conductance, and chlorophyll content of
   kiwifruit leaves. HortScience 19:834-836.

Greer, D.H., Laing, W.A. and Kipnis, T. (1987).
   Photoinhibition of photosynthesis in intact kiwifruit
   (Actinidia deliciosa) leaves. I.Effect of temperature. (In
   Prep).

Greer, D.H. and Laing, W.A. (1987).
   Photoinhibition of photosynthesis in intact kiwifruit
   (Actinidia deliciosa) leaves. II.Recovery and its dependence
   on temperature. (In Prep).

Griggs, W.H. and Iwakiri, B.T. (1956).
   A comparison of methods of obtaining growth curves of
   Bartlett pears. Proceedings of the American Society for
   Horticultural Science 67:91-94.

Gustafson, F.G. and Houghtaling ₙ.ᵦ. (1939)
   Relation between fruit size and food supply in the tomato.
   Plant Physiology 14:321-332.

Gustafson, F.G. and Stoldt, E. (1936).
   Some relations between leaf area and fruit size in tomatoes.
   Plant Physiology 11:445-451.

Hackett, W.P. (1985).
   Juvenility, maturation, and rejuvenation in woody plants.
   Horticultural Reviews 7:109-155.

Harman, J.E. (1981).
  Kiwifruit maturity. The Orchardist of New Zealand. May
  1981 (54)6:126-130.
          127,

Hale, C.R. and Weaver, R.J. (1962).
  The effect of developmental stage on direction of
  translocation of photosynthate in Vitis vinifera. Hilgardia
  33:89-131.

Haller, M.H. and Magness, J.R. (1925).
  The relation of leaf area to the growth and composition of
  apples. Proceedings of the American Society for
  Horticultural Science 22:189-196

Hansen, P. (1967a).
  ^{14}C-studies on apple trees. I.The effect of the fruit on the
  translocation and distribution of photosynthates.
  Physiologia Plantarum 20:382-391.

Hansen, P. (1967b).
  ^{14}C-studies on apple trees. II.Distribution of
  photosynthates from top and base leaves from extension
  shoots. Physiologia Plantarum 20:720-725.

Hansen, P. (1967c).
  ^{14}C-studies on apple trees. III.The influence of season on
  storage and mobilization of labelled compounds. Physiologia
  Plantarum 20:1103-1111.

Hansen, P. (1969).
  ^{14}C-studies on apple trees. IV.Photosynthate consumption in
  fruits in relation to the leaf-fruit ratio and to the
  leaf-fruit position. Physiologia Plantarum 22:186-198.

Hansen, P. (1970a).
  ^{14}C-studies on apple trees. V.Translocation of labelled
  compounds from leaves to fruit and their conversion within
  the fruit. Physiologia Plantarum 23:564-573.

Hansen, P. (1970b).
  ^{14}C-studies on apple trees. VI.The influence of the fruit on
  the photosynthesis of the leaves, and the relative
  photosynthetic yields of fruits and leaves. Physiologia
  Plantarum 23:805-810.

Hansen, P. (1971).
^{14}C-studies on apple trees. VII.The early seasonal growth in leaves, flowers and shoots as dependent upon current photosynthates and existing reserves. Physiologia Plantarum 25:469-473.

Hansen, P. (1977).
Carbohydrate allocation. In Environmental effects of crop physiology. p.247-258. Edited by Landsberg, J.J. and Cuttings, C.V. Academic Press, London. 388p.

Hansen, P. and Christensen, J.V. (1974).
Fruit thinning. III.Translocation of ^{14}C assimilates to fruit from near and distant leaves in the apple 'Golden Delicious'. Horticultural Research 14:41-45.

Hansen, P. and Grauslund, J. (1973).
^{14}C-studies on apple trees. VIII.The seasonal variation and nature of reserves. Physiologia Plantarum 28:24-32.

