CROWN DEVELOPMENT AND RELATED CHANGES IN MORPHOLOGY AND PHYSIOLOGY OF ASPARAGUS PLANTS ASSOCIATED WITH THEIR PRODUCTIVITY

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Te Kunenga ki Pūrehuroa
Inception to Infinity: Massey University's commitment to learning as a life-long journey

ABSTRACT

The results are presented of eight experiments designed to investigate the influence of interrelationships between bud population dynamics and carbohydrate supply from root stores on spear production in asparagus (*Asparagus officinalis* L). These investigations involved studies in the field and the greenhouse, and using aeroponics and hydroponics techniques to facilitate non-destructive studies of plant development. The evidence indicated that spear yield was limited by the number of buds of adequate size for developing into marketable spears, rather than total bud number. It was shown that bud development continues throughout the harvest period. About 14% of these buds contributed to fern production after harvest, but the majority were involved, following a period of dormancy, in development of the next season's spears. Approximately 16% of the new buds contributed to spear yield in the current harvest, 68% were dormant until the following summer and contributed to 18% of total buds at that time. Spear production was most efficient in plants with large crowns, since the effects of correlative inhibition on spear development were greater in small than large crowns. Nevertheless, increase in crown size in terms of root mass is not necessarily accompanied by an equivalent increase in bud number or cluster number, and bud availability is potentially an important yield limiting factor. However, large crowns reduced the period of correlative inhibition within a bud cluster. Crown size and bud population were sensitive to nutrient supply, and it is suggested that control of nutrient supply over the harvest period may be best achieved by use of slow-release fertilizer or split application of nitrogen. Carbohydrate partitioning and possibly photosynthetic rate were also sensitive to daylength, and there was some evidence of genotypic variation in the response to daylength changes and contrasts. Principal component analysis indicated that numbers of buds and bud clusters, plant size and chlorophyll content were the main determinants of spear yield, and cluster analysis demonstrated potentially important genetic variation for these variables in potentially high yielding cultivars. Spear yield is the product of harvest intensity and harvest duration, and harvest duration itself was shown to be sensitive to genotype and management effects on bud initiation and development. A conceptual model is used to illustrate the influence of bud population and bud cluster characteristics on harvest intensity and duration, and on spear yield, and the relative importance of management manipulation of bud dynamics and carbohydrate supply to spear yield.

Keywords: carbohydrate partitioning, yield, hydroponics, aeroponics, bud dynamics, bud clusters, crown size, chlorophyll, yield limiting factor, daylength, plant growth, correlative inhibition, multivariate cluster analysis, principal components.

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Setetes embun membasahi keringnya permukaan tanah

membawa sejemput tali kehidupan.

Sekecil apapun pengetahuan memberikan hikmah

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TABLE OF CONTENTS

List of Tables

LISTS OF FIGURES

CHAPTER 1

GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1. INTRODUCTION

Asparagus (*Asparagus officinalis* L.) is believed to be a native of the eastern Mediterranean (Feher, 1992). It has been cultivated since the times of Greeks and Romans (Salunke and Desai, 1984; Hexamer, 1914 cited in Drost, 1997). Nowadays the plant is widely distributed all over the world including tropical areas (Grubben, 1992; Cueto and Lesnick, 1999) and has become an important international commodity. The demand for fresh asparagus year round is very high in some countries such as European countries and Japan (Bakka et al., 1999; Sato and Motoki, 2002). This means that asparagus has a high value for export and is cultivated in many different countries (Valentine, 2001; Benson, 2002; Guangyu, 2002). In addition to European countries, the USA, Peru, and China are areas of large scale production of asparagus (Feher, 1992; Benson, 1999; Benson, 2002) with smaller amounts grown in countries such as Australia, New Zealand and Canada. Asparagus can be harvested as either white asparagus or as green asparagus. White asparagus production tends to predominate in Europe. The main difference is that the spears of white asparagus are harvested just before they emerge through the soil surface, whereas green asparagus spears are harvested when some 18-25 cm above the soil surface.

Maximizing asparagus production (yield per hectare) of high quality is the goal for every production area including New Zealand. However, compared to production in many countries such as in US (3.39 t.ha^{-1}) (Purdue University, 2003) and in Peru (6 t. ha^{-1}) (http://www.fas.usda.gov/htp2/circular/1998/98-09/aspara.pdf), the average yield of asparagus per ha in New Zealand is still low (2.5 t.ha^{-1}) (NZNAM, 1997; Vegfed, 2003). Asparagus productivity is a function of genotype and environment. Clearly with a perennial crop such as asparagus choice of genotype is pivotal, but the influence of environment (such as temperature and choice of soil type) and susceptibility to pests and diseases can also play a major role.

One of the major constraints on asparagus spear production in the spring relates to carbohydrate level in the storage roots (Robb, 1986). For temperate climates such as in New Zealand, the carbohydrate reserves in the crown for the next harvest season's spear production depend entirely on the efficient replenishment by the fern the previous summer. During spring, spear development uses the carbohydrate reserves stored in the crown the previous summer. Only after harvesting ceases and fern is established does the asparagus plant start to store carbohydrate into the roots. This stage is very important for subsequent potential yield. Both environment and plant can determine accumulation of reserved carbohydrate. One of the current environmental factors believed to influence accumulation of reserve carbohydrate is daylength (Sudjatmiko et al., 1997; Karno, 1999; Woolley et al., 1999). Asparagus spear production will also depend on bud production on each plant, since edible spears develop from these buds. Any limitation to bud number will also affect spear production, but the extent to which this limitation may occur has not previously been explored. Investigation of how bud numbers increases during early plant growth and whether bud number can be modified needs to be studied.

The availability of carbohydrates in storage ensures sufficient support for spear growth during the harvest period. The demand for increasing production and constant availability of asparagus leads to an extended harvest period which exposes the plants to running out of either buds or carbohydrates. Prolonging spear harvest may mean all the larger bud sizes are used for the market and possibly also small buds. As harvesting ends, the plants may only have small buds to develop into ferns, giving poor fern establishment. Factors determining whether plants run out of carbohydrates before bud numbers become limiting or bud number will run out first are not yet known.

The main objective of the research described in this thesis was to study interrelationship between the development of bud numbers during plant development and subsequent spear growth in relation to storage carbohydrate. The specific objectives were as follows:

- to determine the effects of daylength and pot size on asparagus seedling growth;
- to understand the effects of environmental conditions on asparagus plant development in term of morphology and physiology, using soilless culture for easy access to the crown;
- to determine the influence of cutting height, cultivars and plant sex differences on asparagus spear yield;
- to measure spear elongation in relation to correlative inhibition;
- to follow bud distribution under field conditions in relation to potential yield;

1.2. PRODUCTION OF ASPARAGUS

1.2.1. World asparagus production

Approximately 140,000 ha of asparagus were grown world-wide in 1990 (Nichols, 1990). Over the next decade world demand particularly for fresh green asparagus increased, and asparagus areas expanded to 218,335 ha (Benson, 1999), then another 31,110 ha during the next four years (Benson, 2002). In many traditional producing areas of the world the availability of land suitable for asparagus production is limited (Grogan and Kimble, 1959; Yang, 1982; Schofield, 1991), but large expansion has occurred in China (Guangyu, 2002). The cost-effectiveness due to distance, consumption demand and all year long (mother fern) or alternate production has driven some areas to be more profitable than others (Bussel et al., 2002 and 2003). Compared to China for instance, to export fresh asparagus to Japan, New Zealand has to pay considerably more for air freight due to the longer distance. Fortunately New Zealand asparagus production is counter-seasonal to countries in the northern hemisphere, and harvests when most of these countries not producing. Good spear quality is also essential for production to be competitive. In 2001 many US exporters failed to compete with those from countries which produce in large quantity (California Asparagus Commission Newsletter, 2001), New Zealand exporters survived due to maintaining good spear quality.

1.2.2. New Zealand asparagus crop

The current estimated planted area for asparagus in June 2002 was 2015 ha (Wensvoort, 2003) but there are considerable areas of free-draining soils in New Zealand that are also suitable for asparagus production (Schofield, 1991). Annual production is c. 8000 t, of which c. 4000 are processed for export and 1500 t are exported fresh. Domestic fresh consumption is c. 2000 t annually and the domestic market consumes about 500 t of processed asparagus. New Zealand's asparagus production contributes 2% of total world production (Schofield, 1991; NZNAM, 1997). Although it is a small percentage of the world production, total asparagus production for export contributed $ 16,284,576 (FOB) to total export vegetables ($ 481,517,198 of FOB) (http://www.vegfed.co.nz, 2003).

While there is still opportunity in world market for New Zealand asparagus exporters, problems are encountered in raising production. Over-all decline of asparagus production in the 1980's in New Zealand has been reported due to disease such as tip rot (Menzies, 1984), phytopthora (Falloon and Fraser, 1991), *Fusarium* (Schofield, 1991) or carbohydrate depletion because of the plants getting old (Robb, 1983; Falloon and Fraser, 1991).

In temperate climates, asparagus plantings reach peak production after 5 – 8 years and slowly fall thereafter so that the commercial life is c.10-20 years (Falloon and Tate 1986; Bussell and Ellison, 1987). Much of the area that is in production in New Zealand is planted with old cultivars and is nearing the end of its commercial life (Falloon and Fraser, 1991) due to both age and Fusarium. The decline of asparagus productivity has been defined by Grogan and Kimble (1959) as a gradual decrease to the point which it is no longer profitable to maintain. Typical symptoms include a reduced number of fern stalks and thinner stems. Spears may shrivel or wilt at any stage of growth. Ferns are usually yellowed and stunted with reddish brown vascular discoloration and rusty flecks or lesions on the external layers of the lower portion of fern stalks. Reddish discoloration may extend into the crowns from fern sockets or from discoloured fleshy roots. Feeder roots may be absent or shrivelled and where present, show discoloured, reddish areas at the junction with fleshy storage roots. Some of the fleshy roots show vascular discoloration and many collapse completely. Soft rot bacteria or secondary organisms are usually associated with such collapse.

Replanting with new cultivars on fresh sites that are capable of increasing productivity is preferable as replanting old asparagus fields usually results in poor vigour and low yields (Grogan and Kimble, 1959; Elmer and LaMondia, 1999).

1.3. BOTANY OF ASPARAGUS

Asparagus (*Asparagus officinalis* L.) is a vegetable belonging to the genus *Asparagus* of the family *Liliaceae* (Watson & Dallwitzs, 1992; Tutin et al., 1980). There are more than 150 species of asparagus but only *Asparagus officinalis* L. is edible (Nonnecke, 1989). Asparagus is a monocotyledoneous and dioecious perennial plant grown for its edible spears. Asparagus produces male and female florets on separate staminate and pistillate plants. Female and male plants are a very important trait in asparagus potential production (Ellison et al., 1960; Ellison et al., 1990) (see section 1.4.3).

Morphology of asparagus can be divided into two major parts: above ground (aerial) and underground (Fig.1.1). The plant consists of above ground stems (referred to as the fern) bearing cladophylls (which perform as leaves but are actually modified stems) and scale leaves (together referred to as the fern), underground stems (rhizomes), and fleshy (storage roots) and fibrous roots (feeder roots). The fleshy roots serve as storage organs while the fibrous roots are absorption organs. The fleshy roots come from the rhizome and serve as storage organs and also supply moisture and nutrients while the fibrous roots are absorption organs for the uptake of water and nutrients (Nichols, 1988; Nonnecke, 1989).

The plant is grown for its succulent, fleshy spears which, in temperate climates, appear after a winter rest period. The spears develop from the buds, and every bud on the rhizome can potentially develop into a spear. The spears grow and, if they are not harvested, become fern. The true leaves are the scale like structures that appear at the tip of the spear and at each node along its length (Fig. 1.1.). As the plants grow, lateral stems form in the axils of these leaves creating branching foliage sometimes referred to as pre-ferns and these lateral stems also form small, scale-like leaves along their length. Modified stems, or cladophylls come out of the axis scales growing in whorls from the axils of the leaves. When fully developed these constituent foliages give the plant its fern-like appearance (Pierce 1987; Nonnecke, 1989).

In asparagus, cladophylls function as the main site for photosynthesis (Sawada et al., 1962; Downtown and Torokflavy, 1975; Lin and Hung, 1978; Inagaki et al, 1989; Faville, 1999) whereas the main leaves (scales) are lacking this physiological function. Photosynthesis also occurs in stems and green spears (Blasberg, 1932; Inagaki et al., 1989), but not sufficiently to balance out respiration (i.e. no net photosynthesis).

Flowers develop in the axils of scales. Asparagus is a dioecious crop, that is, one plant bears male and the other female flowers. In reality, flowers have both stamen and pistil but in male flower the style and in female flower the stamen is stunted (Jones and Robbins, 1928 in Feher, 1992). Between the two types hermaphrodite forms are also found with viable pistil and stamen. Following pollination the asparagus female flowers develop into berries. When mature the berries are red or brownish-red, and have a diameter of 8 mm (Feher, 1992). Each berry has 3 locules with 1-2 seeds in each.

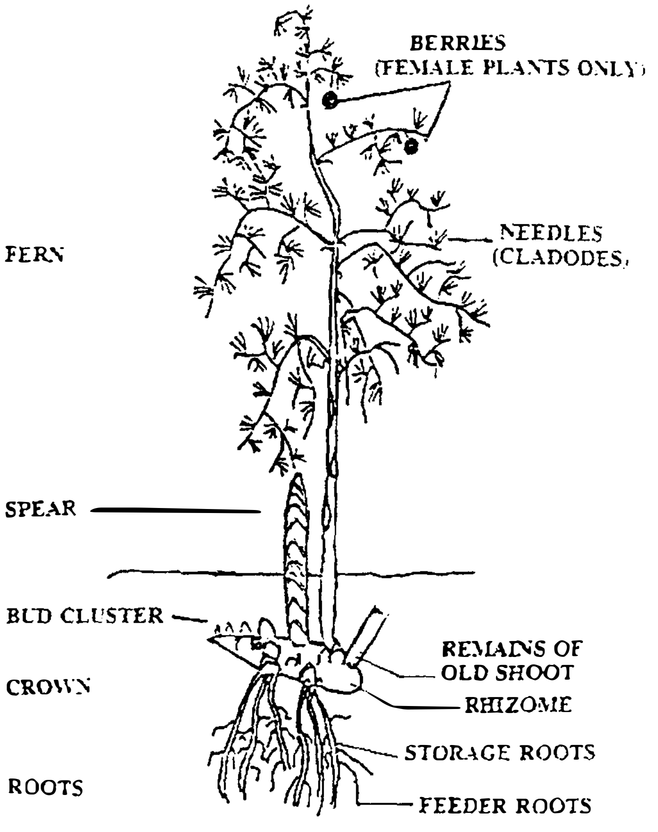


Figure 1.1 The structure of an asparagus plant (After Nichols, 1996).

1.4. MORPHOLOGY AND PHYSIOLOGY OF ASPARAGUS

1.4.1. Plant morphology

1.4.1.1. Morphology of rhizome and buds

Plant morphology is related to development of the plant but not necessarily to growth, which is defined as an irreversible increase in volume (Salisbury and Ross, 1992). Morphological description of asparagus is limited (Feher, 1992), especially as related to bud morphology. Very little study has been done on bud development (Blasberg, 1932; Bigard, 1973; Duangpaeng et al., 2002).

Asparagus plants (see Fig. 1.1) consist of the crown (rhizome plus storage roots as the underground parts) and fern (the above ground parts). The rhizome of asparagus develops from un-elongated basal internodes of old stems (Blasberg, 1932). It is actually a thick, ligneous, underground shoot in a horizontal position with slow sympodial development (Feher, 1992).

Bigard (1973) followed rhizome development from four month-old asparagus plants and from three year-old plants in the field and made a schematic diagram (Fig. 1.2). After the germination and seedling stage, the buds initially developed from the main axis were called “axial buds”. These buds were thought to be the primary axis for future crown development and potential for the yield whereas “lateral buds”, buds at the base of primary (axial) buds remained initially dormant (Blasberg, 1932; Bigard, 1973).

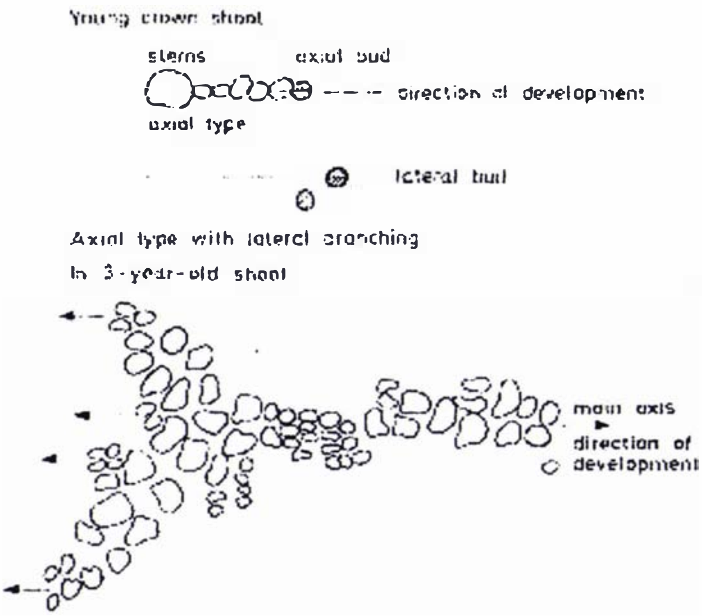


Figure 1.2 Development direction of rhizome with initial lateral branching (after Bigard, 1973).

From observation of the rhizome of three-year old plants, rhizome may develop from the proximal end of the main axis in the opposite direction and the "axial buds" grow further, lengthening the distance of rhizome (Bigard, 1973). Lateral buds may grow out at an angle from the primary axis (rhizome) and form individual clusters that gradually become independent of one another (Bigard, 1973; Nichols, 1988). Eventually the tissue between the clusters disintegrates and a cluster or group of clusters can act as an independent plant.

Duangpeng et al. (2002) observed that the buds from axils of one-year old asparagus plants grew in several directions, and they categorized the initiation pattern of asparagus crowns into three types: A, B, and C. After the first initiation of the primary axis, type A initiated a new group of further buds in one direction opposite to the proximal end. This type only produced one axis (rhizome). Type B produced two groups of new bud groups on the axils; each of the new bud groups grew opposite to one another along with initial buds on the axils. Hence, type B developed new groups of buds as described in Bigard (1973). The third type (C) produced three new bud groups. Two new bud groups were similar to type B, but the third new bud group grew from the side of first initiated group of buds. There is a possibility that the third new group of buds developed from the buds described as “lateral buds” in Bigard (1973). But Duangpaeng et al. (2002) did not specify any “lateral buds” in their study. Therefore, the increase in size of the crown may come from the development of both “axial” and “lateral” buds as in Bigard. In Duangpaeng’s study (2002), dormant buds were those in the first axial group that did not sprout after the following groups of buds grew into spears. No information was given about “lateral buds”.

Matsubara et al. (1991) were able to proliferate more buds from lateral buds by growing them *in vitro* using a combination of 3.9-39% ancymidol and 3% sucrose. An additional supplement of 11.7 μM ancymidol resulted in vitrified shoot formation. Earlier, Yang (1977) developed a tissue culture technique to establish aseptic stock plants from lateral buds of asparagus spears. The rooted plantlets from the buds on the stems of aseptic stock plants were transferred into peat pots and maintained under mist, then transferred into soil pots when shoots start growing. What Bigard (1973) describes as “lateral buds” may be the buds grown from secondary bud clusters branching from the main axes. The branching scheme for bud cluster direction is important since it will determine the extension and uniformity of the crown. The uniformity and extension of bud number will determine the crown size which is important for seedling establishment and yield potential (Krarup et al., 2002; Krarup and Krarup, 2002).

1.4.1.2. Timing of bud formation

Total spear yield of a cultivar will depend on individual spear weight and the number of the spears which developed from the buds. Tiedjens (1924) proposed that few buds and roots were formed during the harvesting season. No increase of bud number occurred or, if any, very few buds were formed during harvesting (Haynes, 1987). Both Haynes (1987) and Robb (1984) indicated that bud and root formation mostly occurred after harvest. But the data of Wilson et al. (1999) appeared to demonstrate that buds were formed during as well as after the harvest period. They distinguished between old and new buds by the colour of buds. Dark brown (old) are those initiated in the previous season and light brown (new) are those produced in the current season. Although they stated that the buds were formed after harvest ended, the number derived from their graphs showed an indication that new buds could have formed before harvest ended. An increase of bud production up to 20-30 buds occurred between early December and 9 January of which about 15 to 20 buds formed in December was obtained in their treatment. The inconsistency of results from different studies regarding bud formation leads to the questions whether bud formation is only associated with carbohydrate production during summer and autumn? An investigation of bud formation during different seasons is needed.

1.4.1.3. Spear production

Once a bud breaks, it grows into a spear (the shoot without branches) (Feher, 1992). The spears grow in a definite order (Blasberg, 1932; Lekholoane, 1997), first the oldest bud followed by the next adjacent bud in the cluster (Hughes, 1992). As time progresses, spears growing at later times are thinner (Poll et al., 1990). Spear size is thought to be cultivar dependent. The buds start growing when the temperature reaches at least 12^{o}C (van Os and Sominse, 1988), 11 ± 3^{o}C (Dufault, 1996) or 10^{o}C (Dean, 1999) providing there is enough soil moisture.

Another environmental factor influencing spear emergence is soil type. Sandy loam produced significantly higher spear yield, spear number, and better spearhead quality than covering with a heavier soil (Kailuweit and Krug, 1995; Liao et al., 1999). In comparison, spear diameter, one of the spear quality characteristics, is often larger from crowns grown in soil rather than those in a forcing system such as hydroponics or potting soils (van Os and Simonse, 1988).

The uppermost part of the spear, the tip, is covered by scales (the true leaves) overlapping each other (Feher, 1992). When the spears are not harvested, these scales open and branches are formed. These spears are not marketable. The elongation of the spears is affected by many other internal and external factors (see section 1.5.2.4). The branches of these shoots will later develop into fern-like structure (cladophylls) around the internodes, functioning for photosynthesis. The stem developed from a spear is called fern, stalk (Uragami et al., 1996) or shoot in different studies. The definition of shoot causes confusion because some studies refer to the shoot as mainly the fern (Hartmann, 1985; Battilani, 1997; Faville et al., 1999a) but others refer to the whole upper parts of the plants (all ferns and spears together). For our study, the shoot refers to the combination of ferns and spears while fern refers to the stem that has already developed cladophylls.

The numbers of ferns and their height are cultivar dependent (Knaflewski, 1985; Uragami et al., 1996). The number of ferns during summer can be 10 – 12 ferns per crown but numbers have been observed as high as 40 ferns on a plant (Feher, 1983 in Feher, 1992).

Along with the shoot development, roots also develop and grow (Duangpaeng et al., 2002). Several buds usually form a cluster and a cluster normally consist of 2 to 9 buds but can be more than 9 buds (Nichols, 1988). New roots develop from the bases of actively growing buds. The roots are very thick and fleshy and are the primary food storage organs of the plant. The large roots have a heavily suberized epidermis, but a few root hairs may be present. The bulk of the mass of the root is loosely fitting cortex, which through cell division gives a considerable increase in diameter.

During seedling establishment, the size of crown and its uniformity are important for transplanting both in the field (Fisher, 1982; Matsubara and Harada, 1996; Sudjatmiko et al., 1997) and in forcing system (van Os and Simonse, 1988; Wagenvoort and Ammerlaan; 1988) and thus for yield performance.

1.4.2. Physiology of asparagus

1.4.2.1. Carbohydrate and life cycle of asparagus

Asparagus yields are dependent on the development of spears from buds initiated in the season prior to crop production (Tiedjens, 1926; Blasberg, 1932). In general it is thought that bud initiation begins after fern development in the summer and continues into the fall (Dufault and Greig, 1983; Haynes, 1987). Thus, bud initiation, fern development and spear harvest are important aspects of the asparagus life cycle.

Spear production will depend on the level of carbohydrate accumulation in the storage roots the previous year. There are four phases of carbohydrate balance in asparagus (Fig. 1.3): dormancy stage, spear production stage, fern renewal stage, and carbohydrate accumulation stage (Nichols, 1996). Haynes (1987) showed that during dormancy, no buds grew and no other activity occurred so there was little reduction in total soluble carbohydrate. But Pressman et al. (1993) working in Israel demonstrated loss of fructans at more than 30% during the dormancy period and suspected this was due to temperature-induced root respiration. The percentage of carbohydrate loss depends on temperature. Hughes (1992) calculated the carbohydrate loss during asparagus harvest at 12.5 ^{O}C (9.8% of dry weight) was lower than at 20^{O}C (14.2% of dry weight). This indicates that carbohydrate loss in dormant asparagus will depend on winter temperature from different geographic regions, and could range from 15 to 30% of stored carbohydrate. Many other studies also showed that the carbohydrate loss due to maintenance respiration could be more than 40% (Danckwerts and Gordon, 1987; Gifford et al., 1984).

Harvest commences in early spring, and total carbohydrate reduces during the spear production stage. Prolonged or excessive harvest during this spear production stage will deplete carbohydrate resources and reduce the plants potential to replenish these reserves during the carbohydrate accumulation stage, and thus a low starting point of total carbohydrates for the following year (Shelton and Lacy, 1980; Haynes, 1987). Total carbohydrates reduce even more between the end of harvest and fern establishment (fern renewal stage). The carbohydrate accumulation stage follows the fern renewal stage. Many studies (Shelton and Lacy, 1980; Haynes, 1987; Pressman et al., 1989) show that an efficient replenishment stage in the asparagus life cycle is crucial to potential yield. In this stage, photosynthesis is active and buds, storage roots and ferns are produced. The utilization of carbohydrates for fern growth may be strongly switched to storage roots in mid February (Sudjatmiko et al., 1997) due to reducing daylength in southern hemisphere. The change of partitioning to the roots after January was also recorded by Faville et al. (1999c) in Waikato (37.25°S), New Zealand. They measured partitioning of ^{13}C in the asparagus field, and noticed that there was very little new fern establishment after January and that the majority of the assimilated ^{13}C was translocated from the labelled fern to the storage roots, and in small amounts to buds and rhizome. These results were similar to Woolley et al. (1999) using ^{14}C.

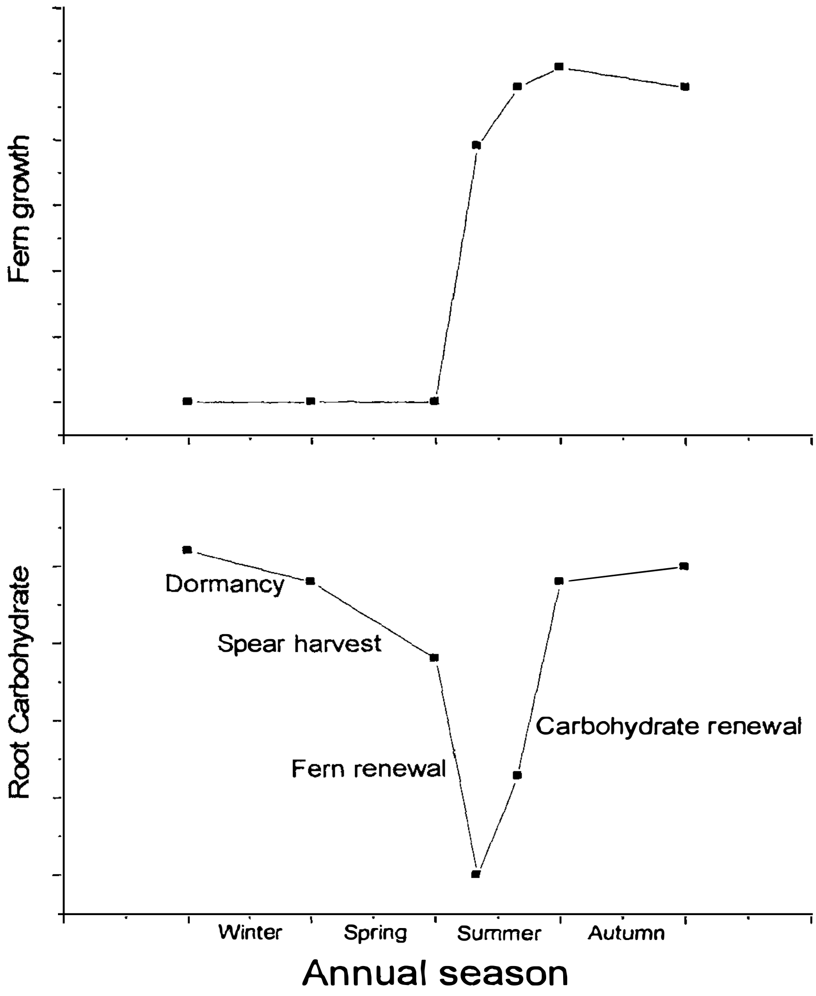


Figure 1.3 Schematic depletion and rejuvenation pattern of asparagus storage carbohydrate and fern growth during an annual growth cycle in temperate climate (Adapted from Pressman et al., 1993; Nichols, 1996; Wilson et al., 1999).

Furthermore, Karno (1999) and Woolley et al. (2002) found that when daylength was reduced to 14 h, there was an abrupt increase in the amount of dry matter partitioning to the storage root compared to the shoot system resulting in changes of root:shoot ratio.

1.4.2.2. Root:shoot ratio

Increasing asparagus root:shoot ratio will produce a larger carbohydrate pool in the storage roots and, as a result, possibly provide a higher potential yield. Root:shoot ratio is commonly used to describe the changes in the relationship between dry weight partitioning to the root and to the shoot. It was found that the use of an allometric relationship between shoot and roots could provide a useful measure of dry matter distribution irrespective of plant size (Hughes et al., 1990).

In a constant environment, the relative growth rates of root and shoot stay at a constant ratio k (the allometric constant) to each other, although a developmental switch such as transition to flowering can alter k. After a change in environment, partitioning between root and shoot alters, usually in such a way as to ameliorate the consequences of the change (Wilson, 1988). For instance, exposure to high concentration of salt in asparagus (Uno et al., 1996) results in relatively more shoot growth, and exposing to limiting concentration of nutrient such as Boron in asparagus (Douglas et al., 1989) results in relatively more root growth. Thus, the allometric constant (k) can indicate plant adjustment to the change of environment.

The growth of asparagus fern during summer is very crucial since the photosynthate during this period can be stored in the roots. The ability of the plants to have good establishment of the fern starts when the plants are in their seedling stage, as Sudjatmiko et al. (1997) showed in their study to support the importance of shoot:root dry weight ratio at seedling stage. The observed increase in root:shoot ratio was probably related to survival of the crown during adverse conditions and could involve inhibition of further shoot growth by established ferns and changes in carbohydrate partitioning brought about by environment. The environmental change is not likely to be temperature as this is fairly constant during late January and early February, but may be daylength (Sudjatmiko et al., 1997; Woolley et al., 1999).

When the partitioning to the shoot and root is expressed in root:shoot dry weight ratio, the ratio does not indicate how many roots or buds are available. The ratio of bud to root number is often used to give information on how many roots support each bud. In addition, bud number is essential for potential yield. The relationship between root number, root mass and bud number in asparagus has never be reported. In general, it is assumed that the heavier the mass the greater the number of roots or shoots, but variation in root or shoot weight may reflect differences in length, thickness or both. It is also generally accepted that there are characteristic differences between cultivars in bud production. Cultivar 'UC157', for instance, produces more spears (buds) than 'Jersey Giant' (Sudjatmiko, 1993), but whether the increase in root mass will necessarily result in the production of more buds on the rhizome has not yet been reported. Dufault and Greig (1983) believed the number of buds produced on asparagus crowns indicated the potential for yield in the following growing season and they did not find a correlation between shoot number and fresh weight with bud number in seedlings, but found bud number and root number to be the best indicators of quality crown production. Over the 10 weeks after emergence, the ratio of root:shoot number steadily increased from 2:1 to about 6:1 for 'UC800' and from 2:1 to 8:1 for 'UC157'. But this increase of root number did not affect the fern:crown fresh weight ratio which remained at 1:1 throughout the season, indicating an equal partitioning of growth between shoots and roots. Looking at shoot:bud number and root:bud number ratios, the shoot:bud number reduced over the season and ratio of root:bud number stabilized toward the end. These ratios indicated that at the beginning the shoots were produced more than the buds, but the buds later on were increasing more than the shoots, stabilising the ratio of root:bud number. Root number and bud number correlated fairly well to crown fresh weight with r = 0.79 and 0.77, respectively. However, root number and bud number were correlated highly significantly (r=0.91) making the root:bud number ratio suitable for predicting potential yield. Hence, bud availability is of interest as well as storage carbohydrate availability to improve yield production.

1.4.2.3. Carbohydrate metabolism in asparagus

Carbohydrate in asparagus is very important because spear growth depends on utilizing reserve carbohydrates. The major reserve carbohydrate in asparagus is in the storage roots, with fructan as a major component. This is often the single most important internal factor determining yield (Shelton and Lacy, 1980).

Fructan is major storage carbohydrate of many 'cool season' (C_3) grasses, particularly members of the sub-family Poaideae (Chatterton et al., 1989). It is a polymer of fructose based on sucrose. Fructans may play a role in drought resistance and low temperature adaptation in many plants (Pollock, 1986; Pressman et al., 1989; Tognetti et al., 1990), and its function for short term and long term storage in many temperate grasses and cereals (Pollock and Cairn, 1991; Bonnet and Simpson, 1992; Yukawa et al., 1995; Henson and Livingstone, 1996) and some other plants including asparagus (Cairns, 1992; Shiomi, 1993) is well recognized. Fructans are stored usually in vegetative parts of the plants such as tubers, rhizomes and roots (Ernst et al., 1995; Schubert and Feuerle, 1997) and to a lesser extent in leaves (Schnyder, 1993, Sims et al., 1993) and stems (Bancal and Triboi, 1993). In asparagus, fructans are the major carbohydrate and are mostly stored in the storage roots (Martin and Hartmann, 1990). Up to about 60% of the root dry weight can be fructan for mobilization during spear, fern and new root growth (Nichols, 1996).

Fructans accumulate when there is an excess of photosynthate over that required for respiration and growth and they are hydrolyzed when current photosynthesis cannot supply the carbohydrate required for growth. For short term storage, carbohydrates are accumulated in the leaves during light period and are remobilized at night during dark period (Pollock, 1986). For long term storage, fructans are stored in the stem, rhizome and roots, and re-mobilized later for growth.

Chemical structure of fructans in the plant is related to sucrose from which they are derived. Three enzyme systems have been identified in fructan metabolism: Sucrose:sucrose fructosyl transferese (SST; EC 2.4.1.99), fructan:fructan fructosyl transferase (FFT; EC 2.4.1.100) and fructan exohydrolase (FEH; EC 3.2.1.80). The first two enzymes are involved in fructan synthesis and the latter is involved in hydrolysis of fructan.

Fructan is first synthesized by transferring one molecule of sucrose to another by sucrose-sucrose fructosyl transferase (SST) to form trischachharidel-kestose (glucose-fructose-fructose) and release one glucose.

$$\text{G-F} \quad + \quad \text{G-F} \quad \xrightarrow{\text{SST}} \quad \text{G-F-F} \quad + \quad \text{G}$$

sucrose sucrose 1-kestose glucose
sucrose (trisaccharide)

In the next stage, a higher degree polymerization is formed by transferring a fructose residue from one fructan to another by fructan:fructan fructosyl transferase (FFT).

$$\text{G-F-F} \quad + \quad \text{G-F-F}_n \quad \xrightarrow{\text{FFT}} \quad \text{G-F-F-F} \quad + \quad \text{G-F-F}_{n-1}$$

1-kestose

Three types of trisaccharides can be formed (see Fig. 1.4). Fructose linked to carbon 1 of the fructose moiety of sucrose forms 1-kestose or isokestose. This group called inulins consists of fructan with β-(2→1) linked fructofuranosyl moieties with a terminal glucose residue. Inulins may reach DP up to 100 but are mostly found up to 30-35 DP in plant parts. The second groups have 6-kestose as the basic structure with

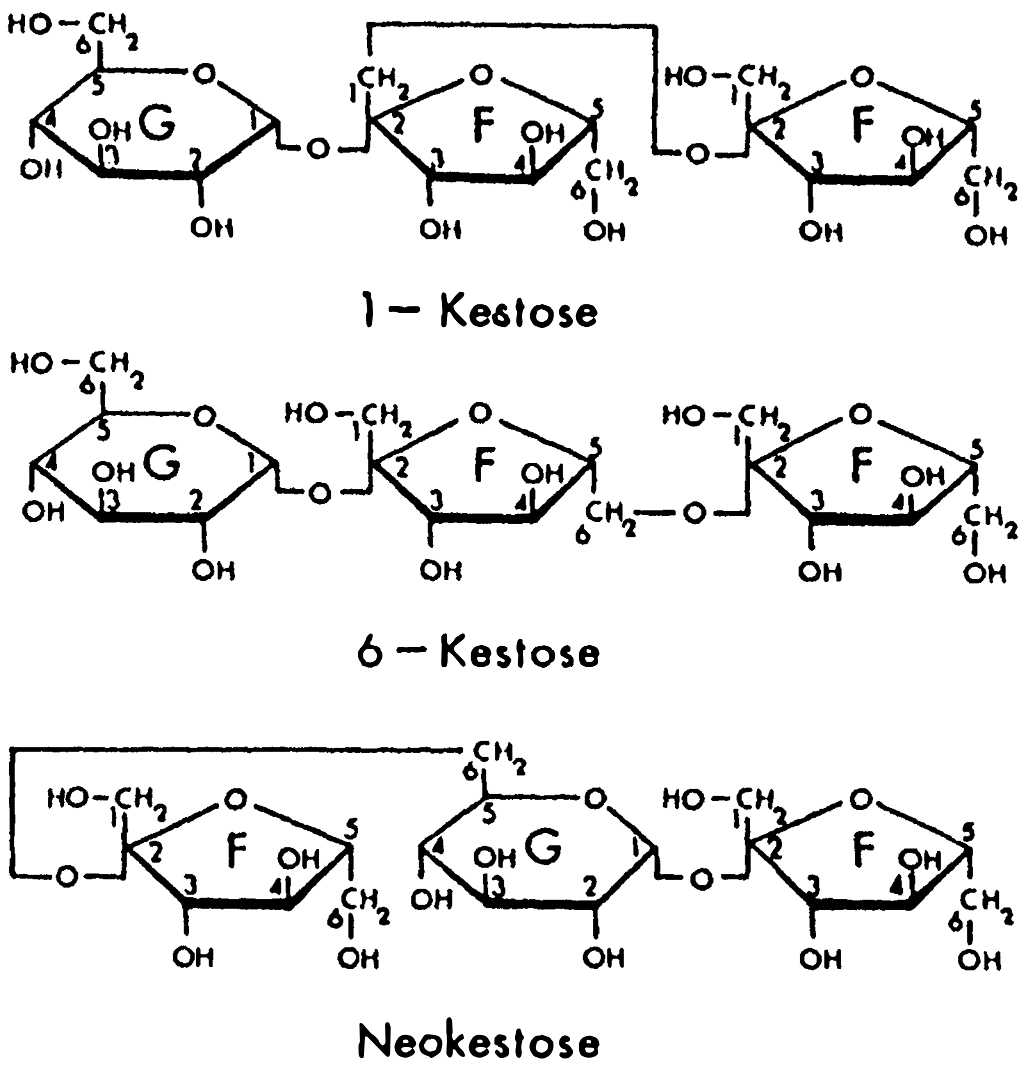


Figure 1.4 Fructan trisaccharides are formed by adding a fructose by adding a fructose molecule to sucrose at the 1-carbon of fructose (1-kestose), the 6-carbon of fructose (6 – kestose) or the 6-carbon of glucose (neokestose). (After Nelson and Spollen, 1987).

connection between one or more fructose moieties forming β-(2→6) linked polymers of fructose with a terminal glucose. This group is called Levans (or phleins) and the degree of polymerization can reach up to 300 in orchardgrass (Yamamoto and Mino, 1985). The third group is similar to inulins but have only fructose moieties at the terminal because the glucose is internal (Nelson and Spollen, 1987).

The last enzyme, fructan exohydrolase (FEH), metabolizes fructans by removing fructose molecules:

$$\text{G-F-F}_n \xrightarrow{\text{FFT}} \text{G-F-F}_{n-1} + \text{F}$$

Eventually, only sucrose is left which can be hydrolyzed by invertase (EC 3.2.1.2.6).

When carbohydrate consumption in sink tissue exceeds supply from current photosynthesis, fructans are hydrolyzed and mobilized. This mobilization occurs when the plants grow under warm conditions following a cool period (Pollock, 1982) such as in asparagus as reported by Nichols (1996) and in perennial grasses in the spring (Pollock and Jones, 1979). The mobilization of fructan in asparagus occurs rapidly during spear growth. In this stage, the loss of carbohydrate can be accelerated when spear removal is frequent during harvest since this reduces correlative inhibition.

1.4.2.4. Correlative inhibition

Each of the many buds on the crown is potentially capable of producing an upright stem. According to Tiedjens (1926) there is a regional inhibition in the crown in the vicinity of the growing spear, delaying the sprouting of adjacent buds until the spear is removed. It is said that the inhibition on bud break and spear growth is caused by apical dominance (Tiedjens, 1924; Kretschmer and Hartmann, 1979). However, unlike apical dominance in most other plants, in asparagus it is the bud at the base that suppresses the buds above. Therefore, in asparagus, the term correlative inhibition is a more appropriate term than apical dominance.

Spear elongation depends strongly on temperature (Poll, 1996). Since the temperature varies among locations, within and between seasons, the time when spears start to emerge and subsequently the optimum interval between harvests both vary (Dufault, 1996). This is due to the fact that the faster the spear elongates, the sooner the release from correlative inhibition occurs. Other factors such as water and nutrients can affect the release of correlative inhibition, probably acting through effects on hormone levels.

Apical dominance, a specific form of correlative inhibition, is the control exerted by the shoot tissues over the outgrowth of lateral buds (Hosokawa et al., 1990). The existence of apical dominance in many crops is extremely significant. There are important agricultural implications for understanding the control mechanism of lateral bud outgrowth by the apical structures of the shoot. The yields of some crops (e.g. pigeon pea, maize, and blueberry) are increased by reduction of apical dominance (Tayo, 1982; Garvey and Lyrene, 1987).

Apical dominance can be demonstrated by tissue removal. If the shoot is decapitated the lateral buds promptly grow out. The major site is not only in young shoots but also in other plant parts such as unfolded leaves, cotyledon and portions of the stem (Hilman, 1984). White et al. (1975) concluded from defoliation studies in *Phaseolus vulgaris* L. that the source of inhibition of bud growth was in the young leaves and not in the shoot apex. Hosokawa et al. (1990) found that within 13 cm of the apical stem growing region there was strong influence, compared to the region 0.5 cm from the tip, on the outgrowth of lateral bud of *Ipomoea nil*. In poinsettia, immature leaves needed to be removed during pinching of the apex to promote rapid lateral shoot development (Berghage et al., 1989). In asparagus, apical dominance, or more strictly correlative inhibition, is thought to play a role in spear elongation (Nichols and Woolley, 1985; Nichols, 1990).

Apical dominance in many plants is influenced by hormones, nitrogen, carbohydrates, and water stress. Auxin had been suspected to have direct action in apical dominance since it is produced in the terminal bud but it is now clear that the action is indirect.

Differences in cultivar sensitivity to apical dominance may sometimes be due to differences in auxin mobility (Brenner et al., 1987) as Salerno and Brenner (1983) showed in their experiment. Little or no mobility was found in 'Craigella' tomato with weak apical dominance but was found in all 5 nodes below the apex and phloem sap in 'BlBl' line which exhibits strong apical dominance.

The fundamental role of auxin in apical dominance has been supported by many experiments. Nevertheless the mechanism of how auxin affects lateral buds remains inconclusive.

Another hormone that is thought to have a great influence on apical dominance is cytokinin. The application of exogenous cytokinin (e.g.kinetin, zeatin, isopentenyl adenine (IPA), or benzyl adenine (BA) directly to inactive lateral buds is able in some speacies to stimulate growth but not in all instances (Fann et al., 1983). The results from many attempts to determine whether a correlation exists between endogenous cytokinin levels and release from apical dominance have been conflicting. This may be due, in part, to technical difficulties of endogenous cytokinin analysis or to differences in tissue sensitivity to cytokinins.

Ethylene, abscisic acid (ABA) and gibberellic acid (GA) have all been implicated in apical dominance, and water and nutrients affect apical dominance, possibly through the effects of hormones such as cytokinins (Cline, 1997)

1.5. YIELD OPTIMIZING

1.5.1. Pot transplants

Asparagus is a perennial plant and takes at least one year for establishment and will produce edible spears in the second year for about 2 weeks of harvest (Benson and Motes, 1982; Robb, 1984; Phillip et al., 2000). Transplanting of crowns may be more cost-effective than direct seeding. In large-scale trials, sowing the seeds in peat pots promoted germination and seedling growth, shortened the seedling production period by 3 months, and eventually increased the spear yield (Chen et al., 1987). Transplanted asparagus plants had more shoots, were taller (Ombrello and Garrison, 1978) and exhibited higher survival than seedlings from direct seeding (Sanders et al., 1990). Fisher (1982) found that the numbers of buds, shoots, and storage roots in transplanted plants were double those in direct seeded plants in the field. The transplants were planted out in the field in early November, and at the same time direct seeded plants were sown. In late April, when plant growth ceased, transplants had produced 24 shoots, 44 buds and 143 storage roots, whereas the direct seeded plants had produced only 12 shoots, 22 buds, and 42 storage roots.

Seedling establishment for transplanting can conserve seeds and therefore it can reduce the cost of hybrid seed. In addition, it reduces the likelihood of early disease, avoids weed problems of seedlings and makes possible the establishment of a uniform line of plants at the desired plant population (Fisher, 1982). The use of hybrid seeds is recommended since variation amongst asparagus plants is well recognized. Another possibility to produce uniform plants is to use a tissue culture technique for clonal propagation. It has been used effectively for other plants but it was not successful in producing uniformity in asparagus plant in the early 1980's (Murashige et al., 1972; Chin, 1982). In recent years, the tissue culture technique has been more widely used but the cost is high.

Seedling quality in terms of bud production as well as plant size can be improved by increasing the phosphorus rate from 10 to 20 ppm (mg.L^{-1}), combined with the nitrogen rate from 100 to 200 ppm (Adler et al., 1984). Total bud number (shoots plus buds) increased from 3.6 to 4.5 when applying phosphorus from 0 ppm to 20 ppm. At the same time, root number also increased. As a result, root: total bud number ratio decreased from 1.13 to 1.08, and significantly increased linearly from 0 to 20 ppm. The use of arbuscular-mycorrhiza fungus enhanced seedling growth at 25°C and 30°C might shorten the seedling-raising period in asparagus (Matsubara and Harada, 1996a and 1996b). Pot size and the depth of pot also influenced asparagus seedlings (Brown et al., 1982; Falloon and Schurink, 1981). Whether the pot size changes the ratio of root:shoot growth is unknown.

1.5.2. Mother fern culture

Mother fern culture is used for continuous harvesting systems designed to allow asparagus growth all year round in tropical and subtropical countries. The system allows one to three spears to develop into fern. Once the fern is mature, the cladophylls produce photosynthate for new spear production (Shen and Hung, 1983). Thus, while the ferns supply the photosynthate the spears can be harvested continuously.

Mother fern culture (Motherstalk method) started as early as 1956 in the Tainan District Agricultural Improvement Station (TDAIS) and has been widely adopted by the farmers in Taiwan since 1961 (Wang, 1965). It has been investigated for use in temperate regions for extending the harvest season so that production can occur when demand and price are high. In New Zealand, asparagus harvests usually cease before Christmas whilst the demand is still high. Robb (1986) conducted experiments to find out whether asparagus harvest duration could be extended using three different methods of mother fern culture: (1) allow 1 mother fern to grow per plant after 6 weeks of harvest, (2) allow 1 mother fern per plant to develop before harvest began, and (3) allow 3 mother ferns per plant to develop before harvest began. She found the best option was to use 1 mother fern per plant after 6 weeks of harvest extending the harvest by 10-14 days compared to normal duration of harvest. However, quality differences were not reported. Previously, Robb (1984a, b) reported that allowing the first spear to develop fern adversely affected spear quality and delayed harvest for 10 days in the spring. Using mother fern culture extended the harvest by 7 days but over-all yield did not differ from conventional method. Similar results from a recent study conducted by Lekholoane et al. (1999) showed that mother fern culture produced considerably lower total and marketable yields, and thinner and seedier spears than the normal spring harvest.

Low temperatures during the autumn may reduce spear emergence (Dufault, 1996) and shorten the assimilation period for mother fern culture in temperate regions (Knaflewski and Krzesinnski, 2002). The shelf life of spears from mother fern culture is also reduced from 4 weeks to 2.7 weeks (Bhowmik et al., 2002). Nevertheless, Reiners and Garrison (1999) using mother fern culture conducted in the greenhouse avoiding moisture stress obtained heavier spears compared to those in the conventional practice, and therefore mother fern culture may allow extension of the asparagus harvest in temperate regions (Reiners and Garrison, 1984). In Japan (Osaka city), asparagus production reached 3.9 t.ha^{-1} using mother fern culture, compared to 3 t.ha^{-1} in conventional production (Araki, 1999). In Hiroshima, Japan, the use of modified mother fern culture has successfully increased total yield by 2.3 times (up to11 t.ha^{-1}) greater than that of conventional practise and prolonged harvest period from 60 to 170 days (Kohmura, 2002). Combination plastic covers to hasten the harvest period together with the use of mother fern culture and allowing three harvest periods in a year, in a greenhouse in Saga, Japan, boosted the yield up to 19 t.ha^{-1} (Sato and Motoki, 2002).

1.5.3. Male plants

Male plants are reported to produce more spears than female plants (Ellison et al., 1990; Moon, 1976; Bohne, 1977; Ellison and Kinelski, 1985; Price and Baughan, 1990; Ellison et al., 1990; Wolyn, 1996). Superiority of male plants over female plants in terms of yield is also due to greater longevity (Ellison et al., 1960). Shorter longevity in female plants may be due to competition between berries and roots for carbohydrate since berries can comprise up to 32% of the weight of female plants (Robbins and Jones, 1923 in Hughes, 1992). The crowns of male asparagus plants were larger than the crowns of female plants and therefore contained more carbohydrate before and after harvest, although there was no difference in their carbohydrate concentration (Hughes, 1992).

Breeding programs for commercially producing male hybrids aimed at increasing the yield qualitatively and quantitatively to achieve higher profit. Earliness, resistance to rust, and spear quality can be achieved by new male hybrids such as Italo, Ercole, and Zeno (Falavigna and Casali, 2002). Male plants produce 20 to 25% more spears than female plants (Wolyn, 1996). But male plants have a lower branching height and smaller basal diameter than female (Roose and Steton, 2002). They found that the lowest branch on male plants were on average of 24.9 cm high whilst the female plants were 28.1 cm. As temperature increases during the harvest period, lower branching height will accelerate head opening, which then can reduce spear quality. Selection for head tightness under high temperature led to very successful, high quality cultivars in many regions (Krarup, 1992).

The use of male hybrids has been reported to increase yield (Falavigna et al., 1998). Furthermore, male hybrids are used since they may increase resistance to some diseases. 'Jersey Giant' is an all-male hybrid with good resistance to *Puccinia asparagi*, *Fusarium oxysporum* and *F. moniliforme* (*Giberella fujikuroi*). It is early and vigorous, producing green spears with purple bracts and tight purple tips during cool temperature (Ellison and Kineski, 1985). It also has low fibre content (Poll et al., 1990).

However, some hybrids from male and female plants such as 'UC157', 'Apollo', 'Grande' and 'Atlas' are still needed. One of the reasons to have female parent for hybrids is to obtain and maintain large spear diameter characteristics. Another reason is for the use of dioecious rather than all-male cultivars was due to the assumption that a dioecious cultivar would have a wide range of adaptability and thus better industry acceptance (Benson et al., 1996). In the current study, several hybrid cultivars were used: 'Apollo', 'Atlas', 'Grande', 'UC157' (Table 1.1). These cultivars are hybrids developed in the US (Benson et al., 1996; Wehner, 2003).

Table 1.1 Horticultural characteristics of Apollo, Atlas, Grande, and UC 157 asparagus cultivars

	CULTIVARS			
	APOLLO	ATLAS	GRANDE	UC 157
GENETICS	Clonal hybrid (3-way)	Clonal hybrid	di-Clonal hybrid	Clonal hybrid
COLORATION				
Spear	green	green	green	Green
Tip	purplish green	purplish green	purplish green	purplish
Butt	purplish green	purplish green	purplish green	Green
Bud scales	purplish green	purplish green	purplish green	purplish
SPEAR CONFORMATION				
Shape	cylindrical	cylindrical	cylindrical	Cylindrical
Cross section	round	round	round	Round
Texture	smooth	smooth	smooth	Smooth
Bud scales	Closely oppressed	Closely oppressed	Closely oppressed	Closely oppressed
Diameter	medium large	medium large	large	Medium
Avg. Spear weight	28 g	28 g	32 g	25 g
DISEASE TOLERANCE				
Fusarium spp	Highly tolerant	Highly tolerant	Highly tolerant	Highly tolerant
Puccinia asp.	tolerant	tolerant	tolerant	Tolerant
Asp. Latent virus 2	free	free	free	Free
TEMPERATURE ADAPTATION	Not available	Tight head under warm to hot growing condition	Tight head under warm to hot growing condition	Tight head under moderate to hot growing condition
Production	Early spring	Early spring to latc cutting season	Early spring to late cutting season	Early spring

Source from: Benson et al. (1996) and Wehner (2003)

Two American hybrid cultivars, 'Jersey Giant' (all-male) and 'UC157', were recommended by New Zealand Asparagus Council in 1990. The production characteristics of the two cultivars have been compared with Mary Washington as a control (Table 1.2).

Table 1.2. Performance of Jersey Giant and UC157 compared to Mary Washington and Beacon

Production characteristics	UC157	Jersey Giant	MW/Beacon
% yield first month's harvest	25	25	10
% saleable spears	77	74	55
Saleable yield	150-200	150-200	100
Export yield	220-380	220-380	100
Stemphyllium susceptibility	Moderate	Low	Moderate
% medium/large spears	60/40	60/40[1]	70/30
Volunteer seedling in the field	Yes	No	Yes
Purple spear colouration	Low	High when cool	Low

Source from: The New Zealand Asparagus Manual, 1990. [1] as it is printed.

1.5.4. Hydroponics and Aeroponics

The use of soilless culture in asparagus is aimed at increasing profit by taking advantage of high prices during off-season harvest production or continuous year-round production (Schrevens et al., 1989; Wagenvoort, 1979; Poll et al., 1990; Nichols, 2002). This practice for asparagus has been reported by many European researchers but has not yet been established commercially.

Traditionally, asparagus cultivation could extend to 15 years of production. But as the crowns age, production tends to reduce and finding new land for asparagus is also limiting (Robb, 1984; Poll et al., 1990). Furthermore, conventional asparagus production has high labour cost, with much manpower needed during the harvest i.e. 750 manhours per ha (Schrevens et al., 1989). On one hand, forcing asparagus in the field to extend the harvest period appeared to be unsuccessful (Robb, 1984; Sanders, 1985; Onggo, 2002) due to thinner spears and earlier opening bracts. Severe effects of extended harvest in the field are also associated with photosynthesis due to late fern establishment, low temperature in temperate regions or high rainfall in wet tropical regions. The option may then become protected cultivation e.g. the use of tunnel houses or soilless production.

Spears from soilless production using hydroponics were thinner than those in conventional cultivation, but they were less fibrous which increased spear quality (Wagenvoort and Ammerlaan, 1988). However, the spears in general were of a lower quality due to crooked stems with poor head tightness. Schrevens et al. (1989) found that exposing the crown to cold treatment before commencing production in hydroponics increased mean spear fresh weight by 58% and spear diameter by 42%. This meant that a fresh weight of 16.2 g for a 22 cm long spear with a diameter of 9.51 mm could increase to 25.61 g fresh weight and 13.49 mm diameter. Wagenvoort and Ammerlaan (1988) reported that from two-year old asparagus, the average spear number ranged from 3.4 to 6.5 for the hybrid varieties with low to high rhizome weight (between 374 to 550 g) whereas, for one year old asparagus plant, they produced between 2.9 to 5 spears depending upon the substrate used in hydroponics (Schrevens et al., 1989). Nevertheless, the average number of spears (9.7) produced by two year old asparagus plants using hydroponics was found to be higher in the study conducted by Poll et al. (1990) than those of Wagenvoort and Ammerlaan (1988). Furthermore, high mean spear weight was not related to the number of spears produced (Wagenvoort and Ammerlaan, 1988; Schrevens et al., 1989). The differences in spear number and spear weight could be attributed to cultivar differences as these researchers used different cultivars.

Total yield production will depend on spear weight and spear number. Poll et al. (1990) found that the average of total yield per crown using hydroponics was lower than those in potting soils using glasshouses. The spear numbers and mean fresh weight of spears were 11.8 spears and 12.1 g and 9.7 spears and 10.4 g for the plants of potting soil and hydroponics, respectively. Soilless culture however is also a convenient research tool to study plant growth in a controlled environment and measure underground portions of the plants without destruction (Ehret and Ho, 1986; Weathers and Zobel, 1992).

Conductivity or electrical conductivity (EC) is the measurement of the amount of electrolyte which is related directly to the amount of nutrient ions that are dissolved in the nutrient solution. The unit of measurement is milliseimens per cm ($mS.cm^{-1}$). EC in soilless culture is important since optimum nutrient solution conductivity is crop dependent. The changes in EC of nutrient solution affects water potential of the solution and therefore affect plant water status.

The level of EC causing stress in vegetable crops is often investigated. Keeping the EC of the solution at 2 $mS.cm^{-1}$ has the benefit of larger spear diameter and fresh weight when compared to higher EC solutions (Schrevens et al., 1989). Spear elongation was greater at EC 2 $mS.cm^{-1}$ than those at higher EC concentration (Schrevens et al., 1989). An increase of EC from 0.4 to 3.6 $dS.m^{-1}$ reduced growth of asparagus (Huett, 1994) while EC of 4 $mS.cm^{-1}$ increased plant growth of sweet pepper (Tadesse et al., 1999). Nonetheless, the effect of EC on plant growth of asparagus has not been specifically investigated. In Chapter 6 of this thesis, different EC concentrations were used to investigate the response of asparagus to EC level.

1.6. SPEAR QUALITY

Asparagus cultivar evaluation is conducted to determine yield potential and suitability for specific growing conditions (Bussell et al., 1984; McCormick and Thomsen, 1995; Uragami et al., 1996). Cultivar evaluation should also consider consumers' demand for specific criteria such as uniformity of color (whether white or green), size (length and diameter) and taste (Yadav, 1998; Piazza, 1998). Hence, asparagus spear quality is an important economic determinant. Environmental factors such as planting depth, plant population, temperature and moisture affect the spear quality.

Planting depth has two purposes (NZNAM, 1990): to control the number, thickness and weight of spears produced and to control the spear height that will be reached before the heads begin to open. Flat or ridged beds can be used to modify the depth of crown in the soil. Flat beds are considered best when the soil is not dominated by clay (NZNAM, 1990). The rhizome moves horizontally in flat beds allowing the buds to grow at similar depths of soil. On the other hand, in ridged beds the rhizome may grow into a folded shape and some roots are constrained to grow sideways (Weaver, 1927). Increasing the depth of crown in the soil reduces the number of spears but they are thicker and heavier (Hartmann, 1985; Kailuweit and Krug, 1995; Liao et al., 1999). The changes in spear number and spear weight tend to offset each other so that overall production is not different due to different planting depth (NZAM, 1990). To increase the yield at the same time as maintaining spear quality by means of spear size, the plant population must be adjusted.

Kaufman and Orth (1990) attempted to construct a model for green asparagus plant population to obtain high profitability due to plant density differences. In their model, a plant density of 92,000 crowns.ha^{-1} would be optimum to give maximum yield for the first half of the productive period (8 years). At a later age, a lower plant population would begin to approximate the yield of the high plant density. Adding to the model other factors such as input cost, plant densities of 45,000 and 30,000 crowns.ha^{-1} would yield optimum production of thin or thick spears of 'Helios', respectively. The recommendation for plant density, however, will vary for different cultivars and specific locations. For instance, saleability and total yield of 'Rutgers Beacon' increased with increasing population from 4,500 to 66,000 plants.ha^{-1} in New Zealand and total yield for 'Limbras', a more vigorous cultivar, increased with increasing population but saleable yield increased only up to 40,000 plants.ha^{-1}(Bussell, 1984). Rogers and Pringle (1984) found that the mean weight of first grade spears declined from 22g per spear to 16g per spear with the increase in plant density and total yield reduced from 1.7 t.ha^{-1} for 1 m x 0.15 m spacing to 0.4 t.ha^{-1} for 2.5 m x 90 cm spacing.

Cultivar choice in some areas will be affected by temperature. Plant adaptation to temperature certainly affects spear quality in terms of spear head tightness (Krarup and Henzi, 1992; Krarup and Centreras, 2002), and lignification (Hennion and Hartmann, 1990). Spear toughening would reduce quality and results from tissue lignification progressing from butt to tip (Buchloh and Hartmann, 1990). Also as spear diameter gets thinner, lignification can be accelerated. Lignification is accelerated by the presence of ethylene (Kevers et al., 1984) and develops as temperatures increase, especially in thin spears, which further reduces spear quality.

Spears are graded for canning or fresh market and either for local or export consumption. Each grading serves different requirements. Most grades are based on spear diameter, head tightness, straightness and lack of any defect such as disease or pest. However, different regions or countries have different standards of grade applied for either fresh or canned spears.

Spear grading criteria from New Zealand Novantis Asparagus Manual (NZNAM) differs slightly from Organization for Economic Co-Operation and Development-Europe (OECD).

OECD (2000) divides asparagus into four colour groups: white, violet, violet/green and green asparagus. For market quality the shoot must be intact, sound, free from damage caused by unsuitable washing, clean, fresh in appearance and fresh-smelling, practically free from pests and from damage caused by pests, un-bruised, free from abnormal external moisture and abnormal smell and/or taste, base cut as clean as possible, neither hollow, split, peeled or broken, the development and condition must enable them to withstand transport and handling and to arrive in satisfactory condition at their destination. Apart from the non-marketable, spears are divided into three categories: superior quality, good quality (class I), and marketable quality (class II). Size, tip, length, and colour must follow certain criteria. In Europe, there are long (17 to 22 cm for white and violet asparagus and 17 to 27 cm for violet/green and green asparagus) and short category (12 to 17 cm). The minimum diameter for green asparagus is 3 mm with maximum variation 8 mm between the thinnest and thickest shoot in the same package or same bundle. There is no division based on spear diameter for different classes in violet/green or green asparagus. For white and violet asparagus, minimum diameter is different for each class: 12 mm for extra (superior), 10 mm for class I, and 8 mm for class II. The tips for superior and class I must be tight while for class II the tips are allowed to be slightly open and "seedy".

NZNAM divides spears into fresh export, canning, freezing, and local fresh. Spear diameters for canning are smaller than for fresh market. The specification for each division is listed in Table 1.3.

Although there are some standards for spear grading, researchers often do not use similar criteria and do not always follow the standards. For example, Bussell et al. (1984) defined the first grade standard of the asparagus spear for both processing and fresh markets as at least 10 mm in diameter at the base for spears that are 18 cm long, straight, with tight bracts. Sanders (1985) divided spear grade into large (spear diameter > 1 cm) and small (spear diameter < 1 cm).

Table 1.3. Asparagus quality standard in New Zealand for different specifications

Specification	Length	Base diameter	Head tightness	Damage
Canning				
First grade	125mm≤ length≤ 180mm	9 mm ≤d≤ 20 mm	Tight and free of “seed”	Free from slug or insect damage
Second grade	125mm≤ length	5 mm ≤d≤ 9 mm or not more than 20 mm	May have visibly seedy heads	Moderately damaged by slugs or insect, distorted shape
Non-marketable	Butts removed from spears over 180 mm	More than 20 mm	Very open seedy heads	Badly distorted, affected by phytopthora or frost
Freezing				
Acceptable	Vary between 137 mm, 150 mm, and 175 mm	Between 6mm and 13.5 mm or between 13.5 mm and 18 mm	Tight and free from visible seed.	Free from any damage from slugs or insect, free from soil
Unacceptable			Open seedy heads	Badly distorted, affected by frost or phytopthora, and infested by aphids, weevil, thrips or other invertebrate
Export fresh				
Small medium	Generally 200mm, trends towards between 220 and 230 mm	6-10mm	Tight	Free from any damage from any slugs, punctures and cracks and free from any disease
Medium		10-15 mm		
Large		16-21 mm		
Jumbo		21+ mm		
Local fresh	In accordance with local buyers, free from crack, damage, pest, soil and open seedy head. Colour and spears in uniform			

Source from: New Zealand Novantis Asparagus Manual (1997)

For forcing asparagus in soilless culture, the spear diameters are usually smaller than those in soil cultivation (Wagenvoort and Ammerlaan, 1988; Poll et al., 1990). Poll et al. (1990) and Poll (1996b) categorized spears based on spear diameter into four grades: A (16-20 mm), B (12-16 mm), C (10-12 mm), and D (8-10 mm). For measuring fibers, Poll and Kruistum (1990) separated the spear according to length and diameter: trimmed to 18 cm at a spear diameter of 10 mm or more, and to 14 cm at a spear diameter between 8 and 10 mm. Based on spear diameter, Krarup (1996) classified spears into Extra (diameter ≥ 21 mm), No.1 (diameter 16-20 mm), No. 2 (diameter 12-15 mm), No. 3 (diameter 10-11 mm), No. 4 (diameter 7-9 mm), and No. 5 (diameter ≤ 7 mm).

Furthermore, McCormick and Thomsen (1990) in New Zealand categorized spears into three classes. Every spear with a diameter less than 9 mm or bent or blemished was non-marketable or class 1. A straight spear and clean with moderately well closed heads was included into class 2, while spears with tightly closed heads showing no seeding were included into class 3 and considered for export. Here, McCormick and Thomsen classified asparagus from lower to high as from non-marketable to marketable. Liao et al. (1999) defined spear quality only based on spear head tightness. They recorded spear head tightness into three categories: 1 (open), 2 (medium), and 3 (very tight). These three categories were also used by Kamo (1999) but in reversed numbering: 1 (very tight), 2 (medium), and 3 (open).

Most of these spear categories for quantifying the spear quality included spear diameter except in Liao et al (1996) and Kamo (1999). The differences in categorizing different ranges of spear diameter may come from different age of the plant, cultivars or cultivation systems that the researchers used.

1.7. RATIONALE

There is increasing demand for asparagus, particularly for fresh green spears especially in Japan and Europe. More and more countries including tropical and sub-tropical countries such as The Philippines establish asparagus cultivation to help meet world demand, creating a competitive market.

To gain economic benefit from a competitive market, high total yield of superior quality spears must be achieved. Compared to other countries, average production of asparagus in New Zealand is still low (2.5 $t.ha^{-1}$) and New Zealand production fulfils only 2% of world production.

The New Zealand Asparagus Council (NZAC) has set a goal of doubling yield of high quality spears by 2010 and promoting the demand for asparagus. To achieve these goals, there are six research priorities: improved varieties, plant disease control, health and nutrition, food safety, innovative, smart products and crop physiology (VegFed, 2003).

Asparagus is in high demand particularly during Christmas time in New Zealand. Very little fresh asparagus is available because most asparagus harvesting in New Zealand ceases before Christmas. Growers decide when to end harvest in order to allow the plant to replenish carbohydrate for the following year's crop. But the basic information to support the decision making process has only just become available based on using the AspireNZ system (Wilson et al., 1999).

Many asparagus growers in New Zealand have used the AspireNZ system to help in deciding the length of the harvest period. The system provides a root storage carbohydrate value based on brix readings from root samples to give an estimate of available carbohydrate in storage roots in term of percent total soluble carbohydrate (TSC).

The extension of harvest length, nevertheless, must consider other internal factors of the plants. With the current system using AspireNZ, the decisions for harvest length is based only on carbohydrate percentage in the storage roots, rather than total carbohydrate available, which would require knowledge of total root mass.

Furthermore total yield will depend on spear weight and number of spears. Since spears are developed from buds, the number of suitable buds could limit the number of marketable spears produced. A limit number of suitable buds could reduce the harvest of high quality spears as well as leaving only small buds to develop into fern, which would then affect future fern vigour for carbohydrate replenishment. However, little work has been carried out on bud number associated with harvest and how the bud number could be modified to make it non-limiting. This is our main research that will verify the importance of bud number in lengthening harvest for achieving high total yield.

An asparagus life cycle is illustrated to give a better overview of the current study (Fig. 1.5). Young shoots (spears) develop from buds in the spring from the underground rhizome. These shoots are initially harvested in spring and early summer to provide the saleable yield. Eventually however the shoots have to be allowed to develop, forming fern-like foliage. The ferns photosynthesise during the summer and early autumn producing carbohydrates (in this case fructans) that accumulate in the storage roots to provide supplies for next season's growth.

This study (printed in bold fonts in Fig. 1.5) is about bud numbers and their relationship to root numbers, root mass, carbohydrate supply and final crop yield.

- How are bud numbers going to be affected by harvest or vice versa?
- Is there any way to modify bud number in relation to root mass when a large root mass is present?
- Is bud number a limiting factor for spear yields?

Eight experiments were conducted to obtain sufficient information to answer these questions.

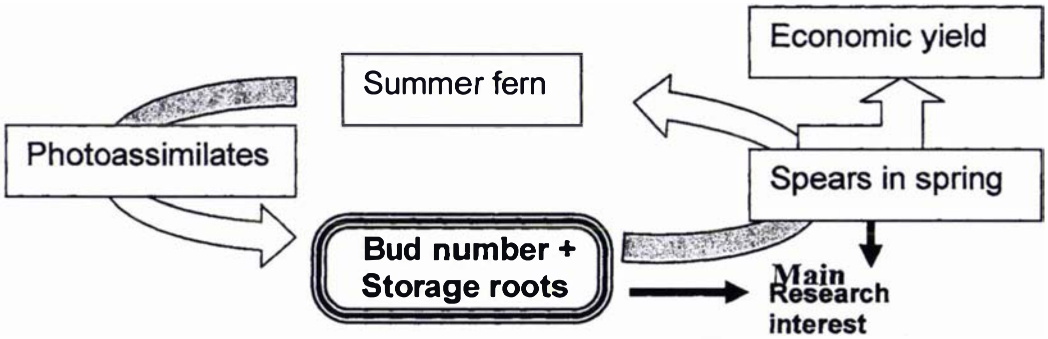
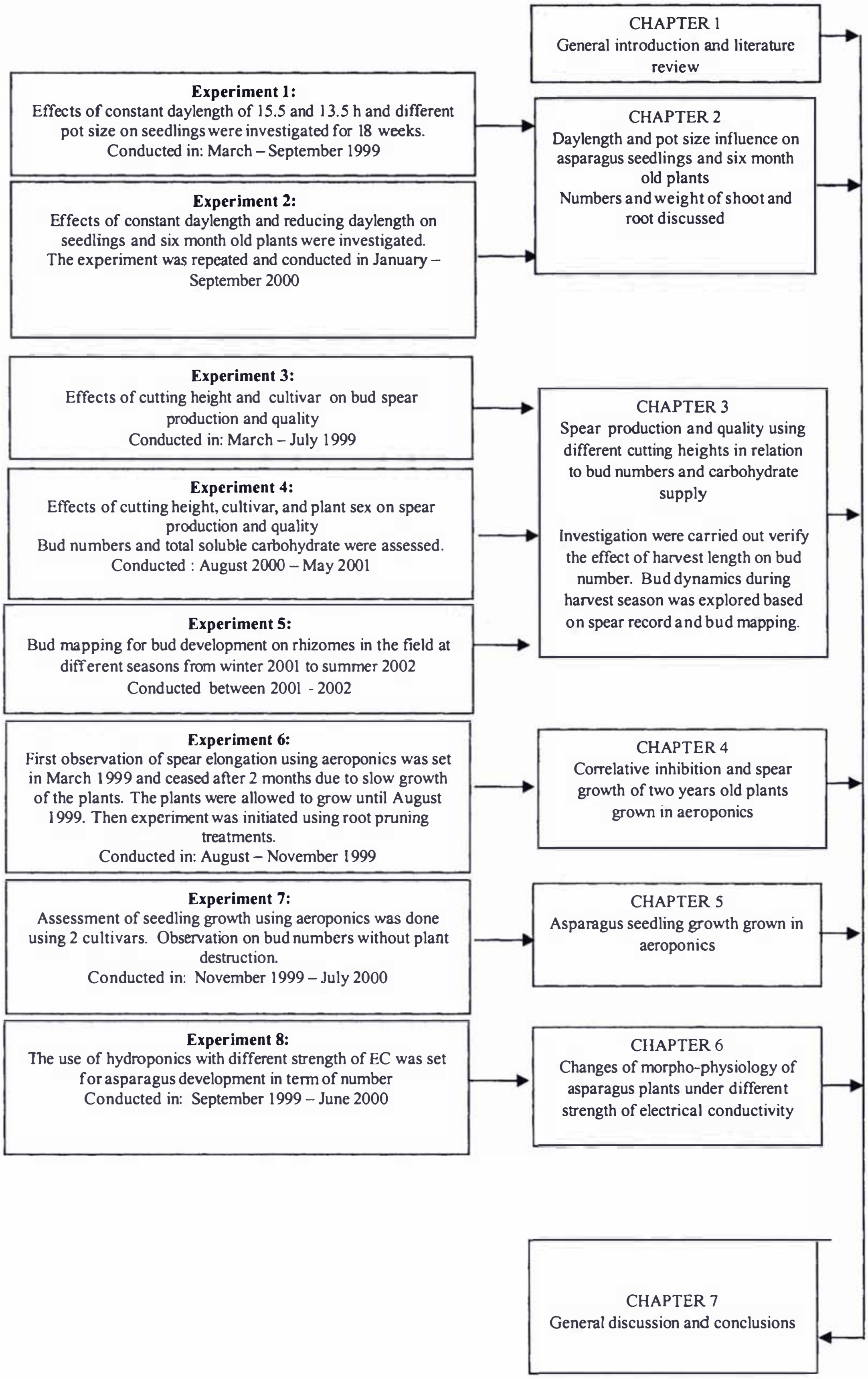


Figure 1.5 Growth cycle of asparagus with economic yield and research interest reported in this thesis (in bold fonts).

To achieve the objective listed in general introduction, a linked series of eight experiments were done from 1999 to 2002. Eight experiments and corresponding Chapters in this thesis are outlined below.



CHAPTER 1
General introduction and literature review

Experiment 1:
Effects of constant daylength of 15.5 and 13.5 h and different pot size on seedlings were investigated for 18 weeks.
Conducted in: March – September 1999

Experiment 2:
Effects of constant daylength and reducing daylength on seedlings and six month old plants were investigated.
The experiment was repeated and conducted in January – September 2000

CHAPTER 2
Daylength and pot size influence on asparagus seedlings and six month old plants
Numbers and weight of shoot and root discussed

Experiment 3:
Effects of cutting height and cultivar on bud spear production and quality
Conducted in: March – July 1999

Experiment 4:
Effects of cutting height, cultivar, and plant sex on spear production and quality
Bud numbers and total soluble carbohydrate were assessed.
Conducted : August 2000 – May 2001

Experiment 5:
Bud mapping for bud development on rhizomes in the field at different seasons from winter 2001 to summer 2002
Conducted between 2001 - 2002

CHAPTER 3
Spear production and quality using different cutting heights in relation to bud numbers and carbohydrate supply

Investigation were carried out verify the effect of harvest length on bud number. Bud dynamics during harvest season was explored based on spear record and bud mapping.

Experiment 6:
First observation of spear elongation using aeroponics was set in March 1999 and ceased after 2 months due to slow growth of the plants. The plants were allowed to grow until August 1999. Then experiment was initiated using root pruning treatments.
Conducted in: August – November 1999

CHAPTER 4
Correlative inhibition and spear growth of two years old plants grown in aeroponics

Experiment 7:
Assessment of seedling growth using aeroponics was done using 2 cultivars. Observation on bud numbers without plant destruction.
Conducted in: November 1999 – July 2000

CHAPTER 5
Asparagus seedling growth grown in aeroponics

Experiment 8:
The use of hydroponics with different strength of EC was set for asparagus development in term of number
Conducted in: September 1999 – June 2000

CHAPTER 6
Changes of morpho-physiology of asparagus plants under different strength of electrical conductivity

CHAPTER 7
General discussion and conclusions

CHAPTER 2

DAYLENGTH AND POT SIZE INFLUENCE ON ASPARAGUS SEEDLING GROWTH[†]

2.1. INTRODUCTION

Carbohydrate balance is very important in asparagus since yield depends on reserve carbohydrate from the previous year. Carbohydrate levels drop dramatically when asparagus spears are harvested and rise after fern establishment (Shelton and Lacy, 1980; Haynes, 1987; Hughes, 1992; Pressman et al., 1993). Once the fern is established it starts supplying carbohydrates to the storage root for the following season's crop (Robb, 1984; Haynes, 1987; Pressman et al., 1993).

Much research on dry matter partitioning has shown that daylength may play a role in controlling dry matter partitioning in plants including asparagus. Sudjatmiko et al. (1997) suggested that decreasing daylength may be the trigger for switching carbohydrate supply from shoot to root in asparagus plants. The critical decrease in daylength in their area (latitude at 40° 23'S) occurs during early February.

[†] Part of this chapter was orally presented at the Conference of the New Zealand Horticultural and Agricultural Annual Convention at Palmerston North Campus, Massey University, June 2000 with the authors and title:

Entin Daningsih, David J. Woolley, K.Karno, Mike A. Nichols, and Keith J. Fisher.

Effect of daylength on carbon partitioning of *Asparagus officinalis* L.

Woolley et al. (1999) conducted research in the same location (latitude at 40° 23'S) and found that there was a change in carbon partitioning between mid summer when 70% of ^{14}C partitioned to the shoot, and late summer when 74% of ^{14}C partitioned to the crown. Later, Faville et al. (1999c) using ^{13}C on asparagus in the field (Waikato, New Zealand, latitude 37°53'S) supported this observation that the time of maximum carbohydrate movement into storage roots for mature asparagus plants was in early February and there was minimum supply of photosynthate to the shoot. Karno (1999) studied the effects of reducing daylength from 15.5 h to 12.00 h (gradually reduced by 15 minutes every four days) and constant daylength (15.5h) on dry matter partitioning of asparagus plants in growth chambers. He suggested that when daylength reduced from 15.5 h to approximately 14 h carbohydrate partitioning favoured the crown rather than the fern. The root:shoot dry weight ratio and allometric ratio between crown and fern of the plants under reducing daylength were higher than under constant daylength at 15.5 h. The plants under reducing daylength showed reduction in plant height, shoot number, number of laterals per shoot, length of lateral, and fern dry weight. However, partitioning to the root system did not continue as daylength declining further. Woolley et al. (2002) suggested that, as plants grew bigger, pot size may have started restricting plant and root growth, over-riding the influence of reducing daylength on photosynthesis partitioning. Further study is needed to clarify these effects.

A large crown may have the potential to produce high yield of spears in the spring. It is also thought that increase in crown size can result in more buds. Robb (1983) stated that root:shoot ratio of the asparagus seedlings is approximately 2:1 (i.e. for every shoot, 2 roots will develop and the root dry weight will be twice that of shoot dry weight). She defines shoots as being both spears (developing shoots) and ferns (shoots already developed with cladophylls). But the root:shoot ratio was found to be dependent on both cultivar and plant age (Karno, 1999). In terms of numbers, the root:shoot ratio of 'UC157' seedlings, for instance, was approximately 5.7:1 at harvest 8, and higher than the other two cultivars, 'Jersey Giant' and 'Italian Hybrid'. Initially the ratios of root:shoot number for the three cultivars were between 2 and 3 roots to 1 shoot. Whilst it is essential to have high bud number with a reasonable support from the root, increase in root weight of asparagus has not been related directly to bud number. Dufault and Greig (1983) attempted to correlate bud number and shoot fresh weight, assuming that bud proliferation would be dependent on shoot activity. As the shoot fresh weight increased more buds would be produced. However, they did not find correlation between the two. The number of buds produced on asparagus crown indicates the potential for yield in the following season (Dufault and Greig, 1983) since the spears are developed from the buds. To achieve high yield then bud numbers on the crown should increase proportionally with root mass (root weight).

The studies reported in this chapter were planned to verify the critical timing of daylength changes on the growth of seedlings and six-month old asparagus plants under controlled environment conditions using two different types of daylength. The first study (Expt 1) was designed to evaluate the effect of constant daylength (15.5 hrs and 13.5 hrs) on asparagus seedling growth. The second study (Expt 2) compared the effects of constant daylength and reducing daylength on six months old plants of two asparagus cultivars. In addition, an investigation of pot size effects under different length of constant daylength (Expt 1) was conducted to confirm the effects on plant growth.

2.2. MATERIALS AND METHODS

2.2.1. Experiment 1: constant long daylength versus constant short daylength

2.2.1.1. Plant material.

Asparagus cultivar 'UC157' was used for this experiment. The seeds were sown on 24th of March 1999 in 60-cell trays. The cells had a volume of 45 ml and were 5 cm deep. The seeds were sown individually in each cell. The growing media used was a mixture of peat, bark and pumice in the ratio of 1:1:1. In addition 100 gram of Ag-lime, 300 gram of dolomite and short term fertilizer of 150 gram Osmocote (16N-3.5P-10.8K)/100 litres was added to the growing media. The seeds were germinated on a bench in a green house, and the seedlings were watered every day. Nine hundred seedlings were transferred into 200 ml pots (small pot size) on 28th April 1999. A similar mixture of peat, bark, and pumice media soil was used, and a long term fertilizer incorporating 100 gram of Ag-lime and 300 gram of dolomite, 200 gram of long term osmocote and 100 gram of short term osmocote was used. After selection for uniform growth appearance, the asparagus transplants were put into growth chambers on 10th May, 1999. After four weeks in the growth chambers, two thirds of the population were transferred into two differently sized pots; medium size 500 ml-pots and large size 850 ml. The plants were watered daily and fertilized three times a week with 50ml of solution of 0.5 gram.litre^{-1} of Peter's fertilizer (Manufactured by Scotts-Sierra Horticultural Product, USA) consisting of 100 ppm N, 37 ppm P and 83 ppm K.

