GROWTH IN THE FIELD AND CO_2 EXCHANGE CHARACTERISTICS IN RELATION TO TEMPERATURE OF YOUNG ASPARAGUS

(*Asparagus Officinalis* L.)

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ABSTRACT

Studies on asparagus plants were conducted in the field and in growth rooms during 1990 to 1992. The field experiment was carried out to study the growth and development of young asparagus using successional plantings, from September to March, with two commonly grown cultivars, namely UC157 and Jersey Giant. The growth room study was divided into three separate experiments with the following four cultivars: UC157, Brocks, Tainan 1 and Larac. The first experiment studied the effects of high temperatures (30/20, 35/25 and 40/30^{0}C) on the ontogenetic changes of photosynthesis, the second the effects of temperatures (20/20, 25/25, 30/20, 35/15 and 40/20^{0}C) on plant respiration and AC_i curve. The final experiment examined the effects of high temperatures (20/20, 25/25, 30/20, 35/15 and 40/20^{0}C) on the light response curve.

In the field experiment, a logistic model based on a heat unit time scale was used to describe changes in total, crown and shoot dry weight. The curves showed that the earlier plantings resulted in larger plants at the end of the season. UC157 performed best from the September planting, while Jersey Giant suffered from low temperatures resulting in the differences between the September and October plantings being marginal. In addition, plant dry weight at the final harvest (autumn) decreased as the planting date was delayed. Planting later than October resulted in inferior plant quality based on carbohydrate storage and shoot, bud and root numbers criteria. In general the effect of treatment was carried over into the spring. A sharp decrease in total plant RGR late in the season was due, in particular, to the fall in shoot RGR. The fall in the shoot RGR was greater than the fall in crown RGR.

The shoot to root dry weight ratio in the first season increased up until February and then decreased regardless of planting date and cultivar. The allometric relationship between shoot and crown dry weight showed a similar trend. It was suggested that the change in the ratio and in the allometric relationship was due to a seasonal factor, probably temperature. In early spring of the second season the ratio increased for a short period of time and then decreased or stabilised.

Shoot, bud and root production increased exponentially for earlier plantings, particularly for UC157. UC157 had a higher number of these three plant parts than Jersey Giant. However, Jersey Giant had larger shoots, buds and roots as the total dry weights of these organs were not different to UC157.

The bud to shoot number ratio increased as the season progressed suggesting that shoot growth predominated over bud production during early growth. Meanwhile the cumulative shoot plus bud to root number ratio was high and similar for all plantings during early growth suggesting that young plants gave priority to shoot and bud development. The ratio then decreased sharply before stabilising late in the season. At the final harvest the cumulative shoot plus bud was supported by about two roots for the early plantings.

The CO_2 exchange studies of asparagus seedlings found that maximum photosynthesis was achieved on fern of an intermediate age regardless of cultivars. Photosynthesis of young and mature ferns was similar. Photosynthesis decreased as temperature increased from 20 to 40^{0}C. Brocks had a lower photosynthesis at 20/20^{0}C compared to Tainan 1 and Larac, while at high temperatures both Brocks and UC157 had a higher photosynthetic rate than Tainan 1 and Larac.

Shoot and crown dark respiration all increased with temperature but the Q_{10} was low. The low Q_{10} of crown respiration was possibly due to low oxygen availability and the capacity of storage roots to conserve storage carbohydrate.

The fern photorespiration and dark respiration also increased with temperature, but at 40/20^{0}C the photorespiration rate decreased. The decrease suggests that photorespiratory enzymes are labile to temperature compared to dark respiratory enzymes. There was a trend for Brocks to have a higher photorespiration rate compared to Tainan 1 and Larac at 20/20^{0}C, while at 35/15^{0}C the photorespiration rate of Brocks was lower compared to the other cultivars.

The CO_2 compensation point (Γ) increased as the temperature increased. The increase was mainly due to photorespiration but at 40^0C dark respiration made a more significant contribution.

The carboxylation efficiency (CE) was the major limitation at low temperature but as temperature increased stomatal limitation (lg) became an important factor. The increase in lg was possibly due to the effect of a high VPD.

Mature fern photosynthesis responded biphasically to increasing light intensities. The only difference in the light response curve between cultivars was at $35/15^0$C, where Brocks had a higher rate of photosynthesis than other cultivars at light intensities ranging from 300 to 750 μmol m^{-2} s^{-1}. Furthermore, the quantum yield (α) and maximum photosynthesis at light saturation (Pmax) decreased and the light compensation point (LCP) increased as the temperature was raised. Tainan 1 had a higher LCP and lower α than other cultivars, while UC157 had a higher Pmax.

Thus overall decrease in carbon accumulation with temperature was mainly due to an increase in stomatal limitation, a decrease in quantum yield, an increase in photorespiration (low carboxylation efficiency), and an increase in dark respiration.

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GLOSSARY OF ABBREVIATIONS

Γ	CO_2 compensation point
ABA	abscisic acid
AC_i	photosynthetic response to internal CO_2
ATP	adenosine triphosphate
CE	carboxylation efficiency
CER	CO_2 exchange rate
C_i	internal CO_2
cv	cultivar
g_i	mesophyl conductance
HU	heat unit
IRGA	Infra Red Gas Analizer
IRGA	Infra Red Gas Analizes
K_m	Michael Menten kinetic
LCP	light compensation point
lg	stomatal limitation
NADPH	nicotinamide adenine dinucleotide phosphate
NAR	net assimilation rate
PAR	photosynthetic active radiation
PCR	photosynthetic carbon reduction
Pg	gross photosynthesis
PGA	phosphoglyceric acid
Pi	inorganic phosphate
PIB	post illumination CO_2 burst
Pmax	maximum photosynthesis at light saturation
Pn	net photosynthesis
Pn700	ratio of photosynthesis at standard light level to maximum photosynthesis
PPFD	photosynthetic photon flux density

Rd	dark respiration
rg	gas phase resistance
RGR	relative growth rate
Rl	photorespiration
rm	mesophyl resistance (1/CE)
RPGR	relative total plant growth rate
Rubisco	Ribulose-1,5 biphosphate carboxylase -oxygenase
RuBP	Ribulose-1,5 biphosphate
Tb	base temperature
TCA	tricarboxylic acid
T_{max}	maximum temperature
T_{mean}	mean temperature
T_{min}	minimum temperature
TPU	triose phosphate utilisation
V_c	rate of carboxylation reaction
V_o	rate of oxygenation reaction
α	quantum yield
Φ	ratio of oxygenase to carboxylase

INTRODUCTION

Asparagus is a perennial plant which will be productive for more than 15 years under good management (Douglas, 1990). Productivity is dependant on the crop storing adequate amounts of carbohydrates below the ground in the storage roots to support spear production in the following spring. The provision of adequate amounts of storage carbohydrates is dependant on the effectiveness of the fern growth stage. The fern growth stage has not been extensively studied, but is the base upon which productivity is built. The starting point therefore for the research outlined in this thesis was the objective to provide a better understanding of the fern growth stage of asparagus. The fern growth stage is the period when the crop is most active photosynthetically and is important not only during cropping but also during crop establishment.

Successful establishment is dependant upon the production of vigorous and healthy plants in the first and second year after planting. Research that has examined the effects of establishment method and time of planting (Bussell, 1984) together with studies on field growth (Dufault and Greig, 1983; Haynes, 1987) has provided information on the growth and development of young asparagus plants in their first season in the field. In an attempt to provide more detailed information on the fern growth stage of young asparagus plants, the effect of time of planting and of seasonal effects on this growth and development, a study using two cultivars and successional plantings was carried out. Regular growth analysis in both the first and during the commencement of the second season of growth in the field was used to provide data on the effects of these treatments on plant performance.

As outlined earlier the fern growth stage is when the asparagus plant is most actively photosynthetically. Asparagus has been grown in both temperate and tropical regions. This suggest that asparagus is adapted to a wide range of temperatures and probably humidities. Important physiological processes which can be used to describe the adaptability of plants to temperature are photosynthesis and respiration. Asparagus has

been identified as a C_3 plant (Troughton *et al.*, 1974) and as having an optimum temperature for photosynthesis in the 15^{0}C to 25^{0}C range (Sawada *et al.*, 1962; Lin, 1983; and Inagaki *et al.*, 1989). The performance of young asparagus plants in the field will be greatly influenced by the interactive relationship between photosynthesis and respiration under the prevailing light and temperature conditions. In an attempt to combine the interests of the present study in the fern growth stage with the objectives of a concurrent research project in the Department of Plant Science on the growth of asparagus at high temperatures a further study was carried out. This research examined the effects of high temperatures, as experienced in the tropics, on photosynthesis and respiration of 4 asparagus cultivars.

CHAPTER ONE

LITERATURE REVIEW

1.1 GENERAL OVERVIEW OF ASPARAGUS

1.1.1 Introduction

Asparagus officinalis L. is a herbaceous perennial, which has been grown in a wide range of environments, including the seashore, the desert, temperate regions and high elevations (Nichols, 1988a; Higgins, 1981; Nonnecke, 1989). These diverse environmental conditions indicate wide adaptability of asparagus to the environment.

1.1.2 Botany and morphology

The Asparagus plant is a long-lived monocotyledonous, herbaceous perennial, is dioecious and is a member of the Liliaceae family (Tutin *et al.,* 1980; Nonnecke, 1989). Ammal and Kaul (1966) suggested that the cultivated asparagus is diploid (n=10). There are at least 150 species of asparagus, but only Asparagus offinales is grown commercially for food (Nonnecke, 1989).

Asparagus plant has two main parts, the above ground part, which is called fern and below the ground called the crown. The fern consists of many shoots. Each shoot has one main stem with many side shoots (Blasberg, 1932). The true leaves are the scale-like structures that form at the tip of the spear and down the stem and side shoots of the fern (Mullendore, 1935; Nonnecke, 1989). Cladophylls are needle-like branches and grow in the axil of the scale leaves (Mullendore, 1935; Nonnecke, 1989) and are considered as the main site of photosynthesis, although photosynthesis also occurs in stems and green spears (Blasberg, 1932; Downton and Torokfalvy, 1975; Inagaki *et al.* 1989). The leaves of asparagus have therefore been reduced in size to form very small scales at the base of the cladophylls. The edible part of asparagus plant is called the spear. The spear is an immature shoot which has not branched (see Figure 1.1).

As a monocotyledon, asparagus has the crown as the critical growth centre. The crown consists of underground stems (rhizomes), fleshy roots, usually called storage roots and fibrous or feeder roots (Nonnecke, 1989; Douglas, 1990). The fleshy roots have two functions serving as storage organs and also supply moisture and nutrients, while the fibrous roots serve as absorption organs (Nichols, 1988b; Nonnecke, 1989).

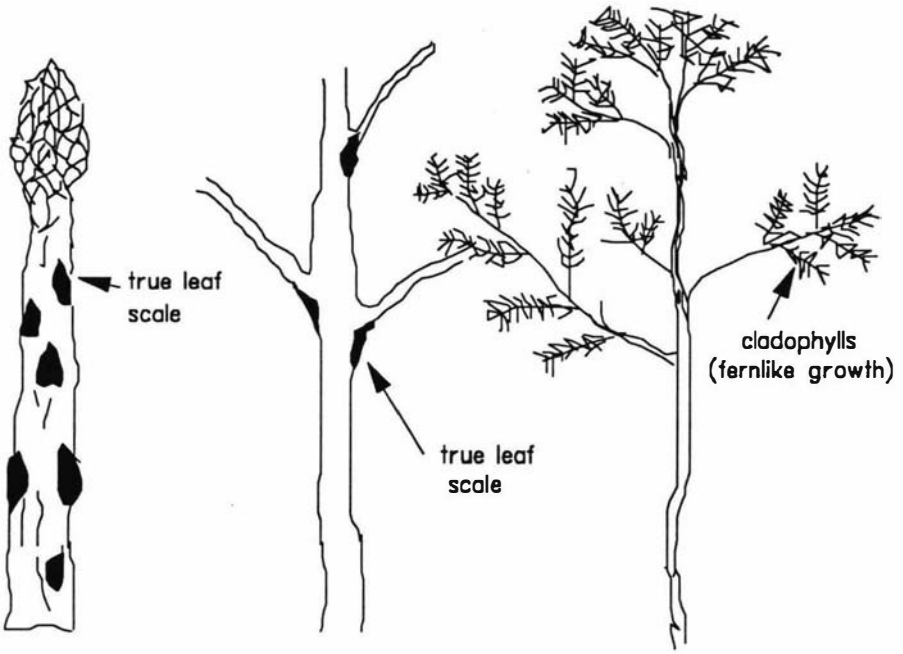


Figure 1.1 The asparagus spear and subsequent fern growth. Scales, so conspicuous in the spear, remain at each leaf base.

The rhizome consists of bud clusters with each bud cluster containing many buds. Each bud cluster has its own connection with storage roots (Nichols, 1988b) (see figure 1.2). Nichols (1988b) suggested that as the plant ages, the bud cluster separate from the main rhizome and has its own identity and behaves like an individual plant. As a dioecious plant, asparagus produces male and female florets on separate staminate and pistillate plants (Nonnecke, 1989).

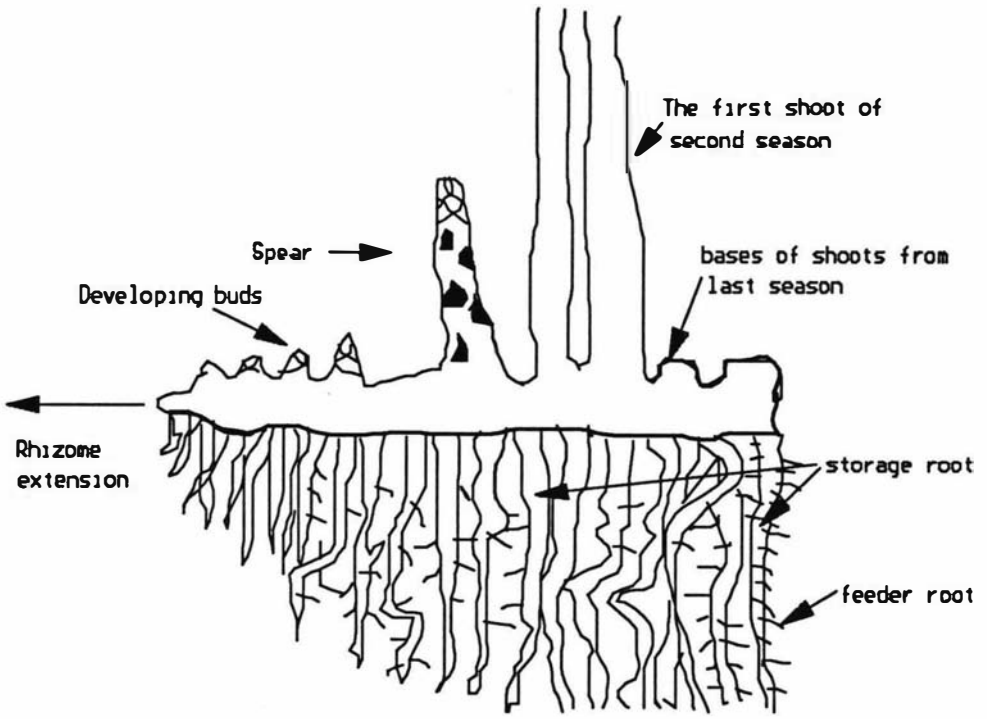


Figure 1.2 The asparagus crown and the attached buds, spear, shoots and roots.

In temperate regions, the growth of the asparagus plant is affected by season. In summer the plant produce shoots which photosynthesize to produce carbohydrate. During this season some part of this carbohydrate will be stored in the storage root. In autumn the shoots senesces because of low temperatures (Hughes, 1992). The plant becomes dormant during the winter. Spear production commences when the temperature is raised above 5^0C during the spring (Hughes, 1992), while the optimum temperature for spear growth is about 25^0C (Nichols, 1988b).

1.1.3 **Physiology**

1.1.3.1 **Shoot growth**

In early spring as temperatures rise and providing there is sufficient soil moisture, budbreak occurs and the asparagus plant start to produce spears and eventually shoots. The plant is dependent on storage carbohydrate to produce spears until the fern opens out and the cladophylls become photosynthetically active (Downton and Torokfalvy, 1975; Lin and Hung, 1983).

There is evidence that the growth of buds is controlled by correlative inhibition (Hughes, 1992). This means that the bud adjacent to the most recently developed shoot will not develop into the next shoot due to plant growth substances produce by the first shoot. The bud will develop into a shoot only after the first shoot has reached a certain stage, or until the first shoot is removed.

1.1.3.2 **Crown growth**

After the first shoot emerges a small bud develops on the crown (Nichols, 1988b). This bud will grow and become the next shoot after the first shoot has reached its full size. The second shoot will have 2 associated roots attached to the rhizome. More buds are produced on the rhizome during the growing season, however, these buds do not develop into shoots until the previous shoot has reached full size. Tiedjens (1924) suggested that the number of buds formed did not depend on the carbohydrate

reserves, but the reserve did influence the size of buds (Tiedjens, 1926). The number of buds which developed into shoots was also dependent on the carbohydrate levels in the storage roots (Tiedjens, 1924).

1.2 GROWING ASPARAGUS IN THE FIELD

1.2.1 Plant establishment

1.2.1.1 Introduction

There are 3 methods of establishing asparagus. By using one year old crowns, by direct seeding and by using seedling transplants. The last method has been used mainly in USA and New Zealand. Research has shown that there are advantages and disadvantages for each of these methods. This review will briefly compare these techniques and then discuss in detail seedling transplants because of the relevance of this technique to the research reported in this thesis.

1.2.1.2 Establishment methods and crop yield

Traditionally asparagus has been established both in the USA (Garrison, 1977) and in New Zealand (Wood, 1983) by using one year old nursery grown crowns. Undoubtably one reason for the use of crowns has been that this has been a simple method of establishing plants below the surface of the soil so that development can take place without the risk of future cultivations and harvesting damaging the crowns beneath. This has been achieved by planting well developed plants (crowns) at the bottom of trenches, which may be 15-30 cm deep (Wood, 1983). Another consideration is that asparagus seed germinates very slowly and the seedlings compete poorly with weeds and also require close monitoring for insect infestation (Garrison, 1977). These are potential problems that are associated with direct seeding. In the reduced area of the nursery bed these issues can be more effectively dealt with.

Direct seeding was trialled for establishing asparagus 15 years ago in USA (Garrison, 1977; Benson *et al.,* 1978a) and in New Zealand (Wood, 1983). 15 years experiment conducted in California demonstrated that direct seeding gave higher yields than crowns for the first 6 years with no differences being observed during the remaining 7 seasons (Benson *et al.,* 1978a). This early differences in yield was a result of increased spear production due to a higher plant density. The reason for using direct seeding at that time was to obtain higher returns early in the life of the crop by using high plant densities. Trials by New Zealand Ministry of Agriculture and Fisheries found that the spear quality from high density plantings was poor due to very thin spears (Wood, 1983). The survival of the seed sown for direct sown crops is often not satisfactory. For example only 23% of the seeds had survived to become established seedlings due primarily to excessive soil moisture and erosion of soil from the sides of the trenches (Ombrello and Garrison, 1978). This low percentage of survival during the first growing season, resulted in the spacing between plants becoming very irregular. Such problems will not exist if asparagus is established using seedling transplant or crowns, because they are much larger and less susceptible to the effect of erosion and post establishment losses (Ombrello and garrison, 1978; Fisher, 1982; Benson *et al.,* 1978b).

Fisher (1982) compared the growth of asparagus established from direct seeding and seedling transplants for 12 months after transplanting. He found that the size of transplants 3 months after planting were equivalent in size to direct-seeded plants at the end of the season. He estimated that 10 weeks in the glasshouse were equivalent to 12 weeks of field growth. At the end of the season the size of transplants was twice than that of direct-seeded plants as also reported by Ombrello and Garrison (1978).

Asparagus establishment from seedling transplants has been carried out commercially in California since the 1970s (Benson *et al.,* 1978b) and experimentally in the UK (Williams, 1979). Although Williams (1979) did not recommend to use seedling transplant he was in agreement with the work of Benson *et al.* (1978b) that establishment with transplants was quicker and that the first harvest could be taken one year earlier than with traditional crowns. In fact Benson *et al.* (1978b) have

proposed that with asparagus established from seedling transplants it might be possible to harvest the spears after one season's growth.

Benson *et al.* (1978b) suggested the advantages of using transplants over crowns were:
(i) the establishment costs were lower due to the use of machine planting with a lower labour cost;
(ii) the time from nursery seeding to harvest was reduced;
(iii) the seed requirement was reduced by almost one-half;
(iv) the injury caused by crown separation from nursery to planting was eliminated;
(v) by growing seedlings in disease-free media in glasshouses the infestation of *Fusarium* sp. should be lower in the new plantation;
(vi) a higher (92-98%) percentage of seedlings become established

The advantages over direct seeding were:
(i) less seed required;
(ii) irrigation requirement at planting was less precise;
(iii) the transplants establish in the field faster and could possible be harvested after one season's growth.

Seedling transplants, however, has some disadvantages. The cost of seedlings are expensive in New Zealand and therefore the use of seedlings is only justified where high-cost hybrids are to be grown (Fisher, 1982). Irrigation, insect control and weed control are more critical than with crowns and the technique is not recommended for land that has previously been used for growing asparagus because of the high level of susceptibility of young plants to Fusarium root rot (Garrison, 1977).

Williams (1979) suggests that establishing asparagus from crowns was more expensive than direct seeding or seedling transplants. This is due to the high labour input required to dig, sort, and handle crowns, and planting the bulky crowns is also very time consuming. Planting the crowns usually takes place in early spring and therefore there can be difficulties in lifting crowns during the bad weather conditions that often occur in that time. Fisher (1983) has suggested that crowns, which often have

damaged roots when planted in the cold wet conditions of early spring, can easily be infected by phytophthora.

In terms of yield, research results are often contradictory. Benson (1979) in the USA and Bussell (1983) in New Zealand reported that crowns produced higher yields than seedling transplants harvested 1 and 2 years after planting. Williams (1979), however, observed that seedling transplants gave higher yields than crowns over 4 years in UK. A recent study reported by Sterret *et al.* (1990) found that although the yield of both crown and seedling transplants was the same in the first harvest season, the crowns gave the higher yield in the second and third season. He suggested that increased yields during the early harvests will be obtained with crowns rather than seedling transplants under dry conditions where adequate irrigation is not available.

Fisher (1983) concluded that the contradiction that is apparent in research results might be due to the quality of the crowns and seedling transplants grown, the level of damage to crowns during lifting and the weather conditions at planting. Crowns should produce higher yields than seedling transplants if they are good quality crowns and experience at planting, conditions which are favourable for growth.

1.2.1.3 **What is a good seedling transplant**

Asparagus crops can be productive for longer than 15 years if the establishment and management of the crop are good. Establishment by using poor transplants will result in a lower return than expected. Therefore, an acceptable asparagus seedlings should have a well developed root system, a number of buds and strong, but not excessive shoot growth (Fisher and Benson, 1984). The reasons are that the root tissues store the carbohydrates on which the seedlings will depend for assimilates and buds are necessary to provide the shoots to enable the plants to establish themselves in the field. Excessive shoot growth was not favoured as it might favour foliage diseases in the nursery.

1.2.1.4 **Production of seedling transplants**

1.2.1.4.1 **Introduction**

Seeds are sown and placed in germination rooms and then using cell transplant technology, the plants are raised in greenhouses before planting out in the field. Such an approach is based on the Speedling system developed in Florida in the USA in the early 1970s (Royle, 1980) and is now widely used with vegetable crops. Liptay (1984) has suggested an alternative approach where the young plants are grown in the field with the seedlings lifted and planted mechanically. The control of weeds is a major drawback of this method. Two advantages of this approach are that no manual handling is necessary and a short time passes between lifting and transplanting of the transplants by machine.

1.2.1.4.2 **Seed treatments and seed quality**

Good quality of seed is very important to obtain even germination and a high germination percentage. Wood (1983) suggested that large seed gives better seedling emergence and produce larger plants more quickly than small seed. This is in agreement with work of Williams and Garthwaite (1973) who found that approximately 50% of the large seed and 30% of the small seed produced good plants, while 4% of the large seed and 15% of the small seed produced inferior plants. Fisher (1983) suggested that the seeds should be dusted with 5 grams of product of both thiram and benlate for each kg of seed to reduce the level of seed born Fusarium.

Brown *et al.* (1982) studied the effect of seed priming on asparagus seed. They found that chitted seed germinated the most rapidly compared to seed primed with polyethylene glycol '6000' (PEG) or the control. The treatment however did not affect the final germination percentage. Seed chitting would therefore be beneficial to reduce the time spent raising seedlings.

1.2.1.4.3 **Cell size, volume, depth and seedling density**

There is no doubt that the cell volume used for raising seedlings has a major influence on the performance of the transplants. Ombrello and Garrison (1978) evaluated the effect of container volume on seedling growth. They found no significant effect on the number of shoots. More recent experiments, however, have demonstrated a strong effect of container volume on seedling growth. For example, shoot and root dry weight, and partitioning of dry weight to the shoot all increased as container volume increased (Fisher and Benson, 1984; Falloon and Schurink, 1981).

Container depth has synergistic effect with container volume on the growth of seedlings. Brown *et al.* (1982) found the total dry weight increased with increasing container depth, but this effect was only significant between the 25 mm and 50, 75, 100 mm container depths. The roots tended to be found only in lower 2/3 of the container at 50, 75 and 100 mm depth. As these containers were all of the same diameter then the effect of depth could well have really been an effect of cell volume. The growth of seedlings in a shallow peat pot, but of a larger volume, was better than that of plants grown in paper pots which were deeper but smaller in volume (Dufault and Waters, 1984).

Problems can arise when containers are too deep (Nikoloff and Falloon, 1986). They found that the roots did not explore the lowest part of the container, as reported by Brown *et al.* (1982), and therefore the roots did not form a compact mass to retain the media. At transplanting the media fell away from the roots, leaving them bare. A reasonable conclusion here is that the larger the cell, the larger the transplant that can be grown. For economic reasons, however, the size of transplant should be such that the seedling can be easily handled and have a good chance of survival. The smaller cells will be ready for planting earlier than the larger cells.

Plant density does not have a major effect on seedling growth. Although statistically not significant, seedlings tend to be taller at high plant densities (Ombrello and Garrison, 1978; Falloon and Schurink, 1981). There was also no difference in the

number of shoots (Ombrello and Garrison, 1978) and shoot growth (Dufault and Waters, 1984). Dufault and Waters (1984) however found that 56% to 66% of the variation in crown fresh and dry weight was due to differences in depth and density. Increasing density decreased crown fresh and dry weight.

Module shape has been investigated by Fisher and Benson (1984). They found that a 20 cm^3 cylinder produced higher shoot and plant dry weights and also shoot number compared to an inverted pyramid cell having a slightly larger cell volume, however, root dry weight was not affected by the treatments. They suggested that an inverted pyramid does not place enough media at the base of the cell for asparagus seedlings. An inverted pyramid, however, has the advantage of being easier to pull out the seedlings from the cell. The recommendation for the ideal container for asparagus therefore should be deep (10 cm), of large volume and have low plant density (Dufault and Waters, 1984). Fisher and Benson (1984) suggested a cell volume of 30 cm^3, with the cell 7.5 cm deep and not too narrow at the base and a plant density of 1000-1100 plant m^{-2} as being commercially acceptable.

1.2.1.4.4 **Media and fertilizer**

Propagation media have been examined as to their suitability for raising asparagus seedling transplants (Dufault and Waters 1984):

(i) vermiculite + peat (VP);
(ii) peat + perlite (PP); and
(iii) perlite + vermiculite (PV).

It was found that the growth of seedlings grown in VP were more vigorous compared to the other treatments. VP seedlings showed superiority in the number of shoots, fresh and dry weight of shoot, number of buds and roots, and fresh and dry weight of crown. At Massey University, a mix of 50% peat and 50% sand has been used for producing a range of vegetable seedlings, including asparagus (Fisher, 1983).

Fisher (1983) recommended adding to each m^3 of media :

1500 gram osmocote (3 months : 15-5.2-12.5)
1500 gram superphosphate
1500 gram lime
3000 gram dolomite
150 gram trace elements

It is a common practice to supply seedlings with liquid fertilizer to media which does not contain an adequate supply of nutrients. This allows the liquid feeding programme to be used to control seedling growth and development as seen in the Speedling system (Royle, 1980). Research has shown that the effectiveness of liquid feeding can depend on the type of fertilizer used. Precheur and Maynard (1983) investigated the effect of varying ratios of NO_3 and NH_4 on the growth of asparagus seedlings grown in sand culture. To maximize growth they suggested to use liquid feeds which contain 75% NO_3-N and 25% NH_4-N. Below 50% NO_3-N, they reported that growth can be restricted. Fisher and Benson (1983) reported that increasing N rates increased shoot and root production and dry weight accumulation, but increasing P decreased root dry weight. In addition (Fisher and Benson, 1984), increasing the N supply to 200 mg l^{-1} to the seedlings only increased shoot and plant dry weight, increased partitioning of dry matter to the shoot, and increased shoot number, but it did not increase root and crown dry weight. They recommended that as 200 mg l^{-1} N gave no commercially beneficial responses that the 100-150 mg l^{-1} N and 15 mg l^{-1} P was more acceptable in practice (Fisher and Benson, 1984). An additional of 100 mg l^{-1} K will bring benefits to the growth of the seedlings (Adler *et al.*, 1984).

Fisher (1983) reported a liquid feed supplying 150 ppm N, 22.5 ppm P and 100 ppm K can be provided by dissolving the fertilizer listed below into 1 litre of water and diluting at 1 : 200.

58.4 gram ammonium nitrate (NH_4NO_3)
18.4 gram MAP
52.6 gram KNO_3

1.2.1.4.5 **Effect of environmental factors and growth regulator on seedling growth**

Asparagus seedlings grow well under warm conditions. Germinating the seed at 25^{0}C is recommended (Fisher 1983). Brown *et al.* (1982) studied the effect of 3 constant temperatures (15^{0}C, 22.5^{0}C, and 30^{0}C) on the growth of asparagus seedlings. Mean plant dry weight increased with increasing temperatures. In conclusion, Fisher (1983) recommended that the temperature range from 16 to 22 ^{0}C would be favourable for seedlings growth.

Desjardins *et al.* (1990) demonstrated the beneficial effect of supplying CO_2 to plants in tissue culture. The root and fern dry weight were increased by 196% by increasing CO_2 from ambient concentration (330 ppm) to 1500 ppm. It was suggested that elevated concentrations of CO_2 may increase net assimilation by reducing photorespiration. Supplemental lighting also improved survival of transplants in the field (Desjardins *et al.*, 1990). Ambient light intensities were not reported in this research.

Although asparagus is considered to be relatively drought tolerant, Drost and Wilcox-Lee (1990) and Wilcox-Lee (1987) suggested that maximum growth occurs in young asparagus plant when the soil water potential is close to field capacity. This suggests that seedling transplants and newly established plantings would benefit from irrigation to minimize moisture stress. Sterrett *et al.* (1990) has confirmed this view as their research showed that vegetative growth of seedlings after transplanting was enhanced by irrigation, regardless of irrigation method. They also found that after the fourth growing season, 83% of transplants with subsurface irrigation still remained compared with 55 % of non irrigated transplants. Wilcox-Lee and Drost (1990) found that plant dry weight was related exponentially to soil moisture.

Soil water salinity also affects asparagus seedling growth. For example, germination was delayed and final germination percentage also reduced at salt levels greater than 9.4 dS m^{-1} (Francois, 1987). He also noted that the first year of seedling growth was

much more salt sensitive than during either germination or the mature stages of growth. From this research it seems that the soil water salinity should be lower than 4.1 dS m^{-1} to be favourable for asparagus.

It has been reported that ancymidol promotes the growth of asparagus roots and shoots in tissue culture (Chin, 1982). Applying this growth retardant to young plant at 1.0 mg $plant^{-1}$ damaged fleshy roots and therefore reduced crown dry weight (Adler *et al.*, 1985). However, they also found that ancymidol enhanced the dry matter in crown rather than fern in plants 7.5 weeks old after seedling. This effect will be beneficial to transplants by making them more tolerant to the stresses of transplanting.

1.2.1.4.6 **Transplant age**

Studies on the effect of transplant age on seedling growth after transplanting were initiated by Ombrello and Garrison (1978). Using 2 different ages of transplants (9 and 12 weeks old) they found that transplant age did not affect height or number of shoots per plant by the end of the season. Plant parameters such as crown and root growth were not determined. In the UK, Williams (1979) reported a similar result. Even a 10 week age difference did not lead to a difference in yield. A later study conducted by Dufault and Waters (1984) demonstrated that 6 weeks old seedlings did not produce as good a quality transplant at planting as did 7, 8 and 10 week old plants. Contradictory results were also reported by Burrows and Waters (1989) who found that transplant size effected field performance resulting from just a 2 week difference in age at transplanting (9 and 11 weeks old). The differences still existed even 12 and 18 months after planting. There is no reported work on the effect of transplant age on yield. It is quite likely that small differences in transplant age does not affect the yield as has been found with cell transplants with cauliflower (Wurr *et al.* 1986).

1.2.1.4.7 **Time of transplanting**

In temperate regions, the time of transplanting of asparagus, whether by using crowns, direct seeding or seedling transplants, is very important in relation to the success of planting. Many researchers have carried out studies of the effect of planting time on the survival and yield of asparagus plants the following year. In Canada, Liptay (1984) compared late August nursery transplants to 1 year old crowns planted the subsequent spring. He found that both survival and yields were not different between the two treatments. Loughton and Baker (1984), however, observed that summer and fall planting of 8 weeks old transplants did not produce good plant stands, particularly seedlings transplanted in mid September, which had very low (27%) survival rates. Seedlings transplanted the following spring performed better in terms of growth and survival. Williams (1979) suggested that late spring or earlier summer would be the preferred time of transplanting as long as irrigation is available. Furthermore, early summer planting of young plants raised in containers gave slightly better yields than early autumn planting of field raised young plants. Using 22 weeks old crowns, the opposite result was obtained by Williams (1979). The crowns planted in autumn had better yields than those planted in spring because the plants produced fern earlier and allowed a light harvest to be taken in the second year.

In New Zealand, Bussell (1984) reported that a 12 week old seedling planted in summer survived the following winter, but the survival and yield were low compared to spring planting. He recommended October and November as the optimum time for planting seedlings in New Zealand. Later planting was unsatisfactory. A recent study which was carried out by Burrows and Waters (1989) in the northern hemisphere gave an indication that fall planting could give a good result. The seedlings transplanted in fall exhibited superior crown and fern characteristics relative to spring planting. It should be noted, however, that spring transplants were significantly smaller than fall seedlings at the time of transplanting. Fall seedlings might also have had the chance to grow and established during autumn before growth ceased.

Research conducted by Dufault and Greig (1983) in the northern hemisphere showed that asparagus field seeded in November and December were killed during the winter in comparison to spring seeding (March to April). Apparently the cause of the losses was due to seed rot.

1.2.2 Growth and development of young asparagus plant

1.2.2.1 Introduction

The growth and development of asparagus plants during their first growing season is a critical period, which has a major influence on the productivity of the plants for the rest of their life. Careful attention and good management during this period will therefore be beneficial to the plants. Successful management of the young asparagus plants requires a knowledge of their growth and development and of factors affecting this growth and development. There have been a number of studies on the growth and development of young asparagus. It should be noted that asparagus is a plant, which has considerable variation between plants within a variety. To draw a conclusion from any experiment using asparagus requires a large sample and specification of the cultivar.

1.2.2.2 Dry matter accumulation and partitioning

Dry matter accumulation of asparagus could be expected to vary between some cultivars. For example, two asparagus cultivars, UC157 (F1 hybrid) and UC72 (open pollinated) were grown in pots and their growth for 2-14 weeks from emergence studied (Benson and Takatori, 1980). They found that these cultivars had different dry matter distribution patterns. The F1 hybrid distributed more dry weight to the root than the OP. The percentage of dry matter distributed into the roots was from 32 to 54% in the F1 and 24 to 48% in the OP. The OP therefore accumulated more dry matter into the fern and this could be in part responsible for the lower yields of UC72 compared to UC157. By contrast, in a field study carried out by Dufault and Greig (1983) showed that even though UC157 initiated more roots and accumulated more

fern and crown fresh weight than UC800 (OP) early in the season, by harvest at 24 weeks after emergence, crowns did not differ in root and bud number, or fructose content (crown quality). This contradiction could be partly due to the root growth restriction in the experiment in the pot carried out by Benson and Takatori (1980). As Brown *et al.* (1982) found that the root growth of asparagus seedlings (cv. Mary Washington 500W) 7 weeks after emergence was inhibited by the lack of depth of the trays. They suggested that the design of the trays is an important factor which affect the rooting of asparagus plants.

Fisher (1982) observed considerable root production of asparagus at 6 weeks after emergence, but the dry matter accumulation to the root did not increase markedly until after 15 weeks had been spent in the field. Root carbohydrate analysis by Dufault and Greig (1983) suggested that carbohydrate concentration tend to decrease coinciding with increased growth, and then increased steadily 14 weeks after emergence until the end of season. Dry matter accumulation into the crown continued up to Autumn (Fisher 1982). This is due to redistribution of dry matter from the shoot (Martin and Hartmann, 1990), which is associated with the induction of the dormancy period (Drost and Wilcox-Lee 1990; Hughes, 1992).

Leaf area increased very little from emergence to 8 weeks, then increased considerably at week 9 (Benson and Takatori, 1980). Leaf area ratio (LAR) however declined gradually with time. They suggested that as plants grow a higher proportion of dry matter was accumulated in nonphotosynthetic tissues, and this caused the shoot/root ratio to decline with time. The decrease in LAR caused the plant relative growth rate (RGR) to steadily fall with time (Brown *et al.*, 1982; Fisher, 1982; Fisher and Benson, 1984). The decrease in plant RGR was more pronounced in asparagus established by using transplants than by direct seeding (Fisher, 1982). In the field Dufault and Greig (1983) also found that shoot/root dry weight ratio continued to increase until summer (July) and then started to decrease along with decreasing air and soil temperature. This probably in response to temperature as asparagus (Hughes *et al.,* 1990) and other species (Farrar, 1988) accumulated more dry matter to the root at low temperature. Photosynthesis of old ferns was also less efficient (Lin and Hung, 1983).

1.2.2.3 **Shoot, root and bud production**

Field studies in New Zealand of young asparagus established from direct seeding showed that the rate of shoot production of OP (Mary Washington 500W) was steady throughout the season (Fisher, 1982). While a study in the northern hemisphere revealed that the shoot growth of an F1 hybrid (UC157) slowed down after 14 weeks, but OP on (UC800) continued their shoot production at least until 21 weeks from emergence (Dufault and Greig, 1983).

F_1 hybrids began producing fleshy roots 6 weeks after emergence and did not cease until the end of experiment, whereas OPs reached the same stage about 3 weeks later and they had little increase after 18 weeks (Dufault and Greig, 1983). Fisher (1982) observed that Mary Washington 500W still produced roots significantly at 18 weeks then declined at 21 weeks. The cessation of root production in OPs seems to be at the expense of shoot production. Shoot production in the autumn, however, might not be beneficial to the plant as it may be too late to translocate the dry matter back to the root in the winter (Nichols,1988b). Spear production in the autumn therefore wastes the carbohydrate resources of the storage roots.

The yield potential of asparagus in the following growing season is indicated by the number of buds produced on the asparagus crown the previous season (Dufault and Greig, 1983). Fl hybrids began their greatest bud production period about 6 weeks after emergence, while OP started about 3 weeks later (Dufault and Greig, 1983). This observations suggests that F1 hybrids have a greater precocity to initiate buds at an earlier developmental stage than OP cultivars. Low temperature did not inhibit bud production in F1 and OP varieties (Dufault and Greig, 1983). Fisher (1982) observed that bud production ceased in autumn. The cessation of bud production coincided with the time of peak shoot numbers (Fisher, 1982) and it was suggested that factors influencing the growth of new shoots also directly or indirectly influence bud initiation.

Bud production was greater as the growing season progressed (Fisher, 1982; Dufault and Greig, 1983). This was indicated by the gradual decrease in the shoot/bud ratio as the season progressed. Root/bud number ratio, however, stabilized about 12-14 weeks after emergence.

1.3 SHOOT-ROOT RELATIONSHIP

1.3.1 Shoot-root ratio

The shoot to root dry weight ratio has been used in many studies to reflect their functional relationship irrespective of plant size (Brouwer, 1962). This method has limitations as it changes with size and phenological development of the plant (Ledig *et al.,* 1970). This is obvious with many crops as the root growth rate generally declines more rapidly than that of the shoot growth rate (Brouwer, 1962; Cooper, 1972). The environment also affects the ratio (Brouwer, 1962). For example, unfavourable condition for shoot or root growth such as low temperatures (Davidson, 1969a; Buggee and White, 1984), low irradiance (Troughton, 1960), drought (Brouwer, 1966) and nutrient deficiency (Davidson, 1969b). The degree of shoot or root response to the those unfavourable conditions will determine the shoot-root ratio (Brouwer, 1963; Davidson, 1969b; Richards, 1983).

1.3.2 Shoot-root allometry relationship

The concept of an allometric relationship between two animal organs can be applied to plant organs (Causton, 1983). The allometric equation is the power function of the two plant parts in the form of :

$$Y = a X^k \qquad (1.1)$$

where X and Y are the size of two organs, and a and k are constants (Causton, 1983). The common function which is used is the natural logarithms of both sides of equation 1.1 to become :

$$\ln Y = \ln A + k \ln X \quad (1.2)$$

The equation (1.2) will produce a straight line relationship between the two organs with k as the slope (Reiss, 1989). Causton (1983) suggested that the k value, also called the allometric constant, represents the ratio of the mean RGR of the shoot to that of the root. The strength of the relationship will be determined by the coefficient of determination (r^2).

The k value is independent of the scale or size of the plant (Troughton, 1960). Therefore, it has been used widely in comparisons of the growth of plants in preference to the shoot-root ratio (Hunt and Burnett, 1973). The k value indicates the degree of functional equilibrium between shoot and root. Reiss (1989) suggested that when the k value equals one thus indicates that the growth rate of shoots and roots are equal. A k value of less than unity indicates that the root has a faster growth rate than shoot, or that both root and shoot growth rate is decreasing but the root growth is decreasing slower, and *vice versa*. The k value also indicates the changing of dry weight partitioning at any particular time (Causton, 1983), which means it describes the adaptation ability of plant growth in response to the treatment imposed. Allometric growth shows that the partitioning ratio is constant over the time interval in which a single allometric function can be used to describe the growth data (Causton, 1983). However it was suggested that over an extended duration more than one allometric function involving a sharp change of gradient was needed to describe the data (Causton, 1983).

1.4 PLANT GROWTH ANALYSIS

1.4.1 Logistic model

The logistic model has been proposed in an effort to smooth out the effect of year to year variation in crop yield (Nelder *et al.*, 1960). The equation which involves four parameter is :

$$dW/dt = k\,W\,(1 - (W/A)\,1/^{\theta}) \quad (1.3)$$

The family of curves defined by equation 1.3 includes several curves with the Gompertz function (when θ=0) as a special case (Nelder, 1961). The characteristic of many growth curve is that the RGR is almost constant when the weight is small compared to the final weight (Nelder, 1961), and he suggested when $\theta > 0$ equation 1.3 can be written in the form

$$W = A/\{1 + e^{-(\lambda+kt)/\theta}\}^{\theta} \quad (1.4)$$

where :

W is dry weight of plant material

λ is the constant of integration (intercept)

A is the asymptotic yield

k is the initial relative growth rate (slope)

t is time

θ is the point of inflection

Time in the model is commonly represented by chronological time, but may be replaced by another 'time scale' when the environment is variable. Nelder (1961) showed a method to fit the data to the logistic model using an iterative technique. Nichols (1970) suggested that the Nelder's technique is only applicable for single sets of data, and described a modification of the technique in order to fit more than one set of data simultaneously to produce a single set of parameters. The modification involves some manipulation of the time scales in order to superimpose the growth curves.

1.5 ENVIRONMENTAL TIME SCALE

1.5.1 General concept

It is very common for the growth pattern for a particular crop to vary markedly

between sowings because of the effects of variable weather conditions (Salter, 1960). For example, when a chronological time scale such as number of days from sowing is used to plot against the growth of plants, the resultant plant growth curves can differ markedly from season to season. Nelder *et al.* (1960) suggested the replacement of the chronological time scale in such growth equations by a time scale based on some suitable combinations of environmental factors. The use of cumulative measurements of the main climatic variables as 'time scales' may thus provide a common scale from season to season.

1.5.2 **Heat unit concept**

Of the various climatic variable which influence plants growth most attention has been given to temperature (Wurr and Kay, 1981; Salter, 1960; Marshall and Thompson, 1987a and 1987b; Wurr and Fellows, 1984). The use of accumulated day degrees or heat unit summation as a time scale is a convenient and simple way of integrating temperature with time to take into account temperature differences over time.

The heat unit system has been used for studying plant temperature relationship. For example, for table grapes maturity determination (Winkler, 1948), and for forecasting the incident of pest (Lienk, 1963) and disease (Boewe, 1953) occurrence. Because of its value it is still used with a variety of crops at the present time (e.g. Friis, Jensen and Mikkelsen, 1986 on peas; Kristenssen, Friss, Henrikssen and Mikkelsen, 1986 and Wurr and Fellows, 1984 on lettuce; Marshall and Thompson, 1987a and 1987b, and Diputado, 1989 on broccoli).

1.5.2.1 **Heat unit system assumptions**

The heat unit theory assumes that:

1. The plant response to temperature is linear over the whole temperature range.
2. Day and night temperatures are of equal importance.
3. There is only a single base temperature over the life of the plant.

4. Temperature is the major environmental factor influencing plant growth and/or development.

The heat unit concept however is far from perfect (Wang, 1960) as :

1. Plants may respond differently to the same environmental factors during various stages of their life cycle;
2. The threshold temperature as it is used in heat unit computations is considered a constant but may change with the advancing age of the plant;
3. Direct proportionality may not exist between growth rate and temperature;
4. Several other environmental factors influence plant growth and development.

1.5.2.2 **Selection of appropriate base temperature**

Arnold (1959) reported that two methods could be used to determine the base temperature, firstly the least variability method and secondly the regression coefficient method. In the former, the heat unit summations from a series of plantings were calculated on a number of base temperatures and the one producing the least variation decided by a process of elimination. The second one involves the calculation of a regression equation relating mean temperature and the heat unit summations. The correct base temperature is the one which gives a zero regression coefficient. Arnold (1959) suggested that there were three procedural errors relating to these methods

1. The use of standard deviation in the first method;
2. The rejection of the right base temperature on the basis that it is too low to be physiologically feasible;
3. The failure to take into account the effect of other environmental factors in the computation of the base temperature.

According to Arnold (1959) the base temperature resulting in the lowest coefficient of variation instead of the standard deviation is the appropriate one.

1.5.2.3 Heat unit calculation

Accumulated heat units above various base temperatures were calculated based on the formula below (Anon, 1954): Where HU is heat units; T_{max} is maximum temperature; T_{min} is minimum temperature; $T_{mean} = (T_{max} + T_{min})/2$; Tb is base temperature.

a. If $T_{min} > Tb$

$HU = T_{mean} - Tb$,

b. If $T_{min} < Tb$ and $T_{mean} > Tb$

$HU = (T_{max} - Tb)/2 - (Tb - T_{min})/4$

c. If $T_{max} > Tb$ and $T_{mean} < Tb$

$HU = (T_{max} - Tb)/4$

d. If $T_{max} < Tb$

$HU = 0$

1.6 PHOTOSYNTHESIS AND RESPIRATION

1.6.1 Photosynthesis in C_3 plants

1.6.1.1 Introduction

More than 50 years progress has been made in the study of photosynthetic pathways. We now accept that there are 3 distinct photosynthetic pathways in higher plants : the Calvin-Benson pathway (C_3 photosynthesis), the Hatch-Slack pathway (C_4 photosynthesis) and Crassulacean Acid Metabolism (CAM) (Lawlor, 1987). Under many environmental conditions C_3 photosynthesis is characterized by (a) high CO_2 compensation point - a condition when net CO_2 uptake is equal to CO_2 released and therefore there is no net gain of carbon and (b) photorespiration - that is respiration

which occurs in the light, over and above dark respiration. The rate of photorespiration is influenced by temperature and O_2 concentration and is most pronounced in C_3 plants.

On the basis of carbon isotope discrimination studies asparagus has been classified as a C_3 plant (Troughton *et al.*, 1974). Asparagus spears and cladophylls also demonstrate typical C_3 characteristics, such as oxygen-sensitive photorespiration and high CO_2 compensation points (Downton and Torokfalvy, 1975). Colman *et al.* (1979) confirmed earlier research that asparagus cell photosynthesis was inhibited by O_2 at low bicarbonate concentrations which again is considered a characteristic of C_3 plants. This review will therefore concentrate on the C_3 pathway because the research reported in this thesis has been conducted with *Asparagus officinalis* L.

1.6.1.2 **The C_3 Pathway**

The C_3 pathway is commonly called the Calvin-Benson cycle. The cycle is also often called the reductive pentose phosphate cycle or the photosynthetic carbon reduction cycle (PCR) to acknowledge the contributions from other scientists in addition to Calvin and Benson. PCR is a cyclic, autocatalytic process in which CO_2 reacts with an existing acceptor in such a way that a new carboxyl group is formed (Edwards and Walker, 1983). This pathway is also called C_3 photosynthesis because the initial product formed is phosphoglyceric acid (PGA), a 3 carbon molecule (Lawlor, 1987). Two molecules of PGA are formed as a consequence of CO_2 combining with ribulose biphosphate (RuBP, a 5 carbon molecules) in a reaction catalyzed by the enzyme ribulose biphosphate carboxylase-oxygenase (Rubisco) (Laing *et al.,* 1974). PGA is converted in a series of steps to regenerate RuBP to keep the cycle functioning. For each cycle one-sixth molecule of glucose is produced (Lawlor, 1987). The energy sources ATP and NADPH, which drive this cycle come from the light reactions of photosynthesis. Both light and dark reactions take place in the chloroplasts (Edwards and Walker, 1983).

Photorespiration can also be regarded as a cyclic sequence of events, which integrate with the PCR cycle (Edwards and Walker, 1983; Lawlor, 1987). According to this concept O_2 can compete with CO_2, giving rise to the alternative RuBPoxygenase reaction, which yields only one PGA (instead of two PGA) together with a C2 product, 2-phosphoglycolate. Lorimer (1981) showed that CO_2 and O_2 compete for the same active site on the enzyme, therefore the rates of the two reactions are determined by the concentration of the two gases. The approximate stoichiometry of C_3 photosynthesis and photorespiration under 0% and 21% O_2 is presented in figure 1.3. For a further discussion of photorespiration see section 1.6.4.

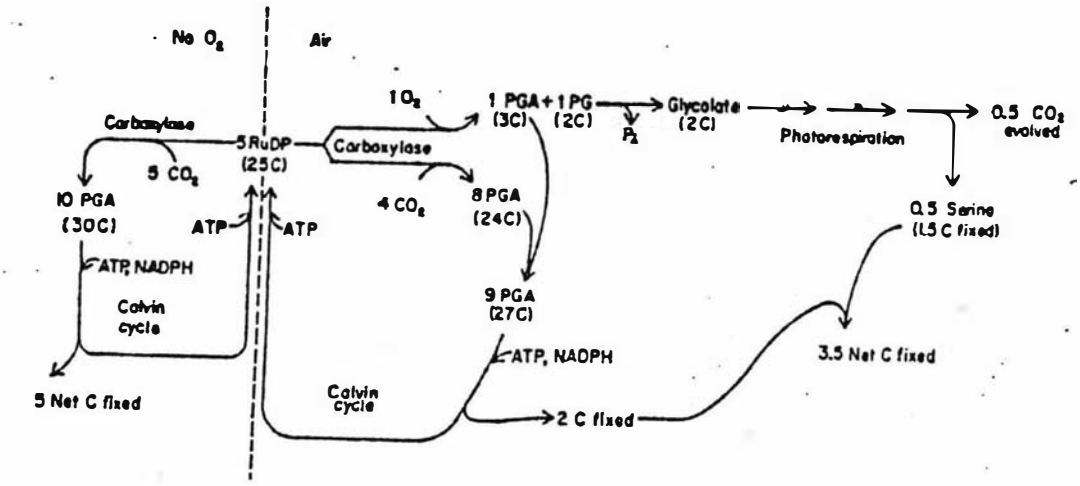


Figure 1.3 PCR cycles in C_3 plants under 0% and 21% O_2 (from Laing *et al.*, 1974)

1.6.2 **Bases for the expression of photosynthetic rate**

A wide range of units expressing photosynthetic rates exist in the literature. In the case of leaves and stems, photosynthesis is usually expressed per unit surface area,

although with leaves or leaf-like structures where all three dimensions are of the same order, such as the linear leaves or needles of conifers, dry weight is often used for convenience. Fresh weight has also been used and other bases include number and volume of cells, chlorophyll a or (a+b), protein or nitrogen content, and activity of the carboxylation enzymes (Sestak *et al.,* 1971). In asparagus, photosynthesis mostly takes place in cladophylls (Inagaki *et al.,* 1989), a small needle-like leaf, and thus it is preferable to express photosynthetic rate on a dry weight basis due to the difficulty of measuring the surface area of cladophylls by using instruments commonly used for flat leaves.

The rate of the process provides maximum information about the process itself if it is expressed on the basis of a plant characteristic which limits or at least strongly influences the process. Thus area of the leaf intercepting radiation provides a suitable basis on which to calculate the photosynthetic rate (Sestak *et al.,* 1971; Wilhelm and Nelson, 1985). Charles-Edward and Ludwig (1975), however, suggested that photosynthetic rate expressed on a leaf area basis alone can be misleading because the leaves can adapt to the environment during their growth. For example, it was found that the ratio of stomatal conductances to combined mesophyll and carboxylation conductances could differ by an order of magnitude higher than 1 in leaves grown at different light levels (Charles-Edward and Ludwig, 1975; Charles-Edward, 1979). McMillen and McClendon (1983) observed that the chlorophyll per unit area remained constant between sun and shade plants, but chlorophyll per unit fresh weight varied inversely with changes in leaf thickness. They suggested that density thickness (fresh weight per unit area) variation is important in photosynthetic adaptation to sun and shade. Gimenez *et al.* (1989) compared the photosynthesis of 2 sunflower hybrids (cv Sungro-380 and cv SH-3622) under water stress. They found that cv SH-3622 had higher photosynthesis than cv Sungro-380 and it was suggested that this partly due to a smaller number and size of cells per unit area of leaf in cv SH-3622. They regarded that smaller cell volume and shorter pathways for diffusion may allow faster transport of materials between cells or cell compartments in SH-6322 than Sungro-380, *e.g.* of the phosphate needed for ATP synthesis and therefore for RuBP regeneration. Thus comparisons among cultivars based on leaf area could be confounded by leaf

characteristics not usually accounted for in such comparisons (Bhagsari and Brown, 1986), this supports the earlier work of Charles-Edward (1978), who suggested that the apparent genetic variability in photosynthesis based on leaf area could be due to simple differences in the size of the assimilatory apparatus, rather than differences in the intrinsic photosynthetic activities of contrasting genotypes. As the absolute rate of leaf photosynthesis is the product of an intrinsic photosynthetic activity and leaf size (Charles-Edward, 1979), the rate of photosynthesis per unit leaf volume is a better indication of intrinsic activity than the rate of photosynthesis per unit leaf area.

Charles-Edward (1978) suggested that the specific photosynthetic rate (i.e. rate of photosynthesis per unit leaf dry weight) is a useful indication of intrinsic photosynthetic activity of contrasting genotypes. Studies showed that correlation of all anatomical variables of *Fragaria vesca* grown at different light and temperature levels were negatively related with photosynthesis per unit dry weight, but were insignificant on a leaf area basis (Chabot and Chabot, 1977). This was possibly due, to a decline in photochemical capacity per unit cell mass (intrinsic activity) as CO_2 resistance per mesophyll cell surface remained constant over a range of light intensities (Nobel *et al.*, 1975; Charles-Edward and Ludwig, 1975). Similarly a later study found that enzymes per unit fresh weight remained constant as leaf thickness varied (McMillen and McClendon, 1983).

From the discussion above it would appear justifiable to use dry weight as the unit of photosynthetic rate, especially when comparing the intrinsic photosynthetic capacity of different genotypes adapted to different environments as in this thesis.

1.6.3 **Factors affecting photosynthesis.**

The main environmental factors affecting the net rate of CO_2 exchange of a leaf are water, the light flux density, the ambient CO_2 and O_2 concentrations, mineral nutrition and leaf temperature. These factors interact with plant age (Lawlor, 1987).

1.6.3.1 **Water**

Water is often the most limiting factor for photosynthesis in natural or agricultural ecosystems (Salisbury and Ross, 1990). The first recognizable symptom of water stress in leaves is a decline in cell enlargement and in rate of leaf area expansion (Shaw and Laing, 1966; Slatyer, 1969) followed by individual leaf photosynthesis (Boyer, 1970). Water stress will also cause the closure of stomata and CO_2 uptake is, therefore, restricted (Troughton, 1969; Farquhar and Sharkey, 1982).

Closure of stomata in response to water stress is associated with the production of ABA (Pierce and Raschke, 1980). They suggested that ABA production begins when leaf turgor is near zero. It is suggested that ABA is partially responsible for the rapid responses of stomatal conductance to reduced water status and in the long term both conductance and photosynthesis decline (Farquhar and Sharkey, 1982). In addition, ABA also reduced the photosynthetic capacity of leaves (ie. a non-stomatal effect), but not of isolated cells or chloroplasts (Raschke, 1982; Cornic and Miginiac, 1983).

While it is generally accepted that the cause of the decrease in photosynthesis of water stressed plants is the increase in stomatal resistance (Shaw and Laing, 1966; Troughton, 1969; Boyer, 1976; Wilcox-Lee and Drost, 1990), recent research with sunflower indicates that losses in chloroplast activity (Sharp and Boyer, 1986) and or the reduction of RuBP regeneration (Gimenez *et al.,* 1989) may be involved, suggesting a direct effect of water stress on the photosynthetic system rather than an indirect effect due to CO_2 supply (Perry *et al.,* 1983). Havaux *et al.* (1986) concluded that in an intermediate stress situation, primary photosynthesis, enzymic activity, CO_2 diffusion and leaf morphology are contributing to the limitation of photosynthesis, but they did not find any extensive degradation of the thylakoid membranes.

It has been suggested that the inhibition at the chloroplast level due to water stress may sometimes be due to photoinhibition, which is light dependent damage to the photosynthetic apparatus (Björkman *et al.,* 1981). Photoinhibition results from the production of excess excitation energy at the photochemical reaction centres (Powles,

1984). This occurs when leaves are illuminated at photon flux densities in excess of that required for saturation of photosynthesis. At low leaf water potential, it has been suggested that if stomata are closed and photorespiration inhibited, the availability of CO_2 would decrease and photosynthesis would quickly become light saturated (Osmond *et al.,* 1980). This might allow a damaging excess of excitation energy to occur.

1.6.3.2 **Light intensity**

Photosynthesis and other photochemical reactions depend not on the total energy in light, but on the number of photons or quanta that are absorbed (Edwards and Walker, 1983). For example, a photon in the blue range of the spectrum has nearly twice as much energy as one in the red range, but the two photons have exactly the same effect on photosynthesis (Lawlor, 1987). Plant scientists therefore often express the quantity of light as the number of photons in the wavelength regions important for photosynthesis, 400 to 700 nm, and called photosynthetic photon flux density (PPFD). The common unit is the $\mu mol\ m^{-2}\ s^{-1}$.

It is well established that the photosynthetic response of C_3 plants to light intensity is biphasic (Lawlor, 1987). Photosynthesis increases with irradiance until it is light saturated and then eventually becomes light inhibited. Between darkness and light saturation there is an irradiance at which photosynthesis balances respiration, this is called the light compensation point (Edwards and Walker, 1983; Lawlor, 1987; Salisbury and Ross, 1990).

Under low light, between 50 and 150 μmol photons $m^{-2}\ s^{-1}$, and CO_2 non-limiting, photosynthesis is proportional to absorbed light, and the initial slope of the line is called the apparent quantum yield (α) or photochemical efficiency (mol CO_2 mol photons^{-1}) (Farquhar *et al.,* 1980; Lawlor, 1987). Ehleringer and Pearcy (1983) suggested that average α for C_3 dicot leaves and grasses is 0.052 and 0.053, respectively. That is about 1 mol CO_2 per 20 photons absorbed. At low O_2 concentration,i.e. low photorespiration, α increased to 0.07 or about 1 mol CO_2 per

14 photons (Lawlor, 1987). Farquhar *et al.* (1980) suggested that at 21% O_2 α increase markedly with increasing CO_2, showing the diversion of the enzyme from oxygenation to carboxylation, but at 1% O_2 the increase occurs only at CO_2 pressures less than 60 μbar. At low O_2 and high CO_2 concentration α of C_3 plants is greater than C_4 plants (Lawlor, 1987). Under water stress, however, α of C_3 plants was strongly inhibited (Sharp and Boyer, 1986; Havaux *et al.*, 1986) due to the inhibition of electron transport (Havaux *et al.*, 1986). Farquhar *et al.* (1980) also suggested that at atmospheric conditions α fell at high temperature, and was further reduced with increasing levels of irradiance, because the potential electron transport rate declined at high temperature. Otherwise, under low O_2 and high CO_2s concentration α is largely independent of temperature.

In C_3 plants under atmospheric conditions, photosynthesis is often saturated, or near saturated, at relatively low light over a wide range of temperatures (Edwards and Walker, 1983). For example, asparagus is saturated at about 1000 to 1400 μmol m^{-2} s^{-1} (Lin and Tsai, 1983; Inagaki *et al.*, 1989), bean at 1000 to 1500 μmol m^{-2} s^{-1} (Ticha *et al.*, 1984), cherry at 800 to 1200 μmol m^{-2} s^{-1} regardless of temperature (Sams and Flore, 1982). In roses the light saturation point increased with temperature (Pasian and Lieth, 1989).

A decrease in light intensity reduced the optimum temperature for photosynthesis in apple and cherry leaves (Seeley and Kammereck, 1977; Sams and Flore, 1982), whereas lowering the growth temperature caused a decrease in the light saturation point and maximum photosynthesis in kiwifruit and roses leaves expressed on a dry weight basis (Laing, 1985; Lieth and Pasian, 1990) indicating a close relationship between temperature and light saturation levels. Low light growing condition causing a decline of the light saturation point and maximum photosynthesis in cherry, chrysanthemum and bean (Sams and Flore, 1982; Sharkey and Badger, 1984; Holcomb *et al.*, 1988). It was found that at low light intensity the rate of electron transport was low and limited the production of ATP and NADPH and therefore limited RuBP regeneration (Sharkey and Badger, 1984; Sharkey, 1985).

Above the light saturation point, photosynthesis in C_3 plants benefit from either an increase in CO_2 or a decrease in O_2 or both (Gaastra, 1959; Ku *et al.,* 1977). At high light levels and relatively high temperatures C_3 plants will benefit from CO_2 enrichment (Edwards and Walker, 1983). Under atmospheric conditions, however, internal CO_2 often becomes limiting and photosynthesis in C_3 plants becomes saturated with light intensities above 1000 μmol m^{-2} s^{-1} (Tolbert, 1980; Farquhar and Sharkey, 1982; Lawlor, 1987), or even decreases at greater light intensities. The decrease of the light saturation of photosynthesis at high temperatures could be due to firstly, excessive energy load on the light-harvesting systems, particularly PSII, which inhibits energy transduction (Lawlor, 1987). Secondly, the limitation of the electron transport rate because the electron carriers cannot turnover fast enough (Sharkey, 1985). Thirdly, the limited availability of RuBP due to the reduction in the capacity of the carbon reactions of photosynthesis (Sharkey and Badger, 1984; Sharkey, 1985). The decrease in photosynthesis under high light is possibly due to a large reduction in photosynthetic electron transport activity because of damage in the primary photochemistry of PSII (Genty *et al.,* 1988; Krause *et al.,* 1990; Sharma and Hall, 1992). Under photoinhibitory conditions the decrease in electron transport activity was more at 5^0C than at 20^0C (Sharma and Hall, 1992). At low temperatures the decrease in CO_2 assimilation was associated with a low rate of triose phosphate utilisation (TPU) (Kobja and Edwards, 1987). The low rate of TPU would deplete the inorganic phosphate (Pi) level and this would limit photophosphorylation and the coupled electron transport promoted photoinhibition (Sage and Sharkey, 1987).

1.6.3.3 CO_2 and O_2 interaction

The response of net photosynthesis (**Pn**) of C_3 leaves to CO_2 in the atmosphere at saturating light intensity depends on O_2 concentration (Edwards and Walker, 1983). In air **Pn** of C_3 leaves is substantially less than gross photosynthesis (**Pg**), due to photorespiration (**Rl**) (Canvin, 1990). With decreasing CO_2 concentration **Pg** also decreases until **Pg = Rl + Rd**, where **Rd** is dark respiration. At this stage **Pn** is zero, and the CO_2 concentration at which this occurs is called the CO_2 compensation point (Γ).

The AC_i curve (see Figure 1.4) have been used to described the relationship between internal CO_2 concentration and net photosynthesis. The curve basically describes 2 responses of photosynthesis to internal CO_2 concentration (C_i) which occur as C_i increase from about 40 ppm (CO_2 compensation point for C_3 plants) to beyond ambient (Farquhar and Sharkey, 1982). The first response is due to a demand function where at low C_i the Rubisco is RuBP saturated. In this region the response of photosynthesis to C_i is linear and the slope is a prediction of carboxylation efficiency (CE) (Farquhar and Sharkey, 1982). The second function is called the supply function where at high C_i the Rubisco is RuBP limited (Farquhar and Sharkey, 1982), the limited RuBP is not due to insufficient irradiance (Farquhar *et al.*, 1980), but due to insufficient electron transport capacity to produce the ATP and reduced NADP for RuBP regeneration, as found by Lilley and Walker (1975) in isolated spinach chloroplasts. That photosynthesis becomes limited by RuBP regeneration is shown by the abrupt change in the slope of AC_i curve (Figure 1.4) (Farquhar and Sharkey, 1982; Layne, 1989).

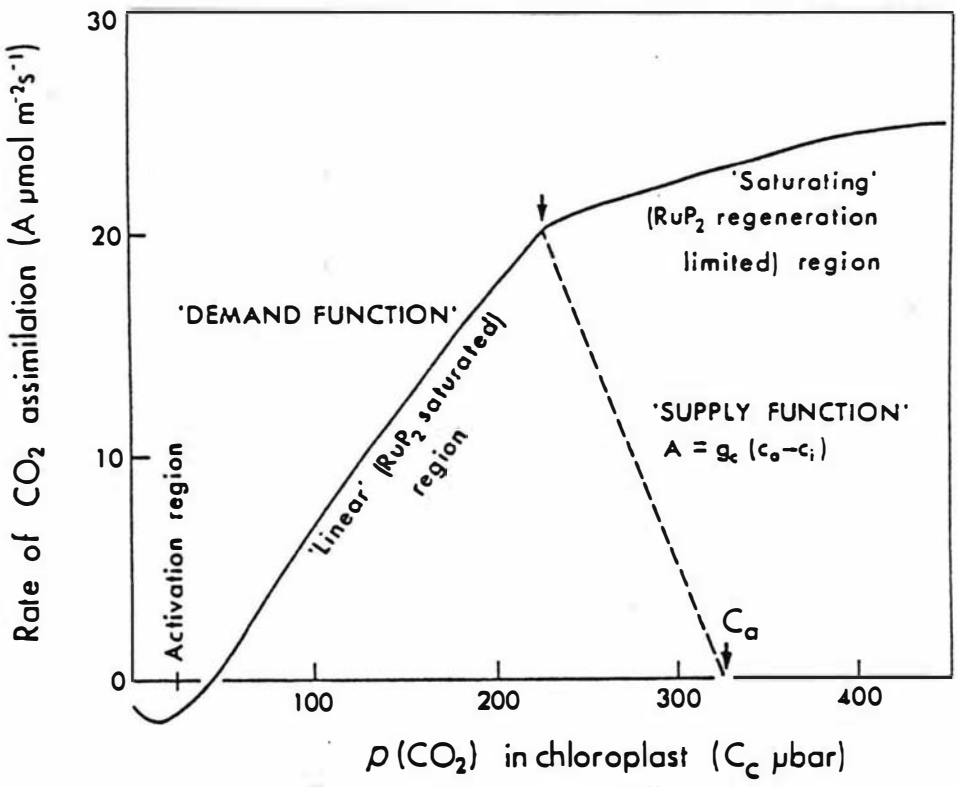


Figure 1.4 The photosynthetic response to internal CO_2 concentration as proposed by Farquhar and Sharkey (1982)

Forester *et al.* (1966a) and Tregunna *et al.* (1966) suggested that O_2 inhibition of photosynthesis was defined as an O_2 inhibition of the efficiency of CO_2 fixation (CE, see paragraph above). Studies showed that CE of bean leaves increased with decreasing O_2 concentration (Laing *et al.*, 1974; Farquhar *et al.*, 1980; von Caemmerer and Farquhar, 1981), with increasing light intensity (von Caemmerer and Farquhar, 1981; Sharkey, 1984) and nitrogen nutrition levels (von Caemmerer and Farquhar, 1981). CE also increased linearly with RuBP carboxylase activity and electron transport (von Caemmerer and Faquhar, 1981). Rising temperatures from 15 to 35^{0}C also increased CE in soybean, wheat, sunflower, watermelon, eggplant and jackbean leaves (Hew *et al.*, 1969; Laing *et al.*, 1974; Ku and Edward, 1977; von Caemmerer and Farquhar, 1981), indicating that at this physiological range of temperatures carboxylase reaction still dominates for RuBP (Farquhar *et al.*, 1980; von Caemmerer and Faquhar, 1981). Temperatures higher than 35^{0}C, however, reduce CE of C_3 leaves (Edwards and Walker, 1983; Lawlor, 1987). Thus high temperatures and a low CO_2/O_2 ratio in the leaf, *e.g.* due to decreasing stomatal conductance, enhances the rate of photorespiration so that C_3 photosynthesis become less efficient as temperature rises.