Hansen, P. and Ryugo, K. (1979).
Translocation and metabolism of carbohydrate fraction of ^{14}C-photosynthates in 'French' prune, Prunus domestica L. Journal of the American Society for Horticultural Science 104(5):622-625.

Hardacre, A.K., Nicholson, H.F. and Boyce, M.L.P. (1984).
A portable photometer for the measurement of chlorophyll in intact leaves. New Zealand Journal of Experimental Agriculture 12:357-362.

Haslemore, R.M., Warrington, I.J. and Roughan, P.G. (1980).
Influence of drying method and post-harvest conditions on total nitrogen, soluble sugar, and starch levels in plant tissue. New Zealand Journal of Agricultural Research 23:355-359.

Havis, A.L. (1962).
Effects of time of fruit thinning of Redhaven peach. Proceedings of the American Society for Horticultural Science 80:172-176.

Henzell, R.F. and Briscoe, M.R. (1986).
Hydrogen cyanamide: a tool for consistently high kiwifruit production. New Zealand Kiwifruit. New Zealand Kiwifruit Authority Conference 1986. p.8-11.

Hilgeman, R.H., Dunlap, J.A. and Sharples, G.C. (1967).
   Effect of time of harvest of Valencia oranges on leaf
   carbohydrate content and subsequent set of fruit.
   Proceedings of the American Society for Horticultural Science
   90:110-116.

Ho, L.C. (1979a).
   Regulation of assimilate translocation between leaves and
   fruits in the tomato. Annals of Botany 43:437-448.

Ho, L.C. (1979b).
   Partitioning of ^{14}C-assimilate within individual tomato
   leaves in relation to the rate of export. In Photosynthesis
   and plant development. p.243-250. Edited by Marcelle, R.,
   Clijsters, H. and Van Poucke, M. The Hague, Junk. 379p.

Ho, L.C., Sjut, V. and Hoad, G.V. (1982).
   The effect of assimilate supply on fruit growth and hormone
   levels in tomato plants. Plant Growth Regulation
   1(3):155-171.

Ho, L.C. et al. (1984) see Addendum pg.321.

Hopping, M.E. (1976).
   Structure and development of fruit and seeds in Chinese
   gooseberry (Actinidia chinensis Planch.). New Zealand
   Journal of Botany 14:63-68.

Hopping, M.E. and Hacking, N.J.A. (1983).
   A comparison of pollen application methods for the artificial
   pollination of kiwifruit. Acta Horticulturae 139:41-50

Hopping, M.E. and Martyn, J.A.K. (1986).
   Spray pollination of kiwifruit. New Zealand Kiwifruit. New
   Zealand Kiwifruit Authority Conference 1986. p.6-8.

Hughes, D.L., Bosland, J. and Yamaguchi, M. (1983).
   Movement of photosynthates in muskmelon plants. Journal of
   the American Society for Horticultural Science
   108(2):189-192.

Jackson, D.I. and Coombe, B.G. (1966).
   The growth of apricot fruit. I.Morphological changes during
   development and the effects of various tree factors.
   Australian Journal of Agricultural Research 17:465-477.

Jackson, J.E. and Hamer, P.J.C. (1980).
   The causes of year-to-year variation in the average yield of
   Cox's Orange Pippin apple in England. Journal of
   Horticultural Science 55(2):149-156.

Jahn, O.L. (1978).
  Fruiting and twig diameter in citrus. <u>American Journal of</u>
  <u>Botany</u> 65(9):1032-1034.

Khan, A.A. and Sagar, G.R. (1966).
  Distribution of ^{14}C-labelled products of photosynthesis
  during the commercial life of the tomato crop. <u>Annals of</u>
  <u>Botany</u> 30:727-743.

Khan, A. and Sagar, G.R. (1969).
  Alteration of the pattern of distribution of photosynthetic
  products in the tomato by manipulation of the plant. <u>Annals</u>
  <u>of Botany</u> 33:753-762.

Koch, K.E. (1984).
  Translocation of photosynthetic products from source leaves
  to aligned juice segments in citrus fruit. <u>HortScience</u>
  19(2):260-261.