2.2.1.2. Growth chamber conditions:

Four growth chambers were used for the experiment with two different light sources in each growth chamber (Fig. 2.1). High intensity light was supplied by 2 x 1000 watt high pressure discharge lamps and 6 x 1000 watt halogen lamps. Low light intensity was provided by 2 x 100 watt incandescent lamps and one 20 watt high efficiency long life tube lamp. Irradiance was measured as mol quanta between 400 and 700 nm using a quantum sensor (LICOR250, Lincoln, Nebraska, USA). The average high intensity light was 303 mol.m^{-2}.sec^{-1} (Table 2.1).

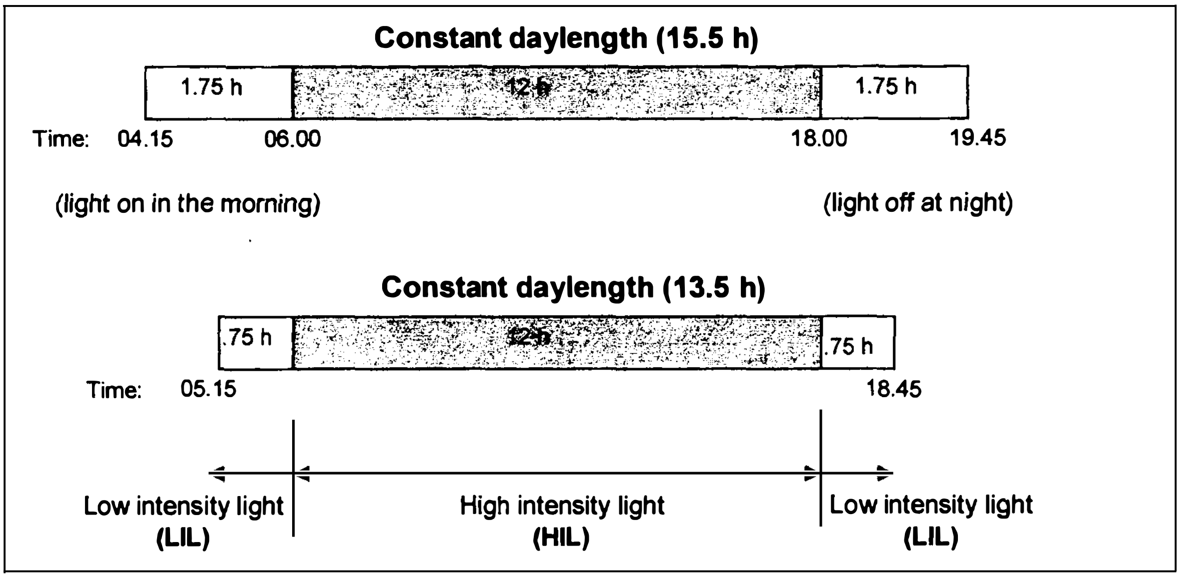


Figure 2.1 The light setting for constant daylength of 15.5 h and 13.5 h for Expt 1. Both have 12 h of High Intensity Light (HIL) but different lengths of Low Intensity Light (LIL).

Both short and long daylength received 12 hours of high intensity light but different lengths of low intensity light (Fig. 2.1). Chambers were set for a constant day/night temperature of 20°C. Air temperature was also recorded daily.

Both daylength treatments received similar amounts of radiant energy. Two pairs of chamber were used for each daylength. The chambers for each pair were matched for light intensity so that chamber 1 and 3 comprised one pair and chamber 2 and 4 was the other pair (see Table 2.1). Within each pair of chambers, the reducing daylength treatments had slightly higher light intensity in order to compensate for the low light intensity energy of the long photoperiod. In this way the total photosynthetically active radiation (PAR) was kept constant for each pair of cabinets.

Table 2.1 Conditions of controlled climate growth chamber.

Growth Chamber	Temperature	High Intensity (μmol..m^{-2} sec^{-1})	Low intensity (μmol.m^{-2} sec^{-1})	Daylength Treatment
1	20°C	318.7	3.2	Constant 15.5 h
2	20°C	320.2	3.2	Constant 13.5 h
3	20°C	287.9	3.2	Constant 15.5 h
4	20°C	288.3	3.2	Constant 13.5 h

2.2.1.3. *Experimental design*

Seedlings were maintained in small pots (200 mls in volume) that were used for the first four weeks of study. A randomized complete block design (RCBD) with two blocks and two different daylengths as treatments was utilized. The two treatments were 15.5 hours and 13.5 hours of constant daylength (Fig. 2.1).The randomised complete block design was then changed into a split plot arrangement after 4 weeks when pot size contrast was introduced.

Pots were arranged in a growth chamber in such a way that any pot size was bordered by the other two pot sizes (Fig. 2.2) in order to have equal light distribution and avoid shading effects. Pots were rearranged to maintain the distribution between pot sizes at each sampling (see 2.2.1.4).

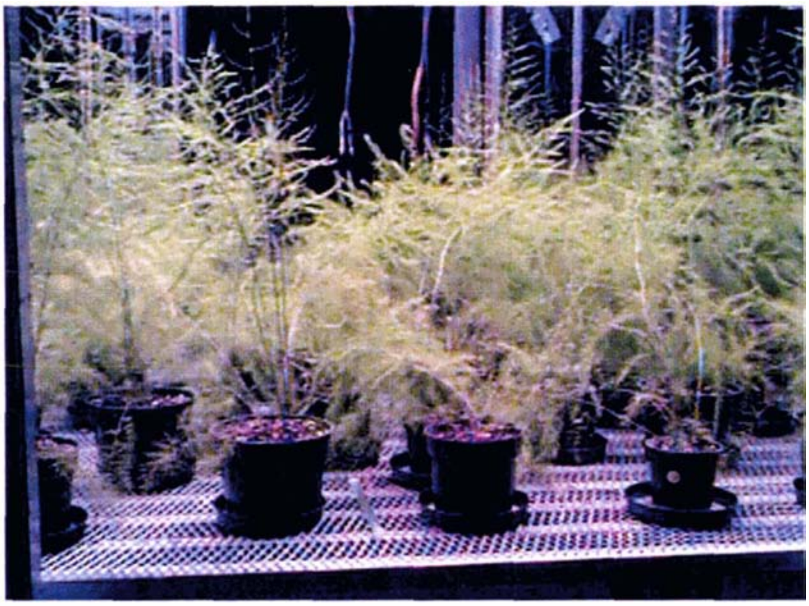


Figure 2.2 Asparagus plants grown in three different pot sizes in growth chambers under constant short (13.5 hours) or long (15.5 hours) daylength in Experiment 1.

2.2.1.4. Collection of the data

Fifteen plants from each chamber were destructively harvested on a weekly basis for the first two weeks. Five samples were obtained thereafter from each growth chamber. Between week 6 and 18, five samples were taken from each pot size within a growth chamber, totalling 15 samples per growth chamber. The plants were removed from the soil and the roots cleaned thoroughly using tap water. Then, the bud, root, and shoot numbers were counted. Shoot number consisted of fern and spear together. Total bud number was shoots plus buds.

Shoot and crown were weighed separately. Plant height was measured from the highest tip of the shoot to the base of each stem on the rhizome. Dry root (crown) and shoot were weighed after the plants were put in an oven for at least three days at 80°C. The times of plant sampling from short and long daylength treatments is listed in Table 2.2.

Table 2.2 Sampling times of asparagus growth influenced by short and long daylength: Expt 1.

No.	Week	Date	Note
1	0	May 11	Initial sampling
2	1	May 18	
3	2	May 25	
4	3	June 1	
5	4	June 8	
6	6	June 22	
7	8	July 6	
8	10	July 20	
9	14	August 15	
10	18	September 12	Final sampling

2.2.1.5. Statistical analysis

A general linear model (PROC GLM of the SAS version 8.2, 1999-2001) with randomised complete block design was used to analyse the numbers of buds, shoots, roots, plant height, and the ratios of root to total shoot number, root to bud number, root to shoot number only, and the ratios of root dry weight to shoot dry weight. One way

ANOVA was used with daylength as the treatments for all measured variables until week 4. After that, analyses of variances for each harvest/sampling were done with three levels of pot size and two levels of daylength as treatments in a split plot design with daylength as main effect and pot size as the split effect.

The shoot-root allometric ratio was calculated using linear regression of $\log_e$ of shoot dry weight against $\log_e$ of root dry weight. Shoot-root allometric ratio is an index of the balance of growth between shoot and root components of the plants integrated over a period of time (Hunt, 1980):

$$\text{Shoot dry weight} = \text{c.Root dry weight}^{k}$$

Or

$$Y = c.X^{k}$$

And the function to fit as linear regression becomes:

$$\log_e Y = \log_e c + k \log_e X \tag{2.1}$$

where:

$\log_e c$ is a constant
k is the allometric constant (the slope)
$\log_e Y$ is natural logarithm of shoot dry weight
$\log_e X$ is natural logarithm of root dry weight

A higher k (allometric constant) values indicates more partitioning of dry matter to shoots while lower k values indicate more partitioning of dry matter to root.

2.2.2. Experiment 2: Constant long daylength versus reducing daylength

2.2.2.1. Plant materials.

Asparagus cultivar 'Jersey Giant' and 'JWC1' were sown on 17 January, 2000 using the medium described in Expt 1 and were germinated on the bench with 28°C air temperature in a greenhouse. The seedlings were transferred into 550 ml pots eight weeks later and removed to another greenhouse. Plants were watered every day and fertilized once a week using a fertilizer solution consisting of 100 ppm N, 37 ppm P and 83 ppm K. On 17th May, 2000 the plants were acclimated in growth chamber in a constant long daylength (15.5 hrs). All the ferns were removed on the 14th June, 2000. The initial measurement was done on 22th July, 2000 and the ferns at that time were already established. The plants were transferred into larger pots (850 mls in volume) four weeks later. The plants were watered daily and fertilized three times a week with a 0.5 gram.litre^{-1} solution of Peter's fertilizer consisting of 100 ppm N, 37 ppm P and 83 ppm K.

2.2.2.2. Growth Chamber conditions:

Table 2.3 Changes of daylength setting and sampling time in Expt 2

Week	Date	Reduce 15 minutes/4 days		Daylength	Note
		Morning	Night		
	16 June	06.15	21.45	15.50	Fern cut
6	24 July	06.30	-	15.25	Start/Sampling
	28 July	-	21.30	15.00	
	1 August	06.45	-	14.75	
8	5 August	-	21.15	14.50	Sampling
	9 August	07.00	-	14.25	
	13 August	-	21.00	14.00	
10	17 August	07.15	-	13.75	Sampling

	21 August	-	20.45	13.50	
	25 August	07.30	-	13.25	
12	29 August	-	20.30	13.00	Sampling
	2 September	07.45	-	12.75	
	6 September	-	20.15	12.50	
14	10 September	08.00	-	12.25	Sampling
	14 September	-	20.00	12.00	
	18 September	08.00	20.00	12.00	
16	22 September	08.00	20.00	12.00	Finish/Sampling

Four growth chambers were used for the experiment. Daylength reduction was arranged according to Table 2.3.

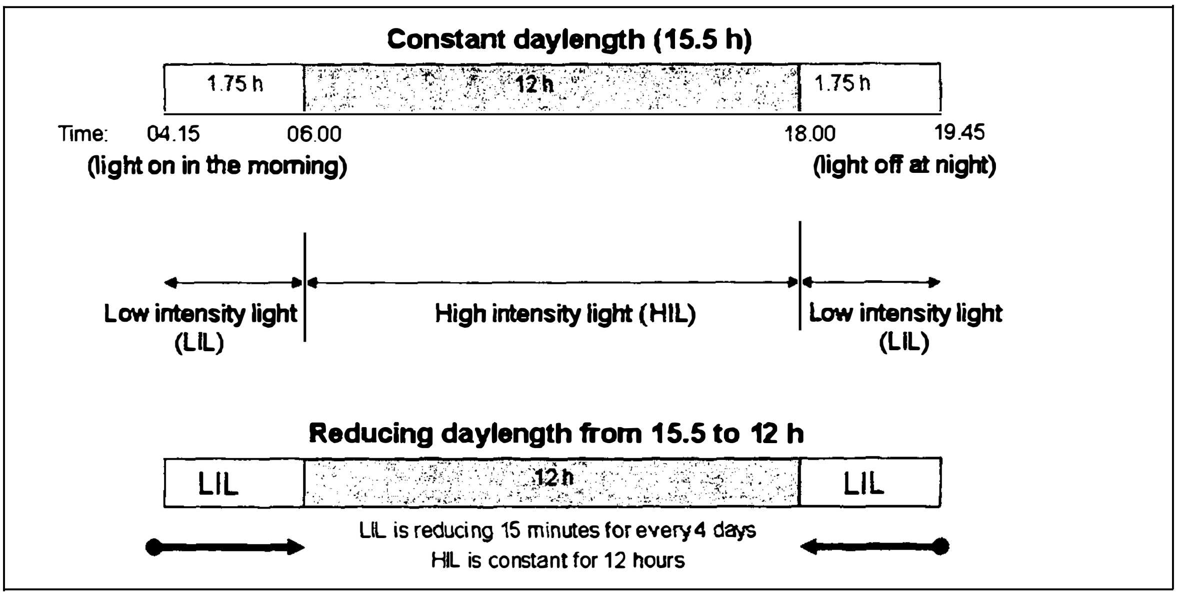


Figure 2.3 Light setting for constant daylength of 15.5 h and reducing daylength in Expt 2. Both have 12 h of HIL and 3.5 h of LIL initially.

Light setting for constant daylength was similar to that in Expt 1. For reducing daylegth, Low Intensity Light (LIL) was reduced by 15 minutes every four days and High Intensity Light (HIL) was kept constant throughout the experiment. Eventually by the end of experiment, reducing daylength had only 12 hours of HIL (see Table 2.4 and Fig. 2.3).

Table 2.4 Conditions of controlled climate growth chamber for Experiment 2.

Growth Chamber	Temperature	High Intensity ($\mu mol.m^{-2} sec^{-1}$)	Low intensity ($\mu mol.m^{-2} sec^{-1}$)	Daylength Treatment
1	20°C	385.03	3.9	Constant
2	20°C	396.68	3.9	Reducing
3	20°C	342.8	3.9	Constant
4	20°C	346.77	3.9	Reducing

Daily temperature in each growth chamber was recorded automatically using DATA LOGGER CR10X (Campbell Scientific, Inc., Logan, USA). Type T thermocouples (Copper Constantan) were used as temperature sensors and CR10TCR probe as thermocouple reference (temperature reference for thermocouple measured with the CR10X).

2.2.2.3. *Experimental design*

A randomised complete block design (RCBD) with 2 replications and with 2 daylength treatments (constant long daylength and reducing daylength) by 2 cultivars ('Jersey Giant' and 'JWC1') was utilized over a four month period.

Pots were rearranged to maintain the distribution between pot sizes at each sampling.

2.2.2.4. *Collection of the data*

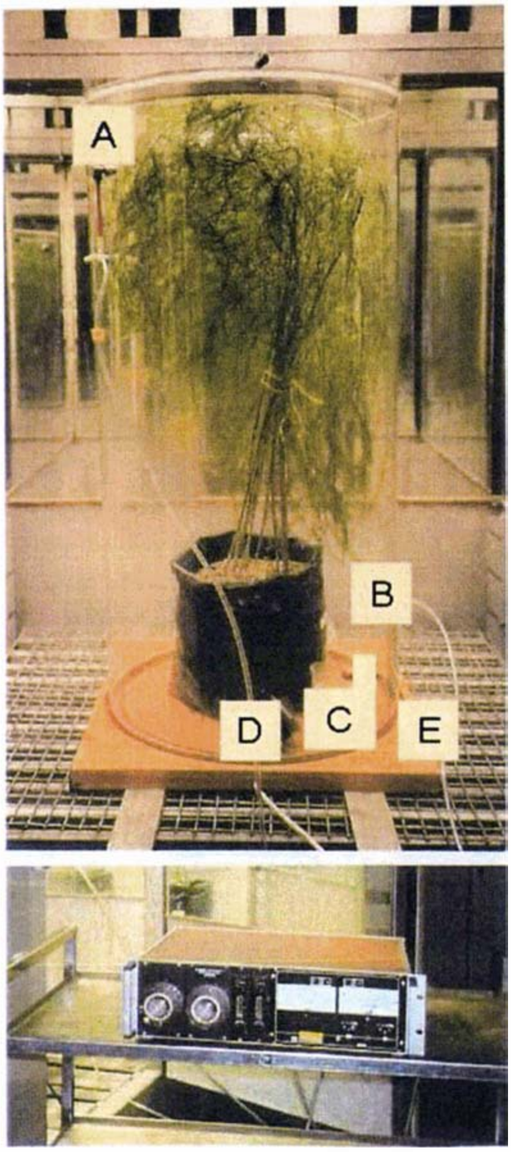
Plants from each chamber were destructively harvested according to the schedule in Table 2.2. Similar measurements as described in Expt 1 (1999) were carried out.

Spears and ferns were counted separately. At the end of experiment net photosynthesis was determined using an Infra Red Gas Analyzer (IRGA).

2.2.2.5. *Infra Red Gas Analyzer (IRGA)*

Measurement of CO_2 fixation using an IRGA was conducted on a total of 16 plants under constant and reducing daylength for the two cultivars at the last measurement. Fresh and dry weight and other growth measurements were obtained from these plants as parts of Expt 2. The measurement was done in a growth cabinet under a temperature of 20°C with irradiance as described in the light setting (Table 2.3). Each plant was put inside an air tight Perspex chamber containing a fan. The base was polyurethaned wood with a water-filled circular groove to form a seal between the perspex and the base. The chamber was connected to a Binos II IRGA (Leybold-Heraeus, GMBH) in a closed loop (Fig. 2.4.) The fan was used to circulate air within the chamber and CO_2 uptake was monitored by IRGA. The CO_2 initially was set at 400 ppm, and measurements were begun at a concentration of 360 ppm and continued for 6 minutes. The volume of chamber was 285.1 l whilst the pots plus plant was 1.1 l.

Assimilation rate was calculated through the assumption that the pressure in the chamber was constant (760 mm). Whilst the volume was constant at 284 l, temperature fluctuated slightly but averaged 24°C. The reduction of CO_2 concentration due to plant photosynthesis in the chamber for every minute recorded through IRGA was converted into μmol of CO_2 per minute for every kilogram of shoot dry weight. These values were regressed against time to obtain the rate of photosynthesis from the value of intercept.



Label:

A: Inlet

B: Outlet

C: Rubber septum

D: Fan

E: Water filled groove in wooden base

Figure 2.4 Measurement of CO_2 uptake by asparagus plants within the chamber (top) and Binos II Infra Gas Analyzer (IRGA) with circulating pump to monitor CO_2 uptake (bottom) (After Karno, 1999)

2.2.2.6. Statistical analysis

A general linear model (Proc GLM) (SAS version 8.2, 1999-2001) for randomized complete block design was used to analyse all variables as described for Expt 1. Protected Least Significant Differences (LSD) at P=0.05 were used to test separation of mean if there were significant differences in univariate ANOVA.

2.3. RESULTS

2.3.1. Experiment 1

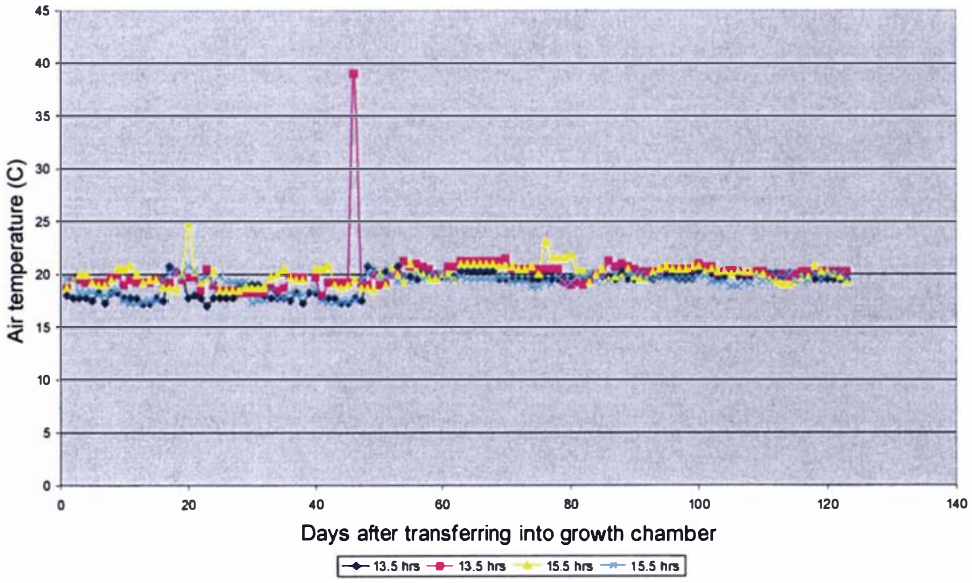


Figure 2.5 Expt 1: Air temperature from four growth chambers in 1999.

Average air temperatures under constant long and short daylength were both 19.6°C. There was one spike of temperature due to temporary fan failure in one growth chamber (Fig. 2.5).

Univariate analysis for each harvest showed there was no significant effect of daylength on growth of asparagus seedlings at any stage for the 18 weeks of observation. When three different pot sizes were used between week 6 and 18, there was no significant interaction between daylength and pot size on plant growth. However, pot size had an effect on growth in some weeks.

Since there was no interaction between daylength and pot size, the results are presented separately.

2.3.1.1. *Number of the bud, shoot, and root under two different constant daylengths*

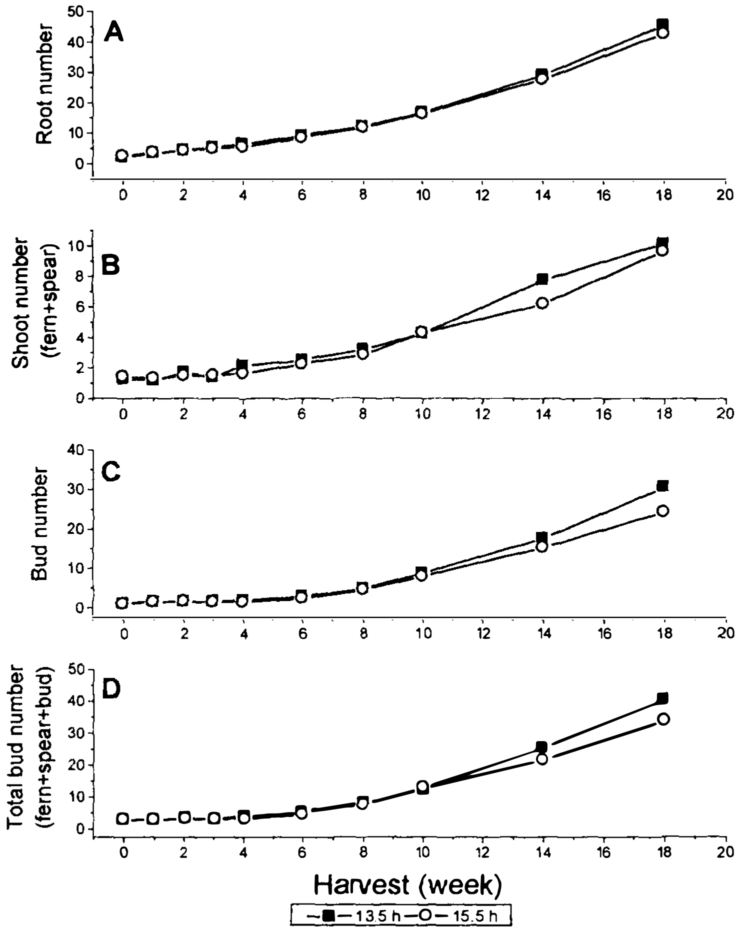


Figure 2.6 Expt 1: Number of root (A), shoot (fern+spear) (B), bud (C), and total bud (fern+spear+bud) (D) per plant of asparagus cultivar 'UC157' at constant daylength at 15.5 h and 13.5 h.

Root, shoot, bud, and total bud number slowly increased over the first four weeks but rates of increase were greater from week 6 to week 18 (Fig. 2.6). Although at the end of the experiment there were some indication of greater root, shoot, and bud number on the short daylength treatment, none of these differences were significant (P= 0.3025 and P= 0.3078 for bud number and total bud number, respectively).

2.3.1.2. *Ratios of root to all combinations of shoot number*

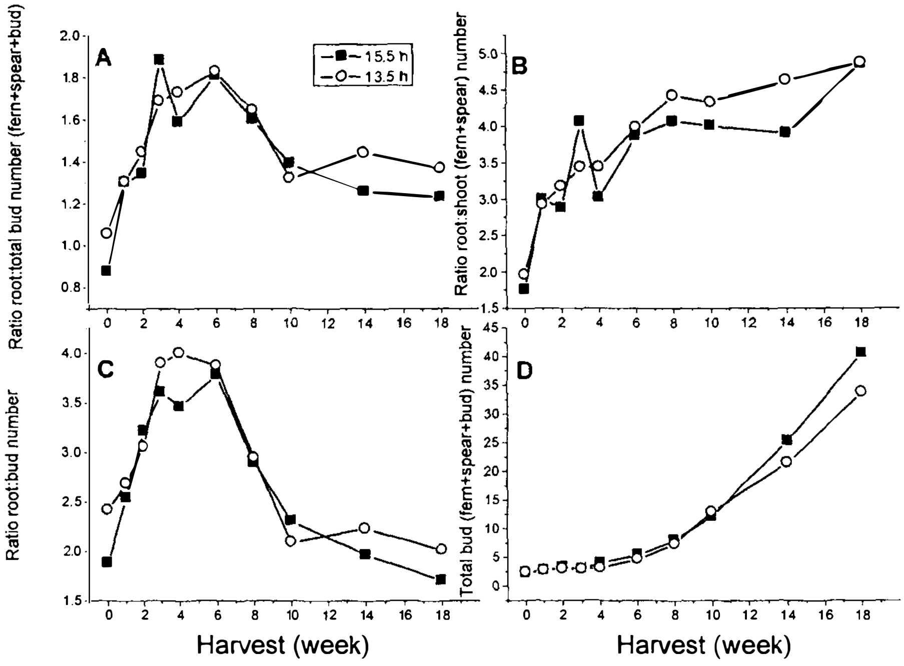


Figure 2.7 Expt 1: Ratio of root:total bud number (A), ratio of root:shoot number (B), ratio of root:bud number (C), and total bud (bud and shoot) number (D) per plant of asparagus cultivar 'UC157' under constant short and long daylength.

There was no significant effect of daylength on any root:shoot ratio (Fig. 2.7). Ratios of root to total bud number (ferns + spears + buds) increased from the first to fourth weeks and gradually reduced beginning at week 6 (Fig. 2.7 A), and stabilised at 1.2 and 1.4 for 13.5 h and 15.5 constant daylength. The pattern of change in the ratios of root:total bud number was similar to the ratios of root to bud number (Fig. 2.7C). But the ratio of root:shoot number (ferns + spears), on the other hand, increased proportionally throughout the experiment (Fig. 2.7. B). Total bud numbers (Fig. 2.7 D) were plotted again as a bases comparison for the other ratios.

2.3.1.3. Dry weight of root, shoot and the ratio of root:shoot dry weight

Root dry weight and shoot dry weight were not affected significantly by daylength (Fig. 2.8), and the ratios of root:shoot dry weight were not different statistically (Fig. 2.8. C). The ratios of root: shoot dry weight increased to about 2.3 at week 3, but showed little change thereafter.

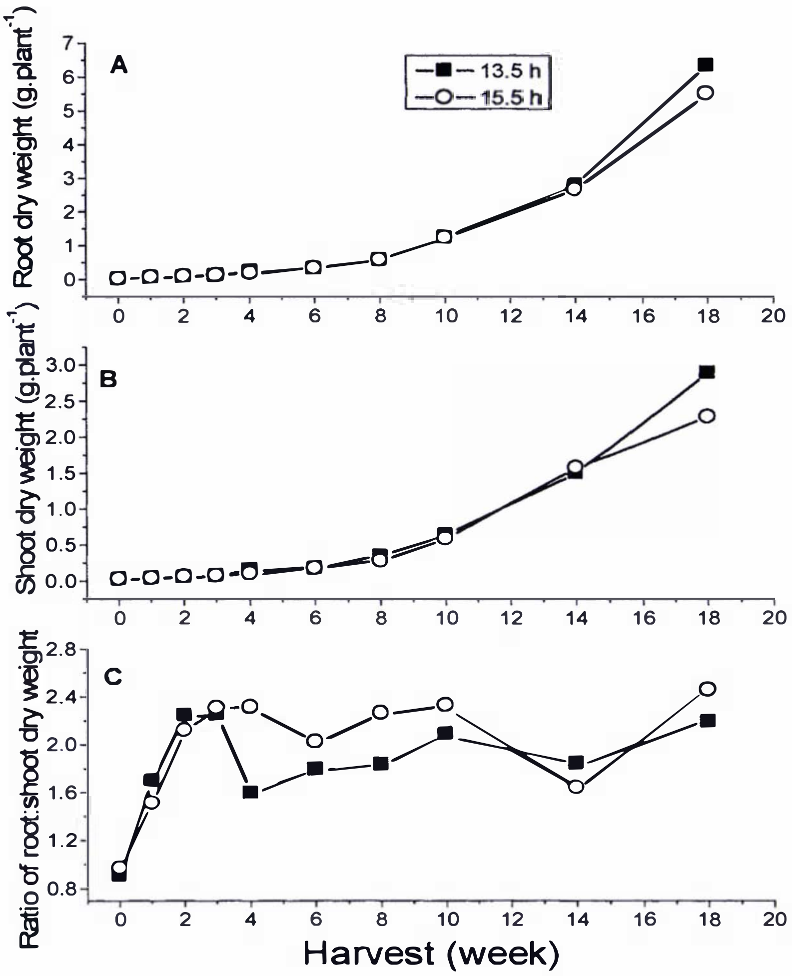


Figure 2.8 Dry weight of root (A) and shoot (B), and ratios of root to shoot dry weight (C) of asparagus 'UC157' grown at different constant daylength.

2.3.1.4. Allometric constant under two different constant daylength

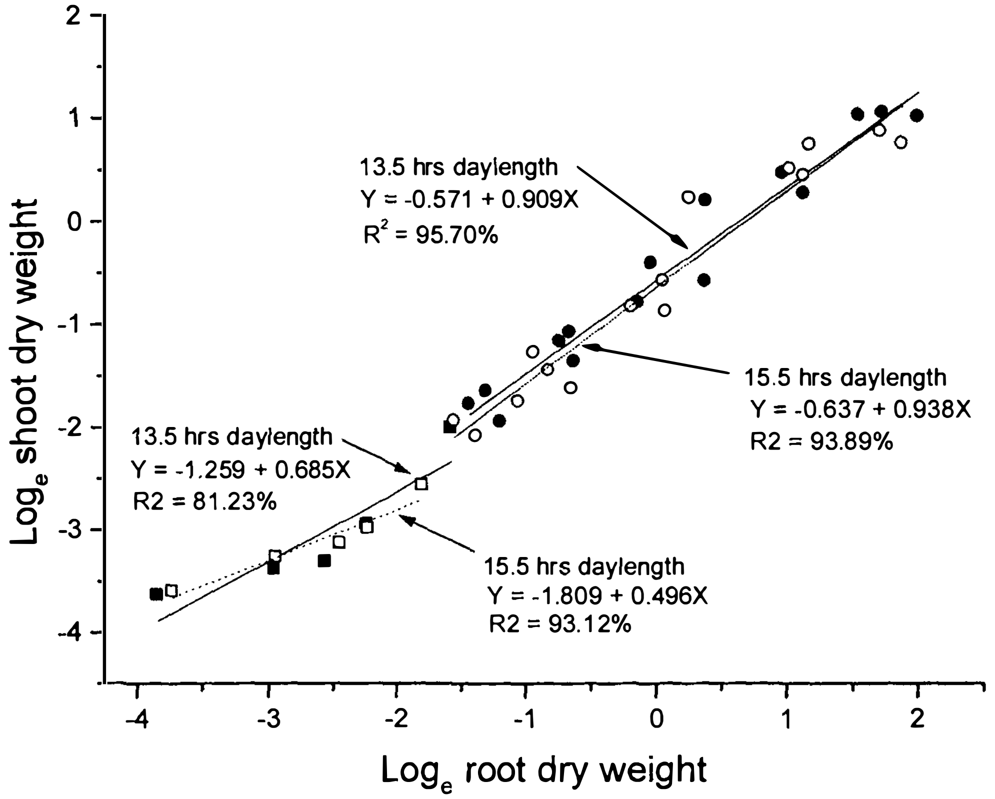


Figure 2.9 Expt 1: Allometric constant log$_e$ shoot dry weight against log$_e$ root dry weight of asparagus 'UC157' grown at two constant daylength (13.5 hrs and 15.5 hrs) for two sections: 0 - 4 weeks and 6 – 18 weeks. Solid and broken lines indicate lines to predict the constant values of allometry. Symbols are for actual values associated with the lines. ■ = constant short day; □ = constant long day; ● = constant short day; ○ = constant long day.

The allometric constants were plotted separately for weeks 0-4, when all plants were grown in the same size of small pots, and from week 6 to week 18 when three pot sizes were used (Fig. 2.9). The two allometric constants under constant long daylength (k =

0.496) and short daylength (k=0.685) were not different statistically for the first four weeks. Regressions explained 81% and 93% of data variation for constant short and long daylength, respectively. Both allometric constants increased to 0.9 over the period week 6 to week 18, and they were not significantly different. The two regression lines within this period explained more than 93% of data variation.

2.3.1.5. Shoot height under different daylength

Table 2.5 Expt 1: Means and standard errors of shoot height of asparagus plant cultivar 'UC157' under two different daylengths

Week	Constant daylength	
	Short daylength (13.5 hrs)	Long daylength (15.5 hrs)
0	19.75 ± 0.74	19.00 ± 0.50
1	19.62 ± 0.50	19.37 ± 0.58
2	19.67 ± 0.49	19.83 ± 0.56
3	22.89 ± 2.57	19.17 ± 3.43
4	28.91 ± 3.61	24.41 ± 1.96
6	30.17 ±1.05	29.93 ± 1.45
8	36.86 ±2.37	33.79 ± 1.50
10	44.48 ± 1.58	43.19 ± 1.49
14	58.15 ± 5.39	66.76 ± 5.63
18	71.45 ± 2.20	69.87 ± 1.66

Shoot height of asparagus was not influenced by daylength within 18 weeks (Table 2.5).

2.3.1.6. *Number of buds, shoots, roots of asparagus plants at different pot size.*

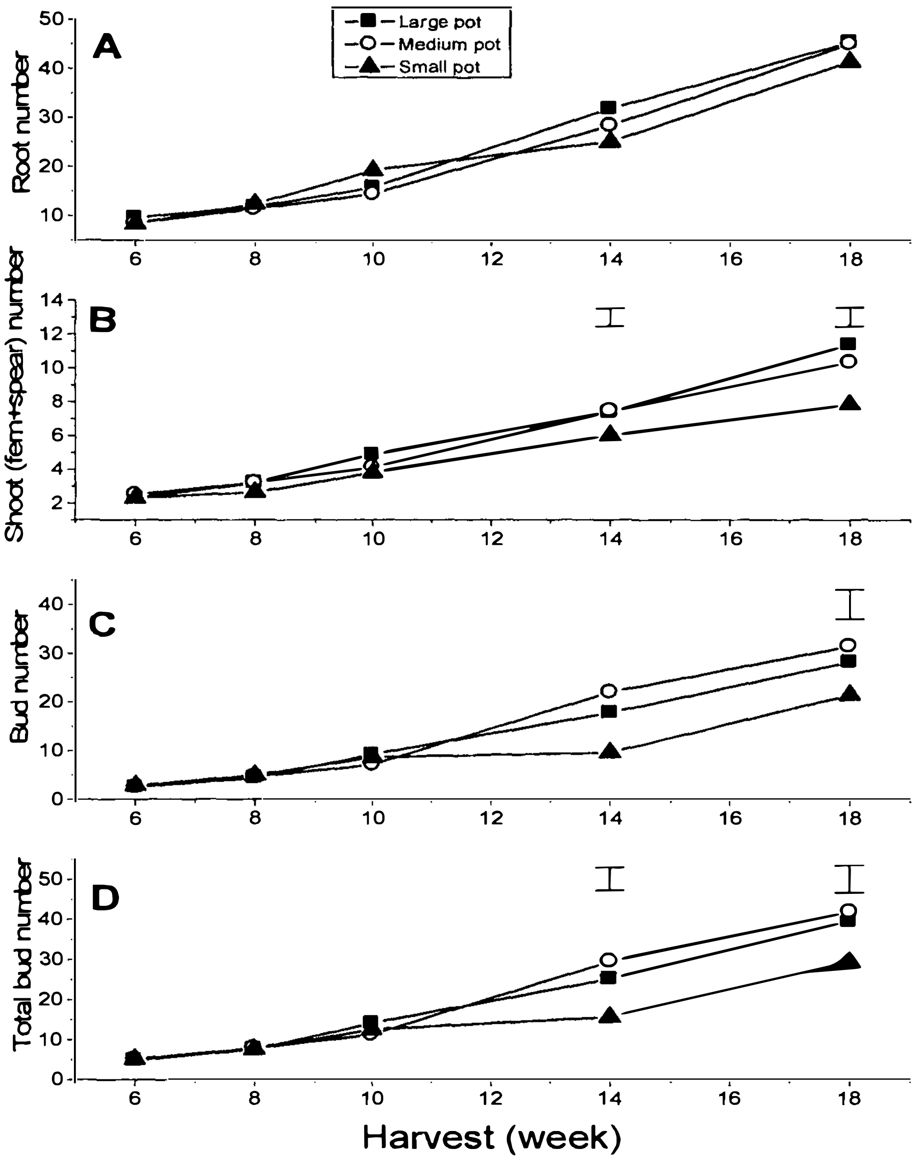


Figure 2.10Expt 1: The influence of pot size on number of root (A), shoot which is fern plus spear (B), bud (C), and total bud (fern + spear + bud) of asparagus 'UC157' grown in growth chamber. Bars indicate $LSD_{0.05}$ to test mean differences among three pot size.

Initially plant growth in terms of bud, shoot, and root number were not influenced by pot size (Fig. 2.10). There was a trend that the plants grown in small pots had fewer roots compared to those grown in large and medium pots at week 14 and 18; but the effect was not significant (Fig. 2.10. A). Bud numbers were significantly higher for the plants in large and medium size pots than those in small pots by week 18 at P=0.0232 (Fig. 2.10 C). Shoot number was also higher in large and medium pots than in small pots at week 14 (P = 0.0323) and at week 18 (P = 0.0021) (Fig. 2.10. B). Significant differences in total bud (ferns + spears + buds) number among 3 pot sizes occurred at week 14 (P = 0.0778) and 18 (P=0.0136) (Fig. 2.10 D).

2.3.1.7. Ratios of root number to all combination of shoot number under three different pot sizes.

The ratios of root to total bud (ferns + spears + buds) number were influenced significantly by pot size at week 10 (P = 0.0367), 14 (P=0.0478) and 18 (P = 0.0249) (Fig. 2.11 A). The ratios of root to total bud number in small pots were relatively constant from week 6 to week 18 (about 1.6), but ratios in large and medium pots dropped sharply at week 10 and continued at about the same values until week 18. The ratios of root to shoot (fern + spear) number were higher in the plants grown in small pots compared to those in large and medium pots at week 8 (P = 0.0385) and 10 (P = 0.0073) (Fig. 2.11 B), but, at week 14 and 18 the ratios of root to shoot number of the plants grown at three different pot sizes were similar. The ratios of root to bud number were reduced from week 6 to week 10 in all pot sizes and were not different from each other. At week 14 and 18, however, ratios of root to bud number in small pots were significantly higher than those in large and medium pots (Fig. 2.11. C). Total shoot number was significantly lower in small pots than those in large and medium pots (P=0.0297) (Fig. 2.11. D).

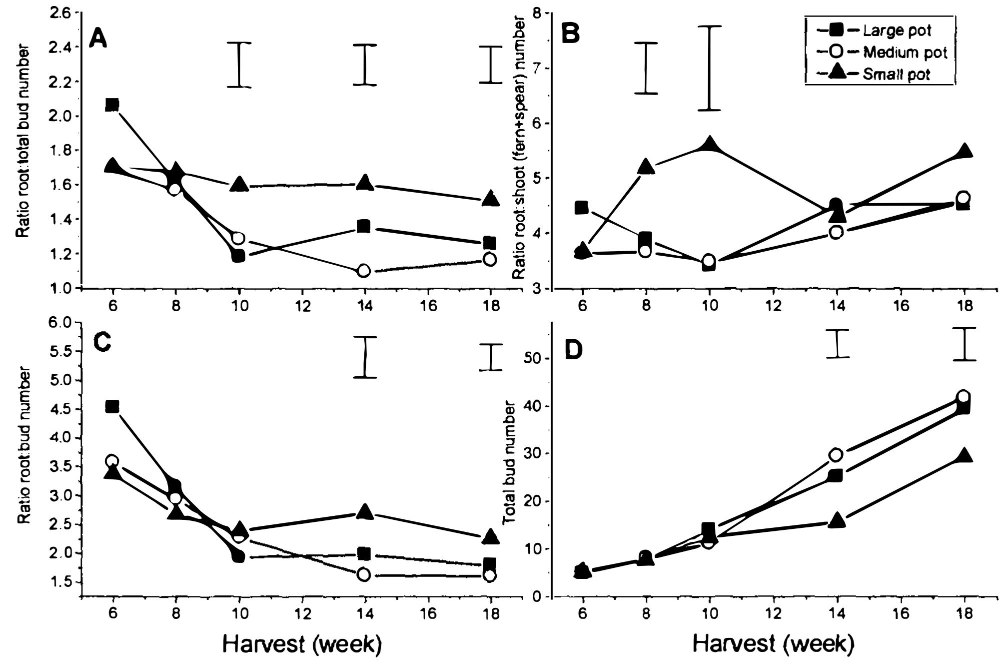


Figure 2.11 Expt 1: The influence of pot size on ratios of root to total bud (fern + spear + bud) number (A), root to shoot (fern + spear) number (B), root to bud number (C), and total bud number (D) of asparagus 'UC157' under controlled growth chamber. Bars indicate $LSD_{0.05}$ to test mean differences among three pot sizes.

2.3.1.8. *Dry weight of root and shoot, and ratios of root to shoot dry weight of asparagus at different pot sizes*

Root dry weights of asparagus plants grown at different pot size were the same from week 6 to 10 (Fig. 2.12. A). At week 14 the root dry weight of the plants from medium and large pots were similar, but significantly greater than those in small pots. At week 18, all the root dry weights were significantly different ($P = 0.0003$) from one another. The shoot dry weight, on the other hand, did not differ at any stage (Fig. 2.12.B). The ratios of root to shoot dry weight were significantly different among pot size from week

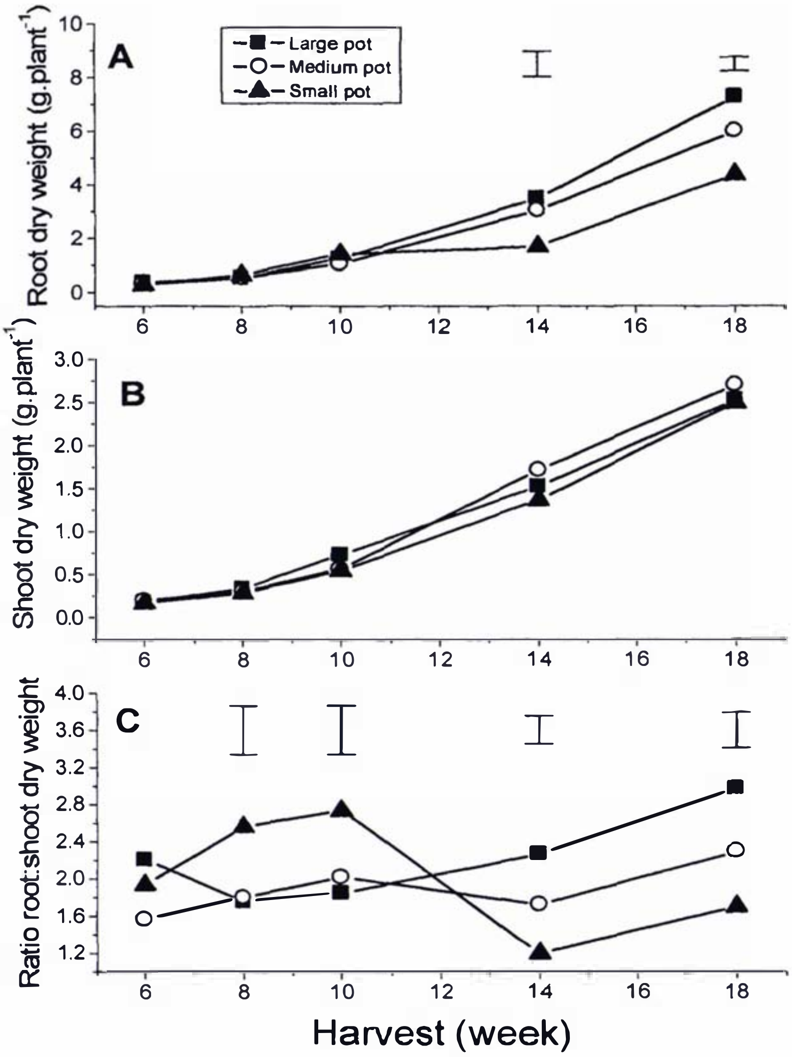


Figure 2.12 Expt 1: Root dry weight (A), Shoot dry weight (B) and ratios of root:shoot dry weight (C) of asparagus 'UC157' grown at three different pot sizes. Bars indicate $LSD_{0.05}$ to test mean differences among three different pot sizes at different harvest time.

8 to week 18 (Fig 2.12 C). Between week 8 and week 10, ratios of root: shoot dry weight of the plants in small pots was significantly higher than those plants in medium and large pots. But in the following two observations, the ratio of root:shoot dry weight increased progressively with pot size.

2.3.1.9. Ratio of root:total bud number and ratio of root dry weight:total bud number.

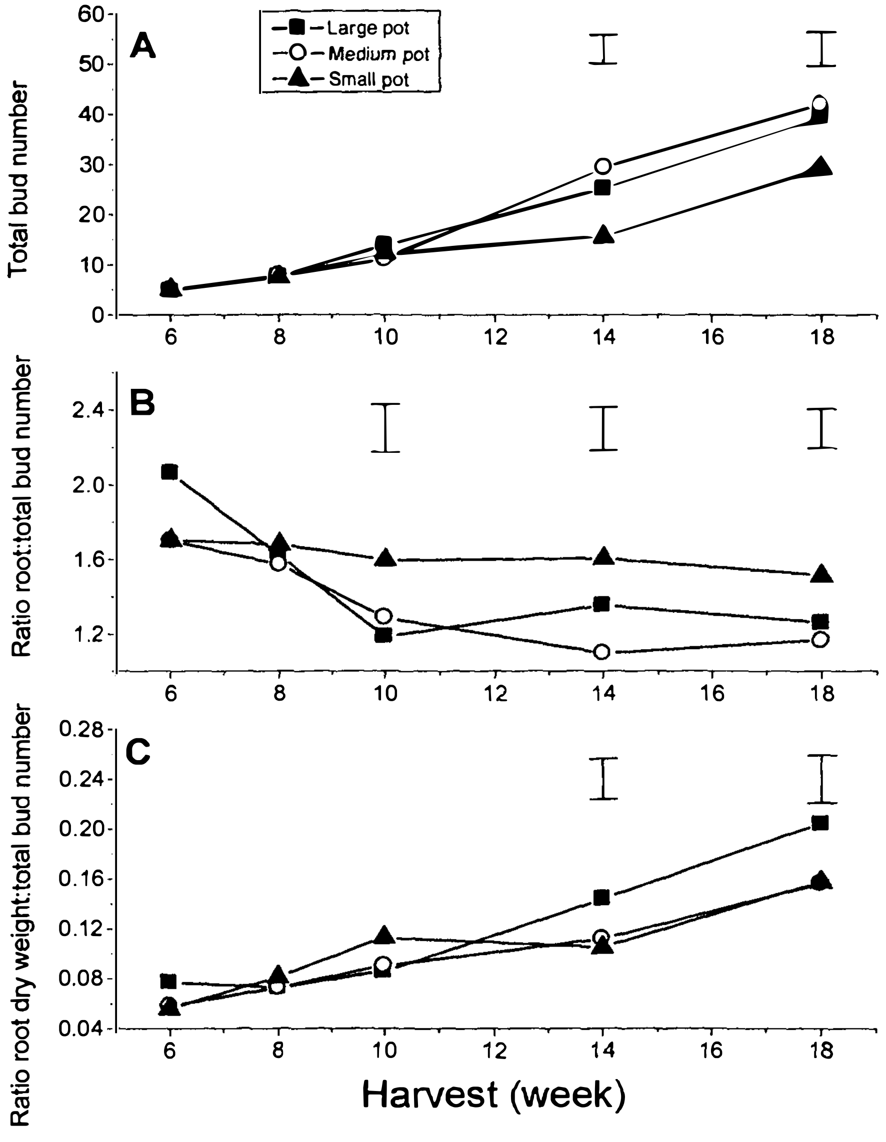


Figure 2.13 Expt 1: Total bud number (bud plus shoot numbers) (A), ratio of root:total bud number (B), and ratio of root dry weight:total bud number (C) of asparagus 'UC157' grown in three different pot sizes. Bars indicate $LSD_{0.05}$ to test mean differences among three different pot sizes at different sampling time.

Total bud numbers (shoot plus bud numbers) were affected by pot size at week 14 and 18 (Fig. 2.13 A). Both plants from medium and large pots produced higher numbers of total buds than those in the small pots. The increase of total bud numbers in the plants from medium and large pots resulted in significant differences in ratio of root number: total bud number (Fig. 2.13B). Whilst the ratio of root number: total bud number from the plants in small pots declined slightly from week 6 to week 10, those in medium and large pots reduced sharply. After that, the ratio remained the same from week 10 to week 18 for those in small pots and slightly fluctuated in medium and large pots. Larger pot size increased dry weight of the root, but did not improve total bud numbers to the same extent. As a consequence, the ratio of root dry weight to total bud number was significantly greater for the plants in large pots by week 14 (Fig. 2.13 C). There were 4.9 total buds per gram of root mass in large pots but 6.4 total buds per gram in medium and small pots. There was no significant difference in total bud number between plants in medium and large pots, indicating that bud numbers per plant may reach a ceiling regardless of root dry weight increases.

2.3.1.10. Allometric constant at the initial small pot size and at the three different pot sizes.

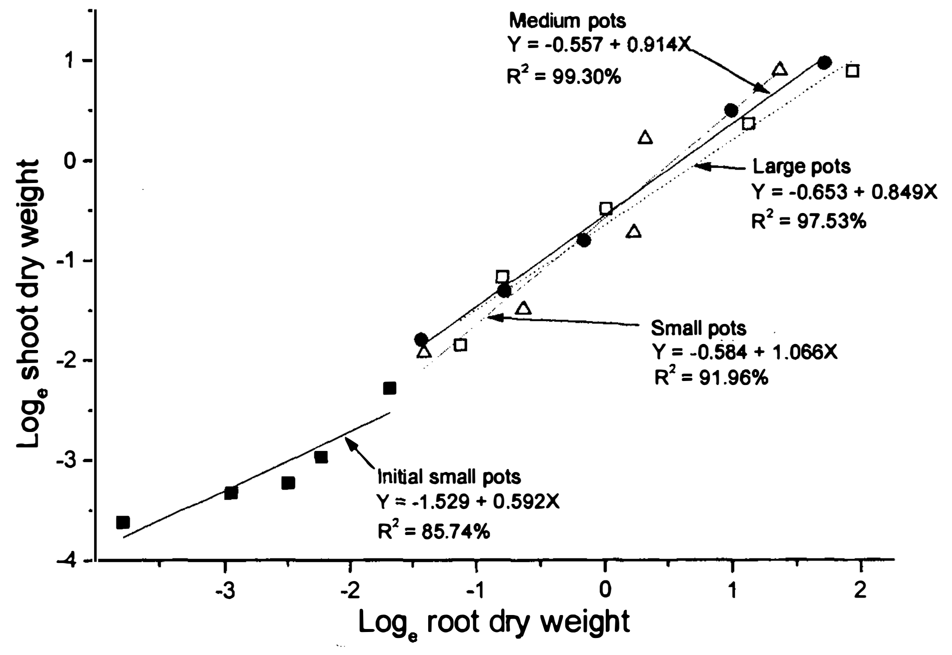


Figure 2.14 Expt 1: Allometric constant log$_e$ shoot dry weight against log$_e$ root dry weight of asparagus cultivar 'UC157' grown in three different pot sizes. Solid and broken lines indicate slopes to determine the constant values of allometry. Symbols are for actual values associated with the lines. ■ = small pots within week 0 and week 4; ▲ = small pots within week 6 and week 18; ● = medium pots; □ = large pots.

The allometric constant during the first four weeks was 0.59 (Fig. 2.14) with the regression equation accounting for 85% of the data variation. When the plants were grown in different pot sizes, the allometric constants changed according to the size of the pot. The allometric constants for small, medium and large pots were 1.066, 0.914, and 0.849, respectively. The allometric constant from large pots was significantly lower than from small pots (P = 0.01) but not from medium pots. The different allometric constants indicated that the plants in large pots produced a proportionally heavier root mass than plants from smaller pot sizes. These allometric constants were obtained from regressions which accounted for more than 90% of data variation.

2.3.1.11. Shoot height of asparagus plants at different pot size

Table 2.6 Expt 1: Means and standard errors of shoot height of asparagus plants 'UC157' grown in three different pot sizes.

Week	Shoot height (cm)		
	Large pot	Medium pot	Small pot
6	29.09 ± 1.59	32.46 ± 1.39	28.60 ± 1.55
8	39.08 ± 2.36	31.86 ± 2.28	35.04 ± 2.46
10	46.21 ± 1.88	40.79 ± 2.12	44.51 ± 1.43
14	57.03 ± 2.15	63.66 ± 2.47	66.68 ± 2.00
18	67.67 ± 2.47	70.12 ± 2.44	74.27 ± 1.99

No difference was found in plant height among the three different pot sizes at any sampling time (Table 2.6).

2.3.2. Experiment 2

Average air temperatures under constant daylength and reducing daylength were 20.17°C and 20.18°C for reducing and constant daylength, respectively (Fig. 2.15).

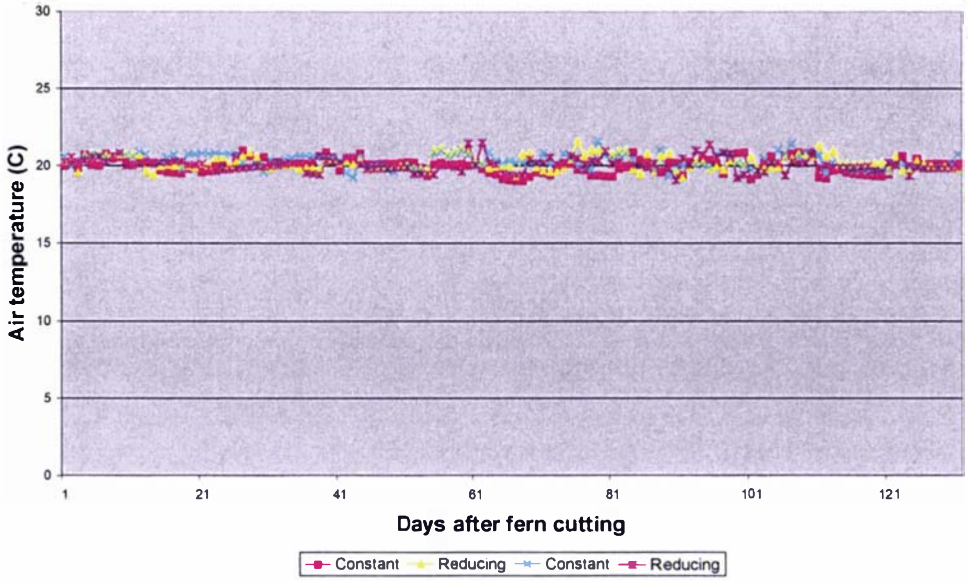


Figure 2.15 Expt 2: Air temperature from four growth chambers in 2000.

No significant interaction between daylength and cultivar was found to affect growth of six month old asparagus plants, so the results of daylength and cultivar effects are presented separately.

2.3.2.1. Daylength effects on the number of roots, total shoots, ferns, spears and buds

The root number (Fig. 2.16 A), total bud number (Fig. 2.16.B) and fern number (Fig. 2.16 C) were not affected by reducing or constant daylength. Total bud number started increasing after the third harvest, at which time daylength was reducing from 14 hrs to 13.75 hrs (Fig 2.16 B).

The significant treatment differences on spear number at harvest 3 and 4 (Fig. 2.16D) appeared to be random effects.

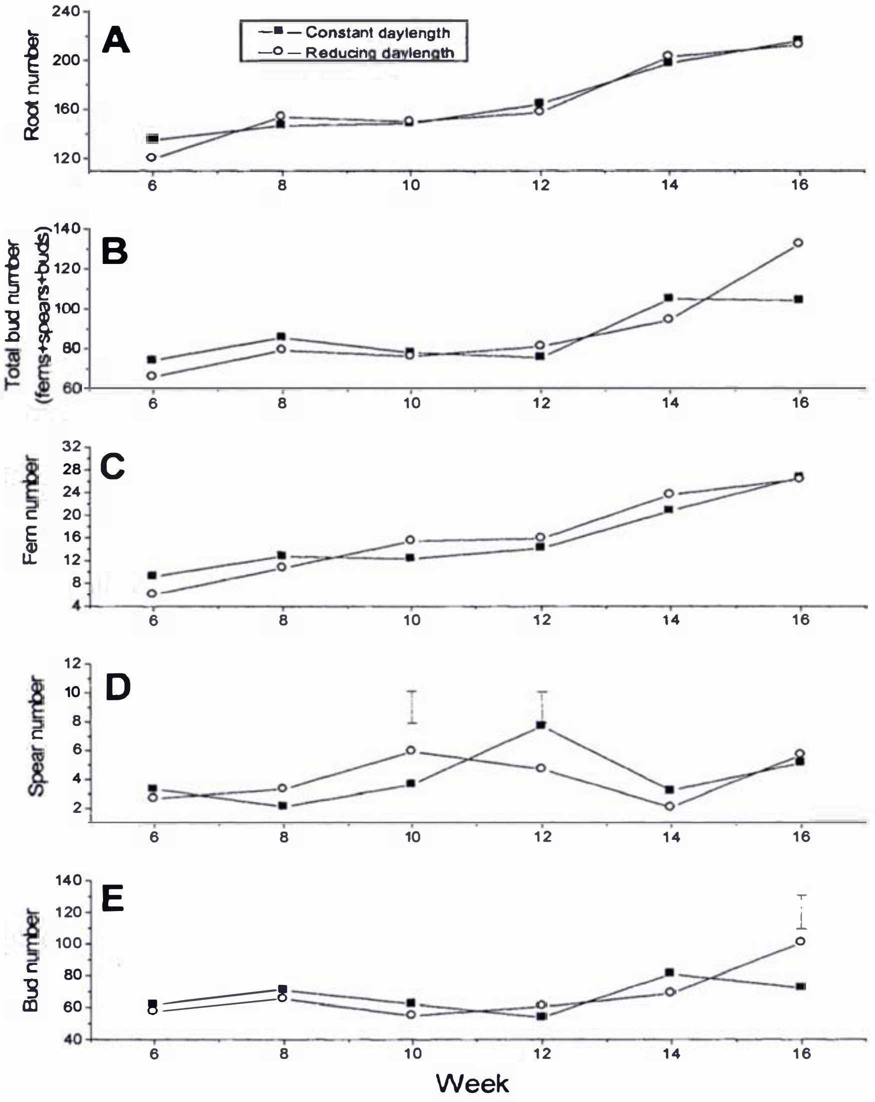


Figure 2.16 Expt 2: Number of root, total shoot, fern, spear, and bud of asparagus under constant and reducing daylength. Bars indicate LSD$_{0.05}$ at different daylength.

The bud numbers of the plants under reduced daylength were initially parallel and lower but not significantly different from those of the constant long daylength (Fig. 2.16. E). Starting at week 12, the bud number of reduced daylength plants increased and was significantly higher at week 16 than that of constant daylength plants. Week 12 coincided with a reduction of daylength to 13.50 hrs.

2.3.2.2. Daylength effects on the ratios of root to total bud number, root to fern number, root to spear number, and root to bud number

There was no significant difference between reducing and constant daylength on ratios of root to total bud number except at the last harvest at $P = 0.05$ (Fig. 2.17 A). Ratios of root to fern number of the plants were similar under constant and reducing daylength, and declined progressively with time (Fig. 2.17 B).

Ratios of root to spear number (Fig. 2.17 C) were significant differently at week 10, 12, and 14, but treatment differences were inconsistent.

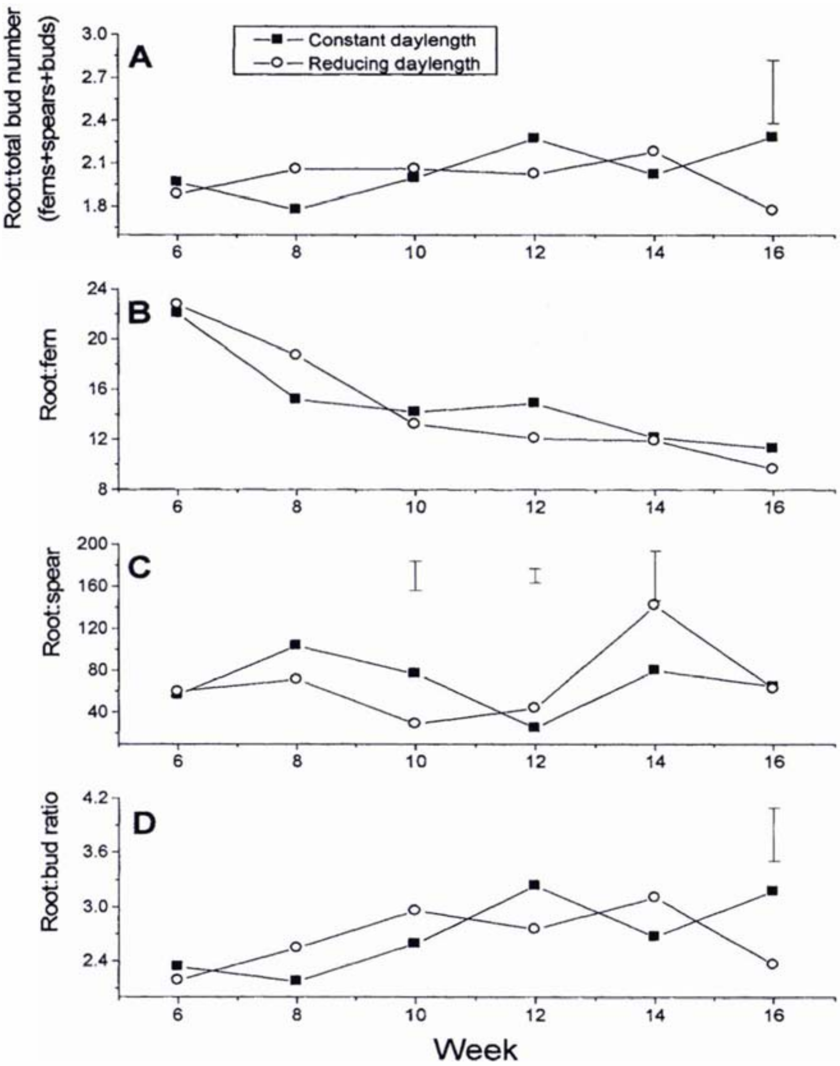


Figure 2.17 Expt 2: Number of buds, spears, shoots and roots of asparagus under two different daylengths. Bars indicate $LSD_{0.05}$ at different daylength.

2.3.2.3. *Daylength effects on root and shoot dry weight and ratios of root:shoot dry weight.*

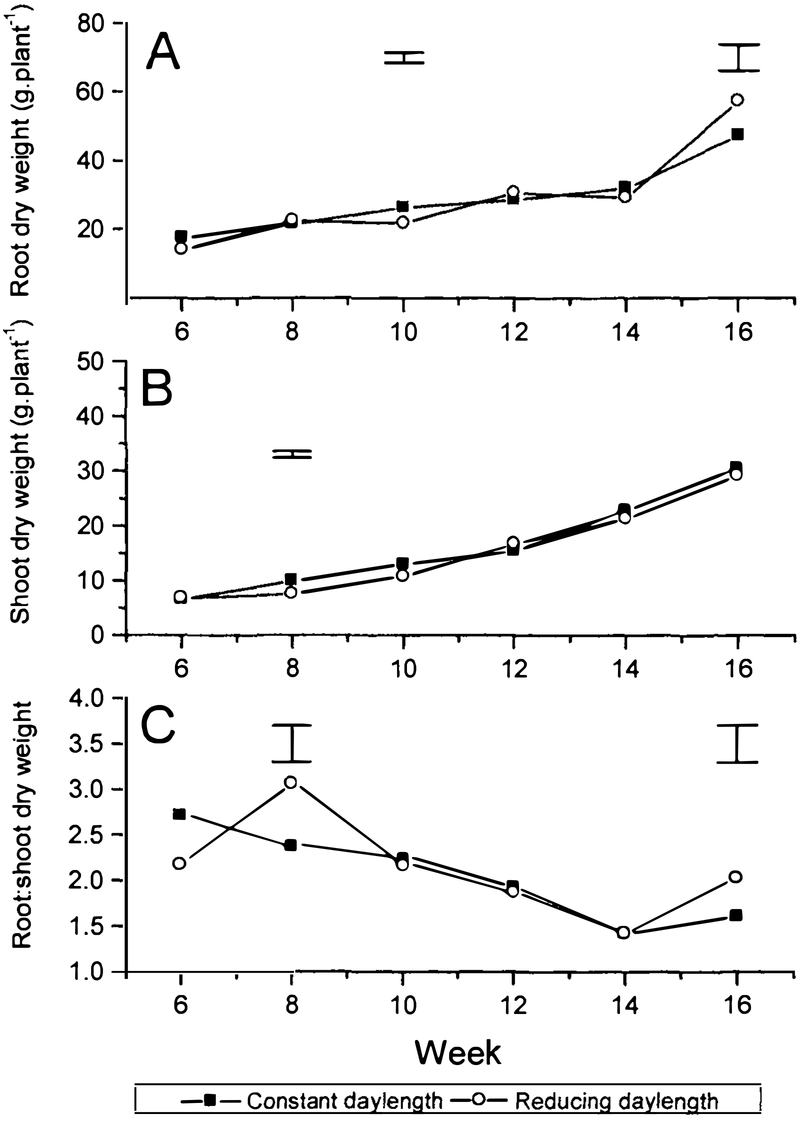


Figure 2.18 Expt 2: Root dry weight (A), shoot dry weight (B), and ratio root:shoot dry weight (C) of asparagus under constant and reducing daylength. Bars indicate $LSD_{0.05}$ at different daylength.

Treatment effects on root dry weight (Fig. 2.18A) shoot dry weight (Fig. 2.18B) and root:shoot dry weight ratio were small and inconsistent.

2.3.2.4. Allometric constant of asparagus plants under constant and reducing daylength

Allometric constants from the plants under reduced and constant daylength indicated differences but (Fig. 2.19) they were not significant.

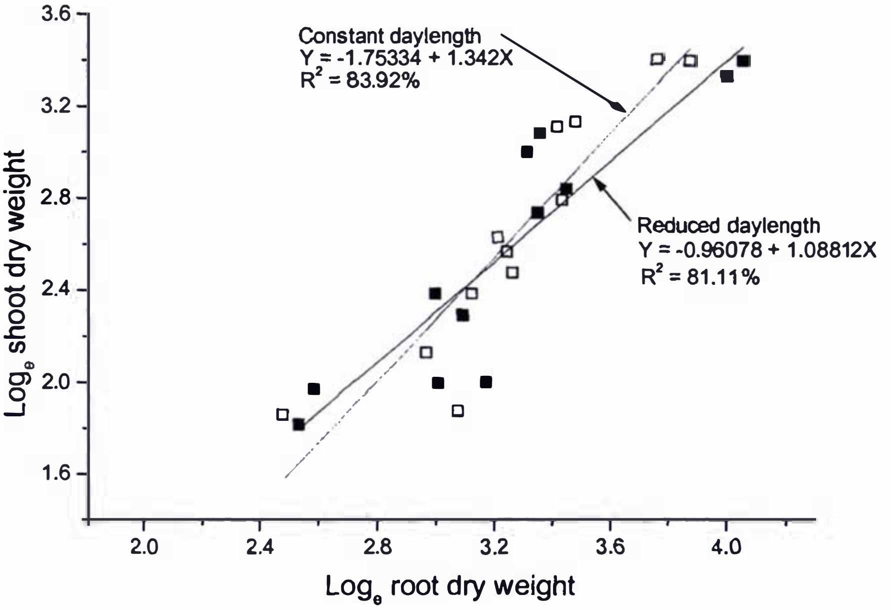


Figure 2.19 Expt 2: Allometric constant log$_e$ shoot dry weight against log$_e$ root dry weight of asparagus at constant and reduced daylength. Solid and broken lines are lines to predict the constant values of allometry. Symbols are for actual values associated with the lines. ■ = reducing daylength; □ = constant daylength.

2.3.2.5. Cultivar effects on the numbers of roots, total buds, ferns, spears, and buds

The root number of 'JWCl' was initially lower but not significantly different from 'Jersey Giant' (Fig. 2.20 A). As the harvest period progressed, the root numbers of 'JWC1' were significantly higher by 50 storage roots than 'Jersey Giant'. This difference occurred from the second to the fifth harvests, but by the final harvest the root numbers were similar between cultivars.

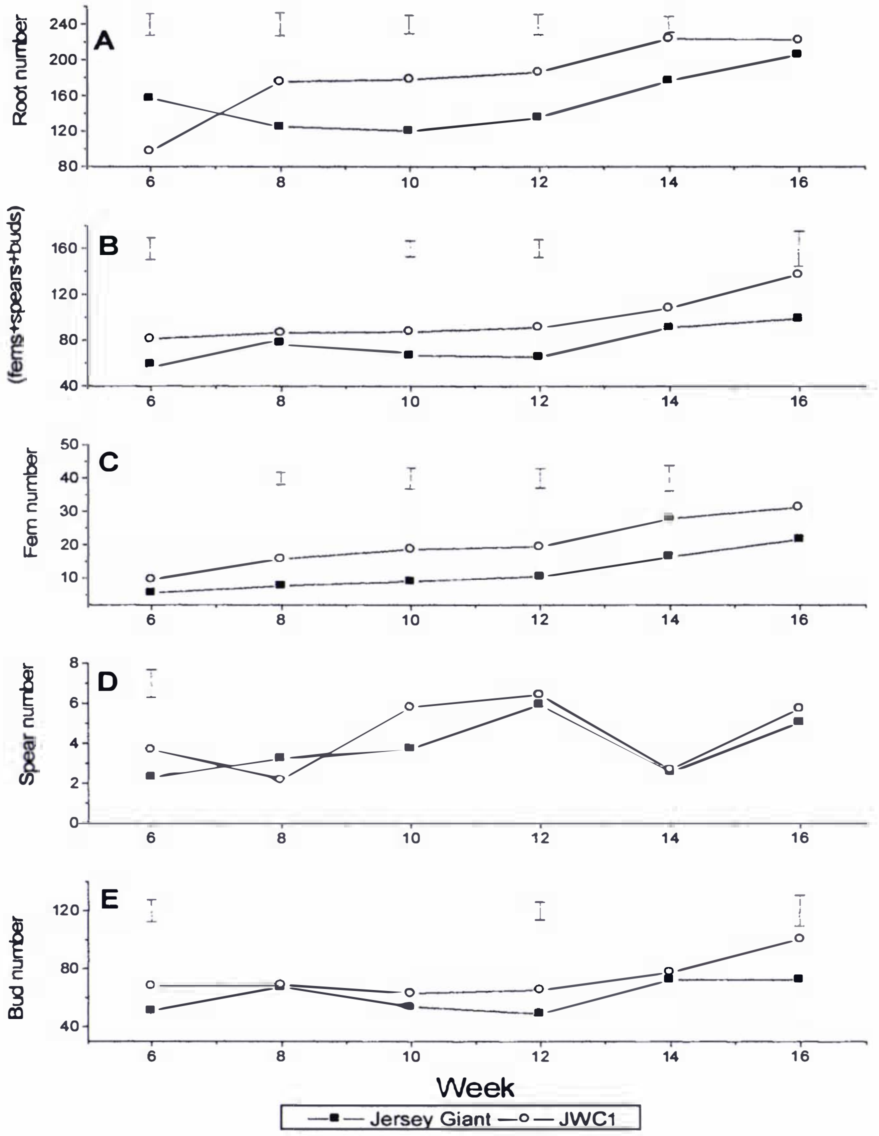


Figure 2.20 Root number (A), total shoot number (B), fern number (C), spear number (D), and bud number (E) of asparagus cultivars 'Jersey Giant' and 'JWC1' across different daylengths. Bars indicate $LSD_{0.05}$ between different cultivars.

Cultivar 'JWC1' produced higher total bud number than 'Jersey Giant' at all times, but cultivar differences were only significant at week 6, 10, 12, and 16 (Fig. 2.20 B). As the bud number increased (Fig. 2.20 E), the total bud number also increased. Fern numbers of 'JWC1' were always higher than 'Jersey Giant' and significant from week 8 to week 14 (Fig. 2.20 C). The spear numbers of both cultivars were almost the same except at the first harvest at which 'JWC1' produced more spears than 'Jersey Giant' (Fig. 2.20 D).

2.3.2.6. Cultivar effects on the ratios of root to total bud number, root to fern number, root to spear number, and root to bud number

Ratios of root to total bud number were significantly higher for 'JWC1' than 'Jersey Giant' at week 8, but this effect disappeared by week 12 (Fig. 2.21 A). Cultivars were similar for root:bud number ratio (Figure 2.21 D). The ratios of root to fern number was higher for 'Jersey Giant' than 'JWC1' throughout the experiment and significant at weeks 8, 12, and 16 (Fig. 2.21 B). These ratios slowly reduced to 12.69 and 8.219 for 'Jersey Giant' and 'JWC1', respectively. Ratios of root to spear number were not different between the two cultivars at any time (Fig. 2.21 C).

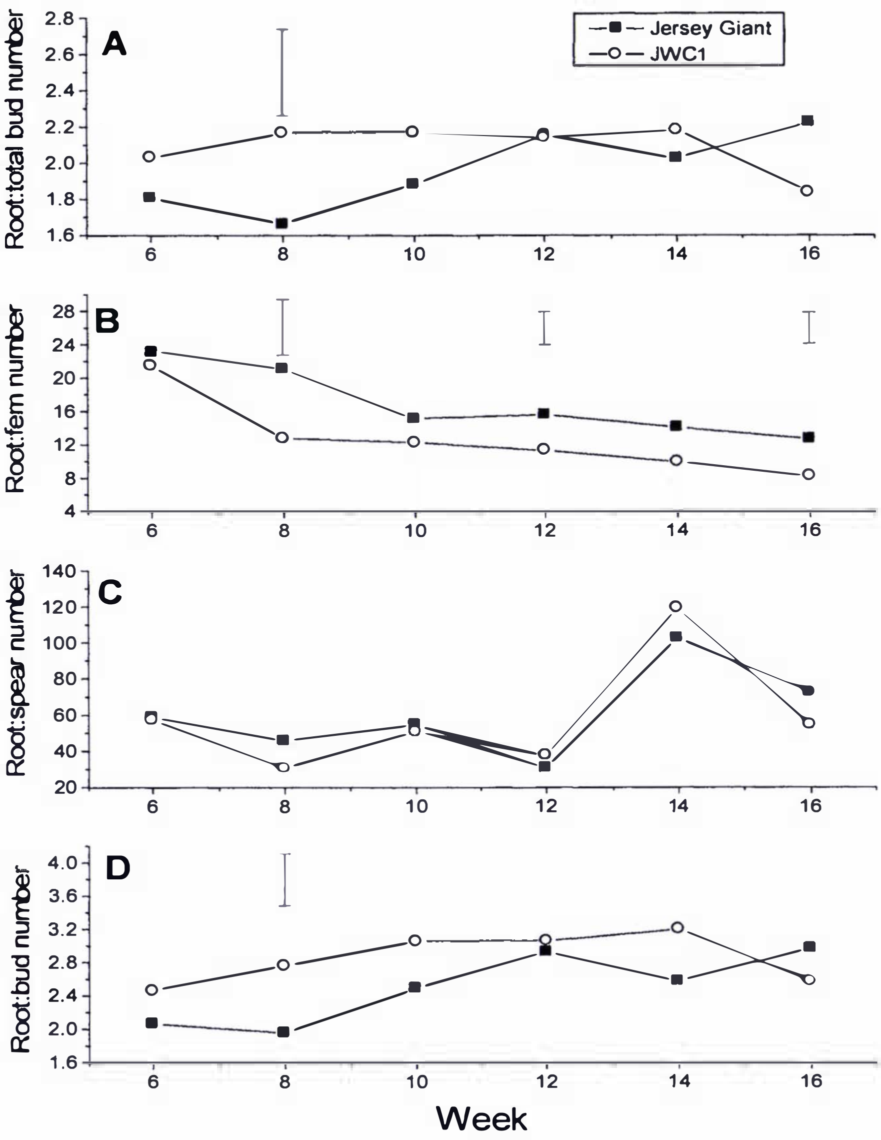


Figure 2.21 Expt 2: Root:total bud number ratio (A), root:fern number ratio (B), root:spear number ratio (C), and root:bud number ratio (D) of two asparagus cultivars grown in the growth chamber across different daylengths. Bars indicate $LSD_{0.05}$ between different cultivars.

2.3.2.7. *Cultivar effects on dry weight of the plants*

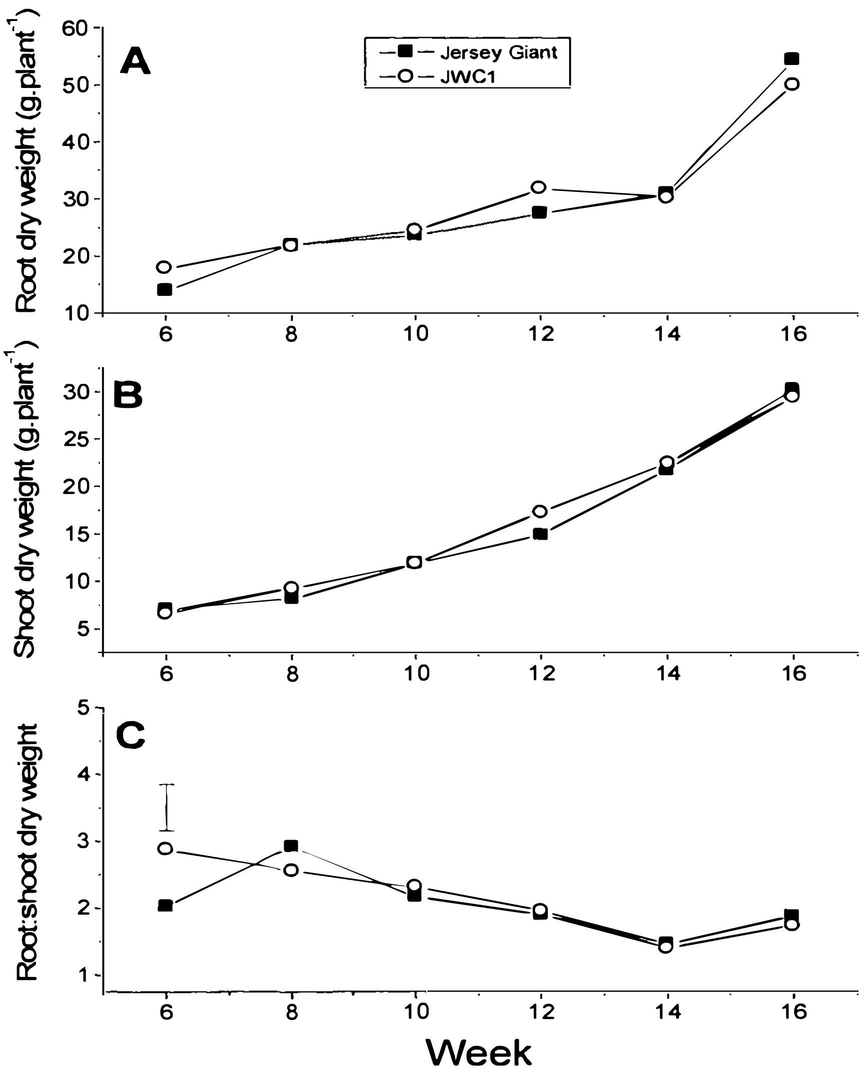


Figure 2.22 Expt 2: Root dry weight (A), shoot dry weight (B) and root:shoot dry weight (C) of two asparagus cultivars grown in growth chamber at different daylengths. Bars indicate $LSD_{0.05}$ between cultivars.