Farquhar *et al.* (1980) derived a kinetic expression which relates the ratio (Φ) of the rate of oxygenase reaction (V_o) to the rate of carboxylase reaction (V_c) :

$$\Phi = \frac{V_o}{V_c} = \frac{V_{cmax}}{V_{cmax}} \times \frac{K_m(CO_2)}{K_m(O_2)} \times \frac{[O_2]}{[CO_2]} \qquad (1.5)$$

under certain condition there will be Φ oxygenation of RuBP for each carboxylation. This ratio is directly proportional to the ratio of O_2 and CO_2 concentrations, directly proportional to the ratio of the V_{max} activities of the Rubisco, and inversely proportional to the ratio of the Michael Menten kinetic term, K_m. Where K_m is the level of substrate at which the rate of reaction is half of the maximum and is a measure (inverse) of the affinity of an enzyme for its substrate. In C_3 leaves, Φ increases with temperature (Berry and Bjorkman, 1980). There are two possible reasons for this increase, firstly, CO_2 and O_2 compete for RuBP at the same active

site on the Rubisco (Laing *et al.*, 1974). The competition between CO_2 and O_2 in the active site of Rubisco determines the relative rates of photosynthesis and photorespiration. Secondly, CO_2 is more soluble in water than O_2 (Edwards and Walker, 1983). With increasing temperature, however, the solubility of CO_2 decreases relatively faster than the solubility of O_2 (Ku and Edwards, 1977). This results in an increased solubility ratio of O_2/CO_2 at higher temperatures. They argued that the dependency of Φ on temperature is mainly due to temperature-dependent changes in the solubilities of O_2 and CO_2 in water. However, as shown in equation 1.5, other parameters in addition to the solubility could affect the temperature dependence of Φ. For example, it was found that the affinity of Rubisco to CO_2 decreased (or $K_m(CO_2)$ increased) more rapidly with temperature than did the affinity for O_2 (Laing *et al.*, 1974; Peisker and Apel, 1977; Servaites and Ogren, 1978; Monson *et al.*, 1982). Therefore the value of the $K_m(CO_2)/K_m(O_2)$ ratio increased with temperature, while that of the V_{max} activities remained fairly constant. Jordan and Ogren (1984) confirmed that only one third could be ascribed to the changing ratio of solubilities of CO_2 and O_2, while the rest, about two thirds, was due to changing kinetic parameters of the enzymes.

1.6.3.4 **Temperature**

At normal physiological temperatures, increasing temperature has little effect on the light-driven split of H_2O or on the diffusion of CO_2 into the leaf, but markedly influences the biochemical reactions of CO_2 fixation and reduction (Berry and Bjorkman, 1980; Edwards and Walker, 1983). Thus increases in temperature usually increase photosynthetic rates until enzyme denaturation and photosystem destruction begin. However, respiration also increases with temperature, and this is especially pronounced for photorespiration. The increase in photorespiration results in net photosynthesis in C_3 plants not being enhanced by increasing temperature nearly as much as might be expected as in C_4 plants (Lawlor, 1987; Salisbury and Ross, 1990).

At low temperatures and bright light, photosynthesis of non-adapted species are reduced because of low Rubisco activity and reduced capacity for electron transport

due to photochemical damage to light-harvesting systems (Berry and Björkman, 1980; Farquhar and Sharkey, 1982). Adapted leaves in high light intensity and low temperatures, however, often had higher maximum rates of photosynthesis per unit of leaf area, because the leaves were thicker and had higher mass, protein, and amounts of rate-limiting components of the photosynthetic apparatus per unit of area (Björkman, 1973; Berry and Björkman, 1980; Patterson, 1980). It was suggested that acclimation to low temperature was brought about by an increase in the capacity of temperature-limited enzymic steps of the photosynthetic process (Berry and Björkman, 1980).

Unlike C_4 plants, C_3 plants do not benefit from high temperature growing conditions (Edwards and Walker, 1983; Lawlor, 1987). For example, increasing temperatures well beyond the normal temperature experienced by plants, reduced electron transport capacity and increases photorespiration greatly (Berry and Björkman, 1980; Edwards and Walker, 1983). At high temperatures it was suggested that ATP and NADPH were not produced fast enough in C_3 plants to promote increases in photosynthesis, so regeneration of RuBP becomes limiting (Farquhar and Sharkey, 1982; Salisbury and Ross, 1990). Activation of Rubisco could decrease at high temperature as found in cotton leaf (Weis and Berry, 1988). High temperatures could also damage photosystem II, with mature leaves more labile to stress (Weis and Berry, 1988; Al-Khatib and Paulsen, 1989) as well as a decrease in the supply of reducing energy within the leaf and a subsequent affect on enzyme reactions which are regulated by the light reaction (Weis and Berry, 1988). Thermal injury due to high temperature stress was accentuated by high light intensities causing decreases in whole chain electron transport, quantum yield, and the light saturation point (Al-Khatib and Paulsen, 1989).

CO_2 compensation point of C_3 leaves is low in cool temperatures with low O_2, but increases as temperature and O_2 rise, particularly when O_2 exceeds the point where oxygenation/carboxylation ratio (Φ) exceeds 2 and temperatures are greater than 35^{0}C (Jolliffe and Treguna, 1968; Farquhar *et al.*, 1980; Lawlor, 1987).

1.6.3.5 **Effect of day and night temperatures on photosynthesis**

Went (1944) suggested that growth of plants is greater when the night temperature is below the day temperature possibly due to small respiratory losses during the night. This might be true only at optimum or supra-optimum temperatures (Ivory and Whiteman, 1978). They found a diurnal variation in temperature gave higher growth rates than a constant temperature for the same daily mean. Otherwise, under suboptimum temperatures conditions a constant temperature gave the highest growth rates and growth rate decreased as diurnal temperature variation increased. They suggested that this was due to the relative effects of night temperature on photosynthesis and dark respiration. Evidence indicated that low night temperatures reduced net photosynthesis significantly during the subsequent day (Izhar and Wallace, 1967; Ludlow and Wilson, 1971b; Tollenaar, 1989; Grantz, 1989). This can be ascribed to a 'feedback' effect on photosynthesis, ie, at low night temperatures respiration rate and photosynthate use for growth slowed, photosynthates accumulates and subsequent net photosynthesis is therefore inhibited (Moldau and Karolin, 1977; Azcon-Bieto, 1983; Azcon-Bieto and Osmond, 1983; Barnett and Pearce, 1983; Sharkey, 1985; Benoit *et al.,* 1986). In another study, McCree and Amthor (1982) grew plants at 30/10^{0}C and constant 20^{0}C and found that net photosynthesis of plants at constant 20^{0}C was higher because of lower day respiration rate.

In contrast, data from several experiments (Dale, 1964; Hussey, 1965; Robson, 1973; Rajan and Blackman, 1975) indicated that night temperatures higher than day temperatures resulted in more rapid growth during the night, a greater leaf area was produced, and photosynthesis was enhanced in the subsequent day.

1.6.3.6 **Stomatal response to temperature and its effect on photosynthesis**

Under normal atmospheric conditions photosynthesis is limited by the internal CO_2 concentration, especially in C_3 plants (Berry and Björkman, 1980; Edwards and Walker, 1983; Lawlor, 1987). At low temperature the dependency is relatively small, but becomes greater as the temperature increases (Berry and Björkman, 1980). They

suggested that stomata may have a strong influence both on the rate and on the temperature dependence of photosynthesis.

Earlier studies showed contradictory results of stomatal response to temperature. While a group of scientists claimed that stomata tend to open with increasing temperature (Stalfelt, 1962; Walker and Zelitch, 1963; Hofstra and Hesketh, 1969; Drake *et al.*, 1970; Drake and Salisbury, 1972; Lange *et al.*, 1974; Ku *et al.*, 1977), others suggested that stomata close at higher temperature (Heat and Meidner, 1957; Rees, 1961; Downes, 1970 ; Wuenscher and Kozlowski, 1971). Berry and Björkman (1980) suggested that the stomata response to temperature is affected by other interacting factors such as internal plant water status and the water vapour pressure difference between the leaf and surrounding air. Evidence showed that stomata remain open in well-watered plants as the temperature increased over a wide range, while that of water stressed plants decreased above a certain temperature (Schulze *et al.*, 1973; Losch, 1979). It was also found that the stomata of *Sesasum indicum* and *Citrus sinensis* closed with increasing temperature when the vapour pressure of the air was held constant, but keeping the vapour pressure difference constant by adjusting the vapour pressure of air, the stomata continued to open with increasing temperature (Hall *et al.*, 1975; Hall and Kaufmann, 1975).

Night temperature also influence stomatal aperture. Zelitch (1963) grew tobacco plants at the same day temperature. He found that low night temperatures (16^0C compared to 27^0C) reduced stomata opening during the day. Therefore it is suggested that inhibition of photosynthesis after cold nights may be caused by the closure of stomata (Zelitch, 1971).

Where plant are not subjected to water stress and high water vapour pressure gradients, stomata tend to respond to temperature following the changing photosynthetic demand for CO_2 (Berry and Björkman, 1980). Evidence showed that the fall in photosynthesis at very high temperature was not caused by stomatal closure, and stomatal conductance even remained high when leaves were heated to

temperatures that damaged the photosynthetic apparatus (Raschke, 1970; Berry and Bjorkman, 1980).

1.6.3.7 **Leaf age**

In general, photosynthesis increases rapidly during leaf development reaching a maximum usually before full leaf area expansion, photosynthesis then decreases slowly but at an increasing rate during the last developmental stages or senescence (Catzky and Ticha, 1980; Sestak, 1981). In the last developmental stage, the maximum photosynthesis and light saturation point of tomato leaf decreased considerably (Peat, 1970), this is probably due to (a) the decrease in the activity of Rubisco and its concentration (Hall *et al.*, 1978; Perry *et al.*, 1983), (b) a decline in the rate of electron transport in the chloroplast (Jenkins and Woolhouse, 1981a and 1981b), (c) the decrease in stomatal (g_i) and mesophyll conductance (Catsky *et al.*, 1976; Constable and Rawson, 1980). Pasian and Lieth (1989), however, did not find clear patterns in photosynthetic efficiency associated with leaf age of roses. They suggested that the range of leaf ages used in their experiment was far from the senescence stage.

Ticha *et al.* (1984) found that the ontogenetic course of photosynthesis was modified by leaf temperature during leaf senescence, the higher the temperature , the slower the decline in photosynthesis. This was, in part, due to stomata and intercellular conductance increasing with temperature (Bennett *et al.*, 1982; Woledge and Dennis, 1982). At lower irradiance Ticha *et al.* (1984) also observed the ontogenetic maximum of photosynthesis was shifted to a later period of leaf ontogeny.

1.6.3.8 **Sink demand**

One internal control of photosynthesis is the rate at which photosynthetic product such as sucrose can be translocated from leaves to various sink organs. For example, it is well established that removal of strong sinks such as developing tubers, seeds, or fruits inhibits photosynthesis (Moss, 1962; King *et al.*, 1967; Salisbury and Ross, 1990). Plaut *et al.* (1987) found that photosynthesis declined due to decreasing sink strength.

such as the removal of developing fruits, as found by Ho *et al.* (1983) and Hammond *et al.* (1984). Peet and Kramer (1980) and Perry *et al.* (1983) also observed that fruiting plants of soybean and cotton had considerably higher net photosynthesis and lower photorespiration rates than did the nonfruiting ones. Perry *et al.* (1983) suggested that the higher photorespiration in nonfruiting plants was due to alteration of the kinetics of Rubisco. Geiger and Giaquinta (1982), however, disagreed that there was simple feedback response in which decreasing export caused the accumulation of photosynthetic products and therefore inhibit photosynthesis. They suggested that the response to the decreases in export occurred slowly, some species even avoiding inhibition of photosynthesis by accumulating starch and sugars. Experimental results appear to depend very much on the ability of the plant to store carbohydrate in alternative sinks.

Lack of sink activity also reduced TPU, ie. starch plus sucrose synthesis (Herold, 1980). Walker and Herold (1977) suggested that TPU is required at one third of the rate of CO_2 fixation, otherwise the level of free phosphate (Pi) will decline and therefore Pi will be unavailable for photophosphorylation, and begin to limit the rate of photosynthesis. Harris *et al.* (1983) observed that in leaves limited by Pi availability, photosynthesis becomes independent of Φ, the ratio of oxygenation to carboxylation, possibly because the rate of photosynthesis equals the rate of triose phosphate production (Sharkey, 1985).

Salisbury and Ross (1990) also indicated that species that have high photosynthetic rates also have relatively high translocation rates. This is consistent with the idea that effective transport of photosynthetic products maintains rapid CO_2 fixation.

1.6.3.9 **General conclusion on the factors affecting photosynthesis**

Water Stomatal closure is suggested to be the major cause of the reduction of photosynthesis when the plant is subjected to water stress. Although some evidence indicated that water stress also directly affects the photosynthetic system.

Light intensity The direct response of photosynthesis to light intensity can be described mainly by quantum yield (α) and photosynthesis at light saturation (Pmax). In C_3 plants the α fluctuates with CO_2 concentration, temperature level and soil moisture content. Meanwhile light saturation point is reasonably stable over a wide range of temperatures and in C_3 plant Pmax is achieved at relatively low light intensities, the value decrease with increasing temperature. Light saturation is reached when CO_2 supply is not sufficient to support the high energy level available.

CO_2 and O_2 concentration The effect of CO_2 and O_2 concentration on the photosynthetic process is determined by rates of CO_2 diffusion and the presence of photorespiration (C_3 plant type). In C_3 plants under normal atmospheric conditions photosynthetic efficiency is determined by the interaction between CO_2 and O_2 concentration and this phenomena has been described by Φ.

Temperature Temperature mainly affects the biochemical reactions of CO_2 fixation and reduction. The optimum temperature for photosynthesis of C_3 plants ranges from 20 to 30^{0}C. The decrease in photosynthesis at higher temperature is due to the increase in photorespiration, the denaturation of photosynthetic enzymes and the destruction of the photosynthetic system. Low night temperature is also suggested to reduce photosynthesis in the following day due to a low rate of dark respiration.

Leaf age Photosynthesis follows a positive quadratic response to ontogenetic changes. The photosynthetic maximum is achieved before full leaf area expansion. The decrease in photosynthesis in the later stages of development is due to the decrease in Rubisco activity, rate of electron transport and conductances.

Sink demand In many cases removal of sink organ, such as fruit, decreases photosynthesis. However, this relationship is not always simple as some species show an ability to accumulate the photosynthetic product (such as starch and sucrose) without having any harmful effect on photosynthesis.

1.6.4 **Correlations of photosynthesis with growth and yield**

The capture and photosynthetic utilization of radiant energy occurs at different organizational levels : the individual leaf, the whole plant, and the crop. At any time, the photosynthetic elements of the crop suffer from climatic limitations, and also environmental constraints such as shading, due to the development of the crop.

Within C_3 and C_4 species, considerable differences have been reported between and within varieties of crop plants in their maximum rates of photosynthesis per unit leaf area (Dornhoff and Shibles, 1970; Elmore, 1980; Bhagsari, 1981; Gifford and Evans, 1981; Zelitch, 1982; Bhagsari and Brown, 1986; Gifford, 1987; Bhagsari and Ashley, 1990). However, there was no consistent association between photosynthesis and crop growth and yield. There is no clear reason for this lack of association (Evans, 1975; Bhagsari and Ashley, 1990). Negative correlation between photosynthesis and leaf area was suggested as a contributing factors (Austin *et al.*, 1982; Bhagsari and Brown, 1986; Gifford and Evans, 1981), or possibly yield is not limited by the potential supply of assimilates (Evans, 1975), but by assimilate distribution. Zelitch (1982) and Bunce (1987) suggested that the lack of correlation between photosynthesis and growth and yield was due to most studies of photosynthesis relying on individual leaves over short periods of time (minutes to hours) at high light intensity, which may not be very reliable because other factors which contribute to production are neglected. Lawlor (1987) suggested that measurement of photosynthesis over longer periods and of larger areas of crop correlated better with production.

1.6.5 **Photorespiration**

1.6.5.1 **Introduction**

Photorespiration, as the name implies, is the additional respiration that occurs in the light. It can be detected in C_3 plant by a number of methods, but it is difficult to measure absolute levels of photorespiration, since under steady-state conditions in the light, photosynthesis, dark respiration and photorespiration are occurring

simultaneously. The existence and importance of photorespiration was first clearly described by Decker (1959). The post-illumination CO_2 burst he observed in C_3 plants decelerated for several minutes following darkness after a period of photosynthesis. Decker (1955) attributed the burst phenomenon to the low levels of photorespiratory substrate remaining in the leaf immediately following withholding light.

1.6.5.2 **Biochemistry of photorespiration**

It is now widely accepted that photorespiration arises because Rubisco has an oxygenase activity as well as carboxylase (Ogren and Bowes, 1971). Under normal atmospheric conditions (330 μbar CO_2, 21% O_2) the carboxylase enzyme appears to fix 4 CO_2 for every O_2 molecule (Long *et al.*, 1975). This ratio of activities has been observed with Rubisco extracted from leaves of soybean (Laing *et al.*, 1974). Under normal atmospheric conditions, it was observed that for every 10 RuBP that cycle through, there will be a net gain of 7 carbons. One CO_2 will be evolved for every 7 carbons gained, resulting in a loss of 14% (Laing *et al.*, 1974).

Induced mutants of *Arabidopsis thaliana* have provided convincing evidence that phosphoglycolate is the only source of carbon for the photosynthetic carbon oxidation cycle (Somerville and Ogren, 1979). In the stroma phosphoglycolate is then hydrolysed to glycolate by a specific phosphatase (Tolbert, 1980; Edwards and Walker, 1983). Glycolate is cycled back into the Calvin cycle via glycine, serine and glycerate using enzymes in both the peroxisome and mitochondrion. The CO_2 released during photorespiration comes almost exclusively from glycine oxidation (Tolbert, 1980; Husic *et al.*, 1987). The accepted stoichiometry is 2 glysines per serine and CO_2 (Berry *et al.*, 1978).

1.6.5.3 **Methods of measurement of photorespiration**

1.6.5.3.1 **Introduction**

Despite our good understanding of the photorespiration pathway, there is still some

disagreement about the rate of photorespiration. For example, Ogren (1984) believes that 15% of the CO_2 used in gross photosynthesis is lost through photorespiration, while Gerbaud and Andre' (1987) claim the rate is between 30 and 50%. These discrepancies could be, in part, due to differences in the method of measurement of photorespiration. There are four different methods which are commonly used for measuring photorespiration. All methods have theoretical or technical problems.

1.6.5.3.2 **Post illumination CO_2 burst (PIB)**

On darkening, glycine metabolism continues longer than does CO_2 assimilation and so efflux of CO_2 from a leaf is observed for 1 to 4 minutes (Decker, 1955). This burst of CO_2 is a good indicator that photorespiration is occurring. The rate of photorespiration is taken as either the slope of the tangent to the CO_2 concentration trace at the end of irradiation period (Decker, 1955) or as the maximum rate of burst (Tregunna *et al.,* 1961). The CO_2 outburst increased with increasing irradiance, increased with higher leaf temperatures between 14.5 and 33.5^{0}C, was unchanged when the leaf was maintained either at the CO_2 compensation point or in atmospheric condition (Decker, 1959; Hew *et al.,* 1969), was inhibited by low O_2 concentration (Forrester *et al.,* 1966a), and declined with increasing CO_2 concentrations (Doehlert *et al.,* 1979; Sharkey, 1985). Maize leaves, however, did not show a typical PIB indicating that photorespiration is low in C_4 species (Forrester *et al.,* 1966b).

There are several disadvantages associated with PIB. First, a variable amount of CO_2 assimilation occurs after the light is turned off (Laisk *et al.,* 1984), which masks the CO_2 burst. Second, the rate of CO_2 release decreases with time, and determination of the maximal rate is subjective (Ludlow and Jarvis, 1971). Third, mitochondrial respiration occurs during this post illumination period (Azcon-Bieto and Osmond, 1983).

This assay, however, is relatively easy and rapid to perform. It can be used at a wide range of CO_2 concentrations and for studying the effects of other environmental factors (Decker, 1959; Treguna *et al.,* 1961, 1966). Ishii and Nagai (1980) suggested

that PIB method was preferable to CO_2 flux into CO_2-free air and extrapolation methods due to the problem of refixation of CO_2 by photosynthesis. Canvin (1979) also suggested that rates of photorespiration computed from PIB using identical systems provide a comparative estimate of the rate of photorespiration since the rate measured from any burst depends on the resolution of the system (volume of plant chamber, etc.) and the resolution of the measuring cell (volume) in the infra red gas analyzer. This was the method selected for the present work.

1.6.5.3.3 **Inhibition of net assimilation by oxygen**

Photorespiration is strongly dependent on O_2 concentration as studies revealed that increases in net photosynthesis of 33% to 50% were obtained in C_3 species when the O_2 content in the atmosphere was decreased from 21% to 1%-3% (Zelitch, 1971). Hence, it is often assumed that the decrease in net photosynthesis with increasing O_2 concentration is a function of the rate of photorespiration. This assay, however, underestimates the magnitude of photorespiration because glycolate metabolism occurs even at low O_2 concentration (Robinson and Gibbs, 1974). Oxygen is always produced by chloroplasts during photosynthesis and may therefore be enriched at the site of glycolate synthesis so that photorespiration cannot be inhibited completely (Zelitch, 1979). Also, loss of O_2 sensitivity has been reported even though photorespiration still occurs in the presence of O_2. This happens when starch and sucrose synthesis limit photosynthesis (Sharkey, 1985).

1.6.5.3.4 **CO_2 efflux into CO_2-free air**

An irradiated leaf is supplied with CO_2-free air and the increase of CO_2 in the chamber, resulting from CO_2 efflux, is measured. This assay is a convenient one. However there are five reasons why this method fails as a quantitative measure of photorespiration. First, the rate of CO_2 efflux is determined in an open system with rapid flow rates and at concentrations of CO_2 close to zero. These conditions limit the sensitivity of the measurement with an infrared gas analyzer and hence the accuracy is limited (Zelitch, 1979). Second, the pool of RuBP can be very low in leaves held

in CO_2-free air (Badger *et al.,* 1984). Third, the rate of CO_2 efflux depends on the rate of photorespiration, the diffusive resistance to CO_2 fixation by the chloroplast, and the stomatal diffusive resistance (Bravdo, 1968). Therefore this method reveals only a portion of photorespiration. Fourth, CO_2 is a competitive inhibitor of photorespiration and thus the rate of photorespiration is enhanced in CO_2-free air relative to normal air (Edwards and Walker, 1983). Fifth, it was found that Rubisco was less active in CO_2-free air (von Caemmerer and Edmondson, 1986).

1.6.5.3.5 **Short-term uptake of $^{14}CO_2$ and $^{12}CO_2$**

If, under steady state conditions of photosynthesis, a leaf is suddenly fed with $^{14}CO_2$ for a short period the initial rate of $^{14}CO_2$ uptake represents gross photosynthesis and will be greater than the previous $^{12}CO_2$ uptake, which measured net photosynthesis (Ludlow and Jarvis, 1971). This method seems to be the most reliable one on theoretical grounds, however there are two significant uncertainties in the measurement of gross photosynthesis. First, it was found that recently fixed $^{14}CO_2$ is respired and recycled so rapidly within the leaf cells that $^{14}CO_2$ released can be detected outside the leaf within 15 to 45 seconds (Ludwig and Krotkov, 1967). Gerbaud and Andre (1987) showed that by ignoring the recycling effect on the specific activity of CO_2 inside the leaf a 20% error in the measurement of photorespiration can arise. The second problem associated with this method is the isotope effects. O'Leary (1981) showed that Rubisco discriminates against $^{13}CO_2$ (a naturally occurring stable isotope) relative to $^{12}CO_2$. However, he also found that the discrimination against $^{14}CO_2$ is about twice that against $^{13}CO_2$, which is about 5.5%. The error is amplified in the calculation of photorespiration and can exceed 25% (Sharkey, 1988). If this method is used with exposure times of several minutes the photorespiration would be greatly underestimated (Zelitch, 1979).

1.6.5.4 **Environmental effect on photorespiration**

This section summarizes the discussion of the effect of environmental factors on photorespiration. The oxygenation reaction is accelerated with increasing O_2 or

decreasing CO_2 concentration (Edwards and Walker, 1983; Lawlor, 1987; Canvin, 1990). These workers suggested that low temperature suppresses photorespiration. Increasing temperature has been found to raise the O_2/CO_2 solubility ratio inside the leaf (Ku and Edwards, 1977) and decrease the affinity for CO_2 (Laing *et al.*, 1974; Servaites and Ogren, 1978; Monson *et al.*, 1982). Both factors are responsible for the increase of photorespiration with temperature. The response of photorespiration to high temperatures depends on species. For example, Hew *et al.* (1969) found that maximum photorespiration rate of sunflower was at 30°C and then decreased. While in tobacco, the photorespiration rates still increased at 40°C (Ishii and Nagai, 1980; Peterson, 1983; Perry *et al.*, 1983).

1.6.5.5 **Role of photorespiration**

Whether there is a positive benefit from photorespiration has long been open to debate. Tolbert (1980) and Ogren (1984) suggested that CO_2 recycling through photorespiration effectively dissipated excess photochemical energy when CO_2 supply to illuminated leaves was limiting. When stomata are closed, atmospheric CO_2 can not enter the leaves, and photorespiration could provide a sink for the electron transport pathway through both RuBP oxygenase activity and the refixation of CO_2 released in photorespiratory glycine decarboxylation (Ogren, 1984). Evidence supporting this theory has been obtained through studies of photoinhibition (Powles and Osmond, 1978; Powles *et al.*, 1979; Heber and Krause, 1980). They found that the internal generation of CO_2 and the orderly dissipation of photochemical energy by the ATP and NADPH requirements of the integrated photosynthesis and photorespiration processes served to protect the photosynthetic apparatus against photooxidative damage when leaves of higher plants were deprived of external CO_2 in the light. For example, daytime stomatal closure during periods of water stress (Heber and Krause, 1980).

1.6.5.6 **The control of photorespiration**

Theoretically formation of phosphoglycolate could be prevented or reduced either by alteration of Rubisco such that the ratio of oxygenase to carboxylase was reduced, or by alteration of the ratio of O_2 and CO_2 available to the enzyme. Modification of Rubisco in favour of carboxylation by using genetic engineering is still in progress (Lindsay and Jones, 1989). For example, mutants of the C_3 plants *Arabidopsis thaliana* and barley that are defective in photorespiration have been found (Somerville and Ogren, 1979; Bright *et al.*, 1984). These mutants are deficient in photoglycolate phosphatase activity and consequently such plants can not survive in natural air because of the accumulation of toxic intermediates of photorespiration (Lindsay and Jones, 1989). This suggests that the modification must occurs in the process before the formation of phosphoglycolate, i.e. modification of the oxygenation reaction for example by decreasing the affinity of Rubisco to O_2 (increase Km for O_2) (Lindsay and Jones, 1989).

In C_4 plants, the ratio of O_2 to CO_2 at the site of Rubisco is achieved by means of the C_4 cycle, a set of reactions which acts as a "CO_2 pump" and therefore increases the CO_2 concentration to a point at which the oxygenase activity is either dramatically reduced or completely absent (Ehleringer, 1979). It is still in doubt wheter the C_4 cycle can be introduced into C_3 plants, because it will involve revolutionary changes in leaf morphology.

1.6.6 **Dark respiration**

1.6.6.1 **Introduction**

Dark respiration is a key physiological process for growth and maintenance. Respiration is much more than a simple exchange of gases. The overall it is an oxidation-reduction process in which compounds are oxidized to CO_2 and the O_2 absorbed is reduced to form H_2O and energy rich ATP formed. Starch, fructans,

sucrose or other sugars, fats, organic acids can serve as respiratory substrates (Amthor, 1989; Salisbury and Ross, 1990).

1.6.6.2 **Respiratory pathways**

Amthor (1989) and Salisbury and Ross (1990) have provided outstanding reviews on dark respiration of plants. They described three different processes of respiration: (*1*) glycolysis followed by (*2*) tricarboxylic acid (TCA) cycle or Kreb or citric acid cycle, and also (*3*) the oxidative pentose phosphate pathway. Basically during respiration, situated in cytosol, starch and sugars are degraded to pyruvate by **glycolysis**, generating ATP. The pyruvate is converted to acetyl-CoA by pyruvic acid dehydrogenase, situated in the mitochondria (Amthor, 1989; Salisbury and Ross, 1990). In the mitochondria, acetyl-CoA enter the **tricarboxylic acid cycle** where it is metabolized to organic acids (α-ketoglutarate, fumarate, citrate), releasing CO_2 and forming NADH. NADH is then oxidized by the mitochondrial electron transport chain with O_2 as terminal acceptor, producing water. Electron transport is coupled to phosphorylation, and this is the source of ATP in respiration. The other source of CO_2 during respiration is an oxidative pentose phosphate pathway. This pathway oxidizes glucose 6-phosphate to 6-phosphogluconate using glucose-6-phosphate dehydrogenase. The enzyme 6-phosphogluconate dehydrogenase then catalyses the reaction of 6-phosphogluconate and NADP in the formation of ribulose-5-phosphate, NADPH, and CO_2.

1.6.6.3 **Respiration of green cells in the light and the dark**

Biochemical evidence suggests that the tricarboxylic acid cycle continues to operate in illuminated leaves at about the same rate as it does in darkness (Graham, 1980). It was previously believed that photosynthesis would drain all the ADP away from mitochondria and so restrict oxidative phosphorylation. However, Lambers (1990) suggested that dark respiration can occur in light for two major reasons. Firstly, because recent discoveries have indicated a source of ADP from a non-phosphorylating path in leaves which allows electron transport to continue. Secondly,

the level of ADP in the mitochondria is not as low in the light as originally believed. It is now no longer a question whether dark respiration continues during light, but rather, to what extent (Gardestrom and Edwards, 1985).

1.6.6.4 **Factors affecting dark respiration**

Several factors affect dark respiration rates. Temperature is one significant factor which strongly influences respiration rate under most conditions. The other factors are substrate availability and photosynthesis (Salisbury and Ross, 1990).

1.6.6.4.1 **Temperature**

Generally an increase in temperature results in an increase in respiration rate (Amthor, 1989; Salisbury and Ross, 1990). Very high temperatures, however, can damage the tissue and metabolic activity and denaturation the enzymes involved in the respiratory process causing a respiration rate decrease (Amthor, 1989; Salisbury and Ross, 1990). Earlier studies showed that respiration rates of various species increased with temperatures up to about 40 to 50^{0}C (Hofstra and Hestketh, 1969; Nevins and Loomis, 1970; Brown and Thomas, 1980; Ludwig *et al.,* 1965; Rice and Eastin, 1986). Gale (1982) suggested that at high temperature, respiration was essential for maintenance of leaf function. He observed that inhibiting respiration during high temperature damaged the photosynthetic apparatus.

For most species and parts, the Q_{10} for respiration between 5 and 25^{0}C is usually between 2.0 and 2.5 (Glover, 1973; Da Costa *et al.,* 1986; Sale, 1974; Salisbury and Ross, 1990). That is respiration approximately doubles for a 10^{0}C rise in temperature. Increasing temperatures up to 30 or 35^{0}C still increases the respiration rate but less rapidly, and therefore Q_{10} decrease (Salisbury and Ross, 1990). They suggested this decrease is associated with the limitation of the rate of O_2 penetration into cells.

1.6.6.4.2 **Substrate availability**

Respiration rate of plants depends on the availability of substrate under many conditions (Osman, 1971; ; Veen, 1981; Ryle *et al.,* 1985; Hansen, 1977; Azcón-Bieto and Osmond, 1983; Penning de Vries *et al.,* 1979; Coggeshall and Hodges, 1980; Moser *et al.,* 1982; Azcón-Bieto *et al.,* 1983; Baysdorfer *et al.,* 1987). Therefore, it is often assumed that increasing substrate levels leads to an increase in respiration rate. For example, respiration rates of leaves are often faster just after sunset than after sunrise, because sugar levels are higher after sunset (Salisbury and Ross, 1990). Some evidence, however, showed that the dependency of respiration on substrate availability only occurs when substrate levels are low (Breeze and Elston, 1978; Fader and Koller, 1984). Other studies revealed that respiration was regulated by the need for ATP or the availability of ADP for oxidative phosphorylation (Hrubec *et al.,* 1985) and limited by the turnover of ATP (Bingham and Farrar, 1988). In contrast Farrar (1980, 1981) suggested that there is no control of the respiration rate by soluble carbohydrate.

1.6.6.4.3 **Photosynthesis**

Dark respiration rates of leaves and whole plants is positively related to the rate of previous photosynthesis (Ludwig *et al.,* 1965; Sale, 1974; Azcón-Bieto and Osmond, 1983; McCree and Troughton, 1966; Veen, 1981; Andre *et al.,* 1982; Massimino *et al.,* 1982). This is presumably due to greater levels of respiratory substrate available or ADP availability. It is, therefore, suggested that dark respiration adapts to the previous rate of photosynthesis (Amthor, 1989).

There is a dependency of root respiration on current photosynthesis by the shoot, and therefore root activity is dependent on the substrate supply from the shoots (Humphries, 1951; Neales and Davies, 1966; Hatrick and Bowling, 1973; Hansen, 1977; Pearson, 1979; Veen, 1981; Ryle *et al.,* 1985; Bingham and Farrar, 1988). They suggested that the effect of reducing photosynthesis, for example by darkening or excising the shoot, will cause a reduction of respiratory substrate supply to the root, and respiration then becomes substrate-limited and eventually falls. This could be a

direct consequence of the translocation of photosynthate from the leaves to the roots (Osman, 1971; Hatrick and Bowling, 1973).

1.6.7 Summary

In summary, there are three classes of rate limitation of photosynthesis : (*1*) supply or utilization of CO_2 (evaluated by AC_i curves, enzyme activity, etc.), (*2*) supply or utilization of light (evaluated by light response curves), (*3*) supply or utilization of phosphate (evaluated by loss of oxygen sensitivity, Pi levels, etc.) (Sharkey, 1985). In addition, Farquhar and Sharkey (1982) suggested that there are three main limitations to supply or utilization of CO_2 : 1. Stomata; 2. Rubisco activity; 3. RuBP regeneration rate.

Photorespiration is considered a wasteful process which occurs in C_3 plants. This process is pronounced at high temperature and high light intensity, high O_2 or low CO_2 concentration (Calvin, 1990). Despite reducing photosynthesis, Tolbert (1980) suggested that photorespiration may be beneficial by protecting the photosynthetic apparatus from photooxidative damage.

Dark respiration provides energy for plant growth and maintenance. Dark respiration appears to continue in the light, even though its magnitude is still under debate. Dark respiration increases with temperatures until enzyme denaturation starts to occur. There is also some evidence that dark respiration of plants (or part of plant) is dependent on substrate availability, including photosynthesis.

CHAPTER 2

A STUDY OF THE GROWTH AND DEVELOPMENT OF YOUNG ASPARAGUS PLANTS IN THE FIELD USING SUCCESSIONAL PLANTINGS

2.1 INTRODUCTION

Knowledge of the growth and development of young asparagus is important to an understanding of both the establishment process and of plant growth. As the young plant is not cropped, but is in the fern stage throughout its growth such plants provide detailed information on fern growth and seasonal effects on this growth. The fern growth stage is of particular importance to the mature plant as it is during this period that assimilates are stored to produce the subsequent crop (Nichols, 1988b; Hughes, 1992).

Research with seedling transplants has found that plant survival and the yield of asparagus was mainly affected by the time of transplanting (Williams, 1979; Bussell, 1984; Dufault and Greig, 1983; Loughton and Baker, 1984; Burrows and Waters, 1989) and less affected by seedling transplant age (Ombrello and Garrison, 1978; Williams, 1979; and Dufault and Waters, 1984). There has however been no research with young asparagus plants in the field using growth analysis as part of a detailed study of plant growth. Researchers with other crops have used successional sowing or plantings with a number of varieties as an effective way of providing information on the seasonal effects on plant growth and development. Examples of such studies are with lettuce (Nichols, 1970) and sprouting broccoli (Diputado, 1989).

In the following experiment two cultivars of asparagus were planted in the field at 4 weekly intervals from September to March. Plant growth and development was studied by taking destructive plant harvests at 4 weekly intervals.

2.2 MATERIALS AND METHODS

2.2.1 Introduction

Two cultivars of asparagus, the clonal hybrid UC157 and the all male single cross hybrid Jersey Giant were used. These cultivars were selected because they are widely grown in New Zealand and overseas. Plants were raised as seedling transplants and were planted out in the field as 8 week old transplants.

2.2.2 Plant raising

Seeds of cv UC157 and Jersey Giant were sown in 100% fine peat contained in cell trays. The cells had a volume of 30 cm^3, were 7.5 cm deep and the seedlings were grown at a density of 1000 plant m^{-2}. Details of the base fertilizers added to the peat and the liquid feed used are shown in Appendix 1 and 2, respectively.

The seed was germinated on a heated bench (25^{0}C) and the seedlings were grown on netting to provide air pruning of the roots. The glasshouse used was located at the Plant Growth Unit, Massey University. Temperatures in the glasshouse were controlled by heating to 16^{0}C, with fan ventilation operating at 25^{0}C. Liquid feed was applied once a day starting four weeks after seed sowing. Regular liquid feeding ceased 2 weeks before transplanting to avoid excessive fern growth.

2.2.3 Planting and irrigation

The seedling transplants were planted out into the field at a site adjacent to the Plant Growth Unit, Massey University, 8 weeks after sowing. The soil type was a Karapoti sandy loam and a soil test (Appendix 3) showed that the pH, calcium, potassium, phosphorus and magnesium levels were at or above target levels for asparagus (Franklin *et al.* 1982; Clarke *et al.* 1986). Nitrogen was the only nutrient applied at the rate of 5 grams of Urea per metre down the line of the row at the time of transplanting.

Sprinkler irrigation was applied at the time of transplanting with the early planting dates (September to December) when there was lack of rain and the soil was dry. For the later plantings irrigation was carried out by hand only to the plants that were being transplanted.

2.2.4 **Disease and pest control**

At transplanting the seedlings were sprayed with Ridomil (Appendix 4) to control phytophthora. Metasystox was used to control aphids and thrips for the first four weeks after transplanting (Appendix 4). As the plants grew larger Metasystox was applied only when considered necessary.

Weed control was by hand in the rows and between the rows a small rotary hoe was used. An electric fence was set up around the experimental area to protect the plants from rabbits.

In winter the ferns were removed and burnt away from the field. In the following spring the field was sprayed with Ridomil to protect the plants from the phytophthora spear rot. Mesurol was used to control slugs (Appendix 4).

2.2.5 **Treatments**

There were 2 cultivars (2.2.1) and 7 planting dates. Plantings were at 4 weekly intervals commencing on 21 September (Table 2.1).

2.2.6 **Successional Harvests**

At 4 weekly intervals, commencing 4 weeks after the first planting, successional destructive harvests commenced. These harvests ceased in autumn (Table 2.2). The number of harvest for each planting date in the first growing season varied because of the differences in planting date. For example, the first planting had 7 harvests, while second planting had only 6 harvests.

Table 2.1 Sowing and planting dates of the 7 successional planting

Successional planting	Sowing date	Planting date
1	20 July 1990	21 September 1990
2	19 August 1990	19 October 1990
3	21 September 1990	16 November 1990
4	19 October 1990	14 December 1990
5	16 November 1990	11 January 1991
6	14 December 1990	8 February 1991
7	11 January 1991	8 March 1991

Table 2.2. Number of successional harvests for each planting date

Planting date	Number of harvest	
	First season	Second season
21 September	7	3
19 October	6	3
16 November	5	3
14 December	4	3
11 January	3	3
8 February	2	3
8 March	1	3

In the second growing season another 3 successional harvests at 4 weekly intervals were taken commencing on 7 October 1991 (Table 2.2). This second series of harvests was taken to provide information on the early growth of the plants after their first period of dormancy. An additional harvest was taken on 19 August of guard plants from between adjacent plots that had been previously harvested. These plants were harvested to provide some information on the dry matter status of plants during the dormant period. Data from this harvest was considered separately because of the questionable status of the plants.

2.2.7 **Experimental design**

There were four replications with 5 plants per plot and 2 guard plants between adjacent plots. The two main treatments, 7 planting dates and 2 cultivars, were arranged factorially, with harvest date as the split plot. The spacing used was 1 meter between rows and 30 cm apart in the row. There were two guard rows of plants along the outside of the experimental area (1 m x 0.5 m).

2.2.8 **Collection of data**

A complete destructive harvest was taken at each harvest. Data collection focused on both the fern and the crown. The crown consists of both the rhizome and storage roots. An attempt was made to recover the entire crown by carefully removing the soil from an area 50 cm around the plant and to a depth of 50 cm.

After harvest the crown was separated from the fern and then washed thoroughly to remove the soil and debris. The parameters which were recorded at each harvest are listed in Table 2.3. The roots longer than 1 cm were separated from rhizome and the number recorded before drying the roots in an oven (80^0C) for 96 hours. Similarly the number of buds located on the rhizome and the number of shoots were determined and then oven dried. The dry weight of roots and rhizome were combined to become dry weight of crown.

Table 2.3 The parameters measured in the study

1. Number of shoots
2. Number of roots
3. Number of buds
4. Shoot dry weight
5. Crown dry weight

2.2.9 **Data analysis**

2.2.9.1 **Logistic model**

The logistic model proposed by Nelder (1961) was used to represent the accumulation of total, crown and shoot dry weight during the first growing season. The model is:

$$W = A/\{1 + e^{-(\lambda+kt)/\theta}\}^{\theta} \quad (2.1)$$

where :

A is the asymptotic yield;

W is dry weight of plant material;

λ is the constant of integration (intercept);

k is the initial relative growth rate (slope);

t is time; and

θ is the point of inflection.

Preliminary examination showed that a heat unit time scale produced a smaller Mean Square for Error (MSE) compared to chronological time (Tables 2.5 and 2.6), therefore a heat unit time scale was chosen to describe data in this present experiment.

2.2.9.2 **Relative Growth Rate**

The relative growth rate is the increase of plant material per unit area of material per unit of time and Radford (1967) suggested the formula was :

$$RGR = 1/W.dW/dt.$$

The traditional use of the formula involves the calculation of RGR over time periods using the formula:

$$RGR = (\text{Log}_e W_2 - \text{Log}_e W_1)/(t_2 - t_1)$$

Hughes and Freeman (1967) fitted their data to the Log_e function so that RGR = $1/W.dW/dt = d(\log_e W)/dt$.

Having determined the logistic equation, dW/dt can be calculated by taking its differential equation :

$dW/dt = k\ W\ (1-(W/A)^{1/\theta})$ (Nelder, 1961).

Then the relative growth rate of total, shoot and crown dry weight was obtained from

$RGR = 1/W.dW/dt = d(\log_e W)/dt$ (2.2)

2.2.9.3 **Shoot crown ratio**

The ratio of shoot to crown dry weight was calculated for all treatment to evaluate the change in dry matter distribution at any particular time (harvest).

2.2.9.4 **Estimation of K-values of the allometric relationship between shoot and crown dry weight during the first season**

The allometric relationship between $\log_e$ shoot and $\log_e$ crown was calculated and represents the ratio of the relative growth rate of shoot to crown (see section 1.5.2). Dry matter data for shoot and crown for all treatments were transformed into natural logarithms. The allometric relationship is calculated from the linear regression equation:

$\ln Y = \ln a + k \ln X$ (2.3)

where : ln a is a constant;

k is the slope;

ln Y is natural logarithm of shoot dry weight;

ln X is natural logarithm of crown dry weight.

To determine the differences in k-values between treatments (cultivars and plantings), mean comparisons were carried out using a t-test (Steel and Torrie, 1986).

2.3 RESULTS

2.3.1 Total dry weight of seedling transplants at the time of transplanting

Analysis of variance revealed that the total dry weight of seedling transplants at the time of transplanting was affected by sowing date and cultivar without any interaction between sowing date and cultivar (Table 2.4). The earliest sowing was significantly lower in total dry weight compared to all, but the September sowing. Although not significantly different, seedling growth was probably best for sowings in October and November. Jersey Giant produced a significantly higher total dry weight than UC157.

2.3.2. Dry weight accumulation during the first and second season

2.3.2.1 Dry weight accumulation during the first season as described by the logistic model

The proposal of Nelder (1961) to reduce variation in crop yield from year to year was adopted in this present study to describe the growth of young asparagus plants grown in the field in the first season. The model, however, was modified as suggested by Nichols (1970) in order to fit 7 sets of data (7 planting dates) simultaneously to produce a single set of parameters. The problem in the present study was that with later planting dates there were few harvests and therefore there was limited data to fit the logistic curve (eg. 2 and 3 harvests for the March and February plantings, respectively).

Table 2.4 Total dry weight (gram/plant) of 8 week old asparagus seedling transplants sown at different times.

Sowing date	Planting	UC157	Jersey Giant	Sw mean[1]
20 July	21 Sept.	0.2038	0.2548	0.23**d**
19 August	19 Oct.	0.2843	0.3423	0.31**ab**
21 September	16 Nov.	0.2668	0.2550	0.26**cd**
19 October	14 Dec.	0.2705	0.3613	0.32**ab**
16 November	14 Jan.	0.2863	0.3683	0.33**a**
14 December	11 Feb.	0.2535	0.3135	0.28**bc**
11 January	8 March	0.2710	0.3198	0.30**abc**
Cv mean[1]		0.26**b**	0.32**a**	
Cultivars (Cv)		**		
Sowing date (Sw)		**		
Cv x Sw		ns		

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Means separation within the column and row by Duncan's Multiple Range Test ($p \leq 0.05$), se = 0.0134 and 0.0072, respectively with $df_{(error)} = 39$.

The results showed that the heat unit time scale gave a lower MSE compared to the chronological time scale (Tables 2.5 and 2.6). The lowest MSE for total and shoot dry weight accumulation was obtained by using the heat unit time scale at base temperature equal to zero (tb = 0), while the lowest MSE for crown dry weight was obtained by using the heat unit time scale at base temperature equal to 3 (tb = 3). The fitted line of the logistic growth curves for $\log_e$ total, crown and shoot dry weight for both cultivars are shown in Figures 2.1 to 2.6. The respective heat unit accumulations for the various harvest dates are presented in Table 2.8.

The fitted line shows that total, crown and shoot dry weight accumulation increased as the season progressed. The calculated relative growth rates, however, indicate that for both cultivars the total plant, shoot and crown relative growth rate followed a similar trend, ie. they fell for the plantings from September to December but not for the late plantings (Figures 2.7 to 2.12).

Total plant, crown and shoot relative growth rate for UC157 were higher than for Jersey Giant (Figures 2.7 to 2.12). In addition although both crown and shoot relative growth rate fell late in the season for the early plantings, but crown relative growth rate fell at a lower rate.

Total and crown dry weights (Figures 2.1 and 2.3) show that for UC157, planting in September did not have a detrimental effect on seedling growth, while for Jersey Giant the differences in dry weight accumulation between the September and the October plantings were marginal (Figures 2.2 and 2.4).

In terms of shoot growth, both cultivars were less affected by planting date as indicated by Figures 2.5 and 2.6, which suggests that only the crown growth rate of Jersey Giant for the September planting was affected by cold weather.

2.3.2.2 **Dry weight at the final harvest at the end of the first season (Autumn)**

Analysis of variance were carried out on the $\log_e$ total plant (Table 2.9), $\log_e$ crown (Table 2.10) and $\log_e$ shoot dry weight (Table 2.11) at the final harvest during the first season (April 1991). The untransformed data for these plant characteristics are included in the tables in brackets. The dry weight of these plant parts all decreased as the planting date was delayed. There was however no significant difference between crown dry weights for the first two plantings. This was particularly noticeable with Jersey Giant.

The only difference between cultivars was in crown dry weight where Jersey Giant had the higher dry weight. There were no cultivar x planting date interaction.

Table 2.5 Logistic growth curve parameters and Mean Square for Error of total plant dry weight of asparagus plants grown in the field during the first season.

Time scale	Log_e A	λ	K	θ	MSE
UC157					
Time*1	5.3308	-8.839	0.3853	0.8803	1.0654
**HU. 0*2	5.4392	-8.857	0.0035	0.6521	1.0607
HU. 1	5.4465	-8.857	0.0037	0.6397	1.0666
HU. 5	5.5062	-8.989	0.0052	0.5561	1.1101
HU. 10	5.7153	-9.564	0.0101	0.3747	1.2943
Jersey Giant					
Time	5.133	-8.484	0.3605	1.4955	1.1398
**HU. 0	5.198	-8.324	0.0032	1.1111	1.0632
HU. 1	5.203	-8.316	0.0034	1.0914	1.0641
HU. 5	5.2401	-8.625	0.0046	1.0806	1.0806
HU. 10	5.374	-8.700	0.0085	0.6836	1.1938

*1. Chronological time scale
*2. HU. 0 etc. = Heat Units above a base temperature of 0.
**. The best fit was obtained at HU. 0 by giving the lowest MSE.

Table 2.6 Logistic growth curve parameters and Mean Square for Error of crown plant dry weight of asparagus plants grown in the field during the first season.

Time scale	Log_e A	λ	K	θ	MSE
UC157					
Time*1	4.8686	-8.129	0.3452	1.1489	0.7762
HU. 0	5.0040	-8.088	0.0031	0.8447	0.6331
**HU. 3	5.0411	-8.131	0.0038	0.7893	0.6169
HU. 5	5.0827	-8.187	0.0044	0.7330	0.6208
HU. 10	5.3692	-8.641	0.0082	0.5027	0.6767
Jersey Giant					
Time	no fit	no fit	no fit	no fit	no fit
HU. 0	4.6487	-7.578	0.0028	1.881	0.7167
**HU. 3	4.6627	-7.581	0.0034	0.7749	0.7028
HU. 5	4.6824	-7.576	0.0040	1.6641	0.7063
HU. 10	4.854	-7.866	0.0079	1.0817	0.7699

*1. Chronological time scale.

*2. HU. 0 etc. = Heat Units above a base temperature of 0.

**. The best fit was obtained at HU. 3 by giving the lowest MSE.

Table 2.7 Logistic growth curve parameters and Mean Square for Error of shoot dry weight of asparagus plants grown in the field during the first season fitted with the base temperature equal to 0 (tb = 0).

	Log_e A	λ	K	θ	MSE
Shoot					
UC157	4.6105	-8.1878	0.00124	0.479	1.8648
Jersey Giant	4.2922	-7.5717	0.00373	0.8145	3.1193

Table 2.8 Heat unit accumulation in relation to harvest date

Harvest date	Heat unit (tb = 0)	Heat unit (tb = 3)
21 September	349.1	262.9
19 October	756.6	584.4
16 November	1200.8	946.6
14 December	1644.2	1306.1
14 January	2153.4	1731.3
11 February	2635.8	2129.6
8 March	3105.5	2515.4

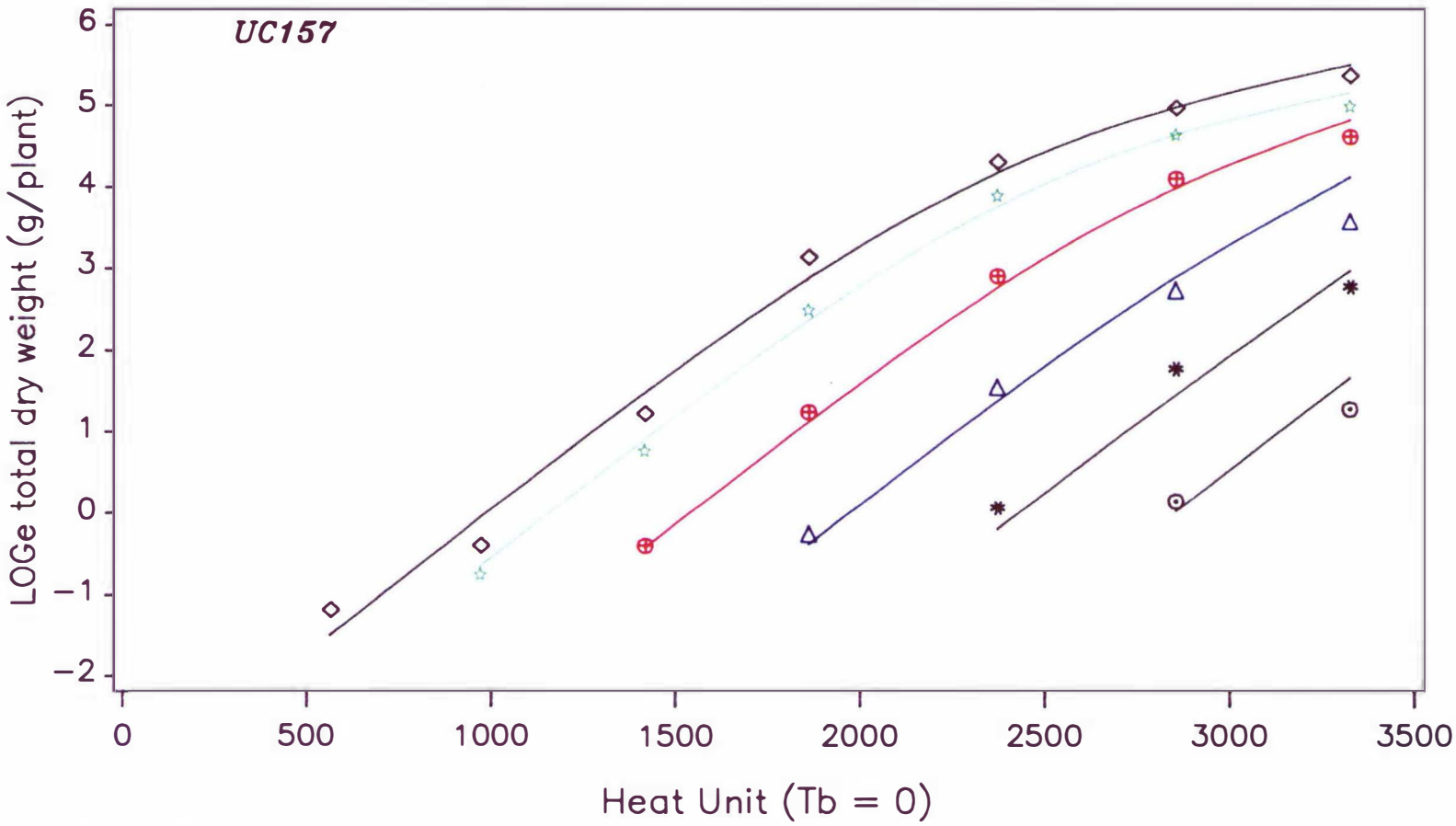


Figure 2.1 Total dry weight of UC157 fitted to the 4 parameter logistic with a heat unit time scale with K constant for all planting (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb).

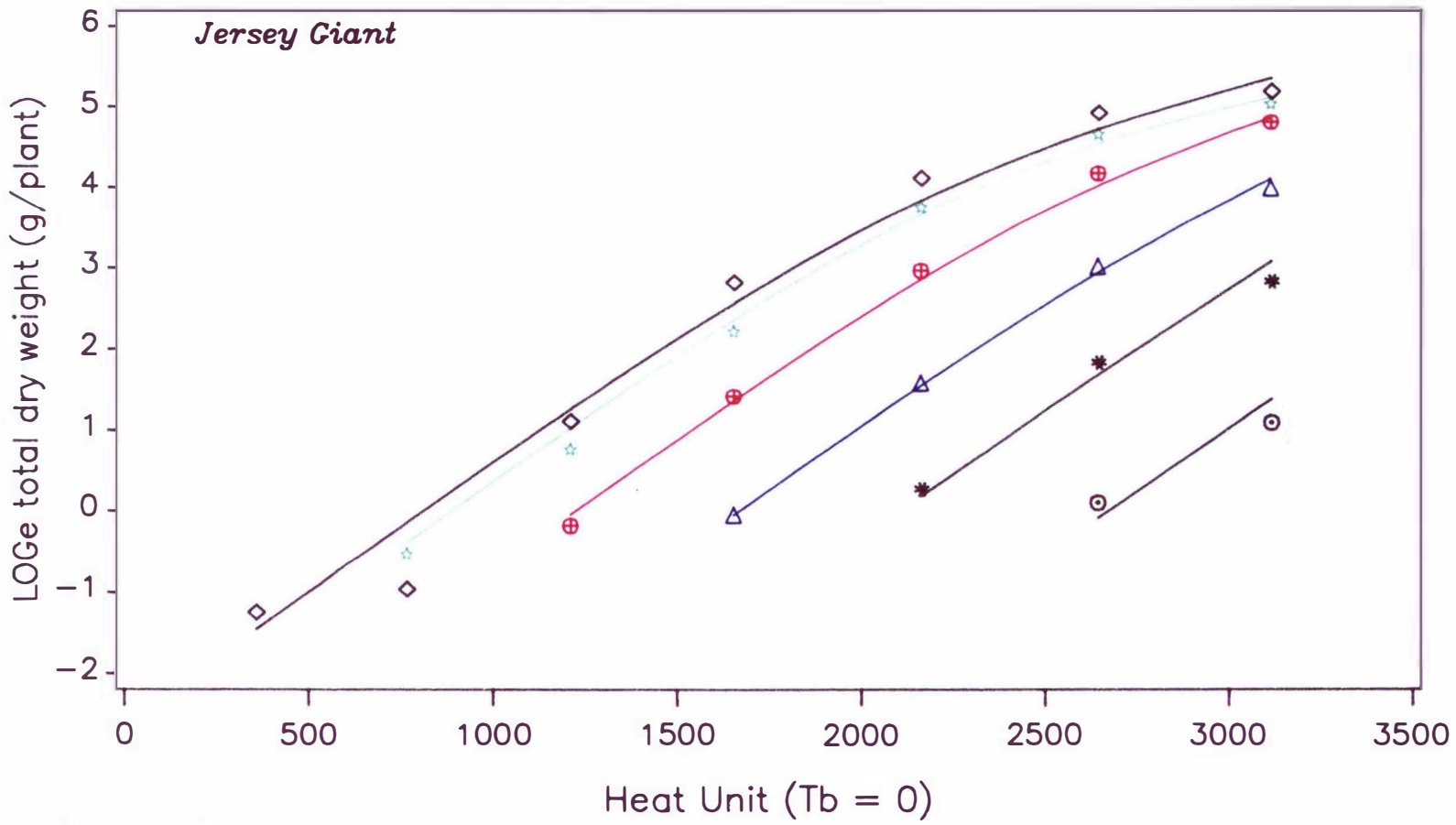


Figure 2.2 Total dry weight of Jersey Giant fitted to the 4 parameter logistic with a heat unit time scale with K constant for all planting (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb).

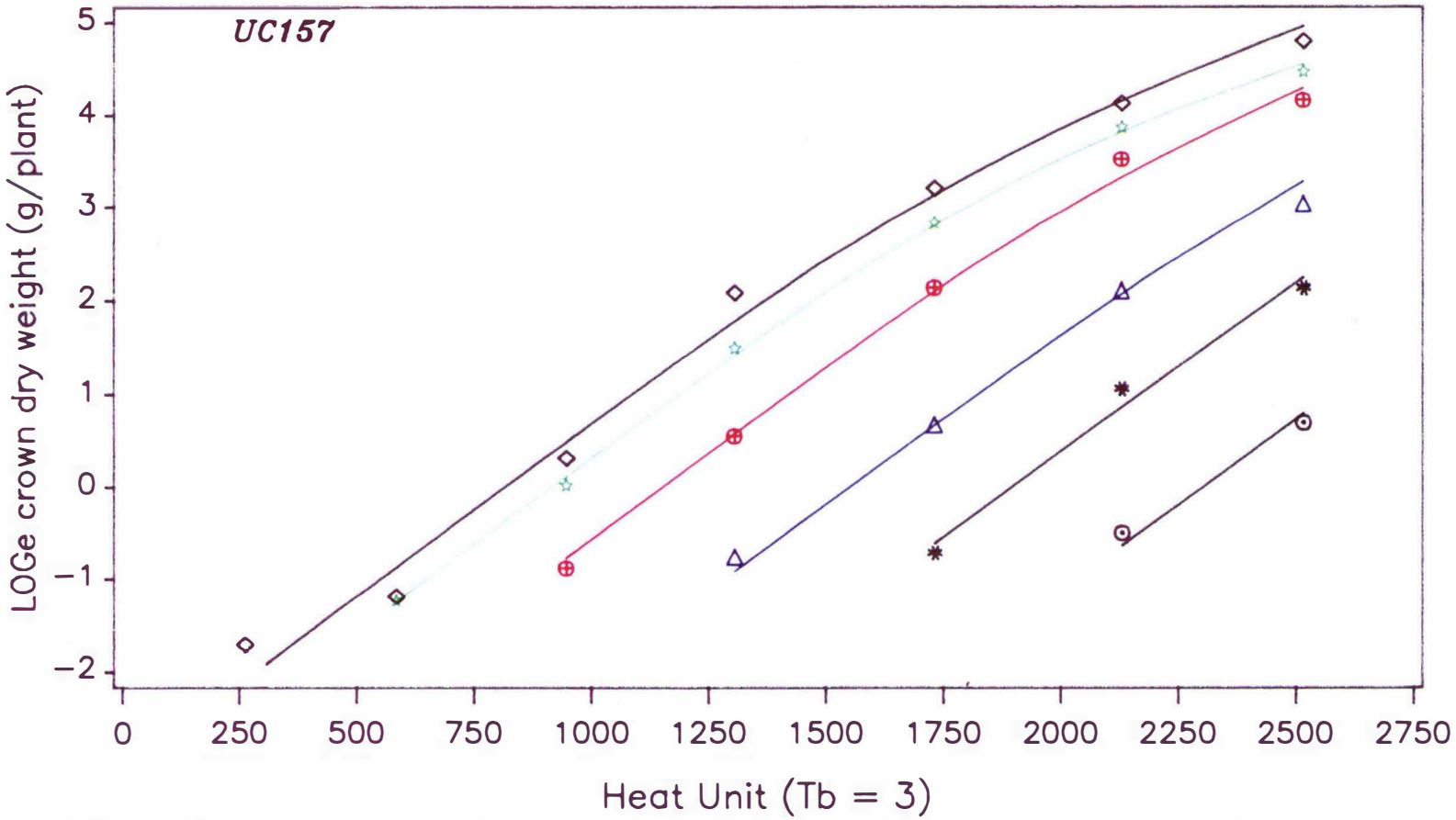


Figure 2.3 Crown dry weight of UC157 fitted to the 4 parameter logistic with a heat unit time scale with K constant for all planting (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb).

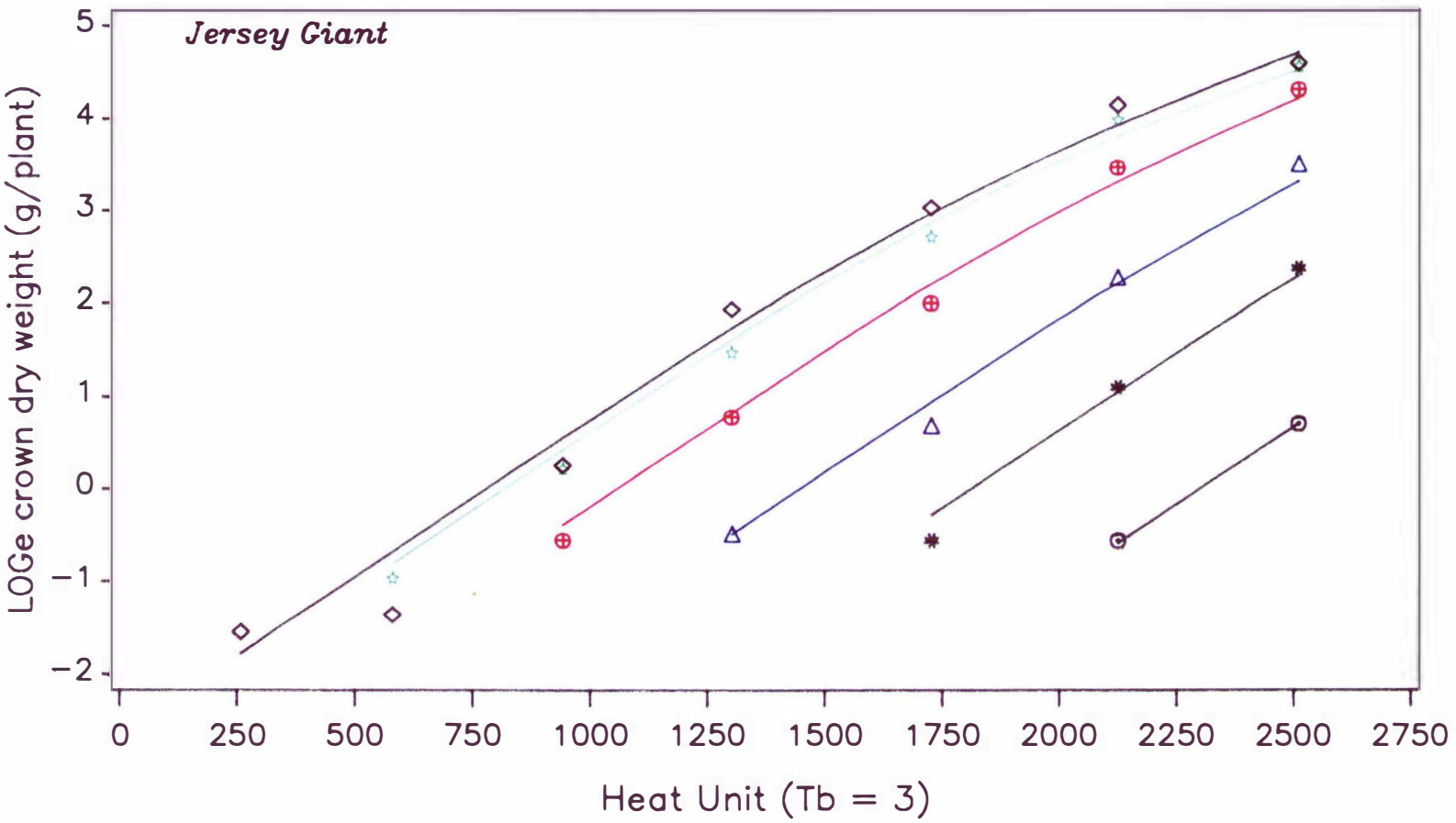


Figure 2.4 Crown dry weight of Jersey Giant fitted to the 4 parameter logistic with a heat unit time scale with K constant for all planting (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb).

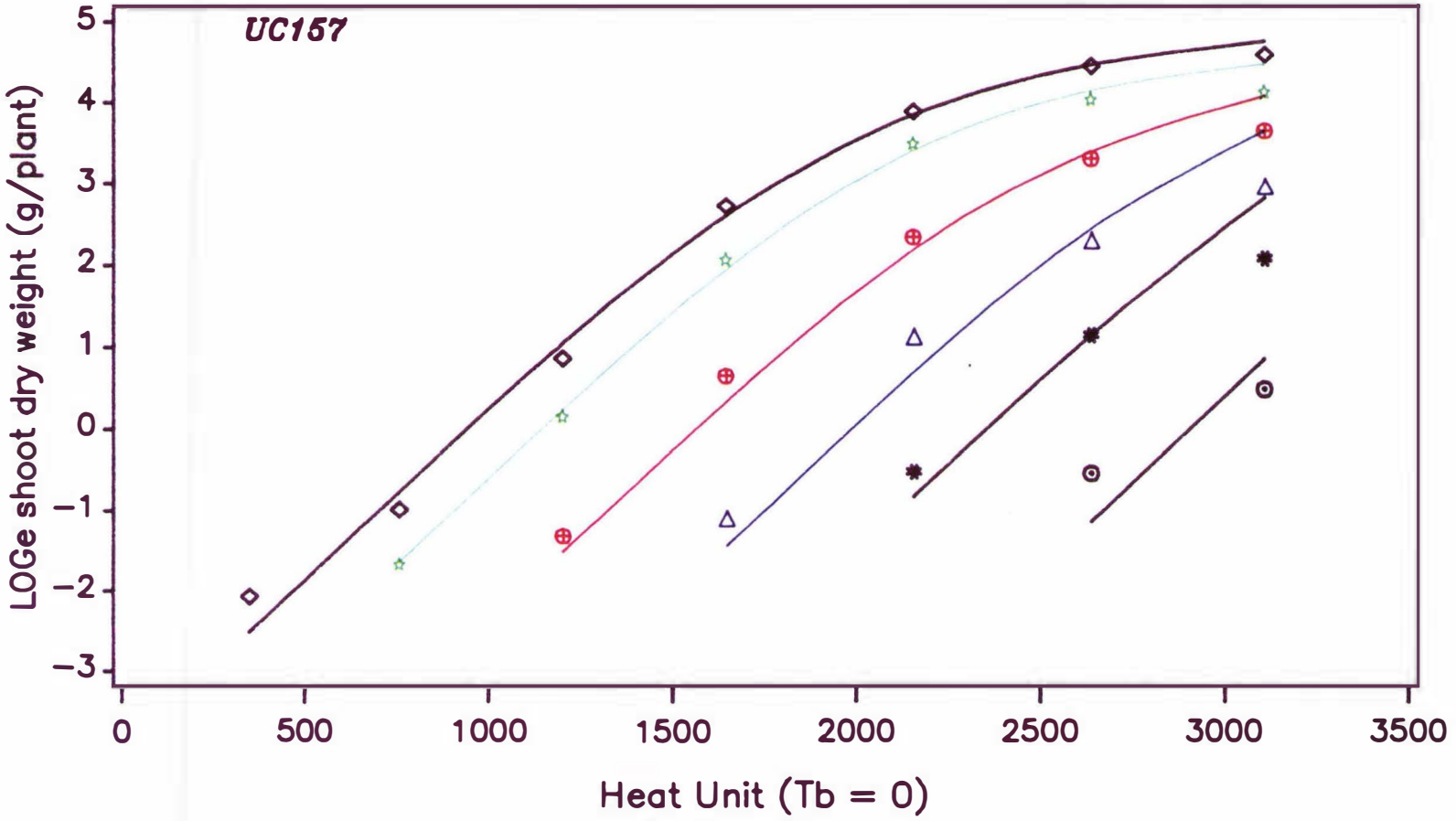


Figure 25 Shoot dry weight of UC157 fitted to the 4 parameter logistic with a heat unit time scale with K constant for all planting (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb).