Kozlowski, T.T. (1968).
  Diurnal changes in diameters of fruits and tree stems of
  Montmorency cherry. <u>Journal of Horticultural Science</u>
  43:1-15.

Kozlowski, T.T. and Keller, T. (1966).
  Food relations of woody plants. <u>Botanical Review</u>
  32(4):293-382.

Kriedemann, P.E. (1968a).
  [14]C translocation patterns in peach and apricot shoots.
  <u>Australian Journal of Agricultural Research</u> 19:775-780.

Kriedemann, P.E. (1968b).
  Some photosynthetic characteristics of citrus leaves.
  <u>Australian Journal of Biological Science</u> 21:895-905.

Kriedemann, P.E. (1968c).
  Observations on gas exchange in the developing sultana berry
  <u>Australian Journal of Biological Science</u> 21:907-916.

Kriedemann, P.E. (1969a).
  [14]C distribution in lemon plants. <u>Journal of Horticultural</u>
  <u>Science</u> 44:273-279.

Kriedemann, P.E. (1969b).
  [14]C translocation in orange plants. <u>Australian Journal of</u>
  <u>Agricultural Research</u> 20:291-300.

Kriedemann, P.E. and Canterford, R.L. (1971).
  The photosynthetic activity of pear leaves (Pyrus communis
  L.). Australian Journal of Biological Science 24:197-205.

Kriedemann, P.E. and Smart, R.E. (1971).
  Effects of irradiance, temperature, and leaf water potential
  on photosynthesis of vine leaves. Photosynthetica 5(1):6-15.

Kuraishi, S. and Muir, R.M. (1962).
  Increase in diffusible auxin after treatment with giberellin.
  Science 137:7650-7651.

Laing, W.A. (1985).
  Temperature and light response curves for photosynthesis in
  kiwifruit (Actinidia chinensis) cv.Hayward . New Zealand
  Journal of Agricultural Research 28:117-124.

Lakso, A.N. (1984).
  Leaf area development patterns in young pruned and unpruned
  apple trees. Journal of the American Society for
  Horticultural Science 109(6):861-865.

Lakso, A.N. and Seeley, E.J. (1978).
  Environmentally induced responses of apple tree
  photosynthesis. HortScience 13(6):646-650.

Larson, P.R. (1975).
  Development and organization of the primary vascular system
  in Populus deltoides according to phyllotaxy. American
  Journal of Botany 62:1084-1099.

Larson, P.R. (1977).
  Phyllotactic transitions in the vascular system of Populus
  deltoids Bartr. as determined by ^{14}C labelling. Planta
  134:241-249.

Larson, P.R. (1979).
  Establishment of the vascular system in seedlings of Populus
  deltoides Bartr. American Journal of Botany 66:452-462.

Larson, P.R. (1980).
  Interrelations between phyllotaxis, leaf development and the
  primary- secondary vascular transition in Populus deltoides.
  Annals of Botany 46:757-769.

310

Larson, P.R. (1983).
Primary vascularization and the siting of primordia. In The growth and function of leaves. p.25-51. Edited by Dale, J.E. and Milthorpe, F. Cambridge, University Press. 540p.

Larson, P.R. and Dickson, R.E. (1973).
Distribution of imported ^{14}C in developing leaves of eastern cottonwood according to phyllotaxy. Planta 111:95-112.

Lavee, S. (1960).
Effect of gibberellic acid on seeded grapes. Nature 185:395.

Lees, H.M.N. (1982).
Kiwifruit (Actinidia chinensis) Hayward variety: increases in fruit size from March to June, during three seasons. The Orchardist of New Zealand. April 1982. p.72-73,75.

Lee, T.D. (1984).
Patterns of fruit maturation: a gametophyte competition hypothesis. The American Naturalist 123(3):427-432.