Both cultivars, 'Jersey Giant' and 'JWC1', had similar root and shoot dry weight (Fig 2.22. A and B), and with the exception of a random contrast at week 6, root:shoot dry weight ratio did not differ (Fig. 2.22 C).

2.3.2.8. The effects of cultivars or daylength on asparagus plant height

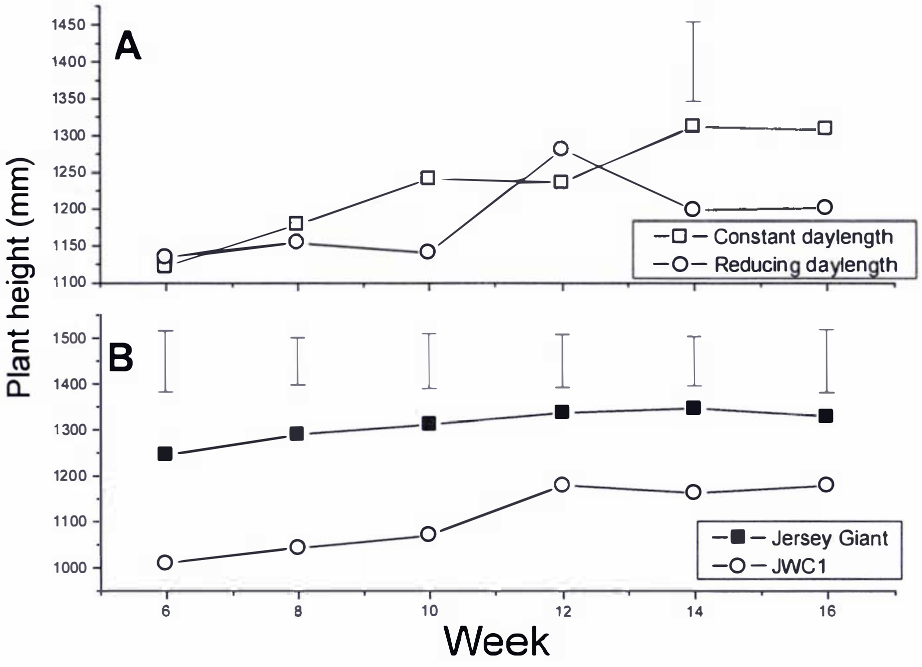


Figure 2.23 Expt 2: Plant height under constant and reduced daylength (A) and between cultivars 'Jersey Giant' and 'JWC1' (B) grown in growth chamber. Bars indicate $LSD_{0.05}$ between cultivars.

Plant height was not affected by daylength (Fig. 2.23 A), but at all times (Fig. 2.23 B) 'Jersey Giant' ferns were approximately 200 mm significantly taller than 'JWC1'. This difference in plant height is illustrated in Fig. 2.24.

Reducing daylength Constant daylength

Figure 2.24 Expt 2: Effects of reducing and constant daylength on asparagus 'JWC1' (first and third from the left) and 'Jersey Giant' (second and fourth from the left) grown in growth chamber.

2.3.2.9. *Allometric constants of asparagus 'Jersey Giant' and 'JWC1'*

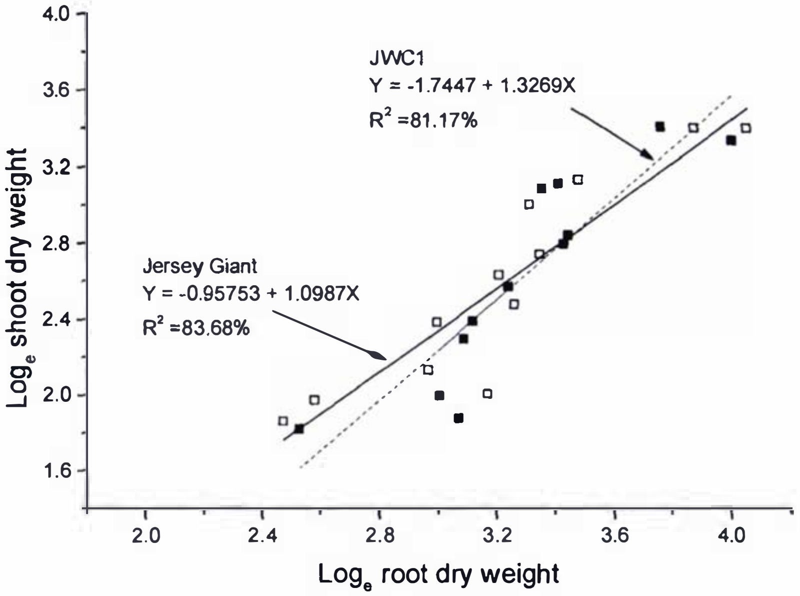


Figure 2.25 Expt 2: Allometric constant ($\log_e$ shoot dry weight against $\log_e$ root dry weight) of two asparagus cultivars grown in growth chambers at different daylengths. Solid and broken lines are predict the constant values of allometry. Symbols are for actual values associated with the lines. ■ = 'JWC1' ; □ = 'Jersey Giant'.

The allometric relationships between $\log_e$ shoot dry weight and $\log_e$ root dry weight ('Jersey Giant' 1.0987, 'JWC1' 1.3269; Fig. 2.25) were not significantly different. The plants with a lower allometric constant, however, tend to partition more assimilate into the root than into the shoot.

2.3.2.10. *Carbon uptake*

Measurements of carbon dioxide assimilation at the last harvest date were conducted on 16 plants from two asparagus varieties at two different daylength treatments. There was no significant effect in daylength and cultivar interaction or daylength itself when analyzed by PROC GLM. 'Jersey Giant' was significantly different from 'JWC1' at $P = 0.05$ (data not shown). From further analysis using regression, 'Jersey Giant' was significantly higher at the intercept than variety 'JWC1' both under constant and reducing daylength. The assimilation rates for 'JWC1' were parallel under reducing daylength and constant daylength. There was an indication that 'JWC1' did not respond differently to reducing daylength whereas 'Jersey Giant' responded differently in term of the assimilation rate (Fig. 2.26).

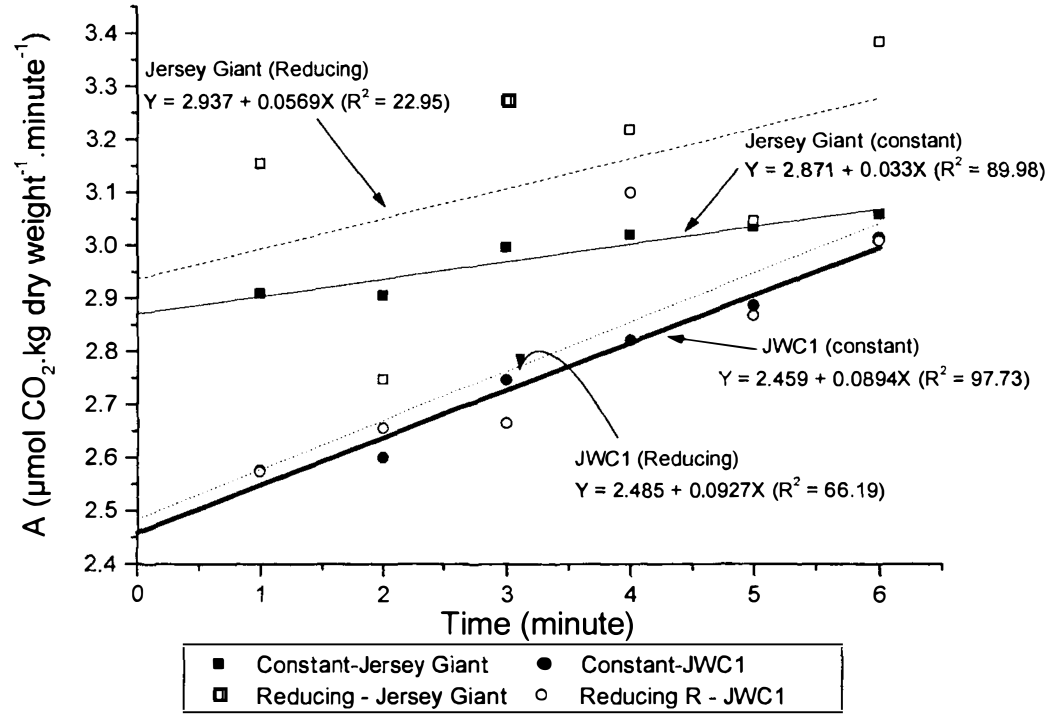


Figure 2.26 Expt 2: Carbon dioxide assimilation rate of asparagus 'Jersey Giant' and 'JWC1' under reducing and constant daylength in growth chamber.

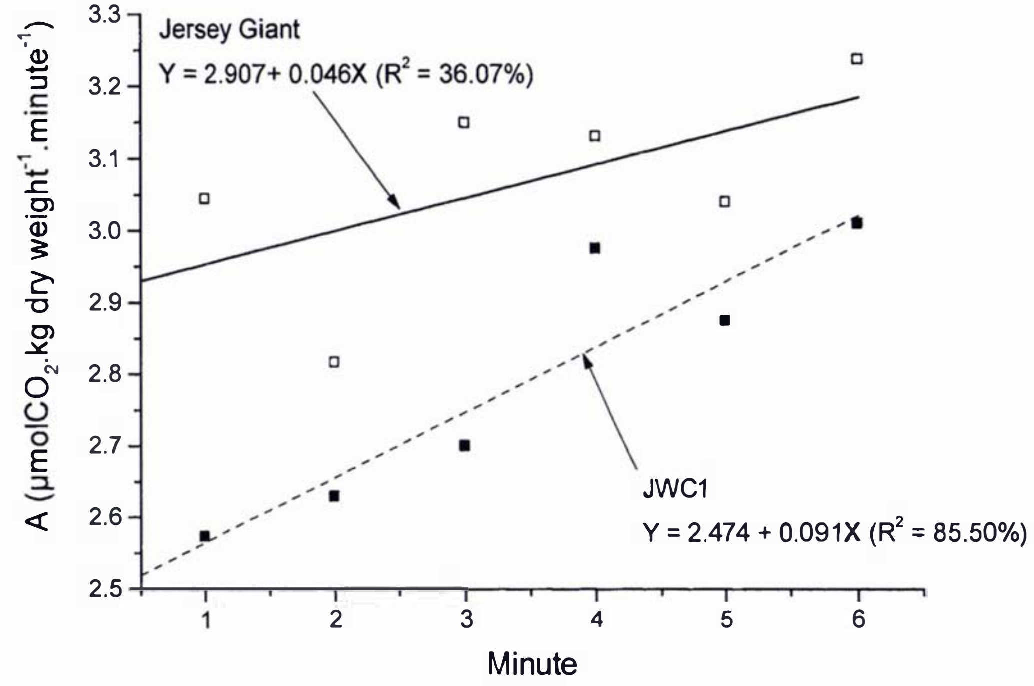


Figure 2.27 Expt 2: Carbon dioxide assimilation rate of asparagus 'Jersey Giant' and 'JWC1' in growth chamber.

Since there was no significant interaction between daylength and cultivar in assimilation rate using PROG GLM, the assimilation rates were plotted for cultivars only (Fig. 2.27). 'Jersey Giant' had higher assimilation rate (*P*<0.01) based on the intercept on the Y-axis (2.907) than 'JWC1' (2.474). High variation in assimilation rates occurred in 'Jersey Giant' and resulted in only 36.07% of data being explained by the model. On the other hand, about 85.50% of data variation fitted the regression model in 'JWC1'.

2.3.2.11. Root:shoot dry weight and allometric constants in relation to carbon uptake

There was an interaction effect of daylength and cultivars at the first observation (week 6) ($P < 0.05$) on ratio of root:shoot dry weight (Fig. 2.28), but this effect disappeared at subsequent observations.

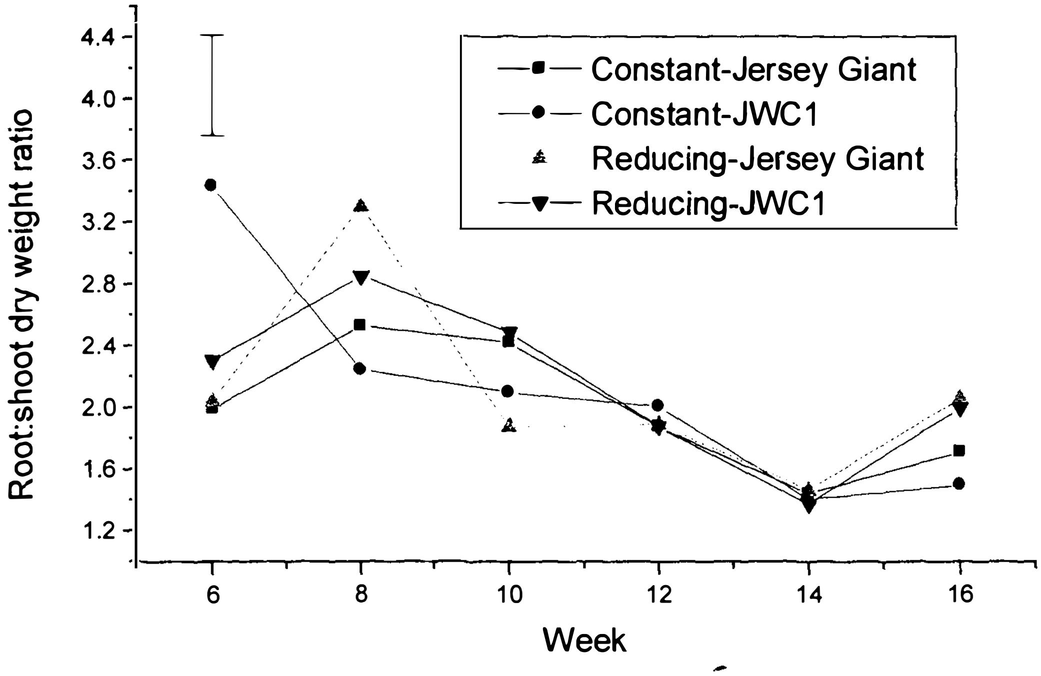


Figure 2.28 Expt 2: Root:shoot dry weight ratios of asparagus 'Jersey Giant' and 'JWC1' in growth chambers. Bar indicates standard error of the mean.

Ratio of root:shoot dry weight of 'JWC1' under constant daylength reduced from week 6 to week 8 and then declined slowly, whilst under the other three combinations ('JWC1' under reducing daylength, 'Jersey Giant' under constant daylength and reducing daylength) the ratio increased at week 8, before declining. The different trends between 'JWC1' under constant daylength and others were reflected clearly in allometric constants (Fig. 2.29), where 'JWC1' under constant daylength differed significantly (*P* < 0.01) from 'JWC1' under reducing daylength and 'Jersey Giant' under constant and reducing daylength.

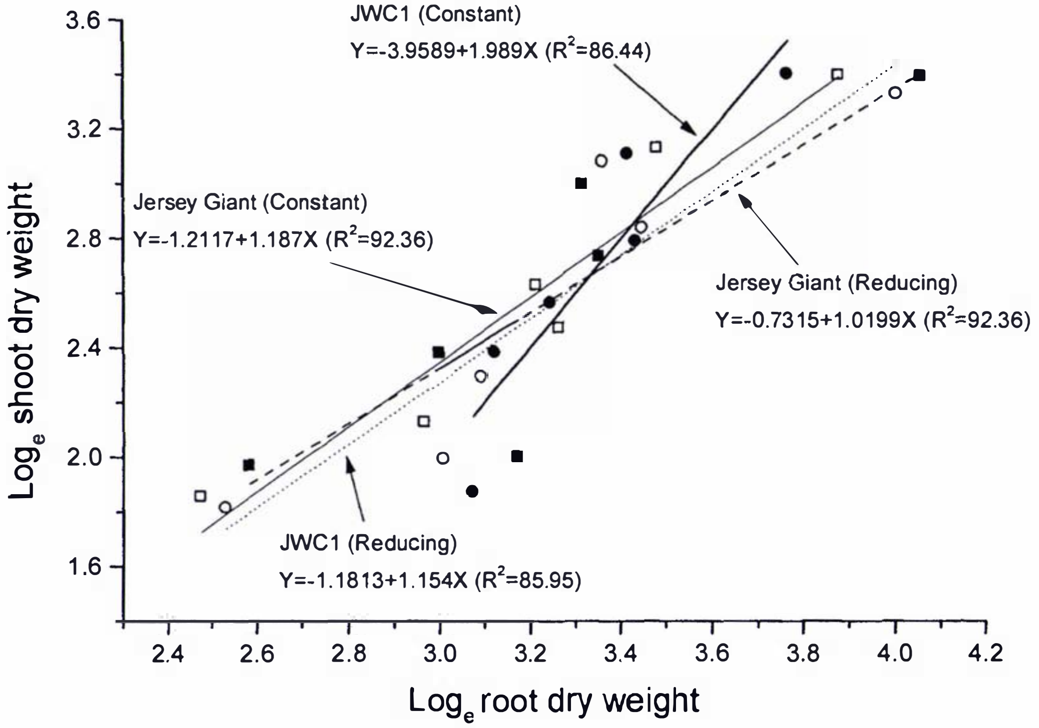


Figure 2.29 Expt 2: Allometric constant ($\log_e$ shoot dry weight against $\log_e$ root dry weight) of two asparagus cultivars grown in growth chambers at different daylengths. Solid and broken lines predict the constant values of allometry. Symbols are for actual values associated with the lines. ■ = Reducing - 'Jersey Giant'; □ = Constant - 'Jersey Giant'; ● = Constant – 'JWC1'; ○ = Reducing-'JWC1'.

2.4. DISCUSSION

2.4.1. The effects of daylength on young asparagus plants

In temperate regions asparagus senesces in the fall season and the ferns dry out. The crown is dormant in the winter but some carbohydrate will be used for respiration. In the spring, the buds grow to form the spears, and ferns, if not harvested. This formation depends on carbohydrate supply and bud availability from the previous season. It is generally stated that once the ferns are established the plant commences to produce more buds (Robb, 1983; Hughes, 1992) and, later, to partition dry matter more into root storage (Shelton and Lacy, 1980; Haynes, 1987). Several growth studies have indicated that daylength might be involved in changing the partitioning from shoot to the root (Sudjatmiko et al., 1997; Woolley et al., 1999).

To provide more detailed information two experiments were conducted under controlled conditions to verify whether daylength is the main cause for this switch in dry matter partitioning in seedlings (Expt 1) and six-month old plants (Expt 2). In Expt 1, two constant daylengths (13.5 h and 15.5h) were chosen to detect if a reduced daylength (13.5 h) affected partitioning differently from long daylength (15.5 h) whilst in Expt 2, a reducing daylength was applied in comparison to a constant daylength of 15.5 h. These daylength treatments were based on the findings of previous research conducted by Sujatmiko et al., (1997), Woolley et al., (1999), and Kamo (1999).

The environmental factors inside the growth chambers were set constant except daylength, but the total photosynthetically active radiation was similar (Table 2.1 and 2.4). In Expt 1 (1999), growth cabinet temperature control once in one chamber resulting in a short term temperature spikes (Fig 2.5), but with no apparent effect on the plants in the affected chamber. A data logger was installed in Expt 2 to provide a continuous record, but air temperature was steady throughout this experiment (Fig.2.15).

In Expt 1, over 18 weeks of observation, there were no consistent significant differences in bud, shoot (fern plus spear), and root numbers between a daylength of constant 13.5 hrs or 15.5 hrs (Fig. 2.6). There was, however, a tendency for total bud production to be higher under a constant daylength of 13.5 h. The effect of this change carried over into the ratio of root:bud number and of root :total bud number (Fig. 2.7) but they were not significantly different.

Root:shoot ratio has been used to show the balance between the supply of nutrient and water to shoots and in return the photosynthates supplied to the roots for their growth and activity (Troughton, 1974). This interdependency was initially described as a size equilibrium between root and shoot corresponding to the need to have an amount of leaves and roots which were functionally equivalent in their capacity to support each other (Brouwer, 1963). Any environmental limitation to the plants such as drought, low temperature or poor light could change root:shoot ratio.

The simplest quantitative expression of the root to shoot relationship is the ratio of their respective dry weights. The ratio of root:shoot dry weight both in short and long daylength in Expt 1 increased initially from 0.9 to 2.2 in week 3 (Fig. 2.8). The increase and fluctuation of root:shoot dry weight ratios were an expression of the development of seedlings into young plants. Here, buds developed into spears and ferns which in turn, produced more buds for more fern to establish; differences in constant daylength did not affect this early growth. At the end of Expt 1, the root:shoot dry weight ratios stabilized at 2.2 and 2.3 for short and long daylength but they were not significantly different (Fig. 2.7). Since dry weight in the plant is the total number multiplied by the individual weight, the changes in root:shoot dry weight ratios were also reflected into ratios of root: total bud number (ferns + spears + buds) and of root:bud number (Fig. 2.7). Within the first four weeks, the ratios of root:bud number increased from 1.9 and 2.4 to 3.6 and 3.9 (Fig. 2.7) for constant daylength of 15.5 and 13.5 h, respectively, and subsequentially declined as seedlings developed into more established plants.

Dufault and Greig (1983) showed that the ratio of root:shoot number increased from 2.1 to 8.4 for 'UC157' and from 1.8 to 6.0 for 'UC80'. They found a positive correlation between the number of storage roots and the number of buds (r = 0.91). From their measurements of root, shoot and bud number and fresh weight of root and shoot of asparagus seedlings of cultivar 'UC157' (hybrids) and 'UC80' (open pollinated = OP), shoot initiation predominated over bud production early in the season (2:1 ratio), but reduced gradually to about 1:2 (0.5) later on. They found that ratio of root:bud number stabilized to about 3:1 in both cultivars at 14 weeks after emergence. These ratios indicated greater bud production later in the growing season. As the seedling growth progresses throughout the season, more and more buds are developed on the crown, and the buds develop to produce ferns which eventually ferns support new bud formation and bud accumulation.

Table 2.7 The effects of constant daylength on ratios of root to different parts of shoot of asparagus seedling at week 18.

Daylength Treatment	Root:total bud number	Root:shoot number	Root : bud number	Root dry weight: shoot dry weight
13.5 h	1.232	4.864	1.703	2.191
15.5 h	1.368	4.879	2.009	2.305
Significance	ns	ns	ns	ns

In the present study, the ratios of root:bud number were 1.7 and 2.0 whilst the ratios of root:total bud number were 1.2 and 1.4 at week 18 for constant short and long daylengths, respectively (Table 2.7). These results were slightly lower than the values given by Dufault and Greg (1983). Derived from their figures of bud, shoot, and root numbers, the ratio of root to total bud number in 'UC157' was 2.1. However, Sudjatmiko (1993) found that the ratio of root to total bud number of asparagus seedling 'UC157' was increasing from 1.38 initially to 3.1 at final harvest. The difference in ratios of root to total bud number may come from plant size as shown in Sudjatmiko's study.

The disadvantage of using root:shoot ratio is it increases with plant size (Ledig et al., 1970) due to exponential growth. In Expt 1, the ratios of root:bud number at week 4 (3.5) were similar to those of Karno (1999) but different thereafter (Fig.2.7). Karno (1999) measured plant growth of asparagus 'UC157', 'Jersey Giant', and 'Italian Hybrid' under the influence of constant daylength of 15.5 h and reducing daylength from 15.5 to 12 h in growth cabinets. In his study, the ratios of root: shoot number of 'UC157' for reducing daylength and constant daylength were about 6.6 and 4.9 respectively whilst in Expt 1 the ratio for constant daylength both treatments were 4.9 (Summary Table 2.7). These different responses could be due to (1) the reducing daylength (Karno, 1999) rather than constant daylength or (2) the change of pot size in Expt 1.

Karno (1999) suggested in his study that asparagus plants started to increase root:shoot ratio when the daylength was reduced from 15.5 h to about 14 h compared to a constant daylength of 15.5 h. In his study, the plants under reducing daylength had higher crown dry weight than those under long constant daylength in harvest 3 (week 6) which is associated with reducing daylength between 14 h and 13.5 h. This higher crown weight was maintained until daylength was reduced to 12.5 hrs, but the effect was not maintained at a daylength of 12 h. Thus reducing daylength, rather than constant daylength may have triggered dry matter partitioning into the root. Woolley et al. (2002) suggested that pot size might have restricted root growth of asparagus towards the end of Karno's study, thus limiting the influence of daylength.

Gradual changes of root:shoot ratio over time are often associated with ontogenic drift, which is the change in plant response as it progresses through its life cycle (Evans, 1972). The changes can also be associated with plant size because plants are growing exponentially. The relationship between root and shoot can be considered more appropriately as an allometric constant. The allometric constant or k value is unaffected by size (Hunt and Burnett, 1973) and it is more widely used in growth comparisons than root:shoot ratio (Hunt and Burnett, 1973).

Environmental factors are often reflected in distinct changes in the allometric ratio of shoot:root dry weight (Hunt, 1990). If the allometric constant changes this indicates a response of the plants toward influential factors of the environment. This situation was reported by Sudjatmiko et al. (1997). They planted asparagus seedlings into the field for seven successive planting dates 4 weeks apart in New Zealand (latitude at 40° 23'S). The planting started as early as 21 September and the latest was on 8 March. They found there was an abrupt change in allometric relationship occurred at the same time in all asparagus plants except for the last two harvests, regardless of plant size and age. This change of allometric constants occurred when daylength was about 14 h (early February). In Karno's study (Karno, 1999), the allometric constants for reducing and constant daylength were 0.69 and 0.86, respectively. In Expt 1, the allometric constants for the seedlings under constant daylength of 13.5 and 15.5 h over the first four weeks were 0.69 and 0.5 respectively, but changed after 4 weeks when the asparagus plants were transferred into different pots (0.9) (Fig. 2.9). In Expt 1 pot sizes rather than different constant daylength may have influenced the allometric constant of seedlings. This pot size effect will be discussed further in section 2.4.3.

In a follow up experiment (Expt 2), reducing daylength was simulated in growth cabinets by daylength extension utilizing two incandescent lamps and one long life tube lamp to produce low intensity light (LIL, 7.5 $W.m^{-2}$). Total radiation was kept constant (see section Materials and Methods) and LIL was the only factor to change in the growth chamber (Fig. 2.3 and Table 2.3). This reducing LIL simulated daylength change in the field from long daylength in summer to short daylength in autumn.

Faville et al. (1999c) found there was very little fern establishment after the end of January which was equivalent to about 14h daylength, so the majority of the assimilate was translocated into the storage roots and in smaller amounts to buds and rhizome. He measured the partitioning using ^{13}C. These results supported previous work done by Woolley et al. (1999) using ^{14}C-photosynthate which found an abrupt change in partitioning of carbon between fern and crown (rhizome plus storage roots) during mid to late-summer. On the 22 January (mid summer) the highest percentage (39.6%) of radioactive label accumulated in young fern followed by 18.4% in the storage roots associated with older parts of the rhizome But later on (late summer) 68.9% of the activity partitioned to the storage roots particularly those with labelled ferns (30.4%). All these results indicated that reducing daylength may have changed the partitioning in asparagus plants.

Six-month-old asparagus plants under controlled conditions, subjected to reducing daylength or constant daylength in Expt 2, responded similarly (Fig. 2.16 and 2.18). However root dry weight and shoot: root dry weight ratio was possibly significantly affected by reducing daylength at week 16, and spear number was significantly affected by reducing daylength at week 10 and 12 (Fig. 2.16 D) equivalent to reducing daylength between 14 h to 13.75h. This is the time when Kamo (1999) and Woolley et al. (2002) found the plants responded significantly to reducing daylength from constant daylength. However, these results were not supported by Exp 1, and could have been a random occurrence. Alternatively reducing daylength may be somewhat more effective than a constant daylength of 13.5 hours in increasing the percentage dry weight partitioning to the roots.

One possible reason why the young asparagus plants in Expt 2 responded poorly, if at all, to reduction of daylength may be the lack of temperature changes. In the field, seasonal changes in daylength are associated with gradual changes of temperature, whilst in Expt 2 temperature was kept constant at approximately 20°C, an optimum temperature (Hughes, 1992) or normal (Yen, 1993) for asparagus growth. Also the data logger record showed a steady optimum temperature throughout the experiment (Fig. 2.15). Changes to low temperature have been reported to affect partitioning in fructan storage from shoot to root, as in perennial grasses in the spring (Pollock and Jones, 1979). In asparagus, exposing to low temperature (15/5°C for day and night temperature) with a 10 h light period for a long period days (50 days) caused a rapid decrease in the sugar content and resulted in concomitant senescence of the shoots, whereas fructan content of the root increased (Pressman et al., 1989). Sudjatmiko et al. (1997) suggested that temperature may not be the main effect since mean temperatures in this study were similar between mid summer and late summer. For the last 11 days of December was 16.4°C, for January was 17.6°C, and for the first 8 days of February was 16.8°C. But the association between decreasing daylength and low temperature could together affect the partitioning in asparagus. Low temperature may be viewed as a natural intensifier of daylength in dormancy related metabolism, which includes the accumulation and storage of fructans for the following season's growth (Pressman et al., 1989). Certainly other phenomena such as dormancy often show an interaction between daylength and temperature. Further study is needed to investigate the possibility of interaction between the effects of decreasing daylength and declining temperature.

2.4.2. Variety differences

Cultivar Jersey Giant is popular in New Zealand for high yield and quality. 'Jersey Giant' was the first all-male asparagus hybrid released by Rutgers University, New Jersey. The plants are highly productive and very vigorous (http://www.inberry.com/asparagus.html). The second variety used in Expt 2, 'JWC1', has thinner spears than 'Jersey Giant' (Personal communication – Stuart Brander). It produces higher yield than 'UC157' (http://aspara. ac.affrc. go. jp/E3IACTCV.htm).

The two cultivars, 'Jersey Giant' and 'JWC1', responded similarly in terms of shoot and root numbers, their ratios and dry weight under reducing or constant daylength treatments (Fig. 2.20 – Fig. 2.22) and the significant interaction effect for ratio of root:shoot dry weight relied on the first observation (Fig. 2.28). Cultivar Jersey Giant was significantly taller and had fewer ferns than 'JWC1' (Fig. 2.23 B); but shoot dry weight did not differ between cultivars (Fig. 2.22). Cultivar Jersey Giant had a higher net CO_2 assimilation rate by 17.5%, particularly when taken as the initial rate, represented by the intercept on the y-axis (Fig. 2.26). Increases in assimilation rate during 6 minutes observation (Fig. 2.26 and 2.27) could have been due to absorption of CO_2 by condensation in the chamber. Furthermore, 'Jersey Giant' tended to have a higher assimilation rate in response to reducing daylength, whilst 'JWC1' produced similar rates regardless of daylength. Whilst the ratio of root:shoot dry weight did not show clear differences amongst all four treatment combinations in Expt 2, the allometric constant of 'JWC1' at constant daylength differed significantly from the other three treatment combinations (Fig. 2.29). This was due to interaction effect between cultivar and daylength on root:dry weight in the first observation (Fig. 2.28) so that initial point of the allometric line for 'JWC1' under reducing daylength was pulled away resulted in a different slope. Since the significant effect was found in one observation and the reason could possibly be sampling effect, the discussion will concentrate on the other three allometric lines, which were similar in their allometric constants. The results suggest that neither 'JWC1' nor 'Jersey Giant' is strongly responsive to reducing daylength. But, assimilation rates of the two cultivars at different daylength in Expt 2 showed 'Jersey Giant' was possibly responsive to reducing daylength (Fig. 2.26). There are several possible explanations for these conflicting results. The large variation in assimilation rates of 'Jersey Giant' at reducing daylength made the daylength effect non-significant. Another reason is that the measurement of CO_2 assimilation at the end of the experiment may not reflect the summation over the plant growth period.

Asparagus has been reported as one of the few crops which show a positive correlation between photosynthesis and yield. Bai and Kelly (1999) found that spear yield and rate of photosynthesis were significantly correlated among eight asparagus cultivars. Their results supported the finding of Faville et al. (1999b) that there was a positive correlation between light saturated photosynthesis (A_{max}) and spear yield among three asparagus cultivars. These results suggest that genetic variation in photosynthetic capacity among asparagus cultivars may contribute to differences in spear yield.

Guo et al. (2002) found a higher carbon export rate in a high yielding cultivar (ASP-69) than a low yielding cultivar (ASP-03) and further found that phloem ^{14}C flux out of cladophyll tissue in ASP-69 was significantly greater than in ASP-03. They suggested that there is a feed-forward effect of rate of photosynthesis on assimilates export in ASP-69 and ASP-03. Comparison of carbon assimilation and partitioning in the two cultivars indicated that greater carbon export rates during the light period in high yielding cultivar ASP-69 were associated with greater rates of carbon assimilation in comparison to the low-yielding cultivar ASP 03. Similarly, ASP-69 accumulated considerably more sucrose in cladophyll tissue during the day than did ASP-03. However, when the average values for export rate during the light period were expressed as a percentage of assimilation rates, both cultivars displayed similar export capacities. Thus, a correlation between sucrose concentration and carbon export rate did not exist. In the current study, 'Jersey Giant' should have produced a greater dry weight gain since CO_2 uptake was higher than that of 'JWC1' (Fig 2.26 and 2.27), but it did not (Fig. 2.22). Whether 'Jersey' Giant' has a higher carbon export rate from cladophylls to roots than 'JWC1' is not known.

'JWC1', a clonal hybrid, which was released in New Zealand in 1994, was reported to have superior yield to 'UC157' and 'Jersey Giant' (http://www.circlepacific.co.nz/pages/aspdev.html; http://aspara.ac.affrc.go.jp/E31ACTCV.htm). However, in Expt 2, the two cultivars did not differ in root:shoot dry weight ratio and root dry weight (Fig. 2.22). The assimilation rate of 'Jersey Giant' was however higher than that of 'JWC1' (Fig.2.27). Whilst Faville et al. (1999) and Bai and Kelly (1999) agreed that asparagus assimilation rate correlated positively with yield, Wilcox-Lee and Drost (1990) did not find a clear cut relationship between photosynthetic rate and productivity. Wilcox-Lee and Drost (1990) found similar photosynthetic rates between a high yielding male hybrid cultivar, 'Syn 4-56', and an open pollinated cultivar 'Mary Washington' but observed higher root:shoot ratio and root dry weight in 'Syn 4-56' than in 'Mary Washington'. In contrast, assimilation rates in Expt 2 were different but productivity in term of root dry weight was similar between 'Jersey Giant' and 'JWC1'.

Amongst other possibilities, cladophylls and plant respiration may play a strong role in determining why different assimilation rates resulted in similar root dry weight between the two cultivars. Cladophylls in asparagus are the main site for photosynthesis

(Downtown and Torokflavy, 1975). Thus any difference in either weight or number of cladophylls could contribute to differences in photosynthesis. Faville et al. (1999c) found differences in diameter and volume per area of cladophylls for 'UC157', 'Jersey Giant', and 'Karopiro' representing low, medium, and high yielding cultivars. As cladophylls diameter and volume increased, photosynthesis increased from 3.8 $\mu mol.m^{-2}.s^{-1}$ in 'UC157' to 6.2 $\mu mol.m^{-2}.s^{-1}$ in 'Karapiro'. In the present study, shoot dry weight of 'Jersey Giant' and 'JWC1' was similar (Fig. 2.22) but fern number of 'JWC1' was higher although it was not significantly different (Fig. 2.20). However, 'Jersey Giant' was significantly taller than 'JWC1' (Fig. 2.23). This suggests that 'JWC1' should have more cladophylls in terms of number but may have smaller cladophyll size compared to those in 'Jersey Giant'. Alternatively, with taller plants and fewer fern numbers than 'JWC1', 'Jersey Giant' may have a smaller ratio of cladohylls to fern but the type of cladophylls in 'Jersey Giant' have higher photosynthetic rate than 'JWC1'. The differences in cladophyll number and size, ratio of cladophylls to fern and the type of cladophylls determining photosynthetic rate possibly exist between the two cultivars; however, cladophylls were not measured in this current study.

Plant respiration can be divided into photorespiration, dark respiration and growth respiration. Photorespiration is the term used to describe the light dependent evolution of CO_2 resulting from the oxygenase activity of the bifunctional enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco, EC 4.1.1.39) It is an energy consuming process that can reduce net photosynthesis in C_3 plants by 25-50% (Ogren, 1984; Gerbaud and Andre, 1987; Oliver et al., 1990). Woolley et al. (1997) showed that 'Larac', an asparagus cultivar adapted to cool temperature, has optimum net photosynthesis at 20°C but that photosynthetic rate declined substantially with increasing temperature, and at 35/15°C (day/night temperature) became less than that of 'Brock Imperial', a cultivar adjusted to hot day and cool night condition. The reduction in net photosynthesis in 'Larac' was also due to higher rates of dark and photorespiration at high temperature. However, there was no difference in crown respiration between the two cultivars.

JWC1 is adapted to cool temperature (http://aspara.ac.affrc.go.jp) and 'Jersey Giant' is broadly adapted from cool (Ellison and Kineski, 1985) to warm temperature (http://aspara.ac.affrc.go.jp). Higher assimilation rate of 'Jersey Giant' (Fig. 2.27) was not reflected in higher plant dry weight compared to 'JWC1' (Fig. 2.22). 'JWC1' may have been optimum in photosynthetic rate, similar to cultivar 'Larac' demonstrated in the study by Woolley et al. (1997), but have lower photorespiration and dark respiration than 'Jersey Giant'. Further investigation measuring plant respiration of the two cultivars is needed to verify this finding, however.

2.4.3. The effects of pot size

Six weeks after transferring into larger pot sizes, asparagus plant growth in terms of shoot and root number (Fig. 2.10), dry weight (Fig. 2.12), ratio between root and shoot (Fig. 2.11 and 2.13) and the allometric constant (Fig. 2.14) varied according to pot size. The bud number and total bud number increased as pot size increased. The increase in bud number was followed by an increase in total bud number. However, there was no difference in shoot dry weight among different pot sizes (Fig 2.12). Although the thickness of shoot was not measured in this study, the observations of similar shoot dry weight of the plants suggested that the plant shoots in larger pots were thinner than in small pots. On the other hand, the numbers of roots were similar for the plants among three different pot sizes (Fig. 2.10), but root dry weight increased with increasing pot size (Fig. 2.12). Differences in root weight may have been caused by differences in root length, root thickness or some combination of the two. Root dimension were not measured directly in Expt 1, but visual assessment of photographic evidence (Fig. 2.30) suggested that plants from large pots have longer roots. Brown et al. (1982) found $\log_e$

of total dry weight in asparagus seedlings was affected by container depth, but this effect was only significant on a contrast between the 25 mm and 50, 75, 100 mm container depths. All of these containers had a constant diameter (50 mm), indicating that the difference was mainly from the depth of the pots. Brown et al. (1982) found that the roots tended to be found only in the lower 2/3 of the container. Dufault and Waters (1984), however, found that the growth of seedlings in a shallow peat pot, but of relatively a larger volume, was better than that of plants grown in paper pots which were deeper but smaller in volume. These effects could be understood since the asparagus roots tend to extend horizontally rather than growing to depth.

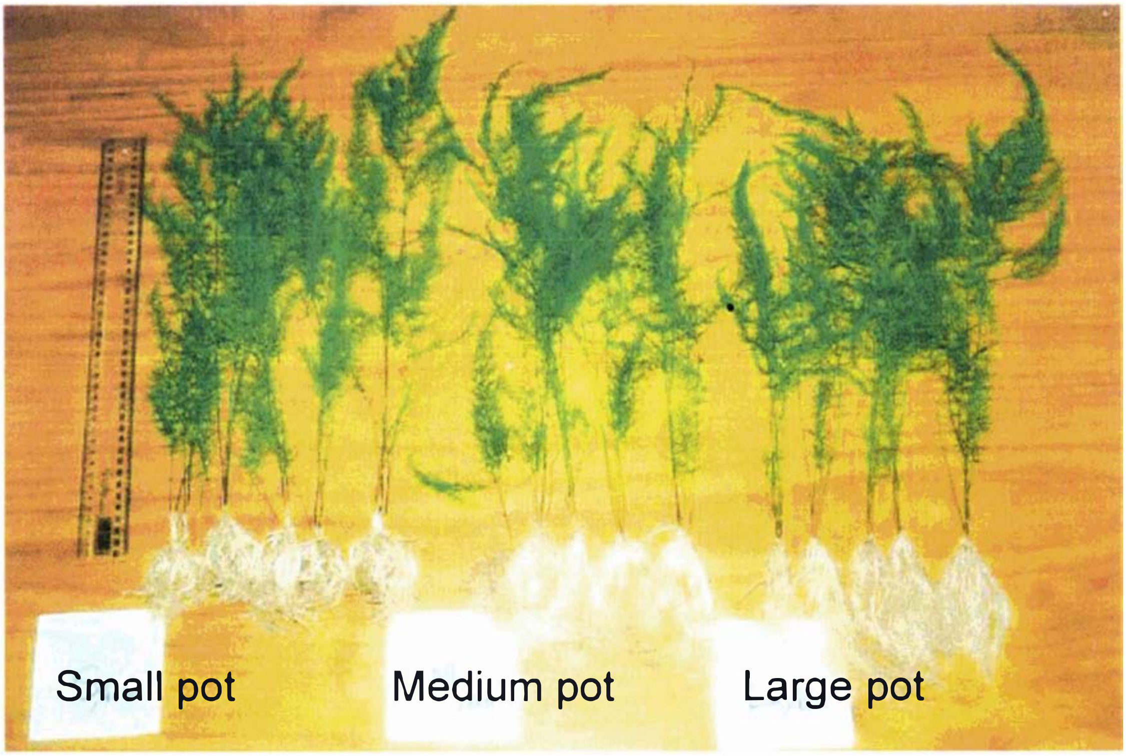


Figure 2.30 The effect of pot size on root growth of asparagus seedlings.

When the container was too deep, the roots did not explore the lowest part of the container (Brown et al., 1982; Nikollof and Falloon, 1986), and therefore the roots did not form a compact mass. In the present work it is not known to what extent root mass increases due to pot size was due to greater length or thickness. This may be important as an indication of partitioning to the root when root space is restricted.

The ratio of root:shoot number in Expt 1 was not correlated with daylength or pot size. The ratio of shoots plus buds or total bud number to **root mass** (root dry weight), conversely, can give meaningful information (Table 2.8). This ratio has not been reported in any research but could be an important determinant of potential yield. Stancanelli and Falagvina (1990) have suggested that the number of "stems + buds", (equivalent to total bud number in our present research), and the dry matter percentage partitioned in the roots of seedlings appeared to be useful for an early screening of asparagus genotypes. They observed that there seemed to be a correlation between "stems + buds" number in seedlings and subsequent plant yield, and this correlation appeared more frequently in their observations compared to other correlations.

Table 2.8 The effects of pot size on ratios of root to different parts of shoot of asparagus seedling at week 18.

Pot size	Root:total bud number	Root:shoot number	Root:bud number	Root:shoot dry weight	Root dry weight:total bud number
Large	1.2579^{ab}	4.5167	1.7855^{ab}	2.97^{a}	0.204^{a}
Medium	1.1637^{b}	4.6245	1.6024^{b}	2.29^{b}	0.156^{b}
Small	1.5114^{a}	5.4705	2.2559^{a}	1.70^{c}	0.157^{b}
Significance	*	ns	*	***	*

ns, *, ***: not significant, significantly different at p 0.05; significantly different at p = 0.001. Mean separation within column by $LSD_{0.05}$. Means with different letters are significantly different

Since asparagus growth relies on soluble carbohydrates in the roots (Shelton and Lacy, 1980; Haynes, 1987; Wilson et al., 1999) which make up a large proportion of root mass, the influence of root mass on bud production and the ratio of total bud number to root mass may be an important yield attribute. Differences in root mass are a major factor affecting changes in the total amount of stored carbohydrates (Haynes, 1987). Benson and Takatori (1980) found that after 12 weeks asparagus seedlings maintain 50% of total plant weight as root, 46% as fern and 4% as rhizome. But in terms of root and fern number, the value depended on cultivars.

In Expt 1, the heavier root dry weight (Fig. 2.12), due to increased pot size, did not increase the total bud number to the same extent (Fig. 2.10). As a consequence, the ratio of root dry weight to total bud number of plants in large pots was lower than that in the smaller pots (Table 2.8 and Fig. 2.13). Thus conditions favouring large root mass and hence high potential yield may be limited by bud numbers. The number of buds produced on asparagus crown indicates the potential for yield in the following growing season (Stancanelli and Falavigna, 1990). Whilst small and medium pots supported about 6.4 total buds per gram, large pots only produced 4.9 total buds.g^{-1} of root dry weight. The implication of this result should affect how we view the relationship between yield, carbohydrate in root storage and bud numbers.

In seedling plants grown in different pot sizes (Expt 1), the increase of root mass did not increase bud number to the same extent. If it is assumed that mature plants will behave similarly, one must consider the extent to which bud number may limit yield in plants with large root systems (high root mass).

2.5. CONCLUSION

Differences in constant daylength (13.5 and 15.5 h) did not affect seedling growth of asparagus 'UC157' or root:shoot number ratios. These results led to the possibility that reducing daylength, instead of constant shorter daylength, may have influenced plant growth as shown by other previous research. Further experiment using reducing daylength, however, did not provide enough evidence to support the conclusion that reducing daylength from 15.5 to 12 h affected growth of asparagus seedling. In the field it may have been the relationship between reducing daylength and declining temperature that affected the partitioning of dry matter. Further controlled environment studies will be needed to investigate this interaction.

Measurements of net photosynthesis of the two cultivars, 'Jersey Giant' and 'JWC1', indicated that the effect of reducing daylength may be cultivar dependent. Whilst the assimilation rate of 'JWC1' did not change with daylength, in 'Jersey Giant' there appeared to be an increase when exposed to reducing daylength but measurements for this particular treatment were very variable.

The allometric constants, derived from the relationship of $\log_e$ shoot dry weight to $\log_e$ of root dry weight was more useful than root:shoot ratio for detecting any environmental effects on plant growth. Pot size changed the allometric constant from 0.5 to 0.9, in both daylengths.

Further division of allometric constants into 3 different pot sizes, indicated an incremental decrease as pot size increased. Plant in large pots partitioned more dry weight to the roots compared to small pots. This result suggests that the partitioning of root to shoot dry weight in the same age of seedlings can be influenced by pot size, but was not conclusive in relation to the previous concern (Woolley et al., 2002) that pot size might have restricted plant growth when daylength was reduced to 12 h.

The greater of root dry weight in large pots was not followed by a similar increase in bud number, thus resulting in a higher ratio of root mass:total bud number in large pots. Every gram of root dry weight therefore supported fewer buds in the large pots compared to small pots. If yield depends on root mass, as is thought, then as management of the crop improves to produce large root systems it seems likely that bud numbers will become a factor limiting spear yield.

The relative importance of bud number and carbohydrate availability in influencing harvest duration and yield quality provide the basis for three experiments (Expt 3, 4 and 5) reported in the next chapter (Chapter 3).

CHAPTER 3

ASPARAGUS PRODUCTION OF FOUR CULTIVARS AT DIFFERENT CUTTING HEIGHTS

3.1. INTRODUCTION

Asparagus harvest in temperate regions starts in the spring. Harvest duration is usually 12 weeks to 16 weeks (Sanders, 1985; Krarup and Henzi, 1992) but may be as short as two weeks (Benson and Motes, 1982; Robb, 1984; Phillips et al., 2000) depending on the age of the asparagus plants. In New Zealand, asparagus harvest can start as early as mid-September and usually ends in early December (Robb, 1986; Bussell, 1997a). However the length of harvest will depend on the age of the plants, temperature, and the level of carbohydrate in the storage roots. Yield and quality may be controlled by these factors in addition to cultivar differences. Under their conditions Takatori et al. (1970) showed that total marketable yield in asparagus was best obtained during the first 60 days of harvest. Lengthening harvest duration to 120 days did not increase total marketable yield since the lengthening harvest only produced more non-marketable spears characterized by opening spear heads, branching, and taper. Different length of harvest periods for 30, 50 and 70 days resulted in 0.6, 1.4 and 2.0 ton.ha^{-1} of marketable yield, respectively (McCormick and Thomsen, 1984). McCormick and Thomsen (1984) found three-year old asparagus plants that were harvested for 50 days the previous year produced higher marketable yield when compared to asparagus previously harvested for 30 days. The differences of marketable spears were from 0.1 to 0.2 ton.ha^{-1}. From a five-year study, Weber (2001) showed that highest yield was obtained with a harvesting period of 10 weeks when yields from 9, 10, and 11 weeks were compared. In terms of carbohydrate depletion, lengthening the harvest season from three to six weeks significantly lowered carbohydrate level in the storage roots during the fern development period for two-year-old asparagus growth (Shelton and Lacy, 1980; Haynes, 1987). The extension of harvest duration resulted in an increased depletion of carbohydrate and increased the requirement for carbohydrate replenishment for the following harvest season. Lengthening harvest duration in any one season is usually done to maximize total yield or to prolong the supply when asparagus prices are high (Bussell et al., 2002). In New Zealand, asparagus harvest mostly ceases before Christmas while the demand for fresh asparagus is still high. Earlier, growers stopped harvesting in late November or early December, allowing plants to replenish enough carbohydrate for the following year's crop (Robb, 1986). However, this practice of stopping asparagus harvest in early December is based on farmers' experiences rather than physiological reasons (Robb, 1983). Nowadays, growers extend asparagus harvest as far as mid or late December.

Asparagus spears are cut for either fresh export market or processing market. The spear length for export market is usually between 210-250 mm while for processing market it is usually about 180 mm (NZNAM, 1997). An increase of spear length for harvest could reduce spear quality in terms of head tightness (Poll, 1996b). Krarup and Centreras (2002) reported that maximum average spear length until significant loss of head tightness, as an average of all cultivars they tested, varied from 37 cm at the beginning of the harvest to 21 cm at the end of harvest. It is also reported that lengthening asparagus spears resulted in spear quality reduction in terms of mineral nutrition (Moreno-Rojas et al., 1992; Amaro-Lopez et al., 1999). For example, Amaro-Lopez et al. (1999) showed a significant reduction of Mg, K, and P from tip to the base of 20-cm asparagus spears with a 2 cm portion interval whilst concentration of Zn reduced linearly away from the tip and concentration of Cr showed a quadratic decrease. They found the tip of asparagus spears has highest mineral content compared to other parts of the spear, and a greater concentration of copper, iron, zinc, manganese, calcium, magnesium, potassium and phosphorus were found in the first 7 cm. Spears that were bigger than 9 mm in diameter had significantly greater concentrations of Fe, Cu, Zn, Mn, Ca, Mg, and K in the apical portion (Moreno-Rojas et al., 1992). Nutrient concentration decreased with the decrease in asparagus diameter, mainly for asparagus smaller than 9 mm in diameter (Moreno-Rojas et al., 1992). This group had significantly lower concentration of Fe, Cu, Mg, and Na.

In Europe, spear lengths between 12 and 17 cm are categorized as short and accepted by customers similarly to long asparagus between 17 and 27 cm (OECD, 2000). When asparagus is cut shorter than 20 cm, the appearance of subsequent spears will not be delayed as long compared to long spears. This is claimed to be due to apical dominance (Nichols, 1996). Asparagus spear growth is thought to be influenced by correlative inhibition (Nichols and Woolley, 1985) in which the growth of subsequent spears is suppressed until the current spear is harvested. A shorter spear height will reduce correlative inhibition and thus spear emergence is likely to be faster. Thus, within a specific time, more buds are used when the spears are cut shorter compared to spears that are cut longer. The number of spears produced depends however on the number of buds available. The availability of the buds in asparagus plants is cultivar dependant. For instance, 'UC157' has more buds per root than 'Jersey Giant' (Sudjatmiko et al., 1997; Wardhana, 1999). Therefore, it is implied that the effect of applying shorter spear cutting height will be cultivar dependent. In addition, asparagus spear growth will depend on the carbohydrate availability in the crown. Many studies reported that an extension of harvest length, meaning cutting more spears in one harvest season, will deplete carbohydrate reserve and lower carbohydrate replenishment for the following season (Hikasa, 2000; Ernst and Liebig, 2001).

While bud number is a good indicator of potential yield of asparagus plants, the effect of bud number on yield has not been studied as much as carbohydrate content in root storage. Wilson et al. (1999) showed a reduction of bud numbers at the beginning of the harvest season and an increase of bud production at the end of the harvest season. They did not correlate bud numbers with yield, however. The bud numbers, however, will dictate how many spears a plant can produce provided adequate carbohydrate is available. Even if the plant has high carbohydrate, if the number of the buds on the rhizome is low, yield will be low. However, it is not clear to what extent bud numbers may limit yield. Furthermore, bud production through one year has not been fully monitored.

In the experiments reported in this chapter different cutting heights have been used as differentially affecting bud number and carbohydrate demand. A low cutting height will place a heavy demand on buds, but a comparatively low demand on carbohydrate. Studies of yield comparison using different asparagus cutting heights are very few (Dean, 1993; Kamo, 1999) with little information regarding the quality of the spear. In fact this type of study can provide information on the relative extent to which bud number or total carbohydrate in the storage roots determines total yield and quality.

Asparagus yield and quality may also vary because of cultivar differences. Some cultivars produce many spears such as ‘UC157’ and some cultivars produce fewer spears of larger diameter, such as ‘Jersey Giant’. As a dioecious perennial plant, asparagus produces male and female florets on separate staminate and pistillate plants. Female plants produce berries which can reduce their potential yield compared to male plants as shown in several studies (Hughes, 1992). Male plants produce more spears and may consequently be higher yielding than female plants (Ellison et al., 1990). However, some cultivars such as ‘Jersey Giant’ are all-male. Individual spears of female plants are generally heavier (Ellison et al., 1960). Thus the bud number of an asparagus plant may depend on its cultivar and plant sex. Male and female plants also differ in distance to first branch on the fern (Benson, 1982) and thus the spear quality may also differ (Ellison and Scheer, 1959; Ellison et al., 1960).

Spear quality is very important especially if the asparagus is for export. High quality spears will be within specific ranges of spear diameter, have compact apical buds (head tightness) (NZNAM, 1997; OECD, 2000) and preferably be of uniform colour (Bussell et al., 1996; OECD, 2000). Kamo (1999) divided spears into three spear quality groups: number 1 if the head was full tight, number 2 or medium if the head was starting to elongate, and number 3 if the head had started opening and already had small cladophylls (seedy). However, his divisions were based on small spears and therefore only considered head tightness. The New Zealand Novantis Asparagus Manual (NZNAM, 1997) uses spear diameter and head tightness to grade asparagus spears that are free from disease and curvature into marketable and non marketable spears. In addition, the marketable spears can be categorized into two different qualities: spear quality 1 and spear quality 2.

The objectives of our experiments were to compare spear yield and quality amongst four asparagus cultivars at five different cutting heights in relation to utilization of carbohydrate and buds present. Plant sex was included in the second year in relation to spear yield and quality. All these comparisons were related to bud number and bud size.

3.2. MATERIALS AND METHODS

Two experiments were conducted in 1999 and 2000. The first experiment (Experiment 3) was conducted during the winter from March to June 1999 and the second experiment (Experiment 4) during the spring from September to December 2000. Both experiments were conducted in a semi-controlled greenhouse at the Plant Growth Unit of Massey University, Palmerston North, New Zealand. In Expt. 3 soluble root carbohydrate levels before harvest were low at 354 to 391 mg.gram^{-1} while in Expt. 4 levels were between 477 and 485 mg.gram^{-1}.

3.2.1. Experiment 3

Objective: to compare the yield and quality of four different asparagus cultivars harvested at five different cutting heights.

3.2.1.1. Plant Materials

Three year old asparagus plants, cultivars 'Grande', 'Apollo', 'Atlas', and 'UC157' were used. During fern growth in the third year, the plants were infected by ***Stemphyllium*** during the summer, so the ferns were cut and allowed to grow again but only for a short time before winter. The crowns were then stored in a cooler at a temperature of 3°C before they were transferred to greenhouse on 19th of March and hand watered for ten days before the experiment started. The experiment started on 29th of March 1999 and ended on 30th of June 1999. The plants were grown in 10 liter plastic pots filled with 1:1:1 bark:pumice:peat mixed media with a base fertilizer of 150 g Osmocote (15% N, 4.8% P, 10.8% K, 1.2%Mg, 3.0% S, 0.4% Ca plus trace elements: B, Fe, Cu, Mn, Mo, and Zn)/100 litres. Temperature set points for heating and ventilating in the greenhouse were 15°C and 25°C, respectively. In addition, temperature at 30 cm above the soil surface was recorded daily. The plants were hand watered after the spears were harvested each morning.

3.2.1.2. Experimental Design

A Randomized Complete Block Design was utilised and treatments arranged as factorial combinations with 20 blocks and 20 treatments and a total of 400 experimental units (pots). Main treatments were four cultivars and five levels of cutting heights (10, 15, 20, 25, and 30 cm). Thus each block consisted of a single pot of each of the treatment combinations (Fig. 3.1).

Figure 3.1 Expt 3: Layout of cutting height experiment on four asparagus cultivars grown in the greenhouse.

3.2.1.3. *Data collection*

The spears were harvested daily, seven days a week in the early morning. Cutting height (CH) was based upon the spear length from the ground to the tip. The spears were snapped manually so that the spear was detached from its base at the rhizome.

After harvest, each spear from each treatment combination was measured for actual cutting height, head tightness and length, base diameter, fresh and dry weight. Spears were not trimmed. The measurement of head tightness was similar to Liao et al. (1999) except the numbering was reversed as described by Karno (1999). The length of the head was measured from the tip to the lowest scale leaf forming the head. The spear base diameter was measured using digital callipers (Model CD-6, Mitutoyo Corporation, Japan). Base diameter was measured on the stem close to the butt.

Spear division into three different qualities was based on the combination of base diameter and head tightness. The division was slightly modified from New Zealand Novantis Asparagus Manual (NZNAM, 1997). Quality 1 spears (first grade of marketable spear) had diameter of at least 9 mm, full head tightness, and free of visible "seed". Quality 2 spears (second grade of marketable spear) had a diameter of at least 5 mm and medium head tightness and may have visible "seeds". Quality 3 spears (non-marketable spears) had badly distorted, open head, seedy, and/or diameter of less than 5 mm.

Spear harvest ended when few spears were produced from the plants and/or most of the spears produced were non-marketable spears.

To obtain dry weights, spears were dried for 3 days at 80°C in a vented oven.

Root samples were taken from ten plants for each cultivar at the beginning of the season (before applying treatment) on 27 March 1999. After washing using tap water, the roots were frozen at –18°C for total soluble carbohydrate determinations.

3.2.1.4. Data analysis

Total harvest length was 13 weeks. There was a total of 93 harvest days in Expt. 3 and harvest days were grouped into 12 weeks plus a final harvest period of 9 days which was called week 13. Daily fresh and dry weight and spear number were summed from each treatment combination for each week and called weekly yield. Weekly yields were accumulated for 13 weeks (cumulative yield) to give total yield of the spears during the harvest season.

The 13 cumulative data points for total yield (without separation of spear quality) were fitted using linear and quadratic models for each cultivar at different cutting heights. First, ANOVA using proc GLM model (SAS® version 8.2, 1999-2001) was run with cultivar (CV), cutting height (CH) and CV*CH interaction together with " Week" and "Weeksq" as variables for linear and quadratic coefficients. This model with the whole data set for 13 weeks would fit into either linear or quadratic effect with main effects and interaction. Then residuals of the quadratic model were plotted to check the model fit. Lastly, proc REG was run individually for linear and quadratic models with 13 cumulative harvest data points according to each cultivar at different cutting heights. Coefficients of linear and quadratic functions for each model are presented together with R-squares to illustrate the yield change over harvest sequences.

The data was then analysed for weekly and cumulative yield to determine the effect of cutting heights, cultivars, and their interaction on cumulative fresh and dry weight, and spear number for both marketable and non-marketable spears as well as for total spears (without separation of spear quality). Statistical analyses were performed using SAS. Univariate ANOVA for cumulative and weekly yield were analyzed with the ANOVA model of RCBD for a 4 X 5 factorial arrangement with general linear model (GLM) procedure for cumulative and weekly yield. Protected Least Significant Difference (LSD) at 5% was used to detect differences among means. LSmeans were used to show the mean value of any interaction.

Results of analyses are presented as: 1) fitting trends of cumulative data during 13 weeks into linear and quadratic models, 2) GLM for cumulative data both total yield and spear quality categories in final week. At the final harvest (week 13), cumulative fresh and dry weight and spear number were presented as total cumulative yield.

Statistical analysis was also performed for total soluble carbohydrate (TSC) of root samples using SAS with ANOVA procedure.

For the purpose of statistical analysis the total spear number is reported to one decimal place.

3.2.2. Experiment 4

Objective: to compare the yield and quality of spears from male and female plants of four asparagus cultivars, at five levels of cutting height and blocked according to available buds on the crown.

3.2.2.1. Plant materials

Four year old asparagus plants, cultivars 'Grande', 'Apollo', 'Atlas' and 'UC157' were used. These plants were previously grown in a greenhouse with drip irrigation for nine months (August 1999 to April 2000). The plants were irrigated for half an hour every morning with commercial Peter's soluble fertilizer with 20% N, 8.7% P, 16.6% K, 0.065% S, 0.05% Mg, 0.007% B. 0.004% Cu, 0.05% Fe, 0.025% Mn, 0.001% Mo, 0.003% Zn at approximate of 0.5% of concentration. Temperature set points for heating and ventilating in the greenhouse were 15°C and 25°C, respectively. Drip irrigation was stopped to dry out the plants for the dormant period in May 2000. Dry ferns were cut from all the plants on 7th August 2000. Plants were transferred from 10 litre to 30 litre pots from August 20 to 27 and hand watered for three days before the experiment started. The growing media was 1:1:1 for peat:bark:pumice mixture with 250 g Osmocote (16N-3.5P-10.8K)/100 liters.

3.2.2.2. *Experimental Design*

The experiment was laid out as a Randomized Complete Block Design with 4 x 5 x 2 factorial treatment combinations. Four cultivars of asparagus, five spear cutting heights, and two plant sexes were used as the main factors (Fig. 3.2). Each treatment combination was replicated (blocked) three times with two plants per treatment combination in each block for all cultivars except 'Grande' which had 1 female plant per treatment combination in each block.

The blocks were separated based on the number of buds on each crown: low, medium or high. Five treatments of cutting spears (10, 15, 20, 25, and 30 cm) were assigned to each cultivar and each sex in each block.

Figure 3.2 Expt 4: Layout of cutting height experiment on female and male plants of four asparagus cultivars grown in the greenhouse.

3.2.2.3. Data Collection

After harvesting, each spear from each treatment combination was measured for actual cutting height, head tightness and head length, base diameter, fresh and dry weight, as described for Expt. 3.

3.2.2.3.1. Root samples

Root samples were taken from each plant at the beginning of the season (before applying treatment) from 23 to 27 August 2000 and at the end of the experiment. Harvest was begun on 2 September and ended on 4 December 2000. Harvest ended when asparagus plants yielded few marketable spears and more non-marketable spears. Once the harvest ended, the crowns were stored at 3°C and root samples were obtained by taking 7 to 14 roots at random around the crown. After washing using tap water, the roots were frozen at −18°C for total soluble carbohydrate determinations.

3.2.2.3.2. Bud numbers

Total buds were counted on each crown before and after the spears were harvested. Bud counting before spear harvest was done between 20 and 28 August 2000. Each crown was removed from its ten-litre pot. All the soil on the top of the crown was removed manually with the assistance of compressed air, to make the rhizome visible. Water was not used in order to minimise spear growth while counting buds of other plants. All buds were assumed viable when the buds were hard when touched by hand. The smallest buds detected were 2 mm in diameter. The ranges of initial bud number (Table 3.1) were used to separate the plants of each cultivar, cutting height and plant sex into three blocks. After counting the buds on each crown, each crown was re-potted into 30-liter pots.

Table 3.1 The ranges of initial bud number per block at different plant sex of four asparagus cultivars grown in greenhouse.

Block	Cultivar	Plant sex	Bud number	
			Lowest	Highest
I	UC157	Female	20	29
		Male	24	32
	Apollo	Female	12	17
		Male	25	29
	Grande	Female	4	11
		Male	5	18
	Atlas	Female	20	26
		Male	26	32
II	UC157	Female	35	49
		Male	33	50
	Apollo	Female	17	29
		Male	30	39
	Grande	Female	12	19
		Male	21	24
	Atlas	Female	26	37
		Male	33	41
III	UC157	Female	53	85
		Male	50	143
	Apollo	Female	29	42
		Male	40	56
	Grande	Female	20	28
		Male	33	70
	Atlas	Female	39	64
		Male	45	84

Bud number was also counted at the end of harvest. All the crowns in the pots were transferred into cool rooms (2 ± 0.5°C) to prevent spear growth while the buds were counted. The buds from plants of the first block were counted from 6th to 10th December 2000. The buds from the plants of the second and third blocks were counted from 17th to 27th December 2000.

3.2.2.3.3. Total soluble carbohydrate

Spear total soluble carbohydrate content was determined for early (first month of the harvest season), middle (second month of the harvest season), and late spears (third month of the harvest season). One to three spears of quality 1 and 2 were collected from each treatment combination. The spears were then divided into five cm lengths from the tip to the base (butt) before they were frozen for determination of total soluble carbohydrate using anthrone reaction (Southgate, 1991). Anthrone reagent was made by dissolving 10 g thiourea and 0.5 g Anthrone (9,10-dihydro-9oxoanthracene) in one liter of 66% (v/v) H_2SO_4 and warming the mixture to 80 – 90°C for 10 minutes. The reagent was stored at 4°C.

Fifty mg dried ground sample was extracted in 5 ml distilled water at 95°C (water bath) for 30 minutes in a thick walled glass test tube. The sample was centrifuged at 3000 g for 15 minutes and another 5 minutes at 1000 g. Then supernatant was taken for the analysis. A fructose solution was diluted to provide a standard curve in the range of 250-7000 μg/l.

Standard amounts of fructose were carried through each series of unknown samples. Fifty μl of sample solution were mixed with 5 ml Anthrone reagent in the tube. The tube was swirled to mix the content and put at 95°C (water bath) for 12 minutes. The samples were cooled and left in the dark at least for 45 minutes before they were measured. The sample absorbance was measured at 620 nm using a spectrophotometer (Hitachi Model U-2000).

3.2.2.4. Data analysis

In addition to the analysis described in Expt 3, analysis of variance was performed with plant sex as an additional main effect besides cutting heights and cultivars.

3.2.2.4.1. Percentage of dry matter

Within harvest duration, dry weight of some marketable spears was not available since the spears were used for total soluble carbohydrate (TSC) sampling. The use of these TSC samplings limited the number of observations for dry matter especially for 'Grande'. Furthermore, spears from each treatment combination were not always available to be harvested and so made incomplete data for weekly analysis. Therefore, thirteen weeks of harvest were pooled and divided into three months with the last month consisting of five weeks. This monthly division was also used for the collection of spear sampling for total soluble carbohydrate. The analysis of variance, then, was run excluding 'Grande' using PROC GLM. Dry matter percentage was analysed for testing amongst spear qualities within each month. LSmeans amongst three spear qualities were tested using PDIFF with Tukey adjustment at P=0.05 when there was significant difference.

3.2.2.4.2. Spear category based on spear diameter

In addition to spear quality similar to that as defined in sections 3.2.1.3, spears were categorized with either head tightness or spear diameter only. The spear diameter ranges for defining quality 1, 2, and 3 spears based only on spear diameter was similar to those described in Expt 3. In the final week, the three methods of defining spear quality were tabulated and compared.

Further analysis of spear production was carried out by dividing spears into 5 diameter categories (Table 3.2) regardless of spear tightness.

Table 3.2 Range of spear diameter (mm) in five spear categories in asparagus harvested from a greenhouse in 2000.

No.	Spear category	Diameter (mm)
1.	Large spears	≥ 9
2.	Medium-large spears	$7 < 9$
3.	Medium spears	$5 < 7$
4.	Small spears	$4 < 5$
5.	Smallest spears	< 4

3.2.2.4.3. Estimated time of maximum production (t_{max})

The time of maximum production (t_{max}) of spear fresh weight and spear number for each category of spear diameter according to Table 3.2 was estimated by using several steps. Univariate ANOVA using proc GLM was first done to test significance of all effects in five categories for spear fresh weight and spear number. Based on these results, subsets of data were produced to find the time of maximum production for the group of plants. For each plant group, the production values (fresh weight or spear number) from each week were plotted against time (week). Gaussian fitting was used to estimate the time of maximum production for each spear category. Maximum production times were obtained from the centre value of Gaussian fitting using ORIGIN^{TM} 5 (Microcal ORIGIN^{TM}, 1997). These time values were then subjected to PROC GLM to test amongst cultivars, cutting heights or plant sex with either five categories of spear size or the first two categories of spear size (see Table 3.2). Total production in terms of fresh weight and bud numbers for each different spear category was analyzed using PROC GLM.

3.2.2.4.4. Bud number

Bud numbers produced during the harvest season in the greenhouse were calculated based on the bud numbers observed before and after harvest and spear number produced during the harvest.

3.2.2.4.5. Total soluble carbohydrates (TSC)

Total soluble carbohydrates content (TSC) of asparagus root and TSC of the spears were analyzed using PROC GLM. Estimation of TSC reduction over the harvest period was based on the following considerations:

Hughes (1992) revealed that the loss of carbohydrate for respiration can reach up to 50%, and varied during asparagus life cycle, and as temperature increased. As a consequence of higher temperature in the spring than in the winter, the carbohydrate loss due to respiration would be more than 15% as Pressman et al. (1993) reported. Pressman et al. (1993) reported that during the autumn when the ferns senesce and the subsequent winter dormant season in Mediterranean areas the roots sustained a constant and significant decrease in fructan content, contributing to a loss of over 30% of the stored fructans. They found that the total soluble carbohydrate of the roots consisted primarily of fructans which made up between 50-80% of the carbohydrate content, depending on sampling date.

Pressman et al. (1993) observed that the loss of carbohydrate in terms of fructan during fern senescence and drying over winter was approximately 20%, and a further reduction up to almost 30% occurred when spears were growing (Figure 1A in Pressman et al., 1993) (Fig. 3.3). Similarly, Haynes (1987) showed that about 20% loss of carbohydrate occurred due to spear growth when harvested for four weeks, and carbohydrate loss increased up to about 50% when harvested for six weeks in two-year asparagus plants.

The relative proportions of carbohydrate loss due to spear growth and root respiration for the current study were estimated by using Figure 1A from Pressman et al. (1993) (Fig 3.3).

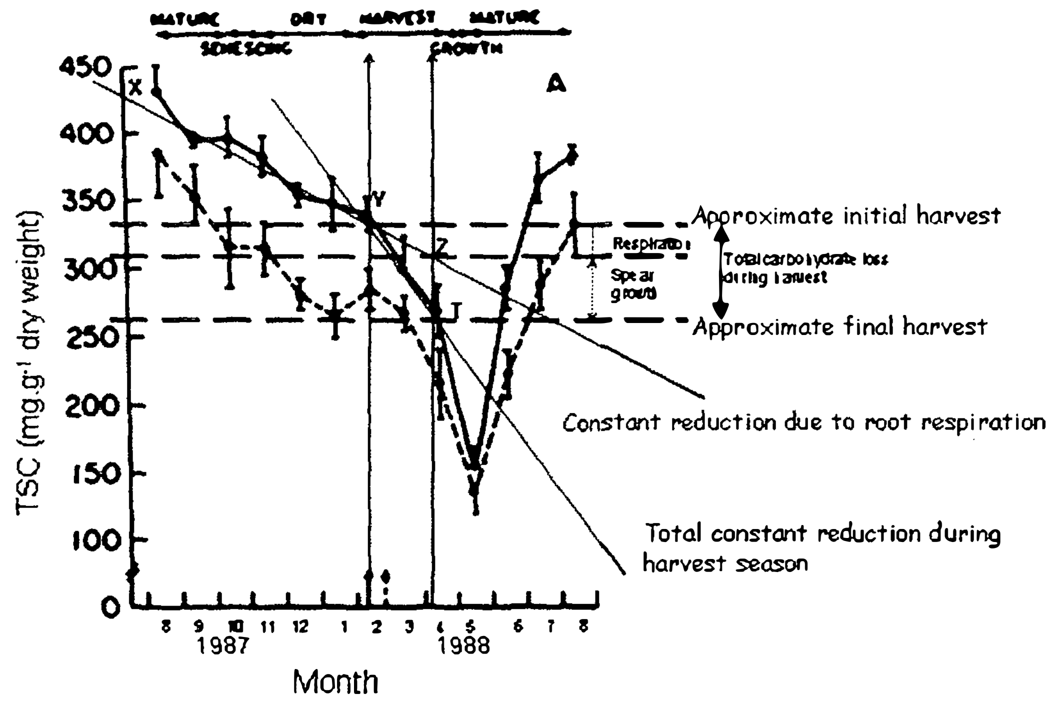


Figure 3.3 Estimation of carbohydrate loss due to spear growth and root respiration for the current study was based on extrapolation from Figure 1 in the study of Pressman et al. (1993).

With the assumptions that temperature did not change during the harvest period and carbohydrate loss was due to spear growth and root respiration, two lines were drawn.

One line (X-Y) was drawn to indicate carbohydrate loss due to the root respiration. A second line (Y-T) was drawn over the harvest period to indicate the total carbohydrate reduction due to both spear growth and root respiration, and extrapolation of the original line X-Y to Y-Z indicated the contribution of respiration to carbohydrate loss over the harvest period. On this basis, levels of carbohydrate loss during the harvest season due to root respiration and spear growth were 30% and 70%, respectively. With these relative percentages and the above assumptions, the estimates of carbohydrate loss were calculated using values of initial and final TSC and weekly spear dry weight.

Then carbohydrate reduction due to spear growth in the current study was estimated using 2 steps:

$$\text{Spear TSC}_n = ((DW_n/DW_{final})*((TSC_{initial}-TSC_{final})*C_{spear})) \qquad \text{(Step 1.)}$$

where:

Spear TSC_n is TSC due to spear growth at week n
DW_n is spear dry weight at week n
DW_{final} is spear dry weight at final week
$TSC_{initial}$ is TSC measured initially before harvest
TSC_{final} is TSC measured at final week of harvest
Cspear is constant of relative percentage of carbohydrate loss due to spear (0.7)

$$\text{Reduction of spear TSC}_n = TSC_{initial} - \text{Spear TSC}_n \qquad \text{(Step 2.)}$$

where:

Reduction of spear TSC $_n$ is the amount of TSC due to spear growth at week n
$TSC_{initial}$ is TSC measured initially before harvest
Spear TSC_n is TSC due to spear growth at week n

The loss of carbohydrate due to root respiration was calculated with the formula:

$$\text{Root TSC}_n = ((\text{TSC}_{initial} - \text{TSC}_{final})/\text{Total number of harvest}) * \text{harvest}_n * 0.3)$$

where:

Reduction of root TSC $_n$ is the amount of TSC due to root respiration at week n
$\text{TSC}_{initial}$ is TSC measured initially before harvest
TSC_{final} is TSC measured at final week of harvest
Total number of harvest is 13
Harvest_n is the week of particular harvest

Total TSC reduction was the sum of TSC due to spear and root respiration in a particular week.

3.2.3. Experiment 5: Bud development in the field

3.2.3.1. Materials and method

Bud numbers were also observed in a commercial planting of asparagus at Bulls, Manawatu Region before and after harvest and in the summer following the harvest season. Two 80 cm lengths of row for asparagus cultivars 'Jersey Giant' and 'Taramea' were chosen randomly. The soil was removed from over the plants which were cleaned with a water jet to reveal the crowns. An 80 x 80 cm grid with 20 cm intervals was laid on the top of the crown. Crowns within this area were mapped and buds were counted. After the buds were counted, the crown was covered with perlite to allow easy access later on after harvest. Soil was then placed over the perlite to form a ridge similar to the whole block. The mapping of bud distribution and bud counting was done before harvest started (30th August 2001), after harvest season (13th December, 2001) and in the following winter (6th June 2002). Bud number, spear numbers and cut spear numbers were recorded. Ferns were counted twice, during summer and autumn (9th January and 26th April 2002).

3.2.3.2. Data analysis

Bud, spear and fern numbers in the field were used to confirm that results from the experiment in the greenhouse were applicable to the field situation. Buds, spears and cut spears from the harvest period in the field were counted from mapping conducted before and after harvest. Ferns were estimated using fern counts conducted at the end of summer and the number of ferns, spears and bud counts in the maps from all observations with assumptions as follows: the bud counts at the first observation (before harvest) were the buds from previous bud season (year 1) and were called initial buds. The spears and cut spears produced during the harvest came from these buds or possibly the buds that were produced during the harvest season, which were called new buds. The ferns came from the initial buds not used to produce spears, or from new buds produced during the harvest period.

3.3. RESULTS

3.3.1. Experiment 3

3.3.1.1. Spear fresh weight.

There was a marginally significant effect of the interaction between cultivar and cutting height (CV*CH) over harvest at $P = 0.0555$ but there were highly significant effects of CV ($P < 0.0001$) and CH ($P < 0.0001$) over harvest on total fresh weight. The model accounted for 90.50% of the data variation.

3.3.1.1.1. The interaction between cultivars and cutting height over time on spear fresh weight.

Fresh weight increased gradually with cutting height in 'UC157' and 'Grande' but not 'Apollo and 'Atlas'. There was a large increase between 10 cm and 15 cm in 'Apollo' while in 'Atlas' the highest yields was obtained at 25 cm rather than 30 cm (Fig 3.4).

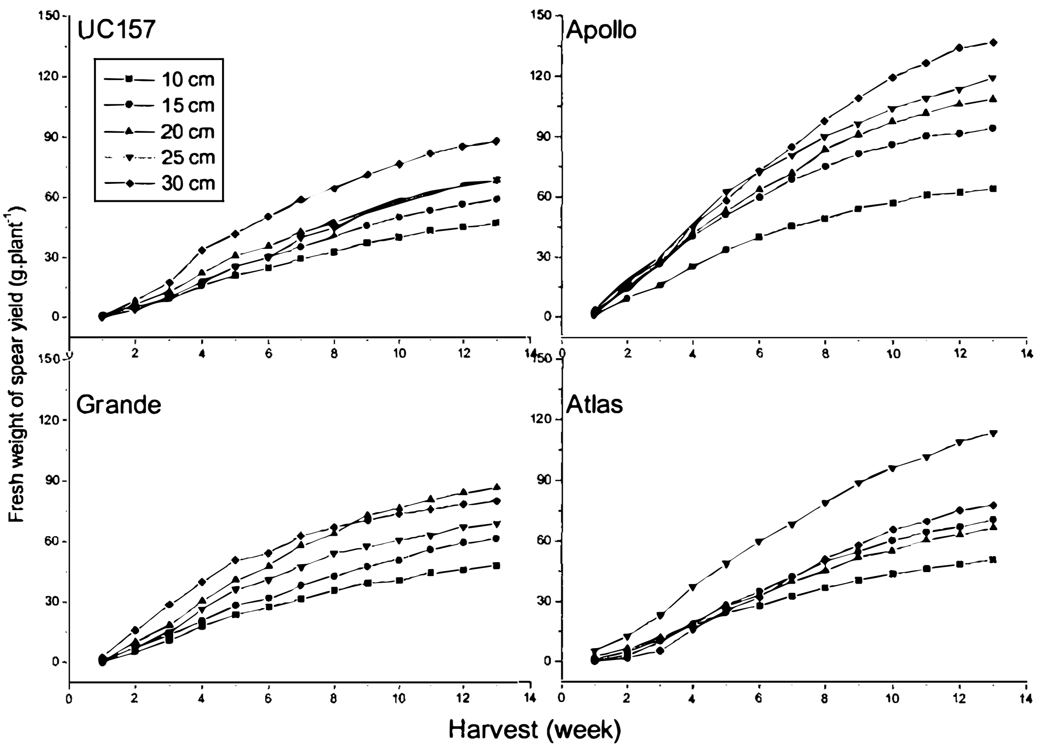


Figure 3.4 Expt 3: Cumulative spear fresh weight of four asparagus cultivars harvested at five different cutting heights during 13 week harvest period.

3.3.1.1.2. Total spear fresh weight

The effect of CV*CH interaction was clearly reflected by total fresh weight in final week (Table 3.4). Cultivar 'UC157' and 'Apollo' increased total spear fresh weight as

CH increased while in 'Grande' and 'Atlas' the peak total fresh weight occurred at CH 20 cm and 25 cm, respectively.

Cultivar 'Apollo' produced the highest total spear fresh weight (104.98 g.plant^{-1}), more than 25% higher than the other cultivars. No significant difference was found among the other three cultivars when tested by LSD ($LSD_{0.05}$ = 10.92 g) (Table 3.3).

Table 3.3 Expt 3: Total spear fresh weight (g.plant^{-1}) of four asparagus cultivars harvested at different cutting heights.

Cutting Height (CH)	Cultivar (CV)				CH mean
	UC157	Apollo	Grande	Atlas	
10 cm	47.04	64.39	47.75	50.73	52.48^{d}
15 cm	58.99	94.58	61.05	70.69	71.33^{c}
20 cm	68.05	108.98	86.65	66.56	82.56^{bc}
25 cm	68.65	119.72	68.69	113.52	92.65^{ab}
30 cm	88.11	137.23	79.79	77.76	95.72^{a}
CV mean	66.17^{b}	104.98^{a}	68.79^{b}	75.86^{b}	
Block	*				
CV	***				
CH	***				
CV*CH	**				

*, **, *** are significant at P=0.05, 0.01, or 0.001 respectively. Within the column and row, means followed by the same letters are not significantly different at $LSD_{0.05}$.

Cutting height (CH) also significantly influenced total spear fresh weight ($LSD_{0.05}$ = 12.21 g). The highest total fresh weight was produced by the highest CH of 30 cm (95.72 g.plant^{-1}) and 25 cm (6.65 g.plant^{-1}), which was significantly different from the three lower CH's. The lowest total spear fresh weight was produced by the lowest CH of 10 cm (52.48 g.plant^{-1}). The total spear fresh weight gradually declined as CH became shorter.