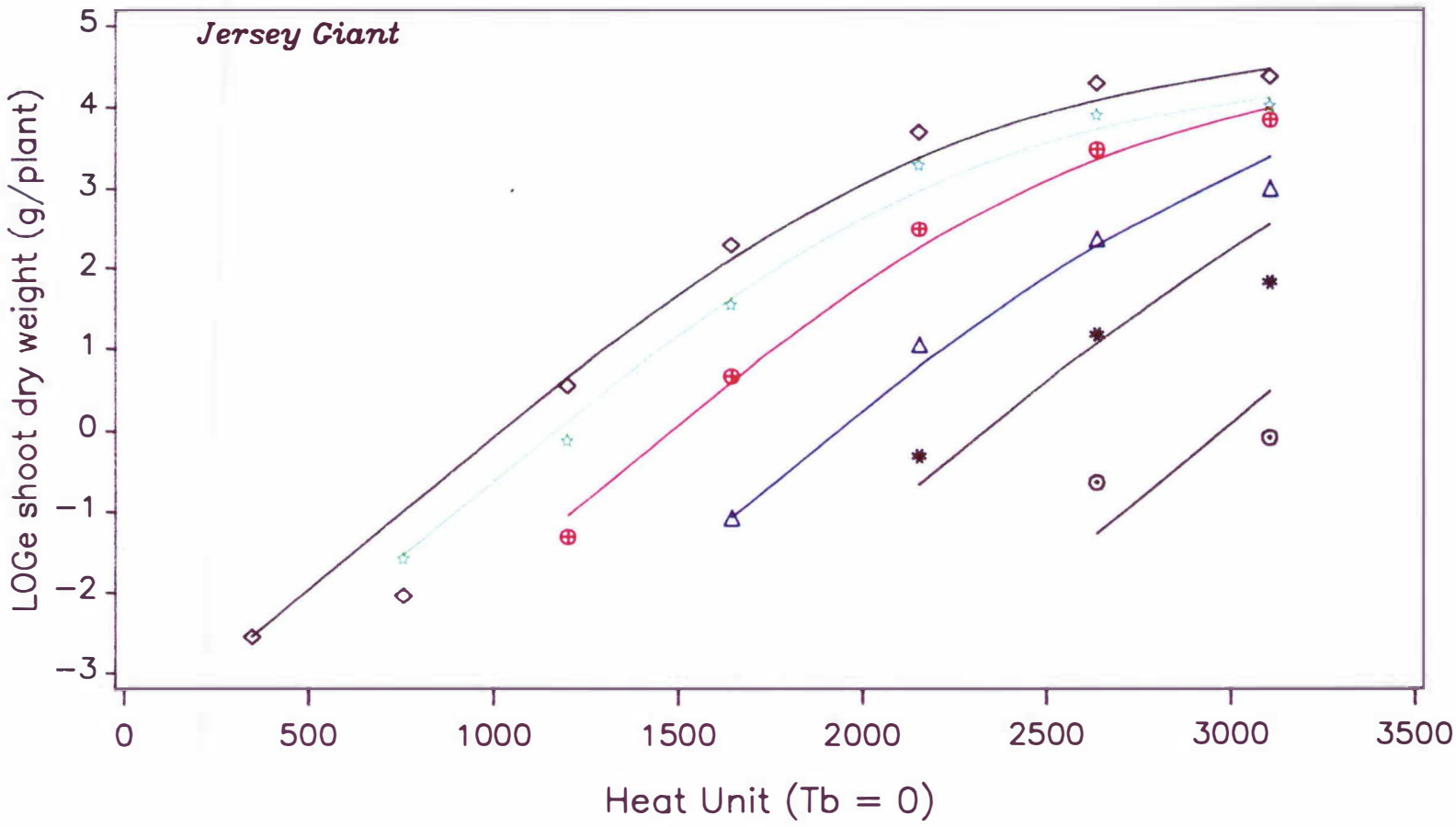


Figure 2.6 Shoot dry weight of Jersey Giant fitted to the 4 parameter logistic with a heat unit time scale with K constant for all planting (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb).

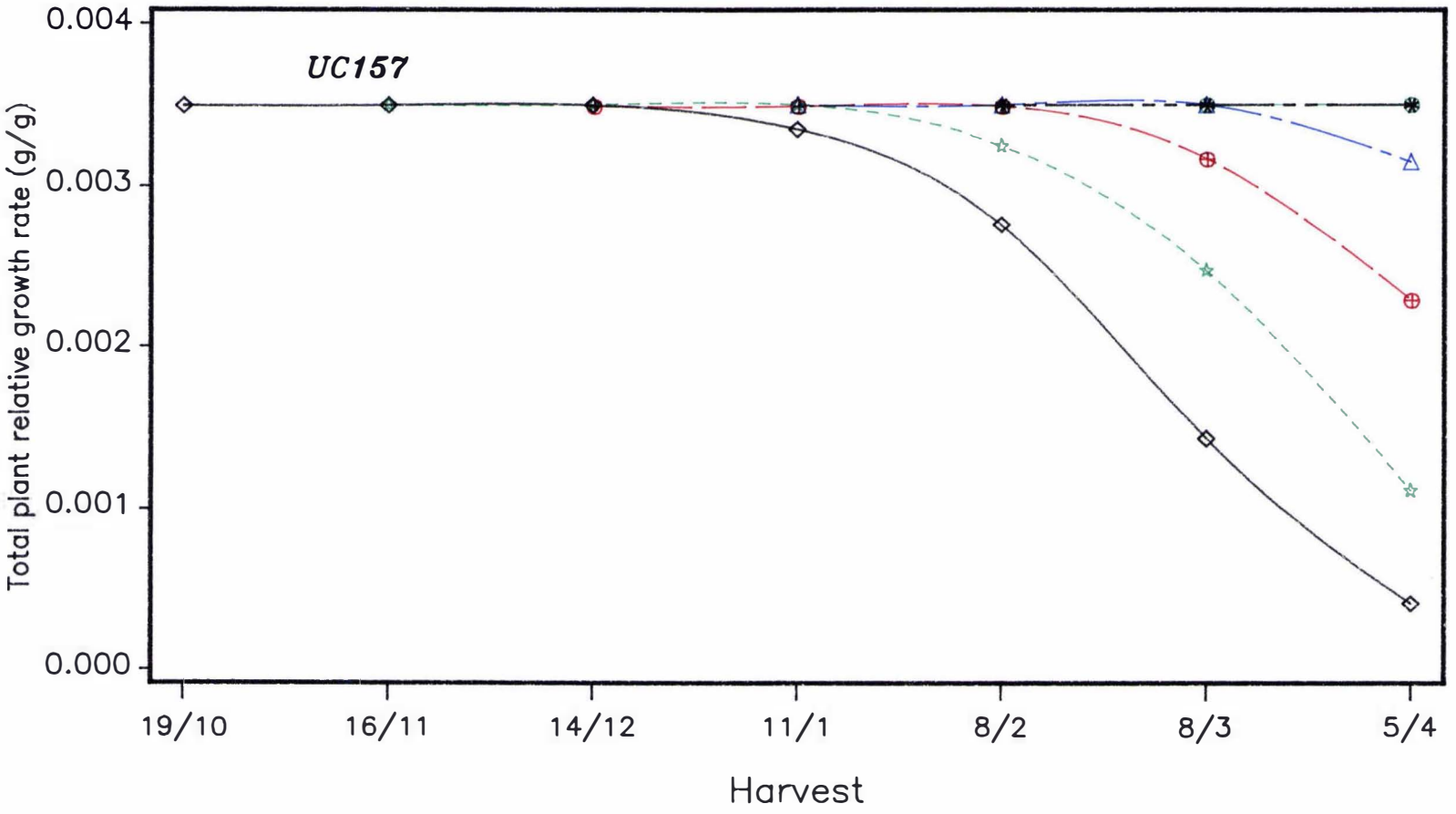


Figure 2.7 Total plant relative growth rate time trends for UC157 in the first season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; △ △ △ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb)

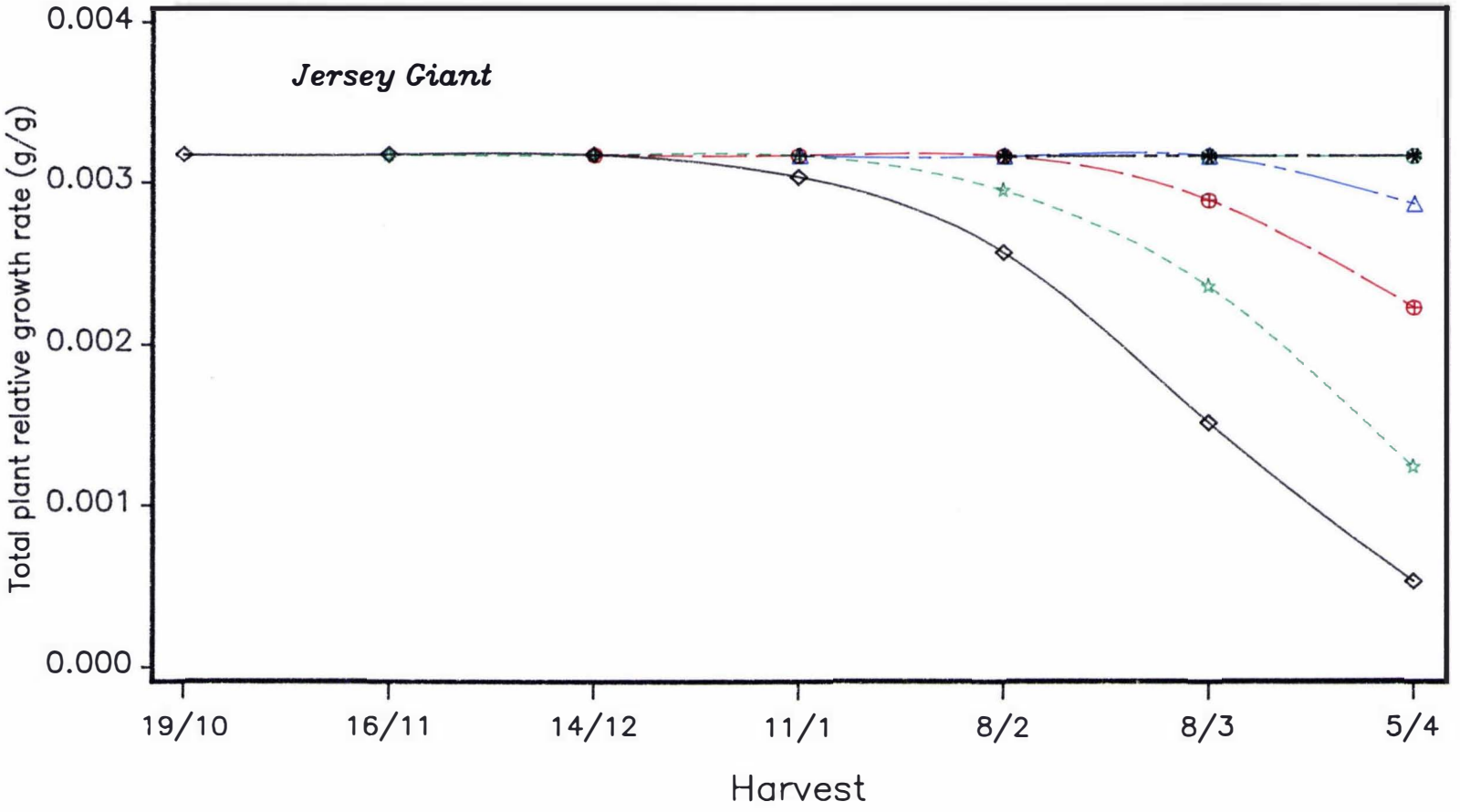


Figure 2.8 Total plant relative growth rate time trends for Jersey Giant in the first season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; △ △ △ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb)

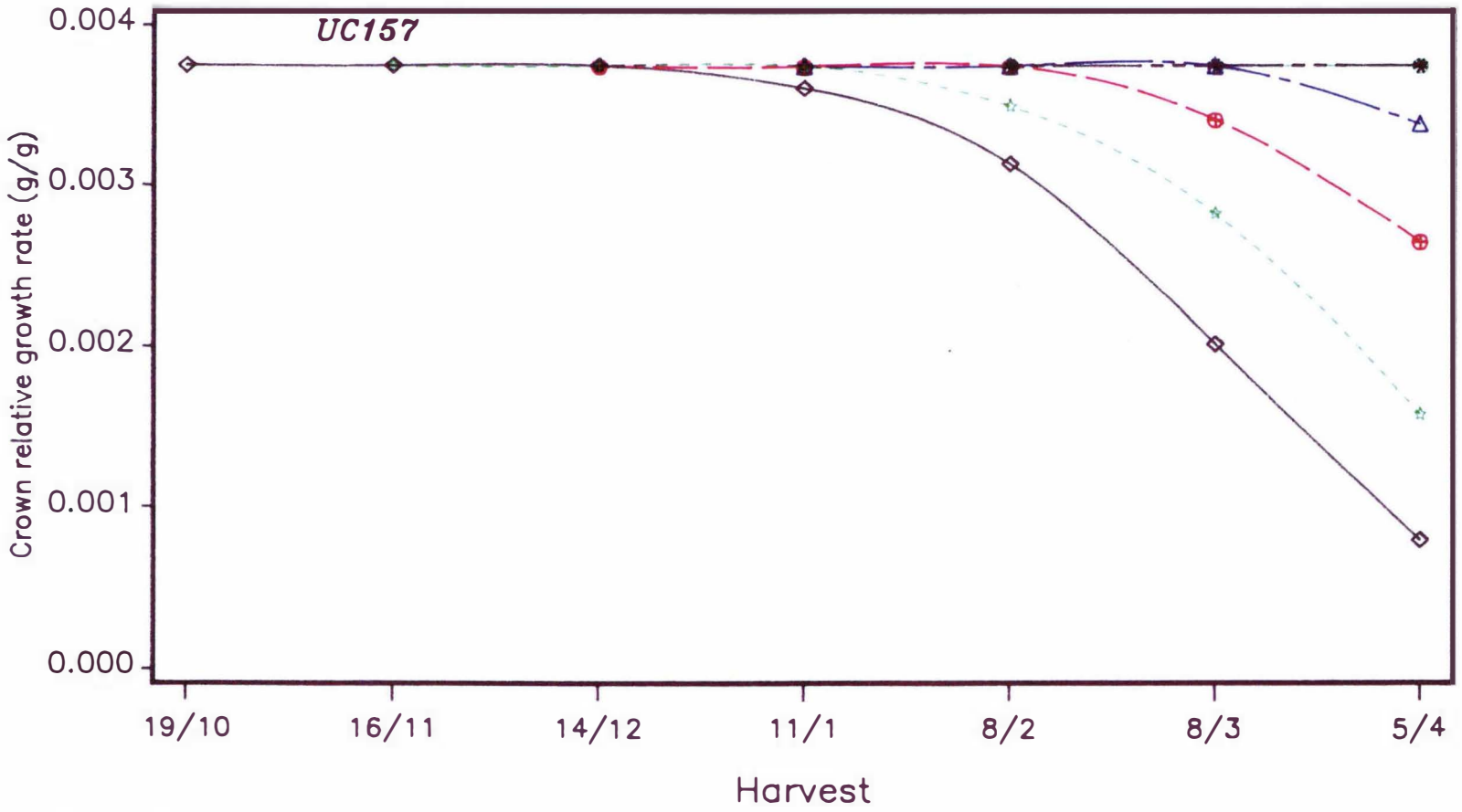


Figure 2.9 Crown relative growth rate time trends for UC157 in the first season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ○ ○ ○ Feb)

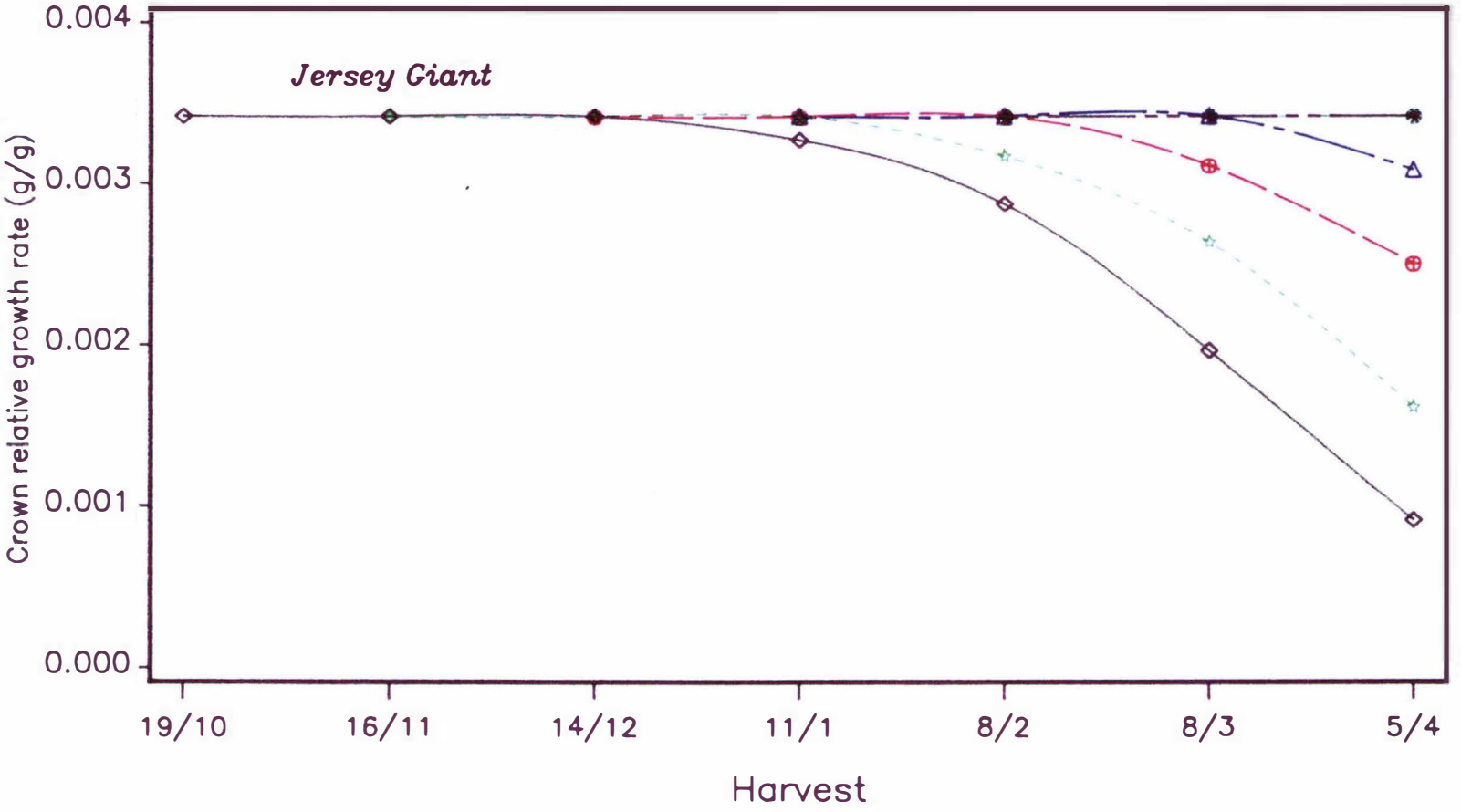


Figure 2.10 Crown relative growth rate time trends for Jersey Giant in the first season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ○ ○ ○ Feb)

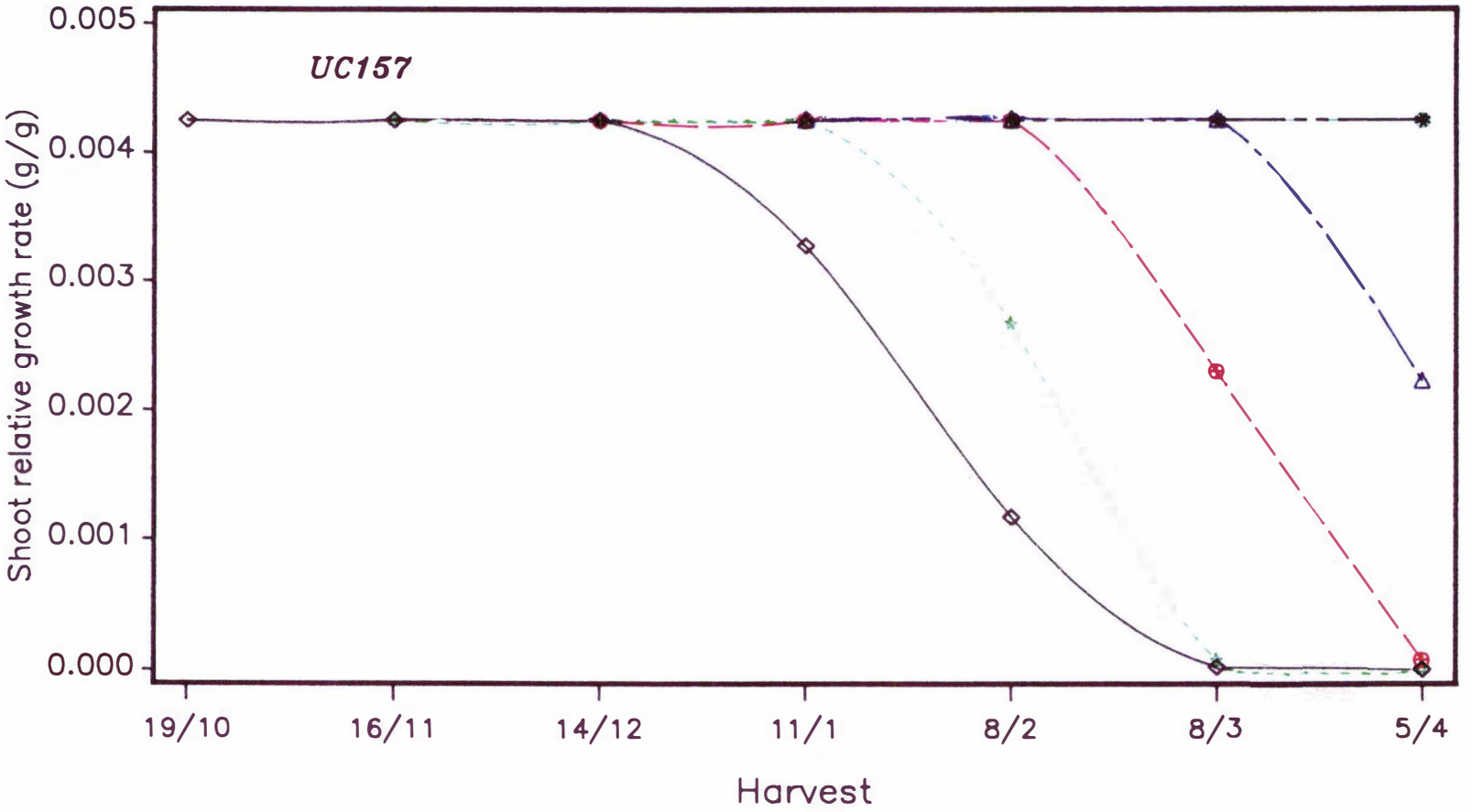


Figure 2.11 Shoot relative growth rate time trends for UC157 in the first season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ▫ ▫ ▫ Feb.)

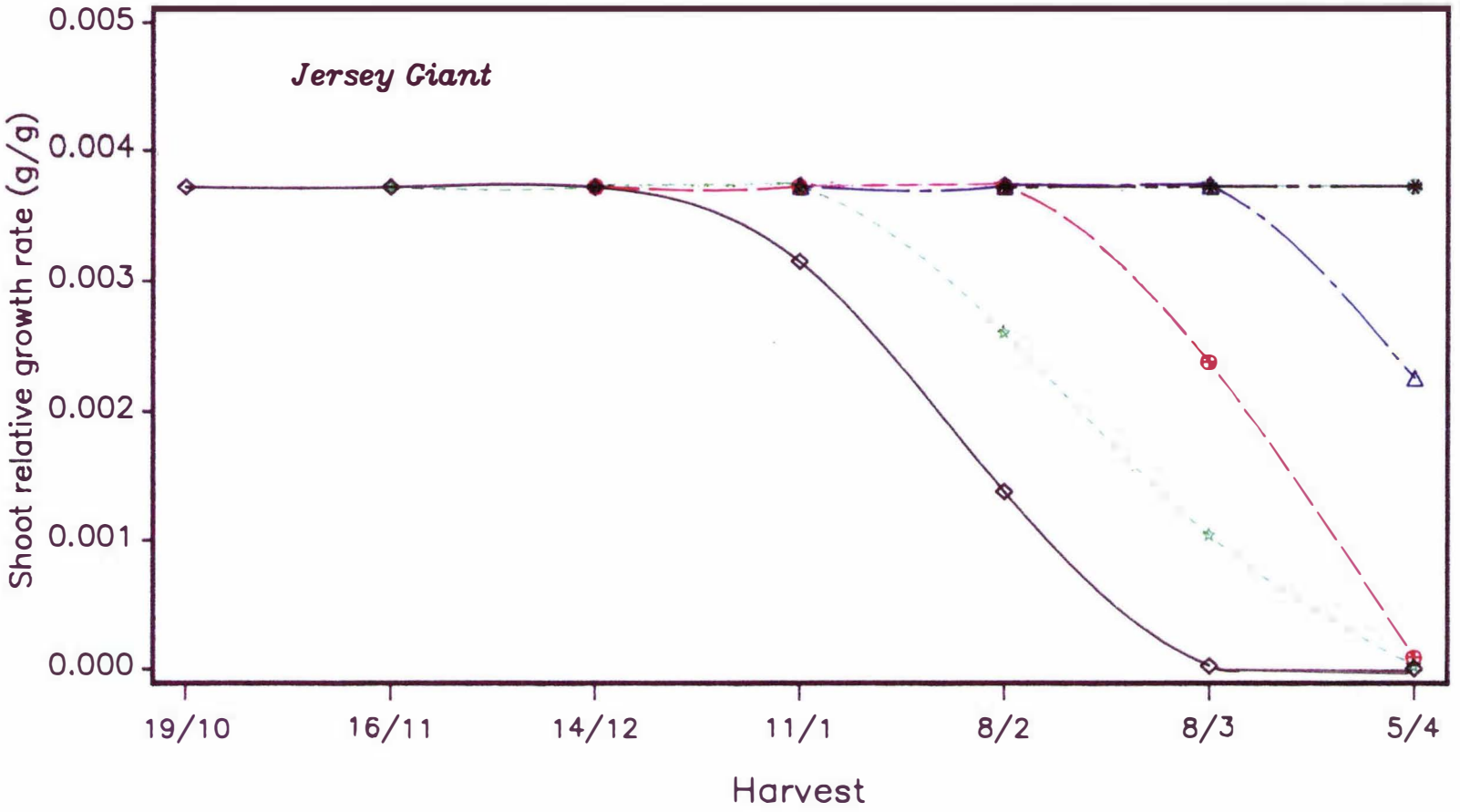


Figure 2.12 Shoot relative growth rate time trends for Jersey Giant in the first season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb.)

Table 2.9 Log_e total dry weight (gram/plant) of asparagus during the first season at final harvest.

Planting	Cultivar		
	UC157	Jersey Giant	Pl mean[2]
21 Sept.	5.363 (213.4)[1]	5.159 (174.0)	5.26**a**
19 Oct.	4.983 (145.9)	5.002 (148.7)	4.99**b**
16 Nov.	4.617 (101.2)	4.798 (121.3)	4.71**c**
14 Dec.	3.580 (35.9)	3.942 (51.5)	3.76**d**
14 Jan.	2.786 (16.2)	2.826 (16.9)	2.81**e**
11 Feb.	1.289 (3.6)	1.063 (2.9)	1.18**f**
8 March	-0.799 (0.45)	-0.689 (0.5)	-0.74**g**
Cv mean[2]	3.12	3.16	
Cultivar (Cv)		ns	
Planting date (Pl)		**	
Cv x Pl		ns	

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Value in the bracket is the untransformed total dry weight;
- 2. Means separation within column and row by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.08297 and 0.0444, respectively with $df_{(error)} = 39$.

Table 2.10 Log_e crown dry weight (gram/plant) of asparagus during the first season at final harvest .

Planting	Cultivar		
	UC157	Jersey Giant	Pl mean[2]
21 Sept.	4.775 (118.5)[1]	4.562 (95.8)	4.67**a**
19 Oct.	4.453 (85.9)	4.558 (95.4)	4.51**a**
16 Nov.	4.127 (62.0)	4.317 (75.0)	4.22**b**
14 Dec.	2.971 (19.5)	3.423 (30.7)	3.20**c**
14 Jan.	2.117 (8.3)	2.373 (10.7)	2.25**d**
11 Feb.	0.697 (2.0)	0.695 (2.0)	0.70**e**
8 March	-1.31 (0.27)	-1.14 (0.32)	-1.23**f**
Cv mean[2]	2.55**b**	2.68**a**	
Cultivar (Cv)		**	
Planting date (Pl)		**	
Cv x Pl		ns	

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Value in the bracket is the untransformed crown dry weight;
- 2. Means separation within column and row by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.0776 and 0.0415, respectively with $df_{(error)}$ =39.

Table 2.11 Log_e shoot dry weight (gram/plant) of asparagus during the first season at final harvest.

Planting	Cultivar		
	UC157	Jersey Giant	Pl mean[2]
21 Sept.	4.552 (94.8)[1]	4.355 (77.9)	4.45**a**
19 Oct.	4.070 (58.6)	3.930 (50.9)	4.00**b**
16 Nov.	3.649 (38.4)	3.816 (45.4)	3.73**b**
14 Dec.	2.769 (15.9)	2.993 (19.9)	2.88**c**
14 Jan.	2.068 (7.9)	1.813 (6.1)	1.94**d**
11 Feb.	0.480 (1.6)	-0.146 (0.9)	0.17**e**
8 March	-1.73 (0.18)	-1.73 (0.18)	-1.73**f**
Cv mean[2]	2.27	2.15	

Cultivar (Cv)	ns
Planting date (Pl)	**
Cv x Pl	ns

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Value in the bracket is the untransformed leaves dry weight;
- 2. Means separation within column and row by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.0971 and 0.0636, respectively with $df_{(error)}$ =39.

2.3.2.3 Total, shoot and crown dry weight accumulation during the second season

2.3.2.3.1 Dry weight accumulation during the spring growing period

Because only three data points were obtained during the second season there was no attempt to fit these data to a logistic model. Instead these data was transformed into $\log_e$ then combined with the first season data as shown in Figures 2.13 to 2.18.

Total plant dry weight accumulation increased slightly from the first harvest to the 2nd of December for both cultivars (Figures 2.13 and 2.14). The slope indicates that the total plant relative growth rate was relatively low during the spring growth period (after dormancy) for the September to December plantings and slightly higher for the later plantings.

Figures 2.15 and 2.16 includes the crown dry weight status at the end of winter (sample was taken on 19 August) and shows that crown dry weight decreased from winter to early spring due to the requirements for shoot growth. There was no significant crown growth until early November, as the data indicate that the crown dry weight were relatively constant over the first 4 week period (October to November) and then increased during the next 4 weeks. The spring growth period returned the dry weight used for fern growth to the crowns.

The shoot relative growth rate of asparagus for September to December plantings increased from early season (October) to mid season (November) (Figures 2.17 and 2.18) and was followed by a decrease. In addition the shoot relative growth rate of the late plantings were relatively higher than the early plantings and constant over the spring period except for Jersey Giant for the March planting. By December the shoot dry weight was greater compared to the shoot dry weight at the final harvest of the first season, regardless of cultivar.

2.3.2.3.2 **Dry weight at the final harvest at the end of the second season**

Analyses of variance were carried out on the $\log_e$ total plant (Table 2.12), $\log_e$ crown (Table 2.13) and $\log_e$ shoot (Table 2.14) dry weights at the final harvest at the end of the second season (2 December 1991). The untransformed data for these plant characteristics are included in the tables in brackets. The dry weight of these plant parts all decreased as the planting date advanced. There was however no significant difference between total plant, shoot and crown dry weight for the first two plantings and between October and November plantings. There were no differences between cultivars and there was no interaction between planting date and cultivar.

Table 2.12 Log_e total dry weight (gram/plant) of asparagus during the second season at final harvest.

Planting	Cultivar		
	UC157	Jersey Giant	Pl mean[2]
21 Sept.	5.67 (290.0)[1]	5.58 (265.1)	5.63**a**
19 Oct.	5.41 (223.6)	5.42 (225.9)	5.42**ab**
16 Nov.	5.29 (198.3)	5.25 (190.6)	5.27**b**
14 Dec.	4.37 (79.0)	4.66 (105.6)	4.52**c**
14 Jan.	3.92 (50.4)	3.83 (46.1)	3.88**d**
11 Feb.	2.17 (8.8)	2.34 (10.4)	2.26**e**
8 March	0.21 (1.2)	0.57 (1.8)	0.39**f**
Cv mean[2]	3.86	3.95	

Cultivar (Cv)	ns
Planting date (Pl)	**
Cv x Pl	ns

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Value in the bracket is the untransformed total dry weight;
- 2. Means separation within column and row by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.0924 and 0.0494 respectively with $df_{(error)} = 39$.

Table 2.13 Log_e crown dry weight (gram/plant) of asparagus during the second season at final harvest.

Planting	Cultivar		
	UC157	Jersey Giant	Pl mean[2]
21 Sept.	4.87 (130.3)[1]	4.71 (111.1)	4.79**a**
19 Oct.	4.66 (105.6)	4.57 (96.5)	4.62**ab**
16 Nov.	4.50 (90.0)	4.44 (84.8)	4.47**b**
14 Dec.	3.57 (35.5)	3.89 (48.9)	3.73**c**
14 Jan.	3.03 (20.7)	2.91 (18.4)	2.97**d**
11 Feb.	1.47 (4.3)	1.64 (5.2)	1.56**e**
8 March	-0.35 (0.70)	0.15 (1.12)	-0.10**f**
Cv mean[2]	3.11	3.19	

Cultivar (Cv)	ns
Planting date (Pl)	**
Cv x Pl	ns

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Value in the bracket is the untransformed total dry weight;
- 2. Means separation within column and row by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.0996 and 0.0532 respectively with $df_{(error)}$ =39.

Table 2.14 Log_e shoot dry weight (gram/plant) of asparagus during the second season at final harvest.

Planting	Cultivar		
	UC157	Jersey Giant	Pl mean[2]
21 Sept.	5.08 (160.8)[1]	5.03 (152.9)	5.06**a**
19 Oct.	4.78 (119.1)	4.86 (129.0)	4.82**ab**
16 Nov.	4.68 (107.8)	4.67 (106.7)	4.68**b**
14 Dec.	3.77 (43.4)	4.04 (56.8)	3.91**c**
14 Jan.	3.38 (29.4)	3.30 (27.1)	3.34**d**
11 Feb.	1.48 (4.4)	1.66 (5.3)	1.57**e**
8 March	-0.76 (0.47)	-0.55 (0.58)	-0.66**f**
Cv mean[2]	3.20	3.29	

Cultivar (Cv)	ns
Planting date (Pl)	**
Cv x Pl	ns

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Value in the bracket is the untransformed total dry weight;
- 2. Means separation within column and row by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.1092 and 0.0584 respectively with $df_{(error)} = 39$.

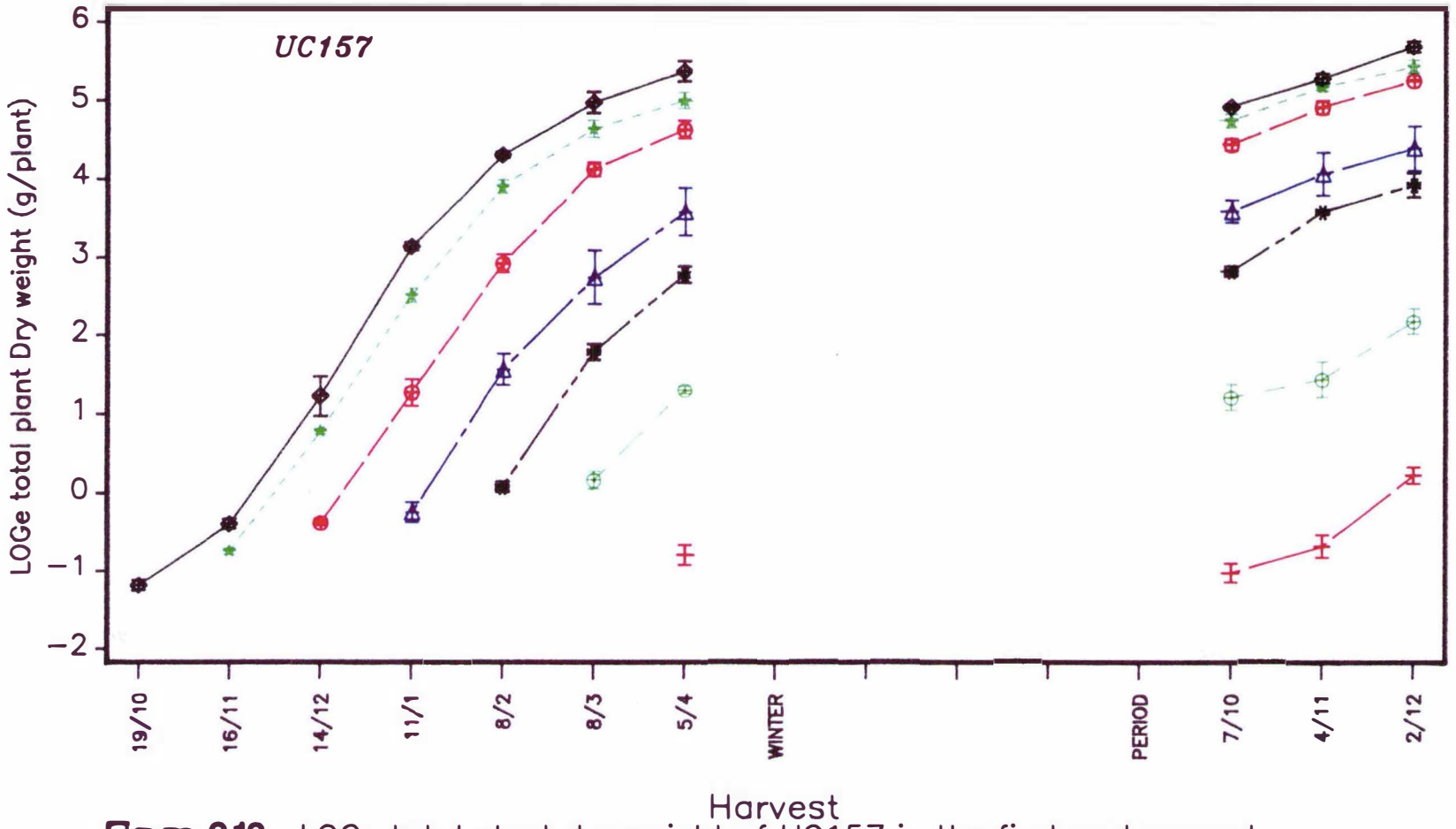


Figure 2.13 LOGe total plant dry weight of UC157 in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb; + + + March). I = Stderr. of means.

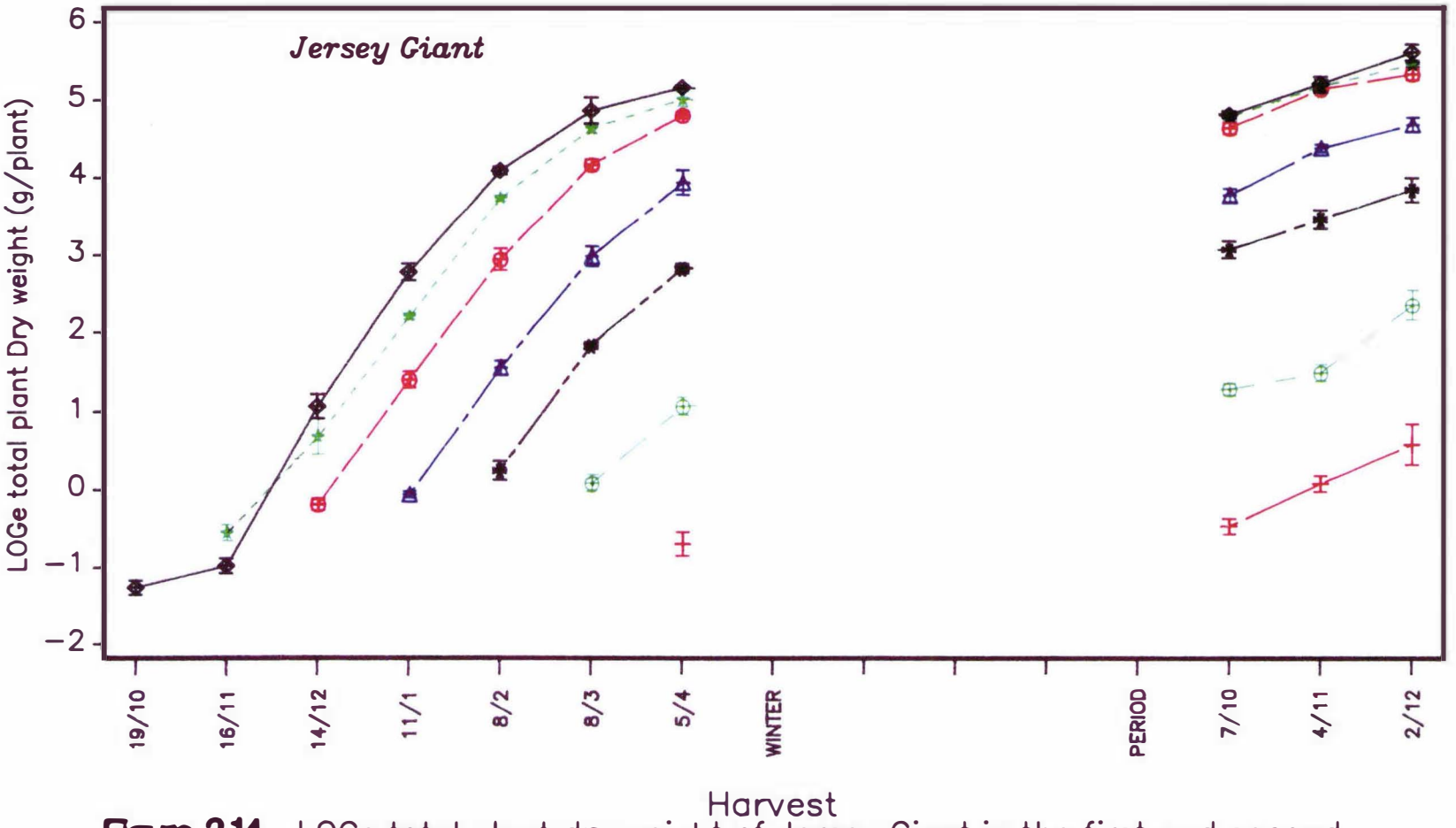


Figure 2.14 LOGe total plant dry weight of Jersey Giant in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb; + + + March). I = Stderr. of means.

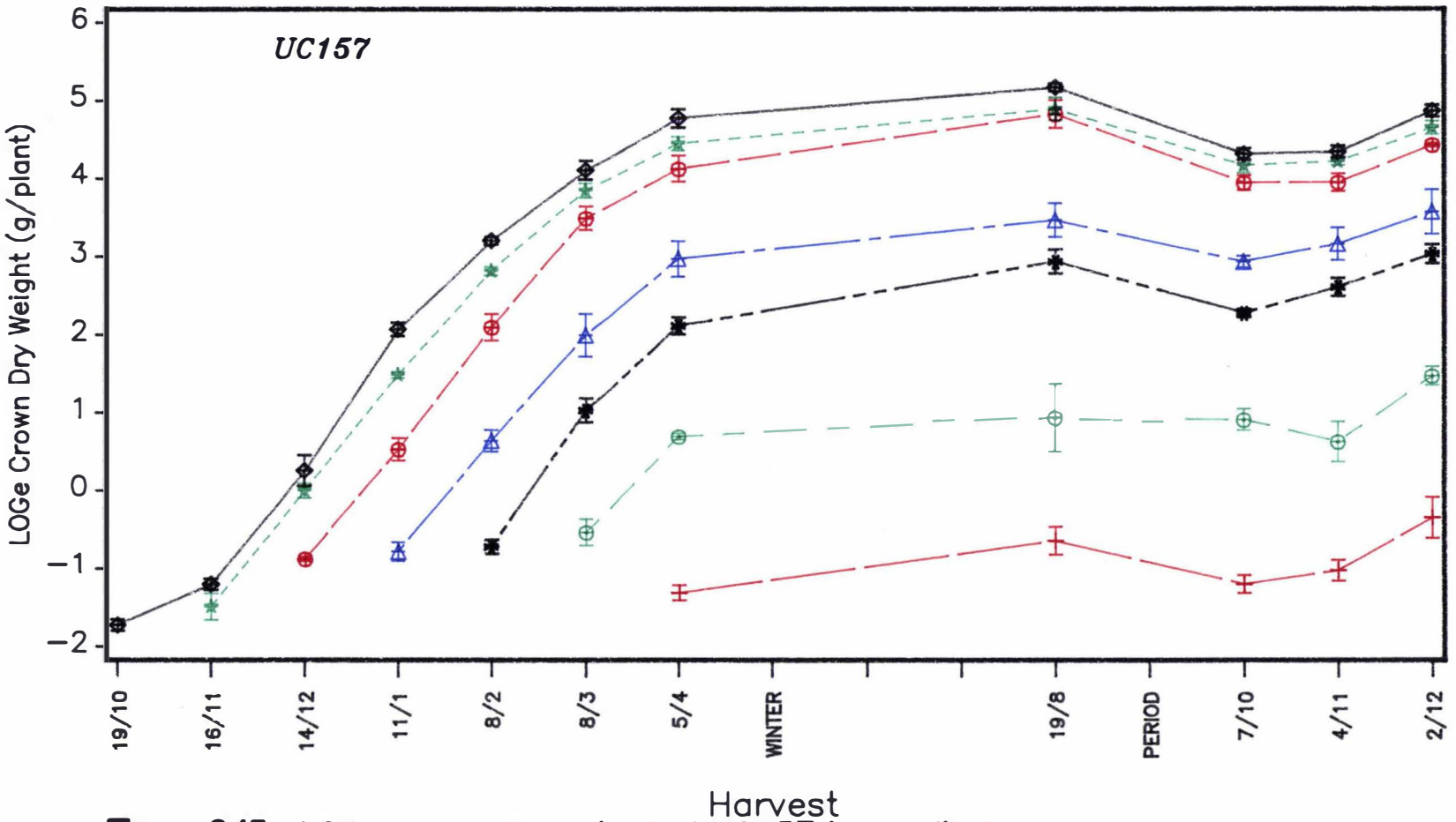


Figure 2.15 LOGe crown dry weight of UC157 in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb; + + + March). I = Stderr. of means.

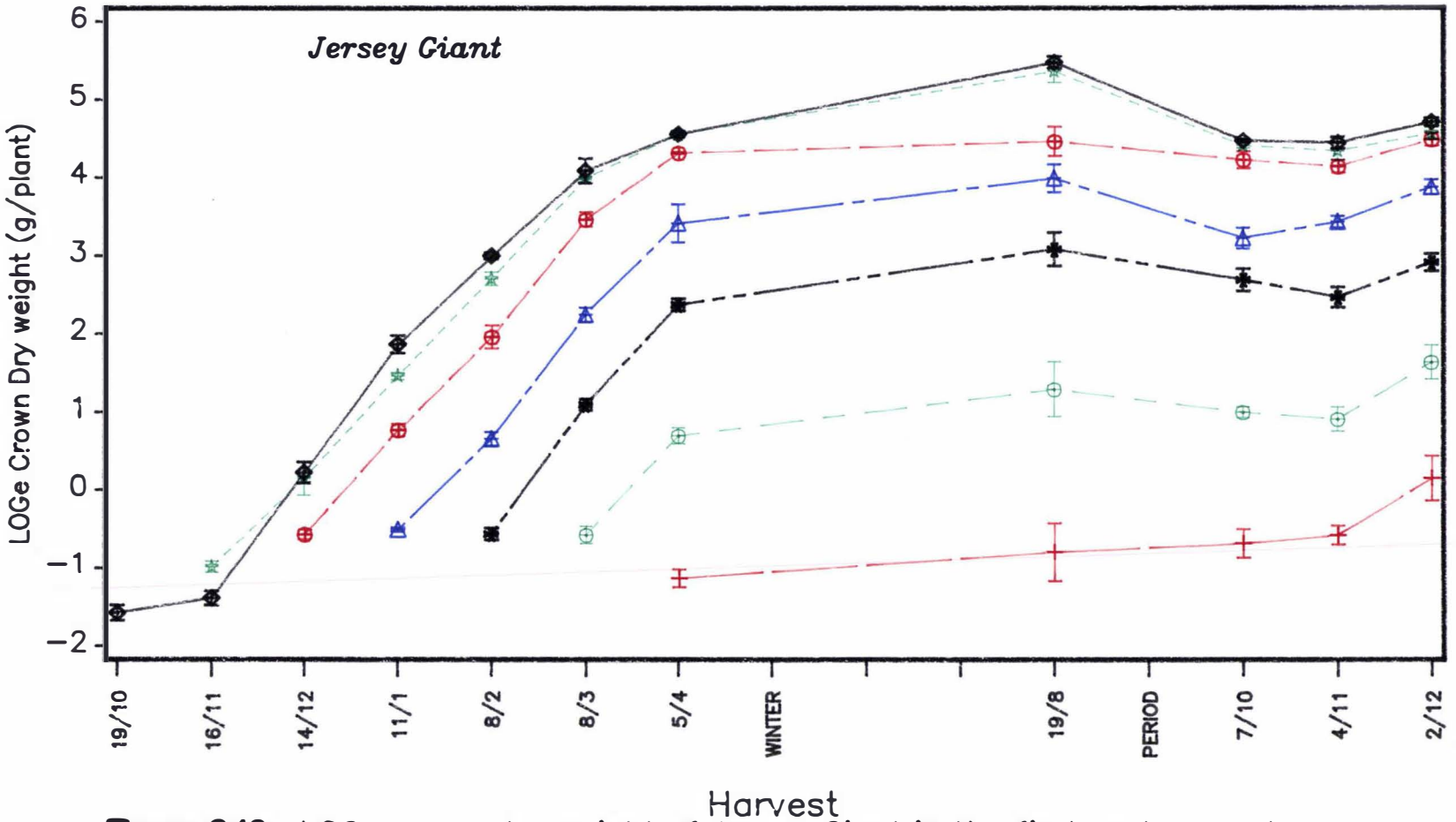


Figure 2.16 LOGe crown dry weight of Jersey Giant in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb; + + + March). I = Stderr. of means.

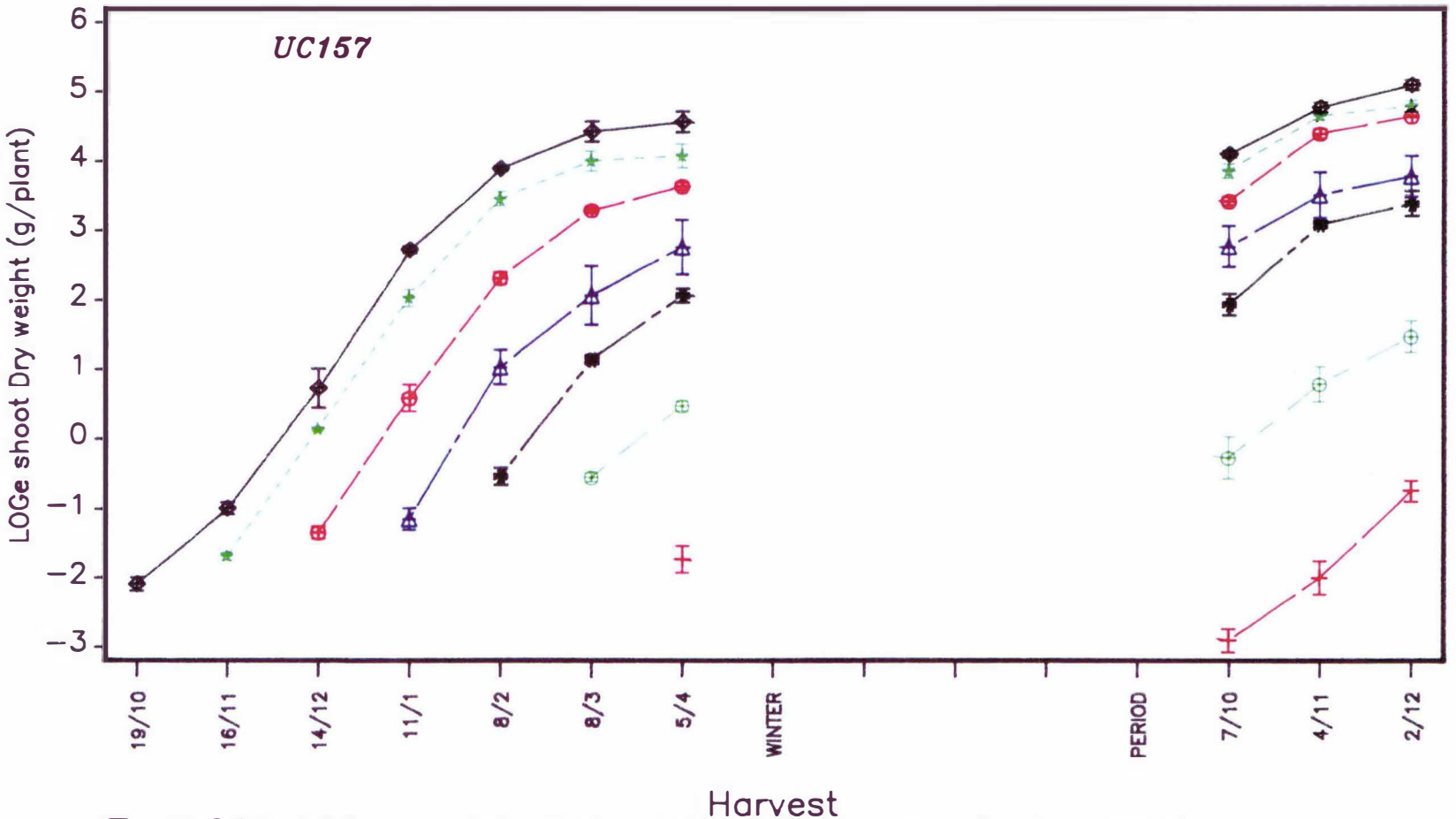


Figure 2.17 LOGe shoot dry weight of UC157 in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ○ ○ ○ Feb; + + + March). I = Stderr. of means.

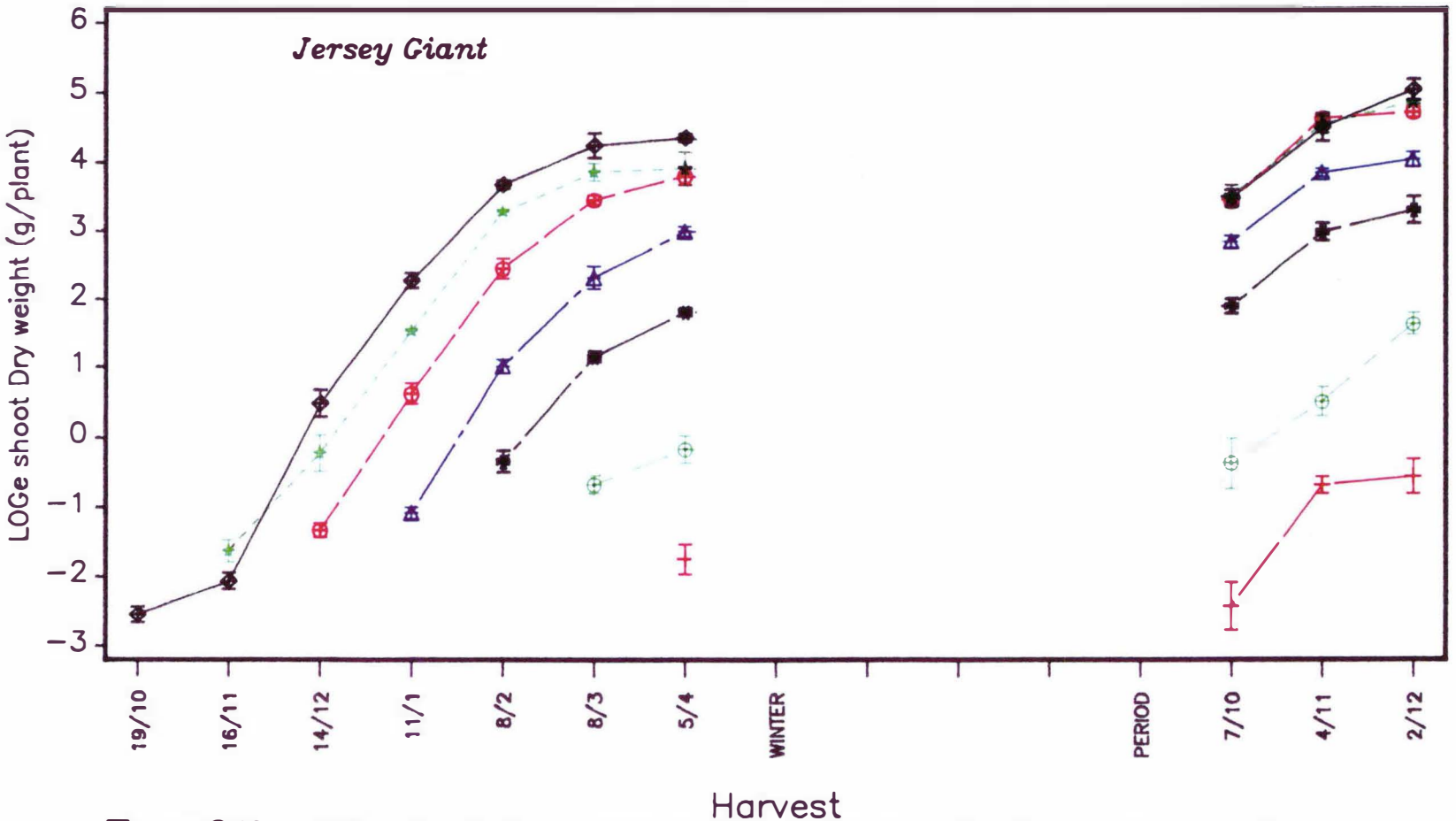


Figure 2.18 LOGe shoot dry weight of Jersey Giant in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ▫ ▫ ▫ Feb; + + + March). I = Stderr. of means.

2.3.3 Shoot to crown dry weight ratios during the first and second seasons

2.3.3.1 Shoot to crown dry weight ratio during the first season

The combined first and second season shoot to crown dry weight ratio is presented in Figure 2.19. Because the ratio was similar between cultivars the average of both cultivars is presented. The ratio increased from 0.5 at an early stage of growth reaching its peak in excess of 1 in February and then decreased to less than 0.8 by early April.

2.3.3.2 Shoot to crown dry weight ratio during the second season

The ratio at the first harvest ranged from 0.3 to 1 (higher for the earlier plantings), then increased to range from 0.5 to 2 in November, followed by a decrease in December to a value of about 0.5 to 1.5, with the late plantings decreasing the least (Figure 2.19).

2.3.3.3 Allometric relationship between shoot and crown dry weight during the first season

Figure 2.20 shows the changes in the allometric relationships between $\log_e$ shoot and $\log_e$ crown dry weight as the season progressed. It should be noted that in order to separate the lines for each planting date the $\log_e$ crown dry weight was offset by 1 gram for each planting. These data suggest that the allometric relationship between $\log_e$ shoot and $\log_e$ crown dry weight changed late in the season (February). Slope (k value) comparisons from these allometric relationships suggests that the k value decreased significantly late in the season for the early plantings regardless of cultivar (Table 2.15c). These data suggest that the allometric relationship was affected by season as the change in the allometric relationships coincided with the decrease in mean weekly temperatures recorded at the adjacent DSIR meteorological site for the period the plants were in the field (Figure 2.21).

The k values for the late plantings were similar to the k values of the early plantings late in the season (Table 2.15c). **K** value comparisons of the early plantings between cultivars found that Jersey Giant had a significantly higher k value for plants planted from September to December compared to UC157 (Table 2.15a).

K value comparisons within cultivars for early growth found that UC157 had a higher k value in the early plantings compared to later plantings. Jersey Giant behaved differently to UC157. Mid season plantings (November to December) had higher k values compared to the early or late plantings (Table 2.15b).

Table 2.15a Initial k value comparison between 2 cultivars of asparagus in the first growing season at the same planting date

Planting	k	se k
Sept.UC (1-5)	1.177b	0.032
Sept.JG (1-5)	1.326a	0.038
Oct.UC (2-5)	1.263a	0.036
Oct.JG (2-5)	1.325a	0.032
Nov.UC (3-5)	1.112b	0.056
Nov.JG (3-5)	1.477a	0.055
Dec.UC (4-7)	1.054b	0.066
Dec.JG (4-5)	1.781a	0.110
Jan.UC (5-7)	0.907a	0.048
Jan.JG (5-7)	0.740a	0.055
Feb.UC (6-7)	0.785a	0.078
Feb.JG (6-7)	0.441a	0.152

- k values from slopes of linear regressions of ln y=ln a + k ln x, where y is shoot and x is crown d.wt. Each parameter estimated from 20 plants.
- Comparisons of k based on t-test ($p \leq 0.05$).

Table 2.15b Initial k value comparison between planting date of 2 cultivars of asparagus at the first growing season.

Planting	k	se k
UC157		
Sept. (1-5)	1.177a	0.032
Oct. (2-5)	1.263a	0.036
Nov. (3-5)	1.112ab	0.056
Dec. (4-7)	1.054bc	0.066
Jan. (5-7)	0.907c	0.048
Feb. (6-7)	0.785c	0.078
Jersey Giant		
Sept. (1-5)	1.326c	0.037
Oct. (2-5)	1.325c	0.032
Nov. (3-5)	1.477b	0.055
Dec. (4-5)	1.781a	0.11
Jan. (5-7)	0.740d	0.055
Feb. (6-7)	0.441d	0.152

- k values from slopes of linear regressions of ln y=ln a + k ln x, where y is shoot and x is crown dry weight. Each parameter estimated from 20 plants.
- Comparisons of k based on t-test ($p \leq 0.05$).

Table 2.15c Changes in allometric relationship between fern and crown dry weight of 2 cultivars of asparagus with time in the first growing season as affected by planting treatment.

Planting	ln a	se ln a*1	k*2	se k*3	R^2 (%)
Sept.UC(1-5)*4	0.234	0.063	1.177a	0.032	99
Sept.UC(5-7)*5	2.341	0.295	0.482b	0.072	82
Sept.JG(1-5)*6	-0.223	0.07	1.326a	0.038	98
Sept.JG(5-7)	2.219	0.259	0.478b	0.065	84
Oct.UC(2-5)	0.024	0.062	1.263a	0.036	99
Oct.UC(5-7)	2.352	0.40	0.403b	0.106	59
Oct.JG(2-5)	-0.345	0.052	1.325a	0.032	99
Oct.JG(5-7)	2.345	0.429	0.361b	0.112	51
Nov.UC(3-5)	-0.172	0.077	1.112a	0.056	98
Nov.UC(5-7)	1.103	0.173	0.615b	0.052	66
Nov.JG(3-5)	-0.465	0.070	1.477a	0.055	99
Nov.JG(5-7)	1.358	0.215	0.583b	0.063	89
Dec.JG(4-5)	-0.166	0.0656	1.781a	0.110	98
Dec.JG(5-7)	0.638	0.138	0.699b	0.057	74
Dec.UC(4-7)	-0.084	0.126	1.054	0.066	95
Jan.UC(5-7)	0.157	0.07	0.907	0.048	97
Jan.JG(5-7)	0.164	0.085	0.74	0.055	95
Feb.UC(6-7)	-0.097	0.051	0.785	0.078	94
Feb.JG(6-7)	-0.426	0.10	0.441	0.152	58

- k values from the slopes of linear regressions of ln y=ln a + k ln x, where y is shoot and x is crown dry weight. Each parameter was estimated from 20 plants.
- Comparisons of k based on t-test ($p \leq 0.05$).

- *1 = standard error of ln a;
- *2 = t test to indicate a significant changes in slope at any planting date;
- *3 = standar error of k;
- *4 = september planting, cv.UC157 from 1 to 5 harvest;
- *5 = september planting, cv.UC157 from 5 to 7 hravest;
- *6 = september planting, cv.Jersey Giant from 1 to 5 harvest.

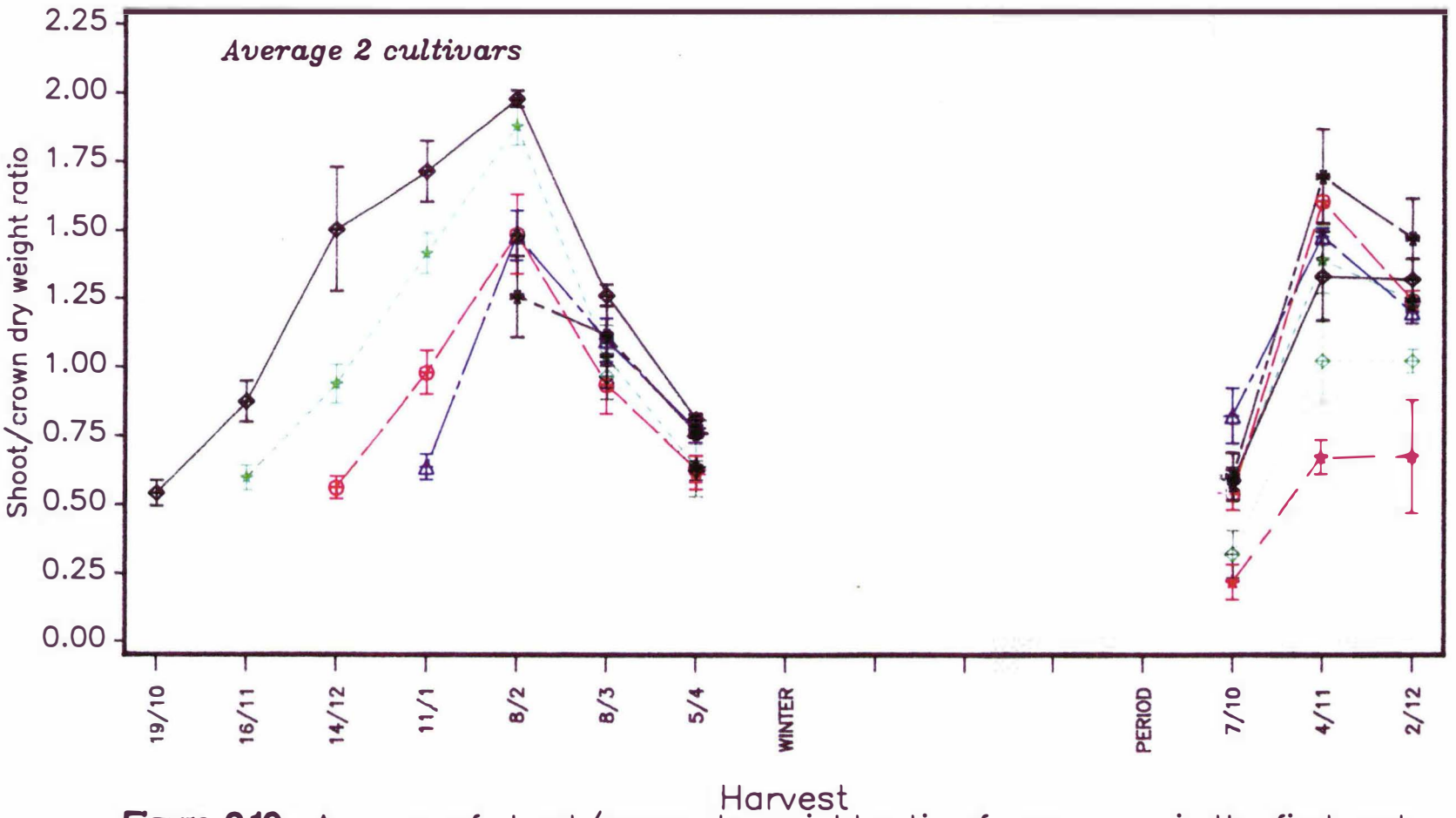
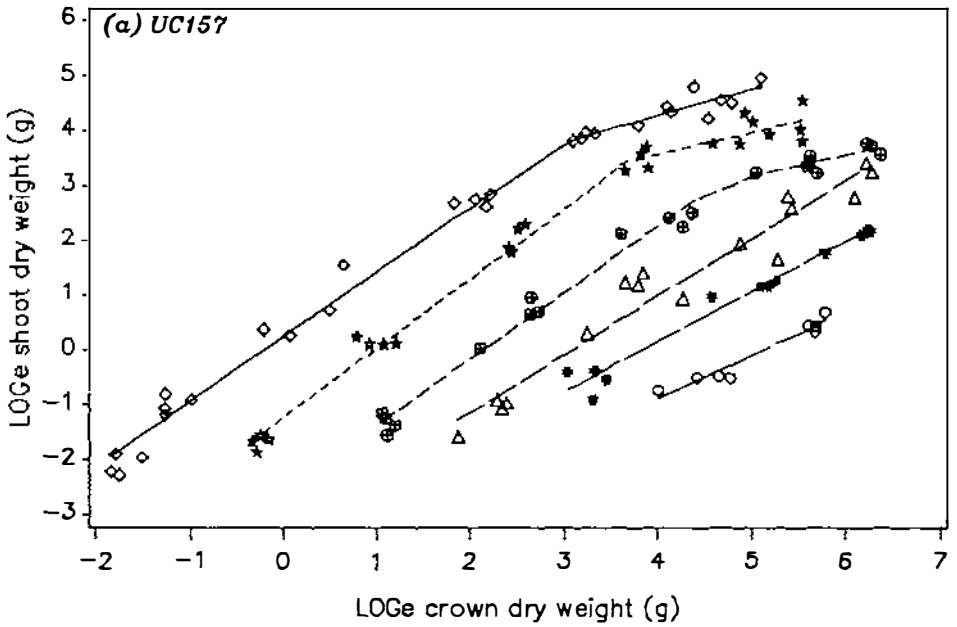


Figure 2.19 Average of shoot/crown dry weight ratio of asparagus in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ◇ ◇ ◇ Feb; ★ ★ ★ March). I = Stderr. of means.