Lee, T.D. and Bazzaz, F.A. (1982).
Regulation of fruit maturation pattern in an annual legume, Cassia fasciculata. Ecology 63:1374-1388.

Lenz, F. (1979).
Fruit effects on photosynthesis, light- and dark-respiration. In Photosynthesis and plant development. p.271-281. Edited by Marcelle, R., Clijsters, H. and Van Poucke, M. The Hague, Junk. 379p.

Leopold, A.C. and Kriedemann, P.E. (1975).
Plant growth and development. 2nd edition. New York, McGraw Hill. 545p.

Llewelyn, F.W.M. (1968).
The effect of partial defoliation at different times in the season on fruit drop and shoot growth in Lord Lambourne apple trees. Journal of Horticultural Science 43:519-526.

Loomis, N.H. (1949).
The effect of pinching off the terminals on yield and cane growth of Champanel grapes. Proceedings of the American Society for Horticultural Science 54:181-182.

Luckwill, L.C. (1939).
On the factors affecting the mean seed weight of tomato fruits. New Phytologist 38:181-189.

Luckwill, L.C. (1968).
  The effect of certain growth regulators on growth and apical
  dominance of young apple trees. Journal of Horticultural
  Science 43:91-101.

Luckwill, L.C. (1970).
  The control of growth and fruitfulness of apple trees. In
  Physiology of tree crops p.237-254. Edited by Luckwill, L.C.
  and Cutting, C.V. Academic Press, London. 382p.

Ludlow, M.M. and Wilson, G.L. (1971).
  Photosynthesis of tropical pasture plants. II.Temperature
  and illuminance history. Australian Journal of Biological
  Science 24:1065-1075.

Magness, J.R. (1928).
  Relation of leaf area to size and quality in apples.
  Proceedings of the American Society for Horticultural Science
  25:285-288.

Magness, J.R. and Overley, F.L. (1929).
  Relation of leaf area to size and quality of apples and
  pears. Proceedings of the American Society for Horticultural
  Science 26:160-62.

Mann, L.K. (1943).
  Fruit shape of watermelon as affected by placement of pollen
  on stigma. Botanical Gazette 105:257-262.

Martin, D., Lewis, T.L. and Cerny, J. (1964).
  Apple fruit cell numbers in relation to cropping alternation
  and certain treatments. Australian Journal of Agricultural
  Research 15:905-919.

Maun, M.A. and Cavers, P.B. (1971).
  Seed production and dormancy in Rumex crispus. II.The
  effects of removal of various proportions of flowers at
  anthesis. Canadian Journal of Botany 49:1841-1848

McAneney, K.J., Judd, M.J. and Trought, M.C.T. (1984).
  Wind damage to kiwifruit (Actinidia chinensis Planch.) in
  relation to windbreak performance. New Zealand Journal of
  Agricultural Research 27:255-263.

McKay, S A. (1976).
  Pollination and other factors affecting fruit-set and size of
  kiwifruits Thesis, M.Sc., University of California, Davis.
  114p.

McPherson, H.G., Green, A.E. and Rollison, P.L. (1983).
The measurement, within seconds, of apparent photosynthetic
rates using a portable instrument. Photosynthetica
17(3):395-406.

Meier, H. and Reid, J.S.G. (1982).
Reserve polysaccharides other than starch in higher plants.
In Plant carbohydrates. I.Intracellular carbohydrates.
p.418-471. Edited by Loewus, F.A. and Tanner, W.
Encylclopedia of Plant Physiology. New Series. Volume 13A.
Springer-Verlag, Berlin. 918p.

Monteith, J.L. and Elston, J.F. (1971).
Micro-climatology and crop production. In Potential crop
production. p.23-42. Edited by Wareing, P.F. and Cooper,
J.P. Heinemann, London. 387p.

Mooney, H.A. (1972).
The carbon balance of plants. Annual Review of Ecology and
Systematics 3:315-346.

Moreshet, S., Stanhill, G. and Fuchs, M. (1975). Aluminium
mulch increases quality and yield of 'Orleans' apples.
HortScience 10:390-391.