3.3.1.2. Spear dry weight

3.3.1.2.1. The interaction between cultivar and cutting height over time on dry weight

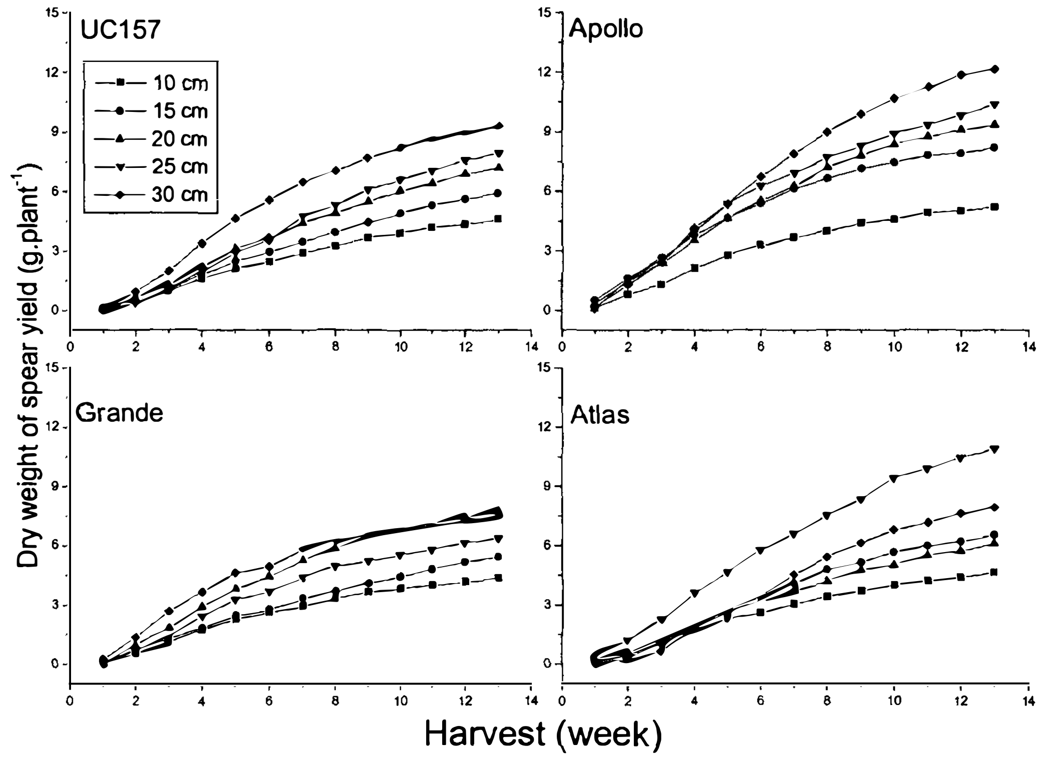


Figure 3.5 Expt 3: Cumulative spear dry weight of four asparagus cultivars harvested at five different cutting heights during 13 week harvest period in the greenhouse.

Spear dry weight followed a very similar pattern to fresh weight. The effect of CV*CH interaction over harvest date was significant at $P < 0.0001$. On individual harvests, interaction of CV*CH significantly affected cumulative dry weight of total spear from week 8 to the last harvest (Fig. 3.5). The responses were similar to cumulative fresh weight of total spear as illustrated previously in Fig. 3.4. CV as well as CH affected cumulative dry weight of total spear at all harvest times except week 1 and 2 for CV and CH respectively.

3.3.1.3. Spear number

3.3.1.3.1. Interaction CV*CH effect on spear number over time

Cultivar (P<0.0001), cutting heights (P<0.0001), and interaction between the two (P<0.0001) significantly affected cumulative spear number over time (Fig 3.6). The trend of spear number increase at different cutting height was different for each cultivar.

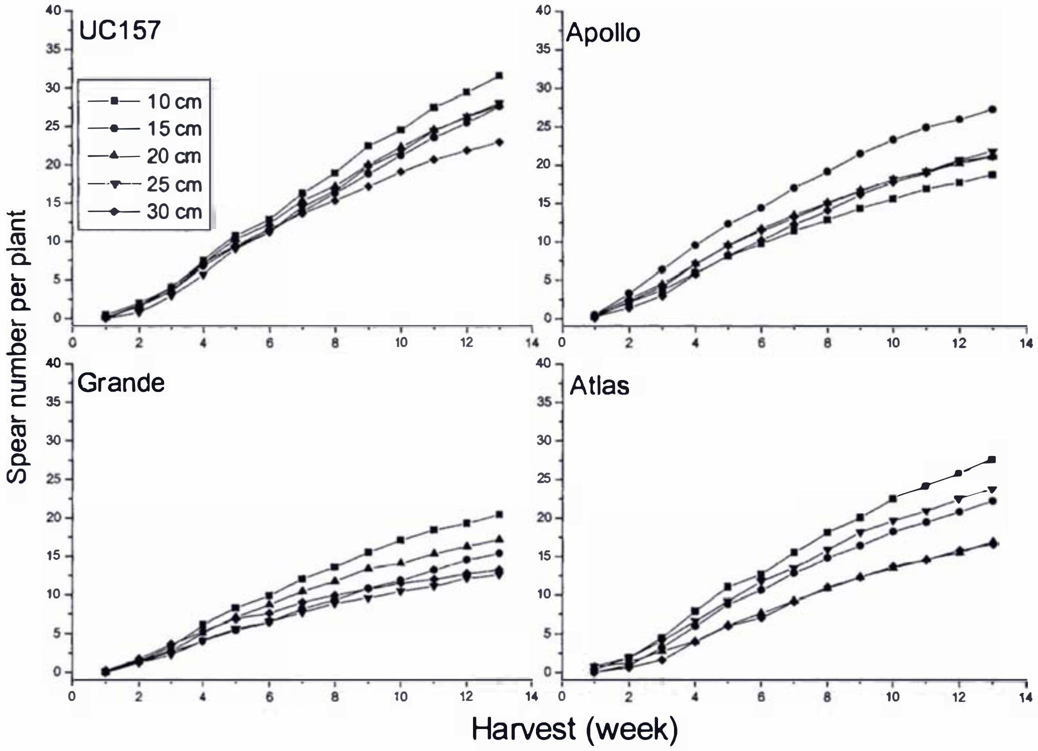


Figure 3.6 Expt 3: Cumulative spear number of four asparagus cultivars harvested at five different cutting heights during 13 week harvest period in the greenhouse.

Cumulative total spear number at cutting height (CH) 10 cm was always the highest in all cultivars except in 'Apollo'. Lowest cumulative total spear number occurred at the highest level of cutting height in 'UC157' and 'Atlas'. However, the lowest cumulative spear number was not at the highest level of cutting height in 'Apollo' and 'Grande'.

3.3.1.3.2. Total spear number

At the final harvest, total spear number was influenced by CV at $P < 0.0001$ and CH at $P = 0.0129$ (Table 3.4) and it was not affected by CV*CH interaction (P=0.0910).

Table 3.4 Expt 3: Total spear number (number of spear.plant^{-1}) of four asparagus cultivars harvested at different cutting heights in the greenhouse.

Cutting Height **(CH)**	Cultivar **(CV)**				**CH mean**
	UC157	Apollo	Grande	Atlas	
10 cm	31.6	18.8	20.5	27.7	24.6^{a}
15 cm	27.7	27.4	15.4	22.30	23.2^{ab}
20 cm	27.9	21.2	17.2	17.0	20.8^{bc}
25 cm	28.1	21.9	12.6	23.8	21.6^{bc}
30 cm	23	21.2	13.3	16.7	18.5^{c}
CV mean	27.7^{a}	22.1^{b}	15.8^{c}	21.5^{b}	
Block	ns				
CV	***				
CH	*				
CV*CH	ns				

Within the column and row, means followed by the same letter are not significantly different at $LSD_{0.05}$. ns, *, *** : non significant or significant at $P = 0.05$ or 0.001to 0.0001, respectively.

Generally as CH increased, total spear number per plant reduced (Table 3.4). The highest total spear number per plant at final harvest was CH 10 cm (24.6 spears) which was not significantly different from that of CH 15 cm (23.2 spears) when tested by $LSD_{0.05}$ at $P = 0.05$ (3.6081 spears). In general, spear number decreased as CH increased but differences were only significant when cutting height differed by 10 or 15 cm. Cultivar 'UC157' produced the highest total spear number (27.7), significantly more than the other three cultivars.

3.3.1.4. *Total soluble carbohydrate*

Concentrations of Total Soluble Carbohydrate (TSC) from storage roots of the four asparagus cultivars were similar to each other (Table 3.5). TSC fell within a range from 354.5 to 390.6 mg.gram^{-1}.

Table 3.5 Expt 3: Soluble carbohydrate concentration (mg/gram) of the four asparagus cultivars before harvest.

Cultivar	Means	Standard error
UC157	373.9	33.8
Apollo	354.5	31.8
Grande	390.6	37.6
Atlas	385.3	34.4
Means	376.1	34.4

3.3.2. Experiment 4 (2000)

3.3.2.1. *Spear fresh weight*

3.3.2.1.1. Effect of cultivar and cutting height over harvest date

Cumulative fresh weight of total spear was affected by the interaction of CV*SEX from week 4 to the last harvest (week 13) (Fig. 3.7). These effects were clearly seen in cultivar 'Grande' where male plants produced almost double the total spear fresh weight of female plants. On the other hand, 'UC157' female plants produced 21.8% more total fresh weight than male plants. Female and male plants of 'Apollo' produced similar total fresh weight.

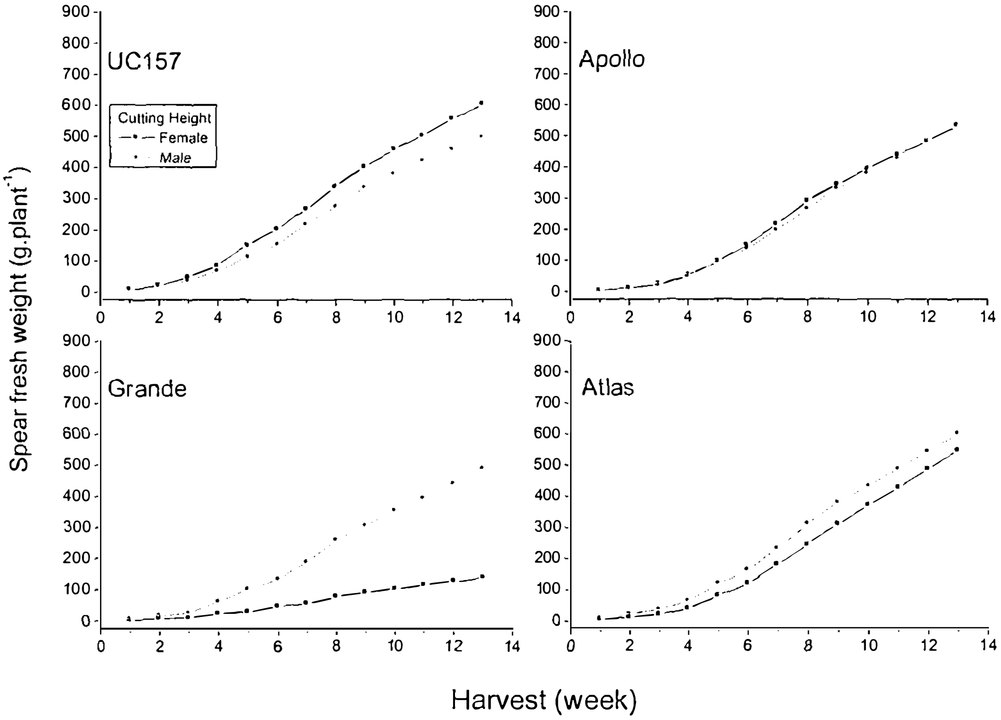


Figure 3.7 Expt 4: Cumulative fresh weight for **two** plants of spears from female and male plants across cutting height of four cultivars grown in a greenhouse during the harvest period.

Cutting height (CH) at 10 cm always produced the lowest cumulative fresh weight whereas CH at 30 cm always produced the highest cumulative fresh weight in all cultivars (Fig 3.8). Within 'UC157', cumulative total fresh weights at CH 15 to 25 cm were similar. In 'Apollo' and 'Grande', cumulative total fresh weights at 20 and 25 cm were close to each other whereas in 'Atlas' cumulative total fresh weights between 10 to

20 cm were similar. However, no significant effect of CV*CH interaction was found on cumulative total spear fresh weight.

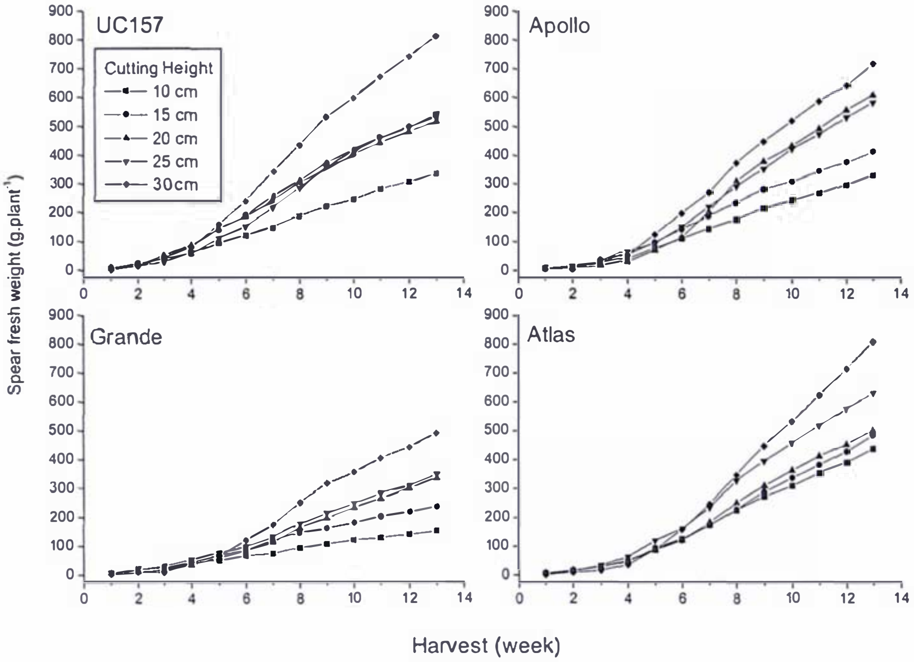


Figure 3.8 Expt 4: Cumulative spear fresh weight for **two** plants of four asparagus cultivars harvested at five different cutting heights during 13 week harvest period in a greenhouse.

Further comparison among these lines from four different cultivars at five different cutting heights was analyzed in SAS using Proc GLM with variables of CV, CH, and interaction of CV*CH, with both Week and Weeksq (for quadratic) or with Week only (for linear) as source of variation. These models accounted for 99.09% and 97.7% of data variation for quadratic and linear, respectively. Residuals from both models were obtained and plotted against its predictor. Residuals from the two models displayed a cubic wave pattern, suggesting a sigmoid model.

Looking at the plot of cumulative total spear fresh weight (Figure 3.8), the values amongst cutting height started to disperse at week 5 or week 6. With this observation, the next models were built from week 5 or 6 to week 13 using Proc GLM with variables of CV, CH, and interaction of CV*CH, together with both Week and Weeksq (for quadratic) or with Week only (for linear) as source of variation. The residuals from both linear and quadratic models using values from week 5 to week 13 were still V-shaped when plotted against its predictor, and the models accounted for 99.91% and 99.56% of data variation for quadratic and linear, respectively. Although the values of Rsquares were different by only 0.35%, the residuals distributions indicated the quadratic model was the better fit.

Coefficients and Rsquares from linear and quadratic models were obtained using Proc REG for each individual line (Table 3.6).

The regression lines across cultivars for every cutting height showed that as CH increased, the quadratic coefficient (c) reduced from -0.282 to -1.201 (Fig. 3.9)

Table 3.6 Expt 4: Coefficient estimates of quadratic and linear models for cumulative fresh weight over 13 weeks at five cutting height of four asparagus cultivars grown in a greenhouse.

		Quadratic Models			R^2	Linear Models		R^2	Rdiff
Cultivar	CH	a	b	c	(%)	a	b	(%)	(%)
UC157	10	43.151	17.275	-0.212	99.89	46.33	15.366	99.81	0.08
UC157	15	58.618	37.304	-1.416	99.97	79.86	24.558	98.66	1.31
UC157	20	58.015	34.319	-1.157	99.95	75.369	23.91	99.02	0.93
UC157	25	32.235	42.628	-1.627	99.83	56.636	27.987	98.50	1.33
UC157	30	67.354	54.854	-1.595	99.90	91.276	40.501	99.28	0.62
Apollo	10	38.180	17.707	-0.242	99.82	41.821	15.522	99.72	0.10
Apollo	15	46.689	25.495	-0.712	99.81	57.374	19.085	99.26	0.55
Apollo	20	8.181	52.246	-1.932	99.71	37.168	34.854	98.50	1.21
Apollo	25	35.753	39.247	-0.902	99.97	49.288	31.126	99.64	0.33
Apollo	30	49.358	48.516	-1.272	99.83	68.434	37.069	99.36	0.47
Grande	10	30.097	9.488	-0.278	98.28	34.262	6.989	97.67	0.61
Grande	15	33.905	17.189	-0.644	99.50	43.571	11.389	98.24	1.26
Grande	20	27.016	23.442	-0.363	99.64	32.468	20.171	99.51	0.13
Grande	25	29.317	25.618	-0.341	99.75	34.433	22.549	99.66	0.09
Grande	30	32.306	49.79	-1.709	99.68	57.947	34.406	98.71	0.97
Atlas	10	38.345	25.515	-0.399	99.89	44.332	21.923	99.76	0.13
Atlas	15	31.119	29.083	-0.374	99.92	36.726	25.719	99.83	0.09
Atlas	20	23.920	36.883	-1.098	99.97	40.394	26.998	99.31	0.66
Atlas	25	35.851	45.303	-1.324	99.91	55.715	33.385	99.28	0.63
Atlas	30	29.915	48.425	-0.229	99.97	33.357	46.359	99.96	0.01
Mean					99.76			99.18	0.5755

The equations for linear and quadratic models used $Y = a + bX$ and $Y = a + bX + cX^2$,respectively.

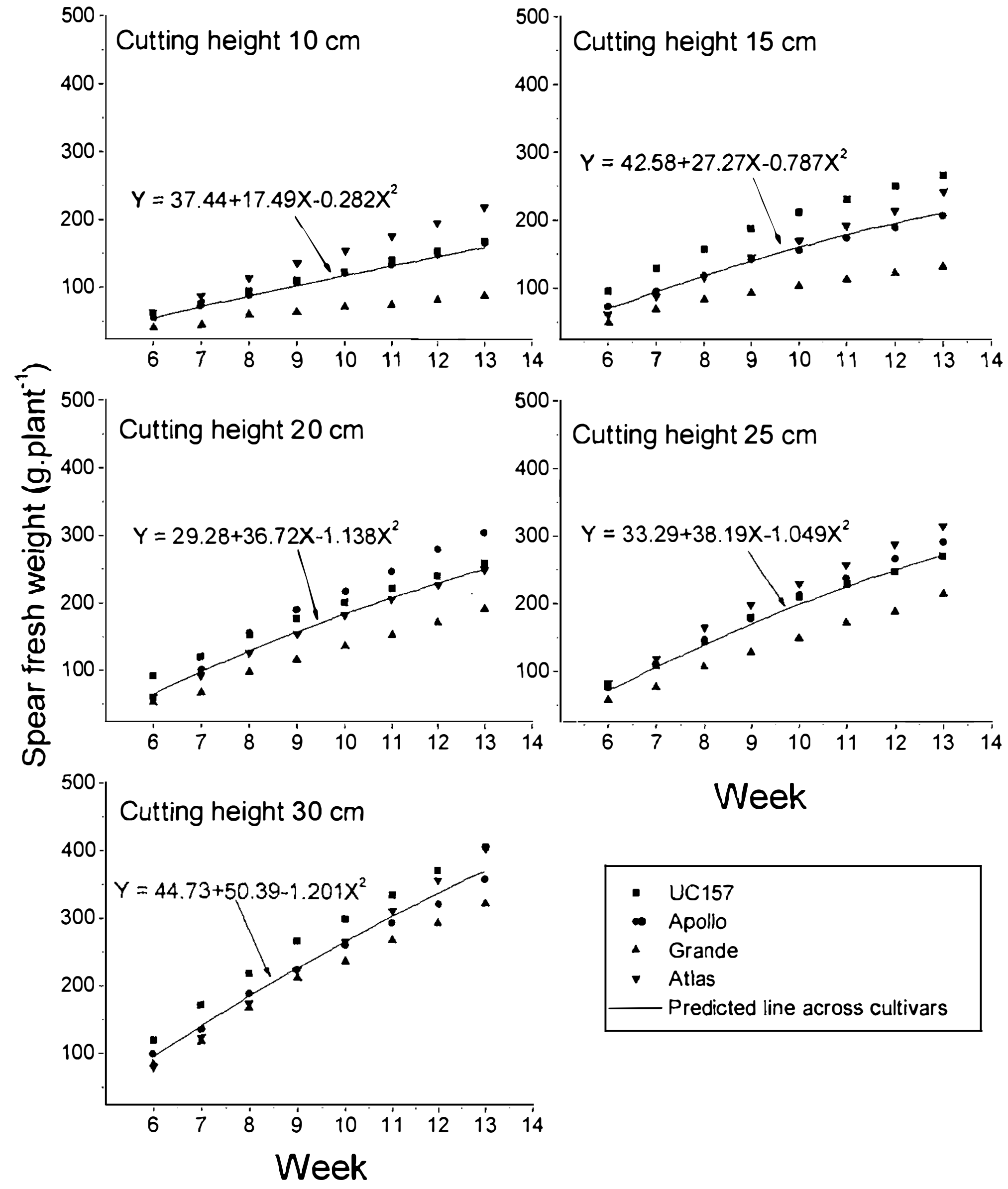


Figure 3.9 Expt 4: Prediction of spear production from four asparagus cultivars at different cutting heights within 13 weeks harvest period.

The trends of weekly total fresh yield in all cultivars were similar (Fig 3.10). Rate of total fresh yield increased until week 7 or week 8 then decreased slowly. After week 9, each cultivar produced similar total yield for each week until the end of harvest. The rate of weekly fresh yield of quality 1 spears increased from week 1 to week 8 and then gradually reduced. The trend of quality 1 spears over the harvest period appeared a bell-shaped. Generally, this trend occurred in all cultivars with slight fluctuation at week 6 in 'UC157' and 'Atlas' and week 5 in 'Grande'. Weekly fresh yield of quality 2 spears also increased during the first eight weeks.

As the harvest progressed toward the end, weekly yield of quality 1 spears reduced while that of quality 2 spears was slightly lower ('UC157'), higher ('Grande') or unchanged ('Apollo' and 'Atlas'). The sum of yield of quality 2 spears was more likely to dominate total yield for the last four weeks before harvest ended. Non-marketable yield increased very little throughout harvest time. Steady production during the last four weeks suggested total yield relied mainly on second grade marketable spears.

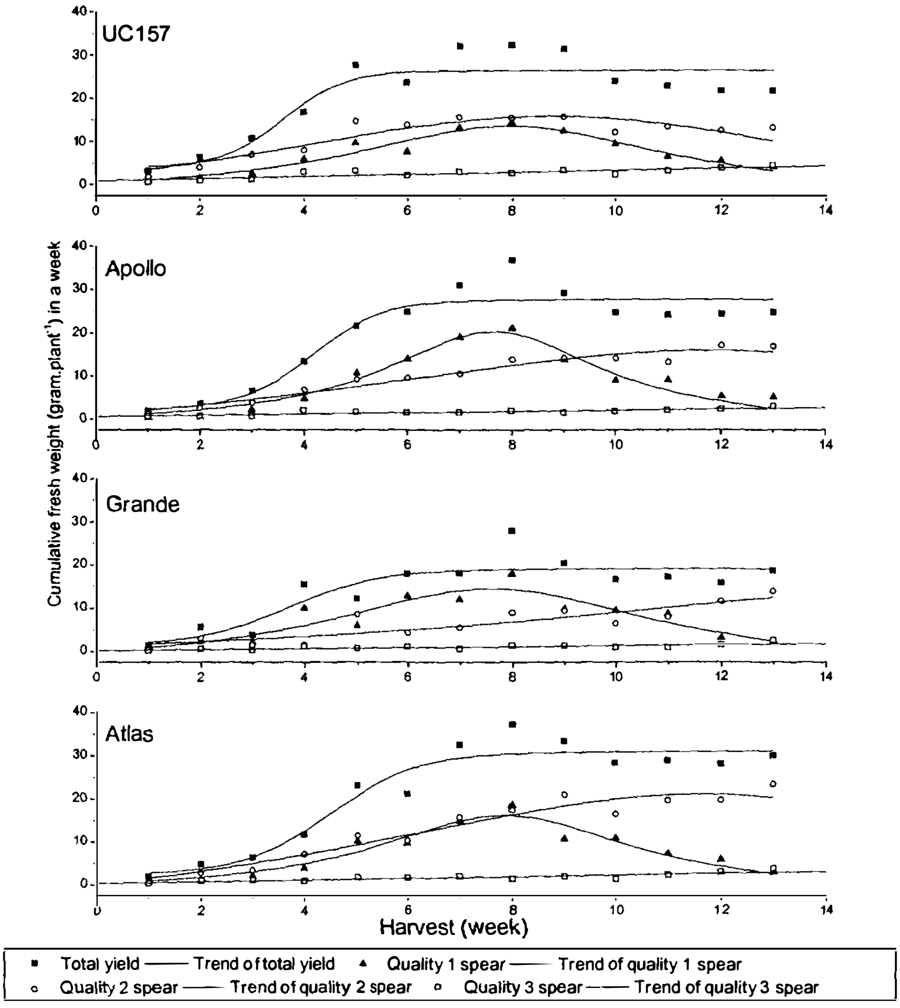


Figure 3.10 Expt 4: The trends of weekly fresh weight of total and quality 1, 2 and 3 spears from four asparagus cultivars harvested for 13 weeks in a greenhouse.

In general, plants produced relatively low fresh weight of quality 3 spears (Fig. 3.11). Weekly fresh weight of quality 1 spears at all levels of cutting heights increased from week 1 to week 8 and started reducing at week 9. Among cutting heights, plants at CH 30 cm produced highest weekly fresh weight from week 6 to week 11. Plants at CH 15 to 25 cm produced almost similar amount of weekly fresh yield while plants at CH 10 cm always had the lowest weekly fresh yield among all cutting height and all harvest times.

Weekly fresh weight of quality 2 spears increased gradually for the first five weeks and then produced similar weekly fresh yields until the last harvest. Nevertheless, plants at CH 30 cm produced more weekly fresh weight from week 5 to the last harvest. After week 7, there were clear trends that as CH increased the weekly fresh yield of spear quality 2 increased. For quality 3 spears, weekly fresh weight was very low regardless of different cutting heights.

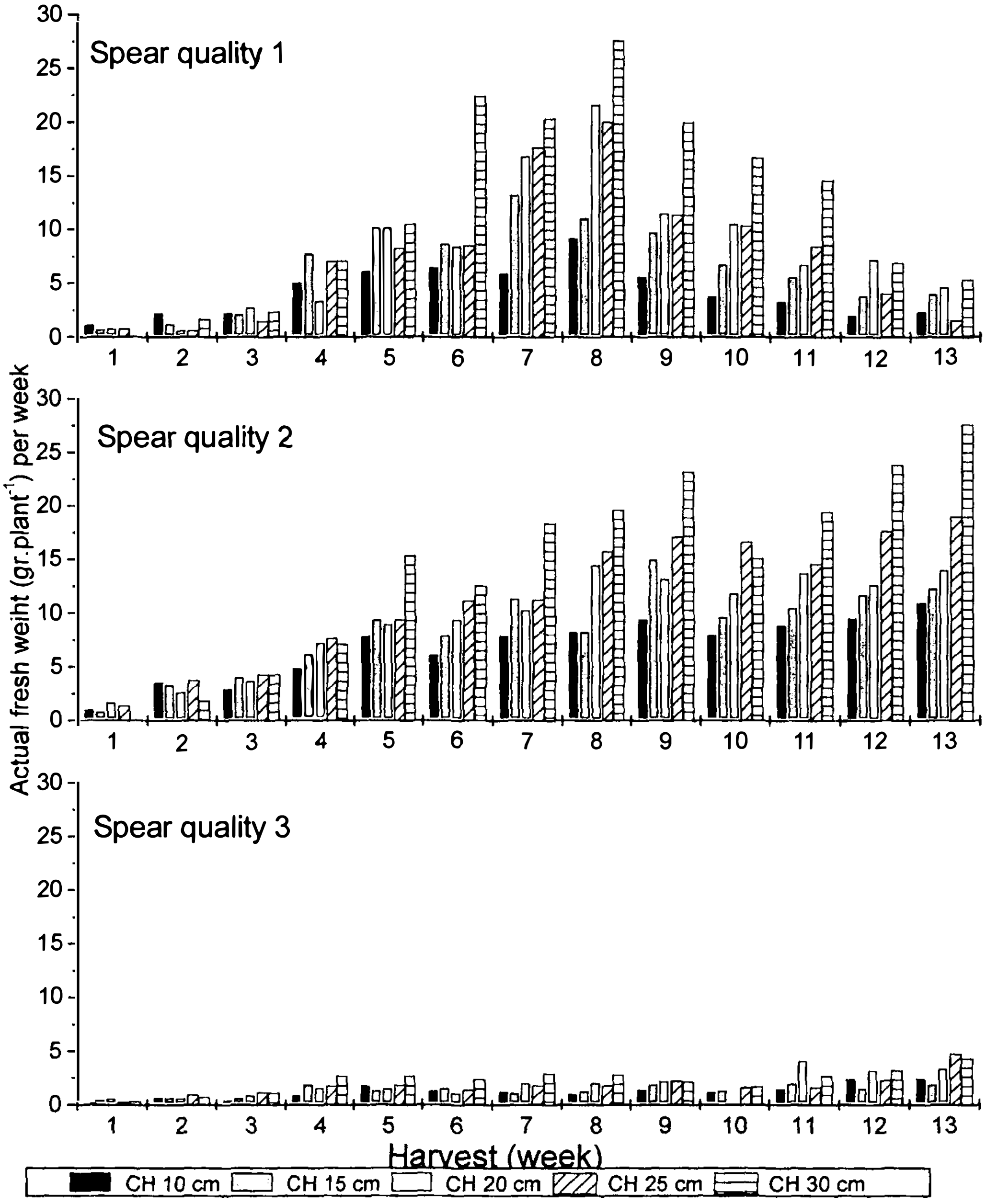


Figure 3.11 Expt 4: Weekly fresh weight of different cutting heights at spear qualities 1, 2, and 3 in each week across four asparagus cultivars harvested for 13 weeks in a greenhouse.

3.3.2.1.2. Total spear fresh weight

Besides being affected by CV*SEX interaction, total fresh weight at final week was also affected by CV ($P < 0.0001$) and CH ($P < 0.0001$) (Table 3.7).

All cultivars except ‘Grande’ (190.3 g.plant^{-1}) produced total spear fresh weight of more than 250 g per plant over 13 weeks of harvest and were not significantly different from each other except for ‘Grande’ (Table 3.26). Total spear fresh weight significantly increased as CH increased from CH 10 cm to CH 30 cm (from 160.6g.plant^{-1} to 373.3g.plant^{-1}).

Table 3.7 Expt 4: Total fresh weight (g.plant^{-1}) of four asparagus cultivars harvested in 2000 at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height **(CH)**	Cultivar **(CV)**				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	168.1	166.1	89.2	218.9	160.6^{d}
	15 cm	266.9	206.5	236.2	241.8	211.8^{c}
	20 cm	259.2	305.0	192.4	249.8	251.6^{bc}
	25 cm	270.8	291.8	214.5	314.6	272.9^{b}
	30 cm	407.0	359.1	323.5	403.6	373.3^{a}
	CV mean	274.4^{a}	265.8^{a}	190.3^{b}	285.8^{a}	

B	Plant sex **(SX)**	Cultivar (CV)				**SX mean**
		UC157	Apollo	Grande	Atlas	
	Female	301.8	266.5	136.9	272.0	244.2^{a}
	Male	247.5	265.0	243.6	299.5	263.9^{a}

C	Plant sex (SX)	Cutting Height (CH)				
		10 cm	15 cm	20 cm	25 cm	30 cm
	Female	164.1	200.7	240.9	255.4	359.9
	Male	157.1	222.8	262.3	290.5	386.8

Block	***	
CV	***	LSD$_{0.05}$ for CV = 43.7
SX	ns	LSD$_{0.05}$ for CH = 48.9
CH	***	LSD$_{0.05}$ for SEX = 30.9
CV*SX	***	
CV*CH	ns	
SX*CH	ns	
CV*SX*CH	ns	

ns, *, *** : non significant or significant at $P = 0.05$ or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at LSD$_{0.05}$.

There were no significant differences in total fresh weight yield of quality 1 spears amongst cultivars (Table 3.8). All cultivars produced similar total fresh weight of quality 1 spear (Table 3.8 Part A). This similarity of total fresh weight of quality 1 spear changed when plant sex was introduced (Table 3.8 Part B). Female plants of 'Grande' produced very low total fresh weight of quality 1 compared to female plants of other cultivars. On the other hand, male plants of 'Grande' produced total fresh weight of quality 1 spears twice as much as that of 'UC157' and higher than the other two cultivars. Cultivar 'Atlas' produced similar total fresh weight of quality 1 spears for both male and female plants. Both 'UC157' and 'Apollo' produced more quality 1 spears in female plants then in male plants whilst 'Grande' was the opposite. Over all, female plants (113.6g.plant^{-1}) produced higher total fresh weight than male plants (86.5g. plant^{-1}). However, total fresh weight of quality 1 spears of female plants did not significantly differ from that of male plants.

Table 3.8 Expt 4: Total fresh weight (g.plant^{-1}) of quality 1 spears of four cultivars harvested at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height (CH)	Cultivar (CV)				CH mean
		UC157	Apollo	Grande	Atlas	
	10 cm	44.5	70.1	26.8	79.63	55.3^{c}
	15 cm	118.0	90.3	69.9	60.0	84.6^{bc}
	20 cm	70.6	160.0	97.6	91.9	105.0^{b}
	25 cm	76.4	106.9	98.5	118.2	100.0^{bc}
	30 cm	156.9	140.3	188.61	135.9	155.4^{a}
	CV mean	93.3	113.5	96.3	97.1	

B	Plant sex (SX)	Cultivar (CV)				SX mean
		UC157	Apollo	Grande	Atlas	
	Female	133.7	143.5	78.63	98.8	113.6
	Male	52.96	83.6	113.9	95.4	86.5

C	Plant sex (SX)	Cutting Height (CH)				
		10 cm	15 cm	20 cm	25 cm	30 cm
	Female	74.6	91.9	108.5	108.9	184.4
	Male	35.9	77.2	101.6	91.1	126.5

Block	ns	
CV	ns	
SX	ns	LSD$_{0.05}$ for CV = 40.3
CH	**	LSD$_{0.05}$ for CH = 45.1
CV*SX	*	LSD$_{0.05}$ for SEX = 28.5
CV*CH	ns	
SX*CH	ns	
CV*SX*CH	ns	

ns, **, ***: non significant or significant at $P = 0.01$, or 0.001, respectively. Within the column and row, means followed by the same letters are not significantly different at LSD$_{0.05}$.

The interaction of CV*SEX also significantly affected total fresh weight of quality 2 spears (Table 3.9 Part B). Generally, responses to the interaction CV*SEX in quality 2 spears were similar to those in quality 1 spears. The differences in fresh weight of quality 2 spears were even more affected by individual main effects. Cultivar 'Atlas' ranked the highest total fresh weight of quality 2 spears followed by 'UC157', 'Apollo' and 'Grande'.

The differences within non-marketable spears (quality 3) were due to CV, SX, and CH but there were no significant interaction effects on total fresh weight of quality 3 spears (Table 3.10). Whilst 'UC157' produced the highest, 'Grande' produced the lowest non-marketable spear total fresh weight (Table 3.10 Part A) and 'Apollo' and 'Atlas' were similar. At CH 10 cm, total fresh weight of non-marketable spears was 16.1g.plant^{-1} and it increased up to 29.4g.plant^{-1} when CH increased to 30 cm. Furthermore, in comparison to female plants, male plants produced significantly higher fresh weight of non-marketable spears.

Table 3.9 Expt 4: Total fresh weight (g.plant^{-1}) of quality 2 spears of four asparagus cultivars harvested at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A Cutting Height **(CH)**	Cultivar **(CV)**				**CH mean**
	UC157	Apollo	Grande	Atlas	
10 cm	101.7	78.51	53.6	122.8	89.2^{d}
15 cm	123.9	94.9	53.9	167.7	110.1^{cd}
20 cm	147.7	125.2	84.4	137.0	123.6^{bc}
25 cm	158.1	169.7	98.2	172.9	149.7^{b}
30 cm	204.8	191.4	120.4	237.4	188.5^{a}
CV mean	147.3^{ab}	131.96^{b}	82.1^{c}	167.6^{a}	

	Cultivar (CV)				**SX mean**
B Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
Female	136.2	105.5	52.5	154.5	112.2^{b}
Male	158.3	158.4	111.7	180.7	152.3^{a}

	Cutting Height (CH)				
C Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
Female	77.1	108.4	154.7	127.9	171.1
Male	92.4	128.4	101.3	138.8	222.3

Block	***	
CV	***	
SX	***	$LSD_{0.05}$ for CV = 23.8
CH	***	$LSD_{0.05}$ for CH = 26.6
CV*SX	*	$LSD_{0.05}$ for SEX = 16.8
CV*CH	ns	
SX*CH	ns	
CV*SX*CH	ns	

ns, *, *** : non significant or significant at $P = 0.05$ or 0.001, respectively. Within the column and row, means followed by the same letters are not significantly different at $LSD_{0.05}$.

Table 3.10 Expt 4: Total fresh weight (g.plant^{-1}) of quality 3 spears of four asparagus cultivars harvested at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height **(CH)**	Cultivar **(CV)**				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	21.8	17.5	8.80	16.4	16.1^{b}
	15 cm	24.9	21.2	8.0	14.0	17.1^{b}
	20 cm	40.9	19.8	10.4	20.9	23.0^{ab}
	25 cm	36.2	15.3	17.7	23.6	23.2^{ab}
	30 cm	45.3	27.5	14.4	30.3	29.4^{a}
	CV mean	33.8^{a}	20.3^{b}	11.9^{c}	21.1^{b}	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	31.4	17.5	5.8	18.86	18.4^{b}
	Male	36.3	22.9	17.9	23.3	25.1^{a}

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	12.4	16.4	24.2	18.1	20.8
	Male	19.9	17.7	21.8	28.3	38.0

Block	***	
CV	***	
SX	**	$LSD_{0.05}$ CV = 6.4
CH	**	$LSD_{0.05}$ CH = 7.2
CV*SX	ns	$LSD_{0.05}$ SEX = 4.5
CV*CH	ns	
SX*CH	ns	
CV*SX*CH	ns	

ns, *, **, *** : non significant or significant at $P = 0.05$, 0.01, or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at $LSD_{0.05}$.

3.3.2.1.3. Percentage of spear dry matter

During the first month, the ANOVA resulted in un-estimable values due to unavailable percentage of dry matter from some quality 1 and 2 spears. Spear quality differences in dry matter percentage were significant in the second and third month (Table 3.11). Dry matter percentage of quality 1 spears was always the lowest (8.2 and 8.01%, for month 2 and 3, respectively) among three spear qualities whereas that of quality 3 spears was always the highest (11.06 and 12.11%, for month 2 and 3 respectively).

Table 3.11 Expt 4: Average percentage of dry matter (%) amongst three different spear qualities at different month of harvest period in 2000.

Quality	Month1	Month2	Month3
Quality 1 spears	NE	8.20^{c}	8.01^{b}
Quality 2 spears	NE	9.10^{b}	8.43^{b}
Quality 3 spears	NE	11.96^{a}	12.11^{a}
Mean	NA	9.75	9.52
Significance	NA	***	***

NE: Not estimable, NA- not available. Within column, lsmeans followed by the same letters are not significantly different using pdiff Tukey adjustment.

Further analysis within each spear quality for month 2 and 3 showed that the average percentage of spear dry matter was similar regardless of cutting height, cultivars, or plant sex (Table 3.12 and 3.13)

Table 3.12 Expt 4: Average percentage of spear dry matter (%) from female and male plants of three asparagus cultivars cut at five different cutting heights in the second month of harvest.

No	Cultivar	Plant Sex	Cutting height	Quality 1	Quality 2	Quality 3
1	UC157	Female	10	8.53	9.27	12.51
2			15	8.26	9.03	11.66
3			20	8.27	9.03	13.26
4			25	7.75	9.05	13.23
5			30	8.40	8.94	15.50
6		Male	10	8.05	9.10	10.11
7			15	8.16	8.94	12.94
8			20	8.76	9.26	16.11
9			25	9.04	8.90	11.27
10			30	7.70	9.06	11.85
11	Apollo	Female	10	7.94	9.88	8.57
12			15	8.26	8.93	10.69
13			20	8.53	8.67	12.64
14			25	8.45	9.08	17.26
15			30	8.20	8.78	12.09
16		Male	10	8.91	9.71	11.06
17			15	8.10	9.13	11.83
18			20	8.11	8.64	11.42
19			25	8.03	9.41	12.02
20			30	7.92	8.61	11.63
21	Atlas	Female	10	7.96	9.17	9.48
22			15	9.00	8.72	14.30
23			20	8.43	8.70	10.9
24			25	9.08	9.82	13.04
25			30	7.71	8.77	11.86
26		Male	10	8.73	8.87	12.05
27			15	8.32	8.39	9.01
28			20	7.72	8.97	10.29
29			25	7.85	8.88	12.23
30			30	7.89	8.51	10.11
	Significance:		Block	ns	ns	ns
			Cult	ns	ns	ns
			Sex	ns	ns	ns
			CH	ns	ns	ns
			Cult*Sex	ns	ns	ns
			Cult*CH	ns	ns	ns
			Sex*CH	ns	ns	ns
			Cult*Sex*CH	ns	ns	ns

ns: not significant

Table 3.13 Expt 4: Average percentage of spear dry matter (%) from female and male plants of three asparagus cultivars cut at five different cutting heights in the third month of harvest.

No	Cultivar	Plant Sex	Cutting height	Quality 1	Quality 2	Quality 3
1	UC157	Female	10	7.83	8.26	12.88
2			15	8.92	8.45	14.65
3			20	7.71	8.52	12.96
4			25	8.49	8.54	13.68
5			30	7.47	8.42	13.26
6		Male	10	8.44	8.57	9.69
7			15	7.72	8.15	13.54
8			20	7.59	8.53	12.03
9			25	8.45	9.15	13.54
10			30	7.34	8.68	10.41
11	Apollo	Female	10	7.07	8.81	10.89
12			15	8.10	8.30	12.39
13			20	7.62	7.82	12.71
14			25	7.37	8.44	13.48
15			30	7.82	8.47	11.68
16		Male	10	7.78	8.65	11.19
17			15	7.41	8.75	12.49
18			20	6.89	7.98	10.43
19			25	7.70	8.54	12.47
20			30	7.29	8.36	14.70
21	Atlas	Female	10	7.99	8.66	10.14
22			15	7.16	8.56	11.52
23			20	8.09	8.45	10.69
24			25	8.28	8.40	11.48
25			30	7.36	8.40	13.99
26		Male	10	7.93	8.58	12.74
27			15	7.94	8.04	10.12
28			20	8.10	8.27	10.56
29			25	9.25	8.24	10.34
30			30	7.85	7.98	12.55
	Significance:	Block		ns	ns	ns
		Cult		ns	ns	ns
		Sex		ns	ns	ns
		CH		ns	ns	ns
		Cult*Sex		ns	ns	ns
		Cult*CH		ns	ns	ns
		Sex*CH		ns	ns	ns
		Cult*Sex*CH		ns	ns	ns

ns: not significant

3.3.2.2. *Spear number in Expt 4*

3.3.2.2.1. Effect of cultivar and cutting height over harvest date on spear number

CV, CH and SEX significantly affected cumulative spear number over harvests, all at $P< 0.0001$. There was no significant effect of CV*CH over 13 weeks of harvest on cumulative spear number. Except for 'Grande', cumulative total spear number at either CH 10 or CH 15 cm was always the highest among other levels of cutting heights in all cultivars (Fig. 3.12).

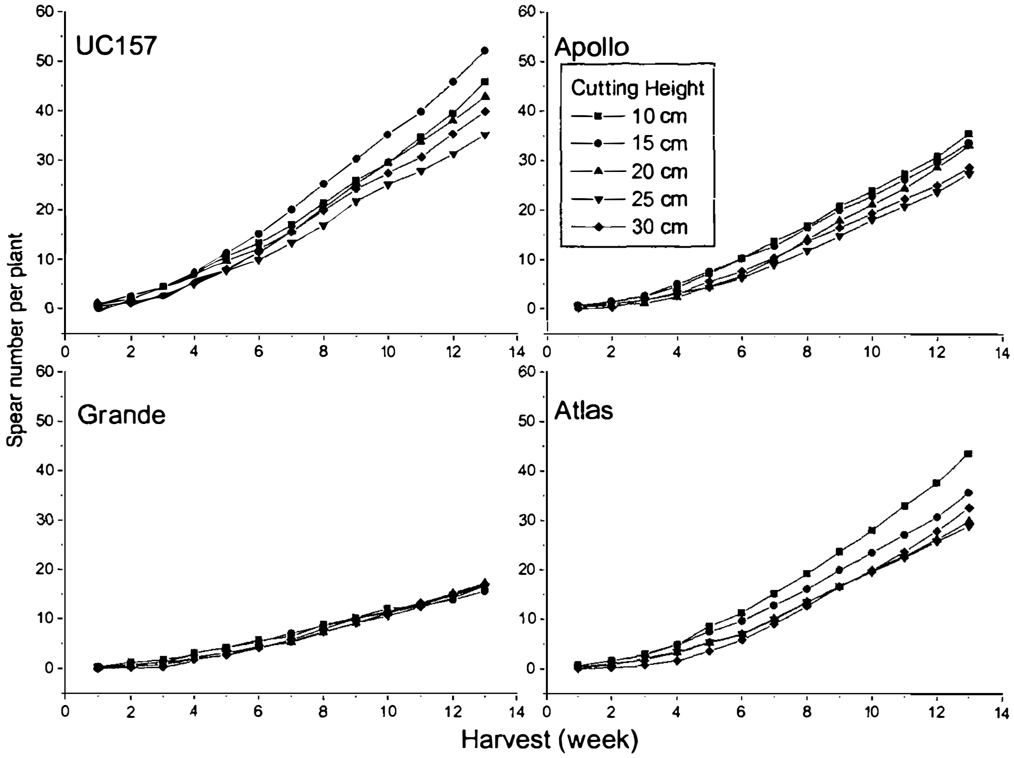


Figure 3.12 Expt 4: Cumulative spear number of four asparagus cultivars harvested at five different cutting heights during 13 weeks harvest period in a greenhouse.

The linear and quadratic models were applied from week 6 to week 13 using proc GLM and residuals were checked. Rsquare (99.93%) from quadratic model in Proc GLM was reduced by 0.11% when the linear model was applied. Proc REG was run to get individual coefficient estimates for each model (Table 3.14).

Table 3.14 Expt 4: Coefficient estimates of quadratic and linear models for cumulative spear number over 13 weeks at five cutting heights of four asparagus cultivars grown in a greenhouse.

		Quadratic Models			R^2	Linear Models		R^2	Rdiff
Cultivar	CH	a	b	c	(%)	a	b	(%)	(%)
UC157	10	10.04	3.197	0.155	99.88	7.724	4.589	99.43	0.45
UC157	15	10.791	4.454	0.084	99.93	9.529	5.211	99.82	0.11
UC157	20	7.48	4.285	0.017	99.93	7.230	4.435	99.92	0.01
UC157	25	5.730	3.991	-0.041	99.80	6.339	3.626	99.75	0.05
UC157	30	7.651	3.948	0.004	99.78	7.584	3.988	99.78	0.00
Apollo	10	7.179	3.082	0.051	99.87	6.408	3.546	99.79	0.08
Apollo	15	7.086	2.929	0.046	99.89	6.391	3.346	99.82	0.07
Apollo	20	3.399	3.359	0.038	99.84	2.828	3.703	99.80	0.04
Apollo	25	3.536	2.656	0.038	99.94	2.966	2.998	99.88	0.06
Apollo	30	4.786	2.854	0.012	99.91	4.606	2.906	99.90	0.01
Grande	10	3.973	1.490	0.009	99.16	3.826	1.578	99.15	0.01
Grande	15	3.952	1.548	-0.014	99.80	4.154	1.427	99.76	0.04
Grande	20	2.686	1.359	0.060	99.84	1.778	1.901	99.44	0.40
Grande	25	2.761	1.349	0.047	99.79	2.061	1.769	99.51	0.28
Grande	30	2.102	1.965	-0.014	99.80	2.314	1.837	99.78	0.02
Atlas	10	7.703	3.452	0.126	99.97	5.808	4.589	99.66	0.31
Atlas	15	6.553	2.964	0.081	99.92	5.343	3.690	99.73	0.19
Atlas	20	3.888	3.083	0.0195	99.96	3.595	3.259	99.94	0.02
Atlas	25	3.615	3.2796	-0.015	99.96	3.835	3.148	99.95	0.01
Atlas	30	2.679	3.048	0.084	99.93	1.4196	3.803	99.74	0.19
Mean					99.85			99.73	0.18

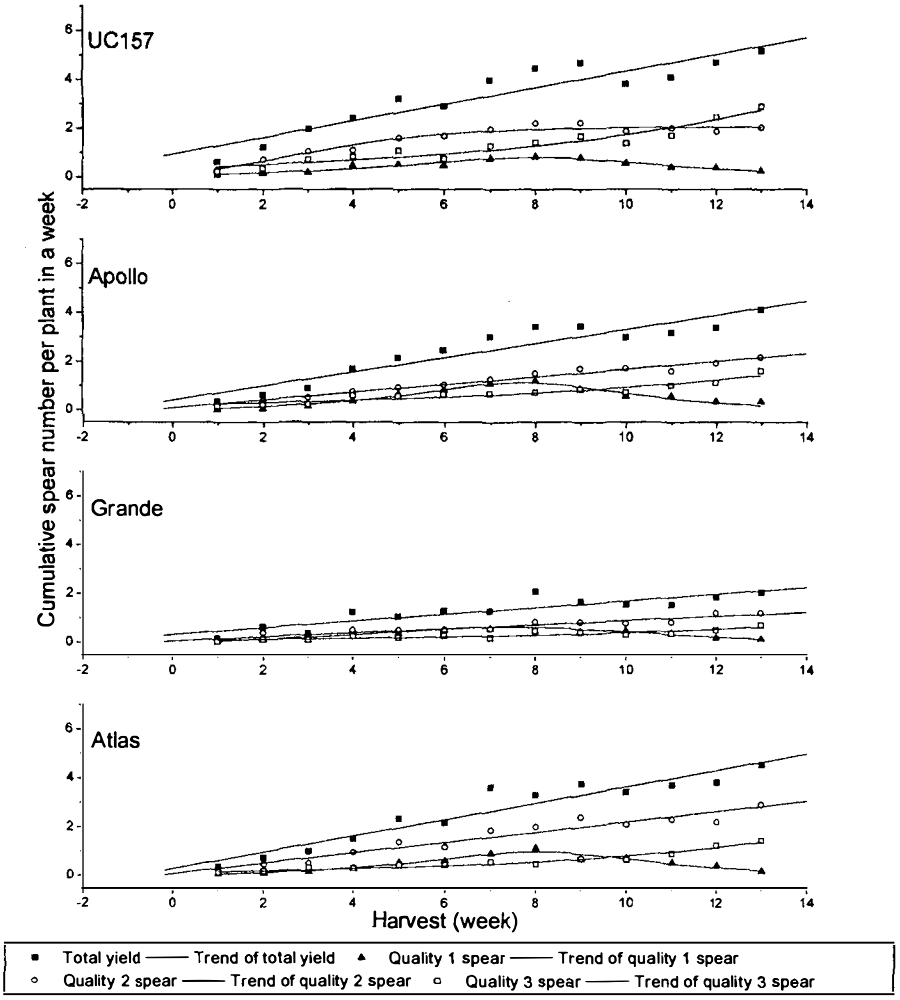


Figure 3.13Expt 4: Weekly spear number of total and quality 1, 2, and 3 in each week from four asparagus cultivars harvested for 13 weeks in a greenhouse.

The trend in total weekly spear number differed from total fresh or dry weight. For total spear number, the trend was an increasing linear (Fig. 3.13). Except for 'UC157', weekly spear number of quality 2 increased similarly to total spear number for all cultivars (Fig 3.13). Weekly spear number of quality 1 increased from week 1 to week 8 and then declined. Weekly spear number of quality 3 increased continuously from the beginning to last harvest. High production of quality 3 spears was particularly observed in 'UC157' as harvest season progressed. For the other three cultivars, more spears of quality 2 were still produced than spears of quality 3.

In general, plants produced more spears of quality 2 than spears of quality 1 and 3 for five different cutting heights for 13 weeks (Fig. 3.14). Within spear quality 2, slightly higher numbers of spears from cutting height 10 and 15 cm were observed in week 2, 5, 7, 9, 11 and 13. The production of spear quality 3 at cutting height from 10 to 20 cm was particularly high in the last four weeks of harvest.

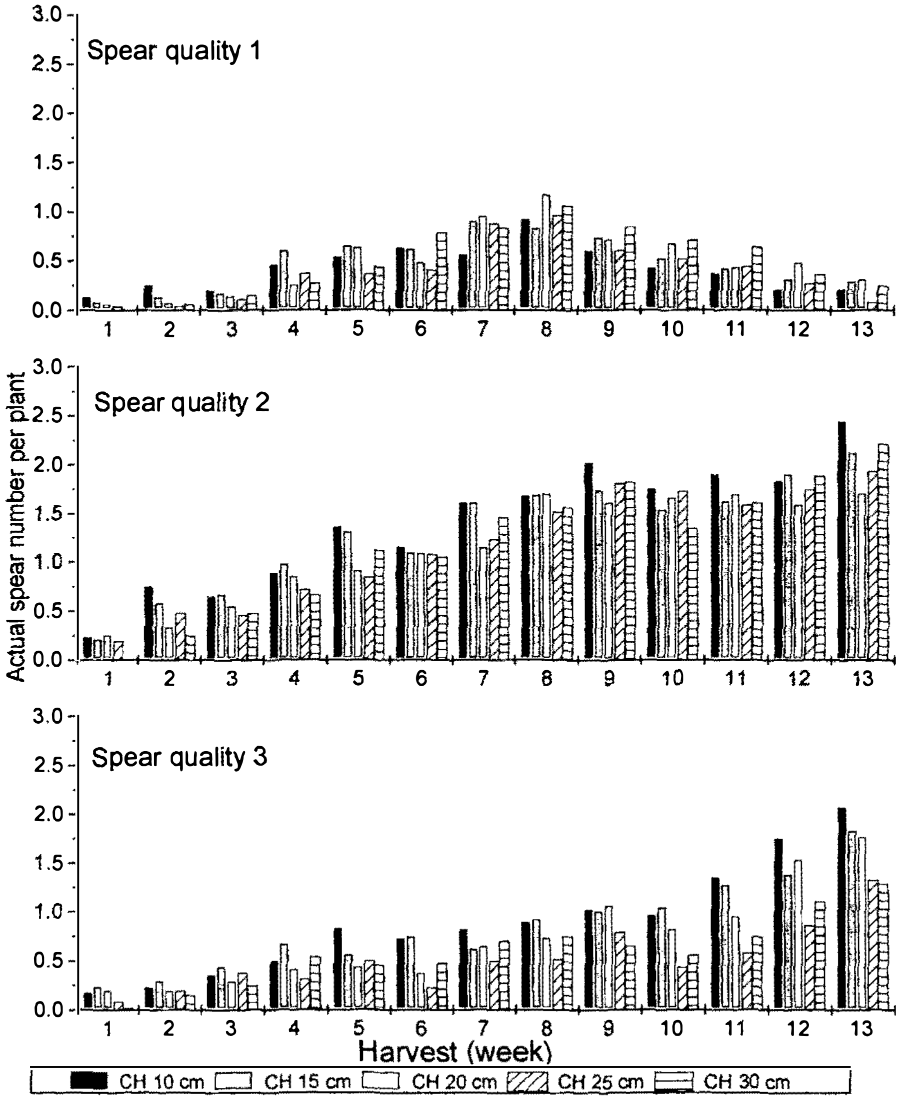


Figure 3.14 Expt 4: Weekly spear number of different cutting heights at spear qualities 1, 2, and 3 in each week across four asparagus cultivars for 13 weeks in a greenhouse.

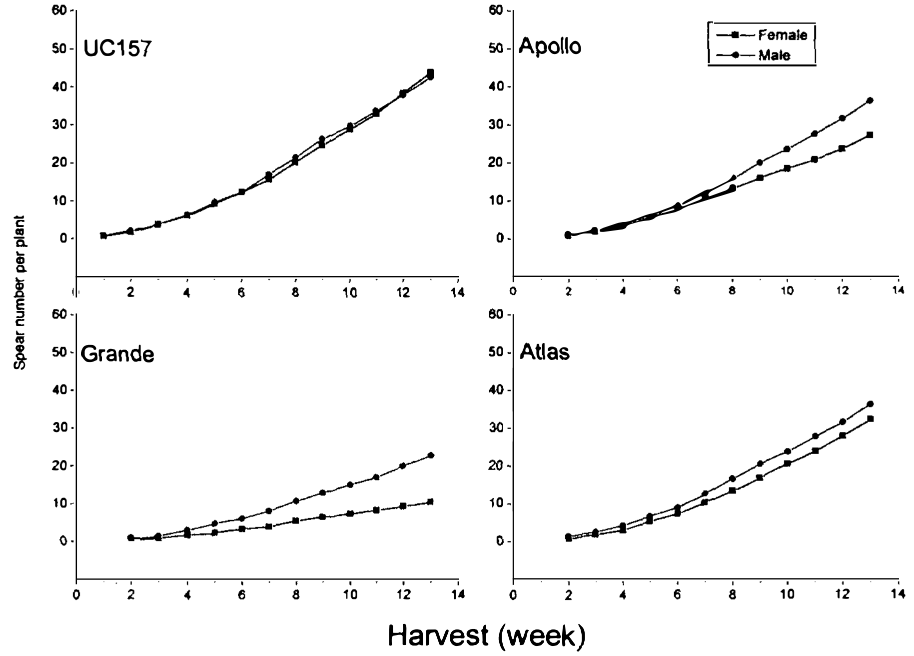


Figure 3.15 Expt 4: Cumulative spear number across cutting height of two plant sexes in four different cultivars harvested during 13 weeks in a greenhouse.

Split plot analysis with harvest date as split factor also revealed that CV*SEX interaction significantly affected cumulative total spear number. Male plants of all cultivars except 'UC157' produced more total spears than female plants especially for 'Grande' (Fig 3.15).

3.3.2.2.2. Total spear number

CH significantly affected total spear number at final harvest (Table 3.15). Most spears were cut in lowest CH (Table 3.15 Part A). As CH increased fewer spears were harvested. Amongst cultivars, 'UC157' produced the highest total spear number followed by 'Atlas' and 'Apollo'. Male plants also produced more spears than female at $P = 0.0001$ (Table 3.15 Part B). The differences between male and female plants were clear in 'Apollo' and 'Grande'. On the other hand, male and female plants in 'UC157' produced the same total spear number. The differences between male and female for different cultivars brought about the significant in CV*SEX interaction (Table 3. 15 Part B).

Although there was no significant effect of interaction CV*CH on total spear number at all harvests, constant low spear numbers across CH in 'Grande' were distinctive compared to other cultivars at final harvest. There was a decreasing pattern of spear number with CH increases in 'Atlas' and 'Apollo' but the pattern of spear number reduction was not obvious in 'UC157' and 'Grande'.

The spear number of quality 1 was only influenced by interaction effect of CV*SEX at $P= 0.0016$ (Table 3.16). Female plants of all asparagus cultivars except 'Grande' produced more spears in quality 1 than male plants (Table 3.16 Part B). Female plants of 'Grande' produced only 50 % of spear number in male, whilst male plants of 'UC157' produced 40% of total spear number in female plants.

The main difference among cultivars occurred in spear number of quality 2 in which 'UC157' and 'Atlas' produced highest spear number followed by 'Apollo' (Table 3.16). 'Grande' produced the lowest spear number (Table 3.17 Part A). Male plants produced significantly more spears than female plants (Table 3.17 Part B). There was no significant effect of CH on spear number of quality 2 spears.

Table 3.15 Expt 4: Total spear number (number of spear.plant^{-1}) of four asparagus cultivars harvested at different cutting height (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height **(CH)**	Cultivar **(CV)**				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	45.9	35.5	16.7	43.7	35.4^{a}
	15 cm	52.2	33.7	15.7	35.8	34.3^{ab}
	20 cm	42.9	33.1	17.3	30.0	30.8^{bc}
	25 cm	35.3	27.4	16.8	29.0	27.1^{c}
	30 cm	39.9	28.7	17.1	32.7	29.6^{c}
	CV mean	43.3^{a}	31.7^{b}	16.7^{c}	34.2^{b}	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	43.9	27.2	10.5	32.2	28.5^{b}
	Male	42.6	36.1	22.9	36.2	34.5^{a}

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	31.6	33.2	29.7	23.1	24.8
	Male	39.3	35.5	32.0	31.1	34.4

Block	***	
CV	***	
SX	***	LSD$_{0.05}$ for CV = 4.1
CH	**	LSD$_{0.05}$ for CH = 4.6
CV*SX	**	LSD$_{0.05}$ for SEX = 2.9
CV*CH	ns	
SX*CH	ns	
CV*SX*CH	ns	

ns, **, *** : non significant or significant at $P = 0.01$ or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at LSD$_{0.05}$.

Table 3.16 Expt 4: Total spear number (number of spears.plant^{-1}) of quality 1 of four cultivars harvested at different cutting height (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height **(CH)**	Cultivar **(CV)**				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	5.3	6.5	2.1	8.2	5.5
	15 cm	8.4	6.7	4.9	5.0	6.3
	20 cm	4.6	9.2	5.2	6.5	6.4
	25 cm	4.4	5.8	4.2	5.9	5.1
	30 cm	7.0	6.7	6.3	5.6	6.4
	CV mean	5.9	6.8	4.4	6.2	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	8.5	8.4	3.0	6.6	6.6
	Male	3.4	5.5	6.1	5.9	5.2

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	7.3	6.5	6.4	5.5	7.4
	Male	3.7	5.9	6.3	4.7	5.4

Block	ns	
CV	ns	
SX	ns	$LSD_{0.05}$ CV = 2.3
CH	ns	$LSD_{0.05}$ CH = 2.8
CV*SX	**	$LSD_{0.05}$ SEX = 1.4
CV*CH	ns	
SX*CH	ns	
CV*SX*CH	ns	

ns, *, *** :non significant or significant at $P = 0.05$ or 0.001, respectively.

Table 3.17 Expt 4: Total spear number (number of spears.plant^{-1}) of quality 2 of four cultivars harvested at different cutting height (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height **(CH)**	Cultivar **(CV)**				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	22.9	15.9	9.7	24.6	18.3^{a}
	15 cm	21.7	15.3	6.9	24.3	17.1^{a}
	20 cm	19.6	14.8	9.1	16.9	15.5^{a}
	25 cm	18.4	16.8	8.6	17.6	15.3^{a}
	30 cm	20.4	15.6	7.4	18.5	15.0^{a}
	CV mean	20.6^{a}	15.7^{b}	8.3^{c}	20.4^{a}	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	18.6	11.7	4.9	18.9	13.5^{b}
	Male	22.6	19.7	11.8	21.8	18.9^{a}

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	15.6	14.2	13.2	12.9	11.8
	Male	20.9	19.9	17.0	17.7	19.2

Block	***	
CV	***	
SX	***	LSD$_{0.05}$ for CV = 3.1
CH	ns	LSD$_{0.05}$ for CH = 3.4
CV*SX	ns	LSD$_{0.05}$ for SEX = 2.1
CV*CH	ns	
SX*CH	ns	
CV*SX*CH	ns	

ns, *** : non significant or significant at P = 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at LSD$_{0.05}$.

Table 3.18 Expt 4: Total spear number (number of spears.plant^{-1}) of quality 3 of four cultivars harvested at different cutting height (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height (CH)	Cultivar (CV)				CH mean
		UC157	Apollo	Grande	Atlas	
	10 cm	17.8	13.1	4.9	10.9	11.7^{a}
	15 cm	22.1	11.7	3.8	6.4	11.0^{ab}
	20 cm	18.8	9.2	3.1	6.6	9.4^{abc}
	25 cm	12.5	4.8	4.0	5.5	6.7^{c}
	30 cm	12.5	6.4	3.3	8.6	7.7^{bc}
	CV mean	16.7^{a}	9.0^{b}	3.8^{c}	7.6^{b}	

		Cultivar (CV)				SX mean
B	Plant sex (SX)	UC157	Apollo	Grande	Atlas	
	Female	16.8	7.1	2.7	6.7	8.3^{a}
	Male	16.6	10.9	5.0	8.5	10.3^{a}

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	8.7	12.5	10.1	4.7	5.6
	Male	14.6	9.5	8.7	8.7	9.8

Block	**	
CV	***	
SX	ns	LSD$_{0.05}$ for CV = 3.5
CH	ns	LSD$_{0.05}$ for CH = 3.9
CV*SX	ns	LSD$_{0.05}$ for SEX = 2.4
CV*CH	ns	
SX*CH	ns	
CV*SX*CH	ns	

ns, *, ***: non significant or significant at P = 0.05 or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at LSD$_{0.05}$.

There was a pattern of decreasing spear number as CH increased in quality 3 spears (Table 3.18). Male plants produced more non-marketable spears than female plants but the difference was not significant. CV effect however was notable on numbers of non-marketable spears ($P < 0.0001$). Cultivar 'UC157' produced the highest number, not only marketable spears, but also non-marketable spears among the four cultivars. 'Grande' always produced lowest spear number for any grade of spears.

3.3.2.3. Average spear head length and spear diameter.

CH significantly increased spear head length of quality 1 spears (Table 3.19), quality 2 spears (Table 3.20) and quality 3 spears (Table 3.21) where quality was based on combination between head length and spear diameter (see section 3.2.1.3). The increases of head length from CH 10 to 30 cm in marketable spears (quality 1 and quality 2 spears) were not as high as in non-marketable spears (quality 3 spears). In quality 1 spears, head length at CH 10 was 2.45 cm and increased up to 3.26 cm at CH 30 cm (Table 3.18). Within non-marketable spears, head length was 2.26 cm at CH 10 cm and increased up to 8.89 cm at CH 30 cm, an increase of almost 300% (Table 3.21). Within spear quality 2, head length was also influenced by interaction of CV*SEX at $P = 0.0225$ (Table 3.20). Cultivar 'Grande' and 'Atlas' had greater head length in male plants than female plants while 'UC157' and 'Apollo' were the opposite.

Neither SEX nor CH significantly affected mean diameter of quality 1 spears (Table 3.22). The difference for CV was due to 'Grande' that produced large spear diameter (11.14 mm). Other factors played a role in determining diameter of quality 2 spears (Table 3.23). Beside CV, CH also increased spear diameter and there was a significant interaction of CV*SEX and SEX*CH (Table 3.23). Diameter of non-marketable spears were influenced by interaction of CV*SEX only (Table 3.24).

Table 3.19 Expt 4: Average spear head length (cm) of quality 1 spears of four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C) during the last harvest month.

A	Cutting Height **(CH)**	Cultivar **(CV)**				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	2.90	2.29	2.26	2.34	2.45^{c}
	15 cm	2.76	2.63	2.32	2.52	2.56^{c}
	20 cm	2.73	2.87	2.56	2.66	2.71^{bc}
	25 cm	2.94	3.50	3.18	2.82	3.11^{ab}
	30 cm	3.17	3.40	3.17	3.28	3.26^{a}
	CV mean	2.90^{a}	2.94^{a}	2.70^{a}	2.73^{a}	

B	Plant sex **(SX)**	Cultivar (CV)				**SX mean**
		UC157	Apollo	Grande	Atlas	
	Female	3.06	3.05	2.71	2.71	2.93^{a}
	Male	2.74	2.82	2.68	2.74	2.73^{a}

C	Plant sex (SX)	Cutting Height (CH)				
		10 cm	15 cm	20 cm	25 cm	30 cm
	Female	2.57	2.54	2.74	3.29	3.28
	Male	2.32	2.57	2.67	2.93	3.23

Block	ns
CV	ns
SX	ns
CH	***
CV*SX	ns
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

ns, *, ***: non significant or significant at $P = 0.05$ or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at $LSD_{0.05}$.

Table 3.20 Expt 4: Average spear head length (cm) of quality 2 spear of four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C) during the last harvest month.

A	Cutting Height **(CH)**	Cultivar **(CV)**				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	2.09	2.13	1.98	2.08	2.07^b
	15 cm	2.34	2.47	2.01	2.32	2.28^b
	20 cm	2.49	2.63	2.33	2.41	2.46^b
	25 cm	3.09	3.43	3.05	4.06	3.41^a
	30 cm	3.47	3.50	3.22	4.59	3.69^a
	CV mean	2.69^a	2.83^a	2.51^a	3.09^a	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	2.73	2.98	2.28	2.67	2.90^a
	Male	2.66	2.69	2.75	3.51	2.64^a

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	2.03	2.23	2.43	3.04	3.59
	Male	2.11	2.34	2.50	3.77	3.80

Block	ns
CV	ns
SX	ns
CH	***
CV*SX	*
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

ns, *, ***: non significant or significant at $P = 0.05$ or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at $LSD_{0.05}$.

Table 3.21 Expt 4: Average spear head length (cm) of quality 3 spear of four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C) during the last harvest month.

A	Cutting Height **(CH)**	Cultivar **(CV)**				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	2.48	2.46	1.89	2.20	2.26^{c}
	15 cm	3.63	4.53	3.19	2.86	3.55^{bc}
	20 cm	5.46	4.70	5.05	3.87	4.77^{b}
	25 cm	7.13	8.51	5.89	8.16	7.42^{a}
	30 cm	8.34	10.59	6.89	9.73	8.89^{a}
	CV mean	5.41^{a}	6.16^{a}	4.58^{a}	5.36^{a}	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	5.56	6.29	3.86	5.32	5.50^{a}
	Male	5.26	6.03	5.30	5.41	5.39^{a}

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	2.15	3.63	4.90	6.73	8.88
	Male	2.37	3.48	4.64	8.12	8.90

Block	ns
CV	ns
SX	ns
CH	***
CV*SX	ns
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

ns, *, ***: non significant or significant at $P = 0.05$ or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at $LSD_{0.05}$.

Table 3.22 Expt 4: Average base diameter (mm) of quality 1 spears of four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C) during the last harvest month.

A	Cutting Height **(CH)**	Cultivar **(CV)**				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	9.99	10.31	10.51	10.92	10.43^{a}
	15 cm	10.58	10.22	10.12	10.55	10.36^{a}
	20 cm	9.91	10.59	12.23	10.11	10.71^{a}
	25 cm	10.14	10.11	10.86	10.73	10.46^{a}
	30 cm	10.61	10.32	11.99	10.99	10.98^{a}
	CV mean	10.25^{b}	10.31^{b}	11.14^{a}	10.66^{b}	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	10.47	10.52	11.23	10.56	10.63^{a}
	Male	10.02	10.10	11.05	10.76	10.48^{a}

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	10.54	10.37	10.91	10.46	11.19
	Male	10.33	10.35	10.52	10.46	10.76

Block	ns
CV	*
SX	ns
CH	ns
CV*SX	ns
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

ns, *, ***: non significant or significant at $P = 0.05$ or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at LSD$_{0.05}$.

Table 3.23 Expt 4: Average base diameter (mm) of quality 2 spears of four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C) during the last harvest month.

A	Cutting Height **(CH)**	Cultivar **(CV)**				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	6.90	6.96	6.73	7.15	6.93^b
	15 cm	6.93	7.31	7.19	7.20	7.16^b
	20 cm	6.74	7.55	7.28	7.27	7.21^b
	25 cm	7.14	7.46	6.28	7.34	7.23^b
	30 cm	7.21	7.60	7.66	7.41	7.47a
	CV mean	6.99^b	7.38^a	7.17^{ab}	7.27^{ab}	

B	Plant sex **(SX)**	Cultivar (CV)				**SX mean**
		UC157	Apollo	Grande	Atlas	
	Female	7.17	7.61	6.99	7.15	7.20^a
	Male	6.80	7.15	7.34	7.39	7.17^a

C	Plant sex (SX)	Cutting Height (CH)				
		10 cm	15 cm	20 cm	25 cm	30 cm
	Female	6.93	7.05	7.11	7.26	7.81
	Male	6.94	7.27	7.32	7.21	7.13

Block	ns
CV	*
SX	ns
CH	*
CV*SX	**
CV*CH	ns
SX*CH	*
CV*SX*CH	ns

ns, *, ***: non significant or significant at $P = 0.05$ or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at LSD$_{0.05}$.

Table 3.24 Expt 4: Average base diameter (mm) of quality 3 spears of four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C) during the last harvest month.

A	Cutting Height **(CH)**	Cultivar **(CV)**				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	3.04	3.27	3.42	3.55	3.32^a
	15 cm	2.71	3.17	4.07	3.89	3.46^a
	20 cm	3.37	3.37	3.26	3.64	3.41^a
	25 cm	3.49	4.09	3.72	3.95	3.81^a
	30 cm	3.74	4.03	3.05	3.83	3.66^a
	CV mean	3.27^a	3.59^a	3.50^a	3.77^a	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	3.11	3.96	3.10	3.85	3.56^a
	Male	3.43	3.22	3.90	3.69	3.56^a

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	3.52	3.25	3.15	4.06	3.55
	Male	3.12	3.67	3.67	3.57	3.78

Block	ns
CV	ns
SX	ns
CH	ns
CV*SX	*
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

ns, *, ***: non significant or significant at $P = 0.05$ or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at $LSD_{0.05}$.

3.3.3. Comparison of total fresh weight among three different spear qualities

Relatively low proportions fell into category of non-marketable spears for all cultivars (Fig. 3.16). In terms of non marketable spears, 'UC157' generally produced the highest percentage (12.5%) of total fresh weight compared to the three other cultivars (6.8 to 8%). More quality 1 and 2 spears produced indicated that more spears had increased diameter, leading to heavier yield.

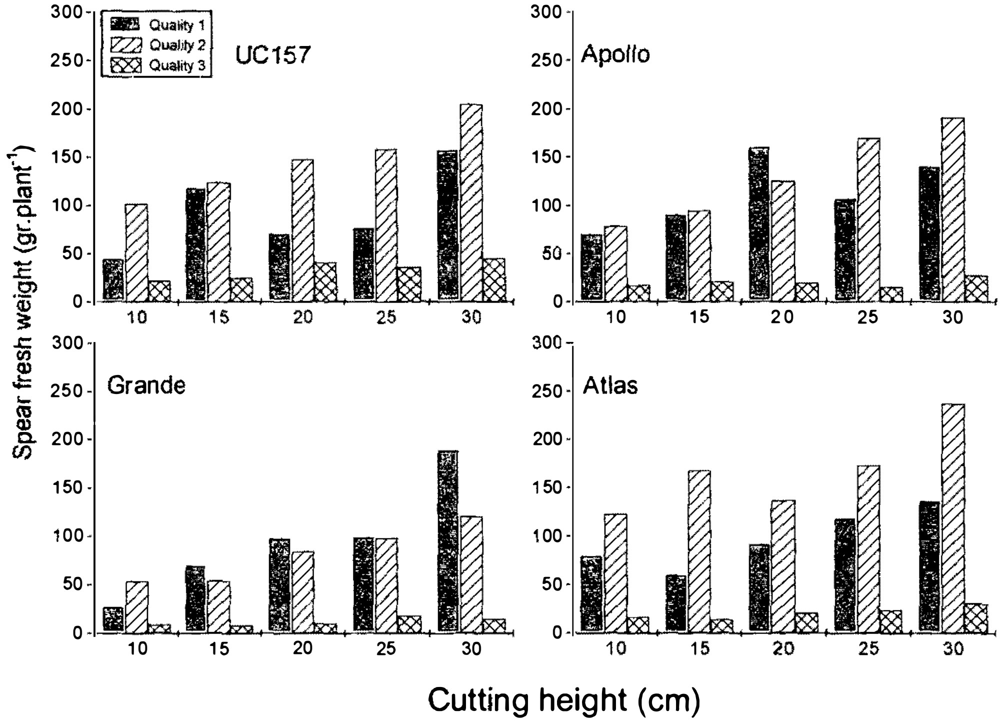


Figure 3.16Expt 4: Spear quality of four asparagus cultivars harvested at different cutting heights.

Among the four cultivars, fresh weight of quality 2 spears increased when CH increased except in 'Atlas' in which spear quality 2 at CH 15 cm was higher than that at 20 cm.

3.3.4. Relationship between marketable and total yield in determining optimum harvest yield in Expt 3 and Expt 4.

3.3.4.1. Total and marketable yield in Expt 3

An increase of total fresh weight of quality 1 spears will contribute to saleable yield. In Expt 3, average first marketable yield (quality 1 spear yield) across four CV was only 18 % of total fresh yield (Table 3.25).

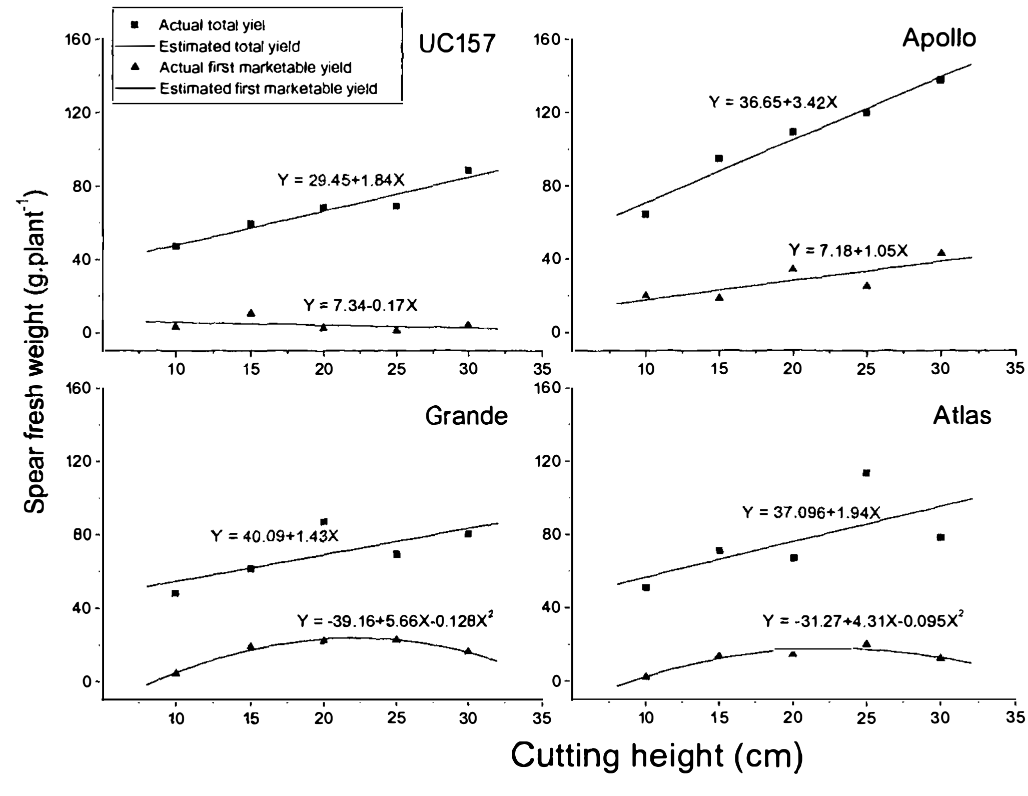


Figure 3.17 Expt 3: The effect of cutting height (CH) on total yield and first class marketable yield (quality 1 spears) of four asparagus cultivars grown in a greenhouse.

As CH increased, the total fresh yield also increased linearly in each cultivar (Fig 3.17) with the highest increase rate in ‘Apollo’. The trend of increases in first marketable yield, however, was different from total fresh yield when CH increased. For 'Grande' and 'Atlas', first marketable yield increased as CH increased from 10 cm to 20 cm, and declined thereafter. The two CV achieved optimum first marketable yield at approximately CH 20 cm. The first marketable yield in 'UC157'reduced linearly as CH increased. On the other hand, 'Apollo' yielded an increase of marketable yield as CH increased.