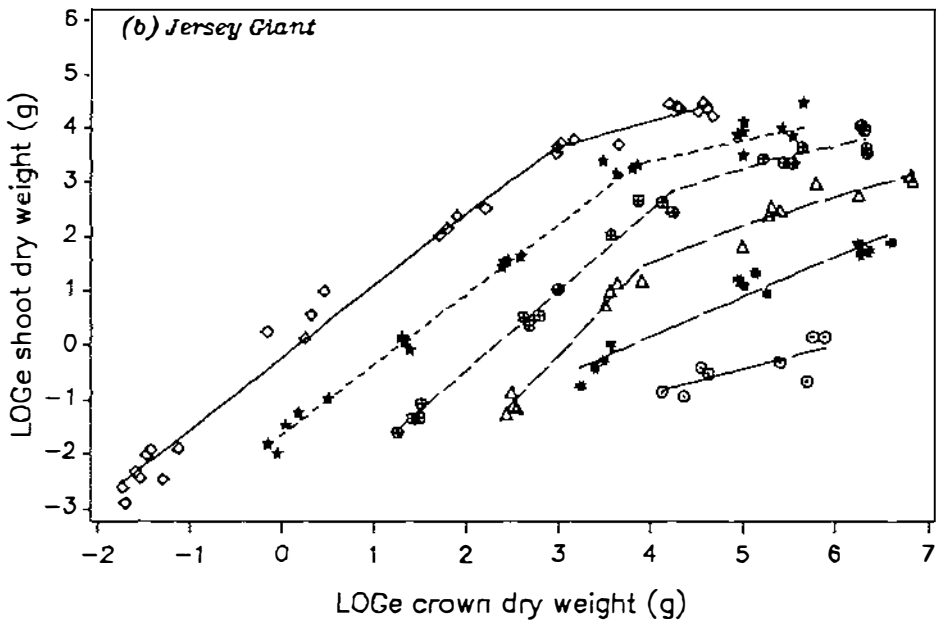


Figure 2.20 Allometric relationships between shoot and crown dry weight (◇ ◇ ◇ Sep; ★ ★ ★ Oct; ● ● ● Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb).

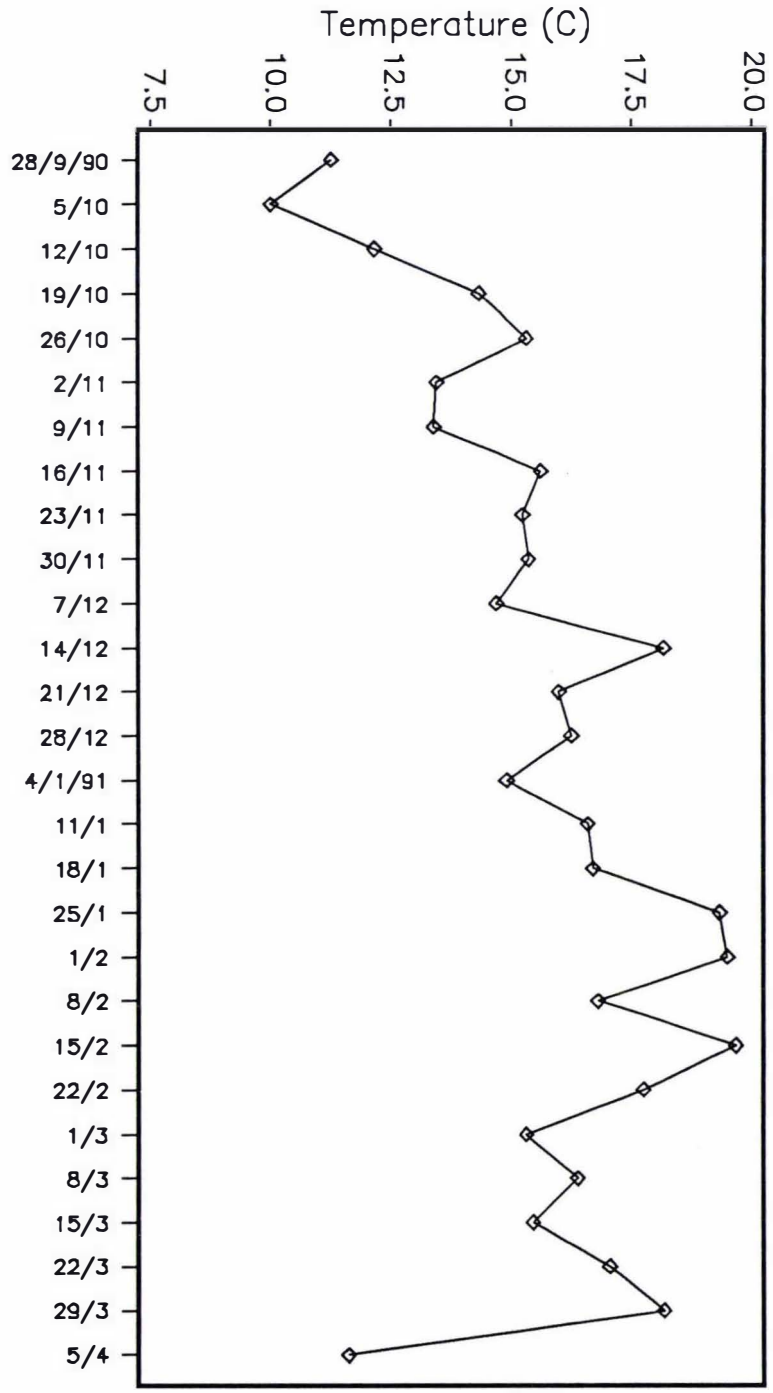


Figure 2.21 Mean weekly temperature from 21 September 1990 to 5 April 1991

2.3.4 **The development of shoots, buds, and roots during the first and second seasons**

2.3.4.1 **Accumulation of shoots, buds, and roots during the first season**

There are three kind of graphs used to describe the number of shoots :

1. The actual shoot number which consists of the green and dead shoots at any particular harvest (Figures 2.22 and 2.23). The analysis of variance on the final harvest was carried out only on this data.

2. The current shoot number which consists of only the green shoots present at any harvest (Figures 2.24 and 2.25). The current shoot number gives an indication of the amount of active photosynthesizing tissue present at any particular harvest.

3. The cumulative shoot number which is the shoot number during the second season plus the number of actual shoots during the first season at the final harvest (Figures 2.26 and 2.27). This is particularly relevant for the ratio of cumulative shoot plus bud to root number during the second season because many roots present during the second season were related to shoots produced during the previous season.

No matter which of the two shoot parameters, which were relevant to the first season were used, shoot production increased as the season progressed (Figures 2.22 to 2.25) and tended to fall away at the final harvest.

Bud number increased throughout the season and did not cease even with the cool temperatures of the autumn (Figures 2.28 and 2.29). Root number increased steadily throughout the season (Figures 2.30 and 2.31). At each harvest UC157 maintained a higher number of shoots, buds and roots than Jersey Giant.

2.3.4.2 **Shoot, bud and root number at the final harvest in the first season**

Analyses of variance were carried out on $\log_e$ number of shoots (Table 2.16), $\log_e$ number of buds (Table 2.17), and $\log_e$ number of roots (Table 2.18) at the final harvest during the first season. The untransformed data are shown in brackets. Shoot number

decreased as the planting date was delayed and UC157 had more shoots than Jersey Giant. October and November plantings had a similar number of shoots. There was no significant interaction between planting date and cultivar.

There were no significant differences in bud numbers for the first three plantings of both cultivars, but from the December planting onwards the number decreased as the planting date was delayed. UC157 produced a greater number of buds than Jersey Giant for all plantings except the December planting. The September planting of UC157 produced about double the bud number of Jersey Giant.

Root number per plant responded similarly to bud numbers, except that the number of roots of UC157 in the November planting was less than the first planting. Apart from the December, February and March plantings UC157 produced more roots than Jersey Giant. The September planting of UC157 produced about double the root number of Jersey Giant.

2.3.4.3 **Accumulation of shoots, buds and roots during the second season**

No dead shoots were observed during the second season and the actual shoot number was therefore equal to the current shoot number. Shoot production increased as the season progressed (Figures 2.22 to 2.27). The rate was the same when expressed on a cumulative basis. The shoot production rate was different between planting dates for UC157. Except for the October and December plantings there was little shoot production from October to November, followed by a high rate in the next 4 week period. During the second season the shoot production rate for Jersey Giant appeared steady over the October to December period.

Table 2.16 Log_e number of shoots/plant of asparagus at final harvest in the first season.

Planting	Cultivar		
	UC157	Jersey Giant	Pl mean[2]
21 Sept.	3.32 (27.66)[1]	2.96 (19.30)	3.14**a**
19 Oct.	3.11 (22.42)	2.91 (18.36)	3.01**b**
16 Nov.	3.06 (21.33)	2.86 (17.46)	2.96**b**
14 Dec.	2.87 (17.64)	2.73 (15.33)	2.80**c**
14 Jan.	2.72 (15.18)	2.46 (11.70)	2.59**d**
11 Feb.	2.07 (7.93)	2.01 (7.46)	2.04**e**
8 March	1.32 (3.74)	1.37 (3.94)	1.35**f**
Cv mean[2]	2.64**a**	2.47**b**	
Cultivar (Cv)		**	
Planting date (Pl)		**	
Cv x Pl		ns	

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Value in the bracket is the untransformed shoot number;
- 2. Means separation within column and row by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.0564 and 0.0301, respectively with $df_{(error)} = 39$.

Table 2.17 Log_e number of buds/plant of asparagus at final harvest in the first season.

Planting	Cultivar		
	UC157	Jersey Giant	Pl mean[2]
21 Sept.	4.24**a** (69.4)[1]	3.59**bc** (36.2)	3.92
19 Oct.	4.16**a** (64.1)	3.80**b** (44.7)	3.98
16 Nov.	4.16**a** (64.1)	3.65**bc** (38.5)	3.91
14 Dec.	3.78**b** (43.8)	3.50**bc** (33.1)	3.64
14 Jan.	3.38**c** (29.4)	2.83**d** (16.9)	3.11
11 Feb.	2.27**d** (9.7)	2.13**e** (8.4)	2.20
8 March	1.04**e** (2.8)	1.21**f** (3.4)	1.13
Cv mean[2]	3.29	2.96	

Cultivar (Cv)	**
Planting date (Pl)	**
Cv x Pl	**

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Value in the bracket is the untransformed bud number;
- 2. Means separation in the table by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.1463 with $df_{(error)}$ =39.

Table 2.18 Log_e number of roots/plant of asparagus at final harvest in the first season.

Planting	Cultivar		
	UC157	J. Giant	Pl mean[2]
21 Sept.	5.73**a** (307.9)[1]	5.04**d** (154.5)	5.39
19 Oct.	5.52**ab** (249.6)	5.10**cd** (164.0)	5.31
16 Nov.	5.34**bc** (208.5)	4.91**de** (135.6)	5.13
14 Dec.	4.70**ef** (109.9)	4.57**f** (96.5)	4.64
14 Jan.	4.27**g** (71.5)	3.86**h** (47.5)	4.07
11 Feb.	3.16**i** (23.6)	3.02**i** (20.5)	3.09
8 March	2.27**j** (9.7)	2.17**j** (8.8)	2.22
Cv mean[2]	4.43	4.10	
Cultivar (Cv)	**		
Planting date (Pl)	**		
Cv x Pl	**		

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Value in the bracket is the untransformed root number;
- 2. Means separation in the table by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.0822 with $df_{(error)}$ =39.

Buds production started at a low rate during the first 4 week growing period for some of the early plantings and then the rate increased in the next 4 week period (Figures 2.28 and 2.29). For the other plantings bud number increased over the whole period. The bud production rate was higher for UC157.

Root production in some cases decreased during the first 4 week period (Figures 2.30 and 2.31). Generally root production did not start until November. In particular there was a marked increase for UC157 for the September to January plantings. For the September to January plantings the root production rate was higher in UC157 compared to Jersey Giant.

2.3.4.4 **Shoot, bud and root number at the final harvest in the second season**

Analyses of variance were carried out on the actual number of shoots (Table 2.19), $\log_e$ number of buds (Table 2.20) and $\log_e$ number of roots (Table 2.21) at the final harvest (2 December) during the second season. The untransformed data are in brackets. The number of shoots was affected by planting date, cultivar and by their interaction. The number of shoots of UC157 in the September to December plantings were not significantly different and were similar to Jersey Giant in the September to October plantings. In addition shoot production of Jersey Giant for the September and October plantings were not different. From December onwards the trend was for shoot number to decreased. UC157 had a higher shoot number than Jersey Giant from November to January.

Bud numbers were significantly affected by planting date, cultivar and their interaction. Within cultivars there were no significant differences in bud number between the early plantings, but bud number gradually decreased as planting date advanced from November onwards, although the differences were only significant between early and late plantings. In addition, UC157 produced more buds than Jersey Giant, apart from the February and March plantings.

The root number was also affected by planting date, cultivar and their interaction. Within cultivars the number of roots was not significantly different between September and October plantings or between October and November plantings. September to November plantings had a significantly higher number of root compared to later plantings (December onward). UC157 had a significantly higher number of roots at all planting dates, except February, compared to Jersey Giant.

Table 2.19 Number of shoots/plant of asparagus at final harvest in the second season

Planting	Cultivar		
	UC157	J. Giant	Pl mean[1]
21 Sept.	9.80**ab**	8.10**abcd**	8.95
19 Oct.	9.10**ab**	8.20**abc**	8.65
16 Nov.	10.00**a**	6.75**cde**	8.38
14 Dec.	10.35**a**	6.70**de**	8.53
14 Jan.	7.65**bcd**	5.30**ef**	6.48
11 Feb.	4.10**fg**	4.05**fg**	4.08
8 March	2.45**g**	3.30**fg**	2.88
Cv mean[1]	7.64	6.06	
Cultivar (Cv)		**	
Planting date (Pl)		**	
Cv x Pl		**	

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Means separation in the table by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.674 with $df_{(error)} = 39$.

Table 2.20 Log_e number of buds/plant of asparagus at final harvest in the second season

Planting	Cultivar		
	UC157	Jersey Giant	Pl mean[2]
21 Sept.	4.08**ab** (59.1)[1]	3.67**cde** (39.3)	3.88
19 Oct.	4.21**a** (67.4)	3.63**cde** (37.7)	3.92
16 Nov.	3.97**abc** (53.0)	3.50**de** (33.1)	3.74
14 Dec.	3.76**bcd** (42.9)	3.37**e** (29.1)	3.57
14 Jan.	3.51**de** (33.4)	3.00**f** (20.1)	3.26
11 Feb.	2.81**f** (16.6)	2.50**f** (12.2)	2.66
8 March	1.70**g** (5.5)	1.86**g** (6.4)	1.78
Cv mean[2]	3.43	3.08	

Cultivar (Cv)	**
Planting date (Pl)	**
Cv x Pl	**

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Value in the bracket is the untransformed bud number;
- 2. Means separation in the table by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.106 with $df_{(error)}$ =39.

Table 2.21 Log_e number of roots/plant of asparagus during at final harvest in the second season.

Planting	Cultivar		
	UC157	Jersey Giant	Pl mean[2]
21 Sept.	5.81**a** (333.6)[1]	5.34**cd** (208.5)	5.58
19 Oct.	5.70**ab** (298.9)	5.2**de** (181.3)	5.45
16 Nov.	5.48**bc** (239.8)	5.05**e** (156.0)	5.27
14 Dec.	5.07**e** (159.2)	4.73**f** (113.3)	4.90
14 Jan.	4.77**f** (117.9)	4.15**g** (63.4)	4.46
11 Feb.	3.80**h** (44.7)	3.68**h** (39.5)	3.74
8 March	2.59**i** (13.3)	2.92**j** (18.5)	2.76
Cv mean[2]	4.75	4.44	
Cultivar (Cv)		**	
Planting Date (Pl)		**	
Cv x Pl		**	

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Value in the bracket is the untransformed bud number;
- 2. Means separation in the table by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.078 with $df_{(error)}$ =39.

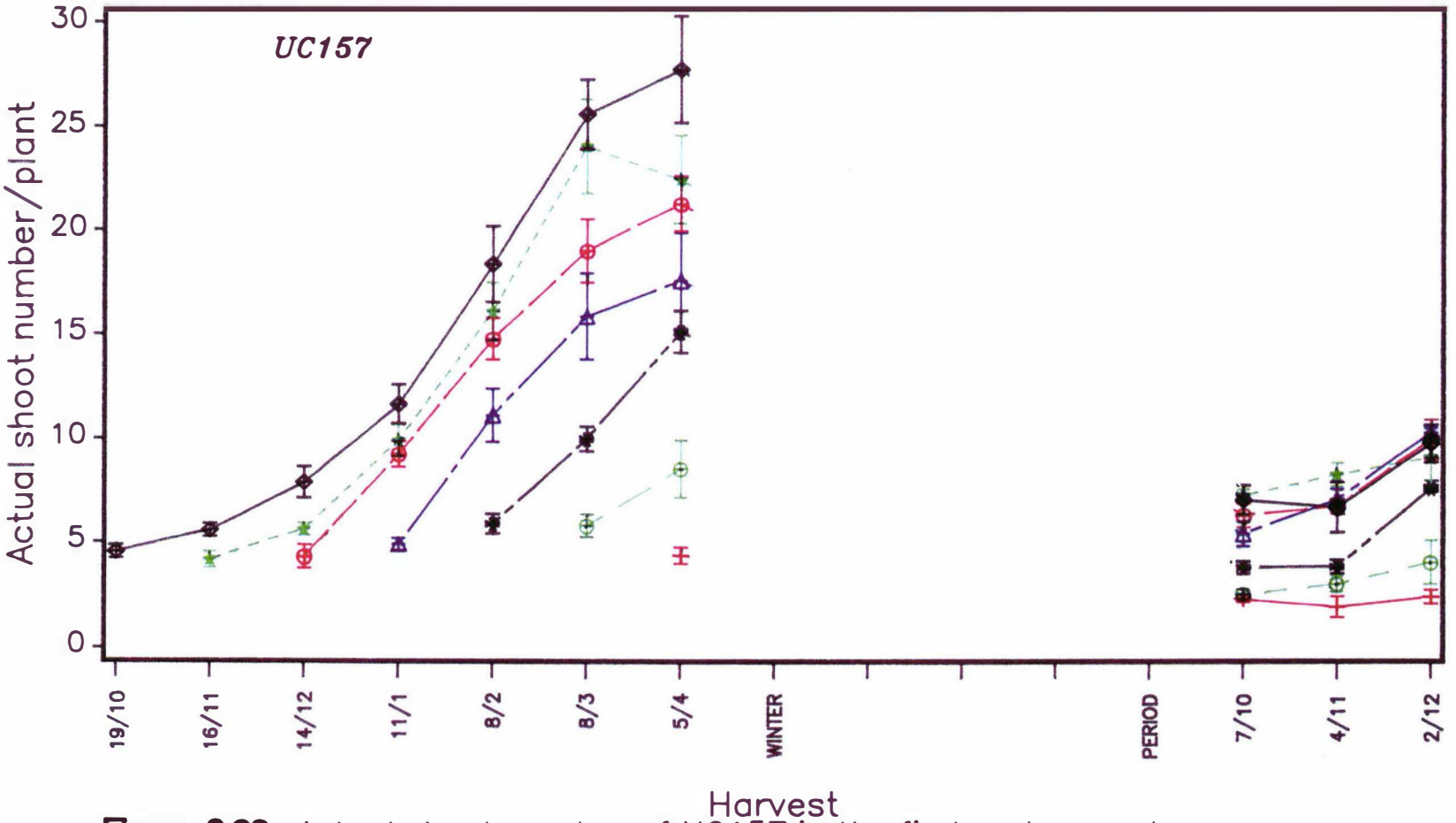


Figure 2.22 Actual shoot number of UC157 in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb; + + + March). I = Stderr. of means.

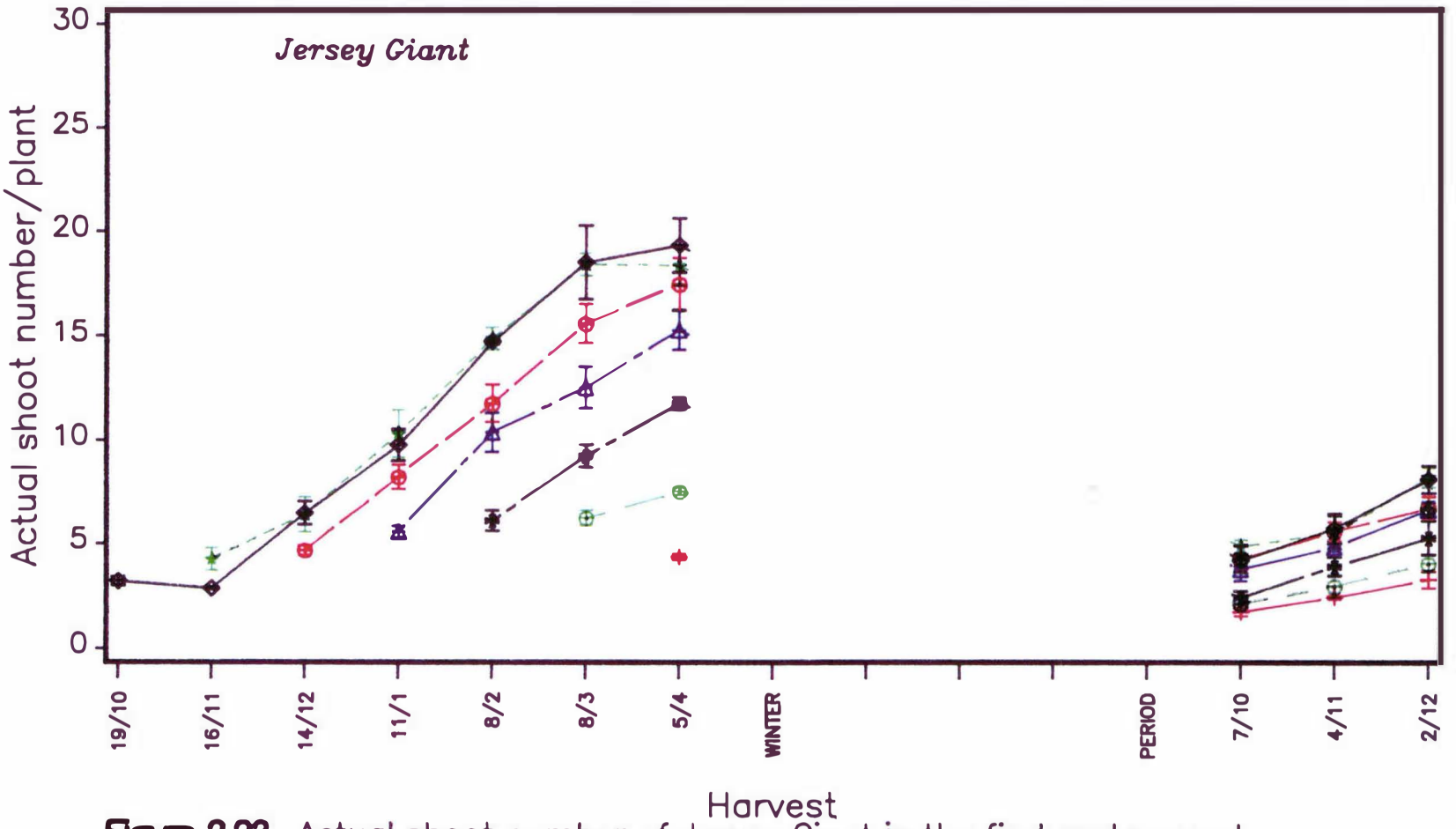


Figure 2.23 Actual shoot number of Jersey Giant in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb; + + + March). I = Stderr. of means.

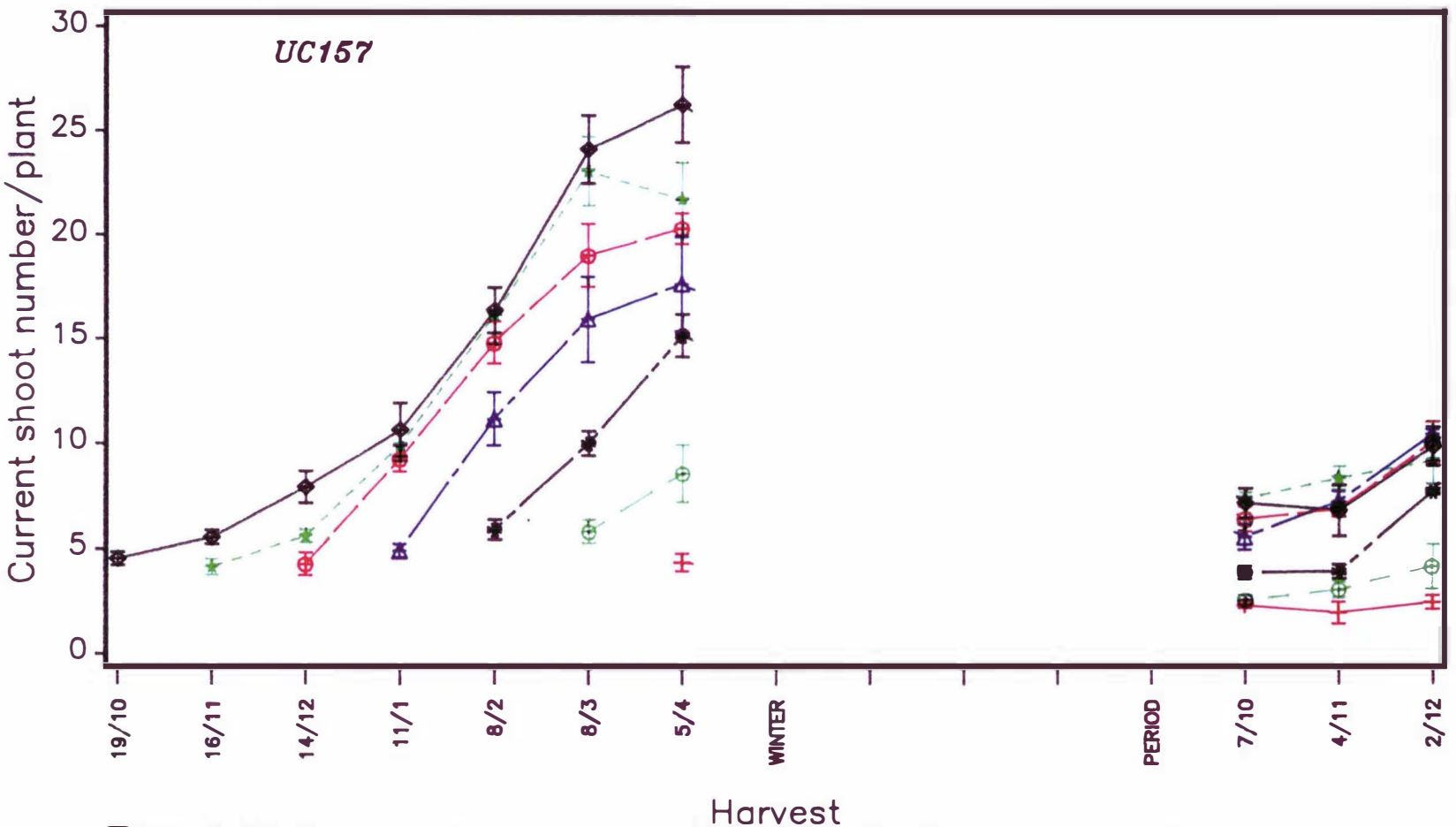


Figure 2.24 Current shoot number of UC157 in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb; + + + March). I = Stderr. of means.

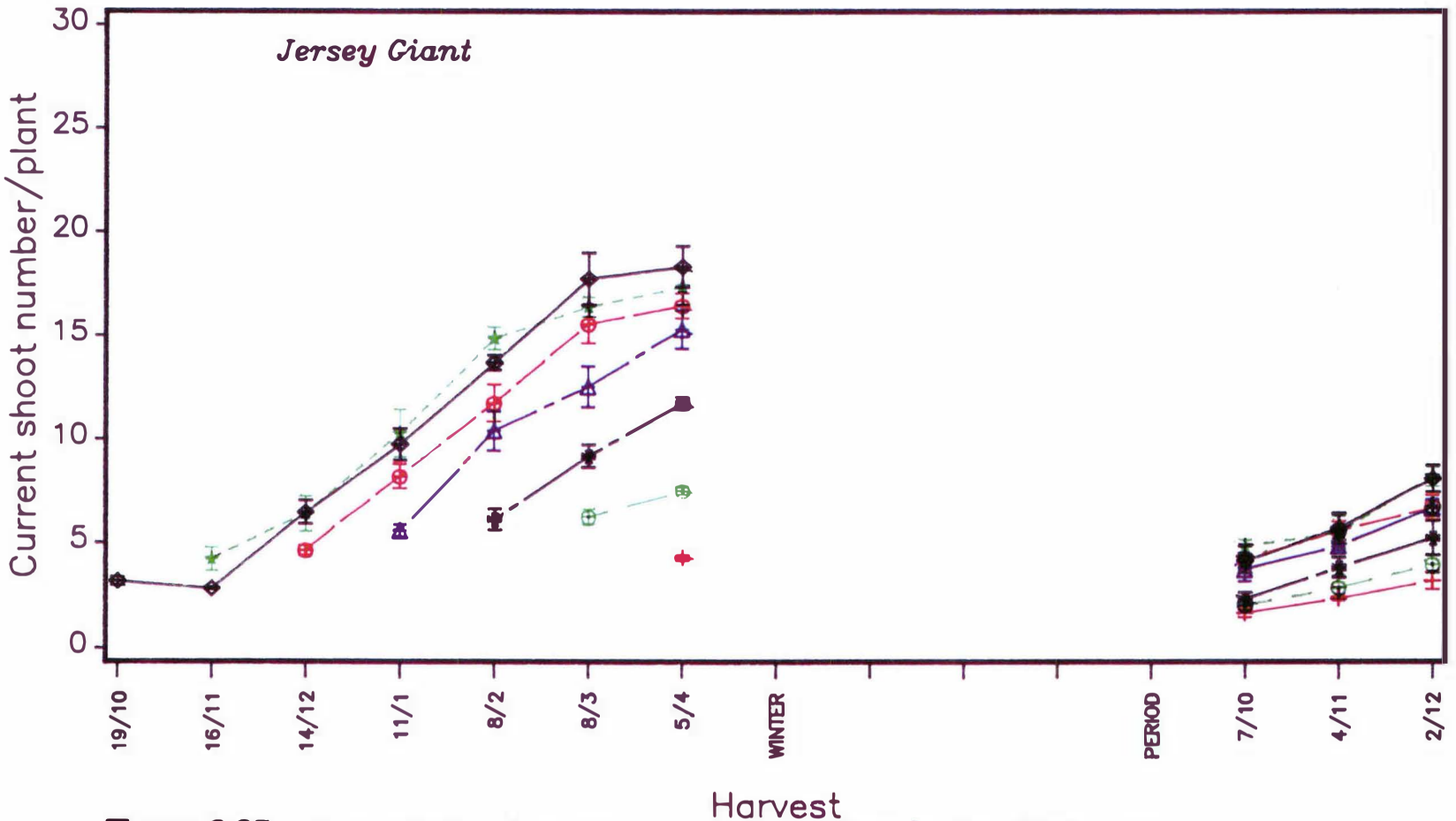


Figure 2.25 Current shoot number of Jersey Giant in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb; + + + March). I = Stderr. of means.

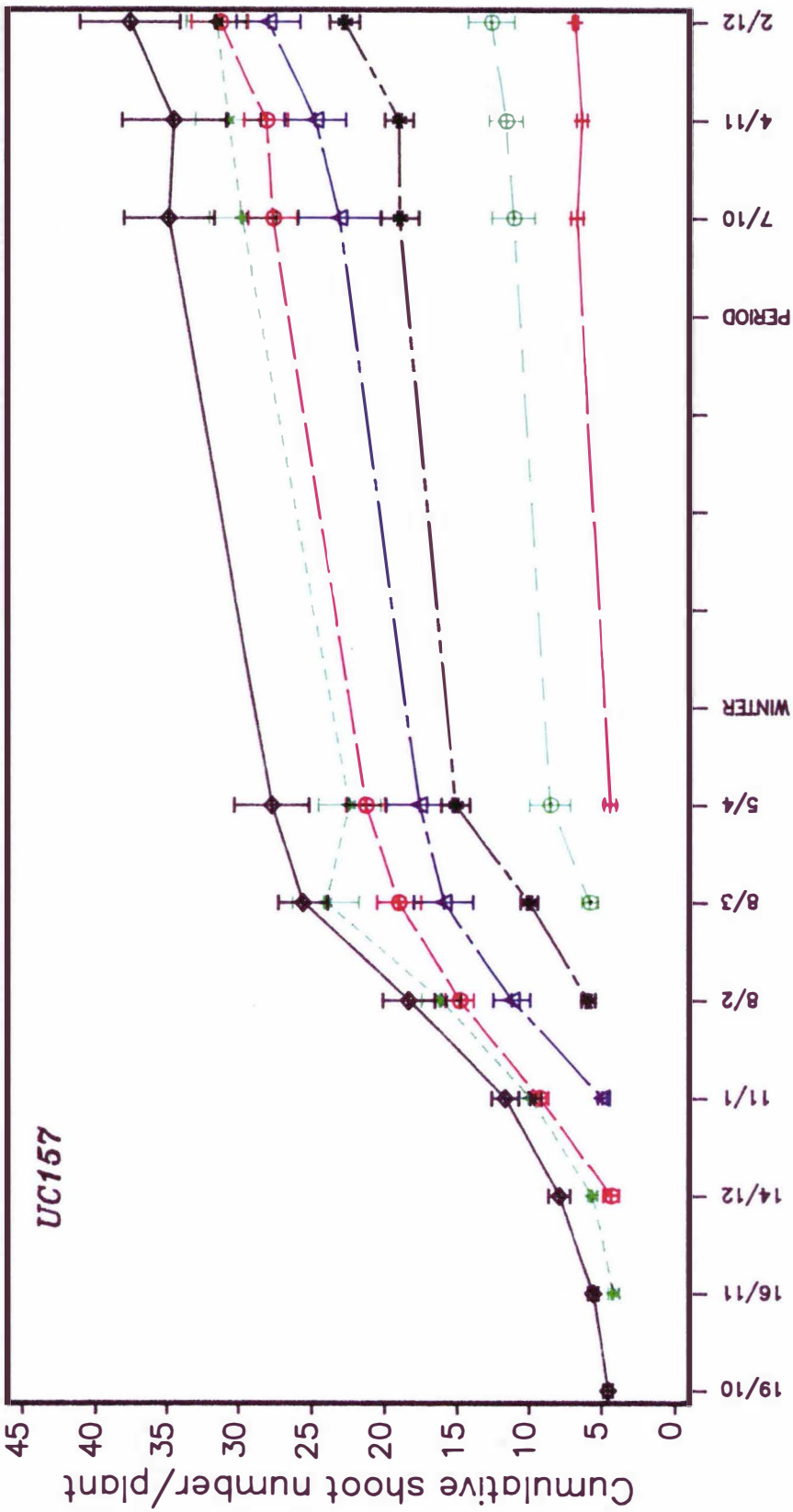


Figure 2.26 Cumulative shoot number of UC157 in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; * * * Jan; ⊙ ⊙ ⊙ Feb; + + + March). I = Stderr. of means.

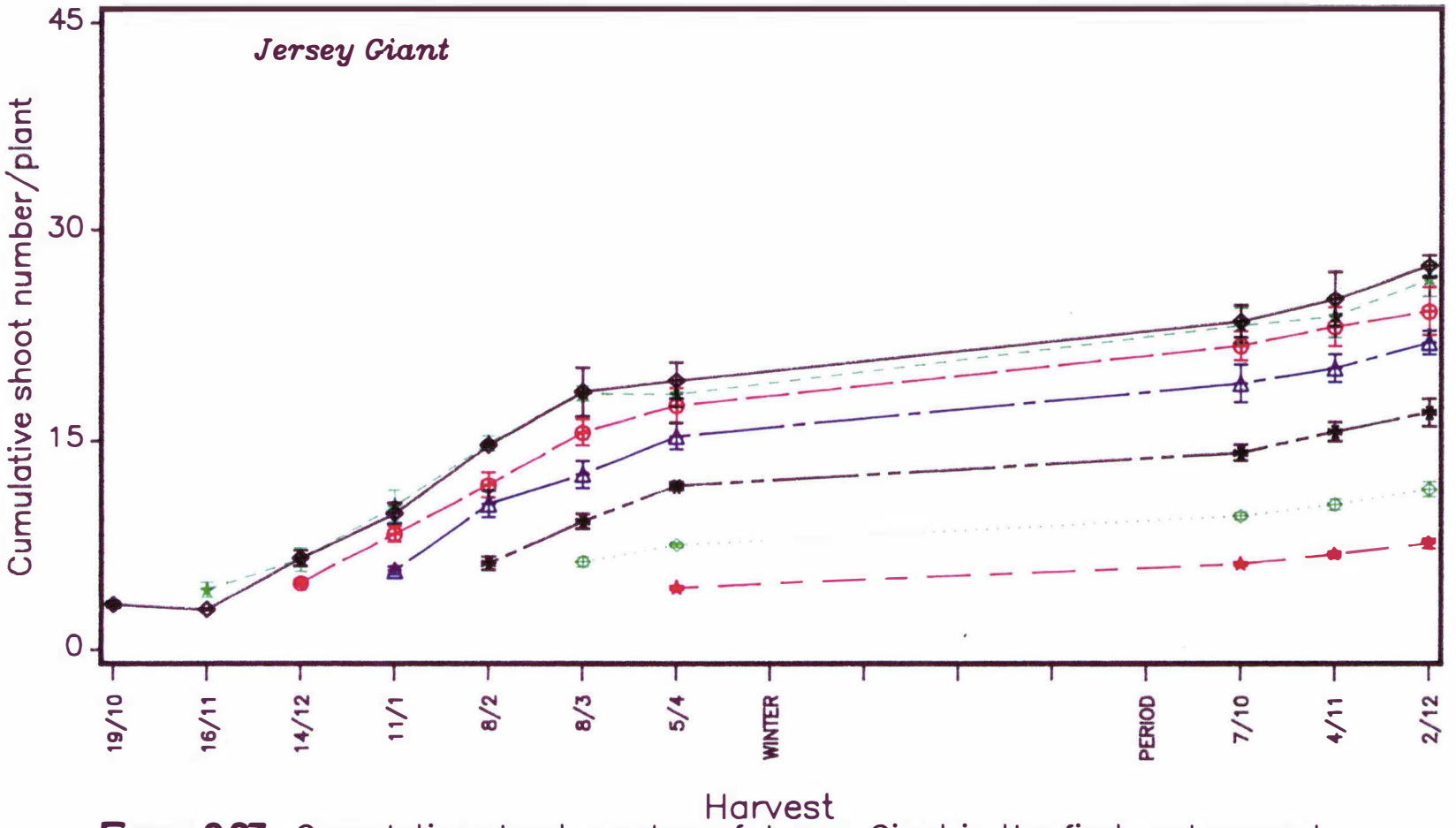


Figure 2.27 Cumulative shoot number of Jersey Giant in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ◇ ◇ ◇ Feb; ★ ★ ★ March). I = Stderr. of means.

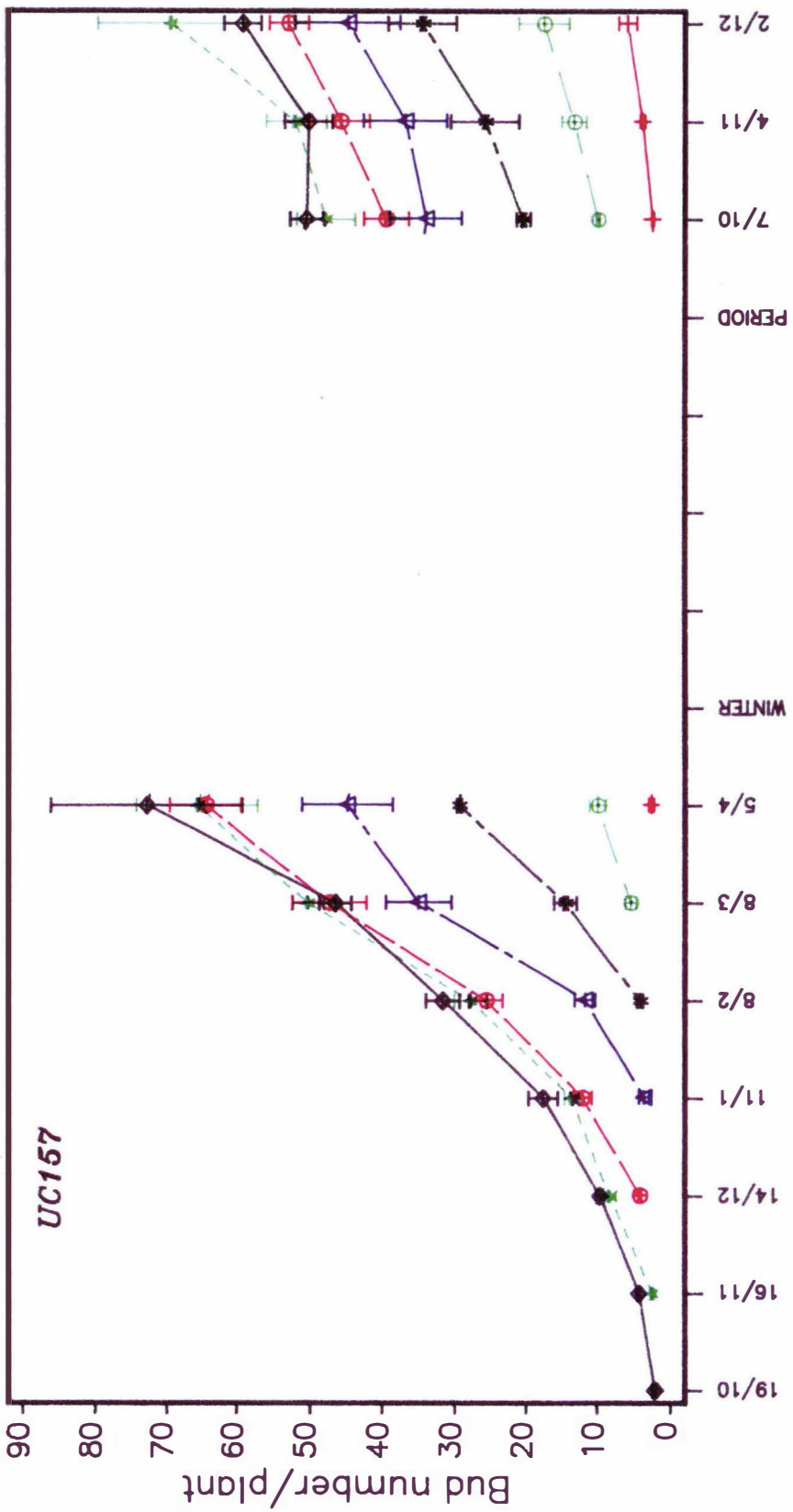


Figure 2.28 Bud number of UC157 in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ N_ov; Δ Δ Δ Dec; * * * Jan; ⊙ ⊙ ⊙ Feb; + + + March). I = Stderr. of means.

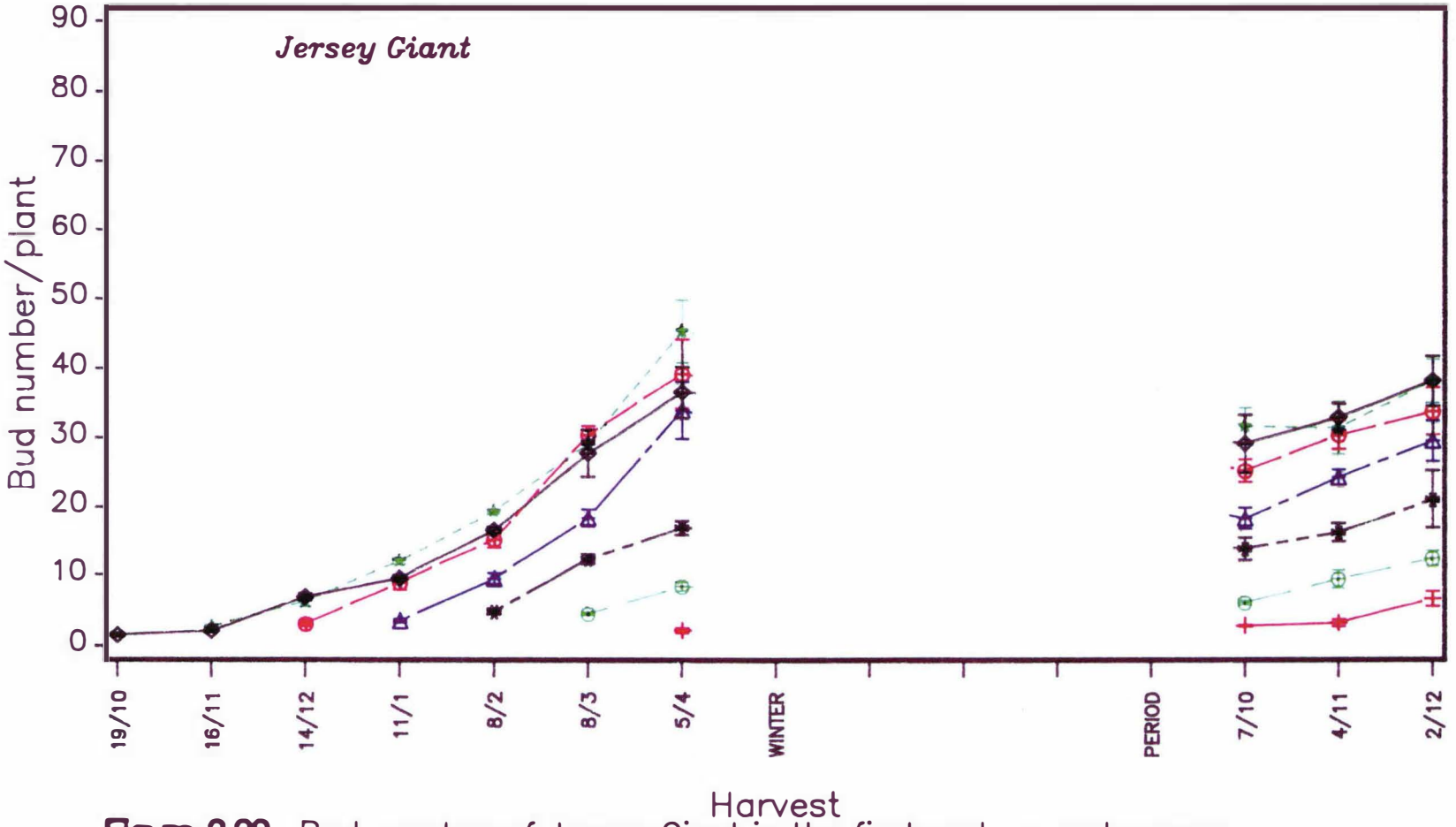


Figure 2.29 Bud number of Jersey Giant in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb; + + + March). I = Stderr. of means.

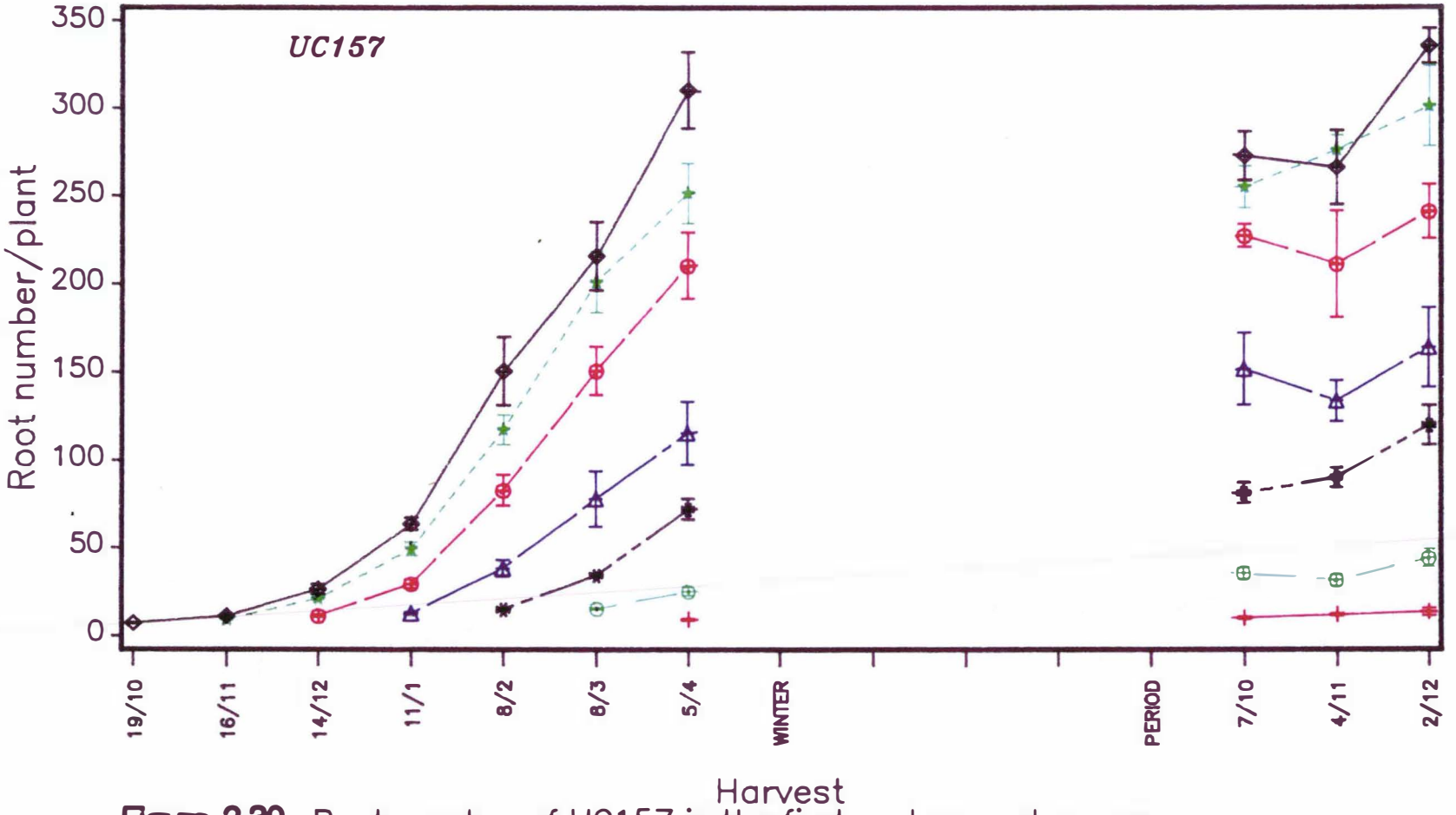


Figure 2.30 Root number of UC157 in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb; + + + March). I = Stderr. of means.

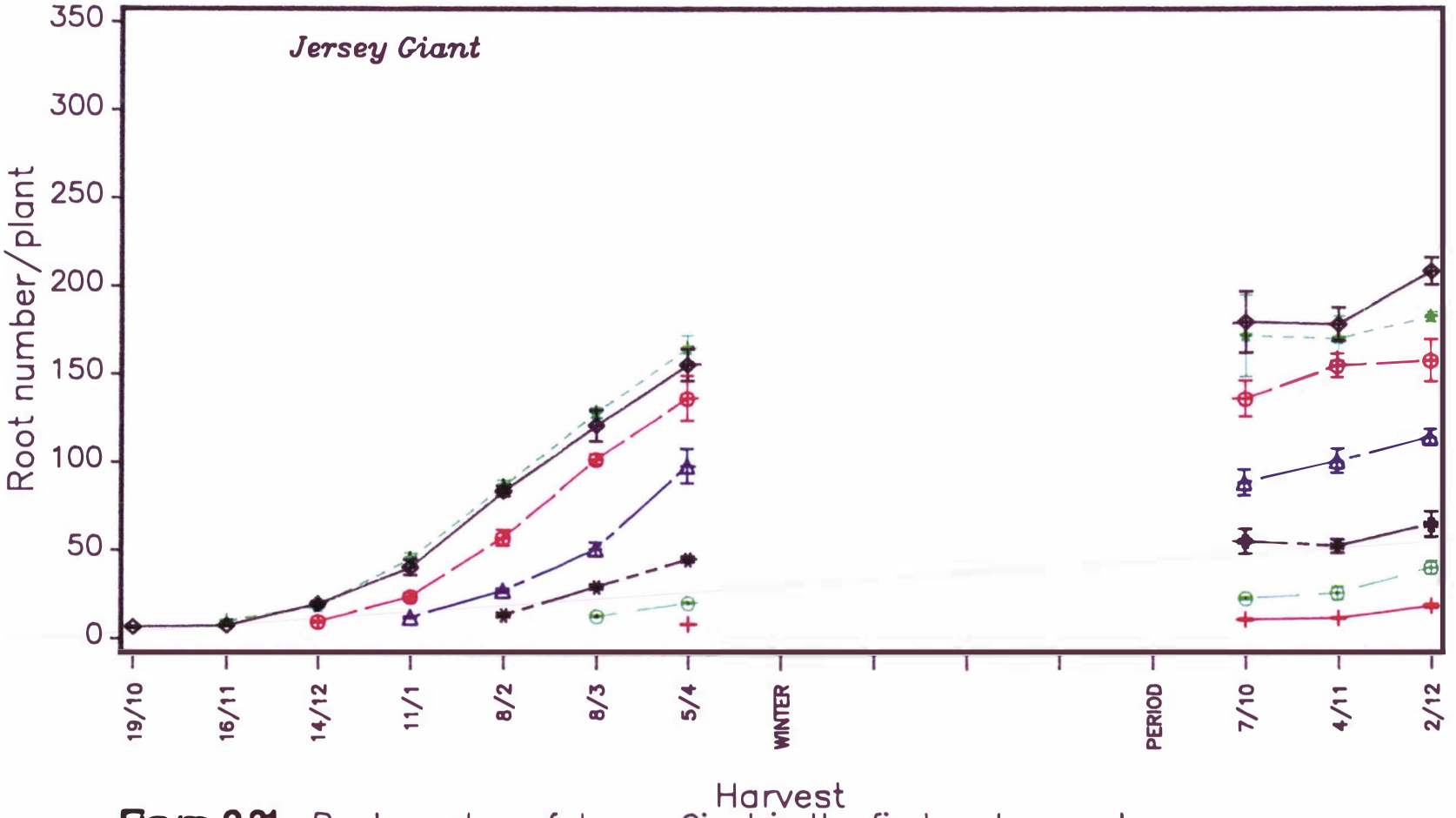


Figure 2.31 Root number of Jersey Giant in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb; + + + March). I = Stderr. of means.

2.3.5 **The ratio of bud to actual shoot number and of cumulative shoot plus bud to root number during the first and second seasons**

2.3.5.1 **Ratios during the first season**

2.3.5.1.1 **Bud to shoot number ratio**

Analysis of variance on the final harvest showed that planting date and cultivar had a significant effect on the bud to shoot number ratio (Table 2.22). The ratio was not significantly different for October to December plantings. The September planting was not different to the December planting. In addition the ratio decreased significantly from December onwards. UC157 had a significantly higher ratio than Jersey Giant.

Although the anova of the final harvest showed a significant different between cultivars, in general the trend was similar between cultivars (figure not shown) and for simplicity the change in the ratio throughout the first and second seasons is presented by the average of the two cultivars (Figure 2.32). The bud to shoot ratio increased steadily as the season progressed. During early growth, shoot number predominated over bud production, regardless of planting date (1:2 ratio). At the end of season the ratio was closed to 2 buds per 1 shoot (2:1 ratio) for early to mid season plantings.

2.3.5.1.2 **Cumulative shoot and bud to root number ratio**

Analysis of variance on the final harvest data found that only the planting date had a significant effect on this ratio (Table 2.23). For simplicity only the average of the two cultivars is presented (Figure 2.33). The trend was that the ratio increased as the planting dates advanced. There were however few differences between the early plantings.

The ratio of cumulative shoot plus bud to root number was relatively constant in early growth followed by a rapid decrease, particularly for the early plantings, and then stabilized at the last three harvest periods (Figure 2.33). It was found that during early

growth that each shoot and bud were supported by about 1.2 roots regardless of planting date. At the final harvest, each shoot and bud of the early plantings were supported by about 3 roots.

Table 2.22 Bud/actual shoot number ratio of asparagus at final harvest in the first season.

Planting	Cultivar		
	UC157	Jersey Giant	Pl mean[2]
21 Sept.	2.57	1.90	2.24**b**
19 Oct.	2.90	2.48	2.69**a**
16 Nov.	3.04	2.34	2.69**a**
14 Dec.	2.57	2.20	2.39**ab**
14 Jan.	1.97	1.44	1.71**c**
11 Feb.	1.20	1.13	1.17**d**
8 March	0.63	0.53	0.58**e**
Cv mean[2]	2.13**a**	1.72**b**	

Cultivar (Cv)	**
Planting Date (Pl)	**
Cv x Pl	ns

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Value in the bracket is the untransformed bud number;
- 2. Means separation within colum and row by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.1546 and 0.0826, respectively with $df_{(error)} = 39$.

Table 2.23 Cumulative shoot plus bud/root number ratio of asparagus during the first season at final harvest.

Planting	Cultivar		
	UC157	Jersey Giant	Pl mean[2]
21 Sept.	0.32	0.36	0.34**e**
19 Oct.	0.35	0.39	0.37**ed**
16 Nov.	0.41	0.41	0.41**d**
14 Dec.	0.56	0.50	0.53**c**
14 Jan.	0.63	0.64	0.64**b**
11 Feb.	0.73	0.78	0.76**a**
8 March	0.72	0.76	0.74**a**
Cv mean[2]	0.53	0.55	

Cultivar (Cv)	ns
Planting Date (Pl)	**
Cv x Pl	ns

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Value in the bracket is the untransformed bud number;
- 2. Means separation within column and row by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.0307 and 0.0164, respectively with $df_{(error)} = 39$.

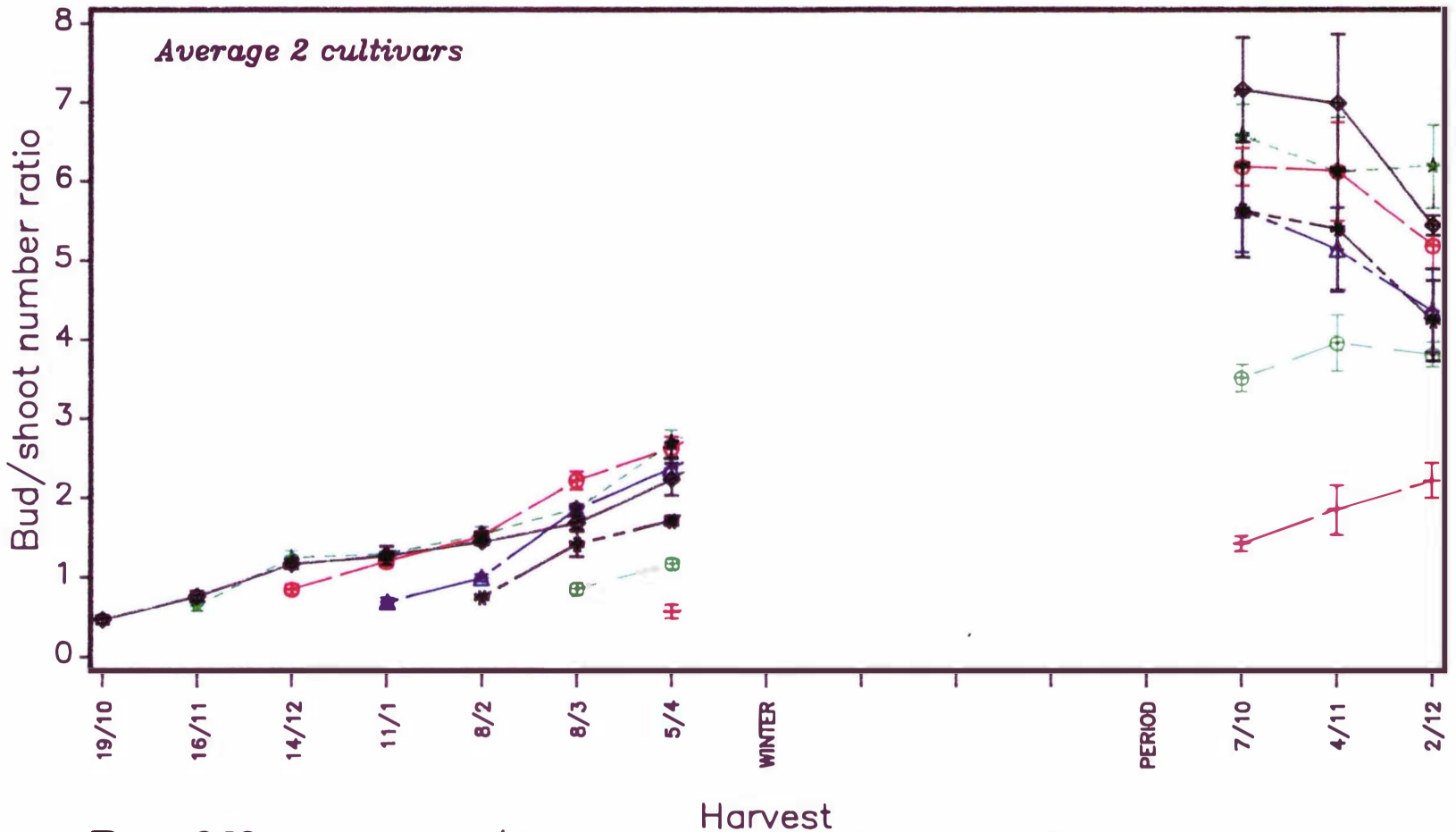


Figure 2.32 Average bud/shoot number ratio of asparagus in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb; + + + March). I = Stderr. of means.

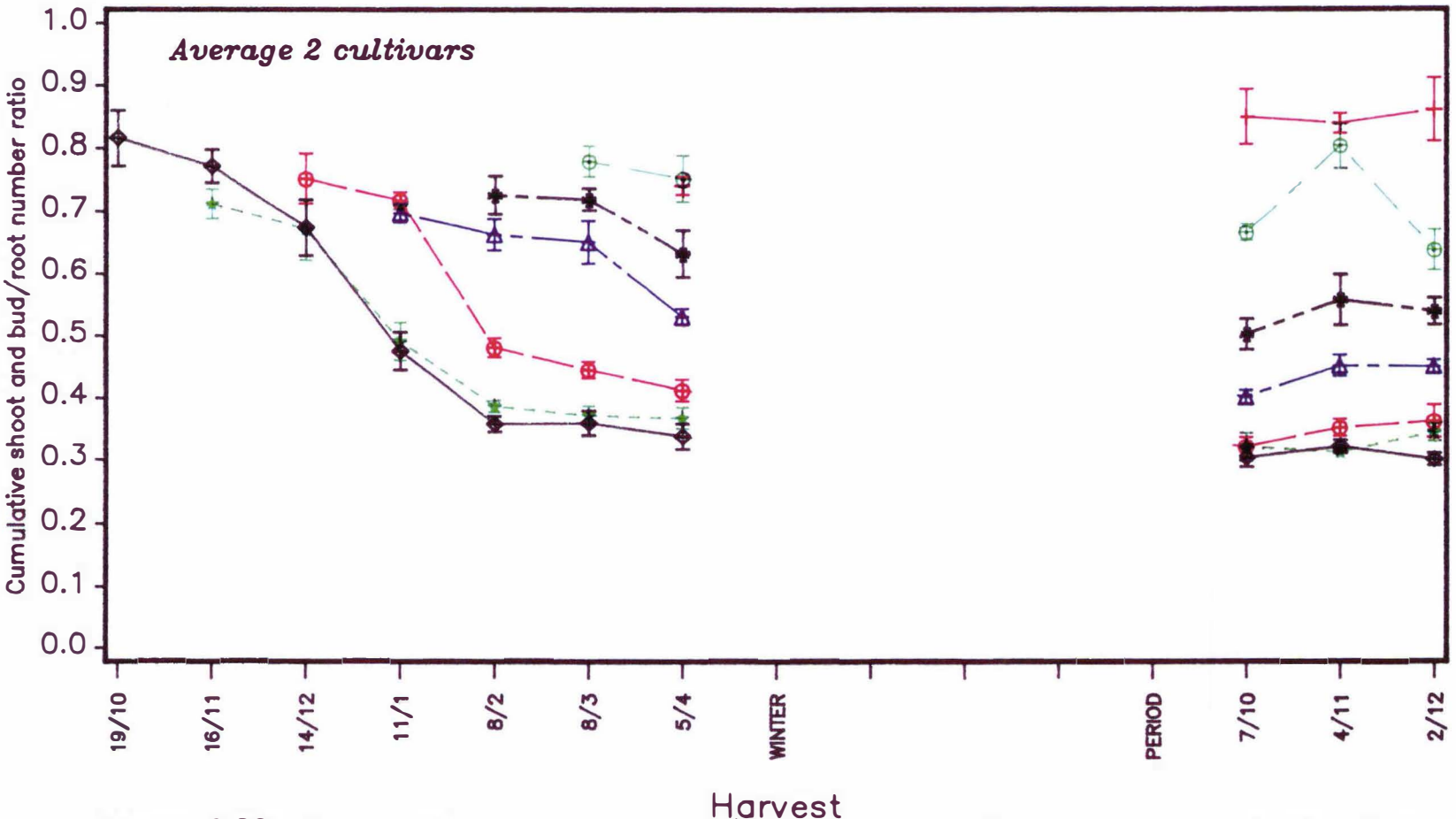


Figure 2.33 Cumulative shoot and bud/root number ratio of asparagus in the first and second season (◇ ◇ ◇ Sep; ☆ ☆ ☆ Oct; ⊕ ⊕ ⊕ Nov; Δ Δ Δ Dec; ✱ ✱ ✱ Jan; ⊙ ⊙ ⊙ Feb; + + + March). I = Stderr. of means.

2.3.5.2 **Ratios during the second season**

2.3.5.2.1 **Bud to shoot number ratio**

Analysis of variance of the final harvest data showed that the ratio was affected by planting date, cultivar and their interaction (Table 2.24). The trend was that the ratio decreased as the planting dates advanced. Between cultivars, the September and October plantings of UC157 had a higher ratio than Jersey Giant, as did the February planting.

The bud to shoot ratio generally decreased as the season progressed, except for the late plantings (Figure 2.32), suggesting that shoot production predominated over bud production, at least during the spring growth period. Early in the second season the ratio was about three times higher than that of the final harvest of the first season.

2.3.5.2.2 **Cumulative of shoot and bud to root number ratio**

Analysis of variance of the final harvest data found that the ratio was affected by both planting date and the cultivar x planting date interaction (Table 2.25). There was no difference between cultivars or planting dates for the first three plantings. The trend was that the ratio increased with the later planting dates. There were differences between cultivars except for the January and March plantings.

The ratio of cumulative shoot plus bud to root number was essentially constant for each treatment except for the February planting (Figure 2.33). In addition the ratio was fairly similar to the ratio at the end of the first season.

2.3.6 **The relationship between number of buds and crown dry weight in the first and second season**

Data of the bud number and crown dry weight were transformed into natural logarithm. It was found that the relationship was highly linear (b = 0.418 and 0.369 with $r^2 = 0.95$

and 0.95 for UC157 and Jersey Giant, respectively; Figure 2.34). Both the slope and intercept of the two cultivars was significantly different (p=0.05 and p=0.01, respectively).