Morgan, D.C., Stanley, C.J. and Warrington, I.J. (1985).
The effects of simulated daylight and shade-light on
vegetative and reproductive growth in kiwifruit and
grapevine. Journal of Horticultural Science 60(4):473-484.

Morgan, D.C., Warrington, I.J. and Halligan, E.A. (1985).
Effect of temperature and photosynthetic photon flux density
on vegetative growth of kiwifruit (Actinidia chinensis). New
Zealand Journal of Agricultural Research 28:109-116.

Mulligan, P. (1986). MAF orchard monitoring. New Zealand
Kiwifruit. New Zealand Kiwifruit Authority Conference 1986.
p.5-6.

Murray, B.J., Mauk, C. and Nooden, L.D. (1982).
Restricted vascular pipelines (and orthostichies) in plants.
What's New in Plant Physiology 13(9):33-35.

Neales, T.F. and Incoll, L.D. (1968).
The control of leaf photosynthesis rate by the level of
assimilate concentration in the leaf: a review of the
hypothesis. Botanical Review 34:107-125.

Nii, N. (1980).
Seasonal changes in growth and enlargement of the Japanese
pear fruit, Pyrus serotina cv Shinsheiki, in relation to
vascular bundle development in the pedicel and flesh.
Journal of Horticultural Science 55(4):385-396.

Nitsch, J.P. (1950).
Growth and morphogenesis of the strawberry as related to
auxin. American Journal of Botany 37:211-215.

Nitsch, J.P. (1970).
Hormonal factors in growth and development. p.427-472. In
The biochemisty of fruits and their products. Volume I.
Edited by Hulme, A.C. London, Academic Press. 620p.

Nitsch, J.P. (1971).
Perennation through seeds and other structures: fruit
development. In Plant Physiology, A Treatise. Volume VIA.
p.413-501. Edited by Steward, F.C. New York, Academic
Press. 541p.

Nobel, P.S. (1980).
Leaf anatomy and water use efficiency. In Adaption of plants
to water and high temperature stress. p.43-55. Edited by
Turner,N.C. and Kramer, P.J. Wiley, New York. 482p.

Noel, A.R.A. (1970).
The girdled tree. Botanical Review 36:162-195.

Nooden, L.D., Rupp, D.C. and Derman, B.D. (1978).
Separation of seed development from monocarpic senescence in
soybeans. Nature 271:354-357.

Olmo, H.P. (1946).
Correlations between seed and berry development in some
seeded varieties of Vitis vinifera. Proceedings of the
American Society for Horticultural Science 48:291-297.

Osmond, C.B., Bjorkmann, O. and Anderson, D.J. (1980).
Physiological processes in plant ecology. Ecological studies
no 36. Springer-Verlag, Berlin. 486p.

Pate, J.S. and Farrington, P. (1981).
Fruit set in Lupinus angustifolius cv.Unicrop. II.Assimilate
flow during flowering and early fruiting. Australian Journal
of Plant Physiology 8:307-318.

Patterson, D.T. (1980).
Light and temperature adaptation. In Predicting
photosynthesis for ecosystem models. Volume 2. p.205-235.
Edited by Hesketh, J.D. and Jones, J.W. Boca Raton-Florida,
CRC Press.

Patterson, M.S. and Greene, R.C. (1965).
Measurement of low energy beta-emitters in aqueous solution
by liquid scintillation counting of emulsions. Analytical
Chemistry 37(7):854-857.

Pearson, J.A. and Robertson, R.N. (1953).
The physiology of growth in apple fruits. IV.Seasonal
variation in cell size, nitrogen metabolism, and respiration
in developing Granny Smith apple fruits. Australian Journal
of Biological Science 6:1-20.

Possingham, J.V. (1970).
Aspects of the physiology of grape vines. In Physiology of
tree crops. p.335-349. Edited by Luckwill, L.C. and
Cutting, C.V. London, Academic Press. 382p.