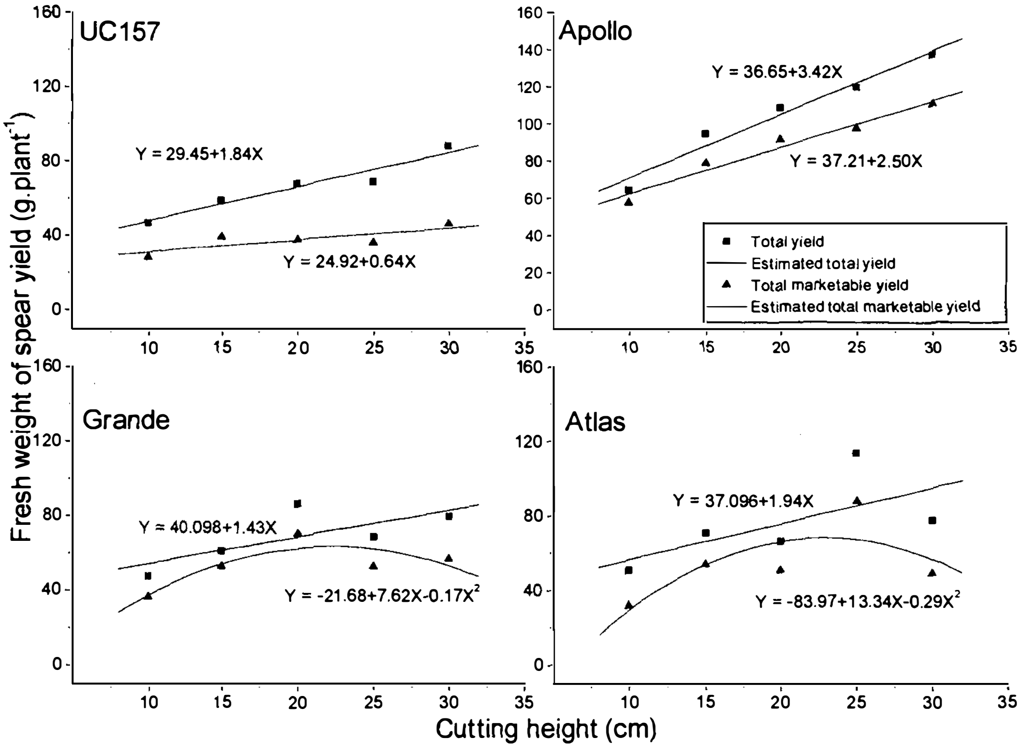


Figure 3.18 Expt 3: The relationship between cutting height and total yield and total marketable yield of four asparagus cultivars.

There was also variation in total yield and marketable yield (quality 1 and quality 2 spears) amongst cultivars. Similar to the patterns of first marketable yield, total marketable yield also showed quadratic responses in 'Grande' and 'Atlas' but linear responses in 'UC157' and 'Apollo' (Fig 3.18).

Different definitions used to categorize spear quality caused different patterns of first marketable yield as CH increased (Table 3.25). Quality 1 spears reduced in all CV as CH increased when only spear head tightness was considered. Using head-tightness only, most spears were categorized into quality 1 spears. However, these patterns of reduction were not clear when spears were categorized based on spear diameter only. Average of quality 1 spears across CH was as low as 6.7% in ‘UC157’ and 15 to 27% for the other three CV. These proportions of first marketable (spear quality 1) yield to total fresh yield were similar to the spear quality division when spear head tightness and diameter were used.

Table 3.25 Expt3: Percentages of spear quality division based on three different definitions: head tightness, spear diameter, and combination of both head tightness and spear diameter on four asparagus cultivars grown in a greenhouse.

Cultivar	Cutting height (cm)	Head tightness†			Diameter			Head tightness & diameter		
		Q1	Q2	Q3	Q1	Q2	Q3	Q1	Q2	Q3
UC157	10	97.5	0.1	2.4	6.4	55.5	38.2	6.4	54.4	39.3
	15	95.7	0.9	3.4	17.8	49.7	32.6	17.8	49.3	32.9
	20	90.9	4.1	5.0	3.2	53.1	43.7	3.2	52.5	44.3
	25	75.1	8.9	16.0	1.0	55.9	43.1	1.0	51.5	47.6
	30	61.5	15.2	23.3	5.2	56.8	38.0	4.3	48.2	47.5
	Average	84.1	5.8	10.0	6.7	54.2	39.1	6.5	51.2	42.3
Apollo	10	98.1	0.9	1.0	31.0	59.2	9.8	31.0	58.4	10.6
	15	95.5	1.6	2.9	19.5	65.3	15.1	19.5	63.7	16.7
	20	94.2	3.5	2.4	33.4	52.2	14.4	31.3	52.8	16.0
	25	82.4	11.2	6.4	21.6	63.6	14.8	21.1	60.4	18.5
	30	82.1	10.1	7.8	32.5	52.2	15.3	31.1	49.5	19.3
	Average	90.4	5.4	4.1	27.6	58.5	13.9	26.8	57.0	16.2
Grande	10	98.0	0.6	1.3	8.3	69.0	22.7	8.3	68.7	23.0
	15	95.2	1.8	2.9	31.2	57.8	11.0	30.8	55.9	13.3
	20	93.5	3.0	3.5	27.2	57.0	15.8	25.1	56.5	18.4
	25	85.5	8.5	5.9	35.4	44.4	20.2	32.3	44.4	23.3
	30	67.2	14.2	18.6	20.4	61.4	18.2	19.9	51.3	28.8
	Average	87.9	5.6	6.4	24.5	57.9	17.6	23.3	55.4	21.4
Atlas	10	98.2	0.3	1.5	4.4	58.9	36.7	4.4	58.4	37.2
	15	97.2	1.9	0.9	18.7	57.6	23.6	18.7	57.3	24.0
	20	91.0	1.4	7.6	21.9	60.1	18.0	21.2	55.3	23.4
	25	82.7	9.5	7.7	17.5	64.5	18.1	17.5	59.9	22.6
	30	63.8	17.5	18.7	16.4	60.9	22.7	15.3	48.2	36.5
	Average	86.6	6.1	7.3	15.8	60.4	23.8	15.4	55.8	28.8

†Closed, medium and open head tightness refers to Q1, Q2, and Q3 for head tightness. The ranges of spear diameter for quality division are spear diameter ≥ 9mm for Q1, 5 < 9 mm for Q2, and ≤ 5 mm for Q3. Combination between spear tightness and spear diameter to categorize spear refers to the text in materials and methods in chapter 3.

3.3.4.2. Total and marketable yield in Expt 4.

In Expt 4, both total yield and first marketable yield for all CV increased linearly as CH increased (Fig 3.19)

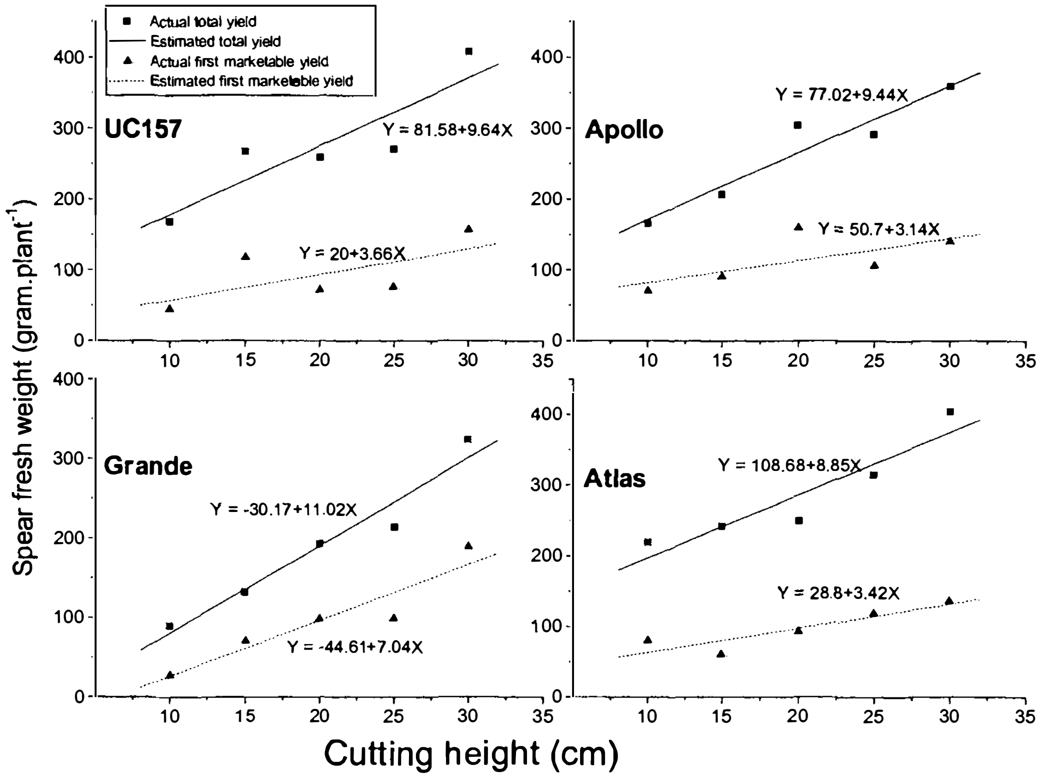


Figure 3.19 Expt 4: The relationship between cutting height and total yield and first class marketable yield of four asparagus cultivars

Average first marketable yield across CH was approximately from 32.9% ('UC157') to 47.6% ('Grande') of total fresh yield (Table 3.26). The proportions of first marketable yield were improved when the spear quality division was only based on head tightness. More than 95% of the spears were categorized into first marketable yield in all CV at CH 10 cm. As CH increased, proportions of first marketable yield reduced from an average of more than 96.5% at CH 10 cm to 70% at CH 30 cm (Table 3.26).

When first and second grade spears were compared with total yield, the patterns were similar and regression lines were very similar especially in 'Grande', 'Apollo' and 'Atlas' (Fig 3.20). These three cultivars had only about 6 to 8% of non marketable yield.

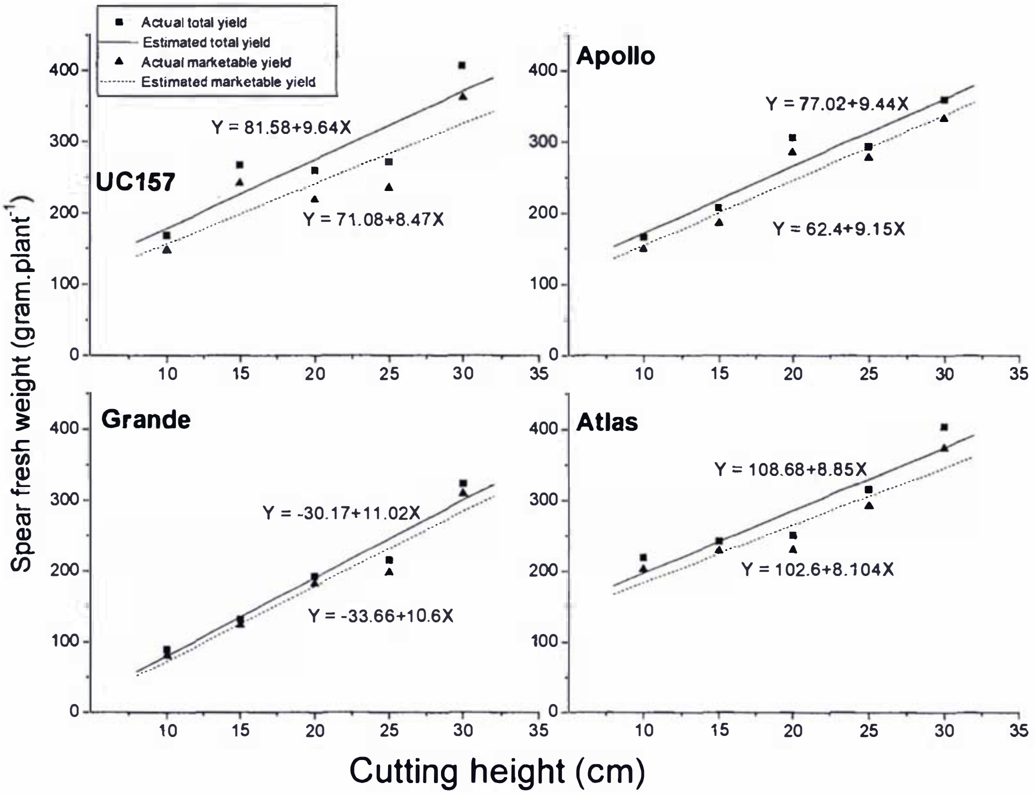


Figure 3.20Expt 4: The relationship between cutting height and total yield and total marketable yield of four asparagus cultivars.

Table 3.26 Expt 4: Percentages of spear quality division based on three different definitions: head tightness, spear diameter, and combination of both head tightness and spear diameter on four asparagus cultivars grown in a greenhouse.

Cultivar	Cutting height	Head tightness			Diameter			Head tightness & diameter		
		Q1	Q2	Q3	Q1	Q2	Q3	Q1	Q2	Q3
UC157	10	97.7	0.9	1.4	26.8	60.9	12.3	26.5	60.5	13.0
	15	95.3	2.7	2.0	44.7	46.6	8.7	44.2	46.4	9.3
	20	90.7	6.2	3.1	27.3	58.0	14.7	27.2	57.0	15.8
	25	79.8	15.2	5.0	30.8	59.1	10.1	28.2	58.4	13.4
	30	76.7	18.9	4.5	40.0	50.8	9.3	38.6	50.3	11.1
	Average	88.0	8.8	3.2	33.9	55.1	11.0	32.9	54.5	12.5
Apollo	10	95.0	3.0	1.9	43.4	47.1	9.5	42.2	47.3	10.5
	15	92.6	4.4	2.9	46.4	45.0	8.6	43.8	46.0	10.3
	20	89.6	8.9	1.4	54.7	39.6	5.7	52.5	41.0	6.5
	25	75.7	22.2	2.1	44.9	51.1	3.9	36.6	58.1	5.2
	30	69.5	26.2	4.3	45.7	50.0	4.3	39.1	53.3	7.7
	Average	84.5	13.0	2.5	47.0	46.6	6.4	42.8	49.1	8.0
Grande	10	97.7	1.2	1.1	30.1	60.4	9.6	30.0	60.1	9.9
	15	94.1	4.2	1.7	55.6	39.6	4.8	53.0	40.9	6.1
	20	91.8	6.8	1.3	52.5	42.8	4.7	50.7	43.9	5.4
	25	79.5	16.5	3.9	51.3	43.6	5.1	45.9	45.8	8.3
	30	74.0	24.3	1.7	74.7	22.0	3.3	58.3	37.2	4.5
	Average	87.4	10.6	1.9	52.8	41.7	5.5	47.6	45.6	6.8
Atlas	10	95.6	3.4	1.0	38.0	55.3	6.7	36.4	56.1	7.5
	15	92.9	5.5	1.6	26.3	69.2	4.5	24.8	69.4	5.8
	20	91.2	6.8	2.1	39.2	54.1	6.7	36.8	54.8	8.4
	25	74.4	22.0	3.6	44.8	50.2	5.0	37.6	54.9	7.5
	30	64.4	31.3	4.3	47.0	47.7	5.3	33.7	58.8	7.5
	Average	83.7	13.8	2.5	39.1	55.3	5.6	33.8	58.8	7.3

*Closed, medium and open head tightness refers to Q1, Q2, and Q3 for head tightness. The ranges of spear diameter for quality division are spear diameter with ≥ 9mm for Q1, 5 < 9 mm for Q2, and ≤ 5 mm for Q3. Combination between spear tightness and spear diameter to categorize spear refers to the text in materials and methods in chapter 3.

3.3.4.3. Initial buds and bud development during harvest season in the green house from Experiment 4

Initial bud number (before harvest) showed differences amongst cultivars (CV), cutting height (CH) and plant sex (SEX) (Table 3.27). For purposes of blocking, plants were sorted with ascending order of bud number. Unintentionally, plants were allocated to CH sequentially and not at random. This effect was removed by using initial bud number as a covariate for relevant analysis. The interaction between cultivar and plant sex on initial bud number was significant. High bud number can indicate high potential yield since more buds can be harvested. While female and male plants of 'UC157' produced similar bud numbers, male plants of other cultivars produced higher bud numbers than female plants. Over-all there were 27% more buds in male plants than female plants. 'UC157' had the highest initial bud number followed by 'Atlas', 'Apollo', and 'Grande'.

Table 3.27 Expt 4: Initial bud number (buds.plant^{-1}) before harvest from four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and female and male plants at different cutting heights (C).

A	Cutting Height **(CH)**	Cultivar **(CV)**				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	42.1	27.6	17.8	35.7	30.8^{c}
	15 cm	44.3	30.3	19.8	35.1	32.4^{bc}
	20 cm	48.6	29.8	21.8	40.2	35.1^{ab}
	25 cm	49.3	31.0	23.6	40.5	36.1^{ab}
	30 cm	54.7	32.1	26.5	41.8	38.8^{a}
	CV mean	47.8^{a}	30.2^{c}	21.9^{d}	38.7^{b}	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	46.1	24.4	15.4	36.0	30.5^{b}
	Male	49.4	35.9	28.4	41.3	38.8^{a}

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	27.2	28.9	31.9	31.4	33.0
	Male	34.4	35.8	38.3	40.8	44.5

Block	***
CV	***
SX	***
CH	***
CV*SX	*
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

Within the column and row, means followed by the same letter are not significantly different at LSD$_{0.05}$. ns, *, ***: non significant or significant at $P = 0.05$ or 0.001, respectively.

After harvest, the bud number was counted again on each plant for all treatment combinations. The buds formed during the harvest season were computed using these bud numbers (before and after harvest) and the spears harvested during the season. Surprisingly it was found that large numbers of buds appeared to develop during the harvest period (Fig. 3.21). The results were analyzed using PROC GLM with covariance for initial bud number.

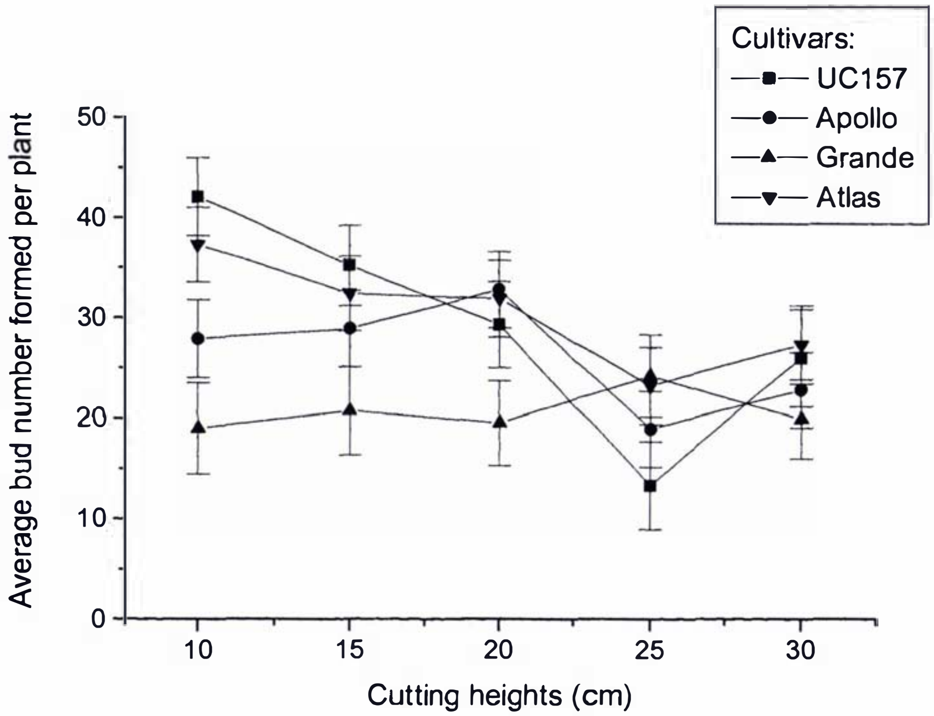


Figure 3.21 Expt 4: Buds formed during harvest season at five cutting heights amongst four asparagus cultivars grown in a green house. Bars indicate standard error of each mean.

The actual number of buds developed during the harvest period revealed interaction effects between CV and CH (*P*=0.0192). All cultivars except 'Grande' produced more buds at lower CH (Fig. 3.21). Clear differences among cultivars occurred at the lowest CH (10 cm). 'Grande' followed by 'Apollo' produced the lowest number of buds at CH 10 cm and they were significantly different from other cultivars. All cultivars except

'Grande' produced fewer buds as CH increased, but 'Grande' produced approximately the same number of buds at all CH. The highest bud number produced was at 10 cm (31.6 buds) and 15 cm (29.3 buds) and these bud numbers were different from those in highest CH (23.9 buds). CV (P=0.0412) or CH (P=0.0007) also affected the numbers of bud formed during harvest season.

3.3.4.4. *The trends of fresh yield and bud numbers over 13 weeks of harvest*

Results from GLM analysis with five different spear categories suggested that only CV, CH and SEX (plant sex) affected spear fresh weight and spear number (data not shown). With these results, groups of plants based on each CV, CH or SEX with three replications were plotted to obtain estimation of the peak time (t_{max}), that is the time when the plants achieved maximum weekly production of total fresh weight or spear number amongst five different spear categories over 13 weeks of harvest.

3.3.4.4.1. Total fresh weight

Estimates of peak time (t_{max}) when maximum weekly spear fresh weight and spear number occurred using Gaussian fitting indicated that large variation and inconsistency of t_{max} occurred within all spear sizes smaller than 7 mm in diameter (data not shown). Nevertheless, estimates of t_{max} for large (≥ 9 mm) and medium-large (7 < 9 mm) were consistent and had low variation. Therefore testing t_{max} amongst CV, CH or SEX was run only for two categories, large and medium-large spears. However it was clear that smaller diameter spears had a much later t_{max} (Fig. 3.22).

T_{max} was significantly different between large and medium-large spears as well as amongst CV (P=0.0166), CH (P=0.0251) and SX (P=0.0241) (Table 3.28). Significant differences due to CV*grade or SEX*grade interactions were also found on t_{max} for spear fresh weight at P=0.0130 and P=0.0392, respectively.

Table 3.28 Expt 4: Time estimates (weeks) of maximum production for large and medium large spear size among four asparagus cultivars, amongst five cutting heights, or between two plant sexes.

Variables	Spear fresh weight				Spear number			
	Large $d \geq 9$ mm		Medium large $7 \leq d < 9$ mm		Large $d \geq 9$ mm		Medium large $7 \leq d < 9$ mm	
Cultivars	Time	stderror	Time	stderror	Time	s.e	Time	s.e
UC157	7.81 ±	0.5494	8.14 ±	0.5494	7.79 ±	0.7388	8.72 ±	0.7388
Apollo	7.80 ±	0.5494	10.71±	0.5494	7.92 ±	0.7388	10.76±	0.7388
Grande	7.76 ±	0.5494	12.73±	0.6894	7.73 ±	0.7388	12.43±	0.7388
Atlas	8.24 ±	0.5494	10.00±	0.6894	8.24 ±	0.7388	10.06±	0.9262
Significance								
Grade	***				*			
CV	*				ns			
CV*Grade	*				ns			
Cutting Height (CH)								
10 cm	7.09 ±	0.4797	9.04 ±	0.6013	7.29 ±	0.6563	9.38 ±	0.8228
15 cm	7.26 ±	0.4797	9.63 ±	0.4797	7.41 ±	0.6563	9.66 ±	0.6564
20 cm	7.89 ±	0.4977	8.93 ±	0.6013	8.14 ±	0.6564	9.42 ±	0.8228
25 cm	8.02 ±	0.4797	9.74 ±	0.6013	8.14 ±	0.6564	10.99±	0.6564
30 cm	8.46 ±	0.4797	11.23 ±	0.4797	8.79 ±	0.6564	11.37±	0.8228
Significance								
Grade	***				*			
CH	*				ns			
CH*Grade	ns				ns			
Plant sex								
Female	8.04 ±	0.3083	11.21 ±	0.4079	8.07 ±	0.8505	11.80±	1.098
Male	7.86 ±	0.3083	8.95 ±	0.4079	7.88 ±	0.8505	10.63±	0.8505
Significance								
Grade	**				*			
Sex	*				ns			
Sex*Grade	*				ns			

ns, *, **,*** : not significant, significant at $p = 0.05$, 0.01 or 0.001, respectively. s.e. = standard error

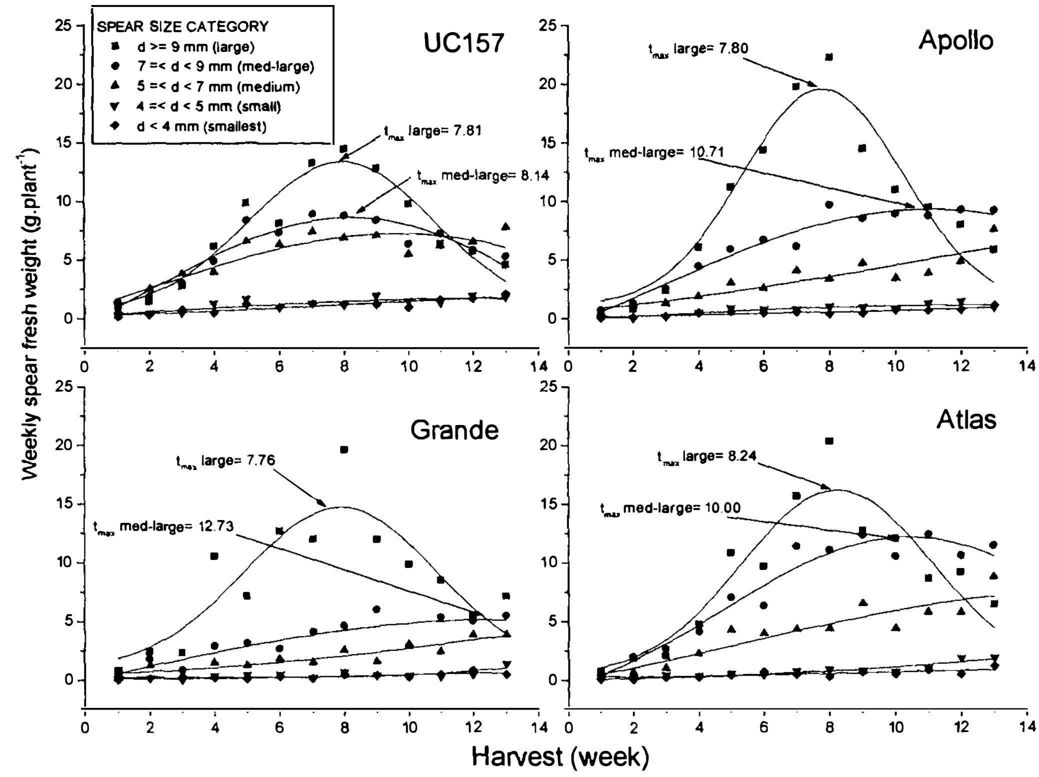


Figure 3.22 Expt 4: The time trends of spear production for fresh weight based on spear diameter category in four asparagus cultivars over 13 weeks harvest. t_{max} = estimated time (weeks) when maximum production occurred.

Estimates of t_{max} for spear fresh weight amongst cultivars were similar (7.76 to 8.24 weeks) for large spears (Fig. 3.22). For medium-large spears, ‘UC157’ produced earlier and reached t_{max} at week 8.14 compared to ‘Apollo’ and ‘Atlas’ peaked at weeks 10.71 and 10, respectively. This is an indication that ‘UC157’ may run out of large spears earlier. ‘Grande’ produced medium-large spears later and reached peak time the latest, at week 12.73. This t_{max} of ‘Grande’ was significantly different from t_{max} of ‘UC157’ but not from the other two cultivars (data not shown).

Although it was not significantly different, ‘Apollo’ had the largest total production of large spears (Table 3.30) amongst the four cultivars while ‘Atlas’ had the largest production of medium-large spears (Table 3.31). Proportionally within cultivar, most of spears of ‘Grande’ were large (58.10%) and medium-large (23.92%), and the rest of spears were less than 7 mm in diameter (Table 3.29). ‘Apollo’ (78.31%) and ‘Atlas’ (76.14%) had similar total proportions of large and medium-large spears whereas ‘UC157’ had similar distribution between medium-large spears (28.29%) and medium spears (25.90%) (Table 3.29) resulting in a significantly higher total medium spear fresh weight than the other three cultivars (Table 3.32). ‘UC157’ had also highest total small spears (Table 3.32) and smallest spears (Table 3.34) compared to three other cultivars.

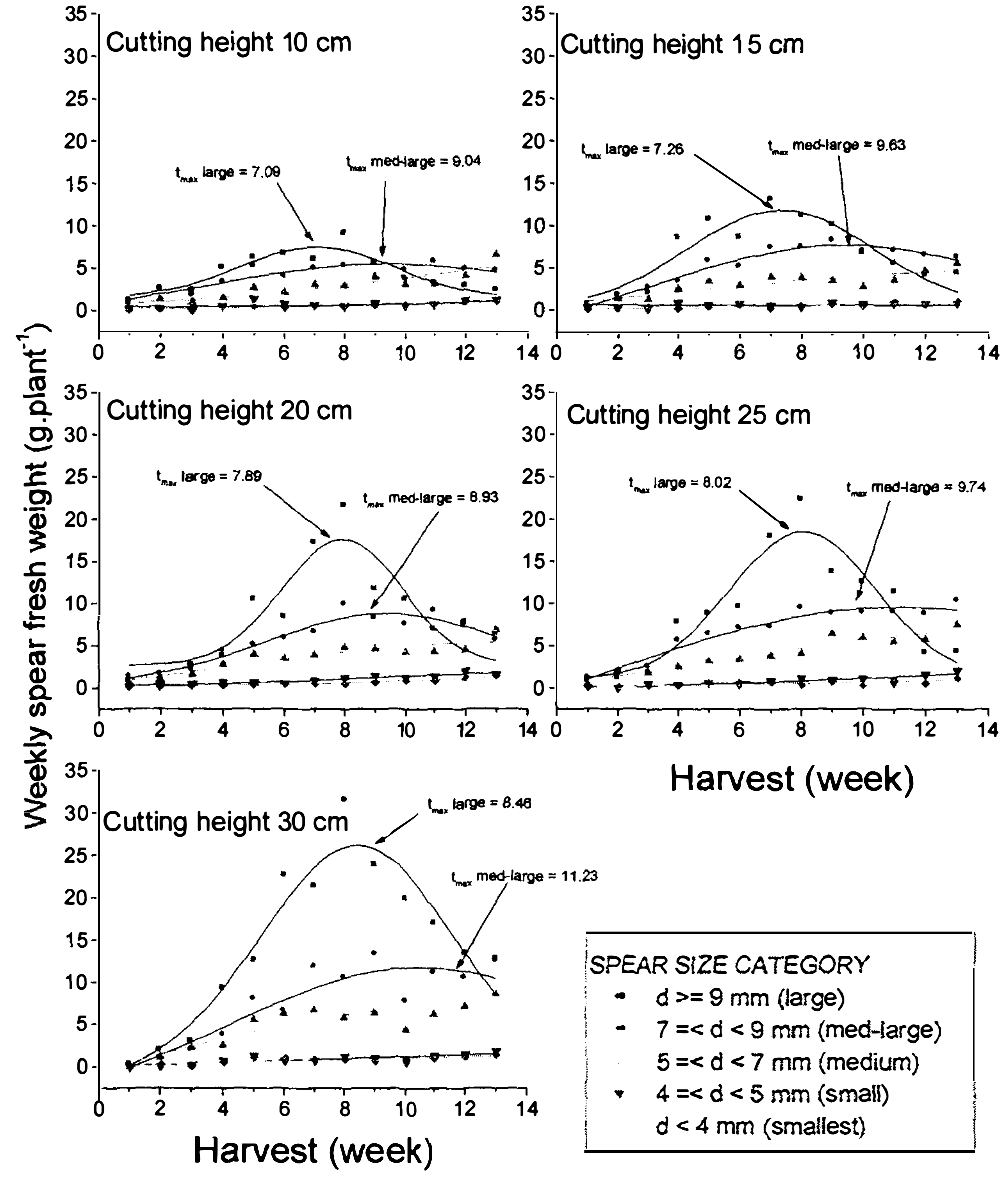


Figure 3.23Expt 4: The time trends of spear distribution for fresh weight based on spear diameter category at five different cutting heights over 13 weeks harvest. t_{max}: estimated time when maximum production occurred.

Amongst CH, it is clear that the proportion of fresh weight due to large spears was highest (50.75%) in the highest CH (Fig. 3.31) but the t_{max} for large spears was not different from the other lower CH (Table 3.28). Nevertheless there were trends of increasing t_{max} as CH increased for both large and medium-large spears (Fig 3.24) and CH increased significantly t_{max} across large and medium spears together (Table 3.28). There were significant main effects but CH trends were similar. The t_{max} of medium large spears was always later than that of large spears (Fig. 3.24).

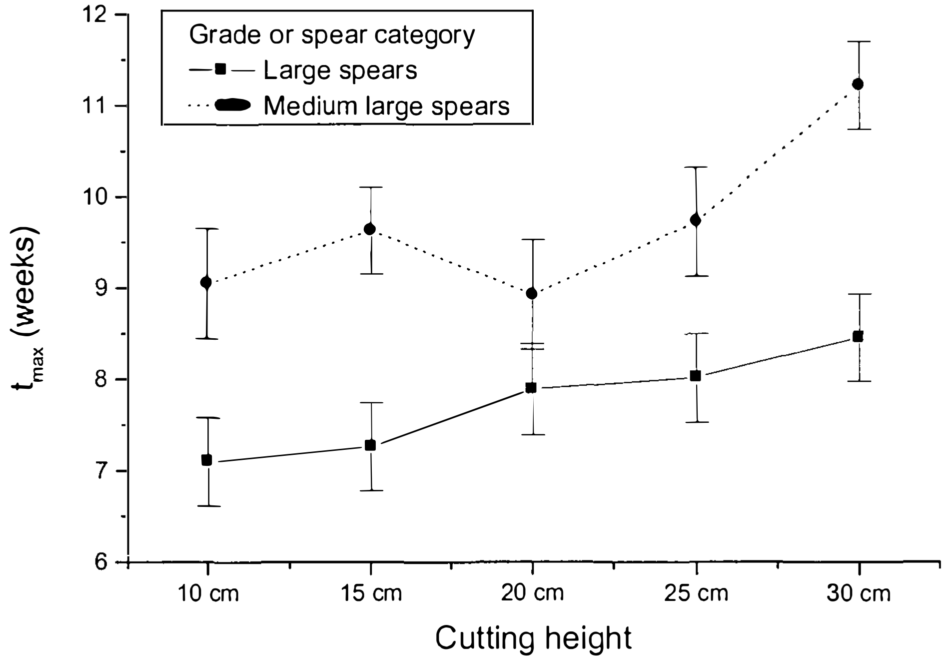


Figure 3.24 Expt 4: The trends of t_{max} between large and medium large spears at five different cutting heights across four asparagus cultivars grown in a greenhouse. t_{max}: estimated time when maximum production occurred. Bars indicate standard errors.

Female plants tended to have a larger proportion of large spears (50.76%) than male plants (37.49%) but the male plants produced significantly more medium-large spears (33.13%) than the female plants (27.00). These proportions were reflected in total fresh weight in large (Table 3.30) and medium large spears (Table 3.31). The t_{max} of medium-large spear production by male plants was 2.26 weeks earlier than female plants (Fig. 3.25), a significant difference at $P = 0.0441$ (Table 3.28).

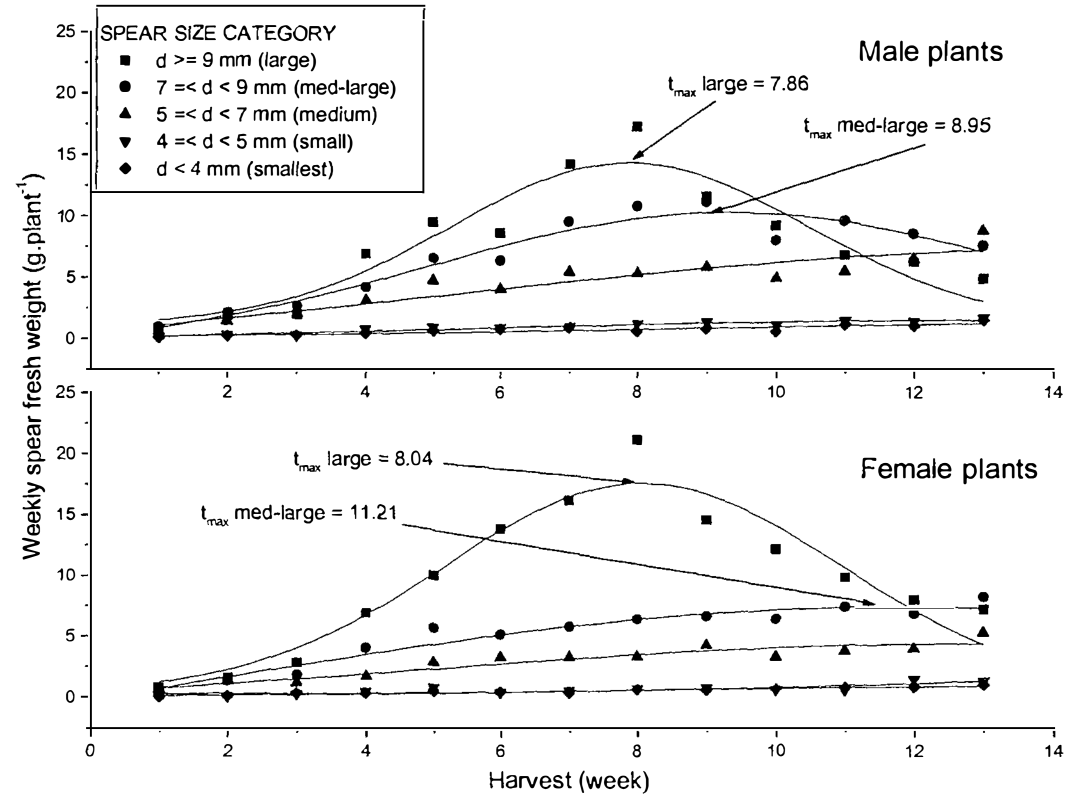


Figure 3.25Expt 4: The time trends of spear distribution for fresh weight based on spear diameter category in male and female plants over 13 weeks harvest. t_{max}: estimated time when maximum production occurred.

Cultivar Grande had the highest proportion (58.10%) for large spears followed by 'Apollo' (47.40%) and 'Atlas' (40.27) and 'UC157' (Fig. 3.22 and Table 3.29). But further GLM analysis for each spear category based on spear diameter showed that only CH and the interaction of CV and SEX significantly affected spear fresh weight within the large spear category (Table 3.30). Unlike male plants in 'UC157' and 'Apollo', the male plants in 'Grande' produced more total fresh weight than female plants whilst male and female plants in 'Atlas' produced similar total fresh weights. The difference in magnitude resulted in significant interaction of CV and SEX on total fresh weight of large spear size (Fig. 3.26).

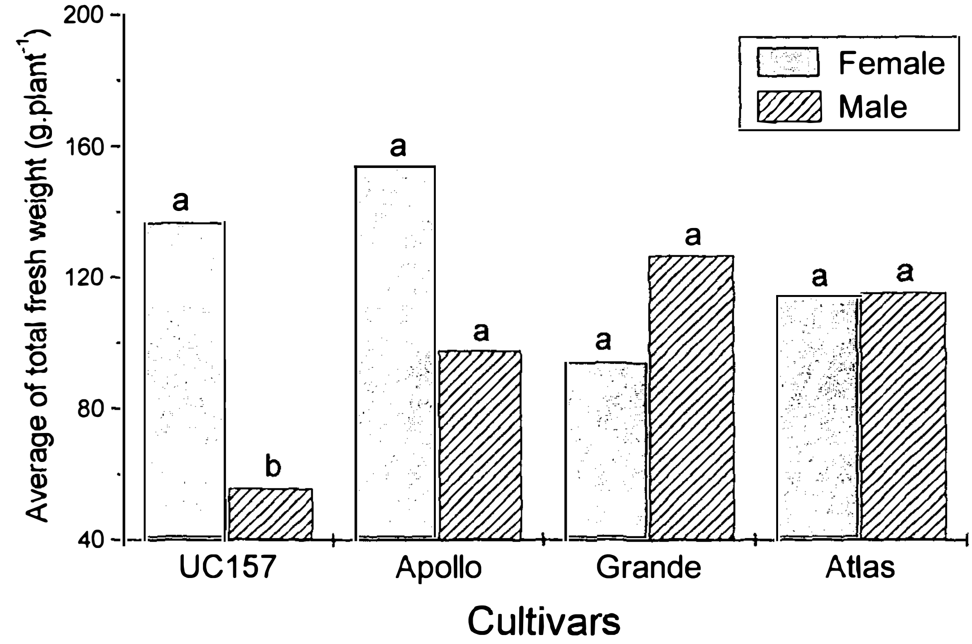


Figure 3.26 Expt 4: The magnitude of average of total fresh weight over 13 weeks in large spears amongst four asparagus cultivars from male and female plants. Different letters within a cultivar was significant at $LSD_{0.05}$

Within medium-large spears, total fresh weight was only influenced by the main effects (Table 3.31). 'Atlas' produced the highest spear fresh weight within medium-large spears, 20% higher than'UC157' and 'Apollo' and more than double 'Grande'. The highest CH always produced the highest yield of large spears. This also occurred in the medium spear category (5 < 7 mm) (Table 3.32). For small spears (4 <7 mm), only CV and SEX significantly affected the total fresh weight (Table 3.33). Male plants produced higher total fresh weight within small spears. 'UC157' produced the highest total fresh weight in small (4 < 5 mm) and smallest spear size (< 4 mm) (Table 3.34).

Table 3.29 Expt 4: Total fresh weight and proportions of fresh weight for each spear category within female and male plants from four asparagus cultivars grown in a greenhouse.

Spear category	UC157			Apollo			Grande			Atlas			Grand Total
	Female	Male	Total	Female	Male	Total	Female	Male	Total	Female	Male	Total	
Large	2053.8	834.115	2887.915	2313.33	1465.965	3779.295	1412.53	1903.46	3315.99	1719.635	1732.55	3452.185	13435.385
	(45.55)	(22.47)	(35.08)	(57.86)	(36.88)	(47.40)	(68.77)	(52.09)	(58.10)	(42.14)	(38.57)	(40.27)	(44.07)
Medium large	1218.575	1110.1	2328.675	1073.38	1391.095	2464.475	351.84	1013.385	1365.225	1344.624	1730.365	3074.989	9233.364
	(26.96)	(29.90)	(28.29)	(26.85)	(34.99)	(30.91)	(17.13)	(27.73)	(23.92)	(32.95)	(38.52)	(35.87)	(30.29)
Medium	846.63	1285.815	2132.445	419.605	840.74	1260.345	202.65	551.715	754.365	809.13	759.715	1568.845	5716
	(18.73)	(34.64)	(25.90)	(10.50)	(21.15)	(15.81)	(9.87)	(15.10)	(13.22)	(19.85)	(16.91)	(18.30)	(18.75)
Small	214.18	260.395	474.575	103.75	175.995	279.745	38.14	115.67	153.81	134.73	162.56	297.29	1205.42
	(4.74)	(7.01)	(5.77)	(2.60)	(4.43)	(3.51)	(1.86)	(3.17)	(2.69)	(3.30)	(3.62)	(3.47)	(3.95)
Smallest	186.505	221.705	408.21	87.755	101.345	189.1	48.77	69.665	118.435	72.42	106.81	179.23	894.975
	(4.13)	(5.97)	(4.96)	(2.20)	(2.55)	(2.37)	(2.37)	(1.91)	(2.07)	(1.77)	(2.38)	(2.09)	(2.94)
Grand Total	4519.69	3712.13	8231.82	3997.82	3975.14	7972.96	2053.93	3653.895	5707.825	4080.539	4492	8572.539	30485.144
	(100)	(100)	(100)	(100)	(100)	(100)	(100)	(100)	(100)	(100)	(100)	(100)	(100)

Number in brackets are proportions in percentage within a column

Table 3.30 Expt 4: Average of total fresh weight (g.plant^{-1}) of spear size with diameter more than 9 mm (large spears) during harvest period from four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height **(CH)**	Cultivar (CV)				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	45.19	72.07	26.80	83.22	56.82^{c}
	15 cm	119.25	95.79	73.22	63.58	87.96^{bc}
	20 cm	70.69	166.80	101.02	97.96	109.12^{b}
	25 cm	83.499	131.15	110.11	141.03	116.45^{b}
	30 cm	162.68	164.07	241.52	189.58	189.46^{a}
	CV mean	96.26	125.98	110.53	115.07	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	136.92	154.22	94.17	114.64	124.99
	Male	55.61	97.73	126.89	115.50	98.93

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	75.91	93.5	112.75	122.09	220.69
	Male	37.73	82.42	105.49	110.80	158.23

Block	ns
CV	ns
SX	ns
CH	***
CV*SX	*
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

ns, *, ***: non significant or significant at $P = 0.05$ or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at $LSD_{0.05}$.

Table 3.31 Expt 4: Average of total fresh weight (g.plant^{-1}) of spear size with diameter more or equivalent to 7 and less than 9 mm (medium-large spears) during harvest period from four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height **(CH)**	Cultivar (CV)				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	55.75	49.41	25.55	82.48	53.29^{c}
	15 cm	69.70	58.52	37.51	110.90	69.16^{bc}
	20 cm	75.54	78.65	59.70	87.29	75.25^{b}
	25 cm	91.43	103.57	56.14	99.22	87.59^{ab}
	30 cm	95.70	120.60	48.64	132.60	99.39^{a}
	CV mean	77.62^{b}	82.15^{b}	45.51^{c}	102.49^{a}	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	81.24	71.56	23.46	89.64	66.47^{b}
	Male	74.01	92.74	67.56	115.36	87.42^{a}

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	45.51	57.22	68.36	74.38	86.91
	Male	61.09	81.09	82.23	100.79	111.87

Block	***
CV	***
SX	**
CH	***
CV*SX	ns
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

ns, *, ***: non significant or significant at P = 0.05 or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at LSD$_{0.05}$.

Table 3.32 Expt 4: Average of total fresh weight (g.plant^{-1}) of spear size with diameter more or equivalent to 5 and less than 7 mm (medium spears) during harvest period from four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height **(CH)**	Cultivar (CV)				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	46.49	28.87	28.28	38.59	35.56^{c}
	15 cm	54.64	34.46	14.67	56.53	40.07^{bc}
	20 cm	74.88	42.15	22.74	47.77	46.88^{bc}
	25 cm	68.52	45.73	37.36	58.66	52.57^{ab}
	30 cm	110.88	58.86	22.68	59.92	63.08^{a}
	CV mean	71.08^{a}	42.01^{b}	25.15^{c}	52.29^{b}	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	56.44	27.97	13.51	53.94	37.97^{b}
	Male	85.72	56.05	36.78	50.65	57.29^{a}

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	31.20	35.03	39.08	45.75	38.77
	Male	39.91	45.12	54.68	59.38	87.39

Block	***
CV	***
SX	***
CH	**
CV*SX	ns
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

ns, *, ***: non significant or significant at $P = 0.05$ or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at LSD$_{0.05}$.

Table 3.33 Expt 4: Average of total fresh weight (g.plant^{-1}) of spear size with diameter more or equivalent to 4 and less than 5 mm (small spears) during harvest period from four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height **(CH)**	Cultivar (CV)				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	11.96	9.04	4.32	8.12	8.36^{ab}
	15 cm	10.86	11.39	2.65	7.0	7.97^{b}
	20 cm	25.17	8.16	5.07	11.93	12.58^{a}
	25 cm	14.03	7.60	7.25	11.18	10.02^{ab}
	30 cm	17.08	10.43	6.34	11.32	11.29^{ab}
	CV mean	15.82^{a}	9.32^{b}	5.13^{c}	9.91^{b}	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	14.28	6.92	2.54	8.98	8.18^{b}
	Male	17.36	11.73	7.71	10.84	11.91^{a}

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	6.63	7.39	12.00	9.14	5.73
	Male	10.09	8.55	13.16	10.89	16.86

Block	***
CV	***
SX	**
CH	ns
CV*SX	ns
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

ns, *, ***: non significant or significant at $P = 0.05$ or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at LSD$_{0.05}$.

Table 3.34 Expt 4: Average of total fresh weight (g.plant^{-1}) of spear size with diameter less than 4 mm (smallest spears) during harvest period from four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height (CH)	Cultivar (CV)				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	8.71	6.74	4.22	6.47	6.54
	15 cm	12.45	6.38	3.74	3.78	6.59
	20 cm	12.89	6.29	3.89	4.89	7.74
	25 cm	13.28	3.93	3.61	4.53	6.34
	30 cm	20.69	5.18	4.29	10.19	10.09
	CV mean	13.61^a	6.30^b	3.95^b	5.97^b	

B	Plant sex (SX)	Cultivar (CV)				**SX mean**
		UC157	Apollo	Grande	Atlas	
	Female	12.43	5.85	3.25	4.83	6.59
	Male	14.78	6.76	4.64	7.12	8.33

C	Plant sex (SX)	Cutting Height (CH)				
		10 cm	15 cm	20 cm	25 cm	30 cm
	Female	4.81	7.58	8.78	4.03	7.76
	Male	8.26	5.59	6.71	8.65	12.41

Block	**
CV	***
SX	ns
CH	ns
CV*SX	ns
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

ns, *, ***: non significant or significant at P = 0.05 or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at $LSD_{0.05}$.

3.3.4.4.2. Total spear number

T_{max} for total number of large spears was significantly earlier than for medium-large spears (Table 3.28) amongst CV (Fig. 3.27), CH (Fig. 3.28) and SEX (Fig. 3.29). T_{max} for large spears was approximately 2.5 weeks earlier than for medium large spears.

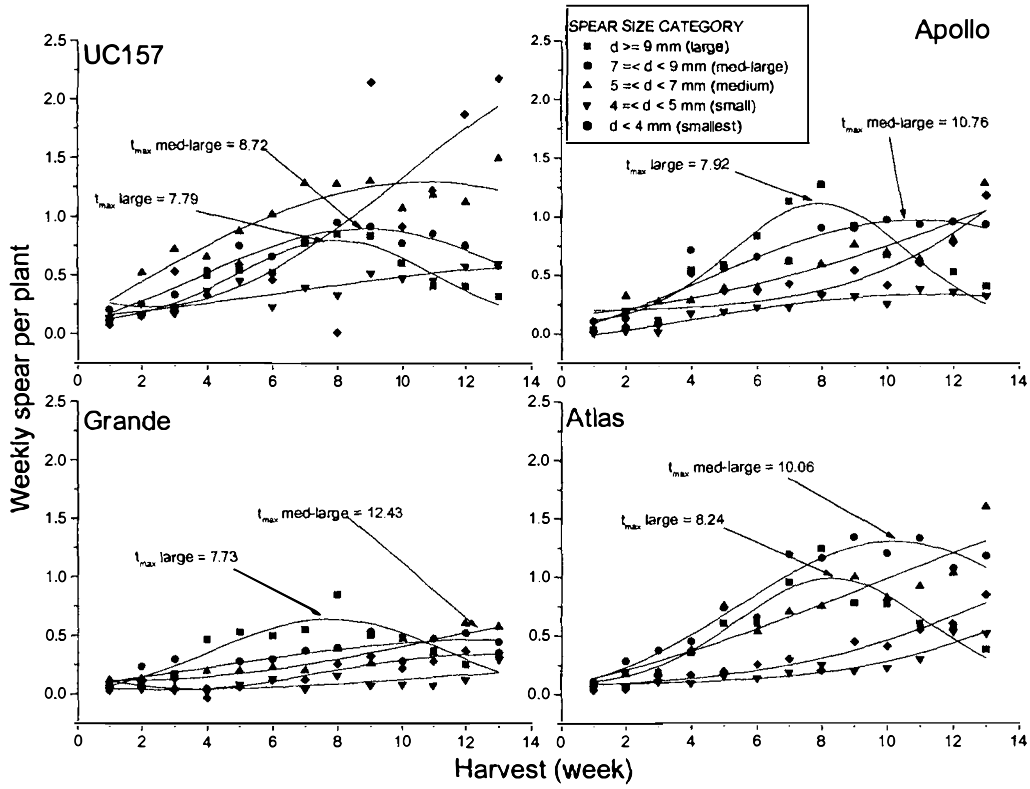


Figure 3.27Expt 4: The time trends of spear number distribution based on spear diameter category in four asparagus cultivars over 13 weeks of harvest. T_{max}: estimated time when maximum production occurred.

The trends of proportions of spear number amongst five spear categories within CV were different (Fig. 3.27). 'UC157' was dominated by medium (5 < 7 mm) to smallest spears (< 4 mm) whilst 'Atlas' was dominated by medium-large and large spears. But the four cultivars showed similar trends in such a way that as large spears (buds) were gradually used up, the number of spears of smaller size increased.

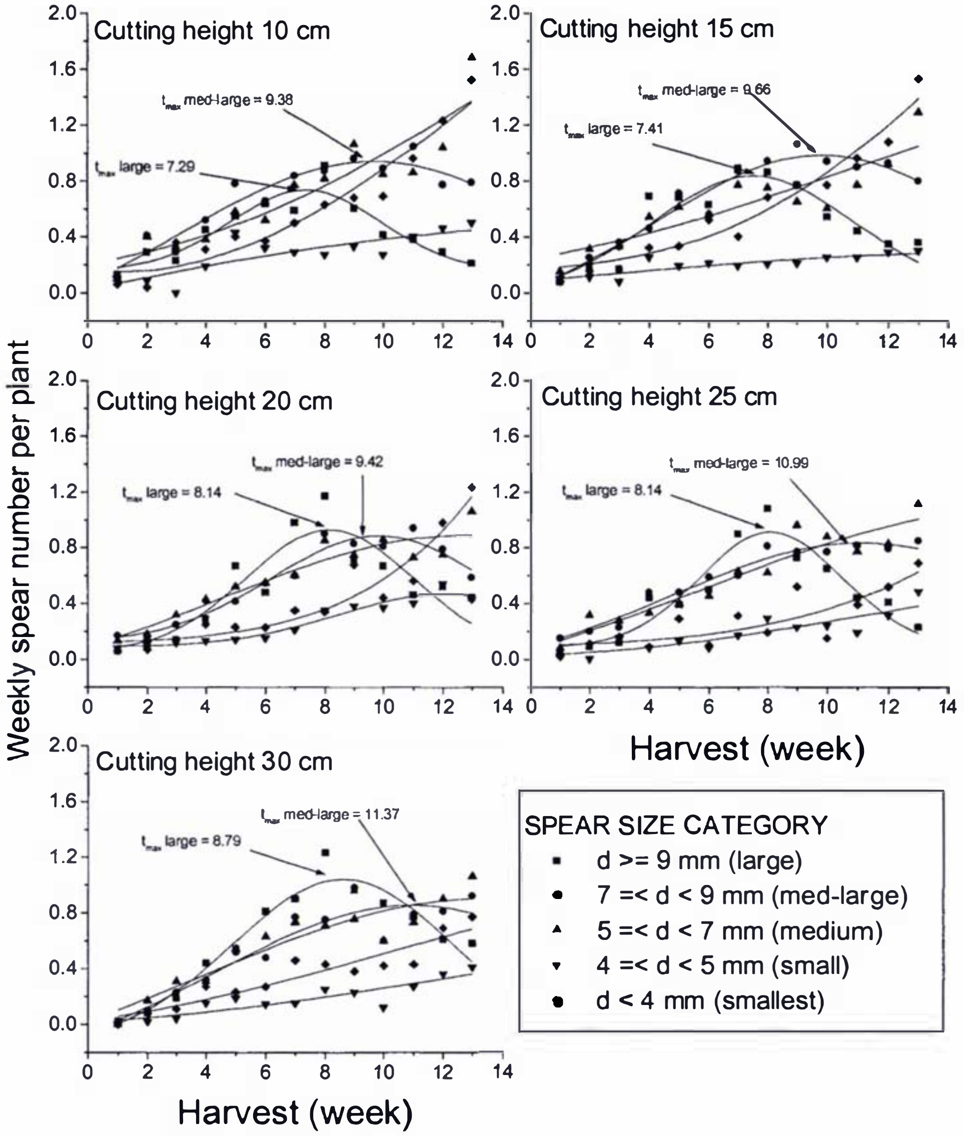


Figure 3.28 Expt 4: The time trends of spear number distribution based on spear diameter amongst five cutting heights of the spears across four asparagus cultivars over 13 weeks of harvest. T_{max}: estimated time when maximum production occurred.

Gaussian fitting indicated that t_{max} for the medium, small and smallest size categories may have been within weeks 12 to 14, 16 to 18 and 22 to 25, respectively (data not shown) with the assumption that a Gaussian curve would fit if harvesting had continued for more than 13 weeks. There were no consistent estimates for t_{max} of spear number at diameter lower than 7 mm.

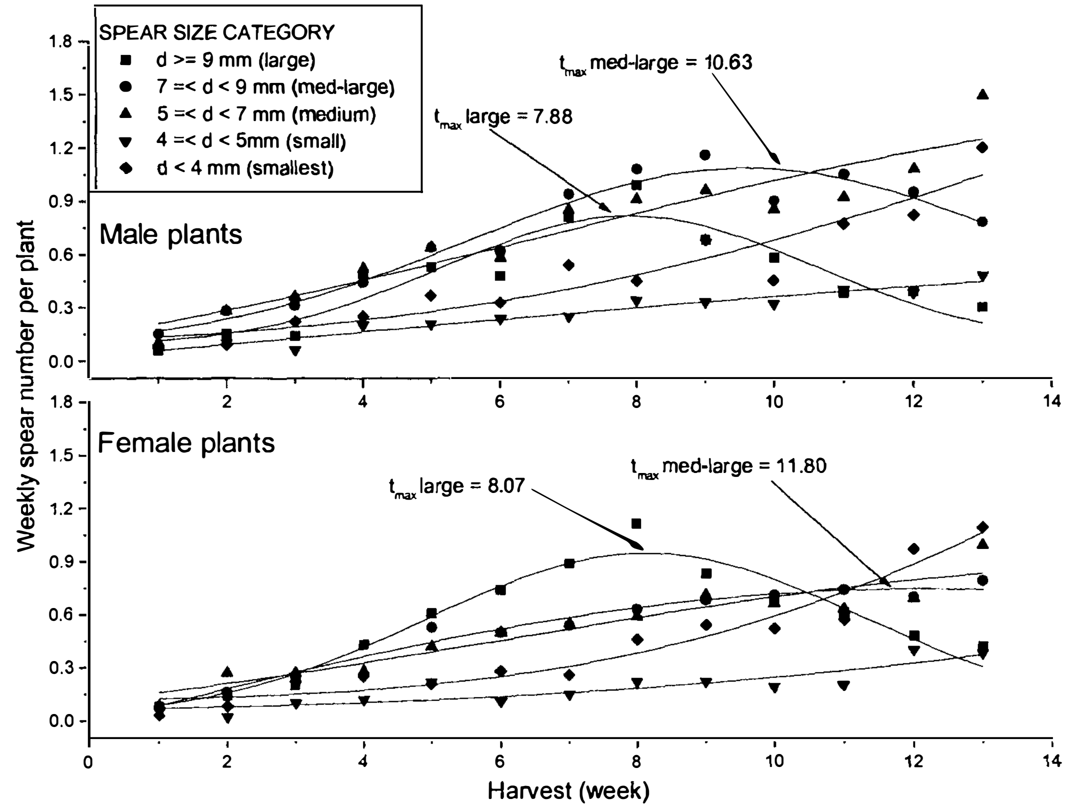


Figure 3.29Expt 4: The time trends of spear number distribution based on spear diameter category from male and female plants during 13 weeks of asparagus harvest.

Although there was an indication that male plants produced spears earlier than female plants, this contrast was not statistically significant (Table 3.28). The male plants produced more medium-large spears than large spears (Fig 3.29) whereas female plants produced more large spears. The spear sizes less than 7 mm were increasingly produced close to the end of the harvest period.

Further GLM analysis showed that CH only affected total numbers of the smallest spear size (Table 3.39) whereas CV and SEX differences influenced significantly total number of medium-large (Table 3.36), medium (Table 3.37) and small size spears (Table 3.38). CV also significantly affected total spear number of smallest size (Table 3.39). It is clear that all cultivars produced similar total numbers of large spear size but different total numbers at smaller spear size.

Within large spears, female plants of 'UC157' produced more total spears than male plants whereas male plants of 'Grande' produced more large spears than female plants (Table 3.35). This resulted in significant interaction between CV and SEX on total numbers of large spear size.

There was an indication that female plants produced more spears only in large spear size, but this was not significantly different from male plants (Table 3.35). At the lower spear size beginning medium to small size, male plants produced significantly more spears than female plants (Table 3.37-3.39).

Within cultivar, 'UC157' produced highest proportion of medium (29.25%) and smallest spears (26.01%) whilst 'Apollo' and 'Atlas' had highest proportions of medium-large spears (26.63% and 32.29%, respectively) (Table 3.40).

Table 3.35 Expt 4: Average of total spear number with diameter more than or equivalent to 9 mm (large spears) during harvest period from four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height **(CH)**	Cultivar (CV)				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	5.3	6.7	2.1	8.7	5.7
	15 cm	8.6	7.4	5.3	5.3	6.6
	20 cm	4.7	9.7	5.4	7.0	6.9
	25 cm	5.0	7.2	4.8	7.2	6.0
	30 cm	7.4	8.1	8.3	8.3	8.0
	CV mean	6.2	7.8	5.2	7.3	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	8.8	9.1	3.6	7.4	7.2
	Male	3.6	6.5	6.7	7.1	5.9

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	7.5	6.8	6.8	6.2	9.0
	Male	3.9	6.5	6.6	5.9	7.0

Block	ns
CV	ns
SX	ns
CH	ns
CV*SX	**
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

ns, **, ***: non significant or significant at $P = 0.01$. Within the column and row, means followed by the same letter are not significantly different at $LSD_{0.05}$.

Table 3.36 Expt 4: Average of total spear number with diameter more than or equivalent to 7 mm and less than 9 mm (medium-large spears) during harvest period in 2000 from four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height **(CH)**	Cultivar (CV)				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	9.7	8.4	3.6	14.2	8.9
	15 cm	9.3	8.3	4.3	13.7	8.9
	20 cm	7.3	7.7	5.5	9.1	7.4
	25 cm	8.3	9.0	4.1	8.8	7.5
	30 cm	7.1	8.8	3.6	9.6	7.3
	CV mean	8.3^b	8.4^b	4.2^c	11.1^a	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	8.5	6.9	1.9	9.6	6.7^b
	Male	8.2	10.0	6.5	12.5	9.3^a

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	7.6	7.2	6.5	6.1	6.3
	Male	10.3	10.5	8.3	9.0	8.3

Block	***
CV	***
SX	***
CH	ns
CV*SX	ns
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

ns, ***: non significant or significant at $P = 0.001$. Within the column and row, means followed by the same letter are not significantly different at $LSD_{0.05}$.

Table 3.37 Expt 4: Average of total spear number with diameter more than or equivalent to 5 mm and less than 7 mm (medium spears) during harvest period from four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height **(CH)**	Cultivar (CV)				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	13.4	7.8	6.2	10.3	8.4
	15 cm	12.7	7.2	2.4	10.8	8.3
	20 cm	12.8	6.8	3.5	7.8	7.7
	25 cm	10.5	7.0	4.6	8.5	7.6
	30 cm	13.9	6.4	2.3	7.2	7.4
	CV mean	12.7^{a}	7.0^{b}	3.8^{c}	8.9^{b}	

B	Plant sex **(SX)**	Cultivar (CV)				**SX mean**
		UC157	Apollo	Grande	Atlas	
	Female	10.5	4.6	2.3	9.1	6.6^{b}
	Male	14.8	9.4	5.2	8.7	9.5^{a}

C	Plant sex (SX)	Cutting Height (CH)				
		10 cm	15 cm	20 cm	25 cm	30 cm
	Female	8.0	7.1	6.8	6.7	4.6
	Male	10.8	9.4	8.7	8.6	10.3

Block	***
CV	***
SX	***
CH	ns
CV*SX	ns
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

ns, ***: non significant or significant at $P = 0.001$. Within the column and row, means followed by the same letter are not significantly different at $LSD_{0.05}$.

Table 3.38 Expt 4: Average of total spear number with diameter more than or equivalent to 4 mm and less than 5 mm (small spears) during harvest period from four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height **(CH)**	Cultivar (CV)				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	5.5	3.8	1.3	4.0	3.6
	15 cm	4.0	3.6	0.7	2.3	2.6
	20 cm	7.1	2.3	1.3	3.1	3.5
	25 cm	3.7	2.0	1.5	2.3	2.4
	30 cm	3.8	2.1	1.1	2.3	2.3
	CV mean	4.8^a	2.8^b	1.2^c	2.8^b	

B	Plant sex **(SX)**	Cultivar (CV)				**SX mean**
		UC157	Apollo	Grande	Atlas	
	Female	4.3	2.1	0.6	2.5	2.4^b
	Male	5.3	3.4	1.7	3.1	3.4^a

C	Plant sex (SX)	Cutting Height (CH)				
		10 cm	15 cm	20 cm	25 cm	30 cm
	Female	2.8	2.5	3.3	2.0	1.2
	Male	4.5	2.7	3.6	2.7	3.5

Block	**
CV	***
SX	*
CH	ns
CV*SX	ns
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

ns, *, ***: non significant or significant at $p = 0.05$ or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at $LSD_{0.05}$.

Table 3.39 Expt 4: Average of total spear number with diameter less than 4 mm (smallest spears) during harvest period from four asparagus cultivars at different cutting heights (A), four asparagus cultivars consisting of female and male plants (B), and asparagus female and male plants at different cutting heights (C).

A	Cutting Height **(CH)**	Cultivar (CV)				**CH mean**
		UC157	Apollo	Grande	Atlas	
	10 cm	12.0	8.8	3.4	6.6	7.8^{a}
	15 cm	17.7	7.3	3.0	3.8	7.9^{a}
	20 cm	11.1	6.6	1.6	3.0	5.6^{ab}
	25 cm	7.8	2.3	1.8	2.3	3.5^{b}
	30 cm	7.7	3.3	1.9	5.3	4.5^{b}
	CV mean	11.3^{a}	5.6^{b}	2.4^{c}	4.2^{bc}	

		Cultivar (CV)				**SX mean**
B	Plant sex **(SX)**	UC157	Apollo	Grande	Atlas	
	Female	11.8	4.4	2.1	3.6	5.5
	Male	10.7	6.8	2.7	4.7	6.2

		Cutting Height (CH)				
C	Plant sex (SX)	10 cm	15 cm	20 cm	25 cm	30 cm
	Female	5.8	9.5	6.3	2.1	3.7
	Male	9.8	6.3	4.8	4.9	5.4

Block	*
CV	***
SX	ns
CH	*
CV*SX	ns
CV*CH	ns
SX*CH	ns
CV*SX*CH	ns

ns, *, ***: non significant or significant at $P = 0.05$ or 0.001, respectively. Within the column and row, means followed by the same letter are not significantly different at $LSD_{0.05}$.

Table 3.40 Total spear number and proportions of spear number for each spear category within female and male plants from four asparagus cultivars grown in a greenhouse.

	UC157			Apollo			Grande			Atlas			
	Female	Male	Total	Female	Male	Total	Female	Male	Total	Female	Male	Total	
Large	131.5 (19.95)	54.5 (8.54)	186 (14.34)	137 (33.58)	97 (17.90)	234 (24.63)	54 (34.18)	100.5 (29.30)	154.5 (30.84)	111.5 (23.08)	107 (19.69)	218.5 (21.29)	793 (21.01)
Medium large	127.5 (19.35)	122.5 (19.19)	250 (19.27)	103 (25.25)	150 (27.68)	253 (26.63)	29 (18.35)	97.5 (28.43)	126.5 (25.25)	143.5 (29.71)	188 (34.59)	331.5 (32.29)	961 (25.46)
Medium	158 (23.98)	221.5 (34.69)	379.5 (29.25)	69.5 (17.03)	141.5 (26.11)	211 (22.21)	35 (22.15	78.5 (22.89)	113.5 (22.65)	136 (28.16)	131 (24.10)	267 (26.01)	971 (25.72)
Small	65 (9.86)	79.5 (12.45)	144.5 (11.14)	32 (7.84)	51 (9.41)	83 (8.74)	9 (5.70)	26 (7.58)	35 (6.99)	37.5 (7.76)	46.5 (8.56)	84 (8.18)	346.5 (9.18)
Smallest	177 (26.86)	160.5 (25.14)	337.5 (26.01)	66.5 (16.30)	102.5 (18.91)	169 (17.79)	31 (19.62)	40.5 (11.81)	71.5 (14.27)	54.5 (11.28)	71 (13.06)	125.5 (12.23)	703.5 (18.64)
Grand Total	659 (100)	638.5 (100)	1297.5 (100)	408 (100)	542 (100)	950 (100)	158 (100)	343 (100)	501 (100)	483 (100)	543.5 (100)	1026.5 (100)	3775 (100)

Numbers in brackets are proportions in percentage within a column

3.3.4.5. Total Soluble Carbohydrate of different segments from the asparagus spears in 2000.

3.3.4.5.1. Total soluble carbohydrate (TSC) concentration in spears

Total soluble carbohydrate concentration (TSC, mg.g^{-1} of dry weight) in the spears varied with harvest time. TSC was significantly higher at the second month ($P \leq 0.0001$) compared to the first and third month of the harvest season (Fig. 3.30).

The TSC concentration of spear segments was higher in the middle of the spears and reduced toward the two ends (tip and butt), fitting quadratic responses indicating greater TSC concentration in the second month than the first and third month (Fig. 3.30).

There was an interaction between spear segment and spear length (Fig. 3.31).

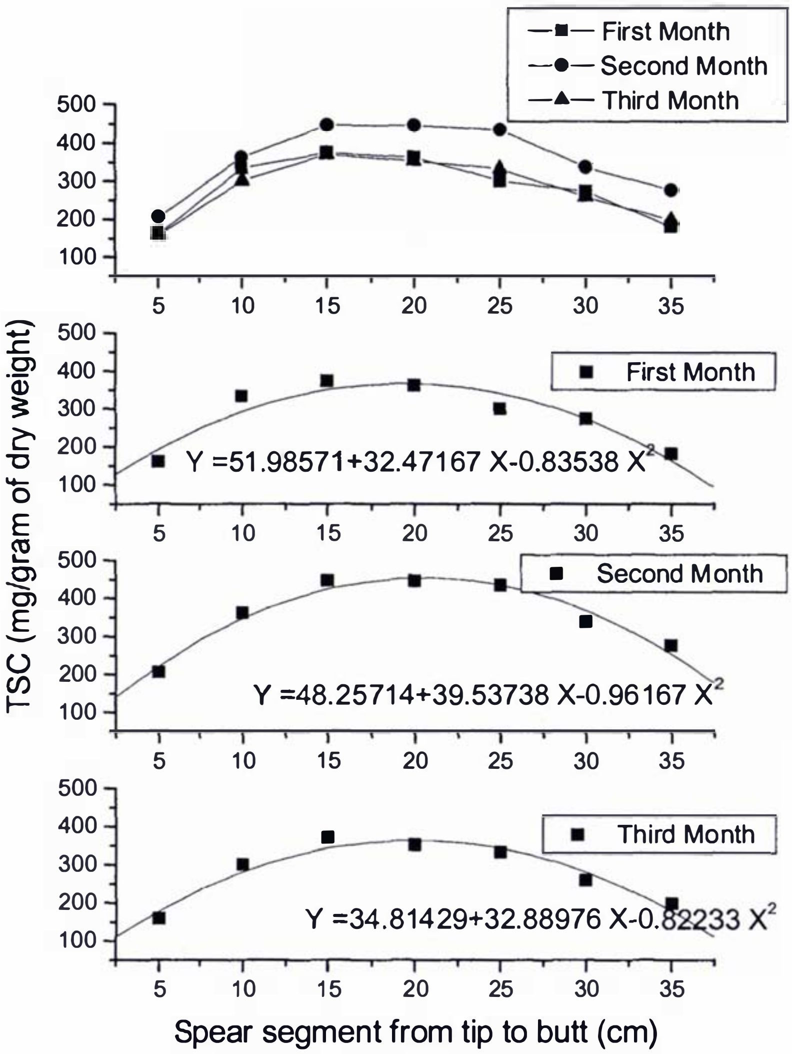


Figure 3.30 Expt 4: Distribution of total soluble carbohydrate concentration ($mg.g^{-1}$ of dry weight) of asparagus spears harvested in different months.

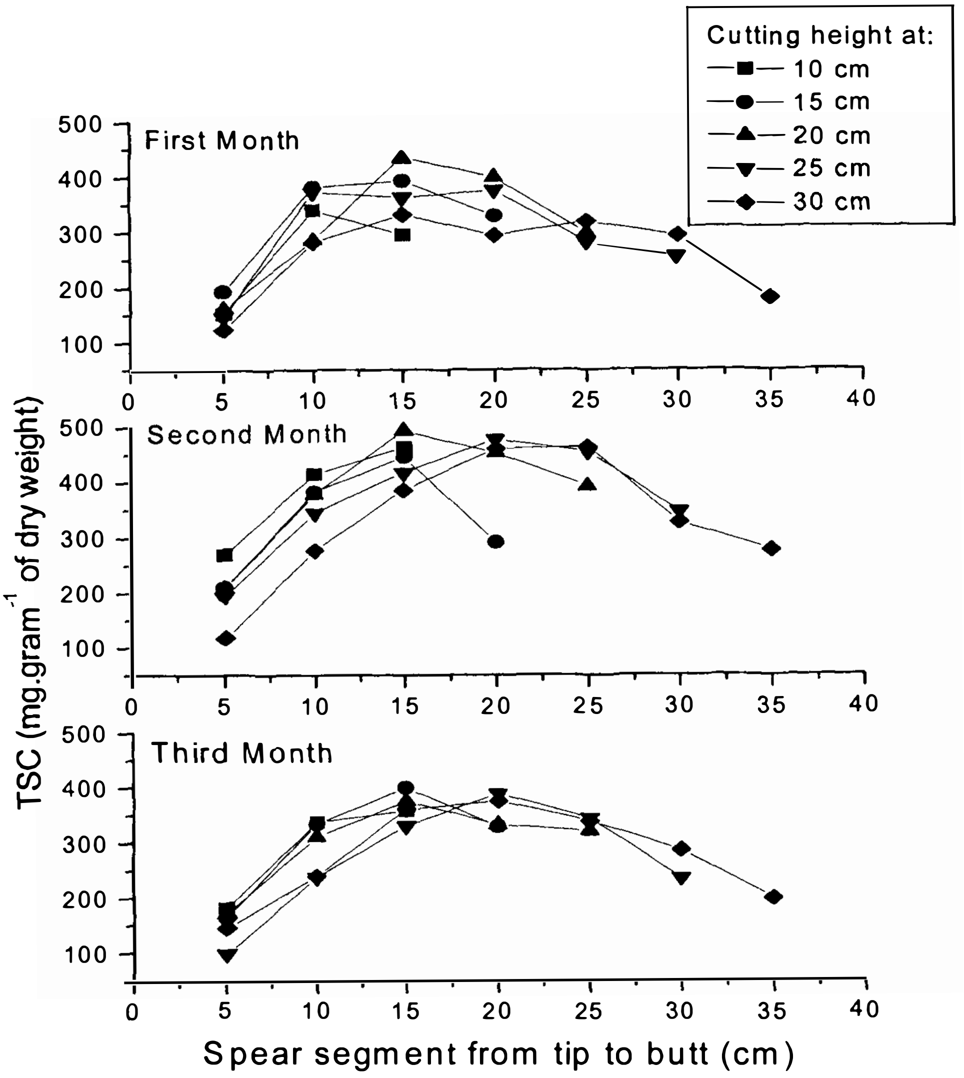


Figure 3.31 Expt 4: Distribution of total soluble carbohydrate concentration (mg.g^{-1} of dry weight) in segments from different asparagus spear length.

3.3.4.5.2. Total soluble carbohydrate concentration (mg.g^{-1} of dry weight) in storage root before and after harvest season in 2000

Although there were significant increases in total spear fresh weight and dry weight as CH increased, no interaction between CV, CH, and SEX was found for TSC of asparagus storage roots either before or after the harvest season. Cutting height did not significantly affect TSC before or at the end of harvest (Fig. 3.32). The total soluble carbohydrate (TSC) concentration of all storage roots ranged from 477.3 to 485.2 mg.g^{-1} of dry weight before harvest. The similarity of TSC amongst CH was also observed after harvest (Fig. 3.32).

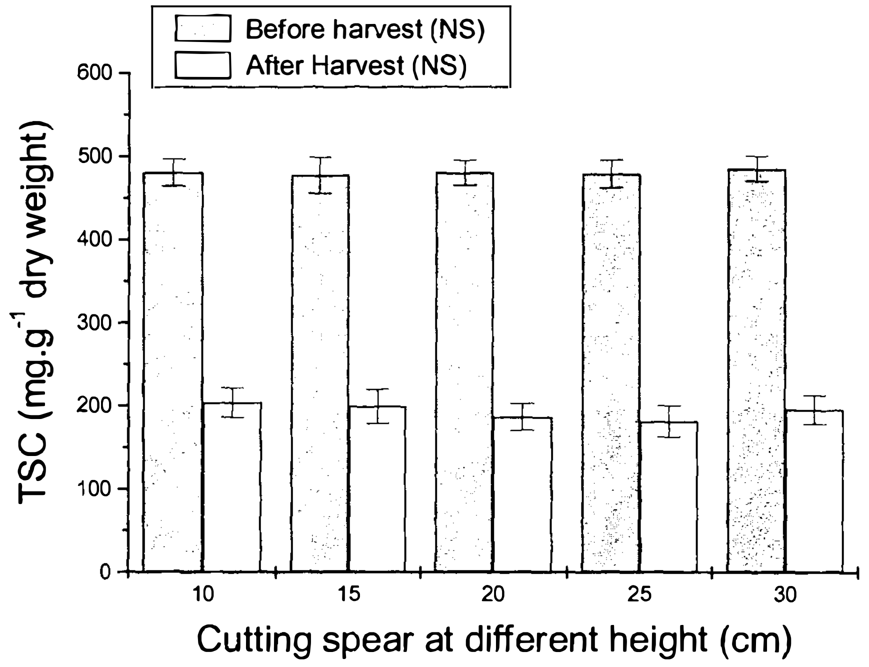


Figure 3.32 Expt 4: Total soluble carbohydrate concentration (mg.g^{-1} of dry weight) of asparagus storage roots before and after harvest for five different cutting heights based on four different asparagus cultivars grown in the greenhouse.

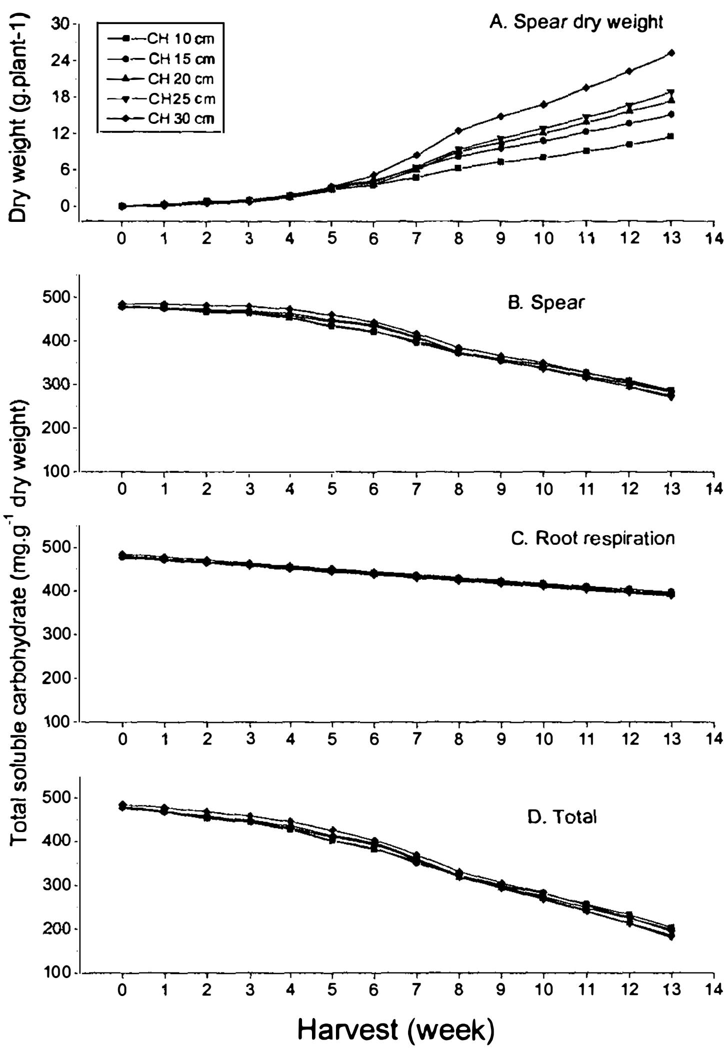


Figure 3.33 Expt 4: Estimated reduction of storage TSC concentration (mg.g^{-1} of dry weight) of asparagus during the harvest period: cumulative spear dry weight production (A); estimation of TSC reduction due to spear growth (B), root respiration (C) and total (D) at five different cutting heights across four different asparagus cultivars grown in the greenhouse, using procedure of extrapolation from Pressman et al. (1993) see section 3.2.2.4.5.

Estimated reduction of TSC concentration was used to compare between the results of TSC from Expt 4 and the current application recommended by AspireNZ, a decision support system for managing root carbohydrate in asparagus. The increase of dry weight was reciprocal with the loss of carbohydrate in terms of TSC concentration (Fig. 3.33).