Table 2.24 Bud/actual shoot number ratio of asparagus at final harvest in the second season.

Planting	Cultivar		
	UC157	Jersey Giant	Pl mean[2]
21 Sept.	6.17**b**	4.73**cd**	5.45
19 Oct.	7.67**a**	4.71**cd**	6.19
16 Nov.	5.34**bc**	5.03**c**	5.19
14 Dec.	4.37**cd**	4.39**cd**	4.38
14 Jan.	4.52**cd**	3.98**d**	4.25
11 Feb.	4.48**cd**	3.16**e**	3.82
8 March	2.34**e**	2.11**e**	2.23
Cv mean[2]	4.98	4.02	

Cultivar (Cv)	**
Planting Date (Pl)	**
Cv x Pl	**

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Value in the bracket is the untransformed bud number;
- 2. Means separation in the table by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.6114 with $df_{(error)}$ =39.

Table 2.25 Cumulative shoot plus bud/root number ratio of asparagus at final harvest in the second season.

Planting	Cultivar		
	UC157	Jersey Giant	Pl mean[2]
21 Sept.	0.29**f**	0.31**f**	0.30
19 Oct.	0.33**f**	0.35**f**	0.34
16 Nov.	0.36**f**	0.37**ef**	0.37
14 Dec.	0.45d**e**	0.45**de**	0.45
14 Jan.	0.48**d**	0.59**c**	0.54
11 Feb.	0.67**c**	0.61**c**	0.64
8 March	0.95**a**	0.77**b**	0.86
Cv mean[2]	0.50	0.49	

Cultivar (Cv)	ns
Planting Date (Pl)	**
Cv x Pl	**

- ns, *, ** Non significant or significant F test at P = 0.05 or 0.01, respectively;
- 1. Value in the bracket is the untransformed bud number;
- 2. Means separation in the table by Duncan's Multiple Range Test ($p \leq 0.05$) with se = 0.0508 with $df_{(error)} = 39$.

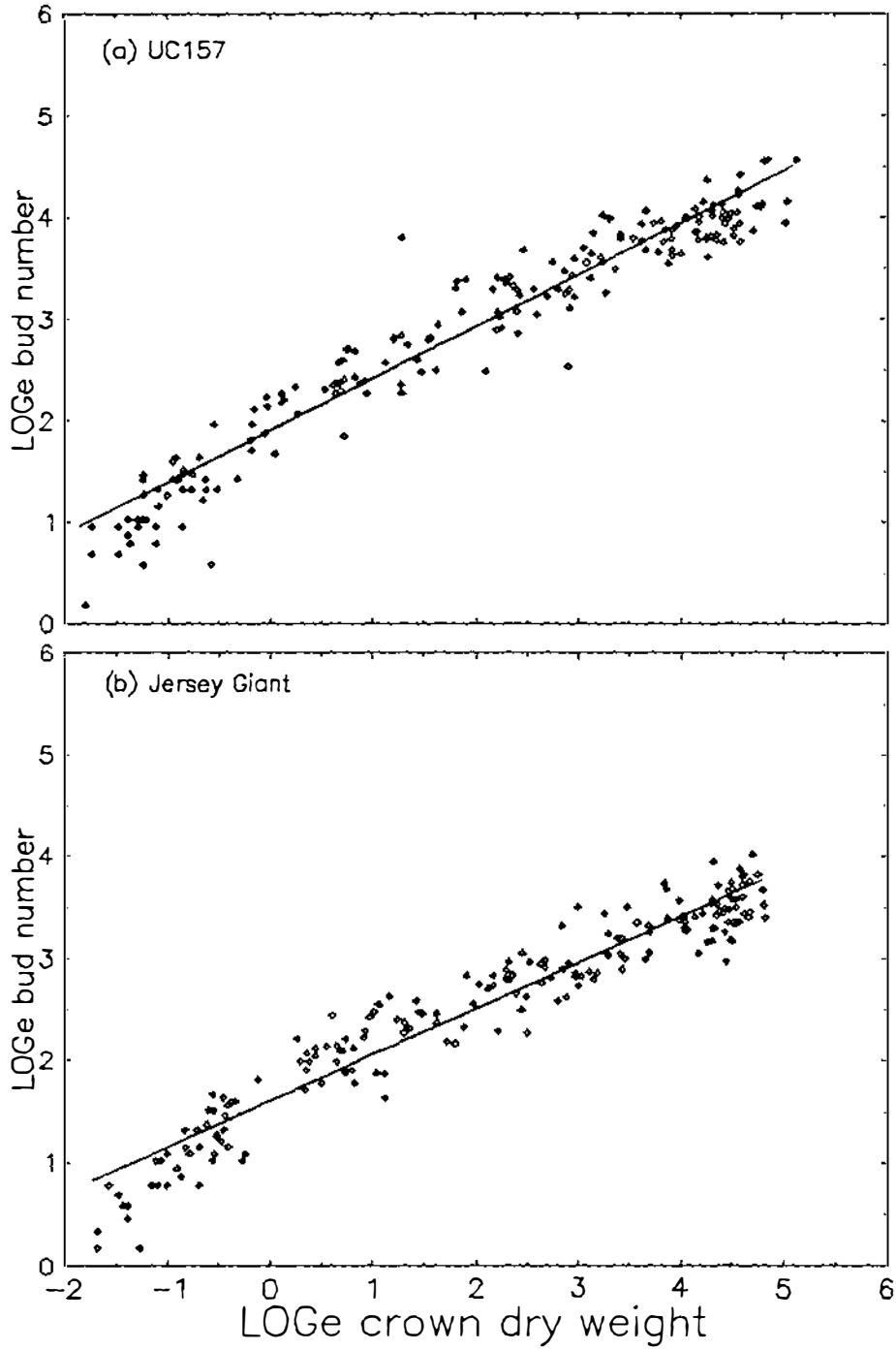


Figure 2.34 The allometric relationships between number of buds and crown dry weight during the first and second season.

2.4 DISCUSSION

2.4.1 Total dry weight of seedling transplants at the time of transplanting

The dry weight of 8 weeks old seedling transplants was affected by sowing date and cultivar (Table 2.4). The very early sowing (mid July) produced the smallest seedling transplants. Probably radiation and temperature influenced the growth of these asparagus seedlings. With the shorter daylength of the early sowing, the seedlings would receive less light for photosynthesis and consequently the growth would be slower compared to later sowings which received more light.

Although temperature settings in the glasshouse were the same for all sowings, during the summer, the temperature inside the glasshouse was usually higher than the ventilation set point (25^{0}C). Studies of the effect of temperature on the growth of asparagus seedlings found that the optimum temperature for seedling growth was 26^{0}C (Yen, 1993). Brown *et al.* (1982) also found that the dry weight of asparagus seedlings increased with increasing temperature from 15 to 30^{0}C. The present study shows that the highest total plant dry weight was obtained by sowing in the early spring (19 August to 16 November), which indicates that at this period of time the seedlings received the most favourable environmental conditions. The growth of seedlings later than November was probably reduced by excessively high day temperatures. Thus, sowing seeds from October to November probably achieved an optimum temperature advantage compared to either early or later sowings. However, there is no practical advantage of sowing seeds from October to November because the seedlings transplants will be too late to be transplanted in the field.

At planting time, except for the September sowing, Jersey Giant had a higher plant dry weight then UC157. This suggests that Jersey Giant had an early advantage (bigger size) and therefore a better chance to establish in the field. Burrows and Waters (1989) also found a significant effect of transplant size on field performance. In other research, however, it has been suggested that differences in transplant size

may not have any effect on the growth of seedlings after transplanting (Ombrello and Garrison, 1978; Williams, 1979; and Dufault and Waters, 1984).

2.4.2 **Dry weight accumulation during the first and second season**

2.4.2.1 **Dry weight accumulation during the first season as described by the logistic model**

Initially the calculation of the logistic model was based on common parameters, ie. the four parameters were considered the same for all planting date. However, this method failed to produce a good fit for this study and therefore it was decided to use another approach which had been found to improve the fit for lettuce and broccoli studies (Nichols, 1970; Diputado, 1989). This was to keep the K value constant while the other parameters changed (Appendix 5). This method produced a better fit by reducing the MSE in the present study.

The logistic curve of total and shoot dry weight (Figures 2.1 to 2.2 and 2.5 to 2.6) indicates that the predicted line for later planting dates did not provide as good a fit as did those of earlier plantings, presumably because of large deviations from the actual initial relative growth rate. The difficulty of this present experiment was that planting dates had different number of harvests. The worst case was for January and February plantings where there were only three and two data points. Therefore it was expected that the fit was not so good for these particular plantings. Asparagus is a perennial plant and becomes dormant in winter, and from this point of view therefore, it requires a longer study (at least a complete one year growing period in the second season) to provide an improved logistic relationship between the environmental time scale and growth as affected by planting dates.

The results show that as far as a heat unit time scale is concerned, that to improve the fit of the model (by reducing MSE) requires a heat sum with base temperatures between 0 to 3^0C. It also demonstrates that an improved fit to the model results from using the environmental time scale (temperature) compared to chronological time.

The unfavourable growth conditions for Jersey Giant planted in the early season (September) was demonstrated by of the logistic curves for total and crown dry weight. September planting being very close to the October planting showing the delay that occurred with the September planting (Figure 2.2 and 2.4).

During early growth the shoot growth of both cultivars (Figure 2.5 and 2.6) was less affected by early planting as the predicted line of the September planting was higher than that of October planting. The poor growth of September planting for Jersey Giant occurred particularly in the early stage of establishment where the growth was checked probably due to very cold temperature conditions. It has been suggested that Jersey Giant should be grown in the North Island of New Zealand (McCormick and Franklin, 1990), and certainly as the temperatures became warmer, the growth rate of Jersey Giant was satisfactory. Williams (1979) found that transplanting young seedlings in the autumn caused near total death of the young fern, but this was followed by new growth in the spring.

Meanwhile UC157 produced higher total plant dry weight (although not significant) from the September planting (Table 2.9) which suggests that UC157 was more tolerant to low temperature growing conditions. The other implication is that the seedling size did not have any effect on the final total plant dry weight as the September planting of UC157 had a lower total plant dry weight than Jersey Giant at transplanting (Table 2.4), but the order had reversed by the end of the season.

For the early plantings the fall in total plant dry weight late in the season (Figure 2.1 to 2.2) was detailed by the fall in total plant RGR over this period (Figure 2.7 to 2.8). That this fall was due in particular to the fall in RGR of the shoot rather than the crown, both of which fell, is shown in Figures 2.9 to 2.12 (see section 2.4.3.1). For plantings later than December the relative growth rate of shoot was higher than the crown (Figure 2.9 to 2.12), which contradicts the allometric relationship results (Table 2.15a to 2.15c). This was due to the fact that the initial relative growth rate of the logistic curve had been set the same for all planting dates (Figure 2.3 to 2.6), causing the initial relative growth rate for late plantings to be higher than the true one.

The fall in total, crown and shoot dry weight accumulation late in the season coincided with the decrease in RGR of total plant, crown and shoot. The decrease was expected as other studies on lettuce and broccoli have found a similar result (Nichols, 1970; Diputado, 1989). The fall in relative growth rate could be due to a seasonal response as the daylength became shorter and the temperature decreased. As RGR=NAR x LAR, the fall in relative growth rate could be accounted by both factors. In lettuce studies, NAR was found to decrease with time as did relative growth rate, meanwhile LAR increased (Nichols, 1970). This probably suggests that the decrease in relative growth rate in asparagus was due to a decrease in NAR.

There are many possible reasons why the shoot relative growth rates fell markedly in February.

1. As the season progressed the shoots became older and therefore their photosynthetic efficiency decreased. In Taiwan where the mother fern technique has been practised for many years, the replacement of the fern is carried out every 3-4 months due to the decrease in the photosynthetic efficiency of the older fern (Lin, 1983). Therefore as the photosynthetic efficiency decreases it is followed by a decrease in the accumulation of dry matter.

2. The growth of new fern is reduced. It was found that the number of new shoots produced late in the season were small and always under the shade of the older shoots which were much bigger in size.

3. As a perennial plant, asparagus is dependent on the storage carbohydrate in the crown for next growing season. In order to survive the plant has developed a mechanism which triggers the crown to become a stronger sink for photosynthates late in the season. This was shown by the fact that the crown relative growth rate fell at a much lower rate.

4. Redistribution of carbohydrate from the shoot to the crown. It has been suggested that at the end of the season transfer of assimilates from shoots to the storage organs occurs (Martin and Hartmann, 1990).

The implication from the last two points is that late plantings have a drawback because in the late summer the plants respond to a change in the environment by

accumulating and/or redistribution more carbohydrate into the crown, and therefore the plants apart from being planted late, also produced less photosynthate with both factors limiting total dry matter accumulation.

2.4.2.2 **Dry weight at the final harvest at the end of the first season**

The common practice in New Zealand is to plant out asparagus seedlings transplants in November in order to avoid the risk of damaging frost. In the present study it was found that this was not as important as originally thought. Williams (1979) has indicated that transplanting during the autumn was satisfactory. This present study found that total plant dry weight at final harvest was related to planting date where the earlier plantings produced the largest plants due to the earlier plantings having a longer growing period. This was demonstrated by the observation that at the end of the season, the size of asparagus planted in November was 47 - 70% of the September planting (Table 2.9).

The only difference in plant growth between cultivars at the final harvest was in terms of crown dry weight, where Jersey Giant produced a larger crown (Table 2.10). There was a similar, but not significant trend for total plant dry weight (Table 2.9). The poor growth of Jersey Giant from the September planting is further demonstrated by the fact that, although the differences were not significant, that for total plant dry weight UC157 was greater than Jersey Giant only for the September planting.

In terms of crown dry weight (Table 2.10) there was nearly a 50% advantage for UC157 by planting in September compared with October, but for Jersey Giant the advantage was probably marginal. Considering that the cost of establishment is probably higher in September, greater glasshouse heating etc., it is recommended that for Jersey Giant establishment should be in October. The emphasize should be put on crown quality because the next season's growth depends mainly on crown quality. Plantings later than October, regardless of cultivar, will be at a disadvantage due to smaller plant size at the end of the first growing season.

2.4.2.3 Total, shoot and crown dry weight accumulation during the second season

2.4.2.3.1 Dry weight accumulation during the spring growing period

The slope (relative growth rate) of the relationship between $\log_e$ total plant, crown and shoot dry weight and time in the second season was much lower than the first season (Figures 2.13 to 2.18). This suggests that as the plants became older that the relative growth rate was slower due to more structural material. Haynes (1987) however found that the relative growth rate of crown transplants was higher in the second season. The growth rate of the crown transplants in first season was apparently was very poor. The present study suggests that establishing the asparagus by using seedling transplants gives a better chance for good growth in the second season. This advantage was carried over into the second season as crown growth had started in November, which was two months earlier than in Haynes's study (1987).

2.4.2.3.2 Dry weight at the final harvest at the end of the second season

After 12 weeks growth in the second season the total plant, crown and shoot dry weight were already greater than at the final harvest in the first season (compare Table 2.12 to 2.14 with 2.9 to 2.11). This was achieved by having high shoot production and therefore high photosynthate production. The shoot growth from November to December provided good support for crown growth. This result demonstrate as far as crown quality is concerned, that during the 12 weeks in the second season, that the plants replaced and then added to the dry weight lost during early growth. At the final harvest there was no difference in dry weight of plant parts between the cultivars. Thus despite differences in shoot and root numbers between the cultivars (section 2.3.4.4) there was no difference in overall efficiency between the cultivars, as dry matter production in the second season was similar. Although the differences were not always significant between adjacent early plantings there was a clear trend favouring early plantings in terms of dry matter production.

2.4.3 Shoot to crown dry weight ratios during the first and second seasons

2.4.3.1 Shoot to crown dry weight ratio and allometric relationship between shoot and crown dry weight during the first season

The present study found that more dry matter were accumulated by the shoot early in the season. As autumn approach there was a change in partitioning which favoured the crown irrespective of plant age (Figure 2.19). This phenomena was interesting because the change was not due to an ontogenetic process as despite large differences in plant age all plantings followed a similar pattern. This is therefore due to a seasonal effect such as changes in temperature, daylength or radiation. It is suggested that temperature probably had a major effect due to the fact that the change in partitioning coincided with the decrease in temperature (Figure 2.21). This is in agreement with the suggestion that more dry matter is accumulated into the crown with decreasing growing temperature (Dufault and Greig, 1983; Hughes, 1992; Yen, 1993). Therefore temperature could be the factor which triggers the redistribution of dry matter from the shoot into the crown. This is possibly a survival mechanism which developed during evolution.

The k value is the ratio of shoot relative growth rate to the crown relative growth rate. The response of the two cultivars appeared to be different with respect to the initial k value (Table 2.15b). Thus with UC157, k fell from the October planting onwards, while with Jersey Giant the k value rose to a peak with the December planting and then fell. These different patterns gave rise to higher k values for Jersey Giant compared to UC157 for November and December plantings (Table 2.15c). These differences may be because the shoot growth of Jersey Giant was more responsive to warm temperatures than UC157. The k values changed abruptly (Table 2.15a and Figure 2.20) in February as demonstrated in Figure 2.20. The fall in k value describes the change in the relationship between the relative growth rates of shoot and crown in favour of the crown. The significance of this change has already been discussed.

2.4.3.2 **Shoot to crown dry weight ratio in the second season**

The shoot to crown dry weight ratio increased from September until November (Figure 2.19). The increase was due to the fact that shoot growth and development was at the expense of crown dry weight, at least until the cladophylls were capable of producing assimilates. Comparing crown dry weight data for the first and second seasons (included the winter sample) shows that the crown dry weight decreased from winter to September, which was due to the carbohydrate reserves being used to produce new shoots (Figures 2.15 and 2.16). Haynes (1987) suggested that storage carbohydrate were not replenished until ferns expanded. As shoots became mature in the early summer and produced assimilate, dry weight accumulation to the crown occurred for most of the plantings causing the ratio to decrease or stabilize. However, during the first season there was has a long period when shoot growth predominated for the early plantings (Figure 2.19). This therefore suggests that the pattern of shoot to crown dry weight ratio was different between the first and second seasons.

This is of course is not surprising as in the second season the initial shoot growth is supported by the crown and there is also a large carry over of crown dry weight from one season to the next. It could be argued that in the second season the peak in shoot production probably was achieved in early summer and then the partitioning of dry matter stabilized throughout the summer period, until the triggering by lower temperatures occurred causing a fall in the ratio. This however needs confirmation by a full growth study in the second season.

2.4.4. **The development of actual, current and cumulative shoots, buds and roots in the first and second seasons**

2.4.4.1 **Accumulation of shoots, buds and roots during the first season**

The higher rate of shoot production in UC157 than Jersey Giant (Table 2.16 and Figures 2.22 to 2.25) was expected as the bud production rate was also higher (Table 2.17 and Figures 2.28 and 2.29). Shoot production has been found to be controlled by

correlative inhibition (Hughes, 1992), which means that buds will not develop into shoots unless the adjacent shoot is removed or has reached certain stage of maturity. It was found that Jersey Giant had stronger correlative inhibition than UC157 due to it having fewer buds and a larger rhizome (Hughes, 1992). The present study is in agreement with Hughes (1992) as Jersey Giant produced fewer shoots compared to UC157. However the shoots produced by Jersey Giant were larger in size as the differences in the final shoot dry weight between the two cultivars was not significant (Table 2.11).

Actual shoot numbers is probably not a reliable parameter to consider in a discussion of plant productivity because it includes some dead shoots. Therefore this study also considered current shoot numbers, which were the shoots actively producing assimilates. It was found however that there were few differences in the pattern between actual and current shoot number production (Figures 2.22 to 2.23 and 2.24 to 2.25). The plant usually lost (dead) only a few shoots late in the season from the early plantings. This suggests that some of the fall in the shoot relative growth rate was accounted by the dead shoots (Figure 2.5 and 2.6).

As the number of buds produced on an asparagus crown indicates the potential for yield in the following season (Dufault and Greig, 1983), one should consider this aspect of crown quality. Bud production followed an exponential pattern, particularly for UC157 (Figure 2.28 and 2.29). At the end of the first season the bud number of UC157 was similar to Mary Washington 500W (Fisher, 1982). It is interesting that the bud numbers were not significantly different for the first three and first four plantings for UC157 and Jersey Giant, respectively (Table 2.17). Tiedjens (1924) suggested that bud production was not dependent on the size of plant (carbohydrate reserve). The allometric relationship between $\log_e$ number of buds and $\log_e$ crown dry weight however shows very strong relationship ($r^2 = 0.95$) for both cultivars (Figure 2.34). This demonstrates that the bud production rate increase was in proportion to the crown dry weight accumulation rate. This suggests a close relationship between bud production and storage carbohydrate. However, during the growth, bud production and crown dry weight accumulation are dependent on source strength, ie. shoot

photosynthesis. Therefore, eventhough there was a strong relationship between these two parameters it does not mean that they are dependent on each other.

In terms of the slope and the intercept, the allometric relationship between $\log_e$ bud number and $\log_e$ crown dry weight of UC157 and Jersey Giant were significantly different. Jersey Giant had a lower slope and intercept. This is because as the season progressed, the crown dry weight accumulation between the two cultivars was fairly similar, but Jersey Giant had a lower bud production rate (Figure 2.28 and 2.29).

As bud numbers were not different, this suggests that the quality of crowns from September to November plantings for UC157 and from September to December plantings for Jersey Giant were not different, based on this criteria. However, the crown dry weight data (Table 2.10) suggests that the buds from the earlier plantings were supported by more carbohydrates compared to the later plantings. Therefore buds from the earliest planting would possibly develop into bigger spears and then shoots as the size of buds is dependent on the carbohydrate reserve (Tiedjens, 1924). It is known that UC157 produces more spears than Jersey Giant. This is understandable because UC157 produced about double the number of buds for the early planting. In terms of spear weight (spear size), however, the differences could disappear as Jersey Giant usually produces thicker spears. This is because Jersey Giant had a higher crown dry weight (Table 2.10). In addition, UC157 had a significantly higher number of roots (Table 2.18; Figures 2.30 to 2.31), but a lower crown dry weight. Since rhizome dry weight accounts for only a small proportion of crown dry weight, it suggests that Jersey Giant's roots were larger.

Shoot number increased with earliness of planting (Table 2.16), but the pattern was not so clear cut for bud and root number for these early plantings (Tables 2.17 and 2.18). It is suggested that this was because shoot growth, the photosynthetic tissue, was an essential pre-requirement for bud and root production. As the temperatures were lower early this showed down shoot growth and delayed bud and root development.

The effect of planting dates on shoot and crown dry weight in the end of first season were similar to its effect on shoot and root numbers, as both parameters decreased as the planting dates were delayed. This was expected since the increase in shoot and root dry weight is related to increase in the shoot and root number.

2.4.4.2 **Accumulation of shoots, buds and roots during the second season**

At the first harvest of the second season the shoot number was already 5 to 8 for the early plantings (Figure 2.22 and 2.23). Most of the shoots were in the spear form. In general shoot number increased with time, although some of the plantings of UC157 were slow to start with. The increase in shoot number continued until the final harvest (December). The majority of the shoots were large and shaded any new shoots. This suggests that even though shoot production still increased, the contribution to dry weight production was small due to too much shading. This confirms the previous suggestion on the shoot to crown dry weight ratio (section 2.4.3.2). Bud production increased from the first harvest, although with some plantings it was slow to start with (Figures 2.28 and 2.29). As root number increase did not start until November this suggests that the carbohydrate needed for bud production had priority over roots. It has been suggested that bud production begins when the shoot growth is well underway (Haynes, 1987), but in this study new buds were present very early in the season.

The bud number at the first harvest of the second season was well below the number at the final harvest of the first season. The decrease was firstly due to some of buds having developed into shoots and secondly probably because some buds had decayed. After 12 weeks of the second season bud numbers were similar to the number at the end of the first season.

There were no significant differences between the first four plantings for UC157 and the first three plantings for Jersey Giant in terms of shoot number at the end of the second season (Table 2.19). This is not surprising as bud numbers at the end of the first season (Table 2.17) showed a generally similar pattern. Also the number of

shoots were not great when one considers the number of buds present on the plant were in the 40-60 range for UC157 and 30-40 range for Jersey Giant (Table 2.20). One can only assume that these large numbers of buds were grouped into perhaps 9-10 clusters for UC157 and 7-8 clusters for Jersey Giant, with each cluster supporting one shoot.

Again as at the end of first season (Table 2.17), there were no significant differences in bud number for the first three plantings (Table 2.20). This is perhaps surprising, but it should be noted that from October onwards the trend was as expected. These buds were supported by crown dry weights (Table 2.10), where there were only differences from October onwards. Without data on yields of spears in the third season, then there could be some support for a suggestion, particularly with Jersey Giant, that the September planting, was not necessarily of great practical advantage, as at the harvest at the end of the first season UC157 generally produced more shoots, buds and roots than Jersey Giant.

The effect of planting dates in the first season was carried over into the end of second season, where shoot and crown dry weight decreased in the same pattern as shoot and root numbers as the planting date was delayed.

2.4.5 **The ratio of bud to actual shoot number and cumulative shoot plus bud to root number during the first and second seasons**

2.4.5.1 **Ratios during the first season**

This experiment confirmed the work of Dufault and Greig (1983) as during the early growth in the first season shoot production predominated over bud production (Figure 2.32). Haynes (1987) also suggested that shoots were produced first followed by the initiation of new roots and buds. As the season progressed however, bud production was higher than shoot production and therefore the ratio increased. At the autumn harvest there were few differences in the bud/shoot number ratio for the early plantings (Table 2.22), but it fell with later plantings. This suggests that with mature

plants there may not be big differences in this ratio. UC157 had a higher ratio than Jersey Giant, which probably relates to UC157 greater ability to produce buds.

The high ratio of cumulative shoot and bud to root number clearly demonstrate that the asparagus plant gives priority to the shoot and bud development in early growth, but as the season progressed the ratio decreases considerably, particularly for the early plantings and stabilises at the end of season (Figure 2.33). A possible explanation for this response could be that after the establishment of sufficient assimilatory tissue to support growth and development, this ratio started to fall until a balance was reached between shoots and potential shoots and storage roots including potential storage roots. Although Figure 2.33 suggests that this occurred in February this was the harvest where these plant parts could be seen clearly enough to count. Initiation would have occurred sometime previously. A functional relationship between 'shoot' and 'root' would not be unexpected even though these tissues do not equate directly to the shoot root ratio of a young annual plant. At the final harvest the cumulative shoot and buds were each supported by 2 to 3 roots for the early plantings (Table 2.23).

Despite the large differences in number of shoots, buds and roots between UC157 and Jersey Giant it is interesting to record that they had similar cumulative shoot plus bud/root number ratios (Table 2.23). Therefore it is suggested that the cumulative shoot and bud to root number ratio is in general similar for all asparagus cultivars.

2.4.5.2 **Ratios during the second season**

The decrease in bud to shoot number ratio was clearly due to the relatively small increase in buds over the experimental period (Figure 2.32) and the requirement of buds to produce shoots to provide the new seasons growth. The much higher ratio in the second season compared to the first season was due to the use of cumulative shoot numbers.

At the December harvest, UC157 maintained a higher bud to shoot ratio than Jersey Giant (Table 2.24) for the first two plantings. This was true of all the plantings for

the autumn harvest. As with the autumn harvest, the ratio fell away with the later plantings. This may have been because these later plantings lacked enough shoots (Figure 2.24 and 2.25) to encourage bud development.

The cumulative shoot and bud to root ratio was relatively stabile compared to the first season (Figure 2.33). This again suggests that the ratio will stay constant for long periods as the plants mature, providing the total number of shoots (past and present) and buds are compared with the number of storage roots past and present. In terms of the ratio at final harvest (Table 2.25) it was fairly constant for the September to November plantings and then increased. The increase was to expected as these plants had not reached a stable ratio the previous season.

2.5 **Summary**

From this experiment it is concluded that :

1. The size of seedling transplants was affected by sowing time. Jersey Giant generally had a higher dry weight except for the September planting.

2. The growth of young asparagus in the first growing season fitted well with the logistic model using a heat unit time scale and base temperatures from 0 to 3^0C. The logistic curves showed that total and crown dry weight was affected by low temperatures at the early planting for Jersey Giant. It also showed that total, crown and shoot dry weight accumulation fell late in the season coincided with the fall in temperature. Crown dry weight accumulation fell at a lower rate.

3. The total plant dry weight at final harvest fell significantly as planting date was delayed. It was found that for both cultivars, the September planting produced the most satisfactory results. However for Jersey Giant, the difference between September and October plantings was marginal. Therefore UC157 and Jersey Giant are best to be planted in September and October, respectively. It was not recommended to plant later than October due to a smaller crown size at the end of the season.

4. In general, Jersey Giant had a higher crown dry weight than UC157 at the end of the first season except for the September planting.

5. The growth of asparagus in the second season was initiated by shoot growth

sometime in September followed by crown growth in November. By December the plants has already replenished the crown dry weight used to produce early shoot growth.

6. There were no differences in dry weight of the shoot and crown between cultivars at the last harvest in the second season. However the trend was that the earlier plantings produced more dry matter than later plantings.

7. The shoot to crown dry weight ratio in the first season increased as the season progressed and then decreased from February onwards regardless of time of planting and cultivar. The allometric relationship between shoot and crown dry weight also changed abruptly in early February. Both changes coincided with the decrease in temperature that occurred at that time of the year. The changes, it was suggested, were not due to an ontogenetic effect but due to environmental changes. The k value for Jersey Giant rose to a maximum in November-December suggesting this cultivar was more responsive to warm temperatures.

8. The pattern of shoot to crown dry weight ratio in the second season was different compared to the first season. In general the ratio increased from early spring to November and then decreased.

9. Shoot, bud and root production rate in the first season increased exponentially particularly for UC157. UC157 generally had a higher number of shoots, buds and roots compared to Jersey Giant at the final harvest in both the first and second seasons.

10. There were no differences in bud number for the first three and first four plantings for UC157 and Jersey Giant, respectively at the end of the first season. This suggests that based on this criteria there was no difference in crown quality between these plantings. November crown dry weights at the final harvest (first season) indicated however, that the quality of first two plantings was better as they had more storage carbohydrate.

11. In the second season shoot production commenced in September, while bud production started in October or probably earlier. Bud number at the first harvest was lower compared to the bud number at the final harvest in the first season.

12. The bud to shoot number ratio in the first season increased as the season progressed indicating that shoot production predominated over bud production.

Meanwhile in the second season, the ratio was constant or decreased with time.

13. The cumulative shoot and bud to root number ratio was similar during early growth and then fell. The ratio then stabilised for the last three harvest for the early plantings. In the second season the ratio was relatively stabile compared to the first season. The ratio was similar between cultivars.

14. The allometric relationship between $\log_e$ bud number and $\log_e$ crown dry weight suggests that bud production rate was in proportion to the crown dry weight accumulation even though it does not mean they were dependent upon each other.

CHAPTER THREE
THE EFFECT OF HIGH TEMPERATURE ON THE PHOTOSYNTHESIS OF YOUNG ASPARAGUS PLANTS IN RELATION TO FERN AGE

3.1 INTRODUCTION

3.1.1 Background to studies on CO_2 exchange of young asparagus plants

In the late 1980s the focus of a concurrent asparagus research programme, in the Department of Plant Science at Massey University, was to study the growth and development of seedlings of a range of asparagus cultivars grown under high temperatures. An interest in the performance of asparagus under tropical conditions had encouraged this work. Growth analysis was used to assess the performance of the seedlings, which were grown in the growth rooms of the Horticulture and Food Research, CRI, Palmerston North.

As the primary objective of the present research, was to study the growth and development of the asparagus plant during the fern growth stage, it was considered appropriate to use some of the plant material of the above programme to study photosynthesis of the fern of young asparagus plants.

Studies on the photosynthesis of asparagus have been confined to work on fern photosynthesis using a range of low temperature treatments (Downton and Torokfalvy, 1975; Lin, 1983; Lin and Hung, 1983; Inagaki *et al.,* 1989). There is a lack of information on the photosynthetic response of asparagus to high temperatures. Thus research with a number of cultivars grown over a range of temperatures, would not only contribute to the high temperature research programme, but would also provide new information on asparagus photosynthesis.

There were 3 experiments studying CO_2 exchange in young asparagus. In the first experiment (chapter 3) it was considered important to develop experimental techniques and to provide some base information on asparagus photosynthesis with the cultivars

over the temperature ranges of interest. This experiment therefore studied photosynthesis of fern of different ages with particular emphasis on the photosynthesis of mature fern over a high range of temperatures. The second experiment (Chapter 4) was focused on plant respiration, in particular shoot and crown respiration, fern dark and photo respiration and also the photosynthetic response to internal CO_2 concentration (AC_i curve) up to ambient concentration. The third experiment (chapter 5) examined light response curves for photosynthesis for the same cultivars over a broader range of temperatures.

3.1.2 **Ontogenetic changes of photosynthesis**

Although some C_3 plants are adapted to high temperature (Bjorkman, 1975), productivity is often low due to photorespiration and low stomatal conductance (Edwards and Walker, 1983; Lawlor, 1987). Asparagus, even though categorized as a C_3 plant, is able to grow in warmer regions, such as in South East Asia, but the optimum temperature for asparagus fern photosynthesis appears to be in the range from 15 to 25^{0}C (Sawada *et al.*, 1962; Lin, 1983; Inagaki *et al.*, 1989). The effect of temperatures above 30^{0}C on asparagus photosynthesis, has not been studied.

Some plants retain their leaves for long periods but most crop plants are relatively fast-growing and produce a succession of leaves. In such species the leaves do not maintain a steady photosynthetic capacity. Photosynthesis tends to be at a maximum at about the time that leaf expansion is completed and thereafter declines, at first gradually and then more rapidly (Catzky and Ticha, 1980; Sestak, 1981).

Even within the same species, populations may differ in their response to light and temperature, and individual leaves can become acclimated to changing levels of climatic variables. Wilson (1973) suggested that in all leaves the photosynthetic rate declines with age, but the rate of decline and the functional life of the leaf varies with species and environment.

The effect of high temperature on the ontogenetic pattern of asparagus fern photosynthesis is not known. In this experiment the effect of high temperatures on photosynthesis of asparagus fern of different ages was studied.

3.2 MATERIALS AND METHODS

3.2.1 Treatments

3.2.1.1 Temperature

This experiment was carried out in parallel to a growth analysis study of young asparagus plants grown at high temperature (Yen, 1993). The temperature treatments applied were determined by the growth analysis study (Yen, 1993).

Growing temperature conditions were alternating 12 hour day and night temperatures of 30/20^{0}C, 35/25^{0}C and 40/30^{0}C providing an average of 25, 30 and 35^{0}C. The experiment was carried out in the climate laboratory at the Horticulture and Food CRI (Crown Research Institute) in Palmerston North. The vapour pressure deficit were kept constant as shown in Table 3.1.

Table 3.1 Environmental conditions in growth room .

Environmental Conditions	Treatment					
	1		2		3	
	day	night	day	night	day	night
Temperature ± 0.5^{0}C	30	20	35	25	40	30
Humidity ± 5%	76	57	82	68	86	76
VPD (mb)	10	10	10	10	10	10
Daylength (hour)	12	0	12	0	12	0

3.2.1.2 **Cultivars**

Four cultivars of asparagus developed for different environments, from temperate regions to the subtropics, were used in this experiment with the expectation that they may show different responses to the high temperature treatments. The cultivars used were:

1. UC157, developed by the University of California. Seed was obtained from California Asparagus Seed and Transplants Inc., Davis, California, USA;

2. Brocks Imperial, developed in South California by Brocks Seed specifically for desert areas. Seed was obtained from California Asparagus Seed and Transplants Inc., Davis, California, USA;

3. Tainan No.1 (called Tainan 1 in the thesis) selected for the humid subtropics in Taiwan. Seed was obtained from Asparagus Research Centre, Tainan 1, Taiwan, Republic of China;

4. Larac, developed for white asparagus production in a cool climate. Seed was obtained from INRA, Versailles, France.

3.2.2 **Propagation and growing conditions**

On 19 March 1990 asparagus seeds were sown in 4.5 litre pots in a growing medium of sieved peat:pumice (50:50 v/v), placed directly into the growth room and the temperature treatments applied. The seeds germinated 3 weeks later irrespective of temperature treatment. The spacing between the plants was approximately 18 x 18 cm and the photosynthesis measurements were made from week 4 to 6. No shading between the plants was observed. The plants were irrigated via an automated microtube system applying a standard mineral nutrient solution (Hoaglands) (Brooking, 1976). The solutions were supplied as follows :

1. Treatment 1 : 3 x 1.5 min pot^{-1} day^{-1} throughout the experiment. Approximately 150 mls of water was supplied within the 1.5 min period of irrigation, which was enough to cause drainage from the pot ensuring sufficient water and nutrient had been supplied to the plant.

2. Treatment 2 : 2 x 1.5 min pot^{-1} day^{-1} for the first six weeks, followed by an increase to four applications for the final four weeks.

3. Treatment 3 : 3 x 1.5 min pot^{-1} day^{-1} for the first four weeks and then 4 x 1.5 min pot^{-1} day^{-1} with an additional 1 x 1.5 min pot^{-1} day^{-1} application of water till the end of the experiment.

The lighting system used in the growth room consisted of 4 x 1000 W Sylvania "metal-arc" high pressure discharge lamps, together with 4 x 1000 W Philips tungsten iodide lamps.

The photosynthetically active radiation (PAR), Wm^{-2} , in the 400 -700 nm wavelength range measured pre-experiment and post-experiment were 151-140, 150-136 and 150-127 for treatments no 1, 2 and 3, respectively. The photosynthetic photon flux density (PPFD), µmol m^{-2} s^{-1}, measured pre-experiment and post experiment were from 714-669, 706-661 and 708-612 for treatments no 1, 2 and 3, respectively.

The day/night and night/day temperature changed linearly over 120 minutes with the light period starting and finishing halfway through the change over period.

3.2.3 **Experimental design**

Within the climate room the plants were arranged in a Randomized Complete Block (RCB). Four replications with one plant per replicate was used and occupied two trolleys in the growth room. Every week the trolleys holding the plants were rotated to reduce the effect of uneven light, water and nutrient distribution.

3.2.4 **Photosynthetic measurement**

Photosynthesis was measured with a closed Infra Red Gas Analyzer (IRGA) system (model Li-6250, Li-Cor Inc., Lincoln, NE, USA) . This portable instrument provides a rapid, simultaneous measurements of photosynthetic rate with minimal change to the environment of the plant material. The Li-6200 consists of a leaf chamber or cuvette, within which leaf and air temperature and humidity measurements are made. The pump in the Li-6250 circulates air from the chamber to the analyzer, where CO_2 concentration is measured, and then returned to the chamber. The photosynthetic rate is obtained by monitoring the rate at which the CO_2 concentration in the air changes over a short time interval (20-40 seconds). The net photosynthetic rate is then calculated by an associated computer using this rate of change, the 'leaf area' in the chamber, the volume of the system, temperature and air pressure.

Preliminary examination showed that 'leaf area' measurement on asparagus fern (tips of fern branches) by using a leaf area meter (model Li-300, Li-Cor Inc., Lincoln, NE, USA) was inaccurate due to the low resolution of the instrument. Therefore, it was decided to use dry weight as the basic unit of photosynthesis instead of leaf area because dry weight could be precisely measured (see section 1.2.2). By default the Li-6200 calculates the photosynthesis based on leaf area. The leaf area is usually entered as cm^2 (kg in this experiment) which the computer converts to m^2. To convert to a dry weight basis a multiplication factor of 10^4 was used. In this study the dry weight of ferns was multiplied by 10^4 before the data was entered into the computer. For example, if the dry weight of fern was 0.05 g then multiplied by 10 to obtain a photosynthetic unit in $\mu mol\ kg^{-1}\ s^{-1}$. This technique was used in the experiments in Chapters 3, 4 and 5.

3.2.4.1 **Measurement procedures**

Before measurement, the Li-6200 was calibrated and tested for leaks each day as recommended by the manufacturer. The boundary layer conductance of 1 $mol\ m^{-2}\ s^{-1}$ was estimated as detailed in the Li-6200 manual. This was achieved by using a narrow

strip of filter paper (Whatman #1) which was of approximately the same dimension as the fern, kept intact but finely divided to give a series of paper 'cladophylls'.

For each measurement, approximately the same amount of fern was placed in a 1 litre chamber in such a way that it contacted the leaf temperature sensor, and then the chamber was closed and latched. Precautions were taken during enclosure of fern into the chamber to avoiding breathing into the chamber. Before starting the measurement the flow rate was adjusted until the relative humidity in the chamber became constant. The photosynthetic measurement is accurate if the RH range changes less than 5% (Li-6200 manual). The light intensity in the chamber was set to a relatively constant value by adjusting the height of the chamber in the growth room. When the CO_2 concentration had changed by 5 ppm, the computer calculated the rate of CO_2 exchange. The fern used was cut and then dried in an oven for 24 hours at 80^0C before recording the dry weight.

3.2.5 **Data collection**

Three stages of fern development were chosen to determine the ontogenetic response of photosynthesis to temperature:

i). Young fern in which cladophylls were slightly open and the colour was light green. Photosynthetic measurement was made at the tip of the youngest lateral branch.

ii). Intermediate fern in which the cladophylls had already opened and the colour was green. Photosynthetic measurement was made from lateral branches located in the middle of the main stem.

iii). Mature fern in which the cladophylls had opened and the colour was dark green. Photosynthetic measurement was made on lateral branches located in the lower part of main stem.

The photosynthetic measurement of young, intermediate and mature fern was taken at 4, 5 and 6 weeks after emergence, respectively, except for the $40/30^0$C treatment where it was not possible to measure young and intermediate fern photosynthesis because growth stopped after 4 weeks. Mature fern photosynthesis was determined

from week 4 to 6 for all temperature treatments. The weekly photosynthetic measurements were always determined on different asparagus plants because the previous week's plants had been harvested for the growth analysis study (Yen, 1993). The fern on which measurements were made are listed in Table 3.2.

Table 3.2 Types of fern measured during the experiment

Week	30/20^{0}C	35/25^{0}C	40/30^{0}C
4	young & mature	young & mature	mature
5	intermediate & mature	intermediate & mature	mature
6	mature	mature	mature

3.2.6 **Data analyses**

The analysis of variance for 2 way classification (cultivar and age of fern) was carried out with Proc GLM (SAS package program) to examine the effect of cultivar and fern age on photosynthesis at a particular temperature (Table 3.3 to 3.5). Trend analysis (orthogonal contrast, within Proc GLM of SAS) at p=0.05 were conducted on the ontogenetic changes of photosynthesis at 30/20^{0}C and 35/25^{0}C.

As in common with growth room studies there was no replication for temperature treatment, therefore it was not possible to analyze the data with the common procedure (eg. RCBD with cultivar and temperature interaction) (Gates, 1991). Another approach was used by using pooled (combined) analysis. This technique commonly employed for field experiment studies to examine the performance of crops over sites or season (Gomez and Gomez, 1984). Gordon (pers. comm.) suggested that this technique would not give much information about the environmental effects since they are confounded. For growth room studies, however, it was considered valid (Gordon pers. comm.) since the climate room was accurately controlled throughout the experiment. The environmental factor of interest is the one that is varied. In the present case this was temperature. Therefore, the pooled analysis using a nested design, was employed to

examine the effect of temperature on young, intermediate and mature fern photosynthesis (Proc GLM of SAS).

Trend analysis (orthogonal contrast, within Proc GLM of SAS) were also conducted on the response of mature fern photosynthesis to high temperatures. Because the source of mature fern were not from the same plant and it was difficult to estimate small differences in fern age, photosynthesis measurements of mature fern for weeks 4, 5 and 6 were pooled.

3.3 RESULTS

3.3.1 Ontogenetic changes of photosynthesis at 30/20^{0}C

3.3.1.1 Between cultivars

There were no significant differences in asparagus fern photosynthesis at 30/20^{0}C between the cultivars at any stage of fern development (Table 3.3).

3.3.1.2 Within cultivars

Trend analysis on ontogenetic changes of photosynthesis showed a quadratic relationship (Table 3.3 and Figure 3.1). The intermediate aged fern had significantly higher photosynthesis than young fern regardless of cultivar and intermediate aged fern photosynthesis was also significantly higher than mature fern for Tainan 1 and Larac. Young fern photosynthesis was not significantly different from mature fern for all cultivars (Table 3.3).

3.3.2 Ontogenetic changes in photosynthesis at 35/25^{0}C

3.3.2.1 Between cultivars

The only significant differences in asparagus fern photosynthesis at 35/25^{0}C between

the cultivars was at the young stage. Here Brocks had lower photosynthesis compared to UC157 (Table 3.4). There was no interaction between cultivars and age of fern.

3.3.2.2 **Within cultivars**

Trend analysis on ontogenetic changes of photosynthesis indicated a quadratic relationship (Table 3.4 and Figure 3.2). The intermediate aged fern had significantly higher photosynthesis than the young and mature fern for the cultivar Brocks.

Table 3.3 Ontogenetic changes in photosynthesis of asparagus fern grown at 30/20^{0}C.

Variable	Photosynthesis (μmol kg^{-1} s^{-1})			
	UC157	Brocks	Tainan 1	Larac
1. Comparison between cvs				
Young ns	263.62	230.70	243.30	213.28
Intermediate ns	333.42	343.77	331.03	357.10
Mature ns	282.77	281.20	260.87	257.83
2. Leaf age within cvs	*	*	*	*
Young	263.63b	230.70b	243.30b	213.28b
Intermediate	333.42a	343.77a	331.03a	357.10a
Mature	282.77ab	281.20ab	260.87b	257.83b
Age_{linear}	ns	ns	ns	ns
$Age_{quadratic}$	*	*	*	*

- Least Square Means for young, intermediate and mature fern with 4, 4 and 12 replications, respectively with $df_{(error)}$=57.
- Means separation within rows (1) and within column (2) by LSD ($p \leq 0.05$), with se = 34.4 .

Table 3.4 Ontogenetic changes in photosynthesis of asparagus fern grown at 35/25^{0}C.

Variable	Photosynthesis (μmol kg^{-1} s^{-1})			
	UC157	Brocks	Tainan 1	Larac
1. Comparison between cvs				
Young **	246.72a	163.05b	227.28ab	228.95ab
Intermediate ns	294.05	290.47	293.85	278.00
Mature ns	252.45	249.86	237.64	225.06
2. Leaf age within cvs	ns	*	ns	ns
Young	246.72	163.05b	227.28	228.95
Imtermediate	294.05	290.47a	293.28	278.00
Mature	252.45	249.86b	237.64	225.06
Age_{linear}	ns	ns	ns	ns
$Age_{quadratic}$	**	**	**	**

- Least Square Means for young, intermediate and mature fern with 4, 4 and 12 replications, respectively with $df_{(error)}$=57.
- Means separation within row (1) and within column (2) by LSD ($p \leq 0.05$) with se = 34.35.

3.3.3 **Mature fern photosynthesis at 40/30^{0}C**

The poor growth of asparagus plants at this particular temperature produced variable growth (section 3.2.5). There were no significant differences in mature fern photosynthesis (Table 3.5).

Table 3.5 The mature fern photosynthesis of asparagus grown at 40/30^{0}C.

Variable	Photosynthesis (μmol kg^{-1} s^{-1})			
	UC157	Brocks	Tainan 1	Larac
Mature leaf ns	140.66	152.56	138.76	132.10

- Each mean figure from 12 replications with $df_{(error)}$=33.
- Means separation within row by LSD ($p \leq 0.05$) with se = 11.59.

Table 3.6 Photosynthesis of young fern grown at high temperature.

Temperature	Photosynthesis (μmol kg^{-1} s^{-1})				
	UC157	Brocks	Tainan 1	Larac	Temp. mean[1]
30/20^{0}C	263.63	230.70	243.30	213.28	237.73
35/25^{0}C	246.73	163.05	227.28	228.95	216.50
Cv mean[1]	255.18	196.87	235.29	221.11	

- Each mean figure was from 4 replications, respectively with $df_{(error)}$=18.
- 1. Means separation within row and column by LSD ($p \leq 0.05$) with se=26.31 and 18.61, respectively.

3.3.4 **The response of asparagus fern photosynthesis to high temperature treatment**

3.3.4.1 **Young and intermediate fern photosynthesis at 30/20^{0}C and 35/25^{0}C**

Pooled analysis found that there was no overall significant effect of temperature and cultivar on young fern photosynthesis (Table 3.6), but intermediate fern photosynthesis decreased significantly from 30/20 to 35/25^{0}C (Table 3.7).

3.3.4.2 **Mature fern photosynthesis at 30/20°C to 40/30°C**

There was a significant effect of temperature and cultivar on mature fern photosynthesis but without any interaction. The mature fern photosynthesis decreased significantly with increasing temperature. For photosynthetic rate combined over all temperatures, LSD test showed only Brocks had a significantly higher rate of photosynthesis than Tainan 1 and Larac (Table 3.8). Further analysis using orthogonal contrasts, also found that UC157 had a higher rate of photosynthesis than Tainan 1 and Larac (p= 0.11 and 0.06, respectively).

The quadratic response of mature fern photosynthesis to high temperatures was similar for each cultivar (Table 3.8, Figure 3.3). Photosynthesis decreased gradually from 30/20°C to 35/25°C, followed by a sharp fall at 40/30°C. The trend was for photosynthesis of Brocks to decrease less slowly with increasing temperature.

Table 3.7 Photosynthesis of intermediate fern grown at high temperature.

Temperature	Photosynthesis (μmol kg^{-1} s^{-1})				
	UC157	Brocks	Tainan 1	Larac	Temp. mean[1]
30/20°C	333.43	343.78	331.03	357.10	341.33a
35/25°C	294.05	290.47	293.85	278.00	289.0b
Cv. mean[1]	313.74	317.12	312.49	317.55	

- Each mean figure was from 4 replications with $df_{(error)}$=18.

1. Means separation within row and column by LSD ($p \leq 0.05$) with se=23.15 and 16.37, respectively.

Table 3.8 Photosynthesis of mature fern at high temperature.

Temperature	Photosynthesis ($\mu mol\ kg^{-1}\ s^{-1}$)				
	UC157	Brocks	Tainan 1	Larac	Temp. mean[1]
30/20°C	282.77	282.20	260.87	257.83	270.88a
35/25°C	252.45	249.86	237.64	225.06	241.25b
40/30°C	140.66	152.56	138.76	132.10	141.02c
Cv mean[1]	225.29ab	227.87a	208.75b	207.22b	
T_{linear}	ns	ns	ns	ns	
$T_{quadratic}$	*	*	*	*	

- Each mean figure was from 12 replications with $df_{(error)}$=98.
1. Means separation within row and column by LSD ($p \leq 0.05$) with se = 13.48 and 8.99, respectively.

3.4 DISCUSSION

3.4.1 Ontogenetic changes in fern photosynthesis

The only differences in young fern photosynthesis between cultivars was detected at 35/25°C, where Brocks had a lower value lower than UC157 (Table 3.4). This could have been because the young fern of Brock was less developed compared to UC157. At 35/25°C it was also found by Yen (1993) that the NAR of Brocks was low during early development and then decreased in a lower rate with increasing age compared to the other cultivars. At the end of the experiment Brocks had a relatively higher NAR than the other cultivars. In addition, at 35/35°C Brocks had a very low NAR and then increased with age while the other cultivars fell with age (Yen, 1993).

Photosynthesis changes significantly with leaf age of various species (Catsky and Ticha, 1980). The results here indicate that the photosynthetic rate of asparagus fern of young plants varied with ontogeny regardless of temperature (Table 3.3 and 3.4, Figure 3.1 and 3.2). In general the results demonstrate that the ontogenetic maximum of photosynthesis,

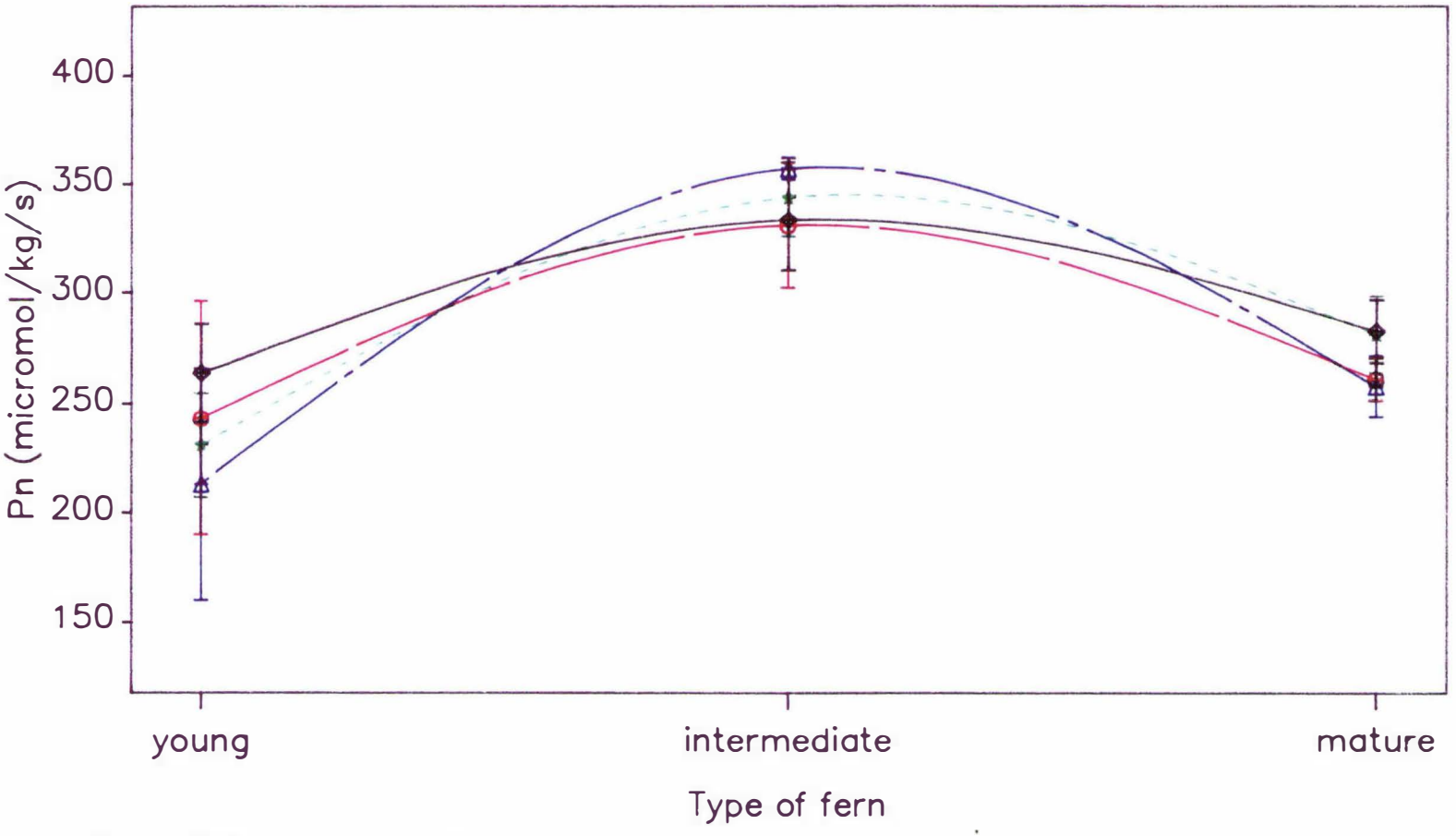


Figure 3.1 Ontogenetic changes of photosynthesis of asparagus fern grown at 30/20C (◇ ◇ ◇ UC157; ☆ ☆ ☆ Brocks; ⊕ ⊕ ⊕ Tainan 1; Δ Δ Δ Larac) I = Stderr. of means.

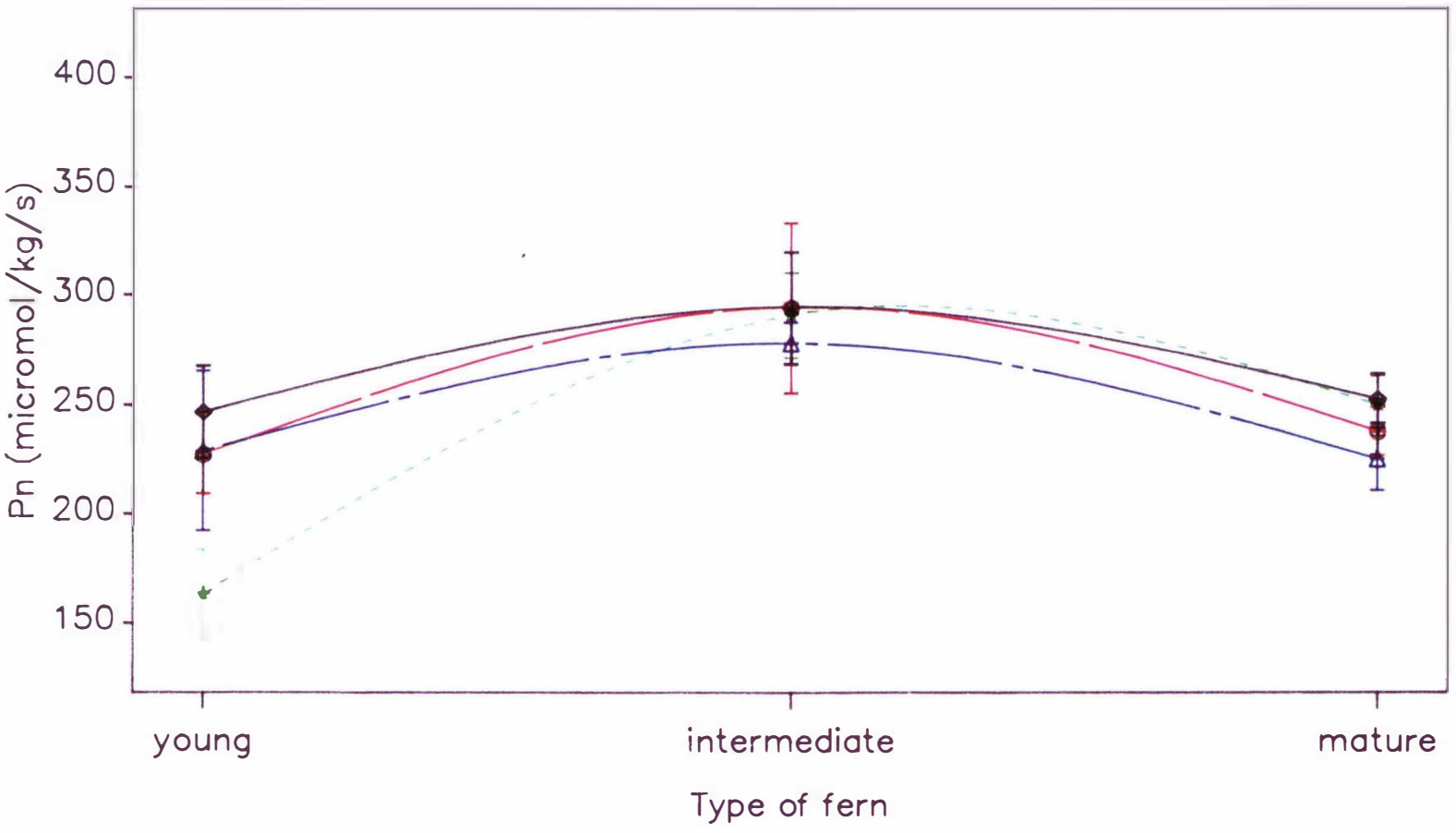


Figure 3.2 Ontogenetic changes of photosynthesis of asparagus fern grown at 35/25C (◇ ◇ ◇ UC157; ☆ ☆ ☆ Brocks; ⊕ ⊕ ⊕ Tainan 1; Δ Δ Δ Larac) I = Stderr. of means.

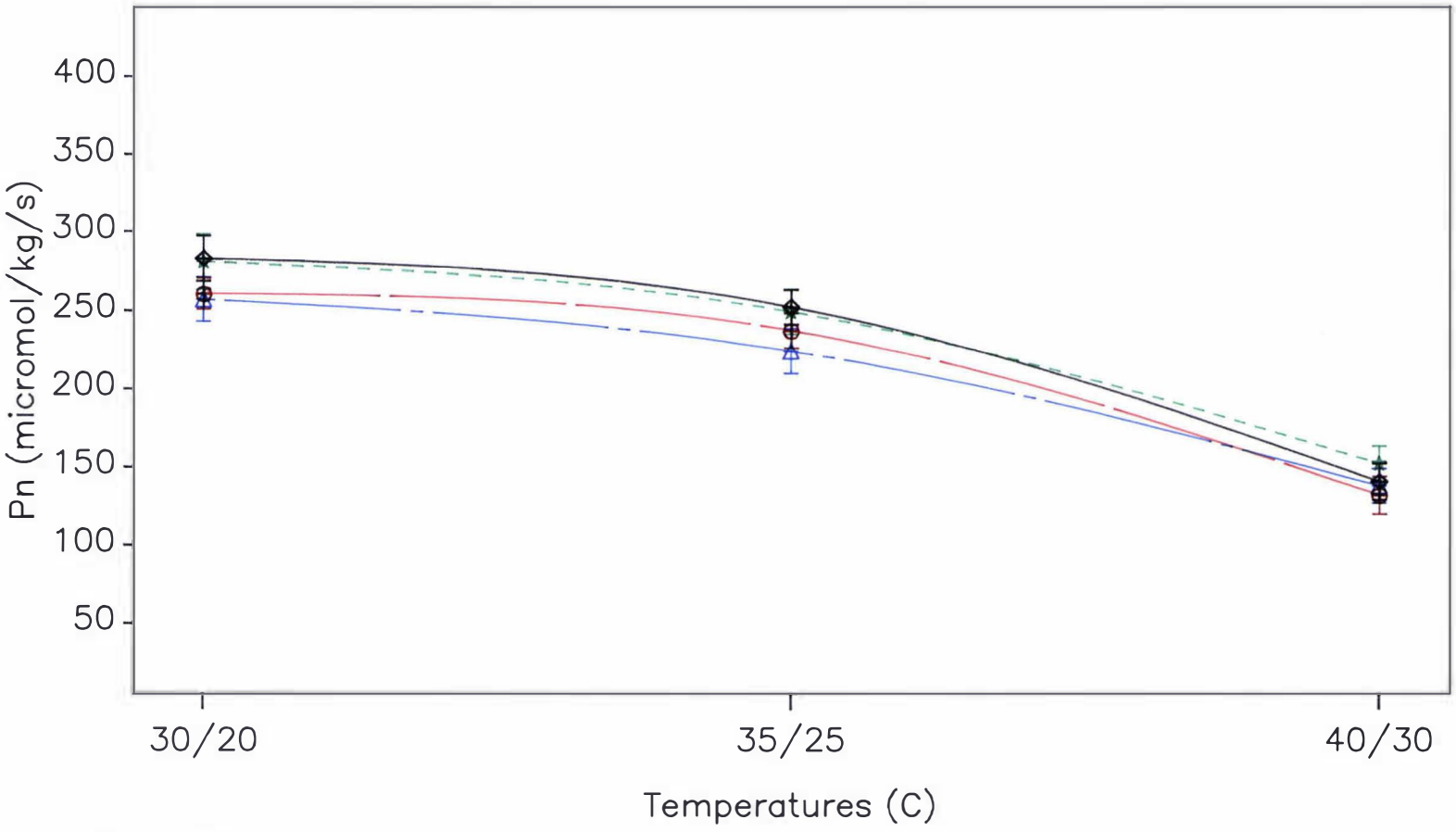


Figure 3.3 Photosynthesis of mature fern average over weeks 4 to 6 after emergence (◇ ◇ ◇ UC157; ☆ ☆ ☆ Brocks; ⊕ ⊕ ⊕ Tainan 1; △ △ △ Larac). I = Stderr. of means.

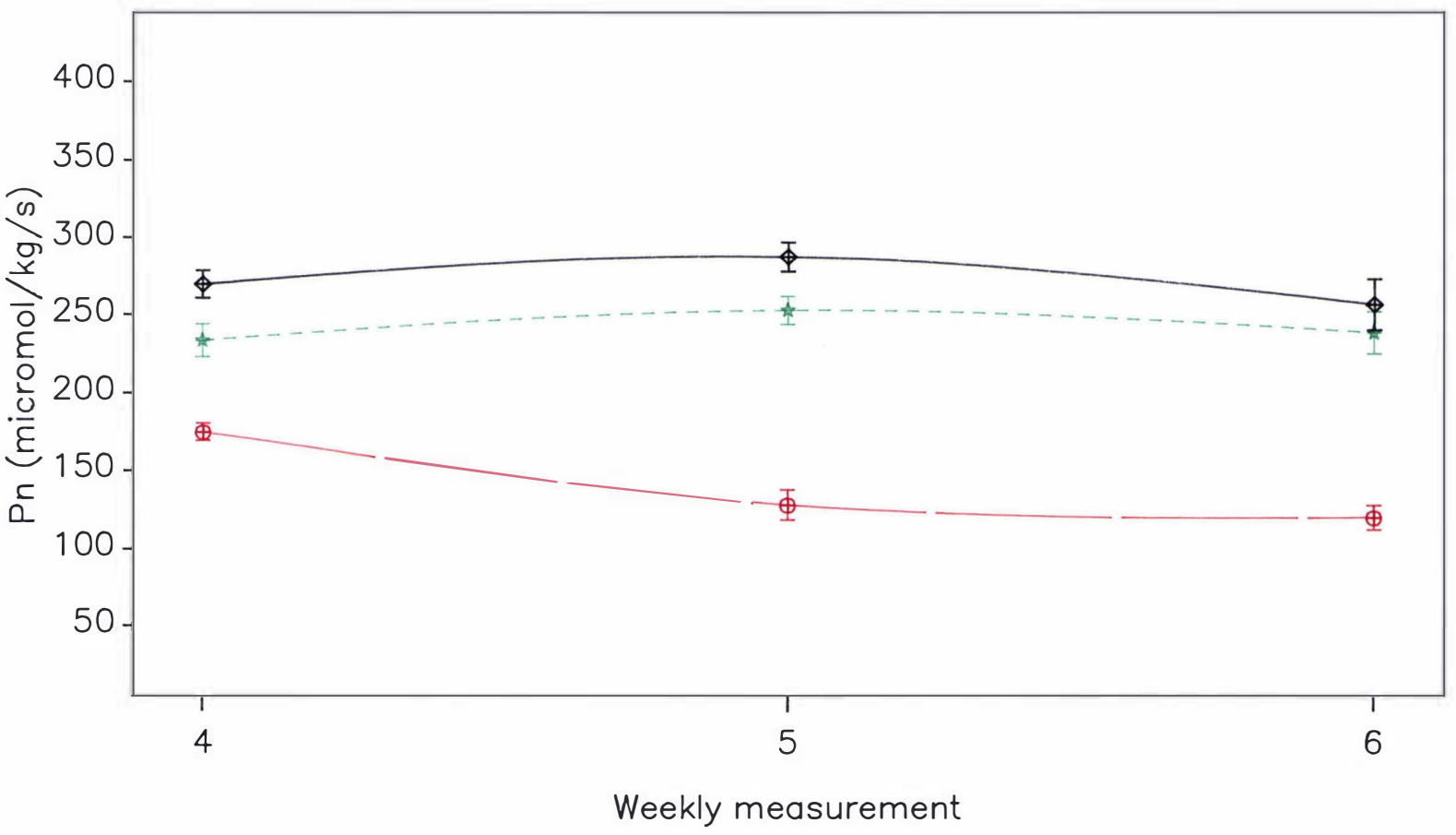


Figure 3.4 Photosynthesis of mature fern average 4 cultivars from weeks 4 to 6 after emergence (◇ ◇ ◇ 30/20C; ☆ ☆ ☆ 35/25C; ⊕ ⊕ ⊕ 40/30C).
I = Stderr. of means.

called "photosynthetic maturity" (Ticha *et al.,* 1984) of young asparagus plants occurred with intermediate aged fern (see section 3.2.5 for the description of fern age), suggesting that at this stage the fern was fully expanded (Catsky and Ticha, 1980; Sestak, 1981). Studies on ontogenetic changes in other species also found that photosynthesis increased as the leaves expand (eg. Ticha *et al.,* 1984 on bean; Sams and Flore, 1982; and Lieth and Pasian, 1990 on roses; Perry *et al.,* 1983 on cotton; Passera, 1981 on barley; Ferron and Sauvesty, 1981; and Leopard and Kriedemann, 1975 on wheat).

Although stomatal development was not studied the lower photosynthetic rate of young asparagus fern could be due to the presence of stomata, which were low in number and immature as has been reported for apple leaves (Slack, 1974). Also in young leaves the photosynthetic system may not have completely developed as biochemical changes continue to occur as chloroplast develop, and the total number of chloroplast may still be increasing (Leech and Baker, 1983; Possingham, 1980).

Although the only differences between intermediate and mature fern photosynthesis were found at 30/20^{0}C for Tainan 1 and Larac and at 35/25^{0}C for Brocks (Tables 3.3 and 3.4), there was a clear trend that the optimum photosynthesis occurred at the intermediate stage. The lack of significant differences between intermediate and mature fern for other cultivars and temperature possibly indicated that the exact position of the fern sample could be important. As has been mentioned previously (section 3.2.5), the sample of the fern was based on the appearance (colour and the closeness of the cladophylls) followed by position without any consideration as to whether the sample came from the first or second shoot.