Prakash, S. and Ram, S. (1984).
Naturally occurring auxins and inhibitor and their role in
fruit growth and drop of mango 'Dashehari'. Scientia
Horticulturae 22:241-248.

Pratt, H.K. and Reid, M.S. (1976).
Chinese Gooseberry: seasonal patterns in fruit growth and
maturation, ripening, respiration and the role of ethylene.
Journal of the Science of Food and Agriculture 25:747-757.

Priestley, C.A. (1976b).
Some effects of ringing and deblossoming branches of young
apple trees on leaf composition. Journal of Experimental
Botany 27:1325-1332.

Priestley, C.A. (1976a).
Some effects of ringing branches on the distribution of dry
matter in young apple trees. Journal of Experimental Botany
27:1313-1324.

Pulawska, Z. (1965).
Correlations in the development of the leaves and leaf traces
in the shoot of Actinidia arguta Planch. Acta Societatis
Botanicorum Poloniae 34(4):697-712.

Pyke, N.B. and Alspach, P.A. (1986).
Inter-relationships of fruit weight, seed number and seed
weight in kiwifruit. New Zealand Agricultural Science
20:153-156.

Quinlan, J.D. and Preston, A.P. (1971).
The influence of shoot competition on fruit retention and
cropping of apple trees. Journal of Horticultural Science
46:525-534.

Quinlan, J.D. and Weaver, R.J. (1970).
Modification of pattern of the photosynthate movement within
and between shoots of Vitis vinifera L. Plant Physiology
46:527-530.

Raschke, K. (1979).
Movements of stomata. In Physiology of movements.
p.383-441. Edited by Haupt, W. and Feinleib, M.E.
Encyclopedia of Plant Physiology. New Series. Volume 7.
Springer-Verlag, Berlin. 731p.

Raven, J.A. and Rubery, P.H. (1982).
Coordination of development: hormone receptors, hormone
action and hormone transport. In The molecular biology of
plant development. p.28-48. Edited by Grierson, D. and
Smith, H. Oxford, Blackwell. 617p.

Rawson, H.M. and Evans, L.T. (1971).
The contribution of stem reserves to grain development in a
range of wheat cultivars of different height. Australian
Journal of Agricultural Research 22:851-863.

Redgwell, R.J. (1983).
Composition of Actinidia mucilage. Phytochemistry
22(4):951-956.

316

Richards, F.J. (1948).
  The geometry of phyllotaxis and its origin. Symposia of the
  Society for Experimental Biology 2:217-245.

Roach, W.A. (1939).
  Plant injection as a physiological method. Annals of Botany
  3:155-226. + 1 plate.

Sale, P.R. (1980).
  Kiwifruit culture. New Zealand Ministry of Agriculture and
  Fisheries Bulletin no.349. 65p.

Sale, P.R. (1981).
  Kiwifruit pollination: male to female ratios and bee
  activity. New Zealand Ministry of Agriculture and Fisheries
  AgLink HPP 233.

Sale, P.R. and Lyford, P.B. (1987).
  Cultural and management practices. In Kiwifruit: science,
  management, and marketing. Edited by Weston,G.C. and
  Warrington, I.J. New Zealand Society for Horticultural
  Science. (In press).

Sastry, K.K.S. and Muir, R.M. (1963).
  Gibberellin: effect on diffusible auxin in fruit
  development. Science 140:494-495.

Satoh, M., Kriedemann, P.E. and Loveys, B.R. (1977).
  Changes in photosynthetic activity and related processes
  following decapitation in mulberry trees. Physiologia
  Plantarum 41:203-210.

Sauer, M.R. (1954).
  Flowering in the sweet orange. Australian Journal of
  Agricultural Research 5:649-657.

Schapendonk, A.H.C.M. and Brouwer, P. (1984).
  Fruit growth of cucumber in relation to assimilate supply and
  sink activity. Scientia Horticulturae 23:21-33.