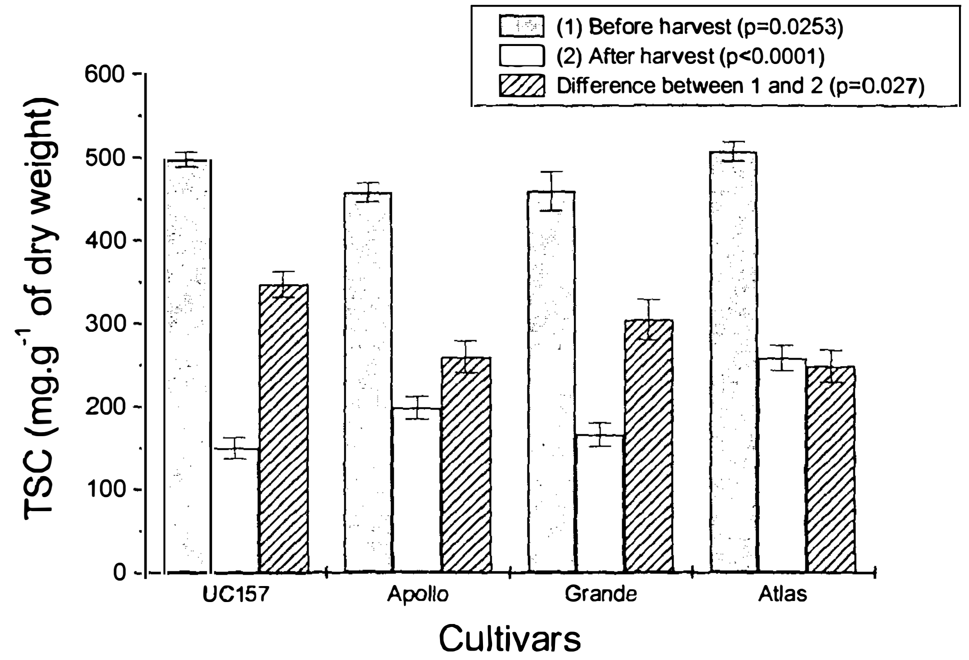


Figure 3.34 Expt 4: Total soluble carbohydrate concentration (mg.g^{-1} of dry weight) of all storage roots before and after harvest and the difference between before and after harvest for four different asparagus cultivars grown in the greenhouse.

TSC concentration was significantly influenced by cultivar before and after harvest at P=0.0253 and P < 0.0001, respectively (Fig. 3.34). The greatest reduction of TSC occurred in 'UC157' (347.5 mg.g^{-1} of dry weight) which then was reflected as the lowest residual TSC among other cultivars, followed by 'Grande' (304.5 mg.g^{-1}dry weight) whereas the smallest reduction occurred in 'Atlas' (248.6 mg.g^{-1} dry weight) followed by 'Apollo' (259.7 mg.g^{-1}dry weight) (Fig. 3.42). Estimated reduction of TSC in 'Atlas' was the lowest (Fig. 3.35).

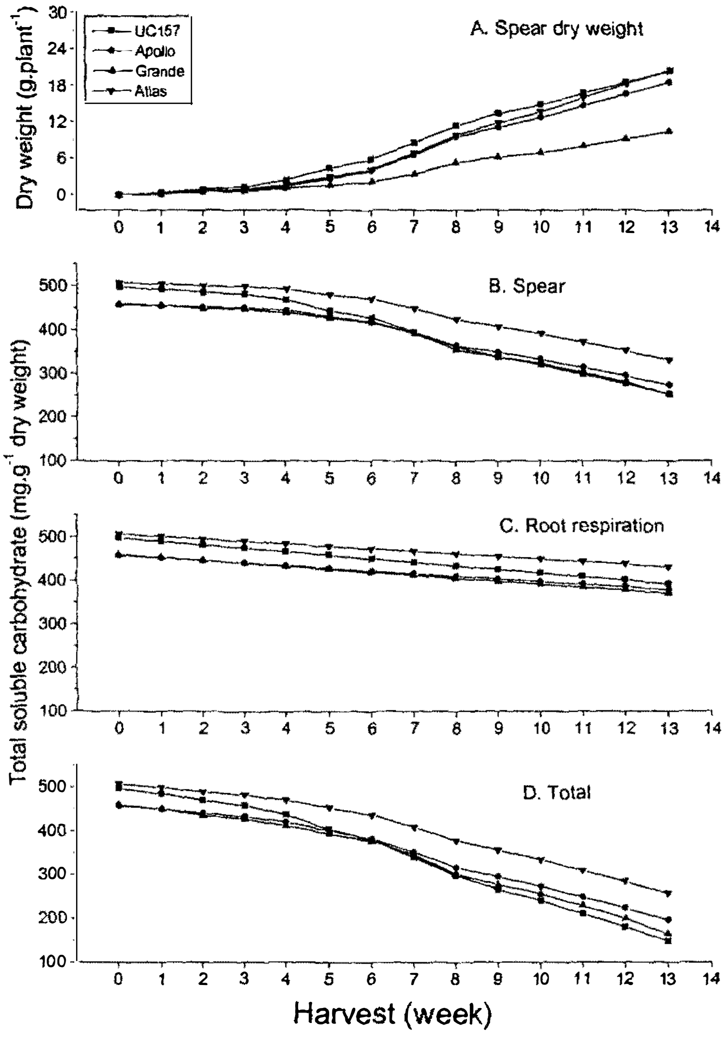


Figure 3.35 Expt 4: Reduction of storage TSC concentration (mg.g^{-1} of dry weight) of asparagus during harvest period: cumulative spear dry weight production (A); estimation of reduction due to spear growth (B), root respiration (C) and total (D) of four different asparagus cultivars grown in the greenhouse.

Initially, TSC of male plants was significantly higher by 39 mg.g^{-1} of dry weight than female plants (499.9 vs 461.29 mg.g^{-1} of dry weight; $P < 0.05$) (Fig. 3.3.36). Once the plants were harvested, the TSC of male plants was reduced further than the female plants, resulting in lower residual TSC for male plants (176.65 vs 208.97 mg.g^{-1} of dry weight; $P < 0.05$).

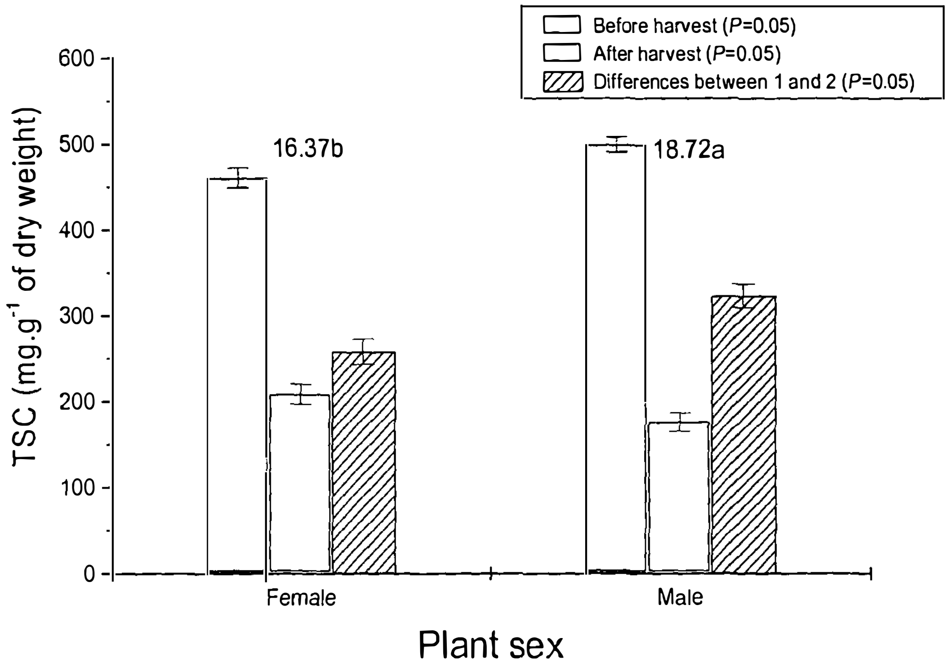


Figure 3.36 Expt 4: Total soluble carbohydrate (mg.g^{-1} of dry weight) before and after harvest for female and male plants based on four different asparagus cultivars grown in a greenhouse. Spear dry weight means followed by the same letter are not significantly different at p = 0.05

3.3.5. Experiment 5: Bud development in the field

3.3.5.1. Asparagus bud numbers in the field

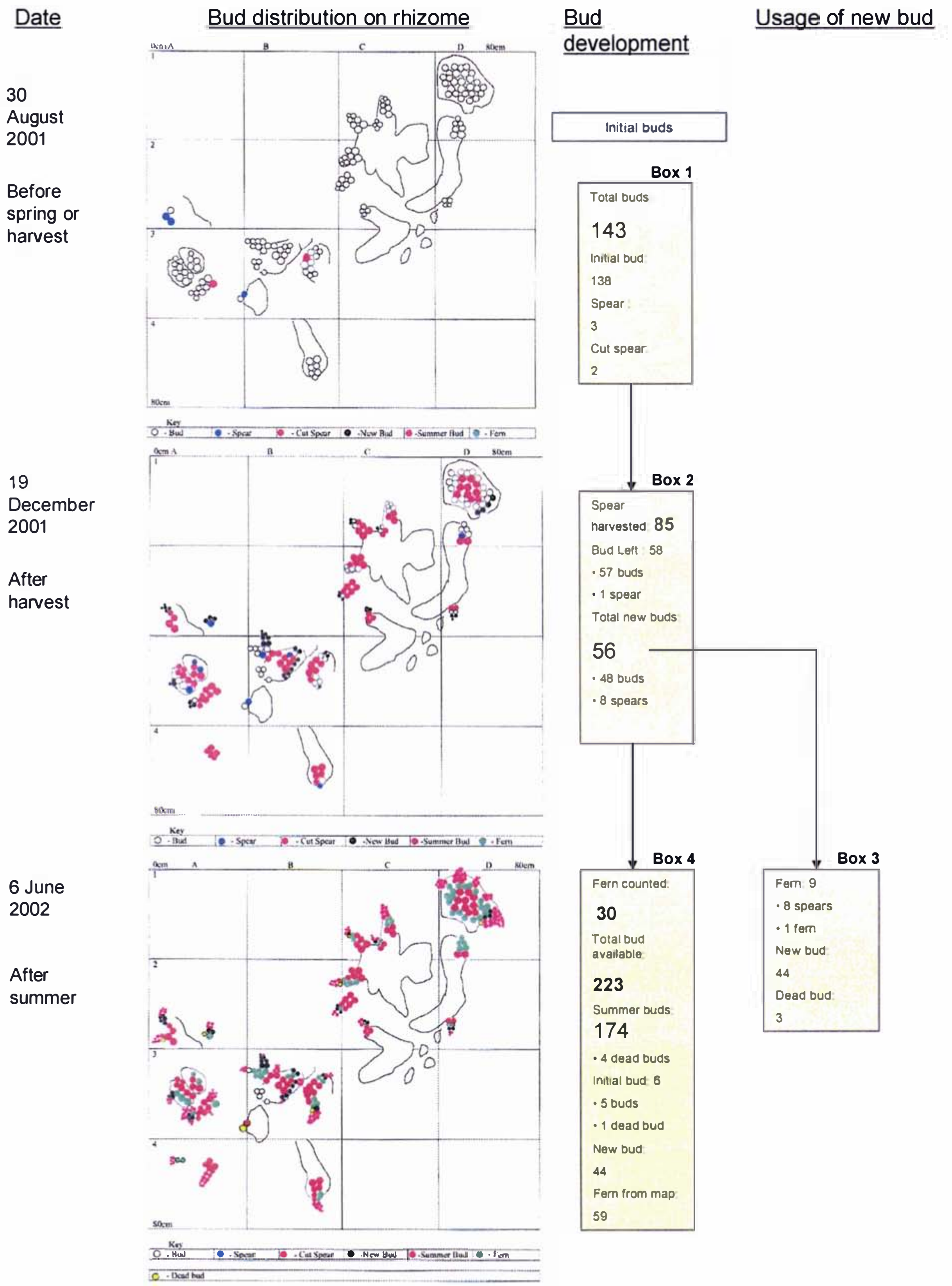


Figure 3.37. Seasonal development of asparagus buds of Jersey Giant in Row 12

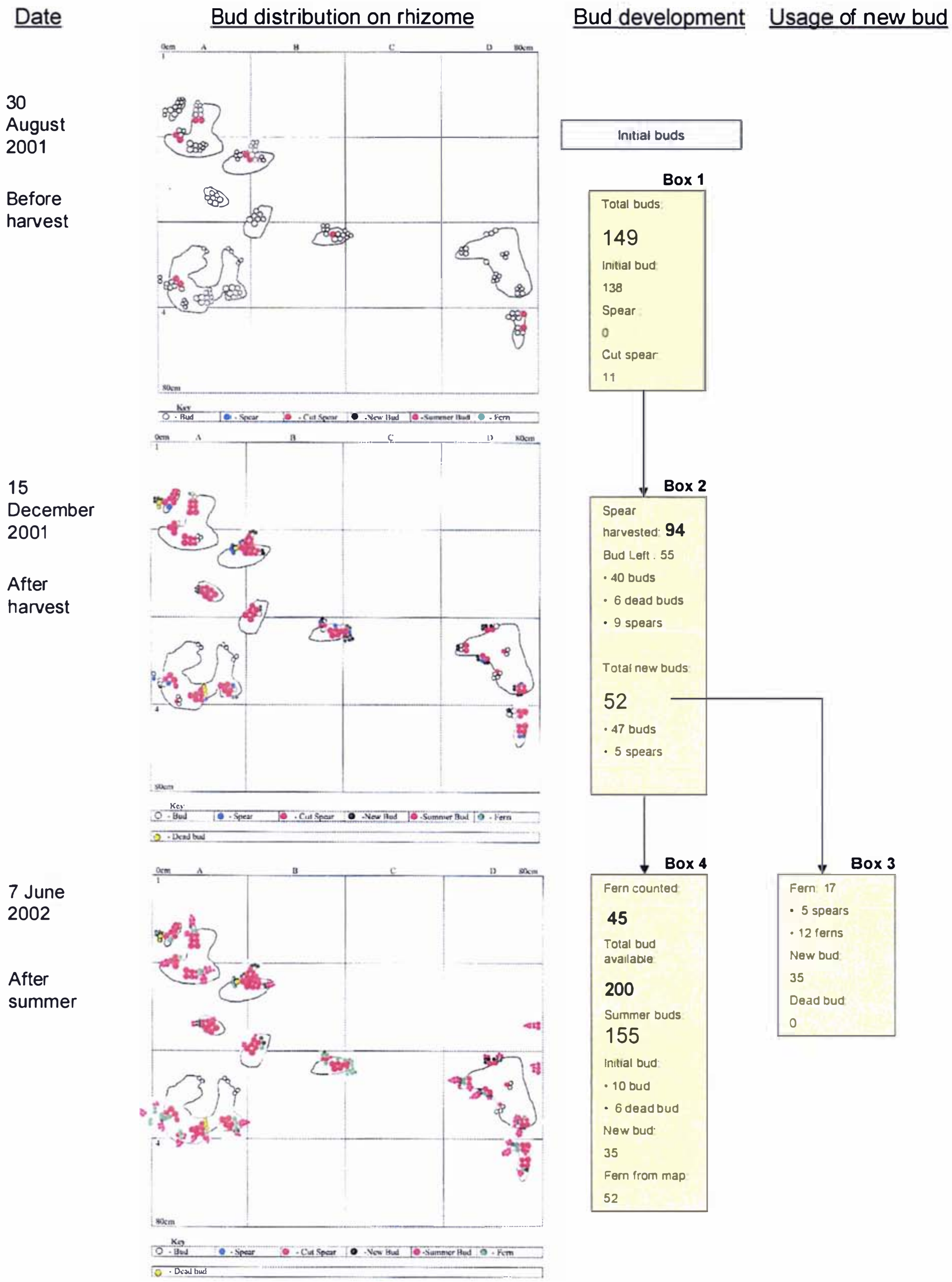


Figure 3.38. Seasonal development of asparagus buds of Jersey Giant in Row 16

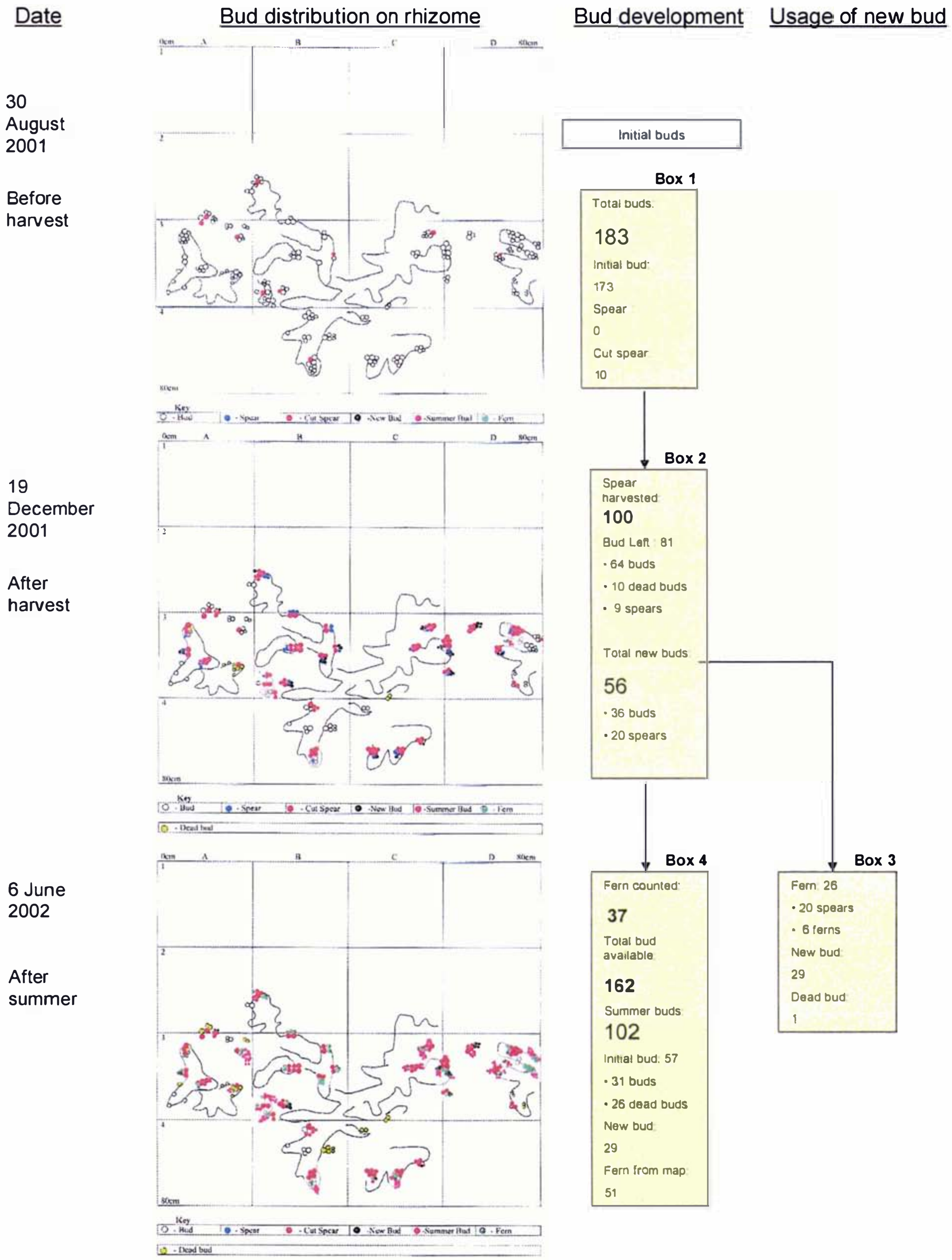


Figure 3.39. Seasonal development of asparagus buds of Taramea in row 6

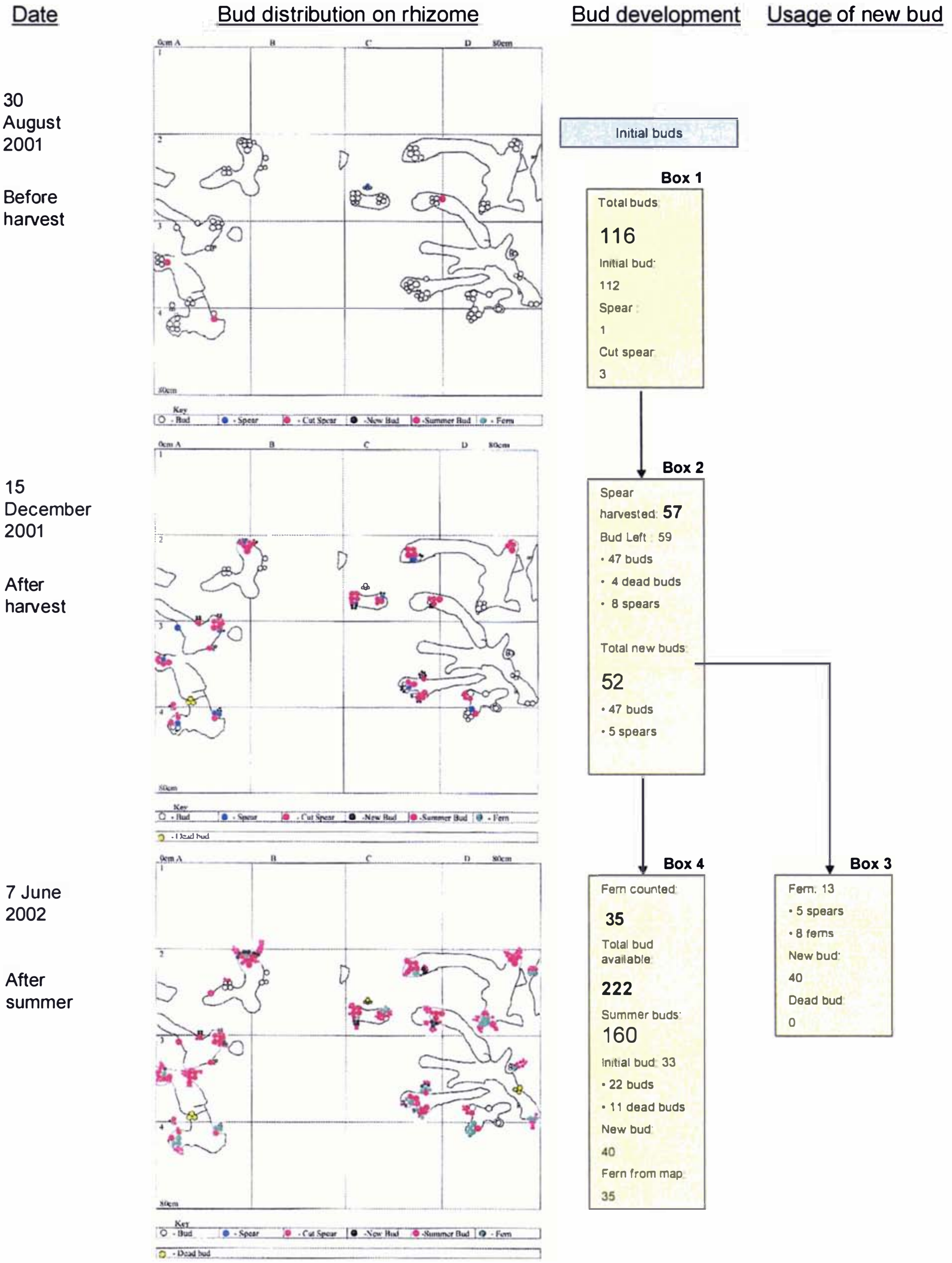


Figure 3.40. Seasonal development of asparagus buds of Taramea in row 10

Bud, spear and cut-spear numbers were obtained at the start of harvest (30 August 2001), after harvest (15th and 19th December 2001) and at the end of autumn (6th and 7th June 2002) whilst fern numbers were counted twice on 9th January and 26th April 2002 from a commercial block at Bulls, Manawatu. The 'Taramea' samples were located at the lower yielding end of the field block.

Cultivar Jersey Giant produced 85 and 94 spears (an average of 89.5 spears per 0.8 m^2) whilst 'Taramea' produced 100 and 57 spears (an average of 78.5 spears per 0.8m^2) (Table 3.41). The total difference between bud numbers before and after harvest indicated additional buds produced during the harvest period. Both cultivars produced on average an extra 54 buds during the harvest period (Table 3.41).

Table 3.41 Bud counts before and after harvest period of two cultivars in the field.

Cultivar	No	Harvest	Bud	Spear	Cut spear	Dead	Total	Differences (After-before)
Jersey Giant	1	Before	138	3	2	0	143	
Row 12		After	105	9	85	0	199	56
Jersey Giant	2	Before	138	0	11	0	149	
Row 16		After	87	14	94	6	201	52
Taramea	1	Before	173	0	10	0	183	
Row 6		After	100	29	100	10	239	56
Taramea	2	Before	112	1	3	0	116	
Row 10		After	94	13	57	4	168	52

Available buds at the end of harvest thus came from both initial buds formed in the previous summer season and new buds that developed during the current harvest period.

Some of the new buds that grew during the harvest period developed into spears (8, 5, 20 and 5 in Box 2 of Fig. 3.37-3.40, respectively). This last statement is based on the difference between total bud number (Box 1 in Fig. 3.37-3.40) and the sum of initial buds left, dead buds, spears and cut spears obtained during the harvest period (Box 2 in Fig 3.37-3.40). For example in Fig. 3.37 total buds were 143 (Box 1) whereas in Box 2 we have 57 initial buds left, plus nine spears (blue circles on the maps) and 85 cut spears (total = 151). Thus eight spears must have developed from new buds (151 minus 143).

Further usage of available buds during the summer was based on bud maps of the second (15th and 19th December 2001) and third observations (6th and 7th June, 2002) (Fig. 3.37 – 3.40) and ferns counted during the summer. Most of initial buds for 'Jersey Giant' developed into ferns as indicated by the low number of initial buds available at the end of summer(6 and 16) but with 'Taramea' considerable numbers of initial buds were still present at the end of summer (Box 4 in Fig. 3.45-3.48). Of the new buds produced during the harvest period 9, 17, 26, and 13 formed ferns (Box 3 in Fig. 3.37-3.40) and live buds remaining were 44, 35, 29, and 40.

The third observation conducted after summer (6th and 7th June 2002) revealed many more buds had formed (summer buds in Box 4 in Fig. 3.37-3.40). Some of the buds previously observed as spears had turned into ferns during the summer. Fern numbers counted in the summer were relatively lower than those in the bud map. The fern numbers from counting did not include very small ferns or ferns that were lost. Summation of initial buds and new buds left during the summer plus summer buds (developed during the summer season) resulted in total buds presumably (but see Discussion) available for the next spring harvest, 223, 200, 162, and 222 (Box 4 in Fig. 3.37-3.40). The average of summer buds produced in 'Jersey Giant' (164.5 buds) was higher than in 'Taramea' (131 buds).

3.3.5.2 TSC from the plants in the field

There was no difference in TSC concentration in the roots between 'Jersey Giant' and 'Taramea' at all times of the observations (Table 3.42). TSC for 'Jersey Giant' and 'Taramea' after the plants were harvested (second observation) reduced to 422.9 and 445.5 mg.g^{-1}of dry weight, respectively. After summer, the plants replenished and increased TSC level up to 523.8 and 559.7mg.g^{-1} of root dry weight of plants for 'Jersey Giant' and 'Taramea', respectively.

Table 3.42 Total soluble carbohydrate concentration of root storage (mg.g-1 of dry weight) from two asparagus cultivars in the field at different seasons.

Observation time		Cultivars		Significance
		Jersey Giant	Taramea	
1.	Initial (before harvest/spring)	570.7	542.1	ns
2.	After harvest	422.9	445.5	ns
3.	After summer	523.8	559.7	ns

ns = non significant using t-test within the same row

3.4. DISCUSSION

Results in this chapter are discussed in the following order:

1. The effect of main treatments and interactions on yield focusing on total spear fresh yield and spear number (3.4.1), and on spear quality (3.4.2) in terms of spear diameter, head tightness, and head length (3.4.1.2)

2. Patterns of yield based on spear quality and total yield over harvest period (3.4.2.2)

3. Further division of buds based on spear diameter to estimate t_{max} (3.4.2.3) regardless of quality definition described in Material and Method Section 3.2.2.4.2.

4. Bud usage derived from mapping in the field supporting and extending bud number observations from greenhouse experiments (3.4.3)

5. The effect of main treatments and interactions on total soluble carbohydrate (TSC) concentration in storage root (TSC_{root}) (3.4.4)

6. The effect of main treatments and interactions on TSC concentration of different segments of the spears (TSC_{spear}) as a quality attribute, over three months (3.4.5)

7. An estimate of total spear fresh yield influenced by cutting height and the proportion of marketable and total yield (3.4.5)

8. Evaluation of the effects of relationships between bud number and TSC_{root} (3.4.6) on spear yield.

9. An estimate of potential production derived from bud number and bud usage (3.4.7)

10. Conclusions

3.4.1. Total yield of asparagus

Asparagus spears were cut over the same harvest period (13 weeks) in Expt 3 and Expt 4. Yield of asparagus grown in the greenhouse in Expt 3 and Expt 4 was influenced by different factors. Over-all, spear yield was higher in Expt 4 than Expt 3 (Table 3.3 and 3.7). In Expt 3, total spear yield, especially quality 1 spears, was very low , probably as consequences of the *Stemphyllium* infection and the corrective management which followed.

Since pattern of spear dry weight was similar to that of fresh weight in Expt 3 (Fig 3.4 and 3.5) as well as in Expt 4, discussion will focus on fresh yield, spear number, spear dry matter percentage and total soluble carbohydrate concentration.

3.4.1.1. Cutting height and cultivar effects on fresh yield and spear number

3.4.1.1.1. Cutting height effects

The effect of cutting height (CH) was the same for each cultivar (CV) in Expt 4 (Table 3.7) but differed in Expt 3 (Table 3.3) possibly because of differences in *Stemphyllium* infection. As cutting height increased, the total yield increased. According to Kamo (1999) who studied the effect of cutting height from 5 cm to 50 cm on the same four asparagus cultivars used in the current studies, total spear fresh weight increased linearly as the cutting height increased from 5 cm to 30 cm, but cutting heights above 30 cm reduced the total fresh marketable yield. However, in Expt 3 total yield increase up to CH 30 cm was only found in 'Apollo' and 'UC157'. Cultivars Grande and Atlas which had similar total yield in fresh weight did not reach the highest total yield at the highest CH (Table 3.3). In Expt 4, the highest yield was found at CH 30 cm in all cultivars (Table 3.7).

The increase in total spear dry weight with increasing CH should equate to increased demand for carbohydrate from the storage root. This is the basis for the suggestion that the pressure of greater cutting height would be equivalent to the pressure of extended harvest duration (Karno, 1999; Nichols and Fisher, 1999) and therefore as the cutting height increased the utilization of carbohydrate reserve should also increase (Shelton and Lacy, 1980).

Cutting height (CH) affected not only total fresh weight but also total spear number. As CH increased, the total fresh yield increased (Table 3.7) whereas total spear number declined (Table 3.15). Highest spear number at the lowest CH (Table 3.15) did not compensate for lower spear weight, so total yield would also be low. Dean (1993) reported that asparagus yield increased as the cutting height increased from 13 cm to 23 cm and showed that the increase of total yield at higher cutting heights was due to higher proportions of large (1.26-1.59 cm) and jumbo (> 1.6 cm) spears. He suggested that carbohydrate supply or other factors that control total yield did not seem to be affected by cutting height above 23 cm. Dean (1993) however, did not measure carbohydrate in his experiment. His suggestion was only based on the trend in his research that as cutting height increased the total yield increased, both in marketable and culled spears. Nevertheless, Karno (1999) showed that CH above 30 cm reduced marketable yield and only increased non-marketable yield. Thus both Dean (1993) and Karno (1999) supported the hypothesis in this current study that the availability of large buds can limit yield and quality.

3.4.1.1.2. Cultivar effects

There were significant differences between cultivars (CV) in total fresh yield (Table 3.3 and 3.7) as well as total spear number (Table 3.4 and 3.15). Cultivars Atlas, Apollo, UC157 and Grande have been reported to have high yield in many different studies, but yield performances for each cultivar were inconsistent, being dependant upon geographical area and field management. Cultivars Atlas, Apollo and UC157 produced fresh yield significantly higher than 'Grande' in Expt 4 (Table 3.7 and 3.15) but only 'Apollo' and 'Atlas' produced significantly higher yield in Expt 3 (Table 3.3 and 3.4). These results were inconsistent with some other studies which were conducted in different countries and managements. Bakka et al. (1999) conducted cultivar trials in Uganda and found that 'Atlas' (2,847 $kh.ha^{-1}$), 'Apollo' (2839 $kg.ha^{-1}$), and 'Grande' (2697 $kg.ha^{-1}$) produced higher yield than 'UC157' (2320 $kg.ha^{-1}$). The high yield of 'Atlas' and 'Apollo' was also reported by Benson et al. from USA (1996) and Anonymous (2000). Cueto and Lesnick (1999) measured the yield performances amongst 7 cultivars in The Philippines and found that 'Atlas' (11,289 $kg.ha^{-1}$) was superior to 'Viola' (10,504 $kg.ha^{-1}$), 'Grande' (9.803 $kg.ha^{-1}$), 'Apollo' (7,816 $kg.ha^{-1}$), 'UC157' (7,649 $kg.ha^{-1}$), 'Jersey Giant' (5,812 $kg.ha^{-1}$), 'Jersey Knight' (5,645 $kg.ha^{-1}$). They found that the superiority of 'Atlas' was due to high spear weight and high percentage of marketable spears as found in Expt 4.

In Expt 3 and 4, an unusually low yield in 'Grande' came from a low number of spears (Table 3.4 and 3.15). Inconsistency of yield amongst cultivars between Expt 3 and 4 may have resulted from poor fern establishment in the previous summer season in Expt 3 causing large variation amongst asparagus plants in term of carbohydrate level (Table 3.5) and bud number (Table 3.4).

3.4.1.1.3. Plant sex effect.

Asparagus is a dioecious plant (Feher, 1992; Ainsworth, 2000). Male plants have been reported to be higher yielding than female plants (Ellison et al., 1990) because male plants produce more spears.

In Expt 4, total spear fresh yield was not influenced by the interaction of CV and CH but the interaction of cultivar and plant sex (CV*SX interaction) was significant (Table 3.7 and 3.15). Male plants of 'Grande' and 'Atlas' produced higher total yield than their female counterparts. On the other hand, female plants of 'UC157' produced higher total yield than male plants (Table 3.26) while in 'Apollo' the differences was not obvious between female and male plants. These patterns of differences between female and male plants within each cultivar continued throughout harvest to the end (Fig. 3.7 and 3.15).

Higher yielding in male plants of 'Atlas' reflected greater spear number per plant for male plants (Table 3.34) and spear weight was more or less the same between plant sexes. Cultivar Grande is well known to produce large spears that can result in higher total yield, but produced the lowest spear number among cultivars in Expt 3 and Expt 4 (Table 3.4 and 3.15). Ellison et al. (1960) reported that individual spears are generally heavier in female plants than male plants. The heavier spears from female plants of 'UC157' and 'Apollo' plants contributed to the increase in total yield of female plants (Table 3.7).

3.4.2. Asparagus spear quality

3.4.2.1. Spear diameter, spear tightness and spear head-length

According to the Manual of the New Zealand Asparagus Council, spear quality for grading is defined as a combination of spear diameter, spear length, spear tightness, and freedom from diseases or pests and physical defects (NZNAM, 1997).

In this study, spear diameter was combined together with head tightness to classify spears into marketable (spear quality 1 and 2) and non marketable (spear quality 3). This classification, based on NZNAM (1997) for canning grade, was modified slightly in the range of quality 1 spear diameters. The percentages of spear qualities based on spear diameter only were different from those using spear head-tightness only, but were close to those percentages based on both parameters (Table 3.25 and 3.26). This suggested that spear quality was more affected by spear diameter, and thus bud size, than spear head tightness in the present study.

In terms of commercial importance, long and tight head can be suggested to be another quality measurement. In this study, spear head-length has been measured as a parameter distinct from head tightness. Head-tightness describes the closeness of the scales at the tip of the spear whether closed tight, medium or open head with internodes showing between the leaf scales. Initially, head-length was measured in response to the results of study by Krarup (1997) who found differences in the height where the heads of spears started to open amongst 28 asparagus cultivars, and suggested that head opening was influenced by temperature. As the temperature increased, spear elongation increased greatly, resulting in higher total yield, but the spear heads tended to open at lower height. Thus head length was an indicator for non-marketable spears in their study. The assessment of spear head length in the current study was conducted in relation to both marketable and non-marketable spears. Spear head-length was not affected by CV, but was affected by CH for all spear qualities. The magnitude of increase in spear head-length in non- marketable spears from 10 cm to 30 cm height was very high in Expt 4. Head-length of non-marketable (quality 3) spears was increased by up to 293% in Expt 4 whilst that of quality 1 and 2 spears increased by 33 % and 72 %, respectively, even though the heads could still be classified as tight. Thus the results for non-marketable spears agreed with the results from Krarup et al. (1997) and Krarup and Contreras (2002) but it is clear that in Expt 4 all spear head-lengths of all cultivars increased as CH increased (Tables 3.19–3.21). Head-length appears to be a function of spear elongation. For commercial interest, long but tight heads may influence the appeal of the spear to the consumer, but further sensory evaluation is needed.

3.4.2.2. Pattern of spear yield and quality over harvest time

Early in the harvest season, few spears emerge and they grow slowly due to low soil and air temperatures. As the season progresses, increase in temperature accelerates spear elongation (Blumenfield et al., 1961; Nichols and Woolley, 1985; Kim and Sakiyama, 1989a; Wilson et al., 1999), which results in more frequent harvest and faster increase in total cumulative yield. The plants in the current study were not grown in the field, but they were in dormancy before they were used for the green house experiments by keeping them in a cool-room at 2°C for Expt 3 and keeping dry for Expt 4. The patterns of cumulative total fresh yield over harvest time in the current study showed a slow increase within the first four or five weeks, followed by rapid increases and levelling off after week 8 or 9 of harvest season (Fig. 3.4, 3.5-3.8, 3.12, 3.15). These trends during the season were similar to the S-shaped curve described in NZNAM (1997) even though the plants were grown in a green house. For the first four or five weeks of harvest duration where the yield was low, few spears, mainly quality 1 or 2, emerged whereas in the last four weeks of harvest either quality 2 or 3 spears contributed more to the total yield (Fig.3.10 and 3.11). During the period of rapid cumulative yield (weeks 5 - 8), quality 1 and 2 spears contributed to the total fresh yield by 52% and 42%, respectively, and quality 3 spears were only 6% of total fresh yield during this period of rapid cumulative yield.

Cumulative total yield of quality 1 and 2 spears increased rapidly but at a decreasing (quadratic) rate (Fig. 3.4, 3.7 and 3.8). This quadratic response over time was dependant on spear diameter and spear number. The relationship between yield and spear number and spear diameter became clear as spear quality degraded from quality 1 to 2 and 3. There was no difference amongst the four cultivars in spear diameter of quality 1 (Table 3.22), but significant differences in spear diameter of quality 2 (Table 3.23). Thus when the spears were categorized in quality 1, which came from large diameter spears (buds), spear number rather than spear diameter determined fresh yield of spear quality 1 (Table 3.16). The effect of cultivar on spear diameter was important in quality 2 spears. Cultivar 'UC157' had smaller spear diameter within quality 2 and lower yield (Table 3.17).

Four-year-old asparagus plants in Expt 4 produced more spears and better quality than three-year asparagus plants grown in Expt 3 that had been infected by *Stemphyllium*.. The results for Expt 4 are summarized in Table 3.43. In Expt 4, only 6 to 12 % of spears were categorised into non-marketable spear by weight, but 22 to 39 % by number (Table 3.43), indicating that a large number of small buds were being utilized.

Table 3.43 Percentages of spear quality based on spear diameter and head tightness in fresh yield and spear number in Expt 4.

Variable	Fresh yield				Spear number			
	Quality1	Quality2	Quality3	Total	Quality1	Quality2	Quality3	Total
Cutting height (CH)								
10 cm	34.43	55.54	10.02	100	15.49	51.55	32.96	100
15 cm	39.94	51.98	8.07	100	18.31	49.71	31.98	100
20 cm	41.73	49.13	9.14	100	20.45	49.52	30.03	100
25 cm	36.64	54.86	8.50	100	18.82	56.46	24.72	100
30 cm	41.63	50.50	7.88	100	21.99	51.55	26.46	100
Plant sex (SEX)								
Female	46.52	45.95	7.53	100	23.24	47.54	29.23	100
Male	32.78	57.71	9.51	100	15.12	54.94	29.94	100
Cultivar (CV)								
UC157	34.00	53.68	12.32	100	13.66	47.69	38.66	100
Apollo	42.71	49.65	7.64	100	21.59	49.84	28.57	100
Grande	50.60	43.14	6.25	100	26.67	50.30	23.03	100
Atlas	33.97	58.64	7.38	100	18.13	59.65	22.22	100

Spear diameters for quality 1, 2, 3 were > 9 mm, 5 < 9 mm, and < 5 mm respectively

Total cumulative fresh weight in Expt 4 was 3-5 times higher than in Expt 3. In Expt 4, yield quality improved in all cultivars as more spears of quality 1 and 2 were produced across the range of CH. An increase of marketable spears as CH increased indicated that at higher cutting rates (low CH) the ability to produce large diameter spears was limited. Most large spears came from buds located at the bases of a bud cluster; therefore most large spears were cut early in the harvest period. Results from studies by

Dufault (1990) and Dean (1993) support this interpretation. However, it is not clear to what extent small buds can grow into large buds during the harvest season. As harvest is extended, a bigger percentage of small spears are produced. This can be illustrated by the t_{max} as explained in the next section (3.4.2.3).

The differences in cumulative fresh weight were due mostly to CH and the interaction between CV and SEX (Table 3.8-3.10). Differences between female and male plants in 'Grande' and 'UC157' contributed to significant interaction of CV and SEX in producing quality 1 spears (Fig 3.7). Amongst all cultivars, 'Grande' produced highest total yield of spear quality 1. Considerably larger spear diameter (Table 3.22) with heavier spear weight (26.2 and 18.7 $g.plant^{-1}$ for female and male plants, respectively) in 'Grande' resulted in more total fresh weight of quality 1 spears produced than in the other three cultivars (Table 3.8). The highest total fresh yield of spear quality 1 was at CH 30 cm for 'Grande', 'Atlas' and 'UC157' but in 'Apollo' spear production in quality 1 was highest at CH 20 cm (Table 3.7). This variation of yield fluctuation between 10 to 30 cm of cutting height was also observed in Karno (1999).

A quadratic response in spear production over time (between weeks 4 to 13) was found in Expt 4 (Fig. 3.7-3.8). The relationship between spear number and spear diameter was clear for all spear qualities. The results suggest that each cultivar had a similar potential number of large spears (> 9 mm) (Table 3.16). Spear number (Table 3.17) and spear diameter (Table 3.23) also determined fresh yield of quality 2 spears (Table 3.9). Thus high proportions of medium sized buds as indicated by spear diameter within quality 2 (5<9 mm) determined total marketable yield as shown in high yielding 'Atlas' (Fig. 3.11). But as spears became less than 5 mm (quality 3), spear number (Table 3.18) rather than spear diameter (Table 3.24) influenced fresh yield of non-marketable spears (quality 3) (Table 3.10) as in 'UC157'. Therefore, spear fresh yields varied more between cultivars when buds were medium or small.

Regardless of different total yield in different cultivars in Expt 4 (Fig. 3.16), the trends of the weekly total fresh yield of all cultivars were similar and gradually increased from week 1 to week 8, and stabilized for the rest of the harvest season (Figure 3.10). Quality 1 spears (> 9 mm, large) and quality 2 spears (5 < 7 mm, medium and medium-large) mostly made up the total yield for the first 8 weeks of the harvesting period in Expt 4. After week 8, yield of spear quality 1 of all cultivars slowly reduced, indicating that large spears (> 9 mm) were used up, whereas there were two patterns of yield of spear quality 2 and 3 to make up steady yield for the rest of the harvest season. In the first pattern, yield of spear quality 2 was unchanged and yield of spear quality 3 increased. This pattern was observed in 'UC157' suggesting the extension of harvest after week 8 risked a high proportion of non-marketable spears (< 5 mm) although still potentially producing spears of quality 2. In this situation, the plants had not used all medium (5<7 mm) and medium-large buds (7<9 mm). Quality 3 spears, which came from small buds (< 5 mm), had higher dry matter percentage than spears of quality 1 and 2 (Table 3.12 and 3.13). High dry matter in the spears could be due to high lignification which is detrimental to eating quality (Billau et al., 1990). The second pattern was that yield of spear quality 2 increased and yield of spear quality 3 was unchanged or slightly increased. In this case, the plants had more medium and medium-large buds (5 < 9 mm) to produce more marketable spears. Cultivars Apollo, Grande and Atlas showed the second pattern. In this pattern, harvest may still be possible until week 11 since large buds are still available, as indicated by the continuing appearance of spear quality 1. From these results, 'UC157' produced many more small buds than the other three cultivars. Therefore, harvest duration depends on cultivar characteristics in term of bud size and bud number. The patterns of different spear quality during the harvest season became more complex when plant sex (SEX) was introduced. But in general, male plants produced more buds with smaller sizes than female plants, as demonstrated by the appearance of more medium to medium large spears (quality 2) (Table 3.9) and small spears (Quality 3) (Table 3.10) in male plants, and the male plants produced medium-large spears (7<9 mm) 2.3 weeks earlier than female plants (Fig. 3.14)

Lengthening harvest to more than 11 weeks only resulted in more non-marketable spears in Expt 4 and this is illustrated well in estimated t_{max} (time at which maximum weekly yields are obtained) for different spear qualities (Section 3.4.2.3).

3.4.2.3. Maximum weekly yield (t_{max}) and bud production

Much emphasize has been placed on the importance of carbohydrate reserves in storage roots in determining final yield. This importance is supported by several studies conducted by Shelton and Lacy, 1980; Haynes, 1987; Wilson et al, 1999. Production is related to the carbohydrate reserves; and the more spears that are cut, the more the carbohydrate reserves are depleted. Many studies have shown that extending harvest time may increase total yield but have little effect on marketable yields (Takatori et al., 1970; Weber, 2001). The appearance of unmarketable spears in a longer harvest was attributed to the loss of marketable spear size (Takatori et al., 1970; Drost 1997) or may be a result of a decrease in the carbohydrate in the roots (Tiedjens, 1926) or may be both (Drost, 1997) and low carbohydrate replenishment due to low vigor of the ferns (Takatori et al., 1970) but many other studies did not discuss bud size limitation. In the current study, bud numbers and size are considered as important additional factors that can limit asparagus yield. Studies of asparagus buds have been relatively few (Bigard, 1974; Wilcox-Lee and Drost, 1991; Wilcox-Lee and Drost, 1997a,b; Wilson et al., 1999; Duangpaeng et al., 2002), and the scarcity of bud information may limit appreciation of the importance of the buds for yield determination.

In the present study, spear diameter was more influential than head tightness in determining spear quality (Table 3.26). This result was used as a basis of spear division for following bud dynamics, illustrating the utilization and limitation of bud number and bud size for yield in asparagus. To simplify the relationship between spear yield and bud number on the crown, the kinetics of spear production in relation to size was traced and illustrated (Fig. 3.22, 3.23, 3.25, 3.27, 3.28, and 3.29). The division based on spear diameter was slightly different from the division of spear quality in section 3.2.1.3. However, most large spears were included in quality 1 spears and most medium-large and medium spears were categorized as quality 2 spears.

Total spear fresh yield based on division of five spear diameters showed those cultivars with higher yield in either large or medium-large spears or both had higher yield in marketable spears (quality 1 and 2) which contributed to higher total yield (Table 3.30-3.34 and 3.35-3.39). The total yields for specific spear sizes can be represented by the areas under a Gaussian fitted curve of spear production against time for each size category (Fig. 3.22, 3.23, 3.25, 3.27, 3.28, and 3.29).

The Gaussian curves indicated that large spears were running out by week 12 and the t_{max} occurred at about week 8 (Table 3.28 and Fig. 3.22 to 3.29). The appearance of medium-large spears followed large spears and reached t_{max} between weeks 8 and 10 for all cultivars except 'Grande' (week 12) (Table 3.28 and Fig. 3.22 to 3.29). Spears of smaller size appeared later and kept increasing towards the end of harvest.

There are several implications of these results. The buds relating to spear 1 quality were harvested first and it was this size of buds that contributed to high marketable yield. As large buds in a bud cluster on the crown were used up, subsequent buds of lower size grew, resulting in the appearance of mostly quality 2 spears. As harvest continued, more buds of smaller size were used, producing thinner spears at later times. Many studies measured carbohydrate reserves but not kinetics (Shelton and Lacy, 1980; Haynes, 1987; Pressman et al. 1993). Takatori et al. (1970) and Drost (1997) have suggested these kinetics as being an important component of limits to spear production. Bud numbers appear to limit spear yield towards the end of a long harvest. This is supported by the current study in the green house where air temperatures were kept as constant as possible. In this situation, spear growth was accelerated, and spears were cut more frequently compared to field conditions. As the temperatures were warm all the time, harvest duration of 13 weeks in this greenhouse could be equivalent to a longer time in the field and therefore can reflect exhaustive use of large, and possibly medium size buds. Once all large and medium bud sizes were used, at least until week 8 – 10 of harvest duration in Expt 4, lengthening the harvest forced smaller sized buds to grow. Bud size is correlated to spear size (Tiedjens, 1926; Blasberg, 1932; Nichols and Woolley, 1985). Small buds produce small spears. When smaller spears are produced, they are more susceptible to lignification (Poll and van Kruistum, 1990) and reduced nutrient content (Moreno-Rojas et al., 1992; Amaro-Lopez et al., 1999) than large spears; thus reducing the quality in addition to spear diameter. The limitation of buds related to yield was therefore in terms of:

a) limiting number of large and medium size buds for producing marketable yield (quality 1 and 2 spears) and,

b) growth of small spears into weak fern influencing photosynthesis and generating less carbohydrate for the next season.

The total bud number itself (Fig. 3.27-3.29) showed no limitation to the yield (Fig 3.6 and 3.20) because new buds continued to develop during the harvest period as indicated by linear regression with time, fitting better than quadratic regression (Fig. 3.13) for bud number.

3.4.3. Bud number and bud usage

As previously described, bud number became a limiting factor in terms of the availability of large to medium-large size buds which contributed to marketable yield when harvest was lengthened, but the total number of buds itself was not a limiting factor. These are the conclusions from the results of the current experiments in a greenhouse and supported by observations in the field.

Bud number between initial and final harvest did not match with total cumulative spear number (Table 3.15). These results indicated there were some new extra buds accounting for the differences. The results from Wilcox-Lee and Drost (1991) indicated there was an increase of buds during the harvest period; however, their destructive sampling of plants during the time course produced large variations in number of bud clusters and buds making over-all conclusions difficult. The authors pointed out that some buds may enlarge over the harvest season, making counting easier and resulting in apparent increase in bud numbers. During the harvest season in Expt 4, uncounted small buds could enlarge over time, and spear harvest could also cause dormant buds to enlarge and grow resulting in increasing numbers of the buds later in the season. Thus, asparagus produced not only spears but also developed buds during the harvest season. Buds developed during the harvest seasons were calculated as the sum of spear numbers produced per plant and the difference between the initial and final harvest bud count. The results of calculations showed that new bud number was highest at the lowest CH indicating that heavy CH pressure stimulated greater bud development.

The discrepancy in bud number or production before and after harvest can now be explained as being due to bud development or production during the harvest period. This finding was supported by mapping work from the field (Fig. 3.37-3.40) which clearly indicated bud development during the harvest period. Low cutting height presumably results in an over-all lower level of correlative inhibition. However, this explanation needs verification. Reduction in correlative inhibition may have been the trigger for faster bud production at lower CH.

In asparagus, correlative inhibition is thought to play a role in spear elongation (Tiedjens, 1924; Kretschmer and Hartmann, 1979; Nichols and Woolley, 1985; Nichols, 1990). In Expt 3 and 4, significantly more spears were obtained at low CH than at high CH. Thus, when the spears were removed more frequently, subsequent buds initiated growth more rapidly. McCormick and Thomsen (1984) compared 50 days and 30 days of harvest period on three-year old asparagus plants, and found that lengthening harvest to 50 days increased marketable yield in the following year. Thus a heavier cutting pressure either due to a longer harvest (McCormick and Thomsen, 1984) or more frequent cutting at lower CH, as in our study, both stimulated bud development. An investigation related to correlative inhibition was conducted and is reported in Chapter 4 of this thesis.

Mapping buds, spears, cut spears and ferns at 3 different times in the field (Expt 5) using ‘Jersey Giant’ and ‘Taramea’ supported the findings in the greenhouse experiment (Expt 4) that buds were formed during the harvest season (Table 3.41). Although final bud numbers were lower than initial numbers, the summation of the differences for bud, spear and cut spear numbers indicated that new buds developed during the harvest season (new buds in Box 2 of Fig. 3.37-3.40).

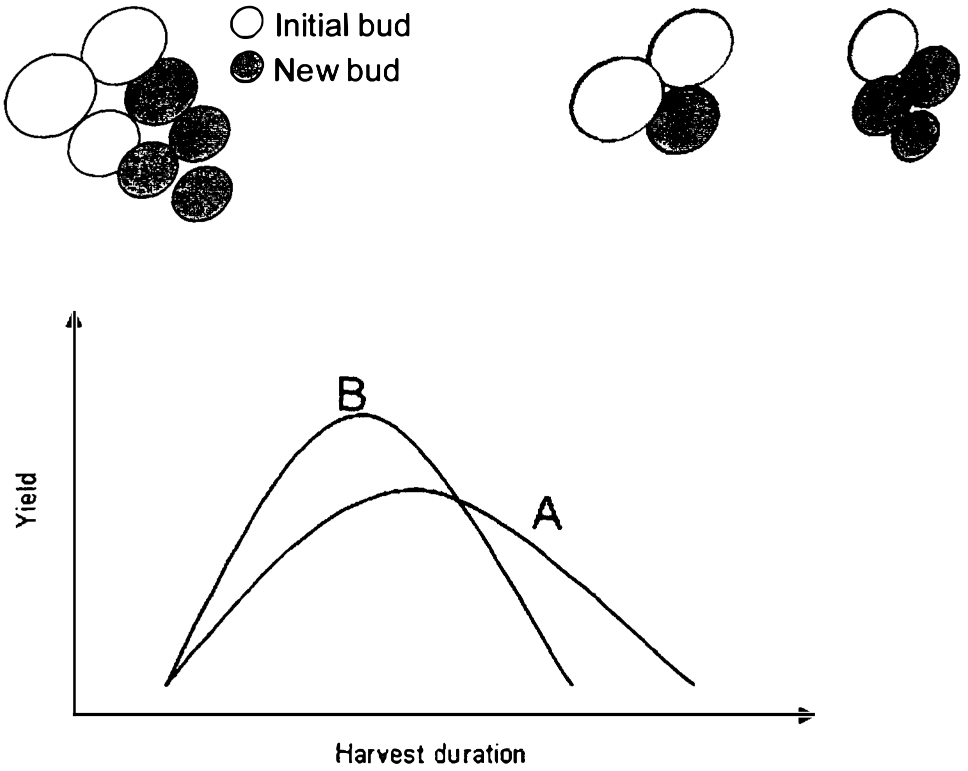
In an earlier study, Bigard (1973) followed bud development in one-year and three-year old asparagus plants and, after removing the leaf scales that covered the last buds in a bud cluster or buds adjacent to the spears, found small structures underneath the leaf scales that could be potential buds. Wilcox-Lee and Drost (1997b) found that bud number and bud size were affected by soil water potential (SWP). As SWP decreased from -0.05 to -0.5 MPa, numbers of total buds and viable buds reduced linearly. The authors claimed that decreasing SWP resulted in fewer medium diameter spears (<7.9mm) and more small (<4.9mm) and large (>8.0 mm) spears. Given the figures of spear diameter distribution from their results, the large diameter spears among treatments and the proportion to total spears harvested were approximately similar regardless of different SWP, and variation occurred in medium and small diameter sizes. This is similar to the current study in that spear fresh yield of large diameter spears (> 9 mm, quality 1 spears) produced were the same amongst cultivars (see section 3.4.2.2). Decreasing SWP may actually suppress bud size development, preventing enlargement of medium sized buds which then produced more medium and small diameter spears as shown in their figures. But it is not clear whether new buds that formed during the harvest season were initiated in early spring and developed during the harvest season, or they really initiated and developed during the harvest season. Further work is needed through rhizome dissection before and during the harvest season to clarify this point.

Some new buds developed during the harvest season had even formed spears or ferns, as shown in Expt 5 (Fig. 3.37-3.40). The usage of new buds rather than using the initial buds available from the previous summer season has several possible explanations.

Firstly, some of the initial buds may be dormant or dead. In Expt 5, buds that would be expected to form large or medium sized spears did not necessarily do so. Some of these buds were isolated (e.g. Fig. 3.38 Quadrat 3 A-B, 3B); some were in a position perpendicular to an adjacent cluster (e.g. Fig. 3.39 Quadrat 1A and 3B); and some were within a cluster that developed some spears (i.e. Fig. 3.38 Quadrat 3B and Fig. 3.40 Quadrat 4B). In Expt 4, when spear production was mainly from the small buds, resulting in thin spears, there were some large or medium buds present at the end of the harvest period that had not grown. These large or medium buds possibly went dormant, and the results complemented the findings in Expt 5. Bigard (1973) found that some buds located on the side of main axes of a cluster were dormant and Duangpaeng et al. (2002) observed that some buds became dormant when new buds developed into spears, whilst Wilcox-Lee and Drost (1997b) noticed that about 37 to 50 % of buds did not grow into spears, due probably to a short harvest period (1 month). The reason for some buds becoming dormant or dying is uncertain.

The second explanation is related to bud mapping. A single bud cluster could comprise 3 buds or as many as 9 buds or even more (Fig. 3.37-3.40). According to Nichols and Woolley (1985), as many as 7 buds on a single crown can start growing at the same time so long they are not in the same cluster. When a crown has many bud clusters but fewer buds within each cluster, harvesting spears could exhaust buds of larger size within a particular cluster, and this may trigger utilization of other clusters. With this situation, spear production may occupy a limited or extended period of time as illustrated in the proportion of the area under Gaussian fitted curves, depending on how many clusters are available and their size (Fig. 3.41). In terms of the crowns in Expt 4, t_{max} of large spears were mostly around week 8, but the production of thick spears went on beyond week 11 (Fig. 3.27). Extended production after t_{max} may involve utilization of new buds. This might have been confirmed either by tracking new buds or by continuously monitoring the buds within their clusters in each plant during the harvest period. However, this was not done in Expt 4. To some extent, Experiment 6 (see Chapter 4) used an aeroponics approach to track buds and spear development within a cluster.

A. Many large buds	B. Many large buds
With few clusters	With more clusters but few buds in a cluster



Possibility:

-Longer harvest due to correlative inhibition	- Shorter harvest because of possibility to grow earlier in small clusters than in large clusters
-Some large spears may be exposed to high temperature at later harvest which results in higher non-marketable yield	- Less prone to loss of head tightness due to earlier harvest and the spears could have tight and long head spear length

Figure 3.41 Possible patterns of harvest distribution based on spear diameter category with different number of buds and clusters on a crown.

The results of Expt 4 and Expt 5, related to t_{max} and bud clusters within a crown, emphasized the importance of bud number and bud size. The total yield of different spear diameters as described under Gaussian fitted curves suggested a dependency on morphology in terms of bud number and cluster distribution on a rhizome (Fig. 3.41). The type of bud and cluster distribution could vary substantially since asparagus is well known to be highly variable, even within cultivars. A possible interpretation of the influence of bud size and cluster distribution on the dynamics of bud production and yield is summarized in Fig. 3.41.

3.4.4. Total Soluble carbohydrate concentration (TSC)

Initial TSC (before harvest) in Expt 4 was higher in male plants than female plants (Fig. 3.36), but probably as a consequence of higher spear fresh yield (Table 3.7), dry weight (Fig 3.36) and spear number (Table 3.15), the male plants had significantly lower TSC than female plants after harvest. Fiala et al. (1979) showed that reserves accumulated in asparagus roots were more strongly utilized by male than female plants during active growth when the spears were formed, and at harvest time, sucrose was reduced more in male than female plants (Fiala and Jolivet, 1982). However, this does not necessarily mean that all-male cultivars will produce higher yields than dioecious cultivars (Benson et al., 1996). Although male plants produced more spears, the spears of male plants in some all-male cultivars were often smaller than female plants (Castanon, 1990). On the other hand, female plants may use carbohydrate reserves for forming berries later in the life cycle (Jones and Robin 1928 cited in Hughes, 1992; Hughes, 1992), resulting in fewer spears from female than male plants (Malhotra, 1930 cited in Moon, 1976).

CH did not affect TSC concentration of the root (Fig 3.32) despite greater dry weight production at high CH. Here, TSC concentration reduced more when producing many more short spears (low CH) compared to longer spears (high CH) even though the latter had higher total dry weight. Lipavska et al. (2000) found a high energy demand during bud break of Norway spruce (*Picea abies* L. Karst) for buds undergoing extensive structural and developmental changes. Applying this argument to asparagus, the requirement of energy for growing 2 spears at low CH should require more energy than when growing a single spear at high CH. Thus extending the harvest could result in proportionally greater carbohydrate reduction due to utilization of more small buds, as shown in 'UC157' in Expt 4 (Fig. 3.34).

3.4.5. Estimate of highest total yield and relationship between marketable and total yield.

Desirable cultivars should have high yield of high quality spears that have specific diameters, tight head and freedom from physical defects from pests and diseases (NZNAM, 1997; OECD, 2000). Many studies also indicate that quality of spears is related to good nutrient content. Measurements of spear nutrient content were mostly made on spear tips as indicators of shelf life (Hurst et al, 1993 a,b) since the tip is active metabolically (Hennion and Hartmann, 1990; Irving and Hurst, 1993) and tip condition is related to tip rot during storage (Lill and Borst, 2001). Amaro-Lopez et al. (1999) indicated that nutrient content was mostly highest close to the tip rather than close to the butt section of spears.

In the present work, total soluble carbohydrate (TSC) concentration of the spear, a contributing quality factor in term of sweetness in the spear, was measured in segments from the tip to the butt from spears at different CH (see Materials and Method section 3.2.2.3.3). The results showed that the average spear TSC concentration was not influenced by CH, CV or plant sex. However, it was influenced by the time the spears were harvested (Fig.3.31), and results suggested that the measurements of spear segments gave more information for whole spear TSC rather than measurement only at the tips. Hurst et al. (1993b) showed that spear tip soluble carbohydrate levels at harvest remained constant throughout the season and are therefore not a determinant of spear shelf life. Closer inspection of their figure of tip soluble carbohydrate showed similar results to the current study.

TSC concentration in spears from the current study was higher in the second month and this result can be related to high cumulative marketable spears during weeks 5 to 8 (Fig. 3.10-3.11). Plants produced highest quality 1 spears during week 5 to week 9 (second month) and higher quality 2 spears (Fig. 3.11), producing large (> 9 mm) to medium spears (5 < 9 mm). Moreno-Rojas et al. (1992) and Amaro Lopez et al. (1999) showed that as spear size decreased the mineral nutrient content also reduced. In Expt 4, TSC concentration as an indicator of sweetness increased when spears were mostly large and medium (quality 1 and quality 2). Thus, when most asparagus quality 1 and 2 spears were produced, within weeks 5 to 9, the spears also had higher TSC concentration, indicating a better quality in terms of nutrient content.

Obtaining high, sustainable marketable spear yield is the aim of every grower. The highest prediction of total yield and marketable yield occurred at CH 30 cm (Fig. 3.19 and 3.20). Marketable yield contributed to 80% of total yield in Expt 4 (Fig. 3.20). But, cutting spears more than 30 cm will only increase non-marketable yield (Karno, 1999).

3.4.6. Influence of bud number and TSC concentration on yield

Selection for high total yield in asparagus is based on both total spear number and spear weight (Cointry et al., 2000). In the current study, the spear number of female plants was not different from male plants for 'UC157' which produced the highest total spear number amongst cultivars (Table 3.14). Female plants of 'UC157' produced a higher total cumulative fresh weight (Table 3.7), indicating that the spears of female plants were thicker than those in male plants. Hughes (1992) found that female plants appeared to be more efficient at producing dry matter than male plants but this efficiency appeared to be dictated by sink demand i.e. berries in female plants. In terms of crown weight, she found male plants had larger crowns than female plants before and after harvest although there was no difference in their carbohydrate concentration. In Expt 4, TSC concentration of male plants was significantly higher before harvest but significantly lower after harvest (Fig. 3.36), but crown weight was not measured. If male plants tend to have bigger root systems but the same or bigger change in TSC concentrations the implication is that carbohydrate is not being used as efficiently. In 'UC157' female plants yielded more than males in our experiments, yet decrease in TSC concentration was less. Fiala and Jolivet (1979) reported that the male plants utilized more carbohydrate to support spear growth. Another possibility is that when TSC concentration is high, the initial carbohydrate is more readily available and used less efficiently.

The reduction of total TSC will be based, not only on spear growth, but also root respiration. Whilst 'Atlas' produced the highest total spear dry weight, the trend of estimated carbohydrate loss due to spear growth (Fig. 3.35B) indicated carbohydrate loss of 'Atlas' were less compared to the other three cultivars. However, root masses of the plants in this experiment were not measured. Because the plants had 9 months of fern establishment in similar sized pots, root mass has been assumed to be the same amongst cultivars before harvest. Cultivar Atlas had a significantly higher TSC concentration but the lowest reduction in TSC concentration during harvest of 49% compared to 69.8 %, 67.9 %, 56.8 % for 'UC157', 'Grande', and 'Apollo, respectively. Higher reduction of TSC by male plants than female plants was observed in 'UC157', 'Grande' and 'Atlas'.

By looking at the total cumulative dry weight of asparagus in Expt 4, 'Atlas' (41.23 g.plant^{-1}) was also the highest followed by 'UC157' (40.83 g.plant^{-1}). It was not clear whether this reduction was related to the efficiency of each cultivar in utilizing the carbohydrate reserve for spear production or for other purposes such as respiration and bud development. In this case, 'Atlas' was able to produce higher yield while TSC concentration reduction was lowest. On the other hand, 'UC157' was almost the lowest yield, close to 'Grande' in terms of total spear dry weight, but TSC concentration reduction was the greatest.

3.4.7. Buds and potential production

It is now clear that buds developed during the harvest season and thus contributed to total buds available during the next season. Some of the new buds, which were developed during harvest, further developed into spears and ferns. The sequence of bud development and usage is summarized in Fig. 3.42, drawing on results from Expt 4 and Expt 5. The field data related to only four 1m^2 plots, and interpretation in the following discussion is based on values for these plants.

Spear production during harvest used up 57% (84 buds) of total initial buds (148 buds) from the previous season (Fig. 3.42 – harvest period) and left 17 buds (12%) as dormant buds (Fig 3.42- summer) potentially able to contribute to the following harvest season (Fig 3.42 – winter). Further usage of buds by extending harvest only led to small spears, demonstrated by the yield in Expt 4, and if the spears were not harvested then they could turn into small ferns. Extending harvest could also trigger the new buds for subsequent development. New buds were reasonably vigorous since only 2% (1 bud out of 54 total new buds) of them were found dead in the summer. Approximately 9 buds (16%) of new buds turned into spears, but were not harvested and further developed into ferns in the summer, and an additional 7 buds (13%) of the buds became ferns and did not develop into spears in the harvest season. The total percentage of new bud usage for spears and ferns was 16 buds (29%), leaving 37 buds (69 %) dormant and potentially contributing to the next harvest season. These new buds could potentially become larger than the buds formed later in the summer, and therefore could be the buds contributing to high marketable yield of large spears in the following harvest. Further mapping just prior to harvesting in the following spring is required to determine just how many of these buds are still viable as considerable bud death can occur over winter.

The ferns counted during the summer were on average 37 whilst there were 49 ferns from mapping, leaving a difference of 12 between the two assessments (Fig. 3.42 – box Fern in summer). These 12 ferns could possibly come from the initial buds since there were about 24 initial buds un-accounted by the end of summer leaving twelve initial buds untraced and possibly decayed (8%) during the summer period. At the end of summer, there were 202 buds counted. The total buds at the end of summer was the summation of initial buds (17 buds), new buds (37 buds), and summer buds which were produced during the summer. Thus during the summer, the ferns actively produced 148 buds, which were called summer buds. These summer buds together with initial (17) and new (37) buds summed to 202 buds available after summer (Fig. 3.42), and may progress through winter into potential production in the following harvest.

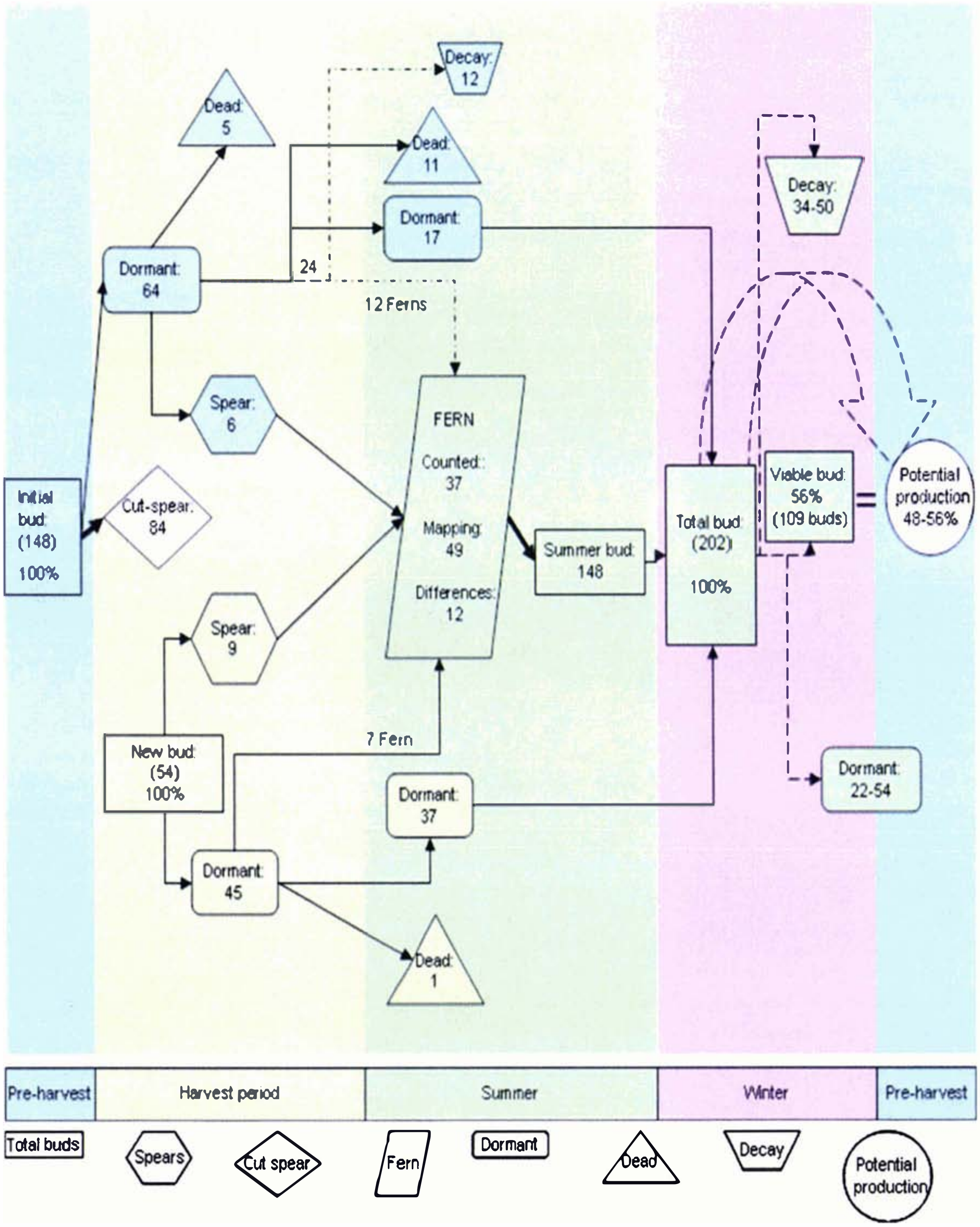


Figure 3.42 Seasonal bud kinetics and potential spear production of asparagus.

During the winter, the buds would be exposed to damage and reduced viability. Wilcox-Lee and Drost (1997b) noticed that there were some buds left after harvest, accounting for 37 to 50 % of the total initial buds. Previously Wilcox-Lee and Drost (1997a) pointed out that decreasing SWP resulted in an increase in non-viable buds. Following these two situations, viable buds could possibly go dormant until the following harvest season, or die. Adverse environmental conditions such as low SWP can reduce bud viability and thus total number of buds available for spear production. In the current study, the evidence suggested that 11-27 % of the buds, counted between harvest period and summer, became dormant and 17-25% may have decayed, leaving 48 – 56 % (96 – 113 buds) of the population potentially available to develop into spears in the next harvest season.

3.4.8. Conclusions

The results from this chapter have indicated the potential importance of bud dynamics and the balance between bud dynamics and TSC reserves in controlling spear number and size. Nevertheless, dealing with underground organs was difficult and conclusions can only be tentative. Experiments conducted in the succeeding chapters were planned to overcome this problem by growing plants in hydroponics or aeroponics.

CHAPTER 4

CORRELATIVE INHIBITION AND SPEAR GROWTH OF MATURE ASPARAGUS PLANTS GROWN IN AEROPONICS†

4.1. INTRODUCTION

The rate of spear growth plays an important role in determining yield of asparagus (*Asparagus officinalis* L.) in a limited growing season. The length of the asparagus harvest season is dictated by environmental factors such as soil and air temperature and plant factors such as bud number and level of carbohydrate storage. As temperature increases in early spring, bud break occurs and the buds grow into spears, the edible part of the asparagus plant. When the temperature increases, spears grow faster (Kailuweit and Krug, 1995; Dean, 1999). As a result, spears need to be harvested more frequently. Estimates of the temperature which optimises the rate of spear elongation vary from an optimum of 20°C (Blumenfield et al., 1961), between 20 and 30°C (Nichols and Woolley, 1985), between 25 and 30°C (Hughes, 1992) depending on the plant age, to between 24.5 and 33°C (Dean, 1999). Effect on harvest frequency will be greater if the spears are cut short (12 - 17 cm length) rather than cut longer (18 – 27 cm length).

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†Part of this chapter was presented in ComBio2000 Meeting, Australia Soc. for Biochem & Mol. Biol., Australia Soc. of Plant Phys., New Zealand Soc. for Biochem & Mol. Biol., New Zealand Soc. of Plant Phys. Wellington, 11-14 December 2000 with authors and title:

Daningsih, E., David J. Woolley, Mike A. Nichols and Keith J. Fisher.
Apical dominance and spear elongation of *Asparagus officinalis* L. in relation to carbohydrate availability

Spear growth in asparagus has been reported to be affected by correlative inhibition between spears (Nichols and Woolley, 1985). This inhibition was variable. If there was separation of growth initiation of buds by at least 12 hr, there was a linear decrease in relative growth rate from spear 1 to at least spear 3 and often spear 6. Any subsequent spears in the same flush showed an inhibited growth rate until most of the earlier spears had been removed, at which time growth rate increased abruptly. If two or more spears started more or less simultaneously (less than 12 hours apart), relative elongation rates were similar (no correlative inhibition). However, the growth rate of subsequent spears was extremely inhibited until most of the spears had been removed. Moreover, Nichols and Woolley (1985) suggested that inhibition in these young crowns could occur between clusters since there was considerable interaction between spears coming from different clusters.

This inhibition of one spear by another was defined as apical dominance by Kretschmer and Hartmann (1979) but defined as correlative inhibition by Nichols and Woolley (1985). Apical dominance itself is the most commonly investigated form of correlative inhibition in which the growth of the apex of a shoot inhibits the development of dominated lateral buds or lower shoots on the same shoot. The bud clusters of the asparagus crown represent a compressed stem, and appear to have a level of correlative inhibition, typical of a plant with a moderate to strong apical dominance (Nichols and Woolley, 1985). However, in the case of spear growth, it appears the basal buds start growing and inhibit spears **above** them, and also possibly spears on other clusters. It is therefore best to refer to this phenomenon in asparagus as one of the many forms of correlative inhibition.

Apical dominance in many plants is influenced by hormones, nitrogen, carbohydrate, and water stress (Woolley and Wareing, 1972a, b, c; McIntyre 1972, 1976, 1977; Nigam and McIntyre, 1977; Braun and Kender, 1985; Cline 1994; Kotov, 1996). The auxin indoleacetic acid (IAA) is thought to be the primary hormone involved in apical dominance, suppressing the growth of lateral buds or shoots in many plants. But how IAA inhibits lateral buds is not clear; and much evidence seems contradictory (Hall and Hillman, 1975; Bangerth, 1989). In asparagus, "apical dominance" was weakened by the application of gibberellic acid (GA) (Kretschmer and Hartmann, 1979), but in another study, GA did not promote spear growth (Mahotiere, 1976). When the auxin naphthalene acetic acid (NAA) was applied to asparagus, spear growth or spear number was not affected (Kretschmer and Hartmann, 1979). Inconsistent results were also found in other plants in apical dominance responses to nutrients, such as nitrogen and carbohydrate, and water stress. The nutrient diversion hypothesis for apical dominance proposes that the apical meristem of a plant acts as a strong metabolic sink, depriving nutrients from the latent axillary meristem and thereby promoting strong directional (e.g. vertical) growth with little branching (Lortie and Aarssen,1997). These authors found that branching was increased by shoot apex removal and was enhanced by the addition of nutrients but only in clipped plants of snapdragon (*Verbascum thapsus*). Thus the nutrient diversion theory does not solely explain the strong apical dominance exhibited by *V. thapsus*. On the other hand, McIntyre (1997) proposed that carbohydrate and nitrate affected apical dominance by a combination of osmotic and nutritional effects. The effect of nutrients such as urea (0.5%) and sucrose (0.5%) spray was exhibited in mango (Sivagami et al., 1989). Urea increased leaf carbohydrate levels but apical dominance was suppressed by growth regulator treatments using cycocel at 6000 ppm (chlormequat), TIBA at 500 ppm, Ethrel at 2000 ppm (Ethephon) or alar at 2500 ppm (daminozide). Furthermore, McIntyre (1973) showed that in some species such as *Agropyron repens* and *Linum usitatissimum,* lateral bud growth can be controlled by varying the nitrogen and carbohydrate supply, while in others such as *Pisum sativum, Phaseolus vulgaris* and *Helianthus annuus*, such control can be achieved only if degree of water stress is sufficiently reduced or if there is no water stress.

The number of spears produced depends on the number of viable buds and the interaction between buds and carbohydrate storage in the roots. Since asparagus growth relies on carbohydrate formed the previous year, the level of correlative inhibition may be influenced by carbohydrate availability. In asparagus, carbohydrate available for spear growth is stored mostly in storage roots, but no study has investigated the relationship between correlative inhibition and root carbohydrate storage. This work was intended to provide information which might serve as the basis for subsequent, more detailed investigation concerning the role of carbohydrate in the regulation of bud activity.

Asparagus spear measurement in the field is very labour intensive (Brown, 1984; Feher, 1992) even when only spear quantity and quality are being determined. Measurement of spear growth rate on a daily basis in the field is also demanding. Wilson et al. (1999) measured spear length in the field from the base at soil surface to the tip. They dealt with soil and air temperature adjustment to make predictions of spear growth rate in the field. To overcome uncertainty about development beneath the soil surface, they made the assumption that below ground spear elongation behaves in a similar way to above ground growth. However, since asparagus crowns are not flat and their depth varies, initial spear lengths below ground would vary. Spear growth rate is also affected by type of soil (Kailuweit and Krug, 1995) and crown depth (Takatori et al., 1974; Lindgren, 1990). Therefore measurement from the base of spears may be more representative of the over all growth pattern. With an aeroponics system the crown is easily accessible, simplifying measurement of buds and roots, as well as total spear length. Planting asparagus in aeroponics thus reduces confounding factors related to spear growth in soil and crown depth, and should assist precise spear measurement.

In the work described in this chapter the kinetics of spear growth in asparagus, grown in an aeroponics solution with differential removal of storage root is reported.

4.2. MATERIALS AND METHODS

4.2.1. Plant Materials: Experiment 6

Asparagus plants 'UC157' were grown in aeroponics over two periods of six months. After the second growing period, plants were harvested between 30 August and 5, September, 1999, and all the ferns and spears were separated from the crowns. The crowns were then cleansed using tap water to remove dead roots and other debris before they were stored at 1°C. The plants were transferred back into the aeroponics system on 21, October, 1999 for the experiment.

4.2.2. Aeroponics system

4.2.2.1. Aeroponics system and plant placement in aeroponics

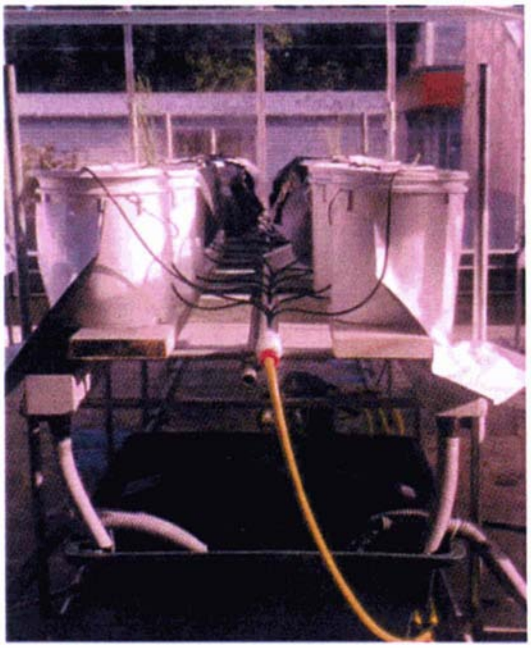


Figure 4.1 Aeroponics system for asparagus plants using rounded plastic containers in a greenhouse.

The aeroponics system was built using 20-litre white plastic containers with lids. There were three blocks, each containing 20 containers which were laid parallel in two rows (Fig. 4.1). The buckets as well as the covers were painted black inside to reduce light and to avoid algae growth. The aeroponics system consisted of five major parts (Fig. 4.2):

(1) Nutrient supply/reservoir was placed on the floor in a large square plastic container. The nutrient solution moved from the reservoir through one irrigation pipe (d=16 mm) connected to a pump.