The trend that photosynthesis decreased from intermediate to mature fern could be related to biochemical and photochemical factors (Tables 3.3 and 3.4). Evidence suggests that such changes were characterised by a decrease in the activity and concentrations of enzymes involved in the photosynthetic reactions, such as rubisco (Sestak, 1969; Peat, 1970; Hall and Brady, 1977; Hall *et al.,* 1978; Passera, 1981; Perry *et al.,* 1983), a decrease in the electron transport rate inside the chloroplast (Jenkins and Woolhouse, 1981a and b), changes in the chloroplast membrane composition (Fong and Heath, 1977),

and decreasing stomata and mesophyll conductance (Catsky *et al.,* 1976; Constable and Rawson, 1980). Photochemical efficiency, however, might not be affected appreciably by age because it was found that there was no significant trend for quantum yield in tomato (Peat, 1970), rose (Pasian and Lieth, 1989), apple (Watson and Lansberg, 1978) and 22 crop plants (McCree, 1972) with leaves of various ages. In contrast, Constable and Rawson (1980) observed that the photochemical efficiency of cotton leaves increased with age up to 15 days and then levelled off from 15 to 40 days. Unfortunately, this present study did not measure the light response curve of asparagus fern at various ages and there is a possibility that dark respiration might cause these differences. Peat (1970) and Pasian and Lieth (1989) found no differences in dark respiration at various leaf ages, while Constable and Rawson (1980) found the reverse.

This experiment was in general agreement with Lin's (1983) study of the $^{14}CO_2$ assimilation activity among various growth stages of asparagus. He found that the young cladophylls (intermediate stage), had the highest $^{14}CO_2$ assimilation activity, about 1.3 fold the activity of mature cladophylls and 2.6 fold that of immature cladophylls (pre-fern stage). This present study found that at 30/20^{0}C and 35/25^{0}C the intermediate fern photosynthesis was 1.26 and 1.2 times (average of 4 cultivars) higher than mature fern, respectively. However, intermediate fern was only 1.45 and 1.37 times (average of 4 cultivars) higher than young fern. This differences with Lin's study could be due to the young fern used by Lin (1983) being still undeveloped compared to the present investigation. Another study conducted by Lin and Hung (1983) found a contradictory result. They observed that the photosynthetic rate of mature cladophylls was 1.3 times higher than intermediate cladophylls. This contradiction could be caused by the different units used in the analysis. For example, in the present investigation and that of Lin's (1983) study, dry weight was used to express the photosynthetic rate while Lin and Hung (1983) used fresh weight. Expressing leaf photosynthesis in fresh weight could underestimate the result. For example, the cell wall of meristematic and newly formed growing cells have only a primary wall, which contains 90-95 % water, while in fully mature cells protoplast deposit more wall material on the primary wall to form the secondary wall (Kochhar and Krishnamoorthy, 1989; Rost *et al.,* 1984). Therefore the photosynthetic differences found between two type of cells (cladophylls) may not be due

to the differences in photosynthetic capacity, but rather to differences in water status. It is also commonly found that expressing photosynthesis in different units can give different results. For example, Chabot and Chabot (1977) found that correlation of anatomical variables of *Fragraria vesca* grown at different light and temperature levels was negatively related with photosynthesis per unit dry weight, but were not significant on a leaf area basis. Poorter and Pothmann (1992) found that photosynthesis of 2 grasses were significantly different when based on dry weight, but not significant on a leaf area basis, while Ottosen (1989) observed that the differences in photosynthesis between clones of *Ficus benjamina* were significant on leaf area basis, but not on dry weight basis. Laing (1985) calculated that the optimal growth temperature for maximal photosynthesis of kiwifruit expressed on a dry weight basis was 25^{0}C, but was at about 17^{0}C when expressed on unit leaf area. Another possible explanation is that Lin and Hung (1983) used a large portion of fern including the lateral stem to determine ontogenetic changes of asparagus fern, while in this experiment only a small section of fern were used, which was a small lateral stem. Previous research has shown that photosynthesis in asparagus was observed mainly in cladophylls (Inagaki *et al.,* 1989). Using fresh weight as the basis unit of 'whole fern' photosynthesis would exaggerate the differences between the present research and that of Lin and Hung (1983), due to the fact that a large part of the tissue included in the study of Lin and Hung (1983) was not major photosynthesizing tissue (Inagaki *et al.,* 1989).

The lack of any differences between young and mature asparagus fern for most of the treatments was surprising (Table 3.3 and 3.4). Downton and Torokfalvy (1975) found that mature cladophyll (fern) had 3.6 times higher chlorophylls content than that of young cladophylls (pre fern), but it has been suggested that chlorophyll content does not have a good relationship with photosynthesis except at very low levels (Lawlor, 1987). Downton and Torokfalvy (1975) also observed that dark respiration and CO_2 compensation point of pre fern were more than 2 times greater than the fern. However, they also found with 1 year old asparagus the photosynthesis of pre fern and fern were not substantially different. It is possible that the low photosynthesis of mature fern in the present study was due to a substantial loss of their Rubisco activity and concentration.

Rubisco has been found to decrease in other species as leaves age (eg. Sestak, 1969 on spinach and radish; Peat, 1970 on tomato; Hall and Brady, 1977 on capsicum; Hall *et al.*, 1978 on grass; Passera 1981 on barley; Perry *et al.*, 1983 on cotton). The role of photorespiration can also not be ruled out. Studies with barley leaves indicate that the glycolate concentration in mature leaves was double that in young leaves (Passera, 1981). He suggested that decreased photosynthesis as leaves age is a consequence of higher photorespiration. Perry *et al.* (1983) also found an increase in photorespiration as the leaves of cotton aged. As tobacco leaves aged both RuBP carboxylase and oxygenase activity decreased, but carboxylase activity decreased at a higher rate (Lurie *et al.*, 1978), causing the ratio of RuBP carboxylase to oxygenase activity to decrease with age. The high ratio of RuBP carboxylase to oxygenase activity of young tobacco leaves, however, was not accompanied by a high photosynthetic rate compared to mature leaves. They suggested that this was due to changes in stomatal conductance, i.e. at a young stage although there was an abundance of Rubisco and photosynthesis was low because of very low stomatal conductance. The assumption that there is significant dark respiration during day periods would support the present finding. It was found that leaf respiration rates are higher in young leaves than in mature ones (Kramer and Kozlowski, 1979). High respiration of young fern therefore will reduce the net photosynthesis.

3.4.2 **Young, intermediate and mature fern photosynthesis of young asparagus plant at high temperatures**

When discussing photosynthesis of asparagus fern it is necessary to state the age status of the plant used. For example, the photosynthetic rate of mature fern taken from 1 year old plants were significantly higher than that of 3 year old plants (Inagaki *et al.*, 1989). In the present investigation very young asparagus plants were used with an expectation that their performance would represent how older plants would respond in similar temperature regimes.

The fact that only young fern photosynthesis was not significantly reduced by high temperature (Table 3.6) suggests that the young fern was more tolerant to temperature than intermediate and mature fern (Tables 3.7 and 3.8). This is consistent with

suggestion that mature leaves are more liable to high temperature damage on photosystem II (Weis and Berry, 1988; Al-Khatib and Paulsen, 1989). This emphasizes the important of leaf age in gas exchange studies with asparagus.

This experiment found that Brocks and UC157 had higher rate of mature fern photosynthesis than Tainan 1 and Larac (Table 3.8, Figure 3.3) suggesting that Brocks and UC157 were more adapted to high temperature conditions. These observation are understandable considering the origins of these cultivars. Brocks was developed particularly for quality improvement in desert areas. As the spear quality is dependent on the carbohydrate storage the improvement probably is achieved by improving photosynthetic rates at high temperatures, while Larac and probably Tainan 1 are more acclimated to low temperature regions and therefore the photosynthetic rate was more affected at high temperatures. The improvement of photosynthesis for Brocks and UC157 was probably through the higher rate of dark respiration during the night. It has been suggested that low night temperature reduced dark respiration and subsequently photosynthesis in the following day (Ivory and Whiteman, 1978; Izhar and Wallace, 1967; Ludlow and Wilson, 1971b; Tollenaar, 1989; and Grantz, 1989). Thus Yen's (1993) results indicated that UC157 and Brocks had a higher relative total plant growth rate (RPGR) at differential temperature regimes (5, 10 and 15^{0}C), while Tainan 1 and Larac have a high RPGR at constant temperature regimes. In addition there is a possibility that Brocks had a genetic improvement in the photosynthesis efficiency. For example evidence indicates that more dry matter is partitioned into the crown at high temperature for Brocks compared to UC157, Tainan 1 and Larac (Yen, 1993). As relative fern growth rate was relatively similar for all cultivars (Yen, 1993) Brocks should have a higher photosynthetic efficiency.

Photosynthesis alone can not be used for selecting cultivars for their adaptability to high temperature as evidence shows that there has been a lack of correlation between photosynthesis and yield (Bhagsari and Ashley, 1990; Zelitch, 1982; Bunce, 1986). The growth analysis study of Yen (1993) , however, also confirms the better adaptation of Brocks and UC157 to high temperatures. For example, Brocks and UC157 had a higher RPGR than Tainan 1 at 35/15^{0}C, but a lower RPGR at 20/20^{0}C than Larac. In addition

Brocks had less variation in RPGR at high temperatures (35/35, 40/20 and 40/30^{0}C) than other cultivars. At low temperatures (20/20^{0}C) Brocks and UC157 had a lower relative crown growth rate than Larac and then the reverse occurred at 30/20^{0}C.

The response of the 4 cultivars over the three temperatures treatments (Table 3.8 and Figure 3.3) clearly show that the photosynthetic rate of mature fern fell with increasing temperature. The fall was particularly marked at 40/30^{0}C. As the data represents pooled measurements from week 4 to week 6 it is possible that the effect of temperature on photosynthesis could be confounded by leaf age. Plotting the photosynthesis data from week 4 to 6 (average of 4 cultivars) however shows that at 30/20 and 35/25^{0}C the photosynthesis was reasonably constant, while at 40/30^{0}C the photosynthesis decreased from week 4 to 5 and 6 (Figure 3.4). These data suggests that the decrease in mature fern photosynthesis from 30/20 to 35/25^{0}C was mainly due to a temperature effect, while at 40/30^{0}C the effect of temperature apparently has been confounded by leaf ontogeny.

3.5 SUMMARY

From this experiment it is concluded that:

1. Fern photosynthesis of young asparagus plants changed with age, regardless of the temperature treatment. The trend was that the photosynthesis increased from young to intermediate aged fern and was then followed by a decrease at the mature stage.

2. There were differences in photosynthesis between the cultivars at the mature stage of fern development with Brocks being the most stable cultivar and Tainan 1 and Larac the least. At 35/25^{0}C young fern photosynthesis of Brocks was lower than UC157 possibly due to Brocks being less developed compared to UC157.

3. The photosynthetic rate of intermediate and mature asparagus fern decreased with increases in high temperature.

CHAPTER FOUR

THE EFFECT OF TEMPERATURE ON SHOOT AND CROWN DARK RESPIRATION AND ON PHOTORESPIRATION, DARK RESPIRATION, PHOTOSYNTHESIS AND THE AC_i CURVE OF MATURE FERN

4.1 INTRODUCTION

The wide range of responses of plants to growing temperature can be partly explained by effects on photosynthesis and respiration processes (Edwards and Walker, 1983; Lawlor, 1987; Salisbury and Ross, 1990). Numerous studies have been carried out on the effect of temperature on photosynthesis and respiration of both C_3 and C_4 plants. In terms of photosynthesis, it has been well established that C_3 plants are sensitive to temperature. The optimum temperature for photosynthesis ranges from 15 to 25^{0}C (Lawlor 1987; Salisbury and Ross 1990). At temperatures higher than 30^{0}C the productivity of C_3 plants tend to be low because of low CO_2 fixation, high photorespiration rate and high dark respiration rate (Edwards and Walker 1983; Lawlor 1987; Salisbury and Ross 1990). Plant respiration of asparagus is an important factor to understand the carbon balance under temperature treatment. However, information on shoot and crown dark respiration of asparagus is scare.

Farquhar and Sharkey (1982), Jones (1985) and Layne (1989) suggested that the response of photosynthesis to internal CO_2 concentration (AC_i curve) provides a powerful physiological tool because information obtained can be used to describe the responses of plants to environments. For example, some of the data generated includes:

i. CO_2 compensation point
ii. Stomatal limitation to photosynthesis
iii. Carboxylation efficiency

AC_i curves are usually generated using elaborate non-portable equipment. Software has now became available for the Li-6200 version 2.01 or 2.02 (Anon, 1991) which

allows AC_i curves to be generated more simply, such as on soybean and cotton as described by McDermitt *et al.* (1989).

The work of Inagaki *et al.* (1989) demonstrated the sensitivity of asparagus to temperature, as would be expected of a C_3 plant. Their study, however, did not include the measurement of AC_i curves. The objectives of this experiment were to determine shoot and crown dark respiration, fern photo and dark respiration, photosynthesis and the AC_i curves of asparagus fern over a broad range of temperature treatments.

4.2 MATERIALS AND METHODS

4.2.1 Treatment

4.2.1.1 Temperatures

The growing temperature treatments used in this experiments were alternating 12 hour day and night temperatures of 20/20^{0}C, 25/25^{0}C, 30/20^{0}C, 35/15^{0}C and 40/20^{0}C. These temperature treatments were determined by the research programmes of Yen (1993). The experiment was carried out in growth cabinets at the Plant Growth Unit (PGU), Massey University, Palmerston North. The experimental conditions are shown in Table 4.1. The lighting system used in the growth room consisted of 6 x 400 W Philips HPI/T mercury iodide high-pressure discharge lamps together with 2 x 1000 W Phillips tungsten halogen lamps, and also 3 x 100 W incandescent lamps are provided on separate timing circuit for low intensity photoperiod. These light combinations gave PPFD ranging from 800 - 900 μmol m^{-2} s^{-1} and PAR (400 - 700 nm) from 170 - 200 W m^{-2}, measured 130 cm below the glass (Wratt, 1977). These conditions are similar in light intensity and quality to the climate rooms of CRI used in chapters 3 and 5.

4.2.1.2 **Cultivars**

The four cultivars used in this experiment were UC157, Brocks, Tainan 1 and Larac (see section 3.2.1.2).

4.2.2 **Propagation and growing conditions**

Asparagus seeds were sown in 100% fine peat contained in cell trays. The cells had a volume of 30 cm^3, were 7.5 cm deep and the seedlings were grown at a density of 1000 plant m^{-2}. Details of the base fertilizers added to the peat and the liquid feed used are provided in Appendix 1 and 2.

The seed was germinated on a heated bench at 25^0C and the seedlings were grown on netting to provide air pruning of the roots. The glasshouse used was located at Plant Growth Unit, Massey University. Temperatures in the glasshouse was controlled by heating to 16^0C with fan ventilation operating at 25^0C.

Eight weeks after germination the seedlings were transfered to larger individual plastic pots, volume of 450 cm^3 and 8.5 cm deep, contained 100% fine pumice. Pumice was used as the media to reduce microorganism respiration during the measurement of the shoot and crown dark respiration. Liquid feed was applied once a day starting four weeks after seed sowing. After three months in the glasshouse the plants were removed to the growth cabinet and allowed to acclimatize for 1 week before measurements were started.

4.2.3 **CER measurement**

4.2.3.1 **Introduction**

Measurement of photorespiration, dark respiration, photosynthesis and AC_i curves were carried out on mature fern using the Li-6200 as described in Chapter 3 (section 3.2.4). Shoot and crown dark respiration were also determined using self designed

closed IRGA system (see section 4.2.3.2 for detail). The parameters measured are shown in Table 4.2. All measurements were made at the day temperature of any particular temperature treatment.

Table 4.1 Environmental conditions during growth cabinet experiments

Treatment	Daylength (12 hrs)	Temperature ± 0.5°C	R H ± 5%
1	day	20	74
	night	20	74
2	day	25	81
	night	25	81
3	day	30	76
	night	20	74
4	day	35	82
	night	15	64
5	day	40	86
	night	20	74

Table 4.2 Parameters studied during the experiment

Parameter	measured on
1. Shoot respiration	individual plant
2. Crown respiration	individual plant
3. Dark respiration	mature fern
4. Photorespiration	mature fern
5. Photosynthesis	mature fern
6. AC_i curve	mature fern

4.2.3.2 **Shoot and crown dark respiration of asparagus plant**

4.2.3.2.1 **Design**

The closed system design for measuring shoot and crown dark respiration is shown in Figure 4.1. The chamber consisted of thin perspex and the height and diameter was 48.7 cm and 52.5 cm, respectively. The total volume of the system was calculated by injecting a known volume of pure CO_2 into the chamber and then the increase of CO_2 concentration in the system was measured (Greer pers. comm.). The volume of the system was determined by the use of the following relationship:

Volume (ml) = A x 10^6/B (4.1)

where A is pure CO_2 concentration (cm^3) and B is the ammount of CO_2 (ppm) increased after injection.

By injecting 30 ml of pure CO_2 the CO_2 concentration increament was 284.18 ppm. Therefore the total volume of system was 105.6 litre.

The system was protected from air leaks using a water seal technique, i.e., by immersing the bottom edge of the chamber into water (see Figure 4.1, inset).

The air inside the chamber was stirred by using small fan mounted on the wood base. The air was stirred to maintain the boundary layer resistance constant throughout the measurement and eliminate gradients of CO_2, O_2 and water vapour across the chamber (Šesták *et al.*, 1971) .

The temperature was monitored with a thermocouple connected to HP data logger (HP-44468A). Magnesium perchlorate was used to reduce the water vapour in the air which went into the IRGA (BINOS II, Leybold-Heraeus GMBH). The air flow was set at 15 cm^3 s^{-1}.

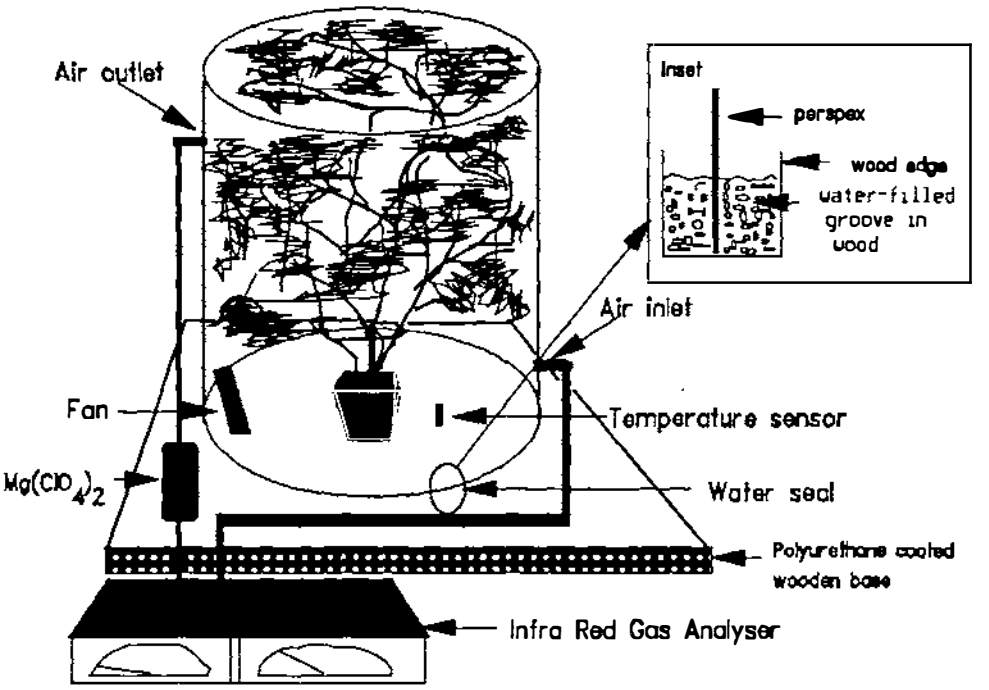


Figure 4.1 Closed system design for plant respiration studies.

4.2.3.2.2 **Calculation and technique of measurement**

a. Calculation

According to Šesták *et al.* (1971) the CER of a closed system can be calculated by the equation shown below:

$$CER = \frac{\Delta C \times V}{t \times A} \quad (4.2)$$

where - CER is efflux or influx of CO_2 (μmol kg^{-1} s^{-1});

- A is the size of shoot or crown (kg dry weight);
- V is the volume of air enclosed in the system (m^3);
- $\Delta C/t$ is the change in CO_2 concentration (ppm) over time (t) in second.

To convert the CO_2 concentration in v/v (ppm) to density unit ($\mu mol\ m^{-3}$) the ideal gas law was used (Layne, 1989), namely PV = nRT.
For example 1 ppm of CO_2 at temperature T °C (T+273 ^{0}K) and pressure P (MPa) is equal to 0.41 (293.15/(T+273)) (P) x 10^3 $\mu mol\ m^{-3}$.

b. Technique of measurement

Shoot and crown dark respiration were measured by enclosing the whole plant in the chamber 20 minutes into the dark period. Measurements were taken for 5 minute periods (t=300 second). After the measurement had been completed, the fern was cut off and the remaining crown was kept in the chamber for respiration measurement.

The fern and crown were then dried in the oven at 80^{0}C for 48 hours before recording the dry weight.

The microbial respiration form the potting mix was determined using an identical container and pumice mix, but no plant and kept in identical conditions to the plants. This respiration was substracted from the values obtained for shoot and crown respiration.

4.2.3.3 **Photorespiration, dark respiration and photosynthesis of mature fern**

4.2.3.3.1 **Photorespiration and dark respiration**

Photorespiration was measured by using the post illumination burst (PIB) method (see section 1.6.4.3.2). The fern was enclosed in the chamber and after 60 seconds the light turned off. The rate at which CO_2 accumulated over 10 second intervals was determined. The maximum rate of initial CO_2 release was considered to be proportional to the photorespiration rate (Tregunna *et al.,* 1961). Recording of CER in the dark continued for another 20 minutes when a steady rate of CO_2 release was obtained, and this data was considered to represent dark respiration. To allow plants to achieve a steady state of photosynthesis after darkness the next measurement of

photorespiration and dark respiration was carried out after the light had been turned on for at least 60 minutes.

4.2.3.3.2 **Photosynthesis**

Photosynthesis was measured at a PPFD of about 750 μmol m^{-2} s^{-1} and at ambient CO_2 concentration (330 ppm).

4.2.3.4 **AC_i curves**

4.2.3.4.1 **Technique of measurement**

To obtain an AC_i curve a special program for the Li-6200 was used (Anon, 1991). This program allows one to calculate the leak rate which is particularly important at low CO_2 concentrations, and correct each assimilation measurement as the chamber CO_2 concentration declined. The equation used was :

$$(dC_{chamber}/dt) = (C_{ambient} - C_{chamber}/\tau) \quad (4.3)$$

where $dC_{chamber}/dt$ is the CO_2 change rate because of chamber leaks (s^{-1}), $C_{ambient}$ is air CO_2 concentration surrounding the chamber (ppm), $C_{chamber}$ is the CO_2 concentration in the chamber, and τ is the leak rate time constant (s). This programme is accessed by function E3 (called Sigit). A leak test can be performed first by reducing the chamber CO_2 concentration to around 100 ppm using a CO_2 scrubber, and then measuring the rate of CO_2 increase ($dC_{chamber}/dt$) with a filter paper leaf replica in the chamber. Since the chamber CO_2 concentration is always known, and the ambient CO_2 concentration can be easily measured, τ can be calculated.

To reduce chamber leakage, frequent renewal of the chamber gasket was necessary. The deterioration of a gasket can be detected from the τ value, a value such as 7000 or less indicating a high degree of deterioration.

The AC_i curve measurement was carried out by subjecting the individual attached ferns to CO_2 levels ranging from 0 ppm to slightly higher than ambient CO_2 concentration (350 ppm). A small fan was positioned 30 cm from the chamber and this kept the chamber temperature acceptably constant during the 30 to 60 minutes needed to obtain the AC_i curves.

To obtain the correct C_i data, leaf area was used in the photosynthetic calculation. Leaf area of fern was measured by considering that the caldophyll is a cylinder and then the surface area can be calculated. After obtaining the C_i, then the photosynthetic data were converted to dry weight basis.

4.2.3.4.2 **Model consideration and data collection**

a. **Model consideration**

Farquhar and Sharkey (1982) referred to the AC_i relationship below ambient CO_2 concentration as a demand function. Layne (1989) and Layne and Flore (1992) used nonlinear monomolecular asymptotic function to fit AC_i relationships. They found that this function produce the best of fit for the AC_i curves evaluated by R^2 and analysis of residuals. The model is:

$$Y = B_1 [(1 - B_2) e^{(-B3 X)}] \qquad (4.4)$$

where Y is the net photosynthesis (A); X is the internal CO_2 concentration (C_i); B_1 is asymptotic value; B_2 is minimum value; B_3 is rate constant; and e = 2.7182818.

b. **Data collection**

From the AC_i curve three related and important parameters can be collected (Layne, 1989) such as :

1) CO_2 compensation point (Γ), predicted by extrapolation of the fitted curve to the C_i at which photosynthetic rate is zero.

2) Stomatal limitation (l_g) which was calculated according to the differential method of Jones (1985) :

$$l_g = r_g/(r_g + r_m) \quad (4.5)$$

$$r_g = -(C_i - C_a)/A \quad (4.6)$$

where: - C_i is internal CO_2 concentration at ambient CO_2 concentration;
- C_a is ambient CO_2 concentration;
- A is net CO_2 assimilation at ambient CO_2 concentration;
- r_g is gas-phase resistance consisting $r_a + r_s$;
- r_m is residual resistance which equals $1/CE_{op}$ (see equation 4.7)

- Carboxylation efficiency at a particular points in the AC_i curve (CE_{op}) is estimated from the slope of the AC_i curve at that point. This is determined from the first derivative of the curve (equation 4.4) :

$$CE_{op} = dA/dC_i = B_1 B_2 B_3 e^{(-B3 X)} \quad (4.7)$$

3) Carboxylation efficiency (CE) was obtained from initial slope of AC_i curve of raw data.

4.2.4 **Experimental design and data analysis**

The plants were arranged in a Completely Randomized Design (CRD). There were four replications with one plant per replicate. Nonlinear monomolecular asymptotic fuction of AC_i relationships were obtained by using the Marquardt compromise method of successive approximations (Proc NLIN, SAS). Data analysis on each particular temperature were carried out using Proc GLM (SAS). Pooled analysis was

carried out to evaluate the main effect (see section 3.2.6). The treatment effects on various calculated values from AC_i curves were determined based on individual fern measurements. Trend analysis of the response of carbon exchange rate (CER) and parameters obtained from AC_i curves were carried out using orthogonal contrasts within Proc GLM in SAS.

4.3 RESULTS

4.3.1 Shoot and crown dark respiration

4.3.1.1 Shoot dark respiration

Analysis of variance on each particular day temperature showed that at 35/15^{0}C Larac had a higher shoot dark respiration rate (p=0.05) than Brocks and Tainan 1 (Table 4.3). Pooled analysis found only temperatures had a significant effect. Shoot respiration did not increase from 20/20 to 25/25^{0}C then followed a significant increase at higher temperatures (Figure 4.2).

The shoot dark respiration of all cultivars increased with temperature and the response was quadratic (Table 4.3). The average Q_{10} of shoot dark respiration between 20/20 to 40/20^{0}C were 1.53, 1.55, 1.50 and 1.56 for cv UC157, Brocks, Tainan 1 and Larac, respectively.

4.3.1.2 Crown dark respiration

Analysis of variance for each temperature found no significant differences between cultivars. Though not significantly different, Larac apparently had the lowest crown respiration rate at all temperatures. This was confirmed by pooled analysis which found a significant effect of temperature and cultivars but without any interaction. Crown respiration of Larac was significantly lower than that of Tainan 1. Crown respiration increased significantly with temperature from 20/20 to 35/15^{0}C and then leveled off at 40/20^{0}C (Figure 4.3).

The response of crown dark respiration to temperature was cubic for all cultivars (Table 4.4). The average Q_{10} between 20/20 to 40/20°C were 1.26, 1.28, 1.25 and 1.3 for UC157, Brocks, Tainan 1 and Larac respectively.

The rate of shoot dark respiration and the Q_{10} was higher than crown dark respiration for all temperature treatments, regardless of cultivars. At temperatures higher than 30/20°C shoot respiration was double that of crown dark respiration (Table 4.3 and 4.4).

Table 4.3. Shoot dark respiration (μmol kg^{-1} s^{-1}) of asparagus at various temperatures

Treatment	cultivars				
	UC157	Brocks	Tainan 1	Larac	Temp.mean[2]
20/20°C ns[1]	6.95	6.68	7.06	7.06	6.94d
25/25°C ns	7.10	8.01	7.97	7.45	7.63d
30/20°C ns	10.30	10.49	9.89	10.24	10.23c
35/15°C **[1]	13.58ab	12.73b	12.54b	13.86a	13.18b
40/20°C ns	16.33	15.95	14.74	17.08	16.28a
Cv. Mean[2]	10.85	10.77	10.64	11.14	
T_{linear}	**	**	**	**	
$T_{quadratic}$	**	**	**	**	
T_{cubic}	ns	ns	ns	ns	

1. Anova on each temperature only found the differences between cultivars at 35/15°C with se=0.43 and $df_{(error)}$=12. Mean separation across the column by lsd (p≤0.05).
2. Mean separation for overall treatment (using pooled analysis) across and within column by Duncan's Multiple Range Test ($p \leq 0.05$) with se= 0.3404 and 0.7613 and $df_{(error)}$= 45.

Table 4.4. Crown dark respiration (μmol kg^{-1} s^{-1}) of asparagus at various temperatures

Treatment	cultivars				
	UC157	Brocks	Tainan 1	Larac	Temp. mean[2]
20/20°C ns[1]	4.04	4.02	4.16	3.77	3.99d
25/25°C ns	4.65	4.51	4.55	4.28	4.50c
30/20°C ns	5.17	5.21	5.04	4.90	5.08b
35/15°C ns	6.35	6.39	6.42	6.20	6.34a
40/20°C ns	6.44	6.58	6.77	6.42	6.55a
Cv. mean[2]	5.33ab	5.34ab	5.39a	5.11b	
T_{linear}	**	**	**	**	
$T_{quadratic}$	**	**	**	**	
T_{cubic}	**	**	**	**	

1. Anova on each temperature did not find any differences between cultivars.
2. Mean separation for overall treatment (using pooled analysis) across and within column by Duncan's Multiple Range Test ($p \leq 0.05$) with se= 0.1176 and 0.2629 and $df_{(error)}$= 45.

4.3.2 **Photorespiration and dark respiration of mature asparagus fern**

4.3.2.1 **Photorespiration**

Analysis of variance for each temperature found only at 20°C did Brocks have significantly higher photorespiration than Tainan 1 (Table 4.5). At temperature higher than 30/20°C photorespiration of Brocks was lower than the other cultivars, though not significantly. Pooled analysis, however, found only temperatures had a siginificant effect on photorespiration. Photorespiration increased significantly from 20/20 to 35/15°C followed by a significant decreased at 40/20°C.

Photorespiration of mature fern, regardless of cultivar, showed a significant cubic response to temperatures (Figure 4.4). Photorespiration increased steeply from 20/20 up to 35/15°C and then decreased at 40/20°C (Figure 4.4). At 35/15°C the average

photorespiration rates were 97.21, 92.23, 95.02 and 96.88 μmol kg^{-1} s^{-1} for UC157, Brocks, Tainan 1 and Larac, respectively.

Table 4.5. Photorespiration (μmol kg^{-1} s^{-1}) of mature fern at various temperature

Treatment	cultivars				
	UC157	Brocks	Tainan 1	Larac	Temp. mean[2]
20/20°C **[1]	39.273ab	41.86a	37.36b	39.55ab	39.51e
25/25°C ns	56.19	57.95	54.89	54.76	55.95d
30/20°C ns	74.30	76.21	77.53	78.33	76.59c
35/15°C ns	97.21	92.23	95.02	96.88	95.33a
40/20°C ns	81.45	78.95	84.12	83.09	81.90b
Cv. Mean[2]	69.69a	69.44a	69.78a	70.52a	
T_{linear}	**	**	**	**	
$T_{quadratic}$	**	**	**	**	
T_{cubic}	**	**	**	**	

1. Anova on each temperature only found the differences between cultivars at 20/20°C with se=1.51 and $df_{(error)}$=12. Mean separation across the column by lsd ($p \leq 0.05$).
2. Mean separation for overall treatment (using pooled analysis) across and within column by Duncan's Multiple Range Test ($p \leq 0.05$) with se= 1.304 and 2.916 and $df_{(error)}$= 45.

4.3.2.2 **Dark respiration**

Analysis of variance for each temperature found a significant differences between cultivars only at 20/20°C where Brocks was significantly higher than Tainan 1 and UC157 (Table 4.6). Pooled analysis found that dark respiration was affected by temperatures, and without any interaction. In general Tainan 1 had a significantly lower dark respiration than UC157. Dark respiration increased significantly with temperatures from 20/20 to 40/20°C.

Trend analysis also indicated that dark respiration of mature fern increased linearly with temperatures (Figure 4.5). The average Q_{10} of dark respiration between 20/20 to 40/20^{0}C were 2.1, 1.8, 2.0 and 1.95 for UC157, Brocks, Tainan 1 and Larac, respectively.

Table 4.6. Dark respiration (μmol kg^{-1} s^{-1}) of mature fern at various temperature

Treatment	cultivars				
	UC157	Brocks	Tainan 1	Larac	Temp. mean[2]
20/20^{0}C**[1]	15.64b	19.82a	16.01 b	18.04ab	17.38e
25/25^{0}C ns	29.01	30.63	29.10	29.24	29.49d
30/20^{0}C ns	41.28	40.35	37.26	40.19	39.77c
35/15^{0}C ns	56.95	50.08	53.30	51.17	52.87b
40/20^{0}C ns	69.21	64.28	63.73	68.82	66.51a
Cv. mean[2]	42.42	41.03	39.88	41.49	
T_{linear}	**	**	**	**	
Tquadratic	ns	ns	ns	ns	
T_{cubic}	ns	ns	ns	ns	

1. Anova on each temperature only found the differences between cultivars at 20/20^{0}C with se=1.5 and $df_{(error)}$=12. Mean separation across the column by lsd ($p \leq 0.05$)
2. Mean separation for overall treatment (using pooled analysis) across and within column by Duncan's Multiple Range Test ($p \leq 0.05$) with se= 1.2053 and 1.3475 and $df_{(error)}$= 45.

4.3.3 **Fern photosynthesis**

Analysis of variance for each temperature found that photosynthesis of Brocks was significantly lower at 20/20^{0}C than Tainan 1 and Larac and Tainan 1 was greater than UC157. Brocks apparently showed a better adaptation at higher temperatures. For example, at 35/15^{0}C the photosynthetic rates of Brocks was significantly higher than

Larac and Tainan 1 and at 40/20^{0}C Brocks was significantly higher than Larac (Table 4.7). Pooled analysis, however, found that only temperatures had a significant effect on photosynthesis. Photosynthesis decreased significantly with temperature from 20/20 to 40/20^{0}C. Optimum photosynthesis was achieved at 20/20^{0}C, where rates were 345.63, 332.33, 360,13 and 352.75 μmol kg^{-1} s^{-1} for UC157, Brocks, Tainan 1 and Larac, respectively.

Trend analysis found that response of fern photosynthesis to increasing temperatures was cubic (Table 4.7 and Figure 4.6).

Table 4.7. Net photosynthesis (μmol kg^{-1} s^{-1}) of mature fern at various temperature

Treatment	cultivars				
	UC157	Brocks	Tainan 1	Larac	Temp. mean[2]
20/20^{0}C **[1]	345.63bc	332.33c	360.13a	352.75ab	347.71a
25/25^{0}C ns	299.59	278.04	290.83	292.01	290.12b
30/20^{0}C ns	262.14	254.38	260.34	259.66	259.13c
35/15^{0}C **	225.37ab	233.64a	221.09b	218.24b	224.59d
40/20^{0}C **	163.60ab	174.71a	172.83ab	158.32b	167.36e
Cv. mean[2]	259.27	254.62	261.04	256.19	
T_{linear}	**	**	**	**	
$T_{quadratic}$	**	**	**	**	
T_{cubic}	**	**	**	**	

1. Anova on each temperature found the differences between cultivars at 20/20^{0}C, 35/15^{0}C and 40/20^{0}C with $df_{(error)}$=12 and se = 6.54, 4.78 and 7.25 respectively. Mean separation across the column by lsd ($p \leq 0.05$).
2. Mean separation for overall treatment (using pooled analysis) across and within column by Duncan's Multiple Range Test ($p \leq 0.05$) with se= 4.7766 and 10.6807 and $df_{(error)}$= 45.

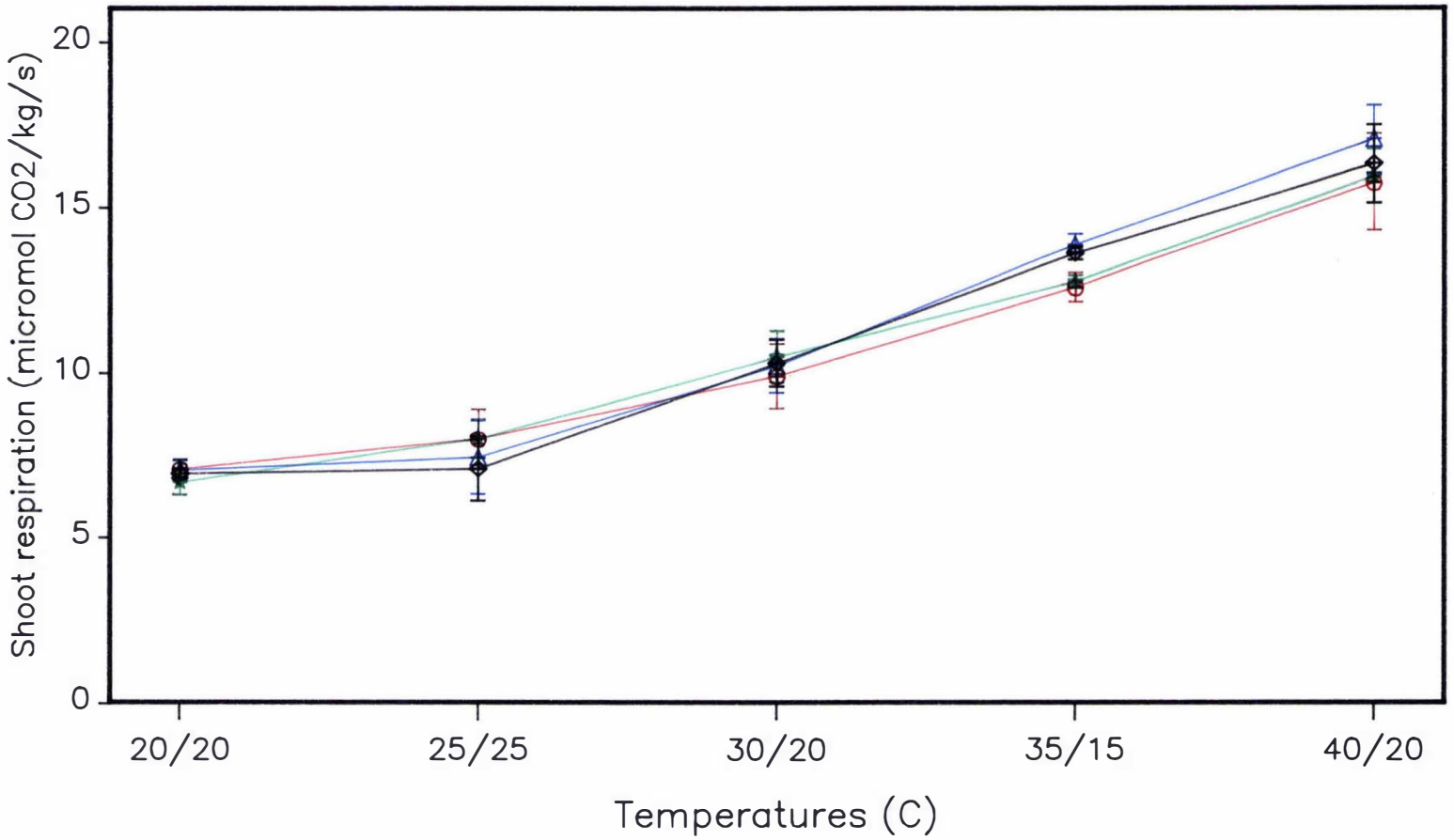


Figure 4.2 Shoot respiration of asparagus plant at different temperatures (◇ ◇ ◇ UC157; ☆ ☆ ☆ Brocks; ⊕ ⊕ ⊕ Tainan 1; △ △ △ Larac). I = Stderr. of means.

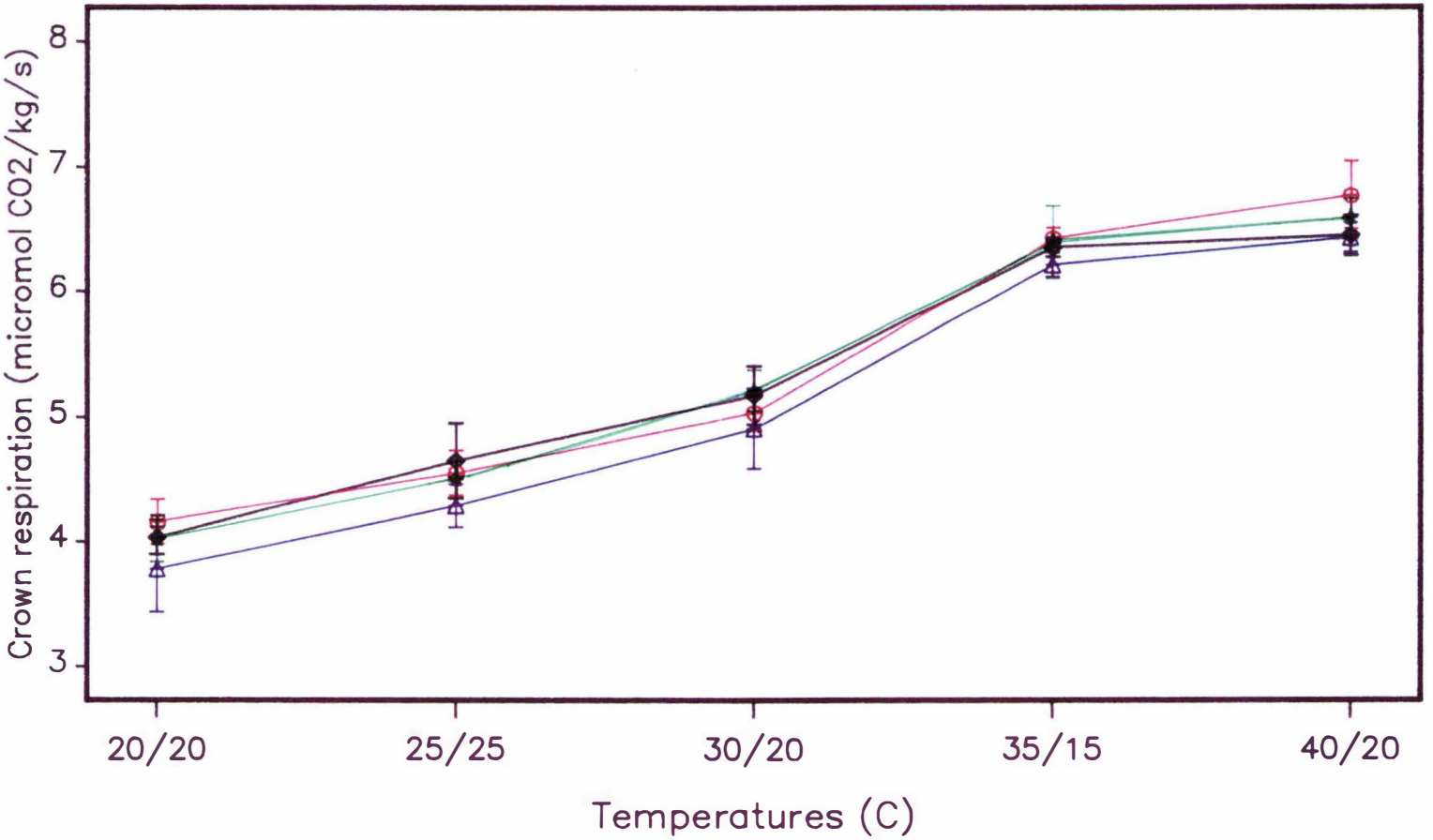


Figure 4.3 Crown respiration of asparagus plant at different temperatures (◇ ◇ ◇ UC157; ☆ ☆ ☆ Brocks; ⊕ ⊕ ⊕ Tainan 1; Δ Δ Δ Larac). I = Stderr. of means.

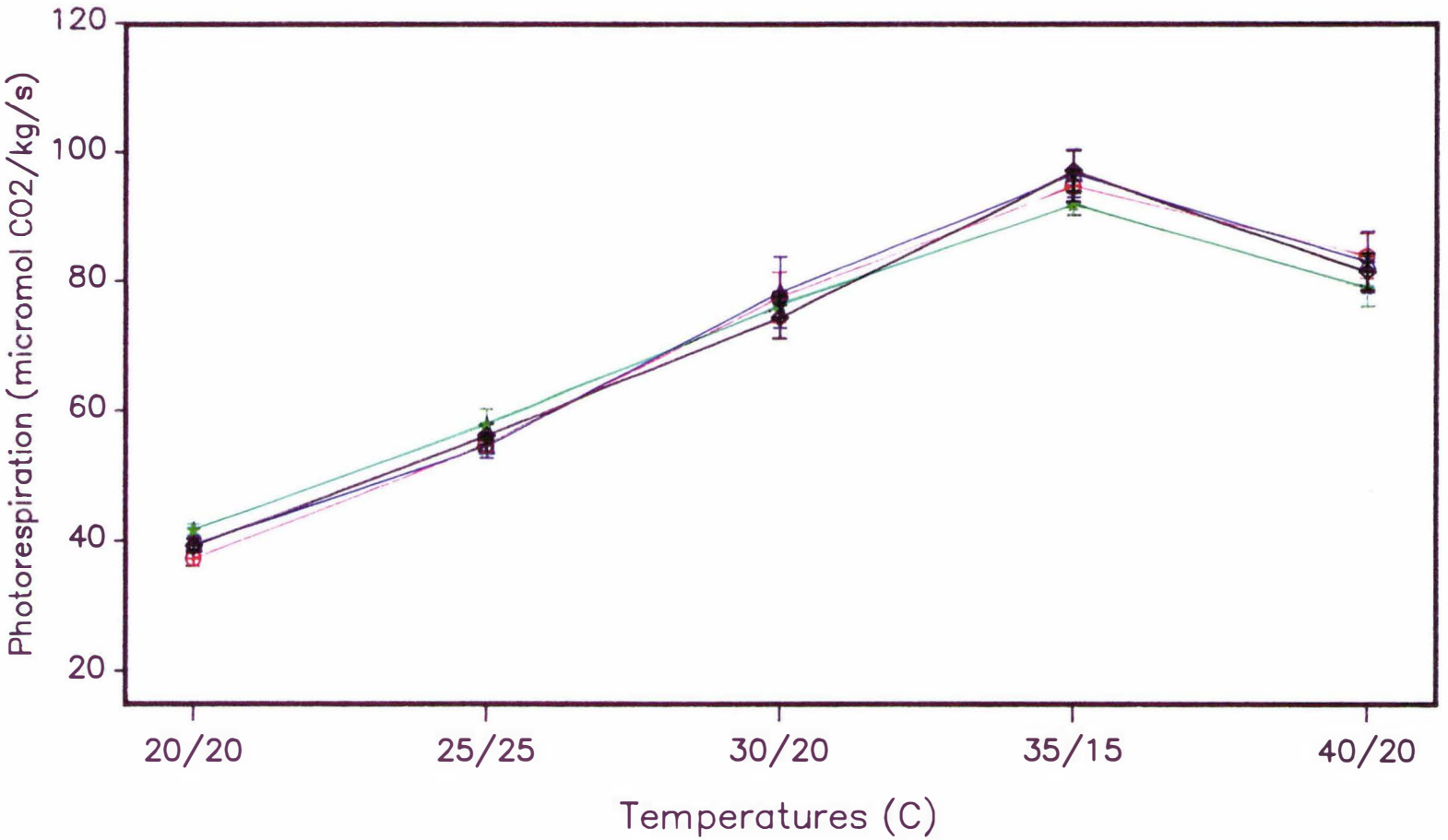


Figure 4.4 Photorespiration of asparagus fern at different temperatures (◇ ◇ ◇ UC157; ☆ ☆ ☆ Brocks; ⊕ ⊕ ⊕ Tainan 1; Δ Δ Δ Larac). I = Stderr. of means.

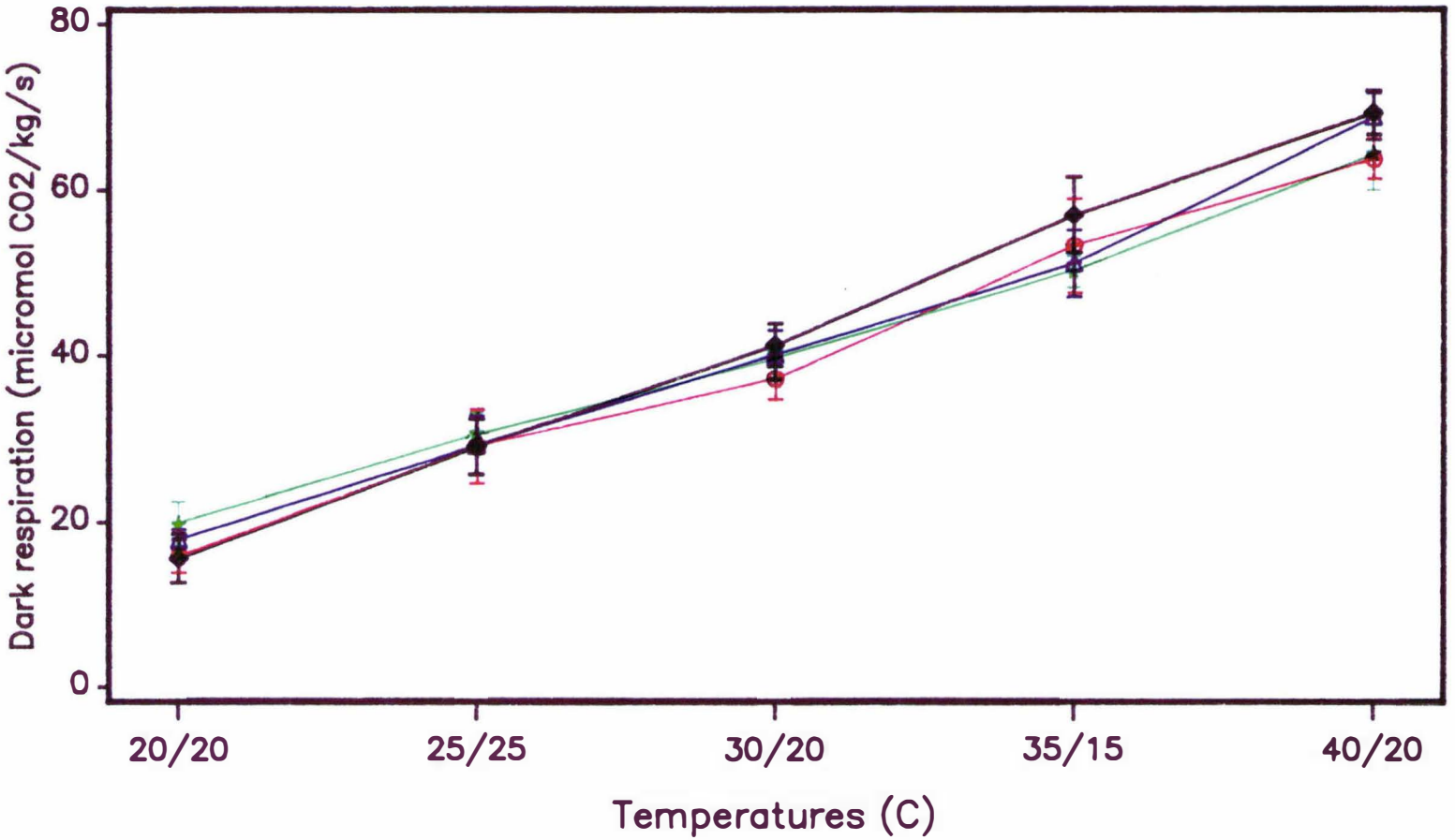


Figure 4.5 Dark respiration of asparagus fern at different temperatures
(◇ ◇ ◇ UC157; ☆ ☆ ☆ Brocks; ⊕ ⊕ ⊕ Tainan 1; Δ Δ Δ Larac).
I = Stderr. of means.

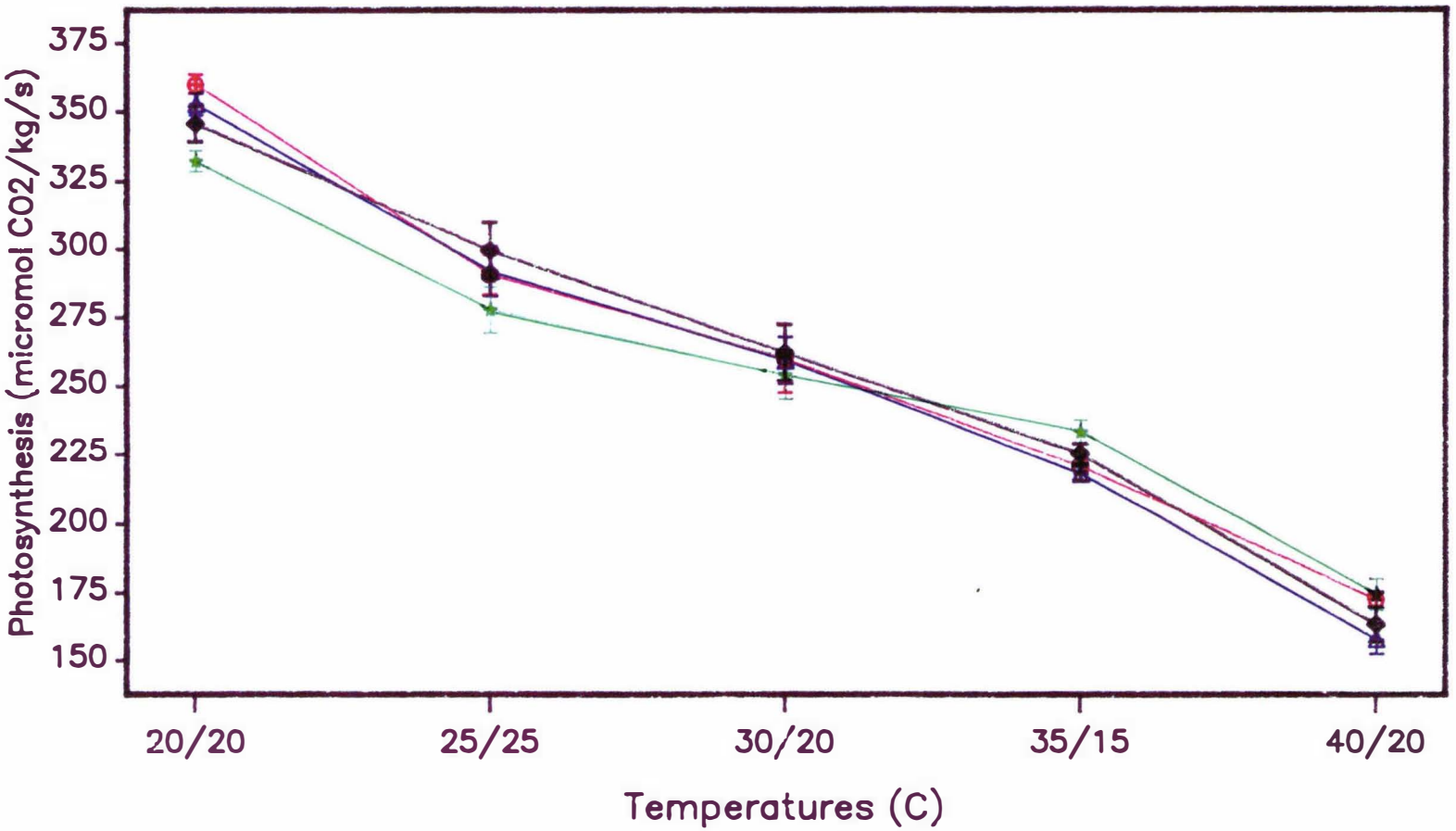


Figure 4.6 Photosynthesis of asparagus fern at different temperatures (◇ ◇ ◇ UC157; ☆ ☆ ☆ Brocks; ⊕ ⊕ ⊕ Tainan 1; Δ Δ Δ Larac). I = Stderr. of means.

4.3.4 AC_i curves

4.3.4.1 AC_i curves of mature fern with increasing temperature

From the AC_i curve three important parameters have been obtained. They were the CO_2 compensation point (Γ), the carboxylation efficiency close to compensation point (CE) and stomatal limitation (lg). The parameters were calculated based on the model considered in section 4.2.3.4.2. It has been suggested that the normal operating point on the AC_i curve is the the transition from RuBP saturation to RuBP limiting conditions, in other words from demand to supply limitation occurs close to the normal internal CO_2 concentration. This concentration was slightly below ambient (Farquhar and Sharkey, 1982; Lawlor, 1987; Layne, 1989). This is important to the present data analysis since the AC_i curves were only measured on the demand function up to about 350 ppm $C0_2$ concentration, slightly higher than ambient CO_2 concentration, and therefore the model proposed by Layne (1989) and Layne and Flore (1992) (equation 4.4) is applicable to these data. The model was then used to fit the lines as shown in Figure 4.7 to 4.10 for UC157, Brocks, Tainan 1 and Larac, respectively. It is still unclear, however, which limitation played the major role in changing the response of the cultivars. Therefore, further calculation was carried out following the suggestions of Farquhar and Sharkey (1982) and Jones (1985, 1989) to provide further information about the source of photosynthetic limitation in particular environments (section 4.3.4.2 to 4.3.4.5).

The AC_i curves of asparagus fern changed with increasing temperatures (Figure 4.7 to 4.10). From the initial slope it can be seen that apparently Brocks did not perform as well as the other cultivars at low temperature but was superior to Larac and Tainan 1 as temperature increased (see section 4.3.4.2).

4.3.4.2 CO_2 compensation point (Γ)

For any particular temperature no significant difference was found between cultivars. However, Brocks and Tainan1 tended to have a higher Γ than UC157 and Larac at

25/25°C (p=0.1) and Tainan 1 had a higher Γ than Brocks (p=0.053) at 40/20°C. Data at 40/20°C was not included in the pool analysis due to the very high variation. Pooled analysis only found a significant effect of temperature on Γ. The overall Γ increased significantly with increasing temperature (Table 4.8). Orthogonal contrast indicated that the response of Γ to increasing temperature was cubic (Table 4.8). From 20/20°C to 40/20°C the Γ increased more than double regardless of cultivar.

Table 4.8. CO_2 compensation point (μmol mol^{-1}) of mature asparagus ferns at various temperatures

Treatment	Cultivar				
	UC157	Brocks	Tainan 1	Larac	Temp. mean[3]
20/20°C[1]	32.80	31.13	29.93	31.73	31.39d
25/25°C	45.73	51.43	51.25	46.23	48.66c
30/20°C	53.70	52.40	51.88	53.35	52.83b
35/15°C	73.55	71.20	70.88	70.33	71.49a
40/20°C[2]	90.08	81.53	101.08	89.63	90.71
Cv. mean[3]	51.44	51.54	50.98	50.41	
T_{linear}	**	**	**	**	
$T_{quadratic}$	**	**	**	**	
T_{cubic}	**	**	**	**	

1. Anova for each particular temperature did not find any significant differences between cultivars.
2. 40/20°C was excluded from pooled analysis.
3. Mean separation for overall treatment (using pooled analysis) across and within column by Duncan's Multiple Range Test ($p \leq 0.05$) with se= 1.48 and $df_{(error)} = 36$.

4.3.4.3 **Carboxylation efficiency close to the compensation point (CE)**

Analysis of each particular temperature found no significant differences between cultivars (Table 4.9). However, there was a trend that at 20/20°C Brocks had a lower CE than UC157, Tainan 1 and Larac (p=0.06, 0.054 and 0.12, respectively), and at 25/25°C Brocks had a lower CE than Tainan 1 (p=0.06), while at 30/20°C UC157 had a higher CE than Tainan 1 (p=0.02). At temperatures higher than 30/20°C Brocks had a higher CE than other cultivars, though not significantly different. Pooled analysis only found a significant effect of temperature on CE. The overall CE decreased significantly with increasing temperatures (Table 4.9). Orthogonal contrasts indicated that the response of CE to increasing temperature was quadratic (Table 4.9).

Table 4.9. Carboxylation efficiency (mol kg^{-1} s^{-1}) of mature asparagus ferns at various temperatures

Treatment	Cultivar				
	UC157	Brocks	Tainan 1	Larac	Temp mean[3]
20/20°C[1]	2.39	2.11	2.40	2.34	2.31a
25/25°C	1.73	1.59	1.83	1.75	1.72b
30/20°C	1.66	1.52	1.42	1.55	1.54c
35/15°C	1.45	1.48	1.36	1.26	1.39d
40/20°C[2]	1.23	1.57	1.12	1.36	1.32
Cv. mean[3]	1.81	1.67	1.75	1.72	
T_{linear}	**	**	**	**	
$T_{quadratic}$	**	**	**	**	
T_{cubic}	ns	ns	ns	ns	

1. Anova for each particular temperature did not find any significant differences between cultivars.
2. 40/20°C was excluded from pooled analysis.
3. Mean separation for overall treatment (using pooled analysis) across and within column by Duncan's Multiple Range Test ($p \leq 0.05$) with se= 0.0571 and $df_{(error)}$ = 36.

4.3.4.4 **Stomatal limitation (lg)**

Analysis of each particular temperature found no significant differences between cultivars (Table 4.10). However, the trend was that at 20/20^{0}C UC157 had a lower lg than Brocks and Tainan 1 (p=0.04 and 0.1, respectively), and at 30/20^{0}C Brocks had a lower lg than Tainan 1 and Larac (p=0.054 and 0.03, respectively). At temperature higher than 30/20^{0}C Brocks had a lower lg than other cultivars though not significantly different. Pooled analysis only found a significant effect of temperature on lg. The overall lg increased significantly with increasing temperatures from 20/20^{0}C to 30/20^{0}C (Table 4.10). Orthogonal contrasts indicated that the response of lg to increasing temperature was linear (Table 4.10).

Table 4.10 Stomatal limitation of mature asparagus fern at various temperatures

Treatment	Cultivar				
	UC157	Brocks	Tainan 1	Larac	Temp. mean[3]
20/20^{0}C[1]	0.088	0.161	0.143	0.124	0.129c
25/25^{0}C	0.217	0.159	0.187	0.168	0.183b
30/20^{0}C	0.219	0.180	0.263	0.278	0.235a
35/15^{0}C	0.253	0.247	0.251	0.306	0.264a
40/20^{0}C[2]	0.264	0.259	0.309	0.307	0.287
Cv. mean[3]	0.194	0.187	0.211	0.219	
T_{linear}	**	**	**	**	
$T_{quadratic}$	ns	ns	ns	ns	
T_{cubic}	ns	ns	ns	ns	

1. Anova for each particular temperature did not find any significant differences between cultivars.
2. 40/20^{0}C was excluded from pooled analysis.
3. Mean separation for overall treatment (using pooled analysis) across and within column by Duncan's Multiple Range Test ($p \leq 0.05$) with se= 0.0185 and $df_{(error)}$ = 36.

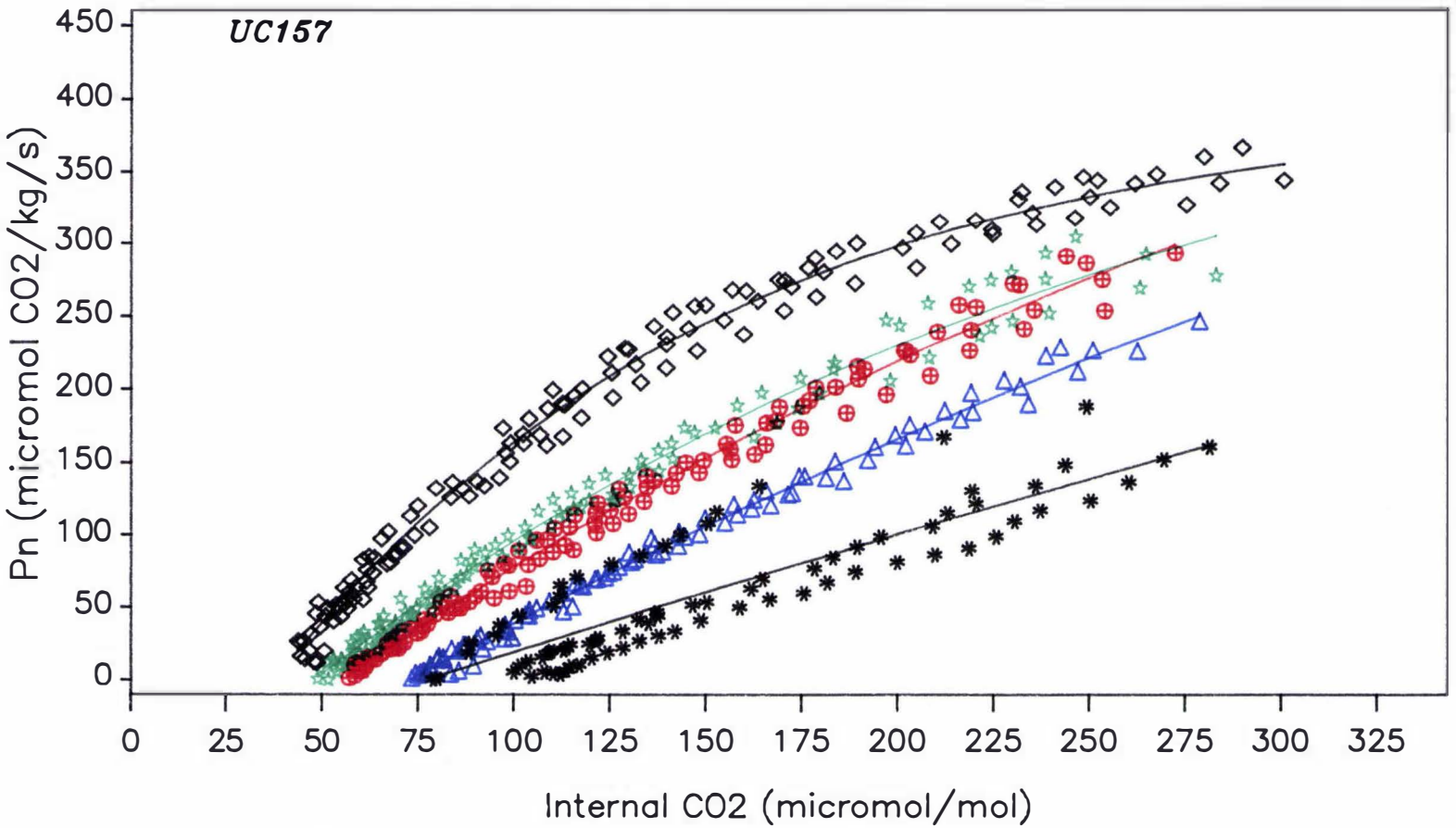


Figure 4.7 ACi response curve of UC157 at different growth temperatures (◇ ◇ ◇ 20/20C; ☆ ☆ ☆ 25/25C; ⊕ ⊕ ⊕ 30/20C; △ △ △ 35/15C; ✱ ✱ ✱ 40/20C). The fitted lines are obtained from equation 5.4.