Schneider, G.W. (1977).
  Studies on the mechanism of fruit abscission in apple and
  peach. Journal of the American Society for Horticultural
  Science 102:179-181.

Seeley, E.J. and Kammereck, R. (1977a).
Carbon flux in apple trees: use of a closed system to study the effect of a mild cold stress on 'Golden Delicious'. Journal of the American Society for Horticultural Science 102(3):282-286.

Seeley, E.J. and Kammereck, R. (1977b).
Carbon flux in apple trees: the effects of temperature and light intensity on photosynthetic rates. Journal of the American Society for Horticultural Science 102(6):731-733.

Seth, A. and Wareing, P.F. (1964).
Interaction between auxins, gibberellins and kinins in hormone-directed transport. Life Science 3:1483-1486.

Setter, T.L., Brun, W.A. and Brenner, M.L. (1980).
Effect of obstructed translocation on leaf abscisic acid, and associated stomatal closure and photosynthesis decline. Plant Physiology 65:1111-1115.

Sharkey, T.D. (1985).
Photosynthesis in intact leaves of C_3 plants: physics, physiology and rate limitations. Botanical Review 51(1):53-105.

Shimshi, D. (1969).
A rapid field method for measuring photosynthesis with labelled carbon dioxide. Journal of Experimental Botany 20:381-340!

Simmonds, N.W. (1953).
The development of the banana fruit. Journal of Experimental Botany 4:87-105.

Singh, B.K. and Pandey, R.K. (1980).
Production and distribution of assimilate in chickpea (Cicer arietinum. L.) Australian Journal of Plant Physiology 7:727-735.

Singh, M,, Ogren, W.L. and Widholm, J.M. (1974).
Photosynthetic characteristics of several C_3 and C_4 plant species grown under different light intensities. Crop Science 14:563-566.

Skene, K.G.M. (1969).
A comparison of the effects of 'Cycocel' and tipping on fruit
set in Vitis vinifera L. Australian Journal of Biological
Science 22:1305-1311.

Skene, K.G.M. (1972).
The effect of ringing on cytokinin activity in shoots of the
grape vine. Journal of Experimental Botany 23(76):768-774.

Smith, G.S., Clark, C.J. and Bulwalda, J.G. (1986).
Seasonal accumulation of nutrients. New Zealand Kiwifruit.
New Zealand Kiwifruit Authority Conference 1986. p.19-22.

Snelgar, W.P. (1986).
Shade and temperature responses. New Zealand Kiwifruit. New
Zealand Kiwifruit Authority Conference 1986. p.14-15.

Snelgar, W.P., Thorp, T.G. and Patterson, K.J. (1986).
Optimal leaf:fruit ratios for fruit growth in kiwifruit.
Acta Horticulturae 175:115-120.

Snowball, A.E. (1986).
Flower development and shoot growth. New Zealand Kiwifruit.
July 1986. p.20.

Spriggs, T.W. (1986).
Curve fitting with constrained b-splines. Plant Physiology
Division, DSIR, Technical report no.23. 30p.

Stephenson, A.G. (1981).
Flower and fruit abortion: proximate causes and ultimate
functions. Annual Review of Ecology and Systematics
12:253-279.

Taylor, T. and Woodfield, J. (1986).
Potassium sprays speed leaf fall. New Zealand Kiwifruit.
March 1986. p12.

Terry, N., Waldron, L.J. and Taylor, S.E. (1983).
Environmental influences on leaf expansion. In The growth
and function of leaves. p.179-205. Edited by Dale, J.E.
and Milthorpe, F.L. Cambridge, University Press. 540p.

Thrower, S.L. (1962).
Translocation of labelled assimilates in the soybean. II.The
pattern of translocation in intact and defoliated plants.
Australian Journal of Biological Science 15:629-649.

Walker, A.J. and Ho, L.C. (1977a).
Carbon translocation in the tomato: carbon import and fruit growth. Annals of Botany 41:813-823.