(2) A pump (Type CP 11 MONO, Model MPE 524-HHG 3-90, 180 watt, rpm 1500) with filter was used to ensure continuous movement of nutrient solution through the system: nutrient coming from the reservoir was filtered then pumped into the system at a rate of approximately 5 litres per minute continuously. From the pump, a branch of three pipes was made from 13 mm ID garden hose. One pipe was connected to each of the three main PVC pipes running between the double rows of chambers in each block. .

(3) Main PVC pipes ran between each double row of buckets: 40 feeding tubes or drip tubes (d = 3 mm) were connected into each main PVC pipe. Two feeding tubes were connected into semi-closed chambers. A jet spray (V-Shape Mister) with 360° directional adjustment was attached at the end of each feeding tube.

(4) Semi-closed chambers were made from 20L plastic containers: the nutrient solution entered each semi-closed chamber through 2 feeding tubes. The position of these 2 feeding tubes was facing one another (180 degree) hanging below the cover of the chamber at the sides of the crown.

A hole with diameters ranging from 6 to 20 cm was made in the middle of each cover to form a support for the crown. This support consisted of two flexible galvanised wires crossing each other at right angles and attached to the edge of the container cover. The cross-wires formed a downward arch into each container.

At the bottom of the chamber, one drainage hole was made for the outlet of nutrient solution return via guttering.

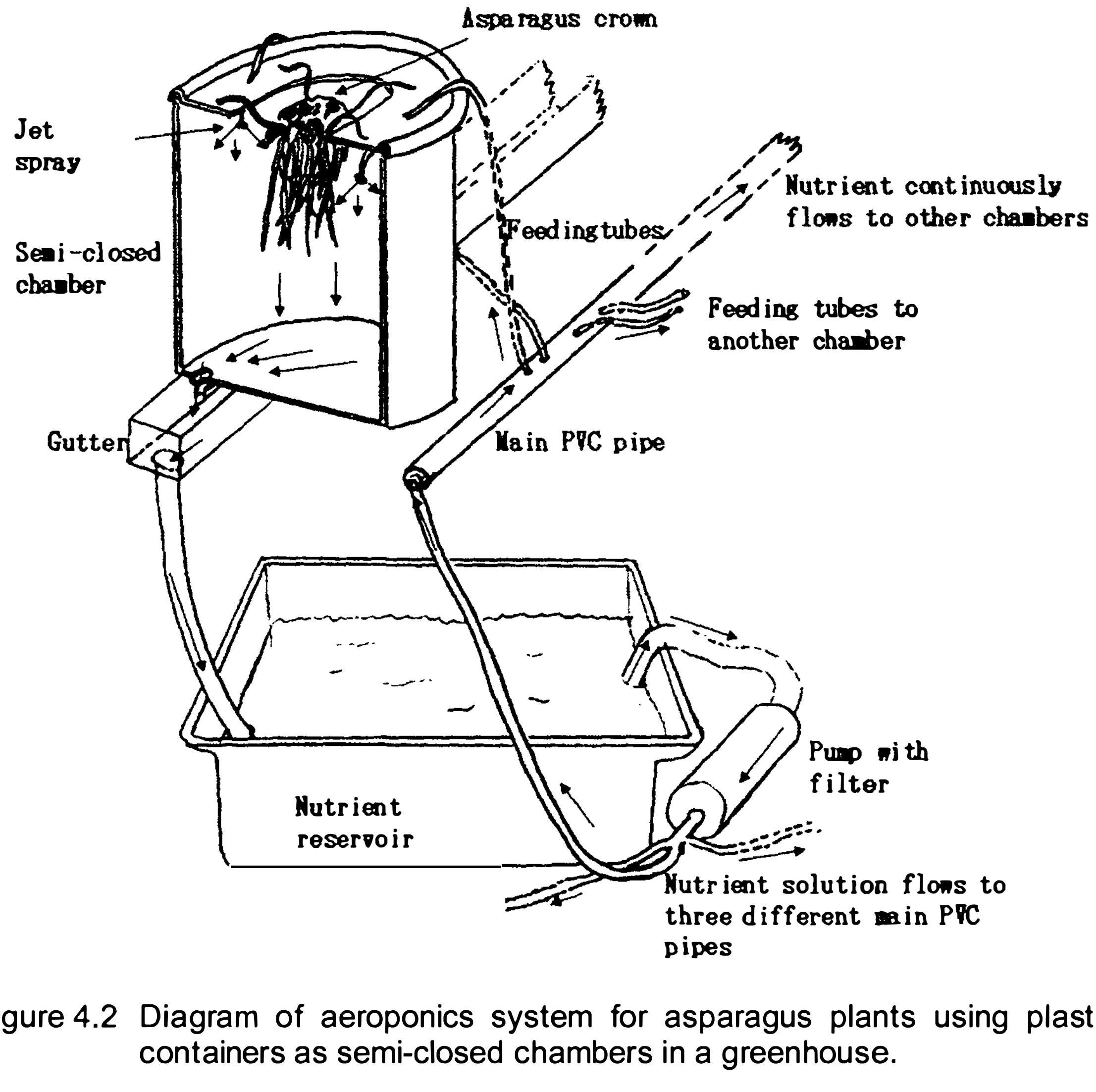


Figure 4.2 Diagram of aeroponics system for asparagus plants using plastic containers as semi-closed chambers in a greenhouse.

(5) Guttering made from square PVC tube was placed beneath each row of containers (chambers) to collect the solution coming from the chambers and return it to the reservoir tank by gravity.

Double sided (black and white) polythene sheets (Panda film) covered the sides of guttering to avoid algal growth during the experiment. The white side faced outward to reflect the light. The nutrient solution tank was covered by Styrofoam and Panda film for the same purpose and to reduce contamination. Panda film was also placed on the top of each cover to reduce root exposure to the light and reduce excessive evaporation.

Nutrient solution misting was applied continuously to the plants at an electrical conductivity (EC) of 2.0 mS.cm^{-1}. Daily checking of EC and pH was done in the morning and pH was kept between 6.0 and 6.5. The nutrient solution was replaced every two weeks to avoid imbalance in nutrients. Checking of jet sprayers and drainage holes from chamber to the guttering was done daily to avoid clogging.

The aeroponics system was placed in a greenhouse automatically heated at 15°C and vented at 25°C. The greenhouse was covered with white shade cloth to reduce sunlight by approximately 20%.

4.2.2.2. *Aeroponics Solution*

Table 4.1 Composition† of aeroponics stock nutrient solutions.

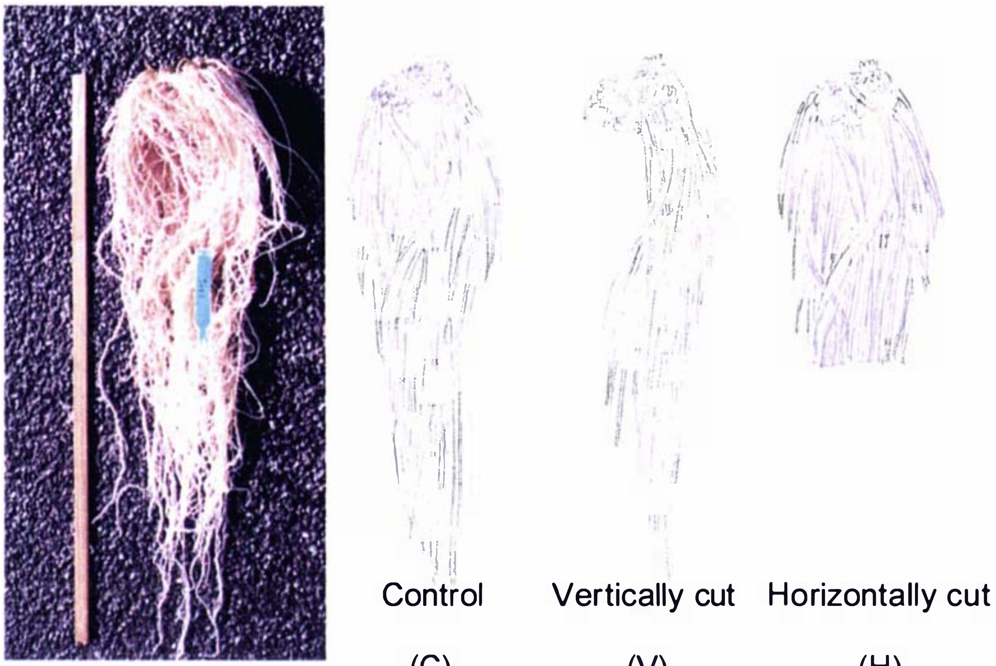
Mixture	Compounds	Quantity (kg/20L)
A	$CaNO_3.4H_2O$ (Calcium nitrate)	1.976
B	KNO_3 (Potassium Nitrate)	1.316
	KH_2PO_4 (Potassium dihydrogen phosphate)	0.544
	$MgSO_4.7H_2O$ (Magnesium sulphate)	0.993
C	FeNa (Chelate iron)	0.158
D	$MnSO_4.H_2O$ (Manganous sulphate)	12.300
	H_3BO_3 (Boric acid)	3.420
	$CuSO_4.5H_2O$ (Copper sulphate)	0.550
	$(NH_4)_6Mo_7O_{24}.4H_2O$ (Ammonium molybdate)	0.184
	$ZnSO_4.7H_2O$ (Zinc sulphate)	0.620

†Modified from Cooper (1979).

The aeroponics solution (Table 4.1) was made by mixing four stock solutions modified from Cooper (1979). Solutions A and B contained macro nutrients whereas solutions C and D contained micronutrients. Equal volumes (60 mls) from each stock solution added to 5 l of water would make up nutrient solution with an electrical conductivity (EC) of 2.1 $mS.cm^{-1}$. A pH of 6.5 was maintained by adding 1% KOH or 10% phosphoric acid during the experiment.

4.2.3. Treatment and experimental design

A Randomised Complete Block Design (RCBD) with three replications was used. The crowns were subjected to three levels of storage root removal as the treatments (Fig. 4.3) by removing the lower half length of all roots (horizontally cut = H), and removing all root from one side of the crown (vertical cut = V), or no removal (control = C). Cutting root horizontally resulted in variation of reduction as a percentage of total crown (plus root) weight between 15 and 28 % by fresh weight whilst cutting root vertically was equivalent to between 11 and 38 % reduction. The crowns were separated into three size categories based on fresh weight. Small crowns weighed from 16 to 60 grams, medium crowns weighed from 85 to 275 grams and large crowns weighed from 331 to 799 grams.



Control (C) Vertically cut (V) Horizontally cut (H)

Figure 4.3 Three levels of asparagus storage root removal: no removal (control=C), removing all roots from one side of the crown (vertically cut = V), removing the lower half length of roots (horizontally cut = H).

4.2.4. Bud mapping and spear harvest

For each crown, bud clusters were mapped to show their position within the crown. The length of each spear produced was recorded daily. The position of individual spears was mapped for each cluster in each crown between 24 September and 15 October 1999 in the cooler before the experiment started. During spear observation, the first spears in each cluster were tagged with coloured plastic-coated wire tied loosely around the base of the spear. Tagging with a different colour for each cluster made easy identification of cluster location. Once the spear was harvested, this colour coded wire was moved to the subsequent spear in the same cluster and so on.

Figure 4.4 Spear elongation and tag within a cluster on an asparagus crown grown in aeroponics.

For this experiment, spear growth was defined as starting when the tip of the bud was not covered by leaf scales and was recognized by the cone-like form (Fig. 4.4). Therefore the initial length of the spear varied in accordance with the size of the bud. Spear elongation was measured by dividers from the base to the tip of the bud. The distance between the two points was obtained to the nearest 0.5 mm. When the spear length reached more than 3 cm, the spear length was measured by using a piece of flexible wire which conformed to the curve of the spears measured. The wire was placed from the base along the side of the spear to the tip and then straightened and measured. Spears were measured daily over a period of 21 days and at approximately the same time each day. The first spear measurements were on block 1, then block 3 and lastly block 2. Spears were harvested once the spears reached at least 200 mm in length and their fresh and dry weights were determined. Base diameter and head tightness of the spears were also recorded. Spear diameter at the base was measured using digital calliper (Model CD-6, Mitutoyo Corporation, Japan). Spears were categorized into 4 groups based on their spear diameter as described in Chapter 3.

4.2.5. Methods to define spear relative growth rate and correlative inhibition

4.2.5.1. Relative Spear Growth Rate (RSGR)

Nichols and Woolley (1985) calculated spear relative growth rate using the natural log of spear length. Exponential spear elongation became linear when converted into natural log. These log transformed data were regressed against time. The slope of the regression was used as a measure of spear elongation rate and expressed as Relative Spear Growth Rate (RSGR). This method is only valid if spear growth is exponential. For the current experiment, some other configurations (shape) of actual spear elongation, as well as natural logs of these, are presented.

4.2.5.2. Correlative Inhibition (CI)

Overlap, lag and inhibition periods were calculated between pairs of spears coming from the same cluster according to the position from the bud map. These periods reflected the stage of the buds: a) dormant period (visually bud did not show any growth activity), b) primed bud (active bud ready to grow but not yet elongated), and c) elongating bud.

An "overlap" period was defined as when two spears grew concurrently. Overlap days were calculated from the day the subsequent spear started to grow until the day the previous spear was harvested (Fig. 4.5).

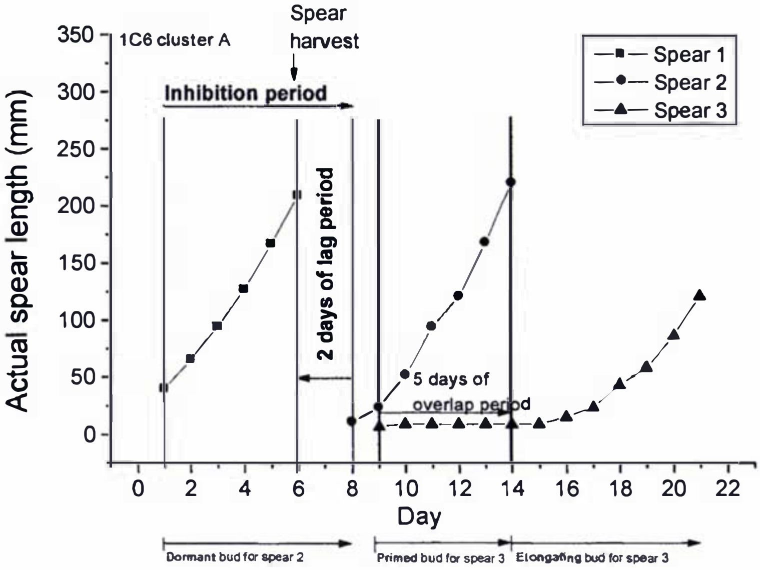


Figure 4.5 Three different periods between pairs of asparagus spears: 1) overlap period (time when two spears grow concurrently), 2) lag period (time between harvest of the previous spear and growth of the following spear), and 3) inhibition period (time was counted from the day of previous spear initially grew to the day the following spear started growing quickly or exponentially).

Positive values indicated an overlap occurrence while negative values indicated no overlap between two spears. Lag period was the time between harvest of the previous spear and appearance of the following spear (Fig.4.5).

When a spear grew before the previous spear was harvested, the lag period was counted as 0. The lag period was counted from the day the previous spear was harvested to the day the following spear started to grow quickly. The inhibition period was counted from the day the previous spear grew to the day the following spear grew quickly or exponentially. These three different categories of periods were used to define whether correlative inhibition existed and to define its strength.

4.2.5.3. *Spear harvest*

Spears were harvested once the length reached 200 mm. Spear diameter at the base and fresh weight of each spear were recorded. In relation to bud dynamics, spear quality was categorized into 5 groups as described in Chapter 3 (section 3.2.2.4.2).

4.2.6. Statistical Analysis

Before the data were regressed against time, the original data of spear length were plotted against time. Each of these graphs was related to its specific crown so that it could be identified as to whether this spear was located on full support, half or minimal storage roots. In the control treatment (no root cutting) all the spears came from full support of storage root (Site A). On the other hand, all spears in half length of cut root had roughly half storage roots (Site B), whereas in vertically cut roots some spears may have come from minimal storage roots (Site C) and some others from full storage roots (Site D). These conditions were built-in as the SITE variable.

Spear length data were transformed into natural logs. The shapes of transformed data were identified as exponential, quadratic, linear, or a combination of these shapes. The shapes of transformed data were tallied according to crown size, treatment or site.

4.2.6.1. *Derived variables and statistical analyses*

Spear length data were transformed into natural log and regressed against time. The slope of the regression was used as a measure of spear elongation and expressed as Relative Spear Growth Rate (RSGR). These RSGR were calculated for spears using the values at the point when growth started near exponential or exponential. This methodology of RSGR has been described by Nichols and Woolley (1985).

Standard analysis of variance using Proc GLM in SAS (SAS Version 8.2, 1999-2001) was used. The RSGR was used to quantify the effect of crown size and root cutting treatments on elongation rates. A simple linear model using proc REG in SAS were fitted to the log of spear elongation (RSGR). These regression equations were fitted to show the changes of the elongation rate pattern of the spears over time with different amounts of storage root. The first set of GLM analyses tested the effects of different amounts of storage root (treatment), size of crown and their interaction. Additional analysis using three groups of cluster numbers was also done. These three groups were 1 cluster, 2-3 clusters, and > 3 clusters per crown.

4.2.6.2. Spear appearance

Shape categories of spear kinetics were defined and assessed through natural log of spear elongation. Counting for each spear shape was done for each combination of root cutting treatment and crown size. The shapes were tabulated for their distribution within each crown size, root cutting treatments and sites. Since the dependent is categorical, testing the distribution of the shapes due to treatments was conducted using Log-linear models in PROC GENMOD. Log-linear model is one of the specialized cases of generalized linear models for Poisson-distributed data. Log-linear analysis is an extension of the two-way contingency table where the conditional relationship between two or more discrete, categorical variables is analyzed by taking the natural logarithm of the cell frequencies within a contingency table (Jeansonne, 2004). In addition, the variables investigated by log linear models are all treated as “response variables” (Jeansonne, 2004). The function used in log-linear analysis is the log of the dependent, y (http://www2.chass.ncsu.edu/garson/pa765/logit.htm).

Periods of lag and inhibition for successive spears were correlated to each other. The lag, inhibition, and overlapped periods of spears were analysed using GLM procedure to test for differences in treatments, crown size, and site as related to spear elongation. Residuals were plotted to check normal distribution of the data, and data transformation was done if necessary.

4.2.6.3. Harvested spears

Proc GLM was run to detect differences in spear fresh weight due to root cutting treatment, size of crown effects at different spear categories described in 4.2.5.3.

4.3. RESULTS

4.3.1. Crown

The numbers of clusters within a crown varied among the three different crown sizes (Table 4.2). Small crowns had mostly one or two clusters within a crown. Medium crowns had from one to six clusters and large crowns had from two to more than 10 clusters. Two large C (Control) crowns had 11 and 13 clusters and one large V (Vertically cut) crown had 16 clusters.

Table 4.2 Expt 6: The number of clusters within an asparagus crown for different sizes.

Size of crown	Trt	Number of cluster										
		1	2	3	4	5	6	7	8	9	10	>10
Small	C	3	2	1	0	0	0	0	0	0	0	0
	H	5	0	1	0	0	0	0	0	0	0	0
	V*	1	3	0	1	0	0	0	0	0	0	0
Medium	C	2	0	2	1	0	1	0	0	0	0	0
	H	1	1	1	1	1	1	0	0	0	0	0
	V	3	1	0	0	1	1	0	0	0	0	0
Large	C	0	1	1	0	1	1	0	0	0	0	2
	H	0	0	1	0	1	2	0	1	1	0	0
	V	0	2	1	0	1	1	0	0	0	0	1
Total		15	10	8	3	5	7	0	1	1	0	3

C = Control (no root removal); H = Horizontally cut; V = Vertically cut
* = one plant was dead

4.3.2. Actual spear elongation

Generally the elongation of early spears was exponential (e.g. 1C3 in Fig. 4.6, where 1C3 = Crown size ***1***, Control ***C***, Rep ***3***), but later spears elongated more linearly rather than exponentially (third spear in cluster A in this case) and later spears tended to have slower rate of growth (second spear at cluster C). In this example there was a lag between harvest and growth of the succeeding spear in all three clusters.

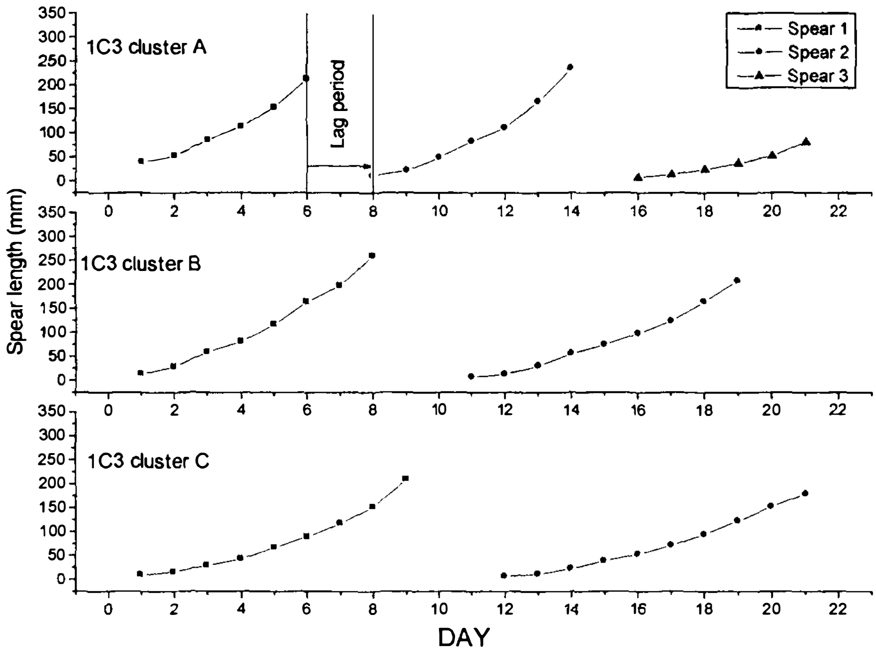


Figure 4.6 Expt 6:Lag period between two consecutive spears and spear elongation within each cluster on an asparagus crown grown in aeroponics in a greenhouse.

In this case spears grew sequentially, but spear elongation was not always exponential, or showed two distinct exponential phases, (see Fig. 4.16 in the next section).

Figure 4.7 illustrates exponential growth for spear elongation, lag periods, inhibition and overlap. In cluster A, the second spear did not grow until two days after the first spear was harvested. The third spear appeared on the second day after the second spear started growing but did not grow exponentially until the second spear was harvested. Here the second and third spears overlapped for 6 days. The third spear grew very little and took another one day lag before growing quickly.

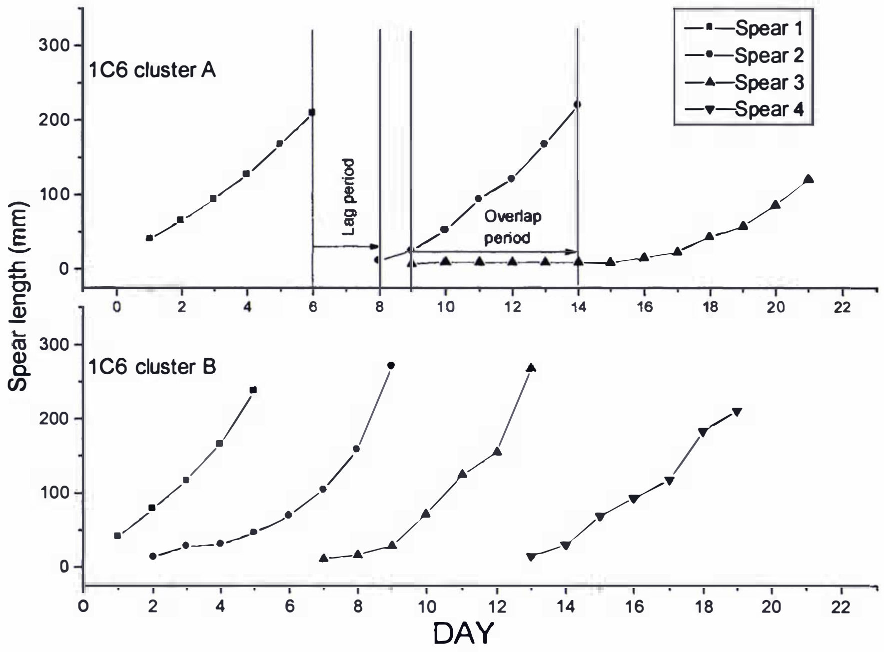


Figure 4.7 Expt 6: Spear elongation, lag period, inhibition period and overlap period occurring in different clusters on an asparagus crown grown in aeroponics in a greenhouse.

However, inhibition of spear elongation in cluster B was weaker than in cluster A. Although there was an overlap period for 4 days between the first and second spears, the second spear still grew exponentially. In addition, three days of overlap between spear 2 and 3 did not totally reduce growth of spear 3.

A more complex situation associated with spear elongation occurred in the following example (e.g. 1C4, Fig. 4.8), where four spears initially grew simultaneously. The first and third spears grew almost at the same rate over 7 days. The second spear was able to elongate at almost a similar speed to the third spear for the first four days. After that, it grew at a very slow rate until one day after the first and third spears were harvested. The fourth spear, however, grew exponentially - at a slightly lower rate than the third spear.

When natural logs were applied to compare elongation between the two spears, the rate of $\log_e$ spear elongation for the third and fourth spears was 0.4849 and 0.4057, respectively. The fifth spear appeared 2 days after the second spear was harvested.

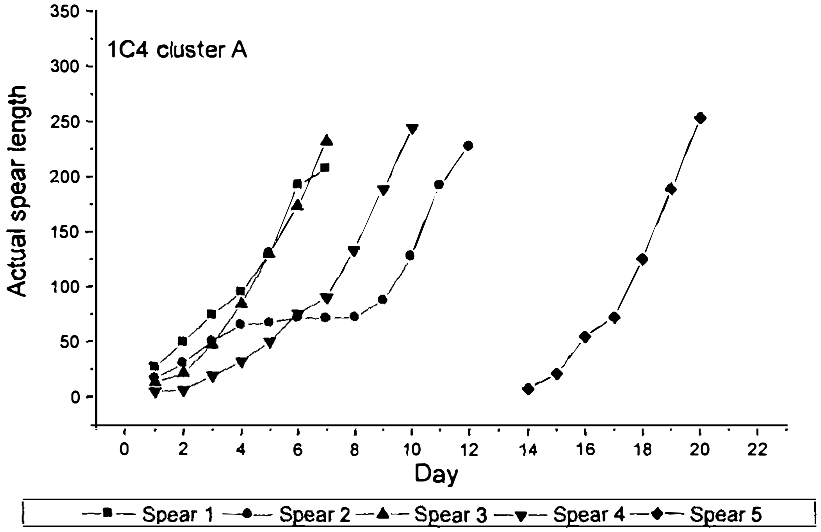


Figure 4.8 Expt 6: Growth inhibition among spears growing at the same time within a cluster on an asparagus crown grown in aeroponics in a greenhouse.

Exponential spear elongation also occurred in horizontally cut (H) crowns, as in Fig. 4.9. A slow rate of spear elongation before growing quickly was noted often on spears within H crowns.

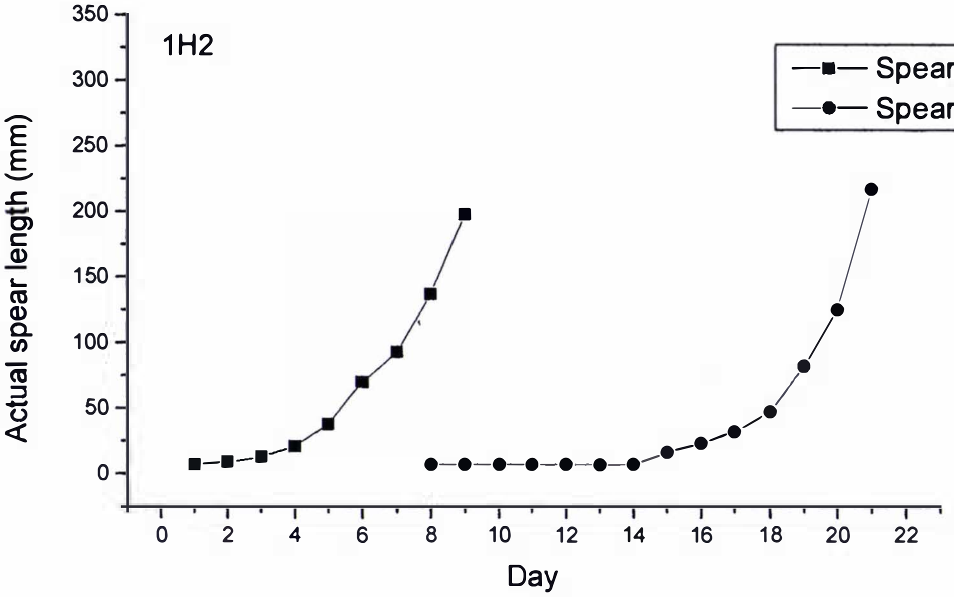


Figure 4.9 Expt 6: Slow growth of 2 consecutive spears within a cluster on a crown with horizontally cut root.

Unique configurations were observed for the following spears (e.g.1H1, Fig. 4.10). When two spears grew together, their responses were different. For the first pair (first and second spears), the two spears grew parallel for 6 days. Then, the first spear grew rapidly until harvest whilst the second spear was inhibited for 4 days, the duration of time for the first spear growing quickly before harvest. The second pair (third and fourth spears) appeared and overlapped for two days with the second spear. Whilst the third spear grew somewhat linearly, the fourth spear grew very slowly for 4 days before growing exponentially within the same time frame as the third spear.

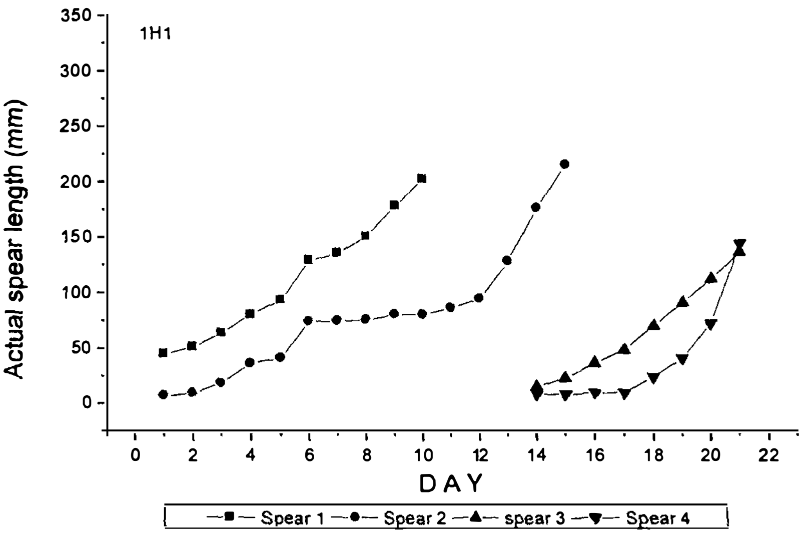


Figure 4.10Expt 6: Possibilities of partial inhibition between a pair of asparagus spears within a cluster when the two spears were growing at the same time.

In the following crown, spears came from sites of different root condition (e.g. 1V4, Fig. 4.11). Spears at cluster A were supported by full roots and grew mostly exponentially. There were some signs of inhibition for 5 days between the first and second spears, 9 days between the second and third spears and between third and fourth spears. Within a pair of spears, the subsequent spear would grow quickly after the former spear was harvested.

Spears in cluster B grew with minimum root support. All six spears grew initially; however, only two spears grew to the height required for harvest.

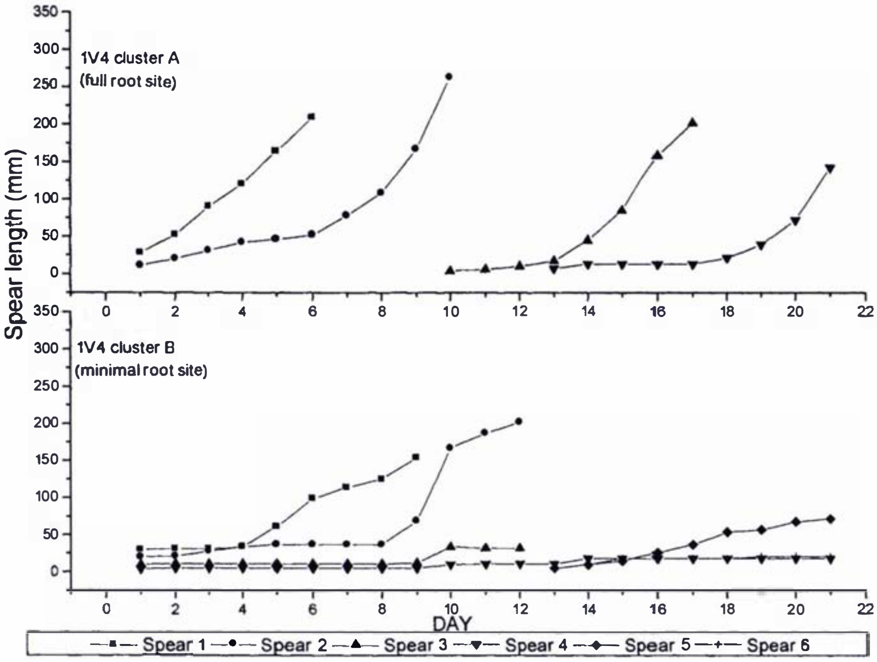


Figure 4.11 Expt 6: Several spears coming from minimal root site of rhizome showed irregular shape of elongation (cluster B), compared to the site with full root support (cluster A). Asparagus crown was grown in aeroponics system in a greenhouse.

In another example, patterns of elongation in spears from two clusters that differed in the amount of root support were similar to patterns observed in control crowns (e.g. 1V5, Fig. 4.12). Lag periods occurred between two adjacent spears. It took 4 days for the second spear to grow after the previous spear was cut at both full and minimal root sites (Cluster A and B). But exponential growth was observed at the full root site whilst linear growth occurred at the limited (minimal) root site.

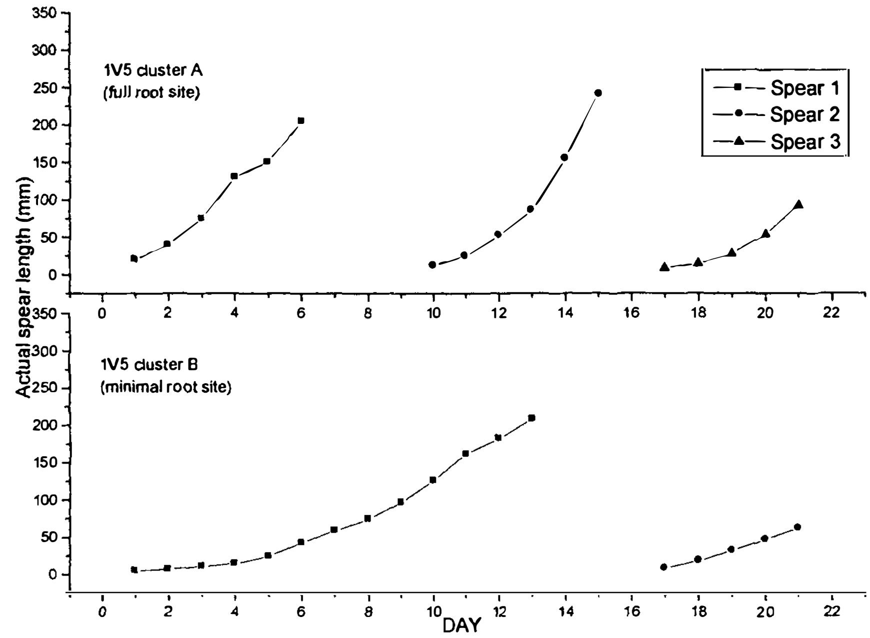


Figure 4.12 Expt 6: Linear and exponential growth of spears from clusters grown at minimal root site and full root site within the same crown. Gap period occurred between adjacent spears at all sites.

When two spears grew together, the more basal spear within a particular pair may partially inhibit the other spear (e.g. 2C1, Fig. 4.13). In the first pair of spears in cluster A, the later spear grew relatively faster than the former spear with natural log slopes of 0.4478 and 0.3270, respectively. Nevertheless, a closer observation of actual spear elongation showed that within the 4 overlapped days, the later spear elongated slower than the former one. Within the second pair in cluster B, the former spear inhibited growth partially by slowing down the speed of elongation of the later one. The relative spear growth rates for these two spears were 0.7833 and 0.5748 for former and latter spears, respectively. Unlike the previous pairs of overlapped spears, the first of the pair of overlapped spears in cluster B showed no inhibition from the preceding spear. In fact, the later spear grew quicker than the former spear, as shown by the natural log of spear elongation.

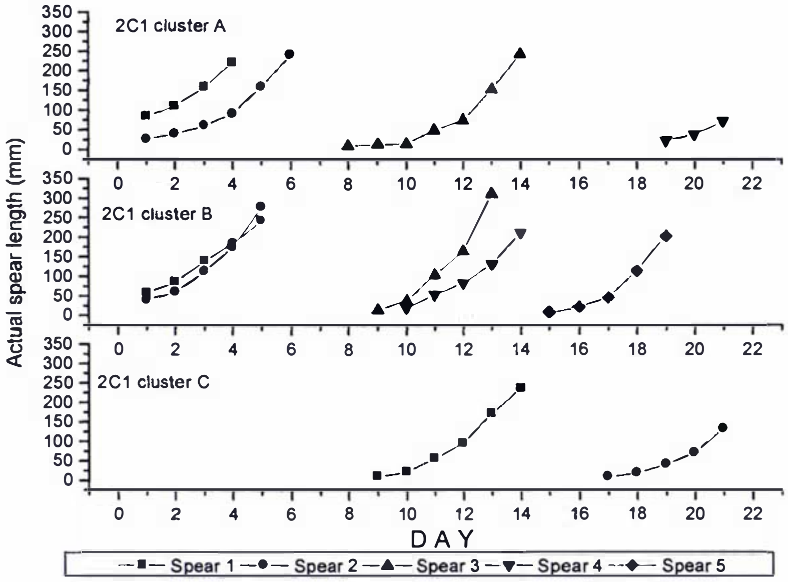


Figure 4.13 Expt 6: Partial inhibition that may exist between a pair of spears in an asparagus crown grown in aeroponics in a greenhouse.

As previously shown in Fig. 4.9 and 4.10, many spears had slow growth at earlier stages of spear elongation. This can be seen clearly in the following figure (e.g. 2H2, Fig. 4.14). An H crown with 7 clusters had produced spears with very slow increase in their elongation except for spears at cluster F.

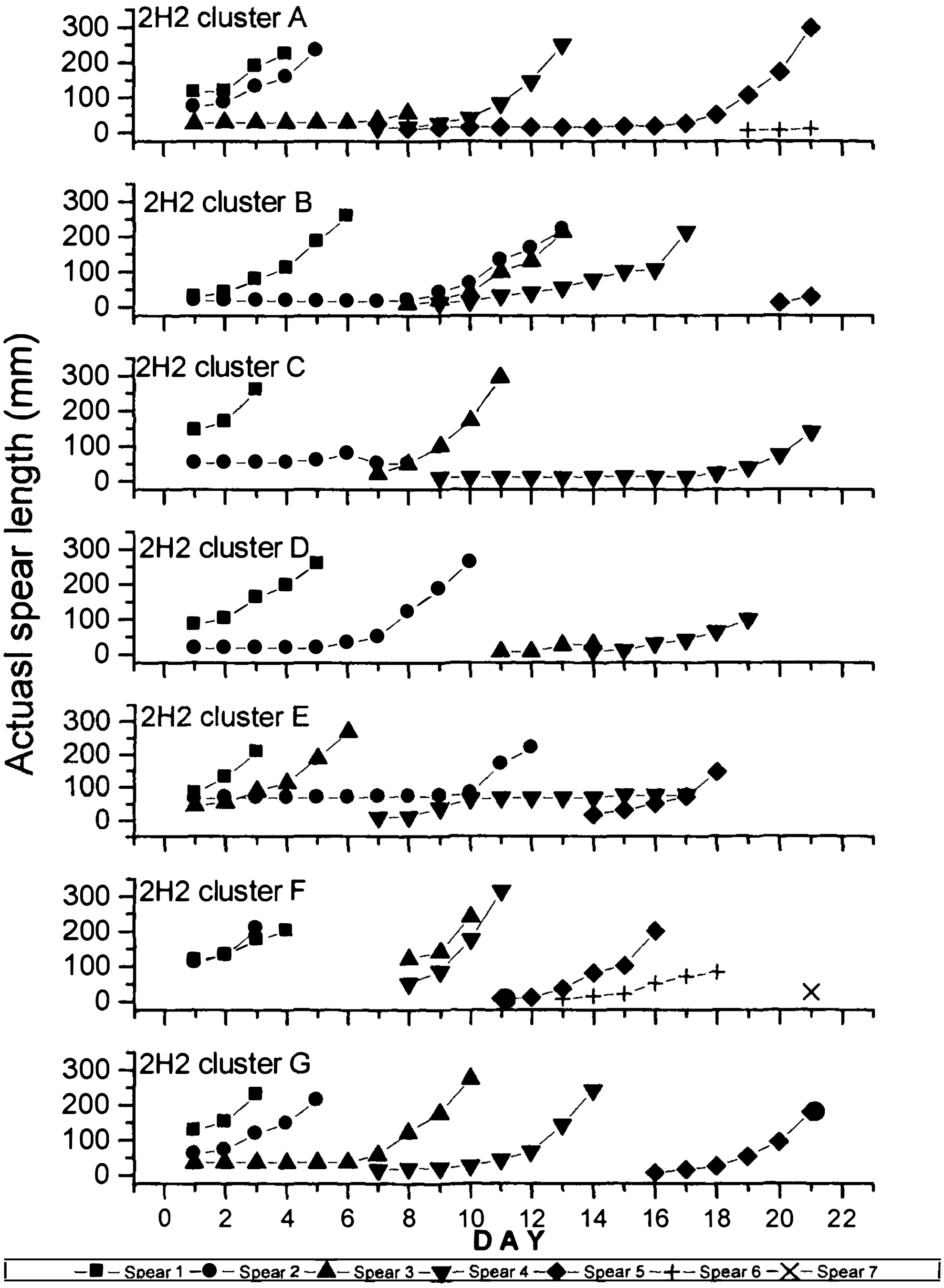


Figure 4.14 Expt 6: Slow growth over some period before asparagus spears quickly elongated either exponentially or linearly in H-crown (a crown with horizontally cut root).

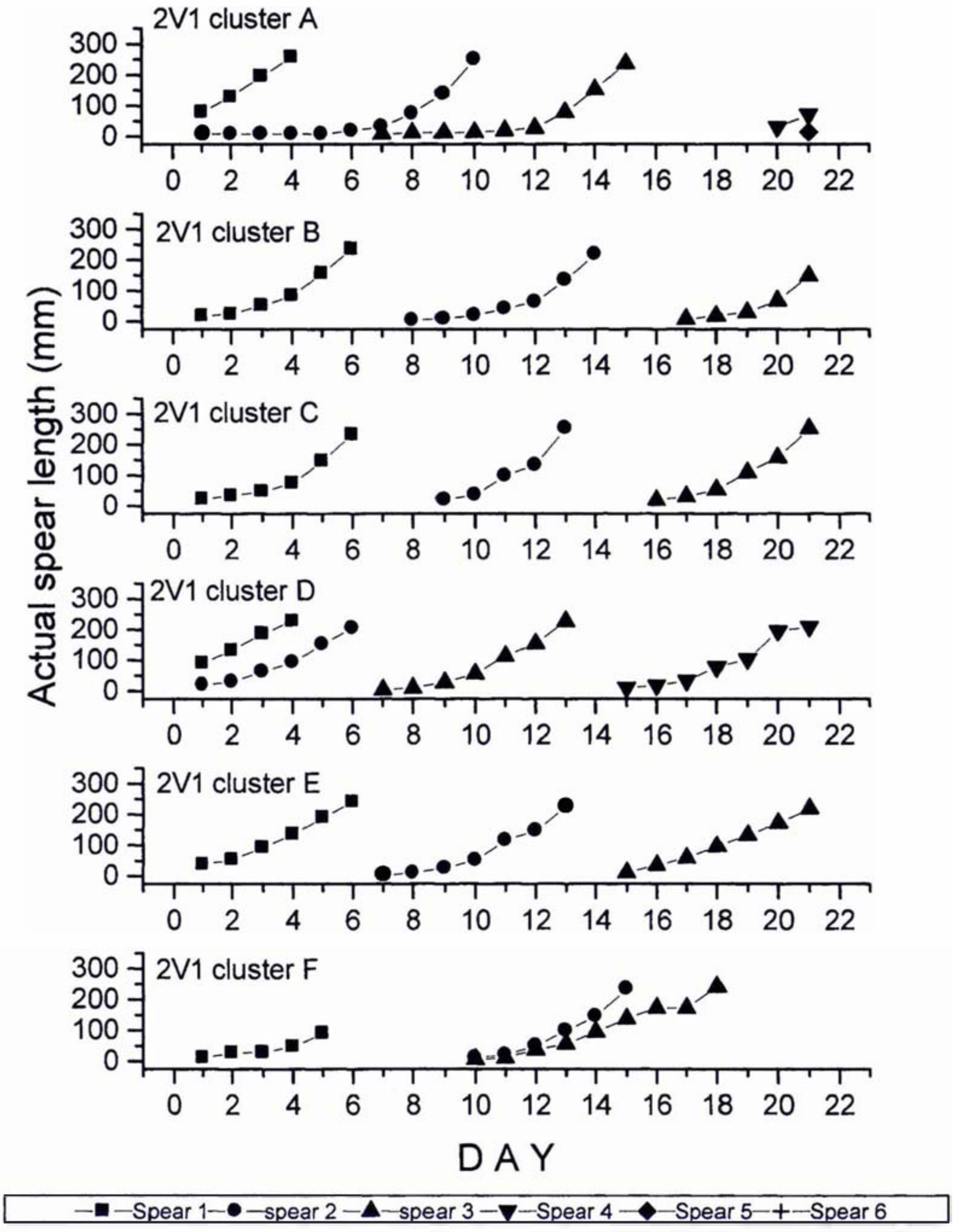


Figure 4.15 Expt 6: Slow elongation of the spears growing with minimal root storage (Clusters D, E, and F) on a crown grown in aeroponics system in the green house.

Slow elongation was also observed when the spears grew in the area of limited (minimal) root availability (e.g. 2V1, Fig. 4.15). Clusters E, F and partially D were located in the site of limited root. Compared to spear elongation from full root (Cluster A, B and C), spears in limited root sites grew at a comparatively slow rate once growth started.

4.3.3. Natural log of spear elongation

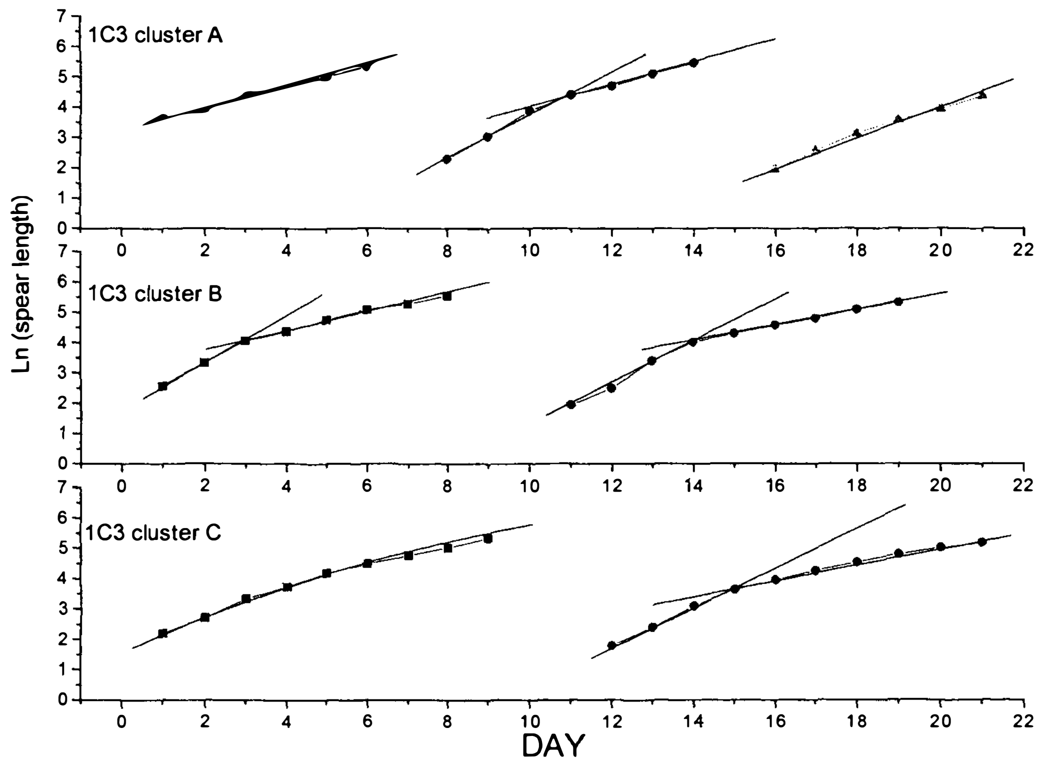


Figure 4.16Expt 6: Natural log of asparagus spear length from the spears of three clusters within C crown grown in aeroponics system in the green house.

There were 19 shapes distinguished for spear length graphs when all values for actual spear length were converted into natural logs. Spears that grew exponentially would fit perfectly into a straight line when converting into natural logs (e.g. 1C3, Fig. 4.16, first and third spears in cluster A). These spears were called **E** (stands for initial shape Exponential) shape in natural logs. Other spears except the first spear in cluster C, would fit into two straight lines intersecting one another, giving two values of slope for each individual spear. This shape suggested two steps of exponential growth in spear length and therefore it is called **EE**. The first spear in cluster C fitted into a quadratic form rather than a linear and was called **Q**.

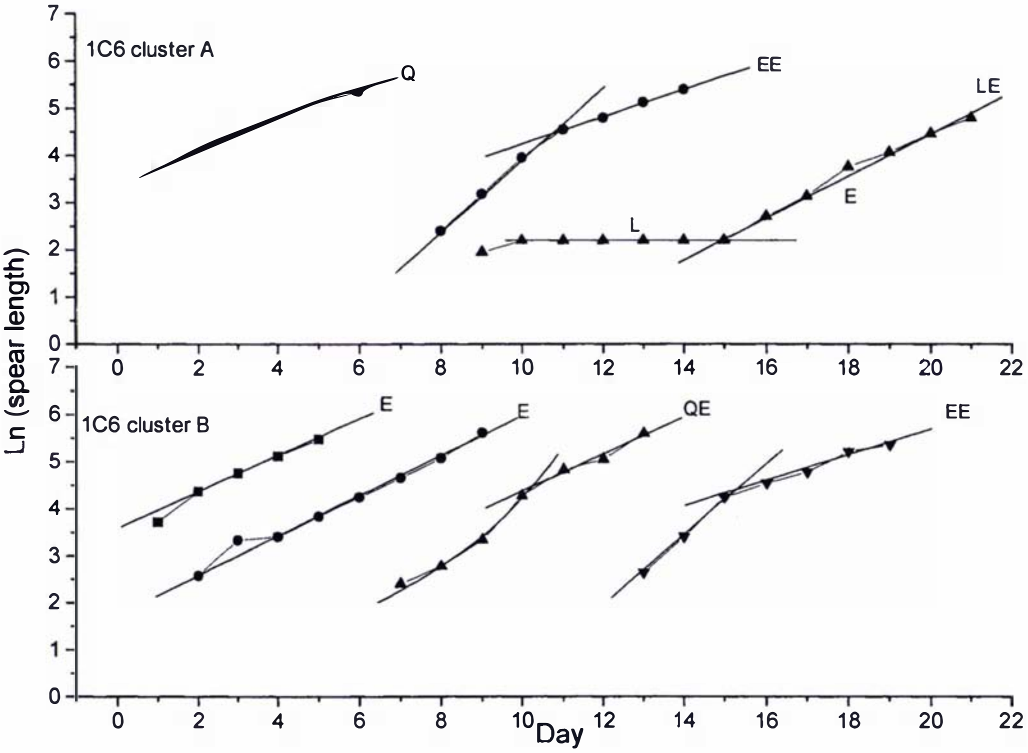


Figure 4.17 Expt 6: Different shapes of $\log_e$ spear elongation that can be found on a crown of asparagus grown in aeroponics system in the green house.

The spears that did not increase in length when overlapped with another spear were flat lines when converted into natural logs. They were given the label **L** (e.g. 1C6, Fig. 4.17, third spear in cluster A).

The separate shapes, based on their natural logs, gave three basic shapes: E, L, and Q. Combinations of the basic shapes may occur in one spear as in Fig. 4.17 third spear (LE) in cluster A and in 1C4 Fig. 4.18 second spear (ELE) in Cluster A. If L shape eventually never increased, it was called LNG (Line Not Growing) (Fig. 4.19).

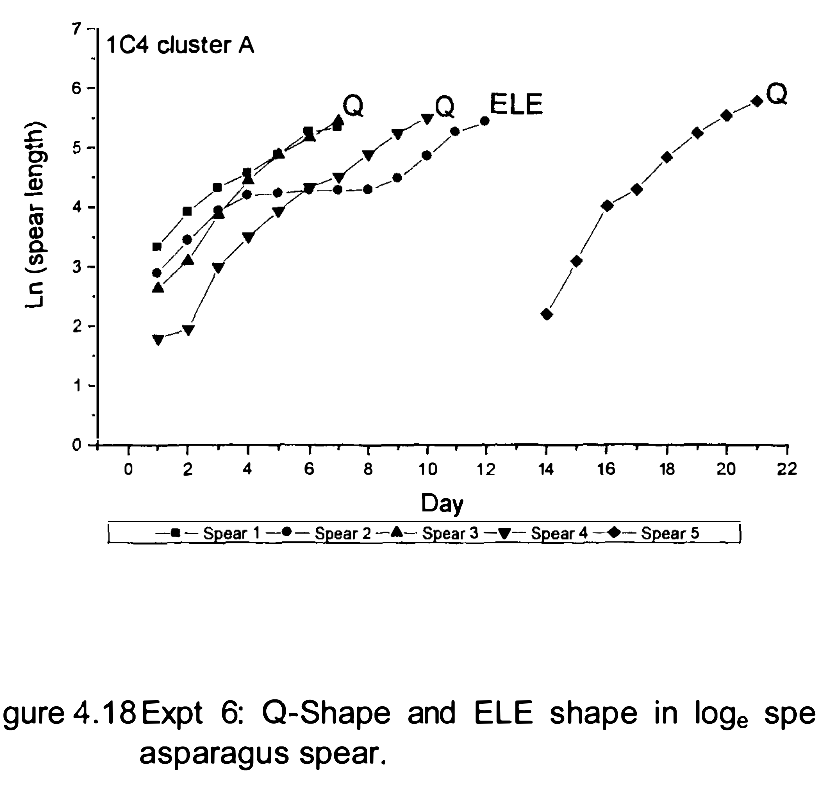


Figure 4.18 Expt 6: Q-Shape and ELE shape in $\log_e$ spear elongation of the asparagus spear.

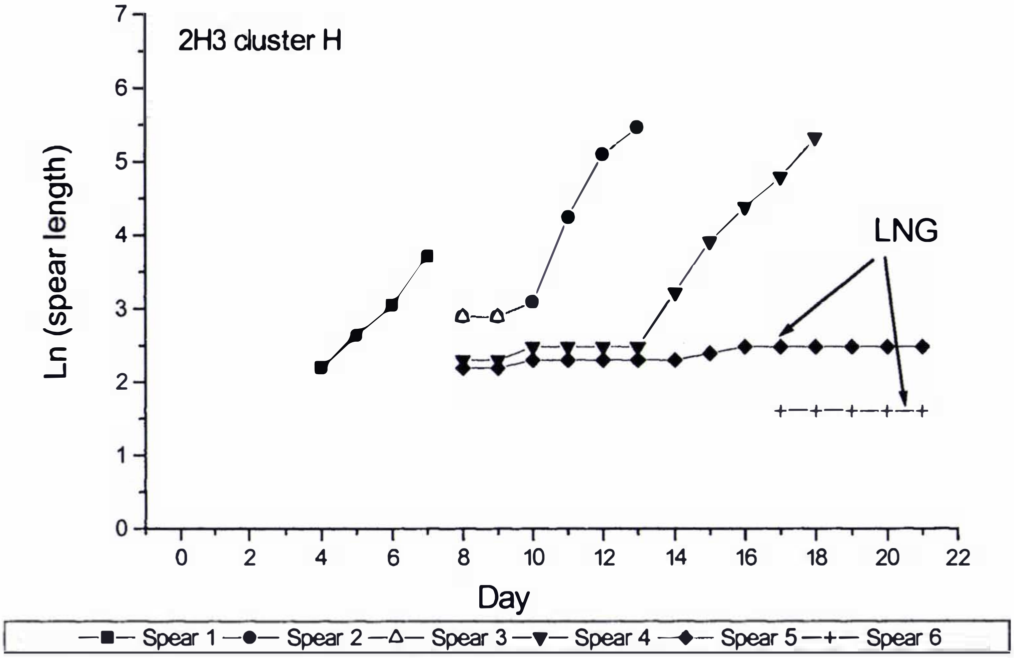


Figure 4.19 Expt 6: LNGs – buds that did not develop were observed in some crowns.

4.3.4. Tabulation of the shapes from natural log of spear elongation

There were 19 shapes identified from the natural log of spear elongation. Among 19 shapes, the most common was E (43.6 %) followed by EE (14.6 %), and Q (12.2 %) totalling 70.5 % out of 732 spears measured (Table 4.3 - 4.6). The next shape, which contributed 7.4 %, was LNG. The spears that did not increase in length (LE), made up 6.7 %. The other four shapes, that totalled 12.1 %, were EL (2.3 %), EQ (3.7 %), LQ (3.6 %), and QE (2.5 %). Each of the other shapes was less than 1%.

Amongst three different sizes of crowns, large crowns had a total of 456 spears (62.3 % of the total) whilst medium and small crowns had totals of 92 (12.6 % of the total) and 184 spears (25.2 % of the total), respectively.

The percentage distribution amongst 19 shapes in each crown size was slightly different, notably in small and large crowns (Table 4.3). The percentage of shape E was lower in small crown (25 %) than in medium (48.4 %) and large (45.4 %) crowns. On the other hand, shape EL was higher in small (8.7 %) than medium (2.2 %) and large (1.1 %) crowns. But large crowns produced more shape Q (15.6 %) than small (7.6 %) and medium (5.9 %) crowns.

Table 4.3 Expt 6: The number and its percentage of 19 shapes of Log_e spear length from small, medium and large crowns of asparagus 'UC157' grown in aeroponics in the greenhouse.

Shape	Crown size						Total	
	Small		Medium		Large			
	Number	%	Number	%	Number	%	Number	%
E	23	25.0	89	48.4	207	45.4	319	43.6
EE	21	22.8	34	18.5	52	11.4	107	14.6
EEE	0	0.0	0	0.0	2	0.4	2	0.3
EL	8	8.7	4	2.2	5	1.1	17	2.3
ELE	2	2.2	0	0.0	3	0.7	5	0.7
ELQ	0	0.0	0	0.0	1	0.2	1	0.1
EQ	5	5.4	6	3.3	16	3.5	27	3.7
LE	7	7.6	11	6.0	31	6.8	49	6.7
LEE	0	0.0	3	1.6	2	0.4	5	0.7
LEQ	1	1.1	0	0.0	0	0.0	1	0.1
LG	2	2.2	1	0.5	1	0.2	4	0.6
LNG	8	8.7	12	6.5	34	7.5	54	7.4
LQ	5	5.4	6	3.3	15	3.3	26	3.6
LQQ	0	0.0	0	0.0	1	0.2	1	0.1
Q	7	7.6	11	5.9	71	15.6	89	12.2
QE	1	1.1	4	2.2	13	2.9	18	2.5
QEL	0	0.0	0	0.0	1	0.2	1	0.1
QL	1	1.1	3	1.6	0	0.0	4	0.6
QQ	1	1.1	0	0.0	1	0.2	2	0.3
Total	92	100.0	184	100.0	456	100.0	732	100.0

Table 4.4 Expt 6 : The number and percentage of 19 shapes of Log_e spear length from three different root cutting treatments in 'UC157' grown in aeroponics in the greenhouse.

Shape	Cutting root treatment						Total	
	Control		Horizontal cut		Vertical cut			
	Number	%	Number	%	Number	%	Number	%
E	117	45.4	108	43.0	94	42.2	319	43.6
EE	43	16.7	35	13.9	29	13.0	107	14.6
EEE	1	0.4	1	0.4	0	0.0	2	0.3
EL	4	1.6	3	1.2	10	4.5	17	2.3
ELE	3	1.2	1	0.4	1	0.5	5	0.7
ELQ	0	0.0	1	0.4	0	0.0	1	0.1
EQ	10	3.9	13	5.2	4	1.8	27	3.7
LE	13	5.0	20	8.0	16	7.2	49	6.7
LEE	2	0.8	2	0.8	1	0.5	5	0.7
LEQ	0	0.0	0	0.0	1	0.5	1	0.1
LG	1	0.4	1	0.4	2	0.9	4	0.6
LNG	22	8.5	17	6.8	15	6.7	54	7.4
LQ	7	2.7	13	5.2	6	5.2	26	3.6
LQQ	1	0.4	0	0.0	0	0.0	1	0.1
Q	27	10.5	27	10.8	35	15.7	89	12.2
QE	6	2.3	6	2.4	6	2.4	18	2.5
QEL	1	0.4	0	0.0	0	0.0	1	0.1
QL	0	0.0	3	1.2	1	1.2	4	0.6
QQ	0	0.0	0	0.0	2	0.0	2	0.3
Total	258	100.0	251	100.0	223	100.0	732	100.0

Average of spear distribution among root cutting treatments was almost similar (Table 4.4). Total spears within control, horizontally cut root, and vertically cut root were 258 (35.2 % of the total), 251 (34.4 % of the total), and 223 (30.5 % of the total), respectively.

Shape distributions within root cutting treatments were also similar (Table 4.4). Shape E was the major shape with the average percentage more than 40 % in each treatment. The following major shapes, EE, Q, LNG, LE and QE, occurred similarly for each root cutting treatment. Shapes of EL, EQ and LQ occurred for more than 1 % in each root cutting treatment, but the percentage distribution slightly differed.

The number of spear distributed amongst the four different root pruning sites was uneven (Table 4.5). Site A (full root) and B (half root length) had similar number of spears accounting for 35.2 % and 34.3 % of the total spears. Site D (full root side from vertical root cutting treatment) had 173 spears (23.6 %) whilst site C (with minimal root support) had the lowest number of spears (50 spears; 6.8 %).

Shape distribution of E, EQ, and Q was lowest in the site with minimal root (C) (Table 4.5). Whilst shape distribution of LQ was lower in site D and was higher in site C, shape Q was highest in site D and was the lowest in site C.

Table 4.5 Expt 6: The number and its percentage of 19 shapes of Log$_e$ spear length from four sites with different amount of root in 'UC157' grown in aeroponics in the greenhouse.

Shape	Full root (A)		Half- length (B)		No root – from vertical (C)		Full root –from vertical (D)		Total	
	Number	%	Number	%	Number	%	Number	%	Number	%
E	117	45.4	108	43.3	16	32.0	78	45.1	319	43.6
EE	43	16.7	35	13.9	7	14.0	22	12.7	107	14.6
EEE	1	0.4	1	0.4	0	0.0	0	0.0	2	0.3
EL	4	1.6	3	1.2	7	14.0	3	1.7	17	2.3
ELE	3	1.2	1	0.4	0	0.0	1	0.6	5	0.7
ELQ	0	0.0	1	0.4	0	0.0	0	0.0	1	0.1
EQ	10	3.9	13	5.2	0	0.0	4	2.3	27	3.7
LE	13	5.0	20	7.9	4	8.0	12	6.9	49	6.7
LEE	2	0.8	2	0.8	0	0.0	1	0.6	5	0.7
LEQ	0	0.0	0	0.0	0	0.0	1	0.6	1	0.1
LG	1	0.4	1	0.4	2	4.0	0	0.0	4	0.6
LNG	22	8.5	17	6.8	2	4.0	13	7.5	54	7.4
LQ	7	2.7	13	5.2	4	8.0	2	1.2	26	3.6
LQQ	1	0.4	0	0.0	0	0.0	0	0.0	1	0.1
Q	27	10.5	27	10.8	5	10	30	17.3	89	12.2
QE	6	2.3	6	2.4	2	4.0	4	2.3	18	2.5
QEL	1	0.4	0	0.0	0	0	0	0.0	1	0.1
QL	0	0.0	3	1.2	0	0	1	0.6	4	0.6
QQ	0	0.0	0	0.0	1	2.0	1	0.6	2	0.3
Total	258	100.0	251	100.0	50	100.0	173	100.0	732	100.0

4.3.5. Shape categories and spear elongation.

4.3.5.1. Shape categories

From the 19 shape categories, 10 categories with less than 1 % representation were combined with larger categories similar in shape to give 9 major categories for further analysis. The final list of 9 categories, and their constituent shape classes, is shown in Table 4.6.

These proportions for 9 shape categories were similar within crown sizes, root cutting treatments and sites (Table 4.3 – 4.5). Small percentages of some categories may be explained by minor modification of a major shape due to random variation or temperature variation. The main categories are indicated in bold font in Table 4.6. Only shape E was used for RSGR analysis.

Table 4.6 Expt 6: Distribution of total number of 19 shapes and their differences to propose new categories of spear shapes of asparagus 'UC157' grown in aeroponics in the greenhouse.

No.	Shape	Total		Proposed Categories (in bold)	
		Number	%	Shape	Number
1	E	319	43.6	**E**	**319**
2	EE	107	14.6	**EE**	**109**
3	EEE	2	0.3	EEE	
4	EL	17	2.3	**EL**	**23**
5	ELE	5	0.7	ELE	
6	ELQ	1	0.1	ELQ	
7	EQ	27	3.7	**EQ**	**27**
8	LE	49	6.7	**LE**	**59**
9	LEE	5	0.7	LEE	
10	LEQ	1	0.1	LEQ	
11	LG	4	0.6	LG	
12	LNG	54	7.4	**LNG**	**54**
13	LQ	26	3.6	**LQ**	**27**
14	LQQ	1	0.1	LQQ	
15	Q	89	12.2	**Q**	**89**
16	QE	18	2.5	**QE**	**25**
17	QEL	1	0.1	QEL	
18	QL	4	0.6	QL	
19	QQ	2	0.3	QQ	
		732	100.0		732

Testing shape distribution using Proc Genmod for the log-linear model with number of shape as the dependent variable showed that the distribution of spear shape was affected significantly ($P = 0.0025$) by interaction of crown size and shape (SIZE*SHAPE), and by shape (SHAPE; $P < 0.0001$) and marginally affected by the crown size (SIZE; $P = 0.0535$) (Table 4.7). The Chi-Square of spear categories (SHAPE) was relatively larger than the interaction, allowing interpretation for SHAPE variable.

Table 4.7 Expt 6: Analysis of variance using log-linear model for the numbers of 9 major spear shapes of asparagus 'UC157' grown in aeroponics in the greenhouse.

Source	DF	Chi-Square	Pr > ChiSq
Intercept			
SIZE	2	5.85	0.0535
TRT	2	0.03	0.9842
SITE(TRT)	1	1.64	0.2000
SIZE*TRT	4	0.78	0.9417
SITE(SIZE*TRT)	2	0.57	0.7521
SHAPE	8	500.72	<.0001
SIZE*SHAPE	16	36.49	0.0025
TRT*SHAPE	16	11.46	0.7800
SITE(TRT*SHAPE)	8	8.51	0.3850
SIZE*TRT*SHAPE	32	37.32	0.2377
SITE(SIZE*TRT*SHAPE)	16	5.97	0.9884
RESIDUAL DEVIANCE	1647	823.87	

Significant interaction of crown size by spear shape is illustrated in Fig. 4.20. Shape E was significantly lower in small crowns than larger crowns; on the other hand, shape EL was significantly higher in small crowns than larger crowns (Fig. 4.20). In addition, shape Q occurred significantly more often in large crowns than small and medium crowns. Other shapes distributed similarly regardless of crown size.

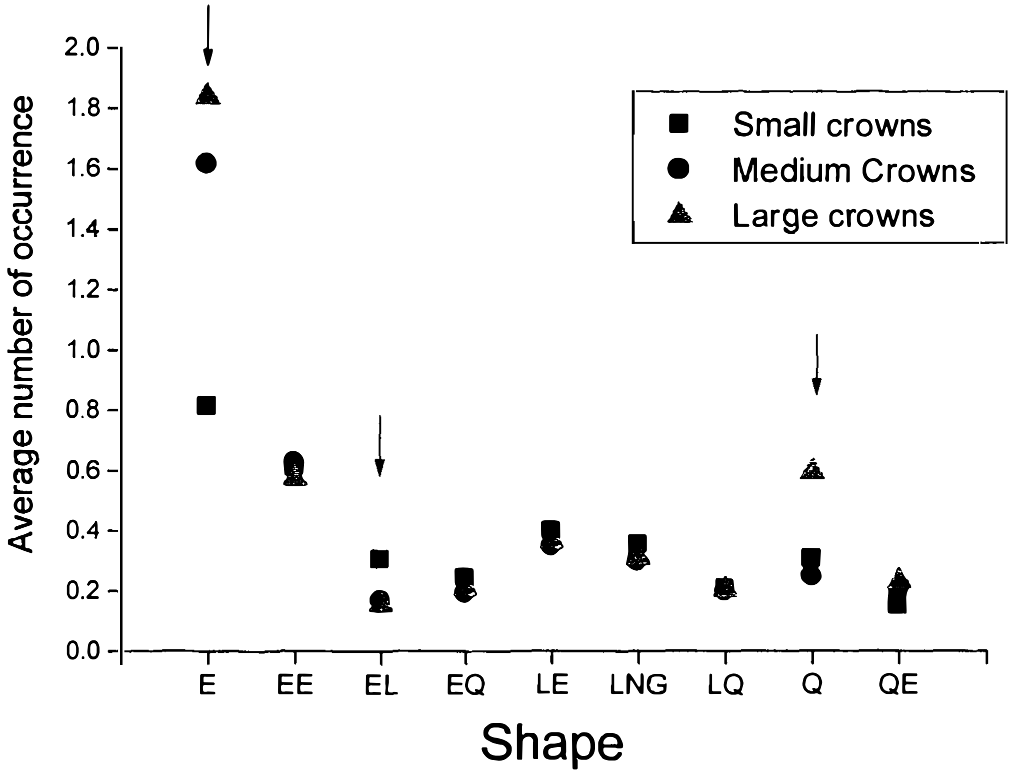


Figure 4.20Expt 6: The average number of shape occurrences affected by interaction between crown size and shapes in asparagus 'UC157' grown in aeroponics. Arrows indicated significances; E, EE, EL, EQ, LE, LNG, LQ, Q, QE stand for Exponential, Exponential Exponential, Exponential Linear, Exponential Quadratic, Linear Exponential, Linear Not Growing, Linear Quadratic, Quadratic, Quadratic Exponential (see text).

4.3.5.2. Spear elongation

Relative Spear Growth Rate (RSGR) as an expression of spear elongation was analyzed using the procedure PROC GLM with SPEAR*SIZE*TRT*CLUSTER*SITE and SIZE*TRT*CLUSTER*SITE as random variables in the GLM model and the model explained 66.8 % of data variation. RSGR was run for 43.6 % of total spears since RSGR can be calculated only for exponential spear elongation (E shape).

Table 4.8 Expt 6: Analysis of variance of RSGR for three different sized crowns and root cutting treatments for asparagus 'UC157' grown in aeroponics in the greenhouse.

Source	DF	Mean Square	F value	Pr > F
SIZE	2	0.0712	3.49	0.0383
TRT	2	0.0886	4.34	0.0185
SIZE*TRT	4	0.0061	0.30	0.8788
SITE(TRT)	1	0.0326	1.60	0.2121
SITE(SIZE*TRT)	2	0.0104	0.51	0.6051
N_CLUST	2	0.0508	2.49	0.0937
SIZE*N_CLUST	2	0.0458	2.24	0.1171
SITE*N_CLUST	6	0.0172	0.84	0.5437
SIZE*SITE*N_CLUST	4	0.1112	5.45	0.0011
SIZE*TRT*CLUSTER*SITE	48	0.0204	0.89	0.6759
SPEAR	6	0.2284	9.92	<0.0001
SPEAR*TRT	9	0.0247	1.07	0.3866
SPEAR*SIZE	8	0.0129	0.56	0.8068
SPEAR*SITE	2	0.0206	0.90	0.4112
SPEAR*N_CLUST	9	0.0237	1.03	0.4204
SPEAR*SIZE*TRT*CLUSTER*SITE	81	0.0147	0.64	0.9833

See text for variables of source of variation.

RSGR was affected significantly by the interaction of crown size (SIZE) with the site at which the cluster was located (SITE) and number of clusters in a crown (N_CLUST) at

$P = 0.0011$. RSGR was also influenced by root cutting treatments (TRT, $P = 0.0185$) and crown size (SIZE) at $P = 0.0383$ (Table 4.8).

Root removal reduced RSGR significantly ($P = 0.0185$) from 0.5595 mm.mm^{-1}.day^{-1} (Control) to 0.5126 and 0.5171 mm.mm^{-1}.day^{-1} for cutting root horizontally and vertically, respectively (Table 4.9). The difference was clear when these RSGR were calculated to predict spear elongation on 2 cm of initial spear height. Control obviously would reach harvested spear height earlier than the other two root cutting treatments (Table 4.9).

Table 4.9 Expt 6: Influence of root cutting treatments (TRT) on asparagus RSGR and the application of RSGR to predict five-day elongation for 2 cm of initial spear height.

Cutting root treatments	Mean (mm.mm^{-1}.day^{-1})	Predicted spear length (cm) on 5 days of initial 2 cm bud height*	Site	Mean (mm.mm^{-1}.day^{-1})	Predicted spear length (cm) on 5 days of initial 2 cm bud height*
Control (C)	0.5595^{a}	32.8 cm	A	0.5595	32.8 cm
Cutting root horizontally (H)	0.5126^{b}	25.9 cm	B	0.5126	25.9 cm
Cutting root vertically (V)	0.5171^{b}	26.5 cm	C	0.4626	20.2 cm
			D	0.5269	27.9 cm

Means with the same letters within the same column were not significantly different when tested at $P < 0.05$.
*Predicted spear length based on $Y = aexp^{rt}$; a = initial bud height, r = RSGR (rate of spear elongation); t = time (days). Site definition: A = full support of storage roots under control, B = half length of cut roots, C = minimal storage roots uncer vertically cut roots, D = full storage roots under vertically cut roots.

Although there was no significance in overall site effect nested under treatment, SITE(TRT), root removal in small crowns had a more profound effect than in medium and large crowns (Table 4.10) when there was an increase of bud clusters. Once there were more than two or three clusters on a crown, the RSGR was reduced in small crowns but not in large crowns (Table 4.10). Increased number of bud clusters in small crowns reduced RSGR by 16 to 32 % (0.092 to 0.194 mm.mm^{-1}.day^{-1}) for site B and A, respectively (Table 4.10), and severest reduction (55 % or 0.241 mm.mm^{-1}.day^{-1}) occurred in the site where roots were minimal (site C). This reduction in site C was also observed in medium crowns with more bud clusters, reducing from 0.4706 to 0.1698 mm.mm^{-1}.day^{-1}. Percentage reduction of RSGR in medium crowns varied whilst in large crown RSGR slightly increased when there were more than 3 clusters at the site of full roots and half length roots. And this interaction among SITE, SIZE and the number of cluster (N_CLUST) was significant at probability 0.0011.

Table 4.10 Expt 6: Influence of site of root removal (SITE) for different crown sizes with different number of clusters on asparagus RSGR (mm.mm^{-1}.day^{-1})

Site	Number of bud cluster	Size of crown		
		Small	Medium	Large
†A	1 cluster	0.5948	0.4805	-
	2<3 clusters	0.4012	0.5672	0.4493
	> 3 clusters	-	0.5186	0.6133
B	1 cluster	0.5503	0.6548	-
	2<3 clusters	0.4587	0.5148	0.4861
	> 3 clusters	-	0.4697	0.5298
C	1 cluster	0.4370	-	-
	2<3 clusters	0.1957	0.4706	0.5081
	> 3 clusters	-	0.1698	0.4312
D	1 cluster	-	0.5767	-
	2<3 clusters	0.4825	0.5775	0.5502
	> 3 clusters	-	0.5148	0.5283

†A = Full root; B = half length root; C = no root from the vertical cutting root; D = full root from the vertical cutting root. - = no available spear.

Within the spear sequence, RSGR was not influenced by any single effects such as TRT, SITE, or SIZE or any interaction of these effects. The first spears had the lowest RSGR, but there was no consistent change in RSGR over spears two to seven (Table 4.11).

Table 4.11 Expt 6: Asparagus RSGR for different spear appearance

Spear number appearance	Mean ($mm.mm^{-1}.day^{-1}$)
First	0.4495^{b}
Second	0.5592^{ab}
Third	0.5996^{ab}
Fourth	0.6278^{ab}
Fifth	0.6083^{ab}
Sixth	0.5048^{ab}
Seventh	0.6286^{a}

Means with the same letter are not significantly different when tested at $LSD_{0.05}$

4.3.6. Correlative Inhibition

Correlative inhibition (CI) was determined from the inhibition period and lag period of spear appearance. When the inhibition period was positive, then the spear elongation was delayed by the presence of correlative inhibition. On the other hand, when the inhibition time was zero, the spears elongated simultaneously without any inhibition from previous spears (no CI).

Analysis of CI was done on log transformed data (Table 4.12) to reduce variance, since plotting residuals using original values of CI resulted in a funnel-like distribution (data not shown). To avoid log zero values, all the values of CI were increased by 0.1.

Table 4.12 Expt 6: Analysis of variance for correlative inhibition (CI) under three different sized crowns and root cutting treatments for asparagus 'UC157' grown in aeroponics in the greenhouse.

Source	DF	Mean Square	F value	Pr > F
SIZE	2	6.1394	3.34	0.0424
TRT	2	2.0676	1.13	0.3314
SIZE*TRT	4	2.3219	1.26	0.2946
SITE(TRT)	1	0.8149	0.44	0.5080
SITE(SIZE*TRT)	2	5.1722	2.82	0.0681
N_CLUST	2	2.1372	1.16	0.3196
SIZE*N_CLUST	2	1.4802	0.81	0.4957
SITE*N_CLUST	6	0.3139	0.17	0.9836
SIZE*SITE*N_CLUST	4	1.8281	1.00	0.4372
SIZE*TRT*CLUSTER*SITE	48	2.0061	0.91	0.7766
SPEAR	6	166.4392	75.21	<0.0001
SPEAR*TRT	9	3.6114	1.63	0.0687
SPEAR*SIZE	8	2.6859	1.21	0.2805
SPEAR*SITE	2	6.7332	3.04	0.0173
SPEAR*N_CLUST	9	3.6918	1.67	0.0789
SPEAR*SIZE*TRT*CLUSTER*SITE	81	2.0061	0.91	0.7766

It took 4 days on average to release suppression from CI in medium and small crowns but only 3.4 days in large crowns ($P = 0.0424$; Table 4.12 - 4.13). This result implied that the strongest CI for subsequent buds occurred in small and medium crowns rather than in large crowns (Table 4.13).

Table 4.13 Expt 6: Correlative Inhibition (CI) existing in different sized crowns of asparagus 'UC157' grown in aeroponics.

Size of crowns	Mean (day)
Small	- 0.1938^{b} (4.13)
Medium	- 0.2081^{b} (4.20)
Large	- 0.0521^{a} (3.44)

Means with the same letters within the same column were not significantly different at $LSD_{0.05}$. Value in brackets is the untransformed data.

CI was also affected by the spear position in a cluster (SPEAR) at $P < 0.0001$ and interaction between SPEAR*SITE ($P = 0.0173$). The mean square of SPEAR was relatively much larger than in the significant interaction, allowing interpretation of SPEAR. Overall CI became stronger as spear positions were further away from the base of a cluster, up to fifth buds, and then reduced thereafter (Table 4.14).

This strength of CI at different positions was affected by their SITE (P = 0.0173). Correlative inhibition (CI) increased up to third spears in all sites, but the trend of increases or reduction varied amongst four sites thereafter (Table 4.14).

Table 4.14 Expt 6: Correlative Inhibition (day) at different spear position and four different sites derived from root cutting treatments of asparagus grown in aeroponics.

Spear number appearance	SITE				Average
	A	B	C	D	
First	- 2.2433	- 2.0893	-2.1587	-2.2490	- 2.1843^{c} (0.13)
Second	0.5673	0.5611	1.1688	-0.0715	0.4687^{ab} (4.80)
Third	1.4579	0.9194	0.9576	1.1286	1.1643^{a} (5.71)
Fourth	0.7755	1.2683	-0.8864	1.4743	1.1071^{a} (5.17)
Fifth	1.8047	0.7875	1.3863	0.2611	1.0102^{a} (5.23)
Sixth	1.3181	0.9263	-2.3026	0.1459	0.5956^{ab} (4.06)
Seventh	1.7918	-2.3026	-	0.0000	- 0.1277^{ab} (4.00)
Eight	-	0.6931	-	-2.3026	- 0.8047^{bc} (1.00)
Ninth	-	-2.3026	-	1.9459	- 0.1783^{ab} (3.50)

Means with the same letter within the column of average are not significantly different when tested at $LSD_{0.05}$. Value in brackets is the untransformed data. A = Full root; B = half length root; C = no root from the vertical root cutting; D = full root from the vertical root cutting. - spears were not available;

4.3.7. Overlap Period

Table 4.15 Expt 6: Analysis of variance for overlap period (OP) under three different sized crowns and root cutting treatments for asparagus 'UC157' grown in aeroponics in the greenhouse.