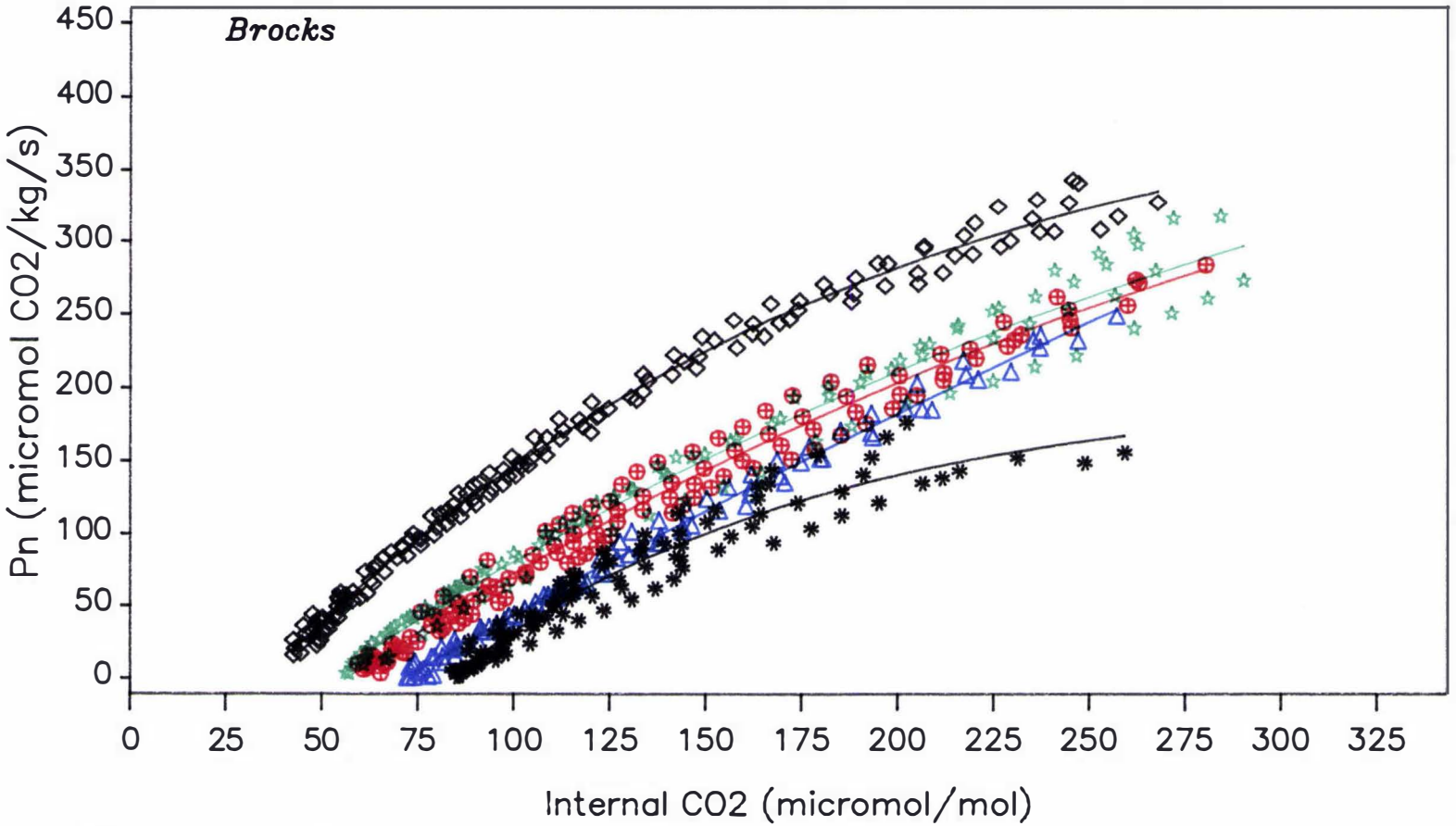


Figure 4.8 ACi response curve of Brocks at different growth temperatures (◇ ◇ ◇ 20/20C; ☆ ☆ ☆ 25/25C; ⊕ ⊕ ⊕ 30/20C; △ △ △ 35/15C; ✱ ✱ ✱ 40/20C). The fitted lines are obtained from equation 5.4.

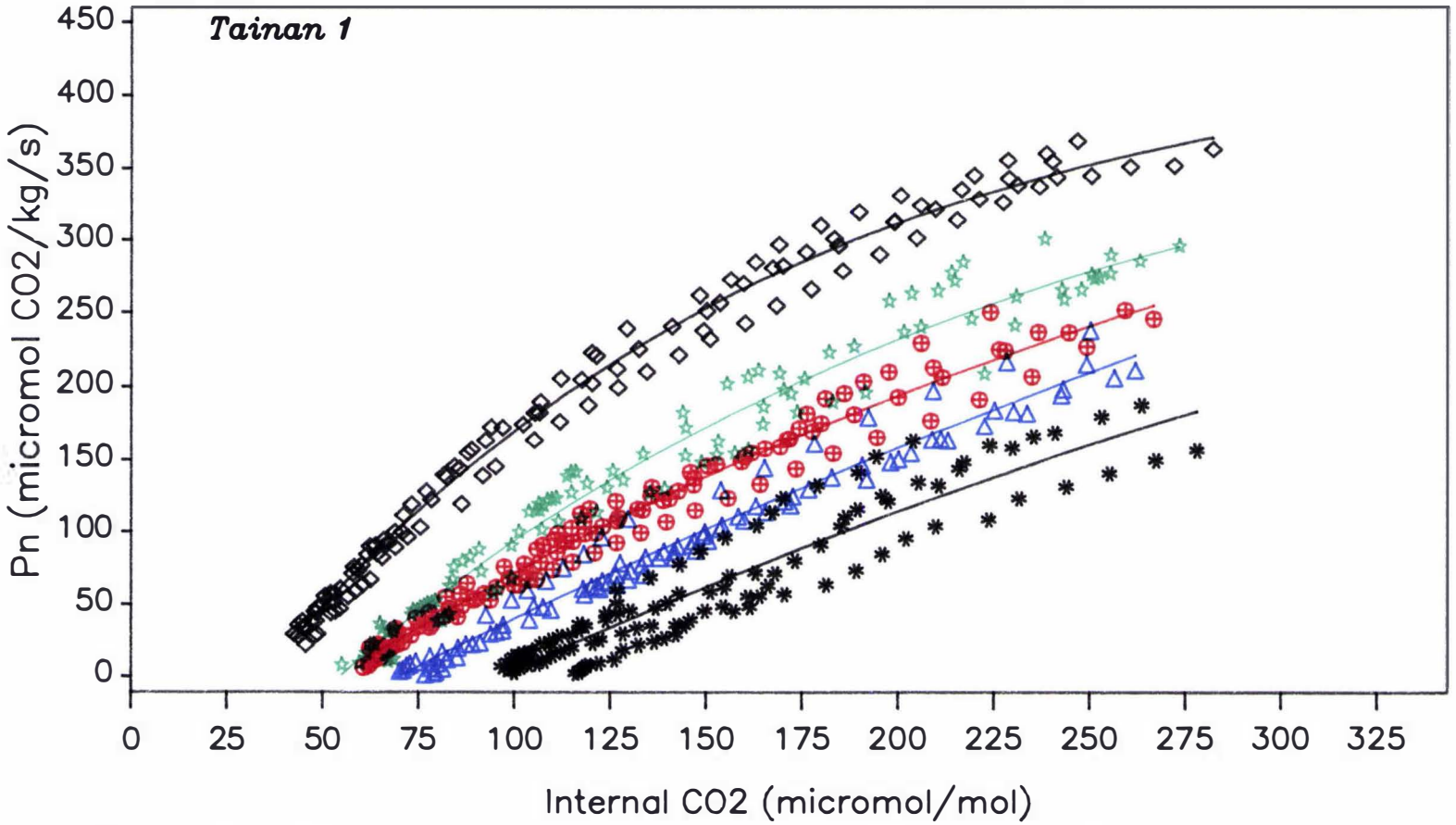


Figure 4.9 ACi response curve of Tainan 1 at different growth temperatures (◇ ◇ ◇ 20/20C; ☆ ☆ ☆ 25/25C; ⊕ ⊕ ⊕ 30/20C; △ △ △ 35/15C; ✱ ✱ ✱ 40/20C). The fitted lines are obtained from equation 5.4.

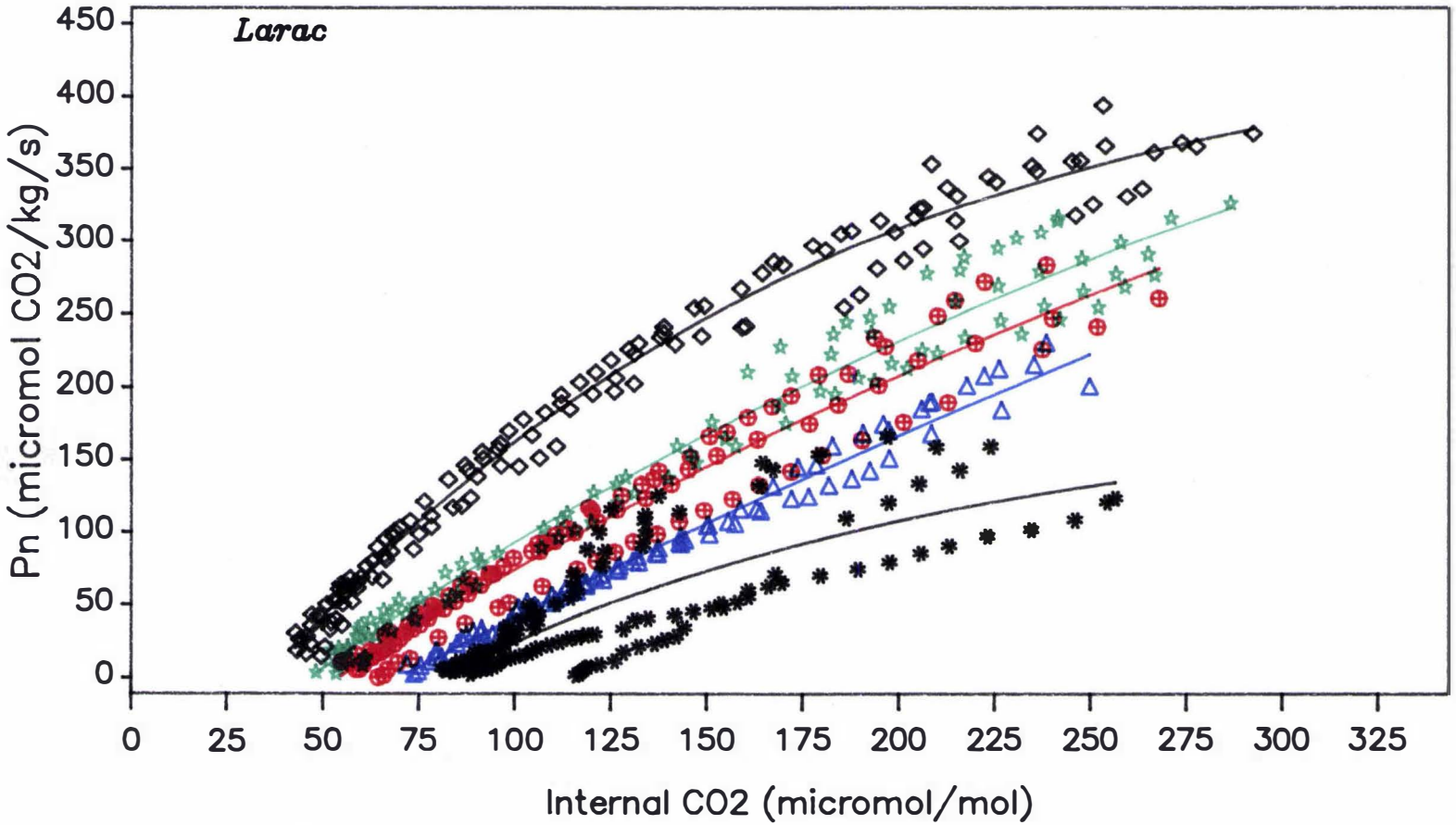


Figure 4.10 ACi response curve of Larac at different growth temperatures (◇ ◇ ◇ 20/20C; ☆ ☆ ☆ 25/25C; ⊕ ⊕ ⊕ 30/20C; △ △ △ 35/15C; ✱ ✱ ✱ 40/20C). The fitted lines are obtained from equation 5.4.

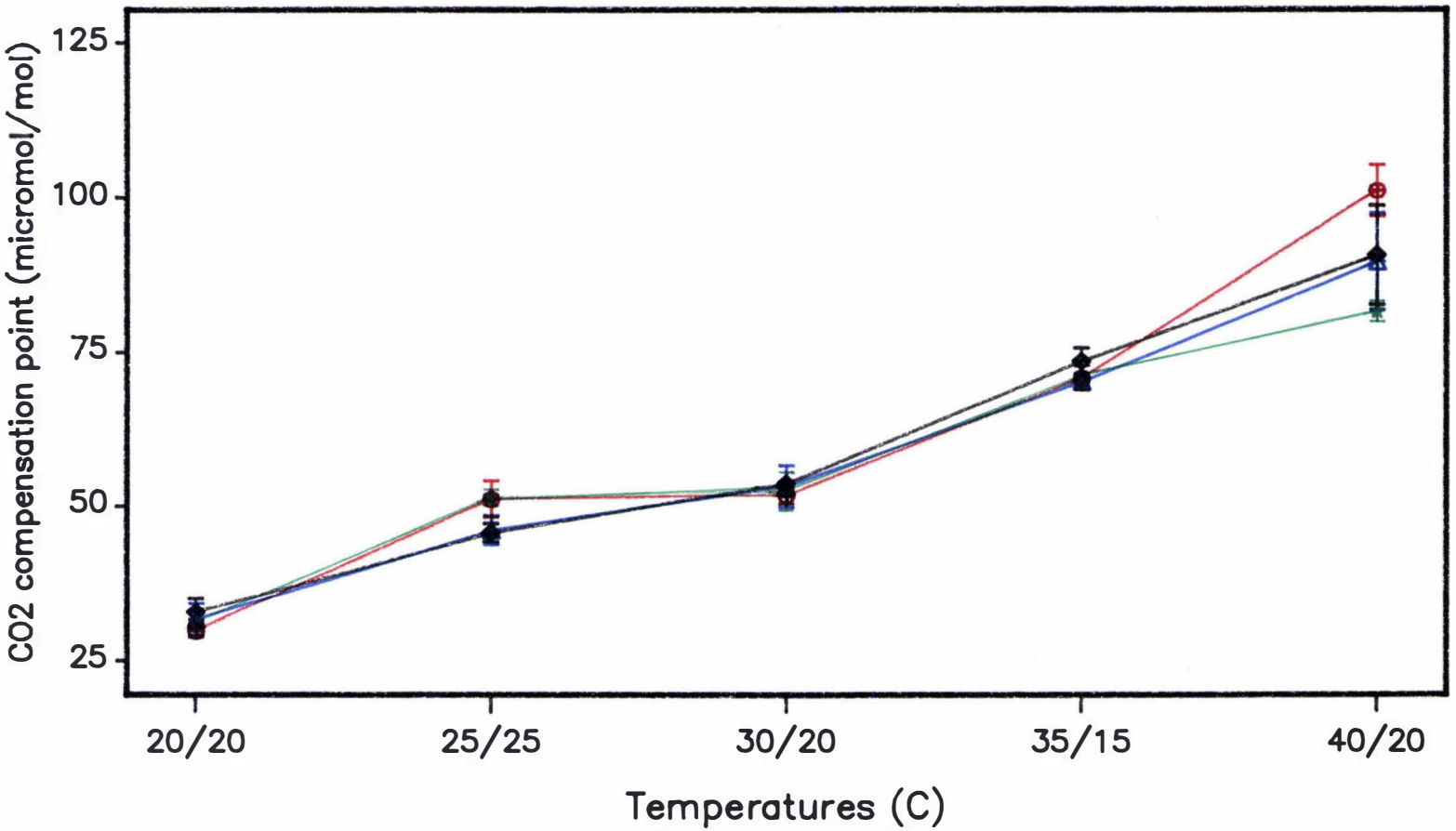


Figure 4.11 CO2 compensation point of asparagus fern at different growth temperatures (◇◇◇ UC157; ☆☆☆ Brocks; ⊕⊕⊕ Tainan 1; ΔΔΔ Larac). I = Stderr. of means.

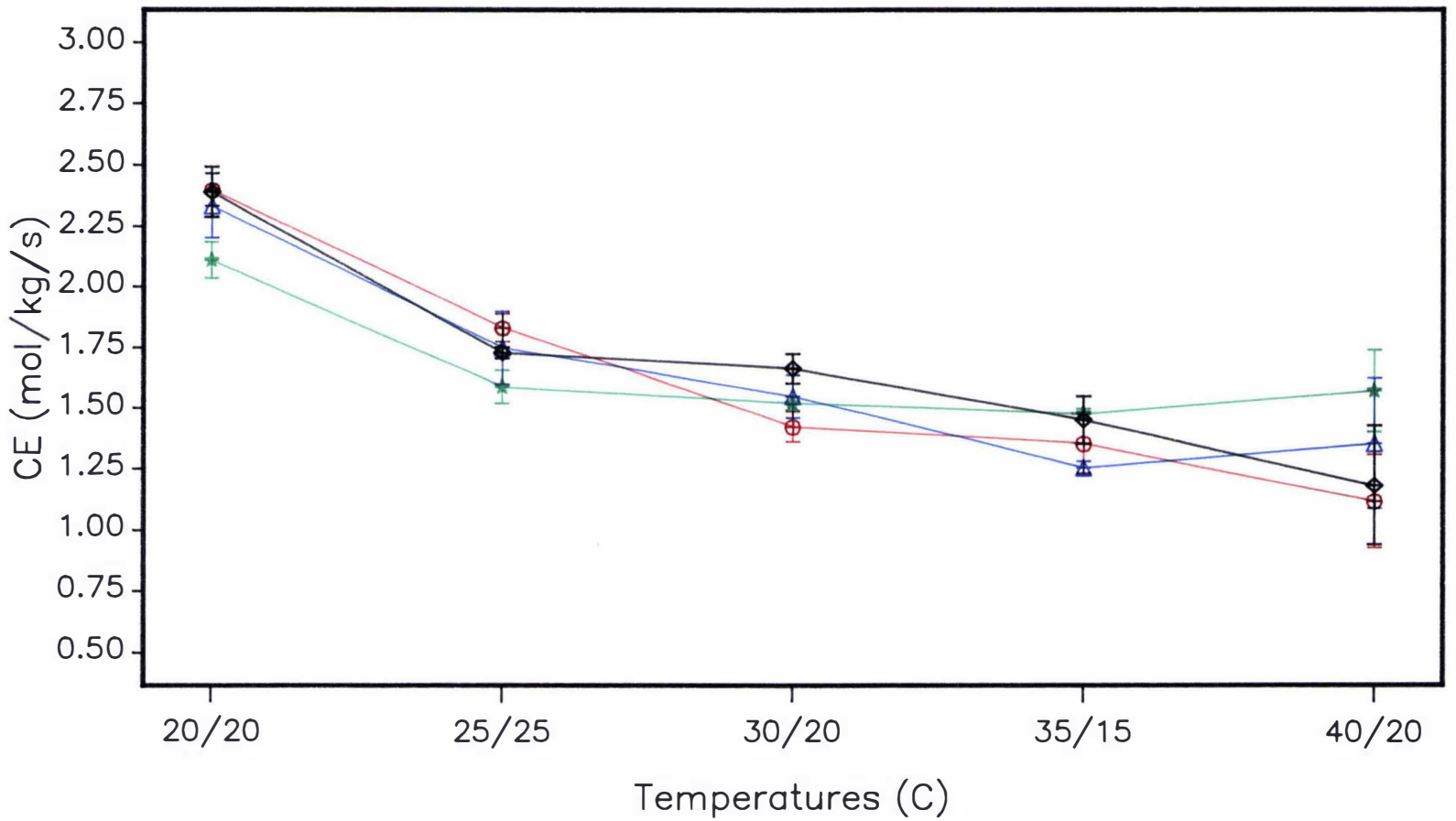


Figure 4.12 CE close to compensation point of asparagus ferns at different growth temperatures (◇ ◇ ◇ UC157; ☆ ☆ ☆ Brocks; ⊕ ⊕ ⊕ Tainan 1; △ △ △ Larac). I = Stderr of means.

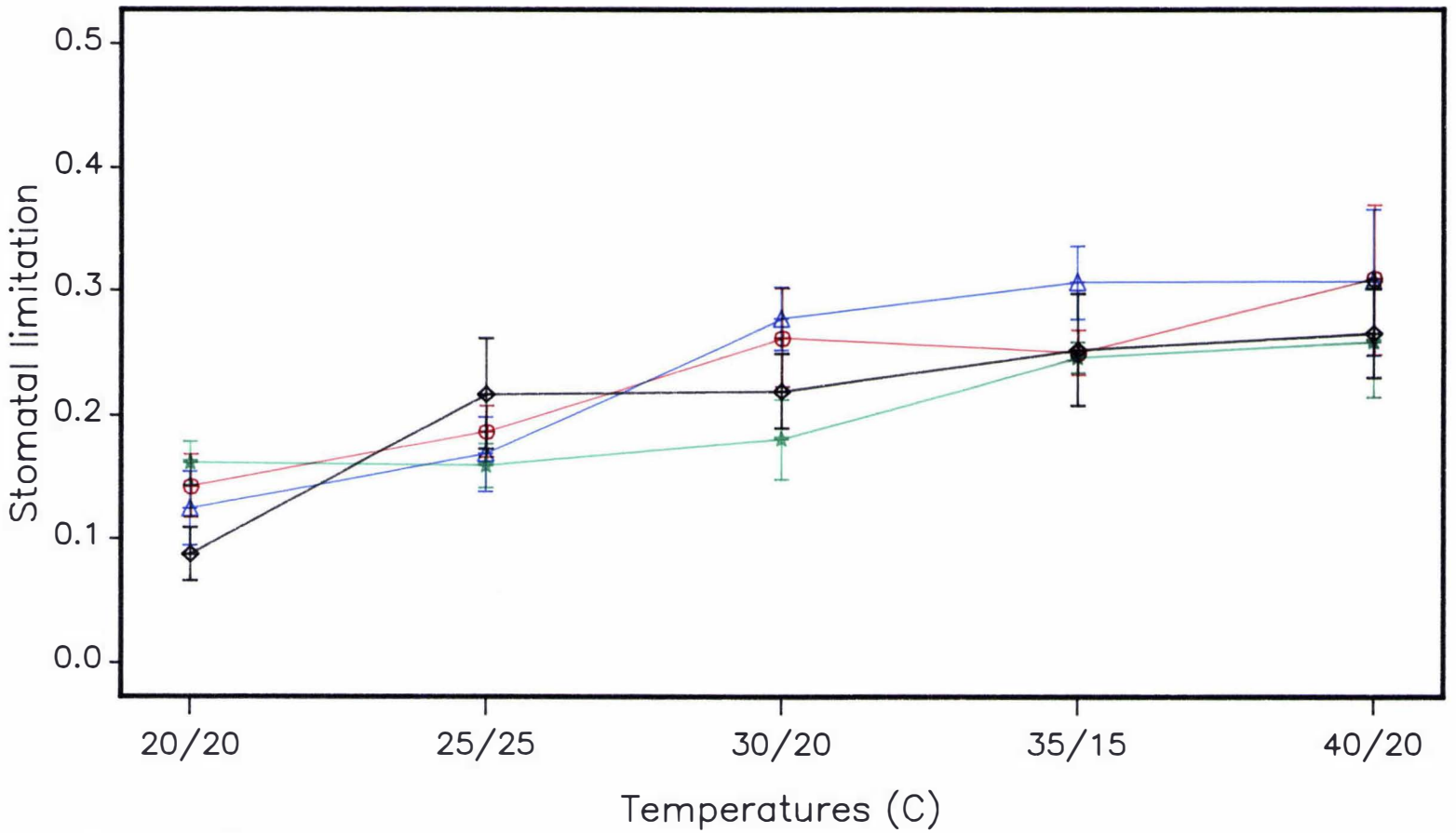


Figure 4.13 Stomatal limitation of asparagus fern at different growth temperatures (◇ ◇ ◇ UC157; ☆ ☆ ☆ Brocks; ⊕ ⊕ ⊕ Tainan 1; △ △ △ Larac).
I = Stderr of means.

4.5 DISCUSSION

4.5.1 Shoot and crown respiration

4.5.1.1 Introduction

Dark respiration is a key physiological process in plant growth and maintenance (Amthor, 1989). In asparagus information on dark respiration is scarce in the literature, but is of importance in relation to the capability of asparagus to adapt in wide range of environments, particularly temperature. It has been suggested that dark respiration consists of respiration for growth (growth respiration) and that associated with the maintenance of the plant (maintenance respiration) (Thornley, 1970). There has been a number of studies describing growth and maintenance and their response to the environment although the three method available to quantify the growth and maintenance respiration are still under debate (Amthor, 1989 and references cited therein). In the present experiment there was no attempt to separate the respiration into growth and maintenance respiration, but in the discussion, both will be considered.

4.5.1.2 Shoot dark respiration

An increase in shoot respiration of all cultivars in response to temperature has been observed in many species (Gerik and Eastin, 1985; Baker *et al.,* 1972). In the present study pooled analysis found that shoot respiration increased from 25 to 40^{0}C. Shoot respiration was related quadratically with temperature which is in agreement with Baker *et al.* (1972) using cotton. On the other hand, Gerik and Eastin (1985) found that of the sixty grain sorghums studied, twenty of them produced significant quadratic responses, while the rest responded linearly. However, the increase in shoot respiration was low as indicated by a low Q_{10}, e.g. between 20 and 40^{0}C the value was around 1.5 or even lower, which was below the value of sorghum and cotton of about 1.86 and 1.8, respectively (Gerik and Eastin, 1985; Baker *et al.,* 1972). Murtagh *et al.* (1987), however, found that the Q_{10} of shoot maintenance respiration of the Kikuyu plant (*Pennisetum clandestinum*), a C_4 plant, was 1.42.

The rate of shoot respiration for all the cultivars were similar to cotton (Hesketh *et al.,* 1971; Baker *et al.,* 1972), ie. about 6 to 17 μmol kg^{-1} s^{-1} within the temperature range from 20 to 40^{0}C, but lower compared to the shoot respiration of soyabean (Ryle *et al.,* 1978; Vessey and Layzell 1987), where, at 20^{0}C, it was 2 to 7 times higher. In sorghum, the shoot respiration was 3 to 5 times higher in the temperature range of 20 to 40^{0}C (Gerik and Eastin, 1985). It is also possible the low shoot respiration rate of asparagus in these experiments was due to a high proportion of senescing cladophylls. There have been a number of studies which found that dark respiration followed ontogenetic development (Baker *et al.,* 1972; Lin and Hung, 1983; Kozlowski, 1992; Hesketh *et al.*, 1971). During the early stages of leaf growth, the synthesis of chlorophyll, proteins, and structural compounds is high, resulting in high catabolic rates to support energy needs (Kozlowski, 1992). As the photosynthetic system matures, the requirement for respiratory energy decreases rapidly (Dickmann, 1971). Hughes (1992) also suggested that the respiratory requirements of asparagus seems to change during the year. The respiratory requirements were higher in the period of rapid fern growth, while Lin and Hung (1983) found that asparagus with the majority of young cladophylls had the highest respiration rate. In the present experiment, during shoot respiration measurement the plants were about 12 weeks old. During the one week of the acclimation period no additional shoots emerged, regardless of cultivar and temperature treatment. It is possible that the growth of the asparagus plants were restricted by the size of the container. The container may have restricted root growth was indicated by the twisted root system. This spiralling root could not grow further because all the container space had been occupied by the roots and as a result plant growth was restricted. If this is correct, then the shoot respiration rate would be low due to the low growth rate which would result in a low Q_{10} value. Under such circumstances shoot maintenance respiration would be the major contributor to total shoot respiration.

The shoot respiration rates of Brocks and Tainan 1 were less sensitive to temperature than that of UC157 and Larac, although analysis of variance for each temperature only detected differences at 35^{0}C where Larac had a significantly higher shoot respiration than Brocks and Tainan 1. If the major part of the respiration was for maintenance,

the higher rate of shoot respiration at high temperatures for Larac, was a disadvantage for this cultivar. The plant would lose substrate without any gain in growth. On the other hand, Brocks and Tainan 1 were more efficient at high temperature and therefore suggesting that these cultivars were more tolerant of high temperature growing conditions.

4.5.1.3 **Crown respiration**

Increasing temperatures from 20 to 40^{0}C produced a cubic response of crown respiration for all cultivars of asparagus (Table 4.4). Farrar (1988) observed that barley root respiration responded cubicly to temperature over the range 4 to 34^{0}C. Osman (1971) on the other hand found that root respiration of wheat increased linearly with temperatures from 10 to 30^{0}C. A similar linear trend was also observed by Nobel *et al.* (1991) for two cacti grown at temperatures from 15 to 40^{0}C. In respect to the asparagus plant, the overall increase in crown respiration from 20 to 35^{0}C (Table 4.4) suggests that crown respiration had been influenced by temperature.

Steep increases in root respiration from 30 to 35^{0}C was an indication that asparagus plants, regardless of cultivars, suffered from high temperatures as indicated by a decreased in RGR of both shoot and crown (Yen, 1993). A further 5^{0}C increase to 40^{0}C, however, only increased crown respiration slightly (Figure 4.3). It has been suggested that increasing growth temperatures to 40^{0}C can cause the respiration rate to decrease, especially when the plant was held in those conditions for long periods (Salisbury and Ross, 1990) due to tissue damage and denaturation of respiratory enzymes (Amthor, 1989; Salisbury and Ross, 1990). It is also possible that the relatively low respiration rate at high temperature was a mean of acclimation to the environment. Lange *et al.* (1974 and references cited therein) described that decreasing dark respiration was related to the acclimation to high temperature. At 40^{0}C, the crown still respired as high as at 35^{0}C (Table 4.4) indicating that crown respiration was still necessary to maintain the root functions and also suggests only very small proportion of respiratory enzymes has been denaturated.

There have been a number of studies confirming the suggestion that root respiration was dependent on the current substrate from the shoot (Osman, 1971; Hansen, 1977; Humphries, 1951; Neales and Davies, 1966; Hatrick and Bowling, 1973; Pearson, 1979; Ryle *et al.*, 1985). Results with asparagus, however, apparently shows no dependencies of crown respiration on photosynthesis because photosynthetic rate decreased with increasing temperature (Figure 4.6) while the reverse occurred for crown respiration. Foster *et al.* (1991) also found a similar relationship with *Ilex crenata*. Poorter *et al.* (1988) reported that the ontogenetic development of photosynthesis and root respiration of *Plantago major* grown at ambient CO_2 were not correlated. Other studies suggested that root respiration of Italian ryegrass was correlated with, but lagged behind, photosynthesis by the shoot (Hansen and Jensen, 1977). The need for ATP or the availability of ADP to oxidative phosphorylation was more important in determining root respiration rate (Hrubec *et al.*, 1985). Farrar (1981) suggested that variations in root respiration of barley was not mediated by assimilate supplies from the shoot. Root respiration of barley was suggested to be controlled by the turnover of ATP (Bingham and Farrar, 1988). It is not surprising, therefore, that there was lack correlation between photosynthesis and crown respiration in asparagus plant. Conflicting results in the literature may have been due to the failure to recognise the rapid shoot-dependent changes in root behaviour, the distinct effect of excision, and the extent of carbon fluxes in the root (Farrar, 1981).

The average Q_{10} of crown respiration for all cultivars of asparagus between 20 to 40^{0}C was around 1.3 much lower than that of 2 for a general rate as suggested by Amthor (1989) and Salisbury and Ross (1990). Other studies, however, found a low Q_{10} of root respiration of *Ficus indica* (1.43) between 25 and 40^{0}C (Nobel *et al.*, 1991); of *Ilex crenata* (about 1.35) between 28 and 40^{0}C (Foster *et al.*, 1991), and of barley, fell from 2.8 to 1.2, over the range 4 to 34^{0}C (Farrar, 1988). The authors did not explain why these Q_{10} values were so low. Low Q_{10} values for crown respiration between 20 to 40^{0}C suggests that crown respiration, increased with temperature, but the response was small. The low Q_{10} was possibly due to limited O_2 availability to the confined, compact root system.

Kozlowski (1992) suggested that respiration of root systems was variable and often was very high. Data from the crown respiration rate of asparagus ranging from 20 to 40^{0}C was similar to data obtained for *Ilex crenata* ranging from 3.5 to 7 μmol kg^{-1} s^{-1}. Compared to other species, however, the crown respiration of asparagus was considerably lower. For example, root respiration of maize at 25^{0}C was 16 μmol kg^{-1} s^{-1} (Heichel, 1971), of soybean at 23 and 30^{0}C were 11 and 12.5 μmol kg^{-1} s^{-1}, respectively (Kishitani and Shibles, 1986). The respiration rate of whole root system of pines were in the range 2.4 to 22.8 μmol kg^{-1} s^{-1} (Kozlowski, 1992). There are number possible explanations why crown respiration of asparagus in this experiment were lower than other species.

1. Root respiration is strongly influenced by ontogenetic development of the plant (Amthor, 1989). For example, root respiration rates of soybean reached a maximum near complete vegetative development and then declined (Kishitani and Shibles, 1986). In this present study, asparagus plants apparently had attained full size with respect to the container as has been discussed previously. Therefore, at the time of measurement, the crown possibly respired at low rate due to very little growth as growth respiration rate is also a function of growth rate (Amthor, 1989), or possibly due to the decrease in the content and activity of respiratory enzymes, associated with the increasing proportion of mature growing tissue and with an increase in the proportion of cellulose (Osman, 1971). Growth respiration, however, possibly contributed a small proportion to the total crown respiration as Nobel *et al.* (1991) predicted that growth respiration of cactus roots only contributes to only a small proportion of total respiration. Szaniawski and Kielkiewicz (1982) also reported root maintenance respiration increased with increasing temperature in sunflower, while root growth respiration was not affected by root temperature. If this is so, then maintenance respiration would account for a large proportion of total crown respiration of asparagus. Penning de Vries (1975) suggested that increasing temperature raised the cost of maintenance respiration due to the stimulation of protein turnover and of active ion fluxes.

2. The majority of the crown is storage root and the proportion of fine roots is low. It would be expected that the respiration rate of a storage organ would be low. For example it was found that at 20^{0}C respiration rate of small potato tuber (1-2 cm) was

4.5 μmol kg^{-1} s^{-1} (Winkler, 1971 as cited by Amthor, 1989). Large , mature potato tubers had very low respiration rate of 0.54 μmol kg^{-1} s^{-1}. As a perennial plant which depends very much on the carbohydrate reserve for next season growth, asparagus should have an inherent capability not to waste carbohydrate reserve.

3. Because of the very compact condition of the root system in the small container, the crown respiration may be limited by low O_2 availability. In addition, Lemon and Wiegand (1962) also suggested that O_2 diffusion to the root cells becomes more limiting to the respiration rate with increasing temperature.

4. Most root respiration occurs in the fine roots as Mamaev (1984) found that the fine roots accounted for more than 95% of the root respiration of *Pinus sylvestris* and *Betula* stands. Asparagus roots have only a small proportion of fine root, the largest proportion being storage root. Therefore, low crown respiration could be caused by low proportion of fine root at all temperature growing conditions.

Over all temperatures Larac had a lower crown respiration compared to the other cultivars as indicated by the pooled analysis. This perhaps means that Larac had a higher respiration efficiency compared to the other cultivars, particularly at low temperatures. Higher crown respiration efficiency at low temperature for Larac was not surprising in view of its origin in cool temperate region.

Shoot respiration of asparagus plants were always higher than crown respiration regardless of cultivars and temperatures. This was in agreement with finding by Heichel (1971) on maize, Poorter *et al.* (1988) on *Plantago major*, Kishitani and Shibles (1986) on soybean, and Hansen and Jensen (1977) on *Lolium multiflorum*. On the other hand, Poorter and Pothmann (1992) reported that root respiration (mg CO_2/kg/s) of 2 cultivar of grasses were higher than shoot respiration. As discussed previously the low crown respiration may be an important mechanism by which asparagus maintains reserve carbohydrate for next seasons growth.

4.5.1.4 **Photorespiration and dark respiration of mature fern**

4.5.1.4.1 **Photorespiration as measured by PIB method**

It has been well established that C_3 plants are photosynthetically less efficient at high temperatures compared to C_4 plants (Edwards and Walker, 1983; Lawlor, 1989; Canvin, 1990), and have higher photorespiration. As a C_3 plant, asparagus is expected to possess a significant photorespiration rate. As photorespiration will reduce photosynthesis, it may be desirable to reduce photorespiration rate in order to increase photosynthetic efficiency. Information of the magnitude of photorespiration of asparagus fern would mean that discrimination of cultivars for their potential productivity based on this factor could be be assessed. However, because the measurement of photorespiration used a PIB method, the steady state of photorespiration can not be obtained (see section 1.6.4.3.2).

This study showed that photorespiration of mature fern, followed a cubic response to increases in temperature, regardless of cultivar (Figure 4.4). Photorespiration increased rapidly from 20°C up to 35°C and than decreased at 40°C. A study on sunflower leaves using the same method found that the highest photorespiration was at 30°C (Hew *et al.* 1969). Peterson (1983) however found that tobacco leaves responded linearly to temperature up to 40°C, while Perry *et al.* (1983) observed that photorespiration rate of cotton increased sharply from 20 to 30°C and then levelled off at 40°C. The decrease in photorespiration rate at 40°C in asparagus was a clear indication that heat stress had occurred.

Brocks had less photorespiration at high temperatures than the other cultivars though not significantly so, demonstrating that this cultivar possibly had better productivity at high temperature. Low temperatures, were unfavourable for Brocks where the trend of photorespiration was high compared to the other cultivars but only was significant different to Tainan 1. There is not any clear answer as to why Brocks had a higher photorespiration at low temperatures. Other cultivars, on the other hand, had similar levels of photorespiration regardless of temperature.

4.5.1.4.2 **Dark respiration**

Dark respiration of mature fern increased linearly with temperature (Figure 4.5). Earlier studies have reported conflicting results regrading the relationship between dark respiration and temperature. For example, wheat leaves grown at temperature ranging from 10 to 40^{0}C showed a similar response to the present study (Azcon-Bieto and Osmond, 1983). However another study with wheat showed a cubic response to temperature, ie. dark respiration increased curvilinear from 10^{0}C to about 30^{0}C and then decreased (Penning de Vries *et al.,* 1979). Data of perennial ryegrass also suggested that a straight line was the best description for the relationship (Robson, 1981). The respiration of sunflower leaves was reported to increase quadratically with temperature from 15 to 40^{0}C (Hew *et al.,* 1969), while Hills (1986) found that asparagus cell respiration increased exponentially with temperature, which was in agreement with the response of leaf respiration of bean, cotton, and sorghum to at least 40^{0}C (Brown and Thomas, 1980). From these reports it seems that the response of leaf dark respiration to increasing temperature was dependent on the species or even the genotype and possibly the method of measurement employed.

The average Q_{10} of dark respiration of mature asparagus fern between 20 and 40^{0}C were 2.1, 1.8, 2.0 and 1.95 for UC157, Brocks, Tainan 1 and Larac, respectively. Hill (1986) also reported the Q_{10} of asparagus cells was 2 over the temperature range of 10-40^{0}C. In general the Q_{10} of most species and plant parts, is between 2 to 2.5 at temperature 5 to 25^{0}C and then decreases with further temperature increase (Salisbury and Ross, 1990). The calculation of Q_{10} of mature asparagus fern between 20 to 30^{0}C and 30 to 40^{0}C showed that the value decreased from 2.63 to 1.68, 2.04 to 1.59, 2.33 to 1.71 and 2.27 to 1.68 for UC157, Brocks, Tainan 1 and Larac, respectively. Denaturation of enzymes involved in the respiratory processes probably did not occur as dark respiration appears to be the most heat-stable of life functions (Alexandrov *et al.,* 1970; Larcher, 1973), but denaturation of photorespiratory enzymes was likely.

The Q_{10} of Brocks was apparently lower compared to the other cultivars. Rainey *et al.* (1987) reported that the Q_{10} differences between genotype of perennial ryegrass

was due to the differences in the amount of two important enzymes (6-phospho-gluconate dehydrogenase and phosphoglucomutase), which regulate the glycolysis and oxidative pentose phosphate pathway. It is unclear, however, how a high or lower Q_{10} might affect productivity (Amthor, 1989). The low Q_{10} of Brocks was apparently caused by significantly higher fern respiration at 20°C than UC157 and Tainan 1, followed by lower rate at high temperatures (Tables 4.6 and Figure 4.5). The higher respiration of Brocks at low temperature can not be primarily related to growth requirements since mature fern were used. Ho and Thornley (1978) suggested that excess respiration may be used for synthesis of compounds (e.g. amino acids) for growth in other parts of the plant and for energy transport of assimilate. It is also possible that carbohydrate was wastefully oxidized in the absence of a major sink, as removing sink demand (reduce sugar export rate) can cause an accumulation of carbohydrate in the fern and raise the respiration rate (Avery *et al.,* 1979; Ho, 1979).

The proportion of dark respiration relative to photorespiration gradually increased with temperature and reached the highest value at 40°C. Hew *et al.* (1969) reported that the proportion in sunflower was constant up to about 30°C then increased at 40°C. The rapid increase of the proportion at 40°C was related to the fall in photorespiration rate while dark respiration still increased (Figures 4.4 and 4.5). It has been suggested that dark respiration is considerably more tolerant of high temperatures than photosynthesis in the same plant (Bjorkman, 1975). As photorespiratory reactions also depend on photosynthetic reactions (e.g. rubisco activity), photorespiration is also less tolerant of high temperature than dark respiration. Consequently, for mature asparagus fern, at 40°C dark respiration increased, while photorespiration decreased.

4.5.1.5 **Mature fern photosynthesis**

Asparagus fern photosynthesis of all cultivars decreased cubicly over increasing temperatures (Figure 4.6). The highest photosynthesis was achieved at 20°C (Table 4.7). This performance was somewhat different to many other C_3 species which have an optimum temperature for photosynthesis around 25°C (Edwards and Walker, 1983; Lawlor, 1987). The steep decrease in photosynthesis of mature asparagus fern in this

study, however, was comparable with a recent experiment conducted by Inagaki *et al.* (1989) who suggested that the optimum temperature for photosynthesis of asparagus fern was 15^{0}C to 20^{0}C. At 30^{0}C Inagaki *et al.* (1989) found that photosynthesis was about 55 % less than optimum. Sawada *et al.* (1962) and Lin (1983) also reported that the optimum temperature for photosynthesis of asparagus was close to 20^{0}C. Perry *et al.* (1983) found that cotton leaf net photosynthesis declined almost linearly as temperature increased from 22 to 40^{0}C. The low optimum temperature for asparagus matches the average natural growth temperature in New Zealand which lies somewhat between 15 to 20^{0}C. The most active growing period for asparagus in New Zealand is from October to January (discussed in Chapter 2) and during this period the range of temperature is about 15 to 20^{0}C. It was surprising that from Yen's (1993) study the maximum increase in total plant dry weight was predicted to occur at a constant temperature of 27 ^{0}C. The possible reason for this contradiction was that the photosynthetic measurement were carried out on 3 month old plants compared to the 4-6 week old plant of Yen (1993). This study showed clearly that photosynthesis of asparagus fern varied during the ontogenetic development (Chapter 3). It also has been well known that there is a lack of correlation between single leaf photosynthesis and growth and yield (Bhagsari and Ashley, 1990; Ottosen, 1989). The short period time employed for taking measurements under optimum conditions might cause this lack of correlation (Zelitch, 1982; Bunce, 1986).

Apparently asparagus cell photosynthesis responds differently to temperature compared to mature asparagus fern. Hills (1986) observed that at saturating light intensity, photosynthesis of asparagus cells increased with increasing temperature from 10^{0}C up to about 35^{0}C and then decreased. Similar results were also was found by Colman *et al* (1979). The differences between fern photosynthesis and cell photosynthesis has been well known (Cataldo and Berlyn, 1974; Hills, 1986). During the isolation process the plasmadesmatal connections between cells are broken (Hills, 1986) and possibly cause the large differences in carbon partitioning in the isolated cells and intact tissue (Cataldo and Berlyn, 1974; Herold, 1980; Hills, 1986). Isolated cell photosynthesis

depends on the pH of the solution and the bicarbonate concentration (Colman *et al.*, 1979). These various limitations could explain why the differences between fern photosynthesis and isolated cell photosynthesis occurred.

This study revealed that photosynthesis undoubtedly was reduced by photorespiration at all temperature treatments. This was shown by the reverse relationship between photorespiration and photosynthesis. By comparing Figures 4.4 and 4.6 it was clear that the decrease in photosynthesis was associated with an increase in photorespiration up to 35^{0}C. The role of photorespiration lessened as temperature increased to 40^{0}C and factors other than photorespiration became more important. Possible factors were firstly, that high temperature caused a reversible heat depression by inducing 'down regulation' of rubisco (Kobza and Edwards, 1987). Secondly, high temperature could reduce the rubisco activation (Weis and Berry, 1988). They reported that at 38^{0}C there was about 60% activation of rubisco in cotton leaves, compared to its activation at 25^{0}C . Thirdly, high temperature reduces the RuBP regeneration due to slower production of ATP and NADPH (Farquhar and Sharkey, 1982; Salisbury and Ross, 1990). Fourthly, high temperature may have caused damage to photosystem II and therefore decreased the reducing energy supply within the leaf and affected enzyme reactions which were regulated by the light reaction (Weis and Berry, 1988; Al-Khatib and Paulsen, 1989).

The fact that the photosynthetic rate of Brocks was inferior compared to other cultivars at low day temperatures, e.g. from 20 to 25^{0}C, but superior at high temperatures, was an indication that Brocks is not a suitable cultivar to establish in low temperature regions, but is more suitable for higher temperature climates. In contrast, Larac apparently has an opposite optimum temperature requirement for growth. At high temperatures (35 to 40^{0}C) Larac had the lowest photosynthesis though only significantly different to Brocks. UC157 and Tainan 1 apparently have relatively wide temperature adaptability in terms of photosynthesis.

4.5.1.6 AC_i curve

4.5.1.6.1 AC_i curves of mature fern with increasing temperatures

The generation of AC_i curves using mature asparagus fern produced some important information relating to the response of photosynthesis to increasing temperature. These parameter were valuable because they provided an explanation of photosynthetic functioning of asparagus fern at different temperatures. In general the model used fitted well to the AC_i curves of asparagus fern, particularly at temperatures lower than 40/20^{0}C (Figures 4.7 to 4.10). At this temperature the combination of high temperature and humidity caused the AC_i measurement to take about 60 minutes and it became difficult to keep the temperature and humidity constant thus causing high variation in the AC_i data.

The results show that increasing temperatures caused a decrease in the initial slope of the AC_i curves, regardless of cultivars and indicated that there was a shift in CO_2 compensation point toward higher values with increasing temperature (Figures 4.7 to 4.10). All the cultivars responded positively with increasing internal CO_2 concentration and there were apparently differences ($p=0.054$ and 0.06) in the carboxylation efficiency between cultivars as will be discussed further in section 4.5.1.6.3.

4.5.1.6.2 CO_2 compensation point (Γ)

For given conditions Γ is characteristic within and between species (Krenzer *et al.*, 1975). Therefore, it is used widely as a rapid method for classifying the CO_2 fixation type. It has been established that plants with high Γ (about 40 µmol mol^{-1} $C0_2$ or higher at 25^{0}C) have a C_3 cycle, while a low Γ (about 5 µmol mol^{-1} $C0_2$ over wide range of temperature) is typical of plants having a C_4 cycle (Edwards and Walker, 1983; Lawlor, 1989; Salisbury and Ross, 1990). The present investigation found that at 25/25^{0}C the Γ ranged from 45 to 51 µmol mol^{-1}, highlighting that asparagus is a C_3 plant.

In the present study the Γ of mature fern increased significantly with temperature (Table 4.8). The trend was cubic (Figure 4.11). This was in agreement with the studies carried out by Bykov *et al.* (1981), Jordan and Ogren (1984) and Nespoulous *et al.* (1989) and also with the model proposed by Farquhar *et al.* (1980).

Canvin (1990) indicated that Γ is closely linked with photorespiratory activity in C_3 plants in which an increasing photorespiration rate has always been associated with an increase in Γ. This study was also in agreement with the previous work (Ticha Catsky, 1981; Canvin, 1990) in that Γ increased in parallel with the increase of photorespiration from 20/20 up to 35/15^{0}C. At 40/20^{0}C, however, the decrease in photorespiration was not followed by a decrease in Γ indicating that there was other sources CO_2 evolution in the light. The only other possible source of CO_2 during the day is dark respiration. It has been suggested that dark respiration exists during the day (Graham, 1980; Lambers, 1990; Gardestrom and Edwards, 1985). Azcon-Bieto and Osmond (1983) reported that the variation in Γ during the day was related to dark respiration in addition to photorespiration, respiration which was predicted to contribute about 25% of the CO_2 efflux measured at Γ. This suggestion was confirmed by reports that adding sugars caused an increase in Γ and respiration (Smith *et al.,* 1976; Tetley and Thimann, 1974).

Brocks tended to have a lower Γ at 40/20^{0}C possibly due to lower photorespiration (Table 4.5). Lower photorespiration is an advantage for Brocks in terms of photosynthetic adaptation at high temperature.

4.5.1.6.3 **Carboxylation efficiency close to the compensation point (CE)**

In terms of photosynthesis, the change in carboxylation efficiency of leaves is an indication that the leaves have been influenced by environmental treatments. From the demand function of the AC_i curve, CE is obtained from the initial slope of the curve (Ku and Edwards, 1977; Farquhar *et al.,* 1980; Edwards and Walker, 1983; Lawlor, 1987).

By analysing the AC_i curve Edwards and Walker (1983) suggested that **CE = Vmax/Km(CO2)**, where Vmax is the maximum velocity of carboxylase and $Km_{(CO2)}$ is Michaelis Constant of the carboxylase for CO_2, ie. the amount of substrate (CO_2) at which the reaction is half of maximum. These two kinetic parameter are dependent on temperature, but in particular the $Km_{(CO2)}$ is strongly affected by temperature (Laing *et al.* 1974; Badger and Collatz, 1977).

Statistical analysis showed that there was a strong effect of temperature on CE. The carboxylation efficiency decreased significantly with increasing temperature, regardless of cultivar. A sharp decrease occurred from 20/20 to 25/25^{0}C. From this data it is likely that the rapid decrease in photosynthesis from 20/20 to 25/25^{0}C was due to mainly competitive inhibition by O_2 since it has been found that the $Km_{(CO2)}$ increases more rapidly with temperature than does the $Km_{(O2)}$ (Laing *et al.,* 1974; Badger and Collatz, 1977).

Ku and Edwards (1977) found that at 25 to 35^{0}C and under atmospheric conditions about 80% inhibition of photosynthesis by O_2 was caused by direct inhibition. Farquhar and Sharkey (1982) suggested that the criteria to establish which resistance, stomata or mesophyll, is dominant in controlling photosynthesis could be evaluated by changes in photosynthesis relative to internal CO_2 (C_i), if photosynthesis and C_i change in the same direction then stomata are the dominant limitation and *vice versa.* From Figures 4.7 to 4.10 it is clear that from temperatures of 20/20 to 25/25^{0}C the decrease in photosynthesis was not followed by decreasing C_i indicating that mesophyll resistance was more dominant, since mesophyll resistance can be considered as the reciprocal of CE (Farquhar and Sharkey, 1982).

Although analysis of variance on each particular temperature did not find any difference between cultivars (Tables 4.9), there was a trend that Brocks had a lower CE at 20/20 and 25/25^{0}C. This was consistent with the photosynthesis data (Table 5.7), which found that Brocks had a significantly lower value than Tainan 1 and Larac at 20/20^{0}C. Increasing temperature apparently only slightly affected the CE of Brocks, while for the other cultivars the CE decreased with temperature.

4.5.1.6.4 **Stomatal limitation (lg)**

At temperature of 20/20 to 25/25^{0}C lg were relatively constant, stomatal limitation accounting for 13% to 18% decrease in photosynthesis (Table 4.10 and Figure 4.13). The steady value of lg at low temperature is not surprising as some studies indicated that stomata open maximally at intermediate temperatures (Hofstra and Hesketh, 1969; Losch, 1977; Neilson and Jarvis, 1975; Raschke, 1970; Sharpe, 1973; Whiteman and Koller, 1967). This result confirms that the decrease in photosynthesis at 20//20 to 25/25^{0}C was primarily due to the decrease in CE. Higher temperature caused lg increased up to 30/20^{0}C. The increase lg (reduced stomatal aperture) was quite possibly due to the increase vapour pressure deficit (vpd) (Hall *et al.*, 1975; Hall and Kaufmann, 1975; Losch, 1977). Table 5.1 shows that vpd during day at 30/20 to 40/20^{0}C were 4 mb higher than at 20/20 and 25/25^{0}C. Thus, stomatal limitation became more important at higher temperature and the data shows that at 40/20^{0}C the overall lg was about 29%, more than double than at 20/20^{0}C. The steep decrease in photosynthesis at the highest temperature treatment clearly due to the combination of decreasing CE and increasing lg.

Although analysis of variance on lg did not find any significant differences between cultivars at all temperatures the trend was that UC157 probably had a lower stomatal limitation at 20/20^{0}C compared to Brocks and Tainan 1. At 30/20^{0}C Brocks had a lower lg than Tainan 1 and Larac (Table 4.10) and at 35/15^{0}C the trend was that UC157, Brocks and Tainan 1 had a lower stomatal limitation than Larac. At 40/20^{0}C UC157 and Brocks tended to have a lower stomatal limitation than Tainan 1 and Larac. This is possibly one explanation of why UC157 and Brocks are more acclimated to high temperature conditions.

4.6 **SUMMARY**

From this experiment it is concluded that :

1. Shoot dark respiration increased with temperature. The response was quadratic. The Q_{10} was of about 1.5. There was differences between cultivar at 35/15^{0}C where Larac

had higher shoot respiration rate than Brocks and Tainan 1.

2. Crown respiration increased from 20/20 to 35/15^{0}C then levelled off at 40/20^{0}C, and the response to temperature was qubic. Crown respiration was low due to low O_2 availability and also crown consists of storage organ.

3. Phorespiration rate, measured by using PIB method, increased from 20/20 to 35/15^{0}C and then decreased at 40/20^{0}C, and the response to temperature was cubic. At low temperature Brocks had higher photorespiration rate than Tainan 1, but with increasing temperature Brocks tended to have lower photorespiration rate than the other cultivars.

4. Dark respiration increased with temperature and the response to temperature was linear. Over all Tainan 1 had lower dark respiration rate compared to UC157. The Q_{10} for all cultivars were about 2.

5. Photosynthesis decreased with increasing temperature and the response to temperature was cubic. The maximum photosynthesis was obtained at 20/20^{0}C regardless of cultivar. Brocks had a lower photosynthetic rate at 20/20^{0}C compared to Tainan 1 and Larac and Tainan 1 was greater than UC157, but Brocks tended to have higher photosynthetic rate at high temperature compared to Tainan 1 and Larac.

6. The present study suggests that CE is a major factor in the reduction of photosynthesis in the 20 to 25^{0}C temperature range. Increasing temperature caused an increase in stomatal limitation and this became an important factor at high temperature.

CHAPTER FIVE
THE EFFECT OF TEMPERATURE GROWING CONDITION ON THE LIGHT RESPONSE CURVE OF MATURE FERN

5.1 INTRODUCTION

In chapter 3 it was found that optimum photosynthesis was achieved with intermediate aged fern. In addition there was differences between cultivars in mature fern photosynthesis at high temperatures. Brocks and probably UC157 were acclimatized better to high temperatures compared to Tainan 1 and Larac based on this criteria. It was considered relevant to further study the differences between cultivars in terms of photosynthesis over a range of temperatures. Therefore the following experiment was carried out to examine the light response curves of photosynthesis for the same cultivars over a broader range of temperatures.

The rationale for this experiment was as follows. Plants have been classified as sun and shade plants, but many species have both sun and shade leaves and have the ability to adapt to a particular light environment. Photosynthetic rates of leaves are therefore influenced by the light intensity in which the plants develops (Fitter and Hay, 1987). In the field under a well managed horticultural system, light intensity is perhaps the most important factor determining the photosynthetic rate. A light response curve describes this relationship between light intensity and photosynthesis under prevailing environmental conditions of temperature, CO_2, water and nutrients. The temperature response of photosynthesis by higher plants has been reported for a wide range of species (reviewed by Berry and Bjorkman, 1980; Berry and Raison, 1981). Most studies, however, have emphasized the rate of photosynthesis at light saturation. Since leaves in their natural environment always encounter a continually changing light environment, it is important to contemplate the interaction of temperature responses with light. If light response curves are generated over a range of temperatures then the photosynthetic rates achieved will relate to the potential of the plant to produce dry matter under those temperature conditions. Light response curve also allow a range of characteristics of the photosynthetic system to be

evaluated such as the light compensation point, quantum yield and maximum rates of photosynthesis.

Thus light response curves describe the potential of the photosynthetic system under the conditions in which they are determined, as well as allowing further description of the photosynthetic system. In term of this research programme it would allow the performance of the photosynthetic system of young asparagus plants to be evaluated with a number of cultivars over a range of temperatures.

In this experiment the light response curves for 4 cultivars of asparagus at a range of moderate to high temperatures were determined with 6 week old seedlings.

5.2 MATERIALS AND METHODS

5.2.1 Treatment

5.2.1.1 Temperature

The growing temperature conditions applied in this experiments were alternating 12 hours day and night temperatures, i.e., 20/20^{0}C, 25/25^{0}C, 30/20^{0}C, 35/15^{0}C and 40/20^{0}C. The experiment was carried out at the climate laboratory CRI (Crown Research Institute) in Palmerston North concurrently with a growth analysis experiment (Yen, 1993). The conditions during the experiment are shown in Table 5.1.

5.2.1.2 Cultivars

The four cultivars used in this experiment were UC157, Brocks, Tainan 1 and Larac (section 3.2.1.2).

5.2.2 Propagation and growing conditions

The propagation method was the same as described in section 3.2.2. The plants were fertigated via an automated microtube system with a standard mineral nutrient solution

(Hoagland solution) (Brooking, 1976) as follows :

Treatment 1 : 3 x 1.5 min pot^{-1} day^{-1} throughout the experiment;
Treatment 2 : 3 x 1.5 min pot^{-1} day^{-1} throughout the experiment;
Treatment 3 : 3 x 1.5 min pot^{-1} day^{-1} throughout the experiment;
Treatment 4 : 2 x 1.5 min pot^{-1} day^{-1} for the first six weeks, followed by an increase to four applications for the final four weeks;
Treatment 5 : 3 x 1.5 min pot^{-1} day^{-1} for the first four weeks and after that 4 x 1.5 min pot^{-1} day^{-1} also a 1 x 1.5 min application of water pot^{-1} day^{-1} till the end of the experiment.

The lighting system used in the growth room has been described (section 3.2.2). The photosynthetically active radiation (PAR), Wm^{-2}, in the 400-700 nm wavelength range, measured before and after the experiment ranged from 151-144, 151-140, 149-148, 150-147, and 149-152 for treatments no 1, 2, 3, 4 and 5, respectively. The photosynthetic photon flux density (PPFD), $\mu mol\ m^{-2}\ s^{-1}$, ranged from 713-690, 714-669, 732-714, 720-710, and 732-736 for treatments no 1, 2, 3, 4 and 5, respectively.

The day/night and night/day temperature changes took 120 min and the light period started and finished halfway through the change overs.

5.2.3 **Experimental design**

The plants were arranged in Randomized Complete Block (RCB). Every week the trolleys holding the plants were also rotated to reduce the effect of uneven light, water and nutrient distribution. For each cultivar four replications with one plant per replicate were used and occupied two trolleys in the growth room.

Table 5.1. Environmental conditions in the growth room

Treatment	Daylength (12 hrs)	Temperature ± 0.5°C	RH ± 5%	V P D (mb)
1	day	20	74	6
	night	20	74	6
2	day	25	81	6
	night	25	81	6
3	day	30	76	10
	night	20	74	6
4	day	35	82	10
	night	15	64	6
5	day	40	86	10
	night	20	74	6

5.2.4 **Measurement of photosynthesis**

5.2.4.1 **Technique of measurement**

Mature asparagus fern was used. The instrument and procedures employed in this experiment were described in section 3.2.4. The CER measurements were taken at six weeks after emergence.

The light intensity was varied from about 15 to about 900 μmol m^{-2} s^{-1}, either by adjusting the distance between the light source and the plant or by using neutral density shadecloth. With any one fern, measurement was first made at the highest light intensity followed sequentially by lower light intensity. At least a 15 minute

acclimation period was allowed between measurement at different environmental conditions (light intensity).

5.2.4.2 **Model consideration**

Many models have been suggested to describe the relationship between photosynthesis and light intensity. The first model was introduced by Rabinowitch (1951) using a rectangular hyperbola. Causton (1983) described the rectangular hyperbola by

$$P = \frac{1}{(a + b/I)} \qquad (5.1)$$

where
P is photosynthetic rate;
I is light intensity;
a is CO_2 resistance (ra+rs+rm+rc);
b is photosynthesis at light saturation.

This model is another version of the Michael-Menten function with the two constants in a different form. Littleton, (1971) (cited by Biscoe *et al.,* 1975), however, found that rectangular hyperbola tended to overestimate the maximum photosynthesis of barley leaves in bright light.

Peat (1970) found that an asymptotic equation fitted better than a rectangular hyperbola (had a smaller sum of mean square deviations). His equation can be written as:

$$P = a + b\,\rho^{I} \qquad (5.2)$$

where P is photosynthetic rate;
I is light intensity;
a, b and ρ are constants with $0<\rho<1$ and $b>a$.

He admitted, however, that the model had no theoretical basis, and for analytical purposes it had the serious defect that the constant ρ could not be defined dimensionally (Biscoe *et al.,* 1975).

Jassby and Platt (1976) examined 8 different models, including a rectangular hyperbola. They concluded that rectangular hyperbola was the worst model in terms of the mean square deviation. They suggested that a nonrectangular hyperbola was the most suitable model to describe the relationships between photosynthetic rate and light intensity. The model is :

$$\mathbf{P = Pmax.Tanh(X)} \qquad \mathbf{(5.3)}$$

and $\mathbf{X = (\alpha.I/Pmax)}$

where P is photosynthetic rate;
I is light intensity;
Pmax is light saturated photosynthetic rate;
α is the initial slope or estimate of quantum yield.

This model is biologically meaningful and also gives the best fit, especially in term of estimating Pmax and α. In this model Jassby and Platt (1976) assumed that respiration was independent of light intensity.

In the present experiment model no. 5.3 was used to describe the relationship between photosynthesis and light intensity.

5.2.5 **Data analyses**

Nonlinear rectangular hyperbola relationships between photosynthesis and light intensity (equation 5.3) were obtained by using the Marquardt compromise method of successive approximations (Proc NLIN, SAS). The light compensation point was predicted by extrapolation of the light response curve of raw data at photosynthesis

equal to zero. The treatment effect on various calculated values (Pmax, α and light compensation point) were determined based on the light response curve of individual fern and then analyzed using the pooled analysis method (Proc GLM of SAS) as described in Chapter 3. Analysis of covariance (within Proc GLM of SAS) was also carried out at temperature 35/15^{0}C to examine the photosynthetic differences between cultivars. Light intensity was considered as a covariate and the photosynthesis data were taken at light intensities from 300 to 750 μmol m^{-2} s^{-1}.

5.3 **RESULTS**

5.3.1 **Light response curve**

The photosynthetic rate of mature fern was positively and strongly hyperbolic in response to increasing light intensity (Figures 5.1 to 5.4). The lines on each graph presented in Figures 5.1 to 5.4 are the fitted curves obtained by using the nonrectangular model (equation 5.3) based on 4 measurements at each the light intensity. The parameters of these curves are given in Tables 5.2 to 5.6 and described below.

By grouping the cultivars into each particular temperature treatment it was found that the differences bewteen cultivars was clearest at 35/15^{0}C and is presented in (Figure 5.5). Analysis of covariance at that temperature indicated that Brocks had a significantly higher photosynthetic rate than other cultivars at light intensities ranging from 300 to 750 μmol m^{-2} s^{-1}. The photosynthetic rate of UC157 was not significantly different to Larac but both cultivars had a significantly higher photosynthetic rate than Tainan 1 at intermediate light intensities.

At 40/20^{0}C the measurement became extremely difficult due to moisture on the fern caused by high humidity causing problems in keeping RH inside the chamber within 5% as required for accurate measurement (see section 3.2.4). These difficulties were reflected in the data, i.e., large variation and poor fits to a nonrectangular hyperbola

model (in fact a straight line fit for Brocks). In addition poor plant growth allowed only 3 measurements to be taken for Brocks and Larac. Because of these reasons the data was not included in the pooled analysis. Yen (1993) also found an unusual value for the allometric relationship between shoot and root at 40/20 and 40/30^{0}C and decided to exclude them from his analysis.

5.3.2 **Effect of growth temperature on the light compensation point (LCP)**

Analysis of variance on each particular temperature found significant differences between cultivars only at 35/15^{0}C where Tainan 1 had a higher LCP than UC157 and Brocks (Table 5.2). Pooled analysis found a significant effect of temperature and cultivar on LCP, but without any interaction. Larac had a higher LCP than that of UC157 and Brocks, and Tainan 1 had a higher value than UC157. The LCP increased significantly with temperature (Table 5.2).

Trend analysis indicated that the change in light compensation point of mature fern with temperatures was quadratic (Figure 5.6). The LCP increased gradually from 20/20^{0}C to 35/15^{0}C followed by a sharp increase at 40/20^{0}C.

5.3.3 **Effect of growth temperature on the estimated photosynthesis at saturating light intensity (Pmax) and the ratio of photosynthesis at standard growth room light intensity to Pmax (called Pn700)**

A significant differences in Pmax between cultivars were only found at 35/15^{0}C where UC157 had a lower Pmax than Tainan 1 and Brocks (Table 5.3). At 40/20^{0}C Pmax dropped considerably for UC157 and Larac and less for Tainan 1 and Brocks. Pooled analysis found a significant effect of temperature and cultivar, but without any interaction. Pmax decreased significantly as temperatures increased. In addition over all the temperatures UC157 had a significantly higher Pmax than the other cultivars (Table 5.3).

The response of Pmax to temperatures was quadratic (Figure 5.11). The Pmax fell from 20/20 to 25/25^{0}C and was relatively constant from 25/25 to 30/20^{0}C and then fell again at higher temperatures.

At the standard growth room light intensites (700 - 750 μmol m^{-2} s^{-1}), photosynthetic rate can be expressed as a percentage of the estimated photosynthetic rate at saturating light intensities (Pmax) and in this thesis this is called Pn700. Pn700 estimates how close the photosynthetic rate at a standard light intensity is to the saturating point, eg. the closeness of Pn700 to unity will indicate that the photosynthetic rate will not benefit significantly from increasing light intensities.

Table 5.2. Light compensation point (μmol m^{-2} s^{-1}) of mature asparagus fern at various temperature.

Treatment	Cultivar				
	UC157	Brocks	Tainan 1	Larac	Temp. mean[3]
20/20^{0}C	16.83	16.95	17.85	18.17	17.45d
25/25^{0}C	20.83	19.60	21.45	21.20	20.77c
30/20^{0}C	26.53	28.00	27.30	29.98	27.95b
35/15^{0}C *[1]	30.25b	31.03b	35.68a	33.98ab	32.73a
40/20^{0}C[2]	44.25	44.5	40.00	45.00	43.25
Cv. Mean[3]	23.61c	23.89bc	25.57ab	25.83a	
T_{linear}	**	**	**	**	
$T_{quadratic}$	**	**	**	**	
T_{cubic}	ns	ns	ns	ns	

1. Anova for each particular temperature only found a significant differences between cultivars at 35/15^{0}C with se=1.68 and $df_{(error)} = 9$.
-. Mean separation for each temperature across column by lsd ($p \leq 0.05$).
2. 40/20^{0}C was excluded from pooled analysis.
3. Mean separation for overall treatment (using pooled analysis) across and within column by Duncan's Multiple Range Test ($p \leq 0.05$) with se= 0.84 and $df_{(error)} = 36$.

Using the term Pn700 it was found that mature fern photosynthesis had reached about 80-90% of its Pmax (Table 5.4). There was a significant differences between cultivars at 35/15^{0}C in which Tainan 1 had a significantly lower PN700 than other cultivars (Table 5.4). Pooled analysis found that there was a significant effect of temperature and cultivar, but without any interaction (Table 5.4). For overall temperatures UC157 had a significantly higher PN700 than other cultivars. Pn700 at 20/20^{0}C was not different from 35/15^{0}C, but both were significantly lower than at 25/25^{0}C. Meanwhile there was no significant differences between Pn700 at 25/25 and 30/20^{0}C.

Trend analysis found a quadratic relationship between Pn700 and temperature (Table 5.4 and Figure 5.7). This was probably due to Pn700 falling markedly at 40/20^{0}C.

5.3.4 **Effect of growth temperature on the initial slope of light response curve** (α).

The use of leaf dry weight instead of leaf area for expressing photosynthesis created difficulties in expressing the α. Alpha is estimated from the slope of the light response curve at low light intensities. The common unit is expressed as µmol CO_2/µmol quanta because the other parameters (m^{-2} s^{-1}) cancel each other. If dry weight is used, as in the present experiment, only s^{-1} cancels out leaving µmol CO_2 kg^{-1}/µmol quanta m^{-2}. This unit is large and illogical, however, the term 'α' here has been used to indicate the quantum yield in relation to temperature. These data, however, can only be used for comparison in this present experiment and cannot be compared to other studies.

Analysis at each particular temperature did not find any significant differences between cultivars at $p = 0.05$. Pooled analysis only found a significant effect of temperature on α. The α decreased as temperature increased, however it was not significant between 25/25 and 30/20^{0}C (Table 5.5).

The relationship of α to temperature was cubic (Table 5.5; Figure 5.8). It decreased from 20/20 to 25/25^{0}C and was then relatively constant from 25/25 to 30/20^{0}C (Figure

5.8). Brocks always had a smaller α at 20/20°C to 30/20°C, though not significantly. At 35/15°C the α of Tainan 1 decreased more steeply compared to the other cultivars though not significantly, while Brocks was relatively constant. At 40/20°C the value for all cultivars fell to the lowest level (Table 5.5).

Table 5.3 Estimated Pmax (μmol kg^{-1} s^{-1}) of mature fern at various temperature.

Treatment	Cultivar				
	UC157	Brocks	Tainan 1	Larac	Temp. mean[3]
20/20°C	401.54	424.26	422.86	416.29	416.24a
25/25°C	303.67	309.74	305.79	305.19	306.10b
30/20°C	290.74	307.29	304.73	303.47	301.61b
35/15°C*[1]	264.85b	286.90a	288.54a	277.71ab	279.50c
40/20°C[2]	213.74	269.98	273.19	234.47	245.47
Cv. mean[3]	315.25b	332.05a	328.38a	327.77a	
T_{linear}	**	**	**	**	
$T_{quadratic}$	**	**	**	**	
T_{cubic}	ns	ns	ns	ns	

1. Anova for each particular temperature only found a significant differences between cultivars at 35/15°C with se= 6.15 and $df_{(error)} = 9$.
-. Mean separation for each temperature across column by lsd ($p \leq 0.05$).
2. 40/20°C was excluded from pooled analysis.
3. Mean separation for overall treatment (using pooled analysis) across and within column by Duncan's Multiple Range Test ($p \leq 0.05$) with se= 5.15 and $df_{(error)} = 36$.