Walker, A.J. and Ho, L.C. (1977b).
Carbon translocation in the tomato: effects of fruit temperature on carbon metabolism and the rate of translocation. Annals of Botany 41:825-832.

Wardlaw, I.F. (1968).
The control and pattern of movement of carbohydrates in plants. Botanical Review 34:79-105.

Wardlaw, I.F. (1985).
The regulation of photosynthetic rate by sink demand. p.145-162. In Regulation of sources and sinks in crop plants. British Plant Growth Regulator Group, Monograph 12.

Wareing, P.F. (1970).
Growth and its co-ordination in trees. In Physiology of tree crops. p.1-21. Edited by Luckwill, L.C. and Cutting, C.V. Academic Press, London. 382p.

Wareing, P.F. (1977).
Growth substances and integration in the whole plant. Symposia of the Society for Experimental Biology 31:337-365.

Wareing, P.F. (1979).
Plant development and crop yield. In Photosynthesis and plant development. p.1-17. Edited by Marcelle, R., Clijsters, H. and Van Poucke, M. The Hague, Junk. 379p.

Wareing, P.F. and Patrick, J. (1975).
Source-sink relations and the partition of assimilates in the plant. p.481-499. In Photosynthesis and productivity in different environments. Edited by Cooper, J.P. Cambridge, University Press. 715p.

Warrington, I.J. and Stanley, C.J. (1986).
The influence of pre- and post-budbreak temperatures on flowering in kiwifruit. Acta Horticulturae 175:103-107.

Warren-Wilson, J. (1972). see Addendum pg. 321.

Watson, M.A. and Casper, B.B. (1984).
   Morphogenetic constraints on patterns of carbon distribution
   in plants. Annual Review of Ecology and Systematics
   15:233-258.

Watson, R.L., Landsberg, J.J. and Thorpe, M.R. (1978).
   Photosynthetic characteristics of the leaves of 'Golden
   Delicious' apple trees. Plant, Cell and Environment 1:51-58.

Weinberger, J.H. (1931).
   The relation of leaf area to size and quality of peaches.
   Proceedings of the American Society for Horticultural Science
   28:18-22.

Weinberger, J.H. and Cullinan.F.P.(1932).
   Further studies on the relation between leaf area and size of
   fruit, chemical composition, and fruit bud formation in
   Elberta peaches. Proceedings of the American Society for
   Horticultural Science 29:23-27.

Williams, G.J.Ⅲ (1974).
   Photosynthetic adaptation to temperature in C_3 and C_4
   grasses: a possible role in the ~~short-grass~~ prairie. Plant
   Physiology 54:709-711.   *Shortgrass*

Wyatt, R. (1982).
   Inflorescence architecture: how flower number, arrangement,
   and phenology affect pollination and fruit set. American
   Journal of Botany 69(4):585-594.

Zelitch, I. (1982).
   The close relationship between net photosynthesis and crop
   yield. Bioscience 32:796-802.

ADDENDUM
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Bjorkmann, O., Troughton, J.H., and Nobs, M (1974).
   Photosynthesis in relation to leaf structure. In: Basic mechanisms in
   plant morphogenesis. Brookhaven Symposia in Biology. No. 25: p. 206-226.
   New York: Brookhaven National Laboratory.

Darron, G.M. and Schander (1941).
   Seed size in blueberry and related species. Proceedings of the American
   Society for Horticultural Science 38:439-440.

Ho, L.C., Bangerth, F., Ebert, A., Flore, J.A., Gifford, R.M., Hoad, G.V.
   and Sjut, V. (1984). Factors affecting final size of fruits.
   p. 45-50. Glasshouse Crops Research Institute Annual Report for 1982.

Warren-Wilson, J. (1972).
   Control of crop processes . In: Crop Processes in Controlled Environments.
   p. 7-30. Rees, A.R., Cockshull, K.E., Hurd, D.W. and Hard, R.G. (eds).
   Academic Press, London and New York.