Table 5.4 Pn700 of mature asparagus fern at various temperature.

Treatment	Cultivars				
	UC157	Brocks	Tainan 1	Larac	Temp. mean[3]
20/20°C	0.87	0.83	0.85	0.83	0.844c
25/25°C	0.91	0.89	0.90	0.91	0.901a
30/20°C	0.91	0.87	0.88	0.87	0.883ab
35/15°C *[1]	0.90a	0.88a	0.82b	0.87a	0.864bc
40/20°C[2]	0.76	0.70	0.70	0.76	0.729
Cv. mean[3]	0.895a	0.866b	0.861b	0.870b	
T_{linear}	**	**	**	**	
$T_{quadratic}$	**	**	**	**	
T_{cubic}	ns	ns	ns	ns	

1. Anova for each particular temperature only found a significant differences between cultivars at 35/15°C with se=0.0204 and $df_{(error)} = 9$.
-. Mean separation for each temperature across column by lsd ($p \leq 0.05$).
2. 40/20°C was excluded from pooled analysis.
3. Mean separation for overall treatment (using pooled analysis) across and within column by Duncan's Multiple Range Test ($p \leq 0.05$) with se= 0.012 and $df_{(error)} = 36$.

Table 5.5 The α (μmol CO_2 kg^{-1}/μmol quanta m^{-2}) of light response curve of mature fern at various temperature.

Treatment	Cultivar				
	UC157	Brocks	Tainan 1	Larac	Temp. mean[3]
20/20°C[1]	0.76	0.69	0.77	0.77	0.744a
25/25°C	0.64	0.59	0.61	0.60	0.609b
30/20°C	0.59	0.55	0.58	0.56	0.569b
35/15°C	0.50	0.51	0.44	0.48	0.483c
40/20°C[2]	0.32	0.32	0.33	0.34	0.326
Cvs mean[3]	0.620a	0.584a	0.592a	0.609a	
T_{linear}	**	**	**	**	
$T_{quadratic}$	**	**	**	**	
T_{cubic}	**	**	**	**	

1. Anova for each particular temperature did not find any significant differences between cultivars.
2. 40/20°C was excluded from pooled analysis.
3. Mean separation for overall treatment (using pooled analysis) across and within column by Duncan's Multiple Range Test ($p \leq 0.05$) with se= 0.021 and $df_{(error)}$ = 36.

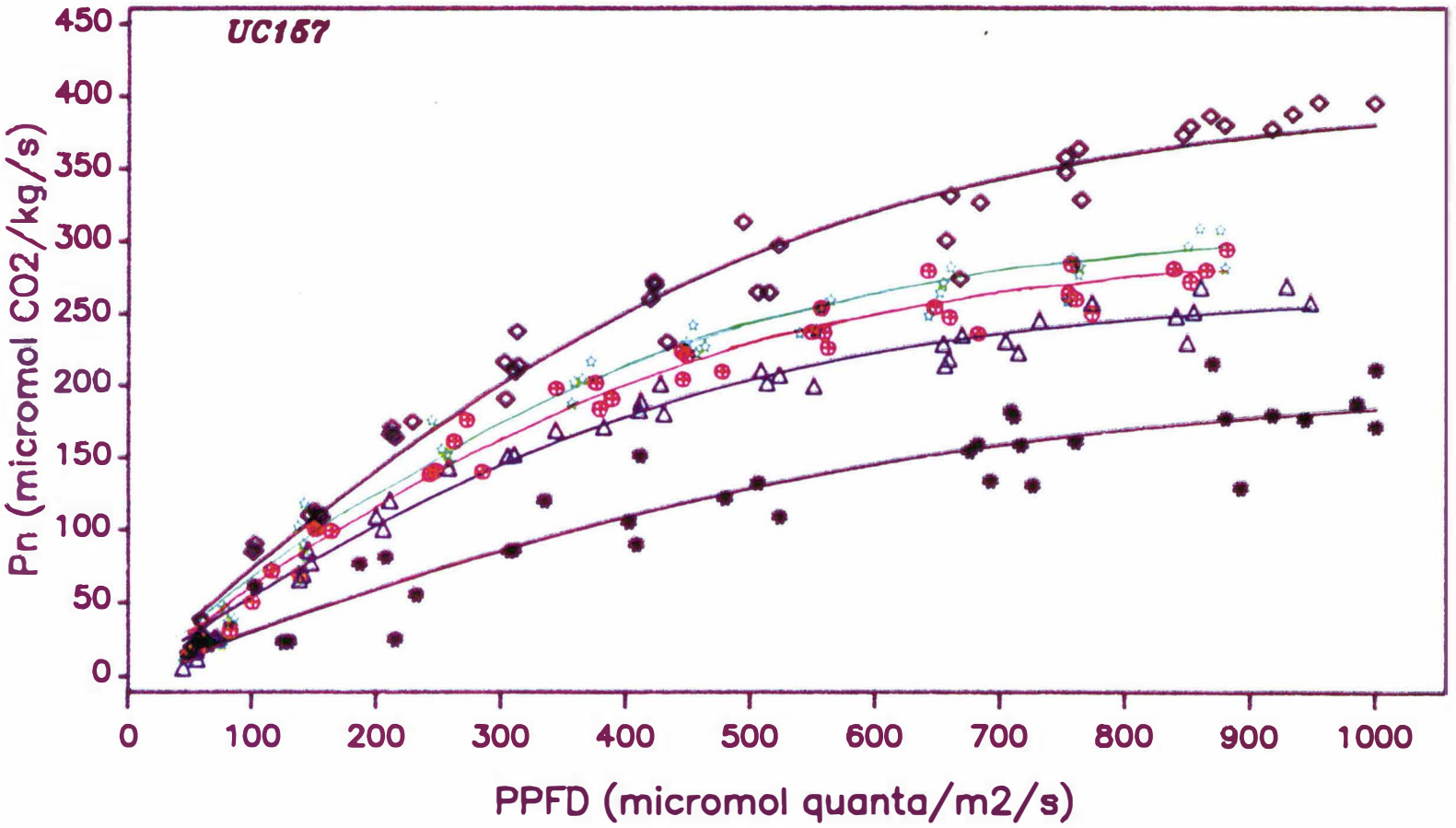


Figure 5.1 Light response curve of UC157 at different growth temperatures (◇ ◇ ◇ 20/20C; ☆ ☆ ☆ 25/25C; ⊕ ⊕ ⊕ 30/20C; Δ Δ Δ 35/15C; ● ● ● 40/20C). The fitted lines are obtained from nonrectangular model (equation 4.3).

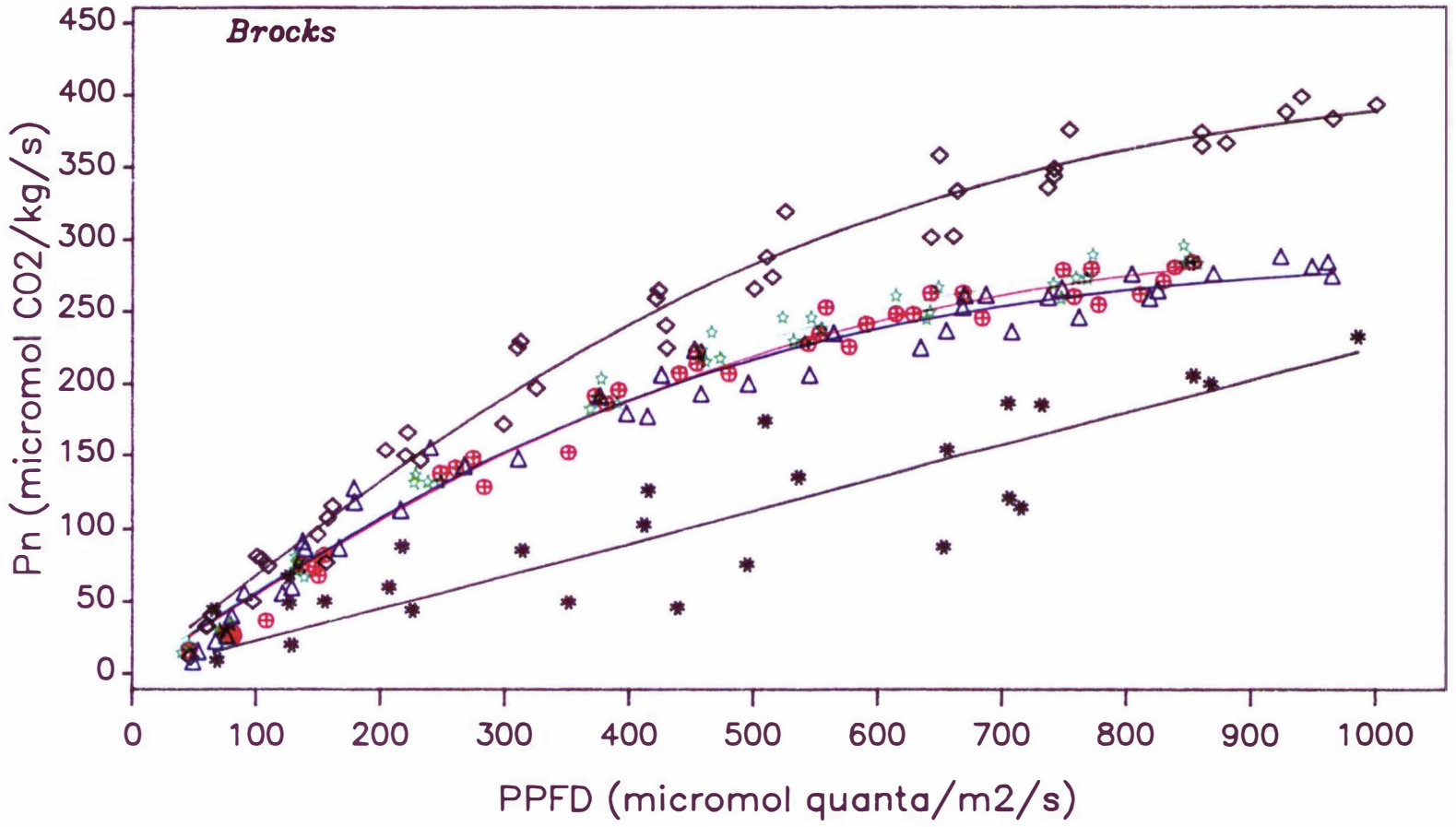


Figure 5.2 Light response curve of Brocks at different growth temperatures (◇ ◇ ◇ 20/20C; ☆ ☆ ☆ 25/25C; ⊕ ⊕ ⊕ 30/20C; Δ Δ Δ 35/15C; ✱ ✱ ✱ 40/20C). The fitted lines are obtained from nonrectangular model (equation 4.3).

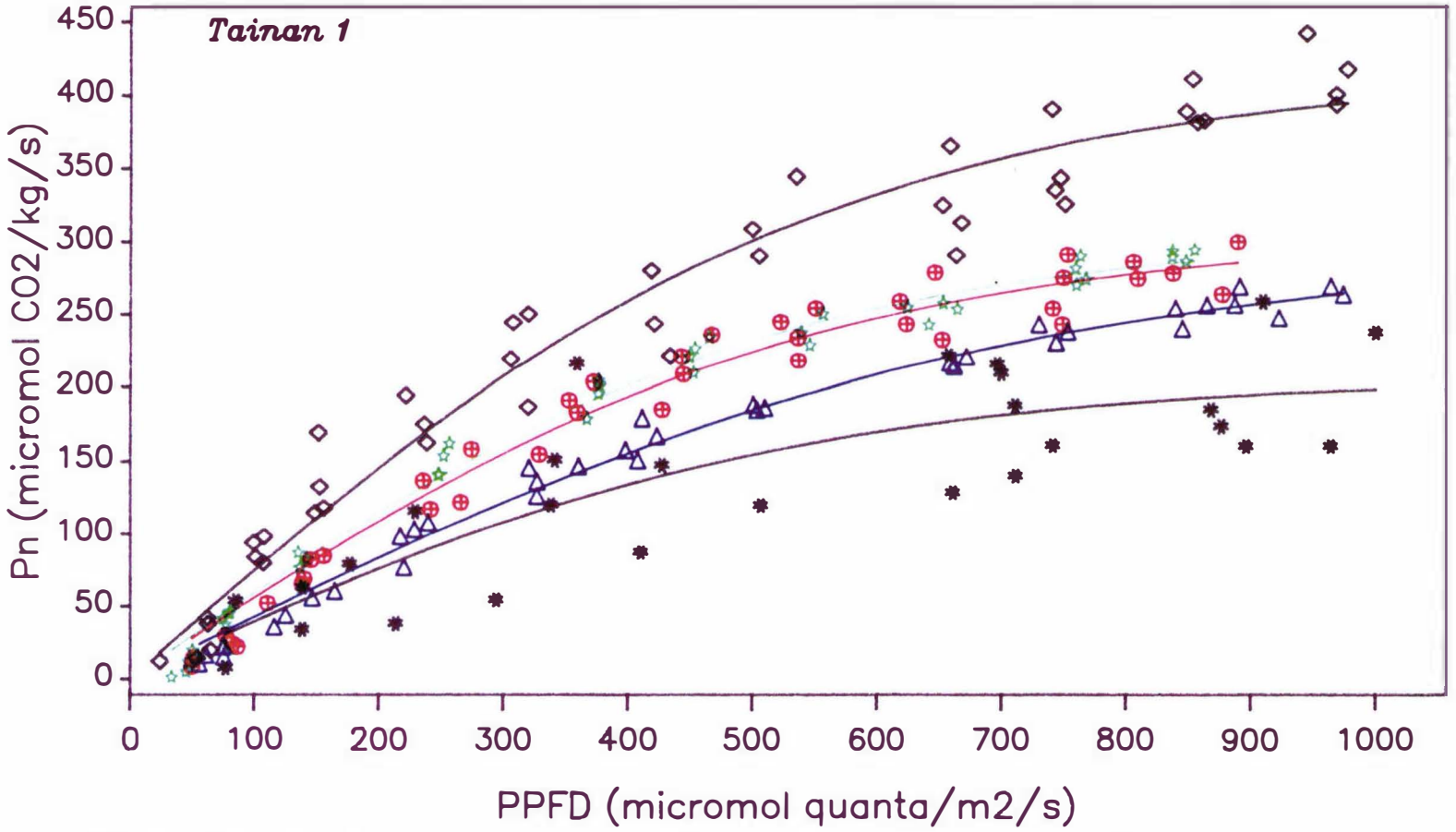


Figure 5.3 Light response curve of Tainan 1 at different growth temperatures (◇ ◇ ◇ 20/20C; ☆ ☆ ☆ 25/25C; ⊕ ⊕ ⊕ 30/20C; Δ Δ Δ 35/15C; ✱ ✱ ✱ 40/20C). The fitted lines are obtained from nonrectangular model (equation 4.3).

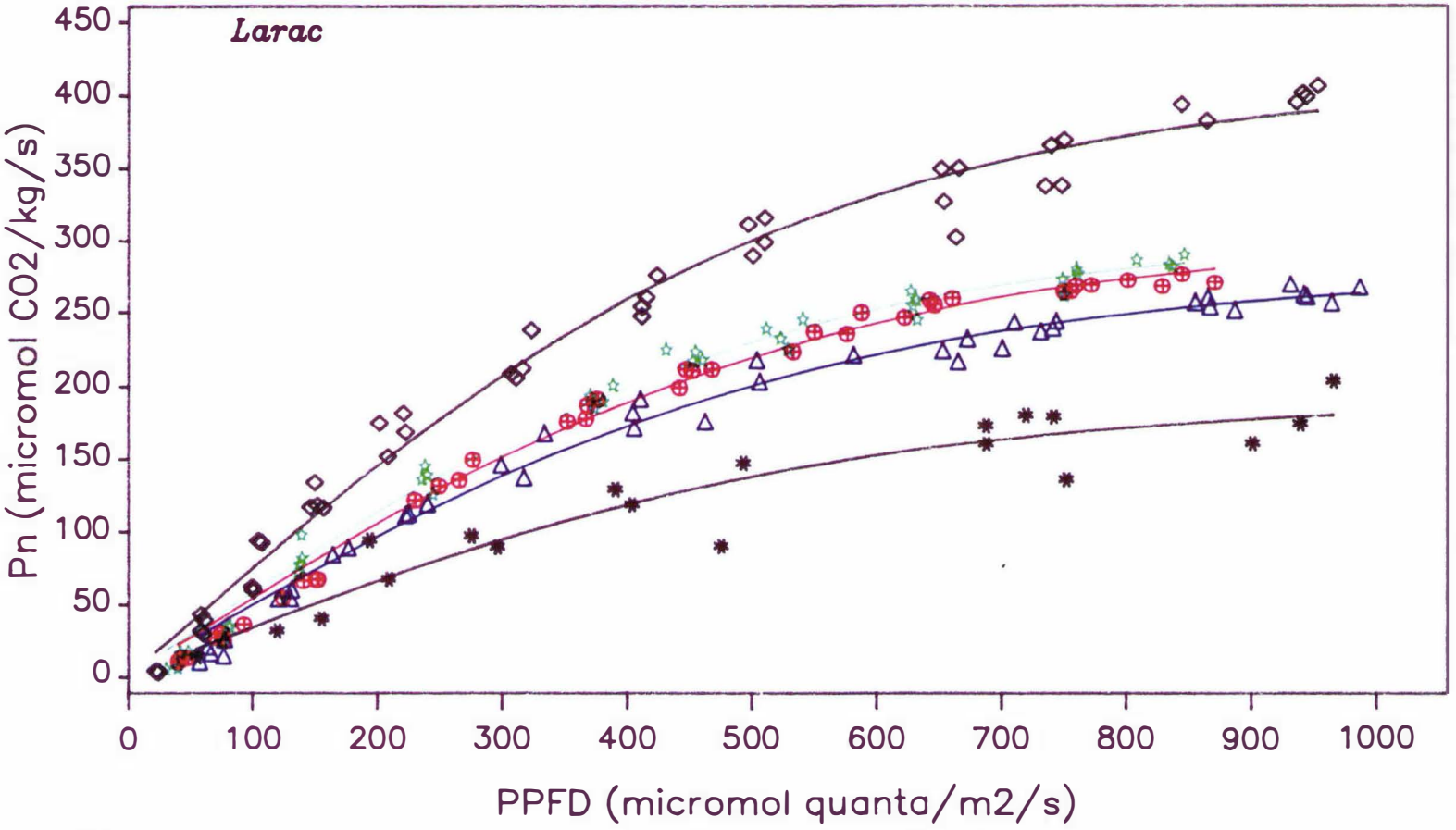


Figure 5.4 Light response curve of Larac at different growth temperatures (◇ ◇ ◇ 20/20C; ☆ ☆ ☆ 25/25C; ⊕ ⊕ ⊕ 30/20C; Δ Δ Δ 35/15C; ✱ ✱ ✱ 40/20C). The fitted lines are obtained from nonrectangular model (equation 4.3).

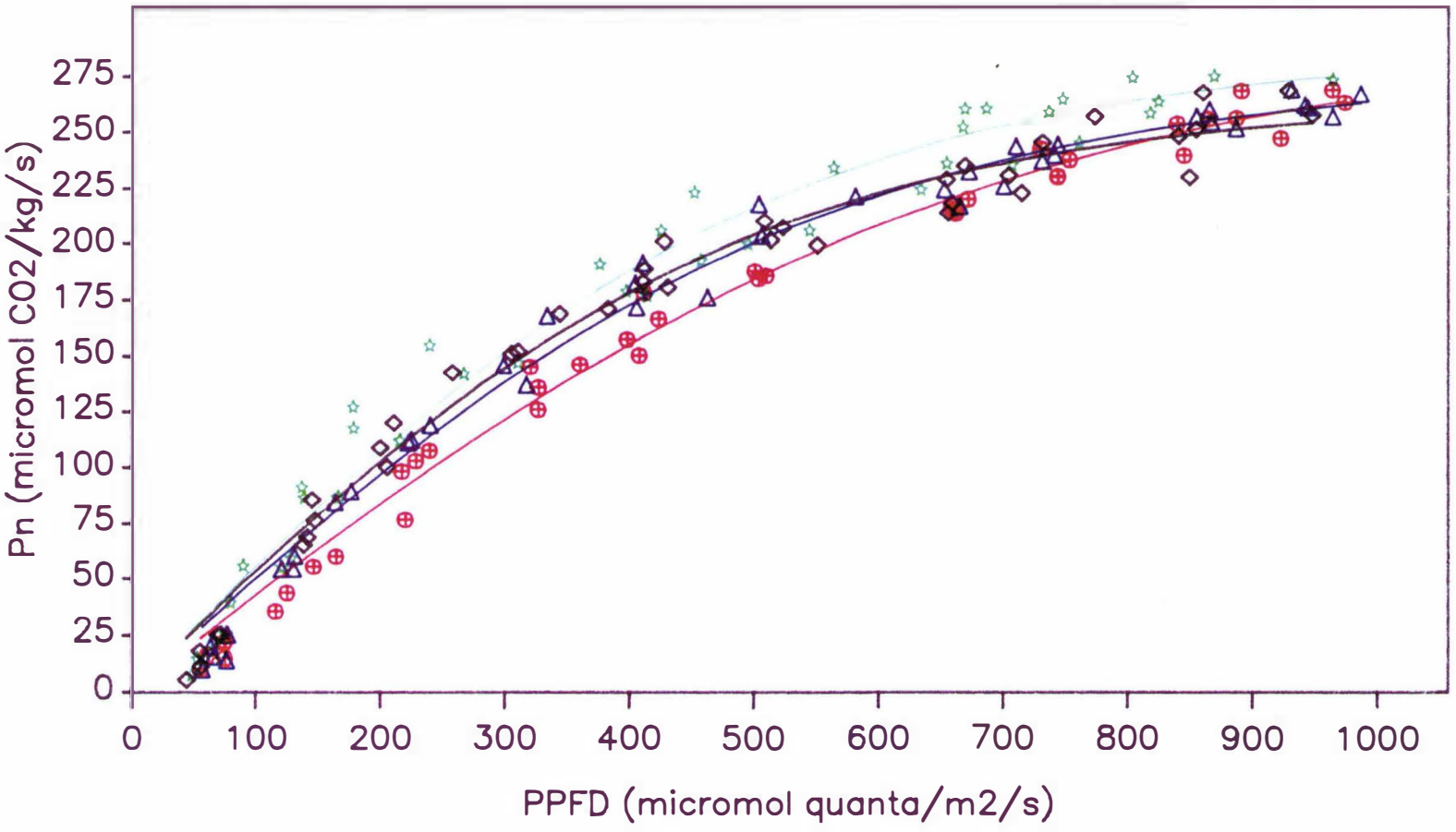


Figure 5.5 Light response curve of asparagus fern grown at 35/15C (◇ ◇ ◇ UC157; ☆ ☆ ☆ Brocks; ⊕ ⊕ ⊕ Tainan 1; Δ Δ Δ Larac).

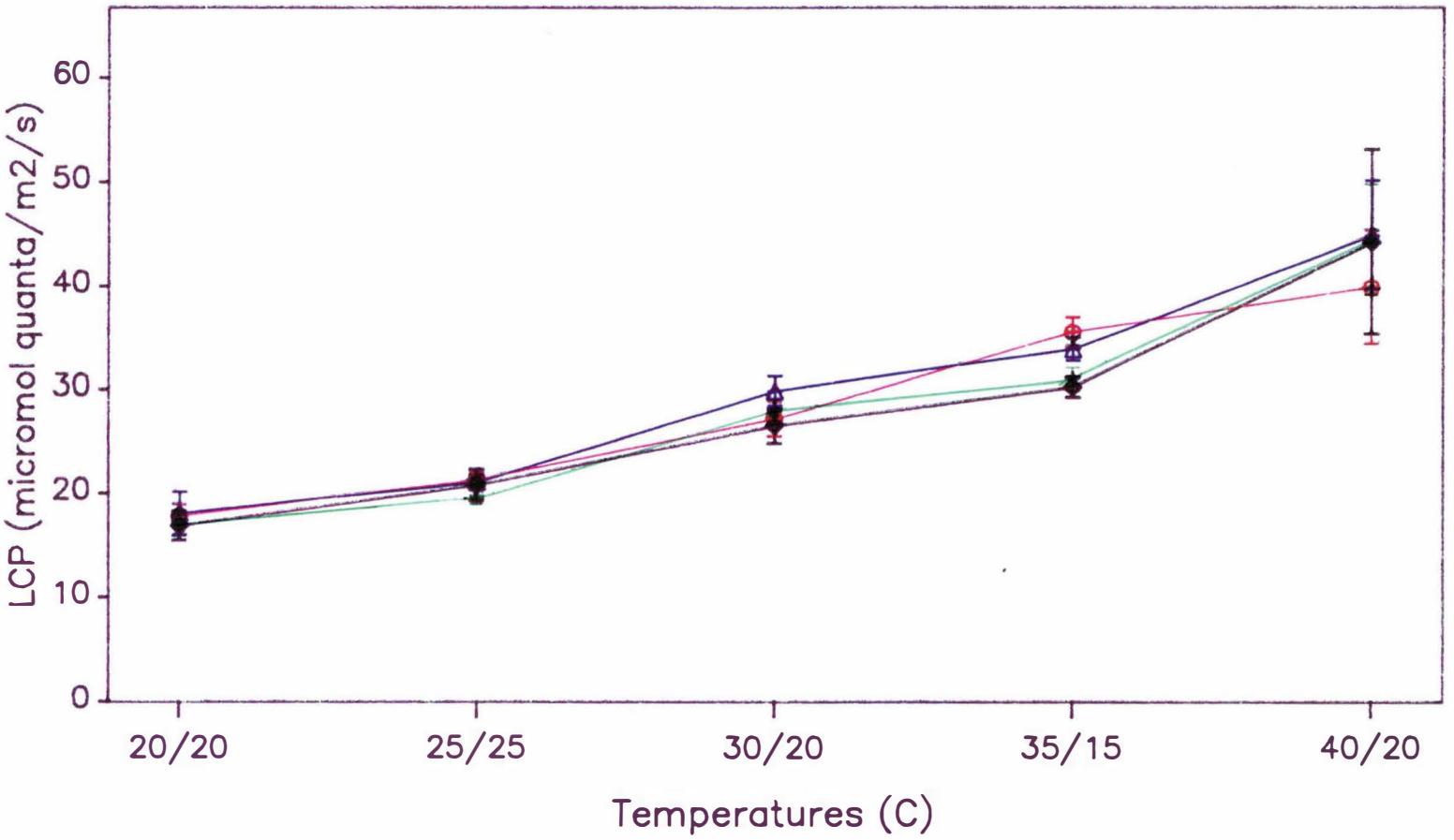


Figure 5.6 Predicted light compensation point of asparagus fern at different temperatures (◇ ◇ ◇ UC157; ☆ ☆ ☆ Brocks; ⊕ ⊕ ⊕ Tainan 1; Δ Δ Δ Larac). I = Stderr. of means.

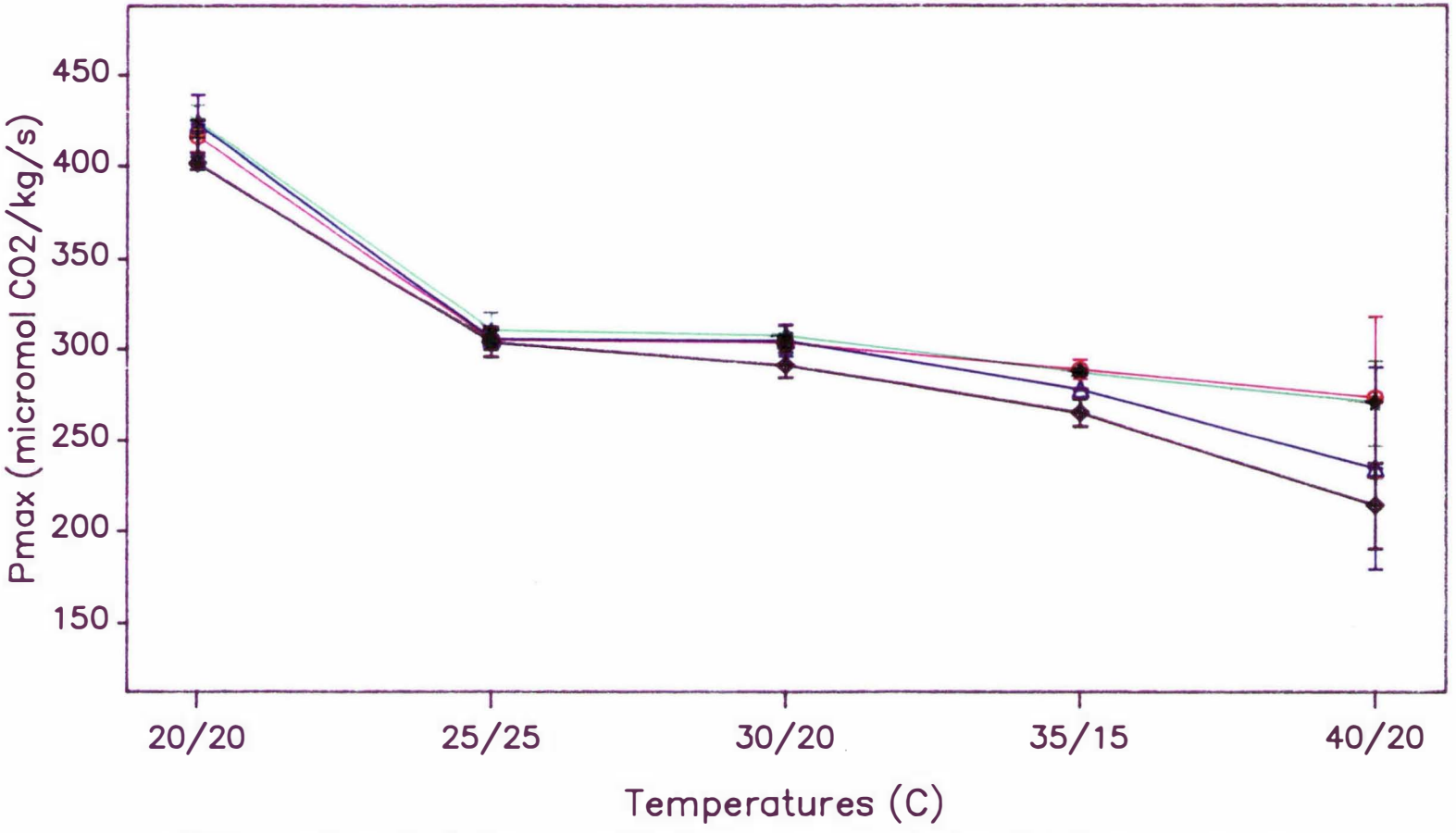


Figure 5.7 Predicted Pmax of asparagus fern at different temperatures (◇ ◇ ◇ UC157; ☆ ☆ ☆ Brocks; ⊕ ⊕ ⊕ Tainan 1; Δ Δ Δ Larac). I = Stderr. of means.

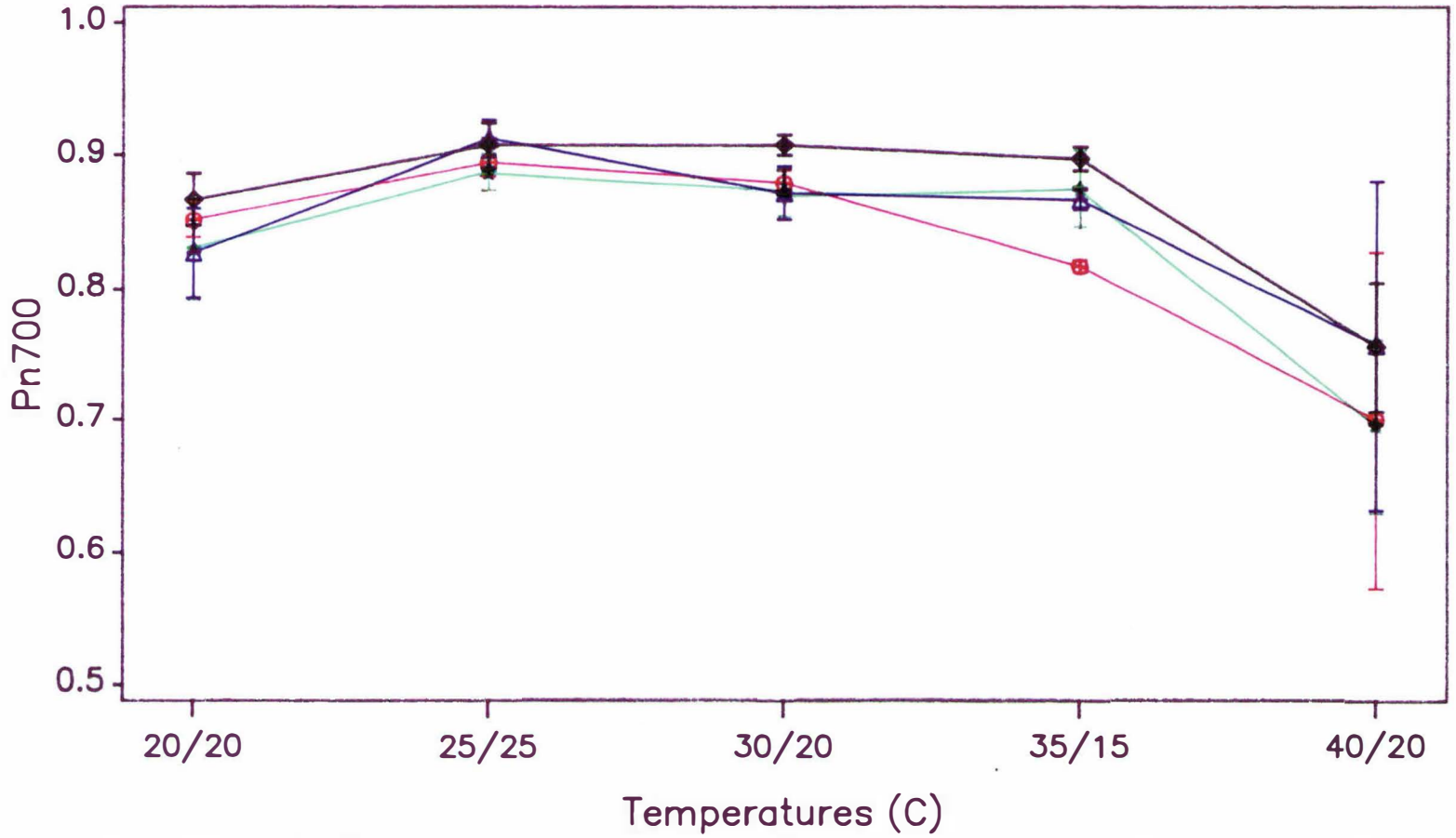


Figure 5.8 Pn700 of asparagus fern at different temperatures (◇ ◇ ◇ UC157; ☆ ☆ ☆ Brocks; ⊕ ⊕ ⊕ Tainan 1; Δ Δ Δ Larac). I = Stderr. of means.

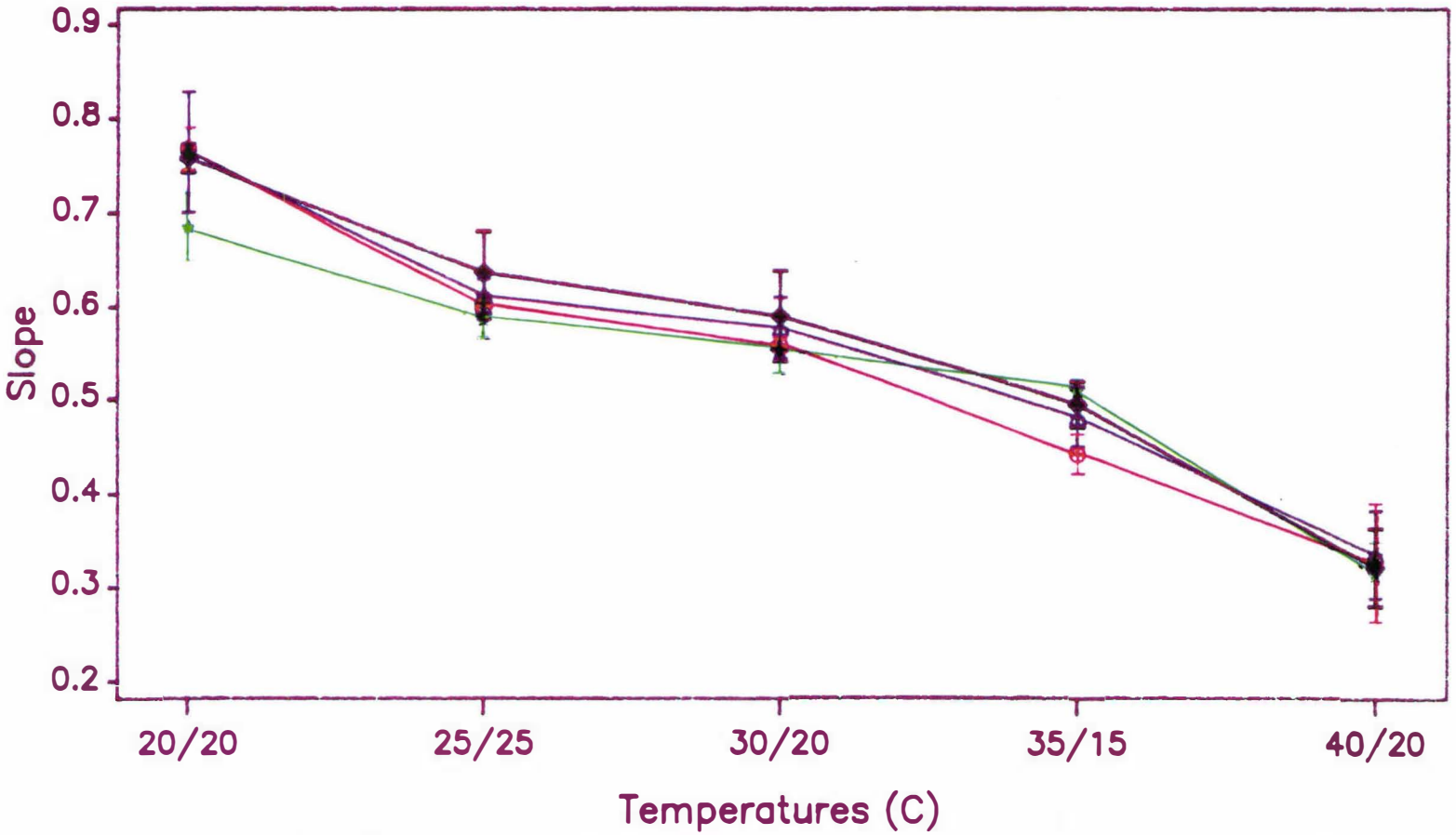


Figure 5.9 The initial slope of light response curve of asparagus fern at different temperatures (◇ ◇ ◇ UC157; ☆ ☆ ☆ Brocks; ⊕ ⊕ ⊕ Tainan 1; Δ Δ Δ Larac). I = Stderr of means.

5.4 DISCUSSION

5.4.1 Light response curve

The present experiment confirms that the response of photosynthesis of mature fern of asparagus to light intensity was hyperbolic over a range of temperatures (Figure 5.1 to 5.4). The general shape of the curve relating photosynthesis and light intensity was similar to that for other crops (tomato, Peat, 1970; asparagus, Inagaki *et al.,* 1989; and Lin and Tsai, 1983; rose, Lieth and Pasian, 1990; cherry, Layne and Flore, 1992; chrysanthemum, Holcomb *et al.,* 1988). It has been suggested that three basic parameters define the light response curve at any given temperature a) the upper asymptote representing photosynthesis at light saturated, Pmax; b) the quantum yield represented by initial slope of the response of photosynthesis to light intensity, α; 3) a measure of the convexity of the hyperbola, θ (Thornley, 1976; Jarvis and Sanford, 1986) (which is approximated by Pn700). Baker *et al.* (1988) suggested that at high light intensity, the effect of temperature on Pmax will dominate, while at limiting light intensity the response to temperature is dominated by an effect of temperature on α. In this study the value of α and Pmax of mature asparagus fern varied with temperature treatment and this will be discussed separately in section 5.4.3 and 5.4.4.

At 35/15°C Brocks had a significantly higher photosynthetic rate than all the other cultivars, while Tainan 1 had the lowest rate. This would suggest that Brocks was more adapted to high temperatures than the other cultivars. The experiment discussed in Chapter 3 also indicated that Brocks performed better than other cultivars at high temperatures. The possibility that low night temperature might affect photosynthesis by feedback inhibition of dark respiration was excluded as in Chapter 4 it was found that dark respiration at 35/15^{0}C was not different between cultivars.

Zelitch (1963, 1971) suggested that low night temperature reduced stomata opening during the day and could cause photosynthetic inhibition. Brocks is a cultivar developed for desert areas (see section 3.2.1.2) in which low night temperatures are typical. One possibility for adaptation would be less inhibition of stomatal opening

following low night temperatures. In this experiment 15^{0}C night temperature was the closest to desert temperatures during the night while 35^{0}C during the day would be close to day temperatures in the desert.

5.4.2 **Effect of growth temperatures on light compensation point (LCP)**

The LCP of mature fern at a range of temperatures was low. At 20/20°C (Table 5.2), the LCP was similar to the value determined in the study on asparagus cells at the same temperature carried out by Hills (1986). A low LCP value is typical of shade plants (Bjorkman, 1981; Lawlor, 1987; Hills, 1986). This experiment was conducted at a standard growth room light intensities of about 700-750 μmol m^{-2} s^{-1}. This light intensity is about 1/3 of maximum natural light intensity in the field. In addition the cladophylls are generally 1 to 3 cm long cylinders, less than 1 mm in diameter. Hills (1986) suggested that about 7 cladophylls grow out from each node and point in many directions, some lie perpendicular to the sun, but many point towards or away from the sun and these cladophylls therefore will receive less light. Therefore many cladophylls of asparagus fern could become adapted to low light intensity environments and behave as typical shade plants.

The increase of LCP of mature fern with temperature (Table 5.2 and Figure 5.6) was similar to many other species such as rose (Pasian and Lieth, 1989), cherry (Sams and Flore, 1982) and hybrid geraniums (Armitage *et al.,* 1981). There are at least two factors which can explain these phenomena. Firstly, since net photosynthesis is equal to gross photosynthesis minus dark respiration plus photorespiration, then net photosynthesis is directly related to dark respiration. Dark respiration has been observed to increase with temperature in various species (Penning de Vries *et al.,* 1979; Gent and Enoch, 1983; Pasian and Lieth, 1989; Berry and Raison, 1981; Amthor, 1989; Lawlor, 1987). The increase of dark respiration will reduce Pn and increase LCP. In asparagus, dark respiration also has been found to increase linearly with temperature (see chapter 4). Secondly there is also a relationship between Pn and photorespiration. It has been established that photorespiration increases rapidly with increasing temperatures (Lawlor, 1987; Edwards and Walker, 1983; Canvin,

1990). Increasing photorespiration therefore will reduce net photosynthesis and increase LCP.

The question now is the extent to which these factors control LCP. Lawlor (1987) suggested that at very low light intensities the effect of dark respiration is dominant, but he also suggested that with high O_2/CO_2 ratios photorespiration is of greater importance than dark respiration. In addition it has been found that increasing temperature increases O_2/CO_2 solubility ratio inside the leaf (Ku and Edwards, 1977). Since Rubisco controls the carboxylation and oxygenation reaction (Lawlor, 1987; Edwards and Walker, 1983), the understanding of the degree to which Rubisco determines the rate of photosynthesis at a particular light intensity is important. It was suggested that at light saturation the Rubisco is the primary limitation to the photosynthetic rate (Seemann and Sharkey, 1986; von Caemmerer and Edmondson, 1986). At subsaturating light intensity, however, the determination of the degree to which Rubisco limits the photosynthetic rate is difficult because reduction of Rubisco activity by regulatory mechanisms becomes more significant (Woodrow and Berry, 1988). For soybean leaves as the light intensity decreased until, at less than 400 μmol quanta m^{-2} s^{-1}, Rubisco activity no longer limited the photosynthetic process (Woodrow *et al.,* 1988 cited by Woodrow and Berry, 1988). They suggested that under these conditions, the photosynthetic rate is most probably limited by the quantum efficiencies of PSI and PSII. Therefore, in this study dark respiration probably affected LCP more than photorespiration. Bjorkman (1981) suggested that for shade plants the very low LCP is caused by very low dark respiration. Azcon-Bieto and Osmond (1983) also found that LCP was strongly correlated with dark respiration in wheat leaves.

The pooled analysis suggested that, as a general trend at the temperature used, Tainan 1 and Larac had higher LCPs than UC157, and Larac had a higher LCP than Brocks (Table 5.2). In addition at 35/15^{0}C Tainan 1 had a significantly higher LCP than that of UC157 and Brocks ($p = 0.05$). Larac also had a similar trend (at $p = 0.06$ and $p = 0.11$, respectively), which probably implies that Tainan 1 and Larac had higher dark respiration. Studies on the dark respiration of mature fern (Chapter 4), however, did

not show a significant differences between cultivars at 35/15^{0}C (Table 4.6). Overall, however Tainan 1 appeared to have a lower dark respiration than UC157. This finding suggests that for asparagus under high temperature condition there are other important factors affecting LCP, such as the reduction of quantum efficiencies in PSI and PSII (Woodrow and Berry, 1988; Barker *et al.,* 1988). Alpha for Tainan 1 at 35/15^{0}C was lower than UC157 and Brocks ($p = 0.07$) (Table 5.5). These result indicated that Tainan 1, and probably Larac, had lower photochemical efficiencies at high temperatures.

5.4.3 **Effect of growth temperatures on estimated Pmax and Pn700**

5.4.3 1 **Estimated Pmax**

The Pmax values in this experiment were obtained from the extrapolation of data, using equation 5.3, as the maximum light intensity obtained in the experiment was only about 900 μmol m^{-2} s^{-1} and still below the saturation point.

Under atmospheric conditions in the growth room estimated Pmax of mature fern decreased sharply from 20/20 to 25/25^{0}C followed by a gradual decline at higher temperatures (Table 5.3 and Figure 5.7). The response of Pmax to temperature varies with species. For example, Pasian and Lieth (1989) found that Pmax of rose leaves was highest when the plants were grown at 30^{0}C compared to 20^{0}C and 37^{0}C, while Armitage *et al.* (1981) found that temperature range from 15 to 32^{0}C did not affect the Pmax of hybrid geraniums appreciably. On the other hand, Sams and Flore (1982) found Pmax of cherry leaves decreased with increasing high temperatures up to 40^{0}C which is in agreement with the present experiment.

The decrease in estimated Pmax of mature fern with temperature was probably due to three factors. Firstly, high resistance of diffusion of CO_2 through the boundary layer and stomata (Baker *et al.,* 1988). The degree that stomatal resistance affects estimated Pmax, however, depends on other factors such as water stress and vapour pressure gradient (Berry and Bjorkman, 1980). In this present experiment, there was differences

in vapour pressure deficit (VPD) between the temperature treatment (table 5.1) where temperature treatments from 30/20 to 40/20^{0}C had a higher VPD. High VPD could possibly increase the stomatal resistance. Secondly, Pmax would be limited by low carboxylation activity of Rubisco due to high rates of the oxygenation reaction with increasing temperature (Farquhar *et al.,* 1980). Thirdly a decline in the maximum rate of electron transport would be expected (Farquhar *et al.,* 1980).

The differences in estimated Pmax between cultivars occurred at a temperature of 35/15^{0}C where UC157 had a significantly lower estimated Pmax than that of Brocks and Tainan 1 (Table 5.3). Overall comparison also indicates that UC157 always had a lower estimated Pmax. In terms of estimated Pmax this result suggested that UC157 was the most affected cultivar, especially under high temperature condition, which is surprising considering that UC157 is considered a high temperature adapted cultivar.

5.4.3.2 **Pn700**

Net photosynthesis at 700 µmol m^{-2} s^{-1} (Pn700) was 80 to 90% of estimated Pmax from 20/20 to 35/15^{0}C (Table 5.4) suggesting that mature fern photosynthesis at the standard light intensity was closed to saturation, which is a typical shade plant characteristic (Hills, 1986; Bjorkman, 1981). Hills (1986) found an even lower light saturation point of about 400 µmol m^{-2} s^{-1} at 20^{0}C for asparagus cladophyll discs. Other studies, found that light saturation point of asparagus has not been achieved at light intensity of 500 µmol m^{-2} s^{-1} at a temperature range of 21 to 23^{0}C (Downton and Torokfalvy, 1975; Yue *et al.,* 1992), while Lin and Tsai (1983) and Inagaki *et al.,* (1989) found a higher light saturation point for asparagus from 1000 to 1400 µmol m^{-2} s^{-1}. The present study found a light saturation point of mature asparagus fern close to that of Lin and Hung (1983) and Inagaki *et al.* (1989) (Figure 5.1 to 5.4). These various studies suggests a considerable variation in light saturating point of asparagus. The variation could possibly arise from the different method of measurement, for example cladophyll discs, cladophylls, or whole plants, as well as the plant age.

The overall comparison shows that UC157 had a significantly higher Pn700 than other cultivars (Table 5.4). Suggesting that this cultivar will became light saturated sooner than the other cultivars. At 35/15^{0}C Tainan 1 had the lowest Pn700 and would benefit the most from increases in light intensities at this particular temperature.

The fall in Pn700 at 40/20^{0}C (Table 5.4 and Figure 5.8) suggested that either the fern required a higher light intensity to reach maximum photosynthesis or other limitations such as electron transport occurred. Further work, using acclimated plants is required to clarify the situation.

5.4.4 **Effect of growth temperatures on α**

At low light intensities photosynthesis is linearly dependent on light intensity and α is constant and maximal (Lawlor, 1987; Edwards and Walker, 1983; Bjorkman, 1981). At higher light intensities the increase in photosynthesis is less than proportional to the increase in light intensity (partial light saturation) and ultimately, photosynthesis fail to increase with increasing light intensity (light saturation). Because of the linear relationships between photosynthesis and light intensity at low light intensity, α is defined as the initial slope of the relationship between photosynthesis and light intensity (Farquhar *et al.,* 1980; Bjorkman, 1981).

The pooled analysis (Table 5.5) indicated that α of mature fern decreased with increasing temperature as for other C_3 plants (Ehleringer and Bjorkman, 1977; Pasian and Lieth, 1989; Powles *et al.,* 1979). The effect of environmental factors, such as O_2, CO_2 concentration and temperature on α of C_3 plants has been well documented (Baker *et al.,* 1988; Berry and Bjorkman, 1980; Farquhar *et al.,* 1980; Bjorkman, 1981; Berry and Raison, 1981; Lawlor, 1987; Edwards and Walker, 1983). They suggested that in normal air (21% O_2 and 0.033% CO_2) α of C_3 plant is temperature dependent. However, when leaves of C_3 plants are provided with low O_2 or high CO_2 concentration during measurement they did not show temperature-dependent inhibition of α, due to the depression of the oxygenation reaction. The decrease in α of mature fern with increasing temperatures in normal air, therefore, was possibly due to

stimulation of the oxidation of RuBP. The rationale is that photorespiration was stimulated under high O_2 or low CO_2 concentrations (Farquhar *et al.*, 1980; Berry and Bjorkman, 1980; Baker *et al.*, 1988; Canvin, 1990). Baker *et al.* (1988) suggested that α reflects the maximum efficiency of utilization of captured photons in the reduction of CO_2, therefore it could be affected by the requirements of ATP and NADPH within the pathway used for CO_2 fixation. This factor is influenced by O_2 and CO_2 concentration and effects of temperature on the kinetic parameters of Rubisco (Berry and Raison, 1981). Increasing temperature increased the proportion of carbon entering the C_2 cycle (photorespiration) and hence increased the demand for ATP and NADPH. In addition at supraoptimal temperatures (35/15^{0}C and 40/20^{0}C) the α was low (Table 5.5 and Figure 5.9), probably due to disruption of photosynthetic enzyme activities (Woodrow and Berry, 1988), low efficiencies of excitation energy transfer within the chloroplast membrane and low efficiencies in the synthesis of ATP and NADPH (Baker *et al.*, 1988).

Alpha was similar in all cultivars (Table 5.5), but though not significant Brocks had a lower α at moderate temperatures, particularly at 20/20^{0}C, and a higher α at 35/15^{0}C indicating that Brocks may have a better photochemical efficiency at high temperatures.

5.5 SUMMARY

From this experiment it is concluded that:

1. The differences between cultivars were apparent at 35/15^{0}C where Brocks had a better photosynthetic performance than other cultivars.
2. Brocks had a lower alpha at 20 and 25^{0}C suggesting that this cultivar was less suited to moderate temperature than the other cultivars.
3. Tainan 1 may be the one most affected by high temperature treatment as indicated by a lower α, higher LCP and lower photosynthetic rate at light intensity range from 300 to 750 μmol m^{-2} s^{-1}.

CHAPTER SIX
GENERAL DISCUSSION

6.1 FIELD STUDY

6.1.1 Introduction

The field study provided information relevant to the use of seedling transplants for crop establishment and to the early growth and development of the asparagus crop.

6.1.2 Crop establishment - seedling transplants

Various studies have emphasized the importance of time of planting to the establishment of asparagus seedling transplants (Williams, 1979; Bussell, 1984; Liptay, 1984; Loughton and Baker, 1984; Burrows and Waters, 1989). The value of an early planting has been confirmed by the present study. The traditional time for planting seedling transplants in New Zealand has been November. Destructive harvests in April at the end of the first season provided evidence that a September planting was an attractive alternative (Table 2.9 to 2.11). The use of a logistic growth model however showed that with UC157 September planting was satisfactory, while for Jersey Giant an October planting may be a better alternative (section 2.3.2.1). This was because, presumably due to lower temperatures, there was little advantage in terms of crown growth in planting in September with this variety. The preference of Jersey Giant for warmer temperatures was also demonstrated by the k value generated when the allometric relationship between shoot and crown dry weight was considered. The k value of the allometric relationship between shoot and crown dry weight describes the ratio of the shoot RGR to the crown RGR. Here the k value for Jersey Giant increased along with the warmer temperatures of early summer to peak in December whereas the k value for UC157 decreased from October onwards (section 2.3.3.3). This suggests that the shoot growth of Jersey Giant was more responsive to warm temperatures than UC157.

Dufault and Greig (1983) emphasized that not only the number of buds, but also the quality and size of individual buds may determine subsequent high quality spear

production. The present study concurred that bud number alone is not a satisfactory descriptor of crown quality. It was suggested that crown quality could be adequately described by considering both bud number and crown dry weight. This was proposed as differences between the early plantings in terms of bud number were not always apparent, whereas differences in crown dry weight were (section 2.3.2 and 2.3.4). The allometric relationship that was established between these two parameters would suggest that these two growth parameters are closely associated with each other (section 2.3.6).

6.1.3 **Growth and development**

The sudden change in this k value to a lower figure from February onwards, irrespective of the age of the plants, provided strong evidence of an environmental factor bringing about an increase in the RGR of the crown in relation to the RGR of the shoot (section 2.3.3). Figure 2.19 detailing the shoot/crown dry weight ratio provided similar evidence. Although this change has been observed in the field before (Dufault and Greig, 1983), the present data clearly demonstrates that it is not an ontogenetic effect because the decrease in the shoot/root dry weight ratio occurred for all planting dates. It was suggested it was a response to lower temperatures. Other workers have reported the effects of low temperatures on the shoot/root dry weight ratio in asparagus (Dufault and Greig, 1983; Martin and Hartmann, 1990; Hughes *et al.,* 1990; Hughes, 1992).

Consideration of the RGR of the shoot and crown throughout the season provides useful information on the relative sink strengths of these organs and the factors which effect them. Thus increasing temperatures appear to favour shoot sink strength and falling temperatures crown sink strength.

The shoot plus bud to root number ratio stabilized for the early plantings in the latter part of the first season and also appeared fairly stable in the second season (section 2.3.5). This suggests that providing all "shoots" and roots past and present are

considered, that a functional relationship exists between the above and below organs not unlike the shoot root ratio of annual plants.

In the second season despite the presence of large numbers of buds on the early plantings, there were relatively few shoots produced - presumably due to these buds being located in a limited number of bud clusters. It is interesting to contemplate that if perhaps two buds per cluster could be encouraged to elongate early in the second season, then a larger leaf area would be established and perhaps as a result a greater production of dry matter would occur during the second season. Removal of early spears at the start of the second season may encourage more shoots.

An interesting observation in the second season was that despite possible losses due to rots and to spear growth the increase in bud number appeared to commence very early in the season.

6.1.4 **The cultivars**

Despite UC157 appearing to be more tolerant of low temperatures and having more shoots, buds and roots (section 2.3.4) there did not appear to be a major difference from Jersey Giant in terms of dry matter production (section 2.3.2). Although Jersey Giant was a slow starter it had caught up by the end of the first season. Both cultivars had similar shoot plus bud to root number ratios and responded similarly in February in terms of changes in RGR of the shoot and the root.

6.1.5 **Further work**

It is suggested that a study using a range of cultivars established from seedling transplants, from perhaps an October planting, where regular destructive harvests were taken over a three year period, would extend the scope of this study. It would provide a better understanding in particular of crown development. It is suggested here that such a study would provide, for example, more detailed information on how buds are allocated to clusters and how these cluster may come into growth during the season.

Information from such a study would also allow the development of predictive techniques for assessing future yield potential. The use of distinctly different cultivars would provide data on where differences between cultivars occurred in terms of dry matter partitioning, general growth and development, and the aspects of growth which appear to be most rigidly constrained. The technical difficulties in recovering roots during the destructive harvest of large asparagus plants is acknowledged, but the return on the effort should be significant.

6.2 CO_2 EXCHANGE STUDIES OVER A RANGE OF HIGH TEMPERATURES

6.2.1 Introduction

The CO_2 exchange study provided information on how four distinctly different asparagus cultivars adapted to high temperatures. This information is of value in terms of our understanding of the fern growth stage and on how the photosynthetic system of asparagus performs at high temperatures. This is relevant to the production of asparagus in tropical regions. It would also be of value to draw up a carbon balance for each cultivar but this can only be done partially with the present data.

Carbon balance in plants can be obtained by measuring whole plant photosynthesis and respiration. The net gain of carbon is represented by the net assimilation rate (NAR). As the environments changes, NAR will depend on the changes in whole plant photosynthesis, photorespiration and dark respiration. In the present study as the temperature increase the net carbon gain decreased. All the parameters to calculate net carbon balance were available, except whole plant photosynthesis as photosynthesis was measured on individual pieces of fern rather than the whole plant. Attempts had been made to obtain whole plant photosynthesis using a closed system but problems were experienced with controlling RH and temperature. However the following summary of the experimental data illustrates how the individual measurements made could be used to determine over all carbon balance and the factors determining it, provided total fern photosynthesis was also measured. The decrease in NAR would

be attributed to changes in carboxylation efficiency, quantum yield, Pmax, stomatal limitation and dark respiration. Any remaining could then probably be attributed to photorespiration.

6.2.2 **Photosynthesis**

6.2.2.1 **Ontogenetic changes in photosynthesis**

Research has shown that photosynthesis follows an ontogenetic pattern (Catsky and Ticha, 1980). The present study confirmed that photosynthesis reached a maximum with intermediate aged fern (section 3.3.1). Even though this study was carried out at only two high temperatures (30/20 and 35/25^{0}C) it is considered that the trend will be similar at other temperatures. This demonstrates that it will be difficult to relate growth to photosynthesis where measurements are determined on single fern of a particular maturity. Thus measurements should be made where possible on whole plants. With large plants this presents major practical problems as indicated in section 6.2.1.

6.2.2.2 **Mature fern photosynthesis**

Mature fern photosynthesis decreased with temperatures from 20 to 40^{0}C (section 4.3.3). In the present study maximum photosynthesis was obtained at 20^{0}C, which confirms the previous studies of Sawada *et al.*, 1962; Lin, 1983; Inagaki *et al.*, 1989. Photosynthesis of course is not the only plant process which may contribute to the adaptability of asparagus plants to environmental conditions. For example partitioning has an important role. Increasing temperatures will encourage shoot growth (Yen, 1993), and even though photosynthesis may be reduced at higher temperatures, an increase in shoot numbers will help to maintain photosynthate production.

6.2.2.3 **The photosynthetic response to internal CO_2 and light intensity**

The present study examined how some aspects of the photosynthetic processes were

affected by increasing temperatures. The model used provided some physiological explanations of the response of mature fern photosynthesis to increases in temperature. The ability of the photosynthetic system to reduce CO_2, decreased as the temperatures increased. Quantum efficiency (alpha) and carboxylation efficiency (CE) appeared to be the most sensitive to temperature. Alpha decreased probably because of loss of ATP and NADP in photorespiration (section 5.3.4), and CE decreased probably because the carboxylation capacity of Rubisco decreased due to competition with O_2 (section 4.3.4.3). These findings suggest that photorespiration is of central importance. However, as the temperature increased, the possibility that the enzymes involved in the photosynthetic process were disrupted cannot be ruled out.

Increasing temperature also increased the light compensation point (LCP) (section 5.3.2), which was due to an increase in dark respiration and photorespiration. There was also a possibility that the increase in LCP was due to reduction in quantum efficiency. High density plantings will cause shading to increase and in areas with high summer temperatures, the increase in temperature may place fern close to their LCP so reducing photosynthate production.

In general the predicted Pmax decreased as the temperatures increased (section 5.3.3) implying that the light saturation also occurred at a lower light intensity. This was shown by the increase in Pn700. At $20/20^0$C Pn700 was around 80% suggesting that in the field that asparagus fern of young plants does not require high light intensities to obtain maximum photosynthesis. High light intensity may even reduce photochemical efficiency, especially during the high temperatures of summer.

The CO_2 compensation point increased with temperature (section 4.3.4.2) as expected with C_3 plants. The increase in the Γ was mainly due to photorespiration. However, at $40/20^0$C dark respiration played a more important role.

In general an increase in temperature increased the stomatal resistance as indicated by an increase in stomatal limitation (section 4.3.4.4). The closure of stomata at high temperature was due either to the response of stomata to increasing temperature or

because of the increase in VPD in this experiment at high temperatures, or both. It is probably that the stomatal closure was in response to an increase in VPD as suggested by Raschke (1970) and Berry and Bjorkman (1980). If this is the case, it suggests that during the summer stomatal limitation is probably is a major factor since lack of rain combined with high temperature, would increase the VPD. In tropical regions, however high temperature is accompanied by relatively high humidity, especially during the rainy season. Therefore there should be a small stomatal limitation.

6.2.3 **Respiration**

6.2.3.1 **Shoot and crown respiration**

Shoot and crown respiration were low compared to other species. The Q_{10} of both parameters were also low (around 1.5 and 1.3, respectively) (section 4.3.1). This was possibly because the asparagus plants, upon which the measurement were made, were not growing vigorously. The low Q_{10}, for crown respiration may also have been because restricted O_2 supply to the tightly compacted root system. As much of the root system of asparagus consist of carbohydrate storage roots, it is also possible that respiration is naturally low. For example small potato tubers only have a respiration rate of 4.5 μmol kg^{-1} s^{-1} at 20^0C, similar to the 4 μmol kg^{-1} s^{-1} of asparagus crowns found in this thesis.

6.2.3.2 **Photorespiration and dark respiration of mature fern**

Both photorespiration and dark respiration of mature fern increased with temperature, but photorespiration then decreased at $40/20^0$C (section 4.3.2). This suggests that the enzymes required for dark respiration are more stable compared to the photorespiratory enzymes. As photorespiration has a major role in determining the photochemical and carboxylation efficiencies, the increase of photorespiration with temperature is a disadvantage for the asparagus plant. Unfortunately, at the present time, there is still no suggestion as how to avoid or reduce photorespiration rate in C_3 plants.

Higher Q_{10} value for fern dark respiration compared to whole shoot respiration suggests that there are differences in respiration of ferns and stems. Inagaki *et al.* (1989) found that asparagus stem respiration was lower compared to the fern respiration. Therefore the low shoot respiration rate and its Q_{10} was probably due to low stem respiration.

6.2.4 **The cultivars**

There appeared to be some differences in the photosynthetic response to increasing temperatures between cultivars. It was perhaps not surprising that Brocks, a high temperature cultivar, was better adapted to high temperature, compared at least to Tainan 1 and Larac, two cultivars developed for subtropical and temperate region. The photosynthetic rate of Brocks was lower than Tainan 1 and Larac at 20°C, but Brocks had a higher photosynthetic rate compared to Tainan 1 and Larac at 35/15°C and higher than Larac at 40/20°C (section 4.3.3). This was because at higher temperatures Brocks apparently had higher photochemical and carboxylation efficiencies and also a lower stomatal limitation. This finding suggest that the photosynthetic adaptation of Brocks to high temperature is a combination of effects on gaseous diffusion, energy trapping and performance of Rubisco. Apparently Tainan 1 and Larac are not well adapted to high temperatures, which is understandable when one considers their origins. Photosynthetic data suggests that UC157 is similar to Brocks in being adapted to high temperatures.

6.2.5 **Further work**

This research was carried out at a range of temperatures which are considered high for asparagus plants. Even though the optimum temperature for photosynthesis and the associated parameters appears to be 20°C further study is required to examine the effect of lower temperatures on the CER since the growth of asparagus in temperate regions will often be at lower day temperatures than 20°C.

In addition the AC_i curves in this study were generated at CO_2 and light intensities at which maximum photosynthesis had not been achieved. CO_2 concentration up to 1000 ppm would provide more convincing data by obtaining a better estimate of Pmax and therefore increase the goodness of fit of the model. An improved technique for generating AC_i curves should be developed if high CO_2 concentration is used as it will take a longer time to generate the curves. For example, the increase in temperature can be reduced by blowing cold air rather than using a fan throughout measurement.

Since the differences between cultivars were small it would be desirable to study whole plant photosynthesis over a longer time period than used in the present work in order to further quantify cultivars differences. Whole plant photosynthesis will also allow one to calculate the carbon balance in the plant as discussed previously (section 6.2.1).

The implication of the cultivar comparisons is that differences do occur between cultivars with respect to their photosynthetic rate at high temperatures. This possibility needs to be further examined with a range of cultivars using larger plant samples than were possible in the present programme.

6.3 AGRONOMIC RELEVANCE

In temperate regions, where day temperature are unlikely to be higher than 25^{0}C during the summer periods, asparagus plants would not experience high temperature unfavourable for fern photosynthesis. Other plant processes may of course have different optimum temperatures. With falling temperatures in autumn, where most of fern will be mature, shoot senescence will reduce photosynthesis (Lin, 1983). These phenomena can be related to the field study (Chapter 2) where the shoot RGR decreased markedly at the beginning of autumn.

In tropical regions asparagus is mainly grown in mountains which have temperatures around 15 to 20^{0}C (it is considered that asparagus is a temperate crop and requires

low temperatures for growth), while temperatures in lowland areas are reasonably high (around 25 to 30^{0}C). Based on the photosynthetic criteria of the present study it is likely that asparagus should still grow well in lowland areas providing suitable sites are available. The advantage of growing asparagus in lowland regions is that the humidity is not that high and therefore the risk of diseases is reduced. It could also be argued that the average temperature range from 25 to 30^{0}C is closer to the range of optimum photosynthesis (20^{0}C) and shoot growth (26^{0}C, Yen, 1993). Therefore the performance of asparagus plants in lowland areas could be better since there is a balance between photosynthetic loss (due to high temperature) and more shoot production at close to optimal temperatures (see also the discussion below).

The implications of the photosynthetic study for plants growing in the field, as described in the field study, are as follows :

1. At light intensity of 750 μmol m^{-2} s^{-1} the photosynthetic rate was close to light saturation (80 to 90%) as indicated by Pn700 (section 5.5). This light intensity should easily be reached in the field during the summer. Thus light intensity will not limit growth, at least for young plants. When the plants become older there will be shading between ferns and light distribution within the ferns will become important. Some fern close to the ground will be at the light compensation point, especially in high density plantings. The removal of old fern, as carried out in the mother fern technique (Lin, 1983), would increase light distribution and therefore improve photosynthate production. However, the cost of fern removal would be considerable.

2. According to Wareing and Patrick (1975) source strength is a measure of assimilate production such that : source strength = source size x source activity

= leaf area x net assimilation rate

Leaf area relates to shoot growth and Yen (1993) has suggested this has an optimum temperature of 26^{0}C. Maximum photosynthetic rates in the present study was obtained at 20^{0}C. Thus temperatures between 20-30^{0}C will probably maximize source strength due to the balance achieved between source size and source activity.

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APPENDIX

Appendix 1. Base fertilizer used (kg/m^3) for peat media asparagus seedling transplant.

Potassium nitrate	1.0
Superphosphate	2.2
Dolomite (lime)	3.0
Micromax	0.6

Appendix 2. Liquid feeds has been used*1 for asparagus seedling transplant (gram/100 litre).

Ammonium nitrate (NH_4NO_3)	13.7
Mono ammonium phosphate (MAP)	13.3
Potassium nitrate (KNO_3)	25.6

*1. This liquid feeds provides 100 ppm N, 135 ppm P and 100 ppm K.

Appendix 3. Soil sample analysis in the field experiment site.

Sample	pH	Ca	P	K	S	Mg	Na
Soil test	6.3	14	53	12	3	26	6

Appendix 4. The disease and pest control programmes

Common name	control	rate
Ridomil	phytopthora	1 kg a.i./ha
Metasystox	aphids and thrips	1.1 l/ha
Mesurol	slugs	5 kg/ha