Source	DF	Mean Square	F value	Pr > F
SIZE	2	166.283	5.21	0.0083
TRT	2	27.475	0.86	0.4281
SIZE*TRT	4	70.1474	2.20	0.0806
SITE(TRT)	1	4.454	0.14	0.7101
SITE(SIZE*TRT)	2	60.5048	1.90	0.1594
N_CLUST	2	2.7454	0.09	0.9177
SIZE*N_CLUST	2	42.1373	1.32	0.2766
SITE*N_CLUST	6	13.362	0.42	0.8635
SIZE*SITE*N_CLUST	4	12.884	0.40	0.8735
SIZE*TRT*CLUSTER*SITE	48	31.904	2.27	< 0.0001
SPEAR	6	150.211	10.67	< 0.0001
SPEAR*TRT	9	15.672	1.11	0.3443
SPEAR*SIZE	8	38.869	2.76	0.0027
SPEAR*SITE	2	46.249	3.29	0.0116
SPEAR*N_CLUST	9	26.449	1.88	0.0409
SPEAR*SIZE*TRT*CLUSTER*SITE	81	16.058	1.14	0.1445

Overlap period (OP) was affected significantly by crown size at $P = 0.0083$ (Table 4.15). Overlap period depended on the position of the spears ($P = 0.0001$), and was significantly affected by the spear position at different crown size (SPEAR*SIZE, $P =$

0.0027), at different sites (SPEAR*SITE, *P* = 0.0116) and at different number of clusters (SPEAR*N_CLUST, *P* = 0.0409).

Overlap period (OP) was longer in small crowns than in medium and large crowns (Table 4.16).

Table 4.16 Expt 6: Overlap period (OP) existed in different size of crowns of asparagus 'UC157' grown in aeroponics.

Size of crowns	Mean (day)
Small	3.59^{a}
Medium	1.29^{b}
Large	1.80^{b}

Means with the same letters within the same column were not significantly different at $LSD_{0.05}$.

Table 4.17 Expt 6: Overlap period (OP) at different spear positions of asparagus grown in an aeroponics.

Spear number appearance	Mean (day)
First	0.00^{c}
Second	2.34^{bc}
Third	2.17^{bc}
Fourth	2.85^{abc}
Fifth	3.07^{abc}
Sixth	6.61^{a}
Seventh	6.00^{ab}
Eight	6.00^{ab}
Ninth	1.50^{bc}

Means with the same letter within a column are not significantly different when tested at $LSD_{0.05}$

Positive overlap period (OP) indicated development of subsequent bud whilst the previous spear was still growing. OP took a longer time as bud position was further away from the base of a bud cluster (Table 4.17). This was true in all cluster number categories, but the degree of increase differed (Table 4.18)

Table 4.18 Expt 6: Overlap period at different bud position as affected by the number of cluster in a crown of asparagus grown in an aeroponics.

Bud position	Number of clusters		
	1 cluster	2 < 3 clusters	> 3 clusters
First	0.00	0.00	0.00
Second	3.29	3.21	1.93
Third	2.42	2.56	2.00
Fourth	2.86	2.31	3.08
Fifth	4.50	3.15	2.81
Sixth	7.50	6.43	6.56
Seventh	9.00	2.00	6.50
Eight	-	-	6.00
Ninth	-	-	1.50

- spears were not available

There were greater differences in OP between spears in small crowns than between spears in medium and large crowns (Table 4.19). OP was 5.2 days for second spears in small crowns but only 1.5 and 2 days in medium and large crowns. Long OP occurred in small crowns for each spear after the first, but in medium and large crowns it occurred only after the fifth spear.

Table 4.19 Expt 6: Overlap period (OP) at different spear position in different sized asparagus crowns grown in an aeroponics.

Bud position	Crown size		
	Small	Medium	Large
First	0.00	0.00	0.00
Second	5.19	1.46	2.01
Third	4.45	1.98	1.74
Fourth	7.00	0.65	2.94
Fifth	4.00	3.11	2.93
Sixth	8.00	7.00	6.38
Seventh	-	9.00	5.00
Eight	-	-	6.00
Ninth	-	-	1.500

- spears were not available

There were increase in period of OP from the first to fourth bud in site A (full root from control), B (horizontal root cutting area) and C (minimal root). The increase of OP was 3 times higher in site C than in site A and B and occurred earlier in site C (Table 4.20). In site D, OP was consistently low.

Table 4.20 Expt 6: Overlap period (days) at different spear positions and different sites of root removal on crowns grown in an aeroponics.

Bud position	Site			
	A	B	C	D
First	0.00	0.00	0.00	0.00
Second	1.66	2.80	1.67	2.93
Third	2.02	2.94	3.64	0.89
Fourth	3.57	2.43	9.33	1.93
Fifth	1.36	4.06	8.00	3.20
Sixth	8.60	6.50	8.00	4.83
Seventh	9.00	8.00	-	3.50
Eight	-	8.00	-	4.00
Ninth	-	5.00	-	-2.00

†A = Full root; B = half length root; C = no root from the vertical cutting root; D = full root from the vertical cutting root. - = no available spear.

4.3.8. Lag period

Delay in appearance of the subsequent spears after the previous spear was harvested (Lag period, LP) correlated well to CI (r = 0. 7148), and LP was affected by the interaction of three variables (SIZE*SITE*N_CLUST) at $P = 0.0433$ (Table 4.21). Crown size (SIZE) also significantly affected LP ($P = 0.0127$). In addition, spear position (SPEAR) significantly affected LP ($P < 0.0001$).

Any type of transformation did not reduce the variance, as indicated by the plots of residuals, and therefore the analysis was based on non-normally distributed population.

Table 4.21 Expt 6: Analysis of variance of lag period (LP) for three different sized crowns and root cutting treatments for asparagus 'UC157' grown in aeroponics in the greenhouse.

Source	DF	Mean Square	F value	Pr > F
SIZE	2	15.881	4.72	0.0127
TRT	2	0.160	0.05	0.9536
SIZE*TRT	4	3.135	0.93	0.4527
SITE(TRT)	1	4.213	1.25	0.2681
SITE(SIZE*TRT)	2	2.567	0.76	0.4714
N_CLUST	2	4.325	1.28	0.2848
SIZE*N_CLUST	2	8.913	2.65	0.0576
SITE*N_CLUST	6	1.888	0.56	0.7597
SIZE*SITE*N_CLUST	4	7.883	2.34	0.0433
SIZE*TRT*CLUSTER*SITE	48	3.368	0.97	0.5500
SPEAR	6	40.757	11.68	<0.0001
SPEAR*TRT	9	1.929	0.55	0.9002
SPEAR*SIZE	8	3.792	1.09	0.3713
SPEAR*SITE	2	8.306	2.38	0.0514
SPEAR*N_CLUST	9	3.461	0.99	0.4533
SPEAR*SIZE*TRT*CLUSTER*SITE	81	3.851	1.10	0.2131

Lag period (LP) was highest for spears 2 – 5, but reduced thereafter (Table 4.22).

Table 4.22 Expt 6: Lag period at different spear position of asparagus grown in an aeroponics.

Spear number appearance	Mean (day)
First	0.13^{b}
Second	1.76^{a}
Third	1.63^{a}
Fourth	1.45^{a}
Fifth	1.26^{a}
Sixth	0.61^{b}
Seventh	0.50^{b}
Eight	0.50^{b}
Ninth	1.00^{ab}

Means with the same letter within a column are not significantly different when tested at $LSD_{0.05}$

4.3.9. Spear yield

Sorting the buds according to spear diameter into 5 different qualities revealed that all spears in small crowns were categorized into quality 5 (<4 mm in diameter) whilst spears in medium crowns were categorized into quality 3 (5 < 7 mm), 4 (4 < 5 mm), and 5 (< 4 mm). In large crowns, some spears were categorized into quality 2 (7 < 9 mm). None of the harvested spears was categorized into first quality (> 9 mm). Data analyses on fresh and dry weight and spear number were based on log-transformed data to reduce variance, indicated by non-normal distribution of residuals.

Root cutting treatment (TRT) did not affect the yield, but crown size (SIZE) significantly affected fresh yield ($P = 0.0007$), dry yield ($P = 0.0016$) and spear number ($P = 0.0278$). As crown size increased, the yield increased (Table 4.23).

Table 4.23 Expt 6: Average fresh and dry yield (g.plant^{-1}) and number of spears in different size of crowns of asparagus 'UC157' grown in aeroponics.

Size of crowns	Average total per plant		
	Weight (gram)		Spear number
	Fresh	Dry	
Small	0.73^{c} (2.57)	- 1.223^{c} (0.36)	0.83^{b} (3.0)
Medium	1.66^{b} (6.28)	- 0.388^{b} (0.63)	0.92^{b} (3.3)
Large	2.28^{a} (13.80)	- 0.028^{a} (1.38)	1.21^{a} (5.6)

Means with the same letters within the same column were not significantly different when tested at $P < 0.05$.
Values in brackets are un-transformed data.

4.4. DISCUSSION

There was substantial variation in the distribution of cluster numbers within the same crown size, although the plants were all of the same variety and age, and grown in the same system (Table 4.2). This non-uniformity of asparagus crowns is well known as one of the problems encountered in yield prediction (Nichols, 1983). In this experiment the problem of crown variation was minimized by blocking for crown size in the analysis.

4.4.1. Shapes of spear kinetics

Once the bud grows and elongates, it becomes a spear. Spears elongating exponentially only accounted for 43.6 % of the total in this Expt 6. Nichols and Woolley (1985) showed that the rate of elongation declined progressively with successive spear appearances. Furthermore, Kim and Sakiyama (1989b) showed that growth of the spears could change to linear growth when the crown size was small, but did not identify differences in the shapes of spear elongation. In fact, spear elongation could be influenced by their position in a cluster and could also be influenced by the timing of the spear appearance as shown in Expt 6 (Fig 4.8- 4.15). These differences in spear elongation may be related to correlative inhibition or source deprivation (see section 4.4.2) or possibly the effect of external factors such as temperature variation (Blumenfield et al., 1961; Nichols and Woolley, 1985; Yen, 1993; Kailuweit and Krug, 1995; Yen et al., 1997; Dean, 1999; Wilson et al., 1999). Assuming exponential growth for spear elongation can result in imprecision in growth models, since less than 50 % of the total spears fitted into the criteria of being exponential.

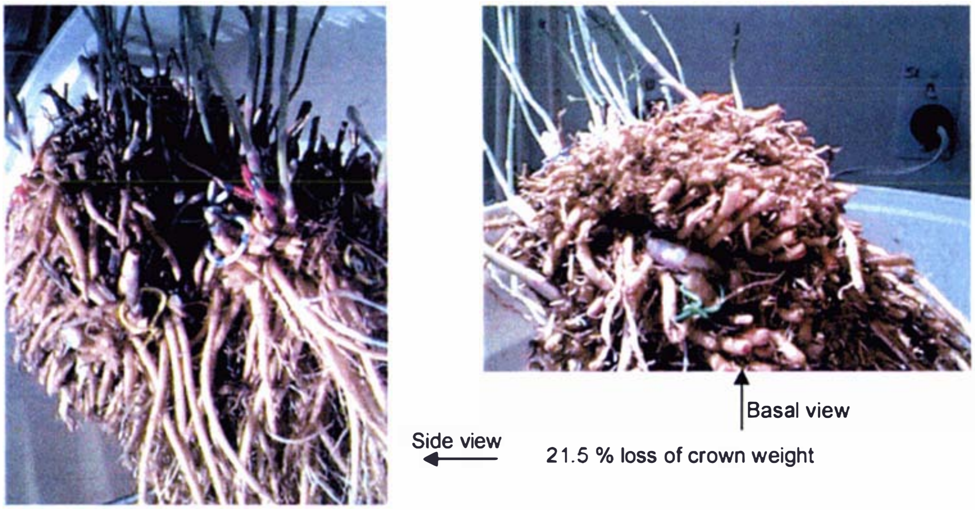
There were 19 identified shapes of spear elongation based on the natural logarithm (Fig. 4.16- 4.19; Table 4.3-4.5). Nine of these shapes of spear growth (spear kinetics) were commonly found in large percentages (from 2.5 % to 43.6 %) whilst the rest were less than 1 %. Amongst nine major shapes of spear kinetics, the distribution of shape E was lower in small crowns (25 %) than in medium (48.4 %) and large crowns (45.4 %) whereas shapes of EE, EL and LG were relatively greater in small crowns than in medium and large crowns (Table 4.3). Percentage reduction in shape E and increases in EE, EL and LG suggested most spears grew slower in small crowns (as was shown in Fig. 4.16). This could indicate longer time to harvest, resulting in potential longer t_{max} of these spear harvests. Statistically, shape differences of spear kinetics in different crown sizes were significant (Table 4.7; Fig. 4.20).

The limitations of carbohydrate in the root as a source to support spear growth could be one of the factors that changes (Kim and Sakiyama, 1989b) spear kinetics as shown in differences in shape distribution amongst root cutting treatments (Table 4.4).

Nevertheless, removal of half the length of roots from the crown did not greatly limit the spear kinetics, as indicated by similar distribution of shape classes over treatments. Removal of half root length reduced crown weight by 19.8 % on average and with this reduction asparagus spears still had sufficient carbohydrate to support growth. Small removal of the root at half length was due to the nature of the asparagus root system. From visual observation in Expt 6, root length was not distributed evenly and the majority of roots occurred within the top two thirds of the root depth, and in the field, occurred in the surface foot of the soil where branching roots are found (Weaver and Bruner, 1927). Cutting roots from half of the crown (vertical root cutting) removed on average 28.7 % of the crown weight. The proportion of root dry weight to the total plant dry weight for 2 to 14 weeks of asparagus seedlings was approximately 20 to 50 % (Benson and Takatori, 1980). Using the values for only rhizome and root dry weight from their results, the root dry weight was about 40 - 90 % of total crown (root and rhizome) dry weight. The results from Expt 6 showed root fresh weight was approximately 20 to 80 % of the total crown fresh weight, depending on crown sizes. It was noticed that small crowns tended to have between 22 and 72 % of root fresh weight whilst bigger crowns could have root fresh weight as high as 80 % of the total crown fresh weight. The root fresh weight was obtained from multiplying by two the root weight removed from the crown vertically. The differences between root proportion in these results and in the results of Benson and Takatori (1980) may come from two reasons.

36.4 % loss of crown weight

26.1 % loss of crown weight



21.5 % loss of crown weight

Figure 4.21 Expt 6: Vertical root cutting treatment on different size of asparagus crowns.

The plants in Expt 6 were raised in aeroponics. Rhizomes freely grew in all directions, including towards the bottom as indicated by some crowns that had some clusters underneath (facing down), making a bulk of rhizome. And when roots were cut in half vertically, the roots were not removed entirely for half total root fresh weight, leaving small partial roots (about 2 cm length from the rhizome) around the bulk of rhizome (Fig. 4.21), resulting in under estimate of root fresh weight removal. Martin and Hartmann (1990) stated that storage roots made up 70 % of the underground dry mass. Average loss of crown weight due to vertical root cuttings in Expt 6 was therefore relatively lower than expected. However, root removal on the average of 28.7 % of the total fresh crown weight influenced the percentage distribution of shape of spear kinetics (Table 4.5).

Although shape E was similar to other treatments, shapes EL, LE, and Q occurred more frequently following the vertical cut. This was due to the effects of two sites (SITE) created by the vertical cutting treatments. One site of the crown had full support of roots and resulted in similar condition to control, the other site was supported by minimal roots, resulting in a reduction of E shape and increases of EL and LQ shapes (Table 4.5 and 4.6). Thus, the severest root removal did not stop spear growth but only suppressed spear kinetics. This condition implied the possibility of transferring carbohydrate from full support (full root at one site) to the minimal root support through living tissue between one cluster and another, which suggested that a growth dependency possibly existed amongst bud clusters on a crown. Effects of one cluster on another in terms of carbohydrate supply could possibly happen if there is living tissue, such as rhizome, to transfer carbohydrate. Martin and Hartmann (1990) showed that a crown (rhizome in this case) serves as a passage for the assimilate stream. In addition, a crown could have 63 % of fructans, suggesting this organ has storage function.

In asparagus, correlative inhibition occurs between adjacent spears (Tiedjens, 1926) within each bud cluster (Kretschmer and Hartmann, 1979) but has not been reported to occur amongst bud clusters. Nichols and Woolley (1985) stated that as many as 7 buds on a crown could start growing within 24 hours of each other, but no two spears ever developed from the same cluster at the same time. However, considerable interaction occurred between those spears, exerted from one bud cluster to others across rhizome tissue (Nichols and Woolley, 1985). Quantitative analysis of correlative inhibition (CI) in Expt 6, however, could not differentiate cluster effects from SITE, TREATMENT, and SIZE on CI (section 4.4.3) since this variable occurred randomly and nested in the interaction of those variables.

4.4.2. Relative Spear Growth Rate (RSGR)

The effect of variation in crown size, which made it difficult to obtain the same number of clusters over treatments, was minimized by putting the size of crown as another source of variation in the anova for RSGR. The analysis of RSGR (Relative spear growth rate) based on the 43.6% of total spears elongating exponentially (Table 4.7) showed there was no effect of crown size (SIZE) although there was a tendency to have lower RSGR in small crowns than medium and large crowns (Table 4.8). Kim and Sakiyama (1989b) found that crown size influenced the pattern of spear elongation. The spears from normal crowns grew exponentially but those from small crowns grew almost linearly. They showed that there were changes in the elongation growth patterns in severely restricted amount of storage roots from those with moderately restricted roots. The decline of elongation rate occurred by the third spear when roots were severely restricted, whilst in moderately restricted roots it was observed in the fifth spear. The sixth spear in moderately and the fourth spear in severely restricted roots showed a drastic reduction in spear elongation. In Expt 6, spears in small crowns still grew exponentially, but at slightly lower rate compared to medium and large crowns. Bud size was positively correlated with spear size (Blasberg, 1932) as suggested by Nichols and Woolley (1985). Cultivar UC157 usually produces medium spear size with high spear and bud number (NZNAM, 1997). Since this experiment only used one cultivar, the bud size would have mainly been affected by the size of the crown.

Root cutting treatments influenced RSGR. Reducing the storage root by cutting horizontally or vertically reduced the RSGR significantly (Table 4.8 – 4.9). Kim and Sakiyama (1989b) showed the different concentration of sucrose, glucose, and fructose on three rhizome sections away from the bud area. The sugar concentration in the rhizome section closest to the bud was only half the sugar concentration in the section furthest from the buds. In their experiment, the storage roots were removed from the rhizome. Their results may explain the maintenance of the spear growth in the restricted storage roots in Expt 6. The spears at site C (minimal root) were still able to grow due to support from neighbouring roots which had tissue connection into the spears with limited storage root. At this site, many spears grew linearly or in irregular patterns as described in the shape distribution in the previous section (4.4.1), indicating the lack of storage roots or carbohydrate. Thus carbohydrate limitation tended to cause spear growth to be linear rather than exponential. Furthermore, total root removal (SITE C) in the crowns with higher numbers of clusters reduced RSGR more in small and medium crowns than in large crowns (Table 4.10). In Norway spruce, changing from dormant state to active buds put the buds into transition of metabolically active sinks and demanded high energy supply to further develop into different structures (Lipavska et al., 2000). Applying this finding to asparagus in Expt 6, clearly simultaneous growth of several spears at the same time exhausted the energy provided by insufficient carbohydrate availability, and resulted in very slow growth in small and medium crowns, reflecting competition for carbohydrate. The energy requirement for bud break and development into spear, however, was not measured in this Expt 6. Apparently, large crowns had capability to grow many spears at once in many clusters regardless of carbohydrate limitation in some parts of a crown. This situation suggested an effective mechanism of transporting carbohydrate to active metabolic buds in large crowns with high carbohydrate content, providing less competition for carbohydrate.

Nichols and Woolley (1985) and Kim and Sakiyama (1989a) showed that as the carbohydrate was used up, the spears growing later lost the ability to maintain the same speed of development as earlier spears. The reduction of RSGR over time for subsequent spears, however, did not occur in this Expt 6 (Table 4.11). There were two possibilities for the RSGR results in this analysis. The data used was only for exponential curves of spear elongation (E) and only accounted for 43.6 % of the total spears. Any other patterns of spear elongation which can be related to timing of spear appearance and possibly more effect of severe carbohydrate competition did not come into account. Thus RSGR analysis that was based only on exponential spear growth (E shape) was not appropriate for analysis of spear growth in this Expt 6 since it could not detect a change of shape as a function of carbohydrate depletion.

Another reason is temperature influence. Spears grow faster at higher temperature (Nichols and Woolley, 1985; Yen, 1993; Kailuweit and Krug, 1995; Dean, 1999; Wilson et al., 1999). As analysis of RSGR in Expt 6 accounted for E shape only, the spears which appeared later were coming from large crowns which were not affected by root cutting treatments and therefore grew as a function of temperature. Although the greenhouse temperature was controlled semi-automatically (see materials and methods), minor variations in temperatures during the experiment was detected (Fig. 4.21).

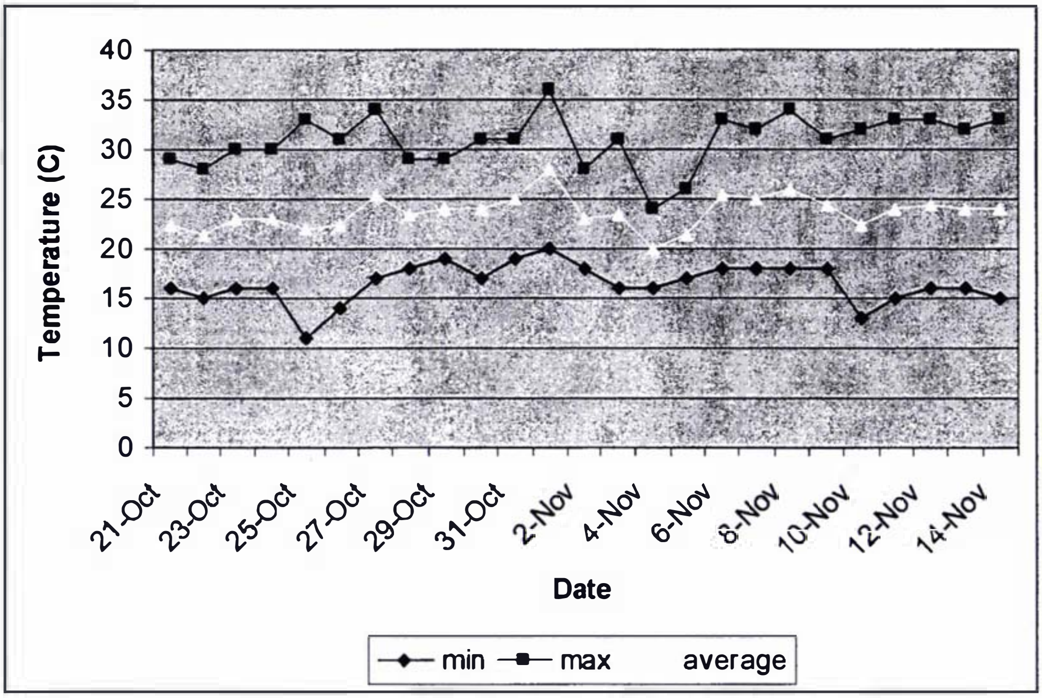


Figure 4.22 Expt 6: The minimum, maximum and average ambient temperature in the greenhouse during Experiment 6, monitored outside growth tanks.

4.4.3. Correlative inhibition

The sequence in which asparagus buds develop into shoots and the time lag between developments of successive shoots is controlled by correlative inhibition (Robb, 1983). There was interest in both the existence of correlative inhibition (CI) and its duration as an indication of its strength. Correlative inhibition (CI) was affected by crown size, as indicated by longer CI in small (4.13 days) and medium (4.20 days) crowns than in large (3.44 days) crowns (Table 4.13). Kim and Sakiyama (1989b) showed a different pattern of spear growth from exponential to linear growth for large and small crown, respectively. But in Expt 6, exponential spear growth still occurred but at lower frequency in small crowns than medium and large crowns (section 4.4.1). Differences in numbers and percentages of major shapes other than E shape indicated changes in spear growth and therefore suppressed the growth of subsequent spears, detected to be significantly affected by their spear position (Table 4.14). In general, CI existed stronger up to fifth spears and slowly reduced thereafter. This is an indication that as harvest progresses, CI gets stronger to some points. Tiedjens (1924, 1926) suggested that correlative inhibition became stronger and rate of production was reduced as the harvesting season progressed. Robb (1984) postulated that correlative inhibition strength was due to hormonal effects, or to carbohydrate content, but much research needs to be done to support her assumptions.

Further results of Expt 6 showed that CI in different spear positions (order of spear appearance) interacted significantly with their site (Table 4.12 and 4.14). These results revealed the relationship between CI and carbohydrate availability. In analysis of RSGR (previous section) on spears growing exponentially (E shaped), reduction of RSGR was noticed if spear growth was supported by minimal roots in small crowns or there were many clusters on a crown in small or medium sized crowns. McIntyre (1997) reported that carbohydrate can influence correlative inhibition by combination of osmotic and nutritional effects. Since the asparagus plants in our experiment were grown in aeroponics, they were subjected to the same level of nutrient and water misting. Each plant would receive similar conditions. McIntyre (1997) provided evidence that lateral buds could be released from the inhibiting influence of the parent shoot apex if the supply of three basic requirements, i.e. water, nitrogen and carbohydrate, was sufficiently increased in *Agropyron repens* (1972), *Pisum sativum* (1971), *Phaseolus vulgaris* (1973) and *Helianthus annuus* (1977). Applying his findings to the growing conditions of asparagus in Expt 6, the earlier spears could have more carbohydrate available to grow than later spears. However, CI was diminishing during later spear growth (Table 4.14). This leads to another possibility that apical dominance in asparagus might happen only in the buds closest to the base. Bud position has been shown to significantly affect the node of floral initiation (NFI) in *Pisum sativum* L cv. Alaska (Stafstrom, 1995). NFI for basal buds on 4 and 7 d plants varied as a function of nodal position and ranged from 5 to 5.7 nodes.

De Kroon and Knops (1990) used terminology of dormant, activated, and elongated buds to describe different stage of buds in two perennial grasses. An activated bud has passed an initial stage of growth, recognized by their cone-like form and short length (< 15 mm). In Expt 6, the measurement started when scale leaves did not cover the tip of the bud and the head appeared to be white and cone shaped and was defined as a primed bud. The primed bud could be implied where the buds started to expand but with very little elongation. OP in Expt 6 was defined as when two spears grew concurrently regardless of the shapes. The existence of OP throughout spear position (Table 4.15-4.20) suggested CI did not entirely suppress the subsequent spear growth. Elongation of subsequent spears at the same time as a previous spear grew indicated that CI was not as strong as when subsequent spears grew very little. The period of primed buds could be related to the suppression of subsequent spear growth when two or more spears grew together and the subsequent spear grew very little or did not elongate. Here the primed bud would relate to the shape of LE (Fig. 4.17) and LQ. From 732 spears, 59 spears (8 %) were categorized into LE shape and 27 spears (3.7 %) into LQ (Table 4.6). Comparison of percentage for LE and LQ amongst 3 crown sizes (Table 4.3), 3 root cutting treatments (Table 4.4) and 4 sites (Table 4.5) indicated similar distribution percentage. This was confirmed by the analysis of Proc Genmod (Fig. 4.20), showing no differences in LE and LQ. But, LE and LQ could also appear without overlap period as shown in Fig.4.9.

Nichols and Woolley (1985) reported that at least a three day lag occurred between removal of a spear at a length of 180 to 260 mm and growth of another bud in the same cluster. In Expt 6, lag period (LP) varied from 0 to 4 days (Table 4.21 – 4.25) depending on crown size, site, the bud position at which the spear came from and the number of bud clusters in a crown. Patterns of LP were similar to the patterns of CI. And indeed, LP correlated positively with CI.

4.4.4. Spear yield

Large crowns produced higher spear fresh and dry weight (Table 4.22), as a function of more large spears as well as spear numbers, whereas small crowns produced fewer spears mainly of quality 5. Small size of the spears (< 4 mm) in small crowns implied bud size was small, but the buds were still able to grow exponentially in some spears as discussed in section 4.4.2. In relation to distribution of shapes, CI and LP, however, it took a longer time to harvest small spears than large spears.

4.5. SUMMARY

Aeroponics provided an easy access to measure daily spear development in terms of length from the base to the tip of the same spears in a cluster on a crown.

Nine major shapes of spear elongation in terms of logarithmic plots were identified in asparagus; spears that grew exponentially only accounted for 43.6 % of the total spears. RSGR estimation worked only for spears that elongated exponentially. Using only E-shape, analysis of RSGR in relation to carbohydrate availability in terms of root storage was not suitable since shape changes may give some more information in response to carbohydrate availability. The distribution of shapes was affected by carbohydrate availability in terms of crown size. Large crowns not only tended to be higher yielding but also produced earlier, indicated by fewer days of CI, OP and LP.

Correlative inhibition (CI) existed amongst spears in a cluster, and was affected by the availability of carbohydrate. CI took about 4 days in small and medium crowns, whilst only 3.4 days in large crowns. The effect of cluster on CI was not detected because cluster identification and site characteristics were confounded. Number and position of bud clusters were not consistent through all the treatment distribution, and statistically the cluster effect could not be separated from other effects. Cluster effect on CI could possibly be detected if using uniform crown size with known distances amongst clusters and initial bud size within a bud cluster.

Increasing bud clusters in small crowns affected spear elongation adversely, indicated by longer time to grow later spears. However, this effect of the number of bud clusters was not found in large crowns. The next two experiments reported in Chapter 5 and 6 were conducted to verify the importance of bud number and bud clusters on a crown for increasing yield in asparagus.

CHAPTER 5

CROWN DEVELOPMENT OF ASPARAGUS SEEDLINGS GROWN IN AEROPONICS†

5.1. INTRODUCTION

Yield of asparagus spears depends on fern and root development, with emphasis on high levels of stored fructans in the roots and high bud number in the crown. The results discussed in Chapter 3 provide some indication of the complexity of the sequences of bud development and carbohydrate concentration, but interpretation was limited because of the difficulty of monitoring the dynamics of these variables in soil culture. There is little information in bud and bud cluster development on crowns (Bigard, 1973; Duangpaeng et al., 2002). Wardana et al. (1999) suggested that an important determinant of the link between sink strength (bud population) and source strength (stored assimilates) is the number of bud clusters present. This was supported by the results from Expt 3, 4, and 5 reported in Chapter 3 and Expt 6 in Chapter 4, but there is a need for more data of bud number and bud cluster distribution to support the suggestion.

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†Part of this chapter was presented in Third Postgraduate Colloquium INR, College of Science, Massey University, Palmerston North, November 2000 with authors and title:

Daningsih, E., David J. Woolley, Mike A. Nichols and Keith J. Fisher.
Shoot and root growth of *Asparagus officinalis* in two different soilless culture systems

For these reasons the experiment reported in this chapter (Expt 7) was planned using an aeroponics technique which allowed continuous monitoring of shoot and root behaviour. It was suggested that this procedure and the control of environmental condition could help to control plant to plant variation which can be a problem in asparagus research (Nichols, 1983; Nichols and Fisher, 1999). Aeroponics has been used successfully for vegetable research and production for many years (Soffer and Burger, 1989; Weathers and Zobel, 1992; van Os, 1994; Lim, 1997; Ota, 2000) but so far has not been used to study asparagus.

Cultivars UC157 and Jersey Giant are hybrid asparagus cultivars, representing low and intermediate levels of annual spear yield, respectively (Faville et al., 1999d).However, 'UC157' was reported to be higher yielding than 'Jersey Giant' (Wardana et al., 1999) when planted under ridge rows, reflecting greater numbers of spears produced rather than greater size of spears.

The main objective of the research reported here was to follow plant growth of these two asparagus cultivars over time in soilless culture (aeroponics), especially in terms of bud number and bud cluster distribution to which time trends of spear production and spear harvesting can be linked.

5.2. MATERIALS AND METHODS

5.2.1. Treatments and experimental design: Experiment 7

Cultivars Jersey Giant and UC157 were used. A randomised complete block design was utilized with four replications with tank as a block. There were two rows of plants in a block, and 30 plants for each cultivar were grown within each row in each block.

5.2.2. Plant materials

Seeds were germinated at 28°C in multi-single cell transplanting plug trays in bark media on 1, November, 1999. On 29, November, 1999, when the seedlings had developed at least two ferns, the transplants were cleansed and transferred into aeroponic tanks.

5.2.3. Aeroponics

5.2.3.1. Nutrient Solution

The aeroponics solutions described in Chapter 4 (Table 4.1) was used by mixing four stock solutions of standard hydroponics solution based on Cooper (1979). Solutions A and B contained macro nutrients whereas solutions C and D contained micronutrients. An electrical conductivity (EC) of 2 was prepared for the aeroponics solution by mixing equal volume from each stock solution. A pH of 6.5 was maintained by adding 1% KOH or 10% sulphuric acid.

5.2.3.2. Tank aeroponics system

An aeroponics system was built using four similar rectangular tanks with volume of (120 x 60 x 56) cm^3 (Fig. 5.1). Each tank was raised 70 cm above the ground on one side and 40 cm on the other side, allowing a water pump (Type CP 11 MONO, Model MPE 524-HHG 3-90, 180 watt, rpm 1500) with filter to be placed under the tank and collection of sprayed solution for recycling. Black plastic was laid down inside the tank to cover all sides.

Figure 5.1 Aeroponics system for asparagus seedlings using four tanks in the green house.

One hole was drilled at the low end of the tank to recycle the solution back to nutrient tank. The nutrient solution was pumped from the nutrient tank, placed under the aeroponics tank, through the lid of the tank using ordinary garden hose (d = 1.3 cm) and connecting to PVC pipes at the base of the tank. Poly Vinyl Chloride (PVC) pipe with diameter of 2.5 cm was used to provide a frame of three parallel lines (Fig. 5.2 A) at the bottom of the tank for delivering nutrient solution. Three spray misters (360 degree) were fitted on the two outside pipes, with four spray misters on the middle pipe (Fig 5.2 B). The distance between spray misters was 33 cm for the two outside pipes and 21 and 23 cm for the middle pipe. After the nutrient solution was sprayed into the air and had misted the asparagus roots, it was then collected at the base of the tank and returned to the nutrient solution tank. The pump then re-circulated the solution.

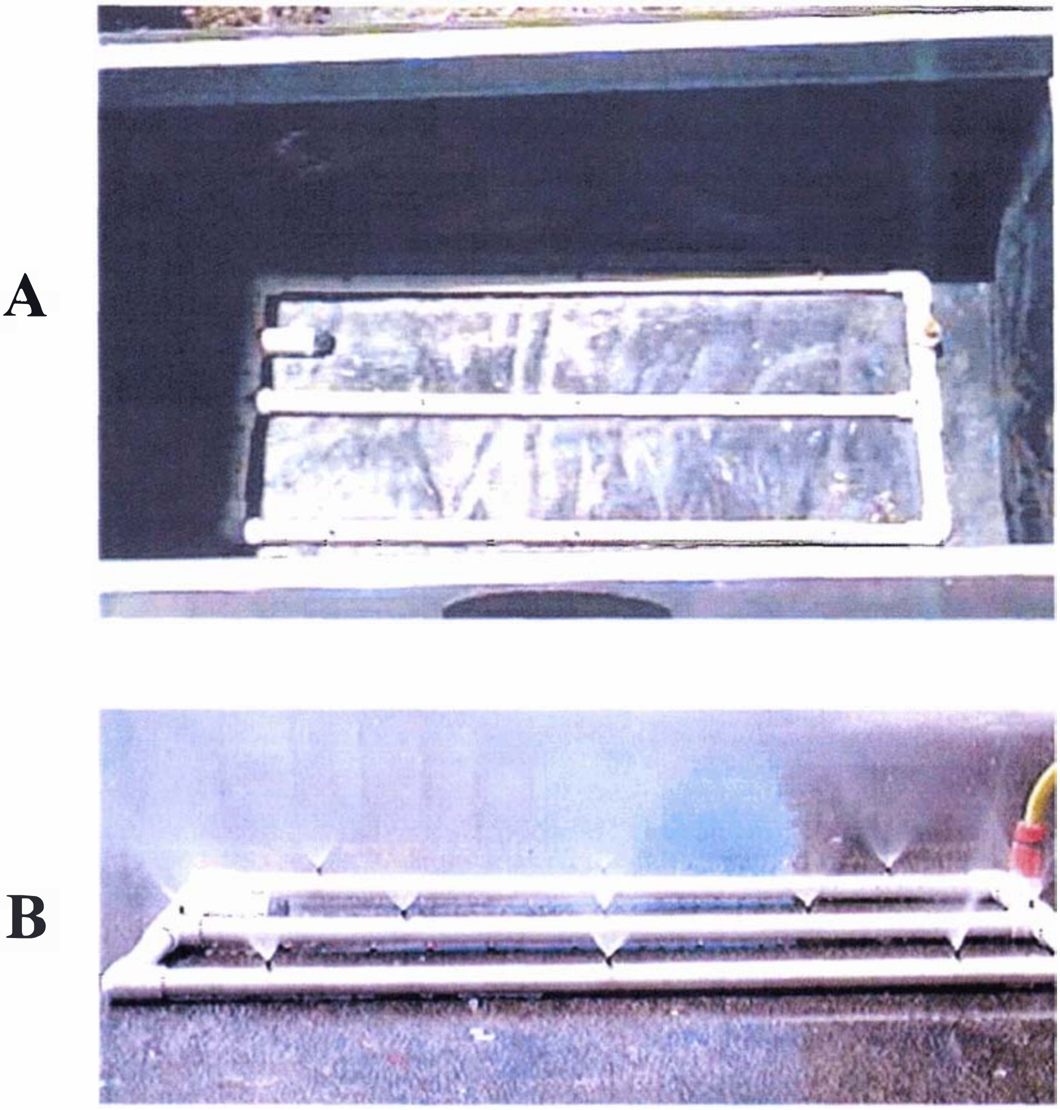

Figure 5.2 Inside aeroponics system for asparagus seedlings using three parallel PVC pipes for circulation of nutrient solution (A) with misting jet (360°) (B). Dimension of life frame was 96 cm (length) x 40 cm (width).

Each pair of tanks shared one nutrient collector tank equipped with one water pump and filter. Polystyrene covered with white plastic covered the top of the tank. Asparagus plants were inserted through holes in the cover, with 15 cm between the rows and 3.5

cm with zig-zag position within a row. The plants were inserted individually using a small loop of wire across the hole which functioned as an anchor for the asparagus crown and exposed the roots to the sprayed nutrient solution inside the tank (Fig. 5.3).

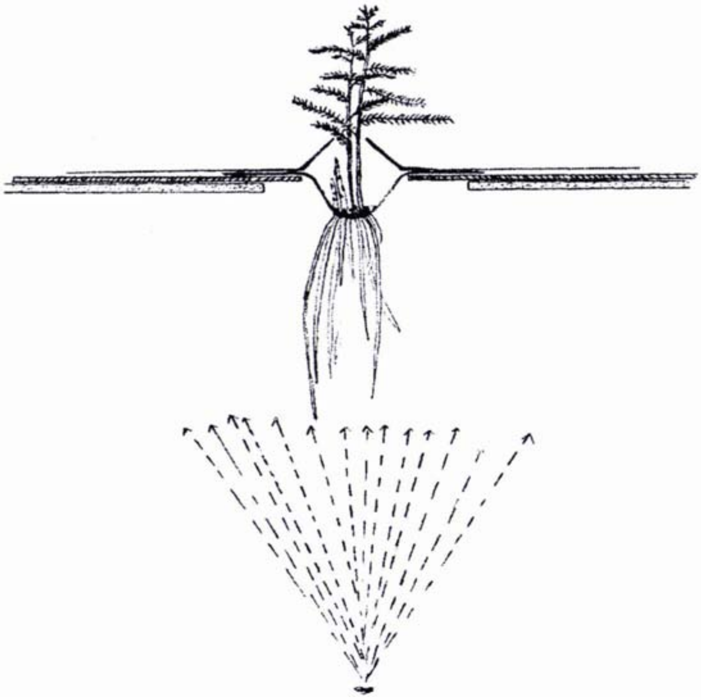

Figure 5.3 Asparagus seedling suspended through a loop of wire on the surface cover with double plastic layers and nutrient solution was sprayed on the root.

Nutrient solution misting was applied continuously for the first two weeks and slowly changed to 6 minutes off and 2 minutes on for another two weeks. Timing was controlled by an automatic clock switch. Collins and Jensen (1983) stated that the misting system is normally turned on for only a few seconds in every 2 to 3 minutes. This is sufficient to keep the roots moist and the nutrient solution aerated. Biddinger et al. (1998) sprayed fine mist for three seconds every ten minutes for tomato plants while Peterson and Krueger (1988) used a misting schedule of 7 seconds at 10 minutes intervals for cucumber. However, misting for 2 minutes and turning off for 6 minutes damaged the asparagus transplants so that a change was made to misting for two minutes and off for four minutes for the reminder of the experiment. The solution pressure pumped into the system was 15 psi with the volume of misting jet of 5 l per minute. The nutrient solution was replaced every two weeks to avoid imbalance in nutrients.

Two weeks after transferring, the green house roof was covered with 40% green shade cloth. The greenhouse temperature heating set point was 18°C and ventilation set point was 25°C.

5.2.4. Measurements

The numbers of buds, shoots (ferns and spears) and storage roots together with plant height and longest root length were measured continuously on a weekly basis for 12 weeks started from 1 December 1999 to 27 February 2000. Total bud number was summation of present buds, spears and ferns. Plants were removed from the aeroponics system for measurements. Plant height was measured from the base of the rhizome to the top of the highest fern.

Ratios were expressed as root:bud number, root:spear number, root:fern number, and root:total bud number (buds + spears + ferns).

At the end of experiment, all plants were harvested destructively. The plants were separated into above ground and below ground (crown including root and rhizome) parts. Both parts were weighed fresh and put in the oven for three days at 80°C for dry weight measurements.

5.2.5. Statistical analyses

All variables were analysed by univariate ANOVA using the SAS GLM Procedure (SAS version 8.2, 1999-2001) for a randomised complete block design with four blocks. Homogeneity of variance at each time of measurement was tested using Levene's test at probability of 5%. Normal distribution was also assessed using PROC CAPABLITY. Values of skewness and kurtosis were examined (http://www.alternativesoft.com/page25.htm). Log transformed data was used to analyze shoot and root fresh weight at the end of the experiment to reduce variance. Values of Protected Least Significant Difference (LSD) at $P = 0.05$ are presented when the two cultivars were significantly different.

Observations from week 6 to 12 were subjected to linear regression against time using proc REG for each cultivar. Regression lines were tested for two cultivar differences by comparing residual sum of squares from PROC GLM with different models. Straight lines of predicted values together with the means of actual data for each parameter measured were graphed to illustrate the goodness of fit of the models of each regression.

5.3. RESULTS

The results of Levene's tests showed that the variances of root, shoot, and total bud numbers and plant height were homogenous for all measurements. The variances for bud number were only heterogeneous at weeks 9, 10, and 11, and for spear number at weeks 9 and 11. Variances of longest root length were heterogeneous at weeks 10 and 11. Since the heterogeneity occurred only in few weeks out of 12 weeks, data were not transformed for the analysis.

The data for all parameters were normally distributed when tested using PROC CAPABILITY.

5.3.1. Plant growth

Green algae grew over the crowns of small seedlings in the aeroponics tanks over time. Plants were water sprayed individually to remove algae before bud counting. It was not possible to discern axial, secondary or tertiary buds clusters and all buds tended to group together.

There was some check to plant growth observed for the first five weeks after transferring the plants into aeroponics. Reduction in plant height, longest root length, and spear number was quite visible. Some ferns wilted, and some spears died so that over-all plant height was reduced. Subsequent plant height measurements were based on new shoots. After six weeks the plants settled into a period of steady growth (Fig 5.4 and Fig 5.5.). Results are illustrated for the full duration of the study, but statistical analyses are largely restricted to weeks 6-12.

5.3.1.1. Plant growth over first six weeks

Within this period, plants were exposed to three different intervals of intermittent nutrient spray. Fluctuation in all parameters occurred as plants adjusted to the change of environment until the plants started to stabilize at week 6 (Fig. 5.4 and Fig 5.5).

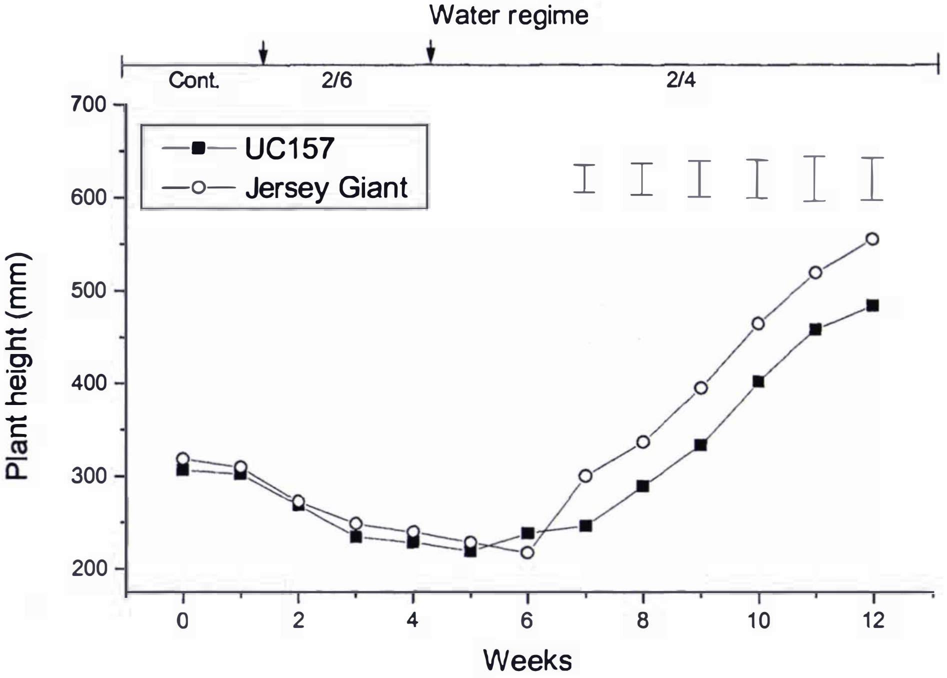

Figure 5.4 Expt 7: Plant heights for cultivar 'UC157' and 'Jersey Giant' grown in aeroponics tank in the green house during summer 1999-2000. Bars indicate $LSD_{0.05}$ at which significant differences occurred. Water nutrient misting were applied continuously (cont.), 2 minutes on and 6 minutes off (2/6), and 2 minutes on and 4 minutes off (2/4).

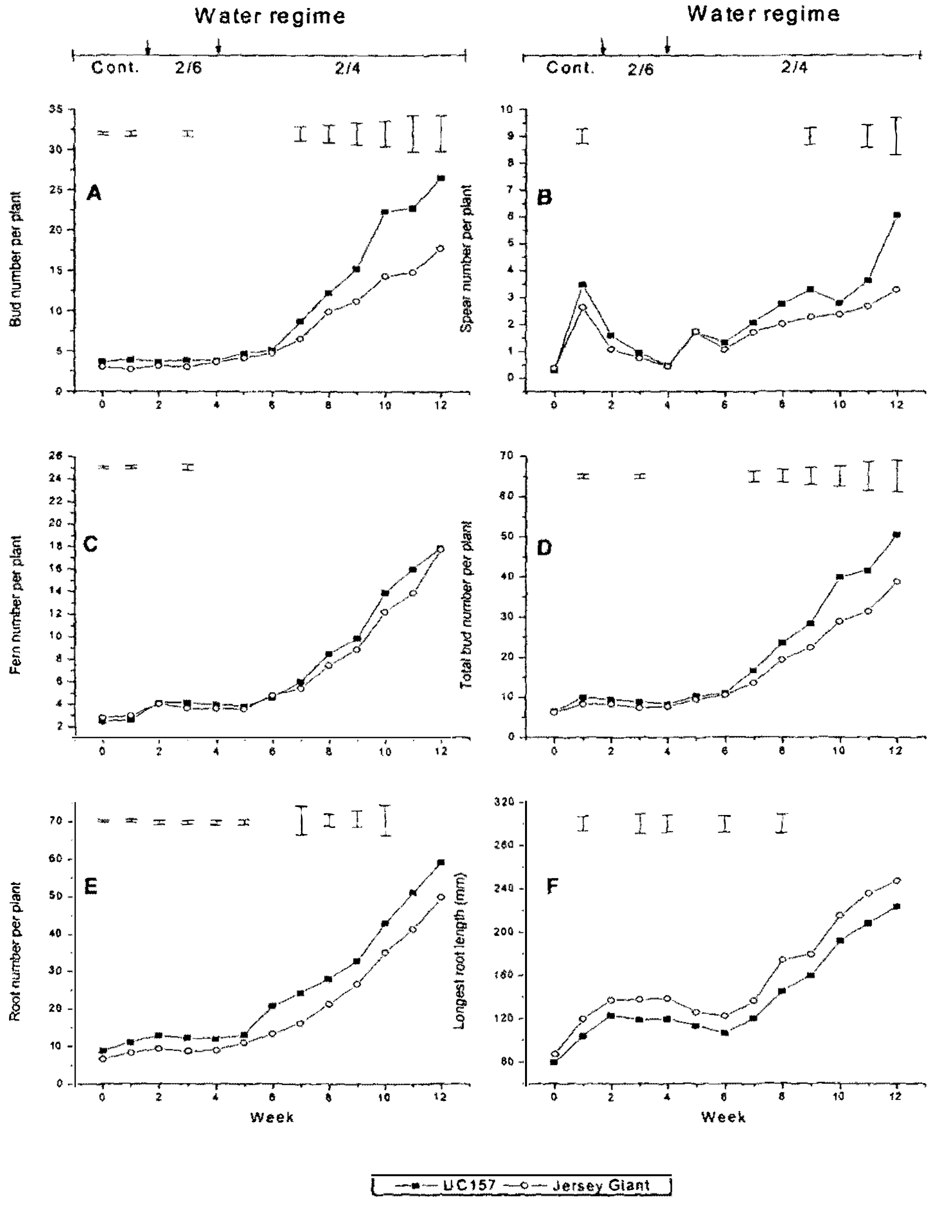

Figure 5.5 Expt 7: Plant growth measurement of bud number (A), spear number (B), fern number (C), total bud number (D), root number (E) and longest root length (F) of asparagus cultivars 'UC157' and 'Jersey Giant' grown in aeroponics tank in the green house during summer 1999-2000. Bars indicate $LSD_{0.05}$ at which significant differences occurred. Water nutrient misting were applied continuously (cont.), 2 minutes on and 6 minutes off (2/6), and 2 minutes on and 4 minutes off (2/4).

5.3.1.2. Plant growth over second six weeks

Within the second six-week period, all measured variables increased (Fig 5.4 and Fig 5.5 A – F). Significant differences between cultivars occurred in all variables except fern number per plant.

By week seven, plant height of 'Jersey Giant' had increased by almost 38% from 217 to 300 mm whereas 'UC157' increased only by 3% (Fig 5.4). The two cultivars then increased steadily in height for the following weeks. The height of 'Jersey Giant' was consistently greater than that of 'UC157'.

Total bud numbers were significantly higher in 'UC157' than 'Jersey Giant' from week 7 to week 12 (Fig 5.5. D). Although the starting point of total bud number was almost similar at week 6, 'UC157' produced buds faster than 'Jersey Giant' in the subsequent six weeks. Cultivar UC157 increased total bud number by 3.6 times while 'Jersey Giant' increased by 2.6 times at week 12 compared to the bud number initially at week 6.

Fern numbers were not significantly different (Fig 5.5. C). Average production of ferns per plant for both cultivars during the second six week period was 2 ferns per week.

Spear number and bud number per plant increased at similar rates. Cultivar UC157 always had higher numbers of spears (Fig. 5.5. B) and buds (Fig 5.5. A). Spear number was significantly different at week 9, 11, and 12, and bud number was significantly different from week 7 to week 12.

The root number of 'UC157' was significantly higher than that of 'Jersey Giant' at week 7, 8, 9 and 10 (Fig. 5.5. E). On the other hand, the longest root length of 'UC157' was always shorter than 'Jersey Giant' but this was significant only at week 8 (Fig. 5.5. F)

5.3.2. Linear regression

Over the second six week period, linear population trends in bud and spear number were significantly different between two cultivars.

5.3.2.1. Bud number

The slopes of bud number against time for 'UC157' and 'Jersey Giant' were 3.65 buds per week and 2.12 buds per week (Fig. 5.6). These slopes were detected significantly different at $P \leq 0.0001$.

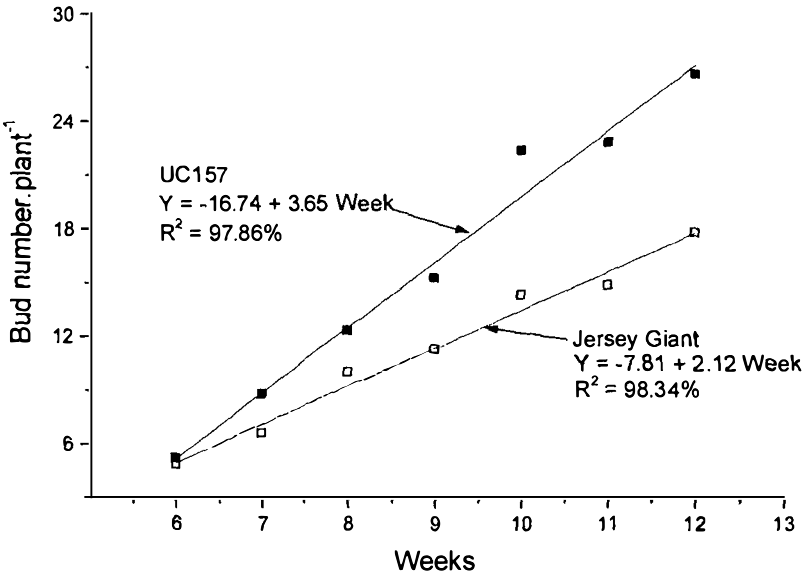

Figure 5.6 Expt 7: Regression of bud number against time (week) for cultivar 'UC157' and 'Jersey Giant' grown in aeroponics tank in the greenhouse.

5.3.2.2. Spear number

The slopes of spear number were 0.62 and 0.32 spears per week for cultivar 'UC157' and 'Jersey Giant', respectively (Fig. 5). The spear number of cultivar 'UC157' was almost double that of cultivar 'Jersey Giant' and was significantly different at $P = 0.0015$.

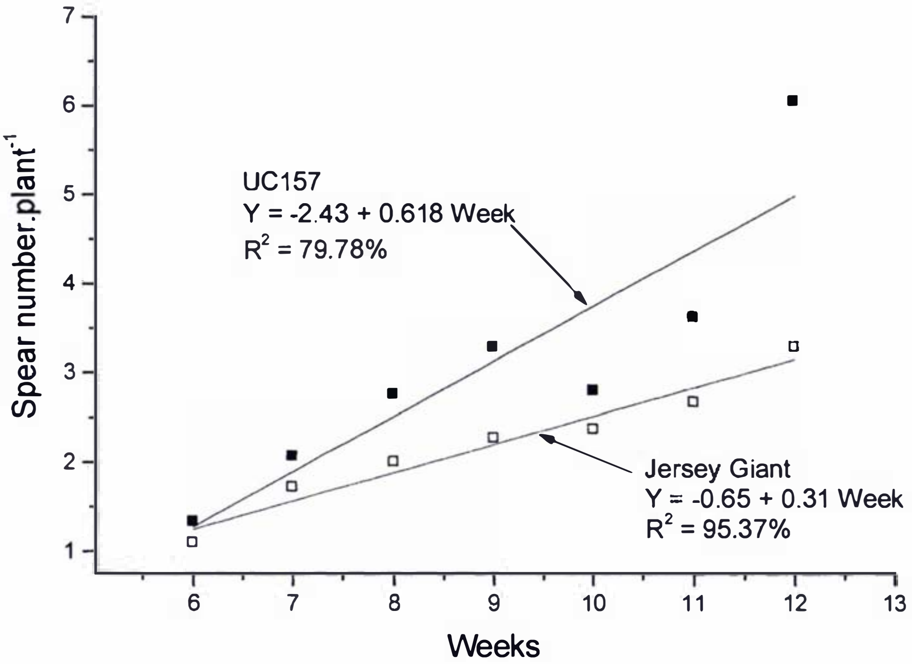

Figure 5.7 Expt 7: Regression of spear number against time (week) for cultivar 'UC157' and 'Jersey Giant' grown in aeroponics tank in the greenhouse.

5.3.2.3. Fern number

Unlike bud and spear number, the slopes of fern number against time for both 'UC157' and 'Jersey Giant' were not different statistically (Fig. 5.8).

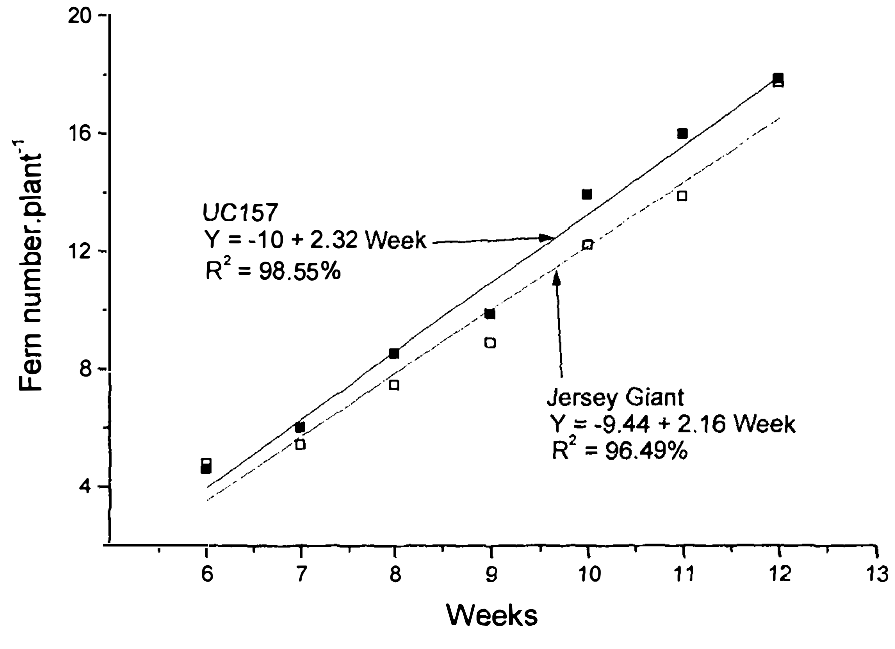

Figure 5.8 Expt 7: Regression of fern number against time (week) for cultivar 'UC157' and 'Jersey Giant' grown in aeroponics tank in the greenhouse.

5.3.2.4. *Total bud number*

The slope of total bud (fern + spear + bud) number between cultivar 'Jersey Giant' and 'UC157' was significantly different at $P = 0.0005$. Cultivar 'Jersey Giant' and 'UC157' produced 4.6 and 7.57 total bud number per week, respectively (Fig. 5.9).

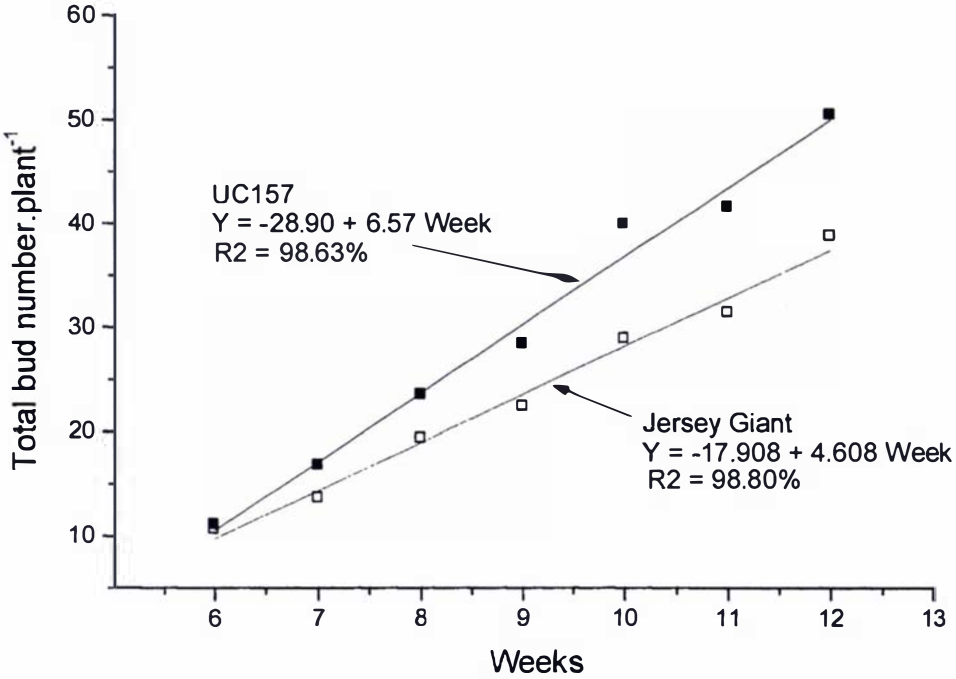

Figure 5.9 Expt 7: Regression of total bud (fern + spear + bud) number against time (week) for cultivar 'UC157' and 'Jersey Giant' grown in aeroponics tank in the greenhouse.

5.3.2.5. *Plant height*

There was marginal differences ($P = 0.07$) in plant height increase between cultivar 'UC157' (47.7mm per week) and 'Jersey Giant' (54.2mm per week) when tested using individual slopes (Fig 5.10). The two lines were significantly fitted as parallel lines, with UC157 consistently being shorter.

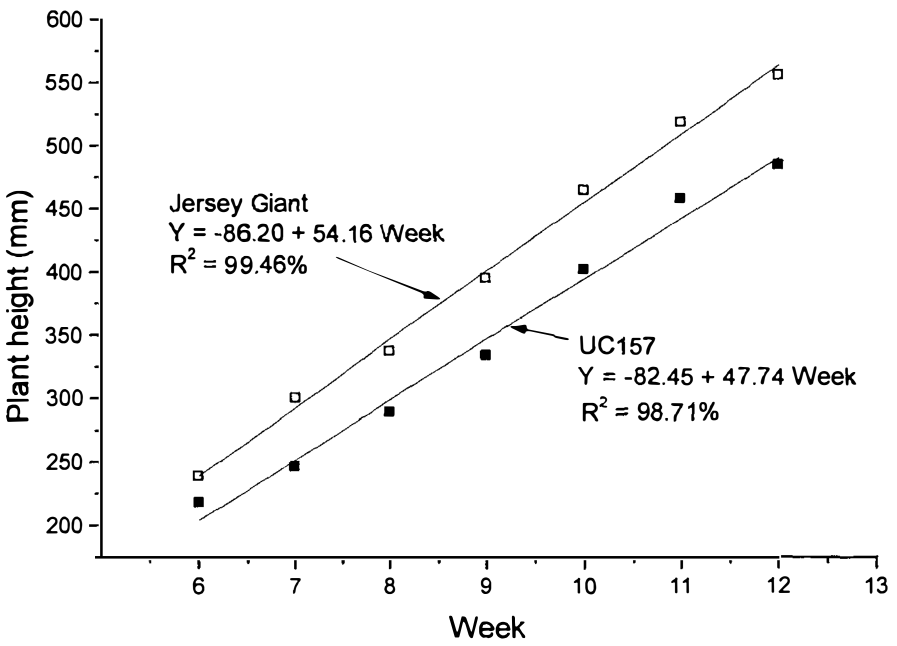

Figure 5.10 Expt 7: Regression of plant height against time (week) for cultivar 'UC157' and 'Jersey Giant' grown in aeroponics tank in the greenhouse.

5.3.2.6. Root number

The slopes of root number were not statistically different between cultivars 'UC157' and 'Jersey Giant' when tested using individual slopes with proc GLM. The lines fitted as two parallel lines (Fig. 5.11), with Jersey Giant consistently having fewer roots.

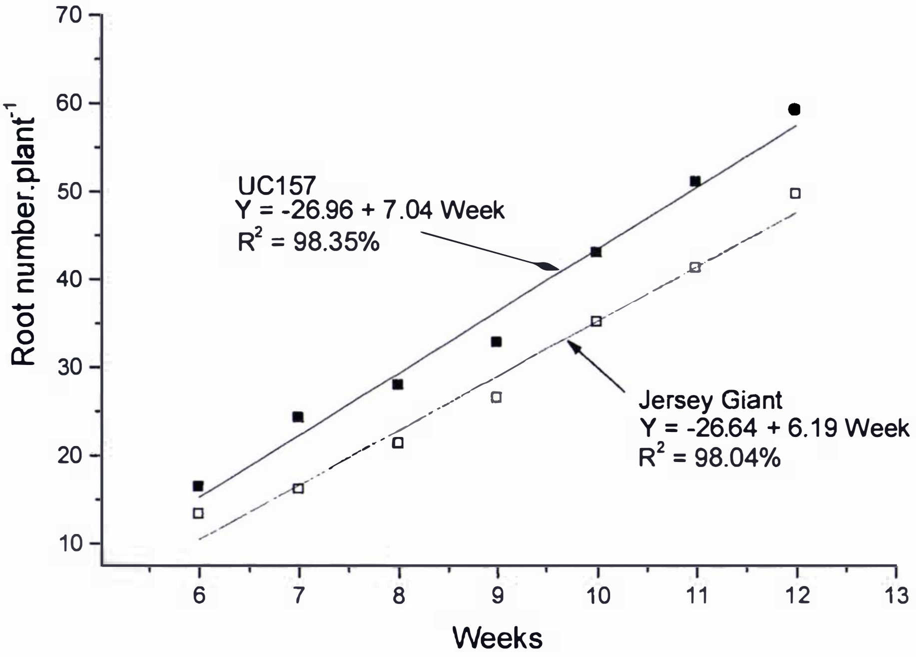

Figure 5.11 Expt 7: Regression of root number against time (week) for cultivar 'UC157' and 'Jersey Giant' grown in aeroponics tank in the greenhouse.

5.3.2.7. *Longest root length*

Similar rates of root length increase in the two asparagus cultivars were found (Fig. 5.12) but the two lines fit significantly as parallel lines with 'Jersey Giant' consistently being longer.

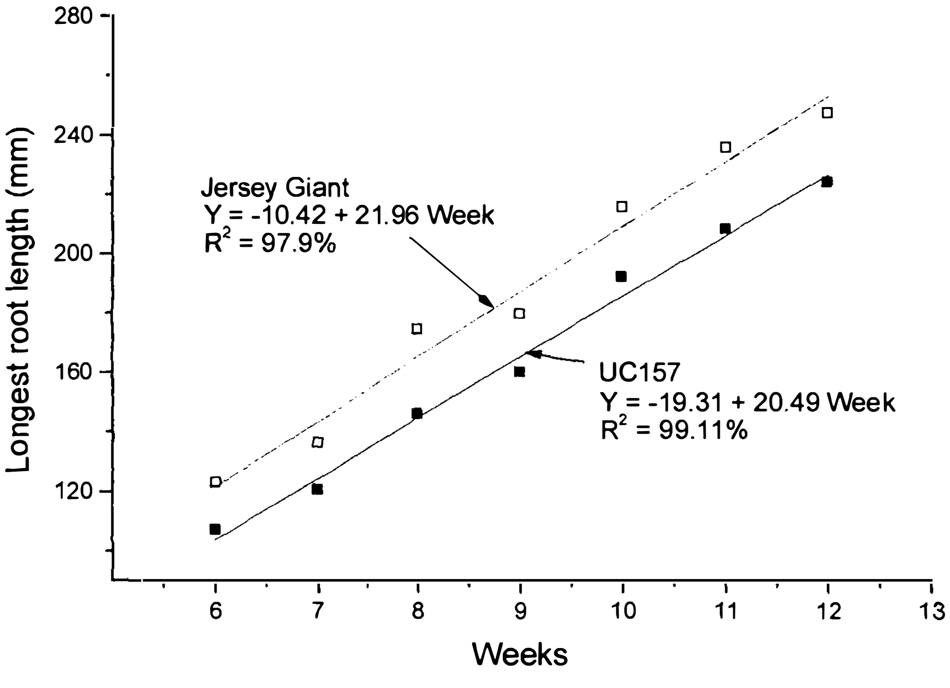

Figure 5.12 Expt 7: Regression of longest root length against time (week) for cultivar 'UC157' and 'Jersey Giant' grown in aeroponics tank in the greenhouse.

5.3.3. Ratio between root number and components of shoot number

The ratios between root number and various components of shoot number (bud, spear, fern, and total bud number) are listed in the following tables.

5.3.3.1. Ratios of root to bud number

From week 6 to weeks 12, both cultivars gradually reduced the ratios of root to bud number. Within this second six-week period, the ratios of root to bud number in 'UC157' were eventually lower than 'Jersey Giant' (Table 5.1).

Table 5.1 Expt 7: Ratios of root number to bud number of asparagus plants grown in aeroponics tank.

Week	Cultivar		Significance
	UC157	Jersey Giant	
6	4.0750	3.2556	ns
7	3.0076	2.8848	ns
8	2.4671	2.2569	ns
9	2.3513	2.4055	ns
10	2.0100	2.5091	*
11	2.4789	2.9892	ns
12	2.3289	2.8764	**

ns, *: non significant or significant at 0.05

5.3.3.2. Ratios of root to spear number

There was not any significant difference between cultivars in ratios of root to spear number (Table 5.2).

Table 5.2 Expt 7: Ratios of root number to spear number of asparagus plants grown in aeroponics tank.

Week	Cultivar		Significance
	UC157	Jersey Giant	
6	16.920	16.966	ns
7	15.242	12.386	ns
8	14.962	14.055	ns
9	12.666	13.945	ns
10	20.19	20.662	ns
11	17.426	18.751	ns
12	13.102	21.980	ns

ns : non significant.

5.3.3.3. Ratios of root to fern number

The ratios of root to fern number between the two cultivars were not significantly different except at week 6 (Table 5.3). The ratios of root to fern number of both cultivars increased similarly. At the final harvest, the ratios of root to fern number for cultivar 'UC157' and 'Jersey Giant' were 3.4482 and 3.1027, respectively.

Table 5.3 Expt 7: Ratios of root number to fern number of asparagus plants grown in aeroponics tank.

Week	Cultivar		Significance
	UC157	Jersey Giant	
6	3.9419	2.9444	**
7	4.4139	3.1338	ns
8	3.3795	2.9821	ns
9	3.4336	3.1145	ns
10	3.1440	2.9273	ns
11	3.3273	3.0048	ns
12	3.4482	3.1027	ns

ns, **: non significant or significant at 0.01, respectively.

5.3.3.4. Ratios of root to total bud number (bud+spear+fern)

From weeks 7 to weeks 12, the ratios of root to total bud number were gradually decreasing and they were not significantly different between the two cultivars except at week 6 (Table 5.4).

Table 5.4 Expt 7: Ratios of root number to total bud (fern + spear + bud) number of asparagus plants grown in aeroponics tank at different harvest.

Week	Cultivar		Significance
	UC157	Jersey Giant	
6	1.6305	1.3055	*
7	1.5031	1.2565	ns
8	1.2196	1.1279	ns
9	1.1883	1.1959	ns
10	1.1234	1.2141	ns
11	1.2557	1.3178	ns
12	1.2067	1.3190	ns

ns, *,: non significant or significant at 0.05, respectively.

5.3.3.5. Comparison between two cultivars on "predicted ratios" of root to components of the shoot during second six weeks

Predicted values from the regression lines in Figs. 5.6-5.9 were used to calculate "predicted ratios" of root to spear number, root to fern number, and root to total bud (bud + spear + fern) number, and these "predicted ratios" were plotted in Fig. 5.13. The ratios of root to bud number (Fig. 5.13.A) in 'Jersey Giant' increased whereas in 'UC157' reduced progressively, approaching constant values at 2.686 and 2.119 for Jersey Giant and 'UC157', respectively.

The ratios of root to spear number of 'Jersey Giant' increased too (Fig 5.13.B). On the other hand, the ratios of root to spear in 'UC157' had relatively little change from 11.975 at week 6 to 11.54 at week 12.

Root to fern ratios changed very little in 'Jersey Giant', but declined progressively in 'UC157' (Fig. 5.13.C). The reduction of ratios of root to fern number was an indication that ferns were produced at faster rate than root.

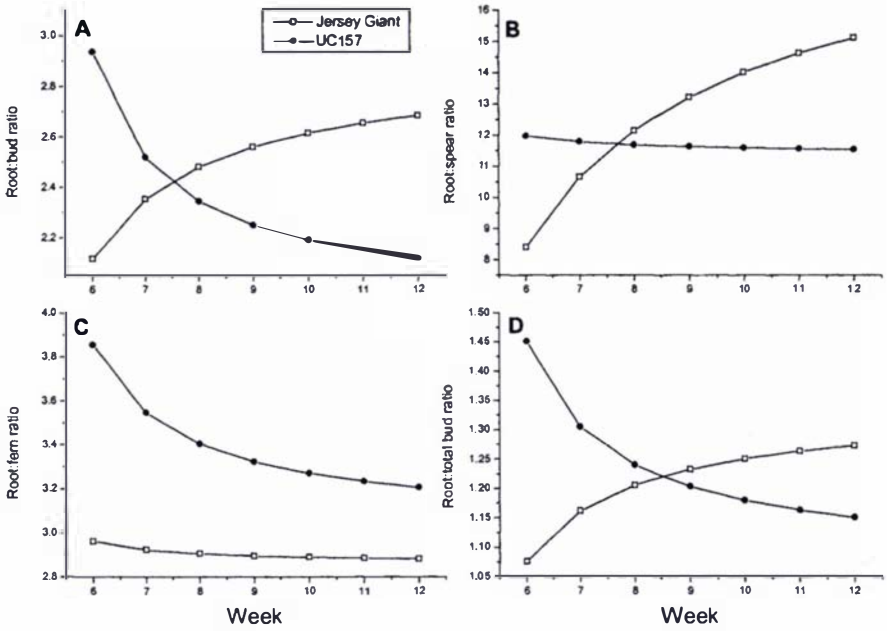

Figure 5.13 Expt 7: Ratios of root number to bud number (A), spear number (B), fern number (C), and total bud number (bud+spear+fern) (D) based on predicted values of two asparagus cultivars grown in aeroponics tank in the green house.

Ratios of root to total bud number are plotted in Fig. 5.13.D. Trends indicated a declining ratio for 'UC157' and increasing ratio for 'Jersey Giant' such that by the end of the experiment the ratios of roots to total buds were similar for the two cultivars.

5.3.4. Fresh and dry weight

Results from testing homogeneity of variance and normal distribution showed only fresh weight of shoot and root were heterogeneous and were not normally distributed (data not shown). Log transformed data was used for analysing shoot and root fresh weight. Variation was large and both log transformed data of fresh shoot and root weight were not significantly different between cultivars (Table 5.5) (Untransformed data shown in brackets).

Table 5.5 Expt 7: Final shoot and root fresh weight of asparagus plants grown in aeroponics.

Variables	Cultivar		Significance
	UC157	Jersey Giant	
Shoot fresh weight (g)	3.57 (50.43)	3.65 (76.97)	ns
Root fresh weight (g)	3.79 (62.33)	3.92 (91.09)	ns

ns: non significant. value in parentheses is the untransformed value.

Cultivars were not different in shoot and root dry weight and the ratio of root:shoot dry weight (Table 5.6).

Table 5.6 Expt 7: Final shoot and root dry weight and ratio of root to shoot dry weight of asparagus plants grown in aeroponics.

Variables	Cultivar		Significance
	UC157	Jersey Giant	
Shoot dry weight (g)	9.71	11.84	ns
Root dry weight (g)	11.64	14.89	ns
Ratio root: shoot dry weight	1.213	1.322	ns

ns: non significant.

5.4. DISCUSSION

5.4.1. Plant growth within the first six weeks

Strong healthy seedlings are important for a good stand (Bussel, 1997b). In this early aeroponics system, the misting regime used initially caused a detrimental effect for plant stand, longest root length and spear number of both cultivars. A reduction in plant height occurred mainly due to fern wilt so that the measurements were made on new spear and fern height.

Root zone aeration is important to the plant since it provides enough oxygen for aerobic respiration (Armstrong, 1980). Obviously the aeroponics system provides oxygen exposure to the plant root (Zobel et al., 1976). This oxygen exposure is very important especially in water culture because depletion of oxygen will have an adverse effect on the plant. By misting the plant root with high pressure in aeroponics system, the root surface is supplied enough oxygen beside adequate water. Unlike in lettuce (Nir, 1982) and cucumber (Peterson and Krueger, 1988) in which plants grew well with an intermittent misting system for 10 to 15 s every 7 to 8 minutes and 7 s at 10 minutes intervals respectively, the intermittent misting in this asparagus experiment involving a period of six minutes without nutrient solution reduced plant stand, longest root length and spear, bud, fern and root number. When a shorter interval between intermittent misting was applied the growth of all plant parts improved (Fig. 5.4 and 5.5). Drost and Wilcox-Lee (1990, 1997a, b) found that bud production was quite sensitive to water stress, and our findings confirmed that asparagus seedlings of the 'Jersey Giant' and 'UC157' produced no buds during the stress occurrence.

In all of these responses 'UC157' was more sensitive than 'Jersey Giant' to misting treatment. This finding contrast with common beliefs about the habit of each cultivar.

Cultivar UC157 is adapted to hot regions (Wehner, 2003) whereas 'Jersey Giant' is better adapted to cool regions (McCormick and Geddes, 1996)

5.4.2. Plant growth from week 6 to week 12

Cultivar 'Jersey Giant' produced fewer total buds than 'UC157' in the second six week period (Fig 5.5 D), reflecting differences in both spear numbers (Fig. 5.5 B) and bud numbers (Figs. 5.5 A). The difference in bud number was followed by greater spear number in UC157 (Fig. 5.5 B and Fig. 5.7) but not greater fern number (Fig. 5.5 C). Sudjatmiko et al. (1997) found that 'UC157' had more ferns in the first season than 'Jersey Giant' but these differences were less marked in the second season. They suggested that the number of bud clusters present at the start of the second season, rather than the number of buds per se determines the number of shoots present. Bud distribution itself from both cultivars in this Experiment 7 could not be distinguished between axial, secondary, and tertiary clusters because under aeroponics, bud clusters of both cultivars tended to group together. This condition may have resulted in the same fern number for the second six week period.

The increase in total buds is important in terms of potential yield of asparagus and often expressed as root: bud ratio or root: total bud ratio. Root number was always greater in 'UC157' than 'Jersey Giant' (Fig 5.5 E). Root number of asparagus plants is very important since the storage roots will supply the carbohydrates for bud break and spear production later on. For asparagus seedlings, continuous production of new roots and total buds will influence the development of rhizome. No matter what the condition, 'Jersey Giant' consistently produced fewer root number than 'UC157' (Fig 5.5 E and Fig. 5.11) but had tendency to have longer root length (Fig 5.5 F and 5.12). A longer root length in 'Jersey Giant' than 'UC157' would be thought to indicate a better adaptation for drought conditions. Root length has been used in other plants to indicate a possibility for survival when water is limited (Schmidhalter et al., 1998; Price et al., 2002; Matsui and Singh, 2003). Thus 'Jersey Giant' had ability to adapt better than 'UC157'. The ratio between aerial (top) and underground growth supported this result.

According to Robb (1983) the root:shoot ratio of seedlings is approximately 2:1. For every shoot, 2 roots will develop and the dry weight of the root system is twice that of the shoot system. Hence Robb refers to shoot as the fern. However, Robb (1983) did not mention the age of seedlings. From Expt 1 reported in Chapter 2, root:total bud ratio varied with plant age as observed by (Dufault and Greig, 1983; Sudjatmiko, 1993; and Karno 1999). The ratios between aerial (top) and underground parts of asparagus are reflected in Fig. 5.13 using predictive values. Cultivar Jersey Giant was less sensitive than 'UC157' after being exposed to stress conditions in the first six weeks, resulting in better growth of 'Jersey Giant' than 'UC157'. This was supported by increases in all values of ratios except root:fern ratio (Fig. 5.13c). An increase in ratios of root to aerial components indicates growth partition favouring to the roots. Further comparison of ratios between root number and various parts from the first and second six week periods (Table 5.1 – 5.4) supported better development of 'Jersey Giant' than that of 'UC157'.

The results in Expt 7 agreed with the findings of Sudjatmiko et al. (1997), showing that 'UC157' performed better than 'Jersey Giant' in term of bud and total bud number but not fern number. In Sudjatmiko et al. (1997), total bud production was 75% higher in 'UC157' than in 'Jersey Giant' at the end of first harvest but only 42 % higher in the second harvest season. However, they showed that both 'UC157' and 'Jersey Giant' had similar ratios of root to total bud number and slightly higher ratio of root to fern number at the end of first and second harvest. In the current experiment (Expt 7) this was not the case because of similarity in fern number which could have been the result of a tendency to have bud clusters grouping together. In addition, Expt 7 used seedlings whereas Sudjatmiko et al. (1997) measured transplanted plants that grew in field conditions.

In contrast with other results (Feibert et al, 1996; Bakka et al., 1999; Faville et al., 1999d), Wardana et al. (1999) showed that the yield was higher in 'UC157' than 'Jersey Giant'. Wardana et al. (1999) suggested that it was the number of spears rather than individual spear weight that contributed to higher total yield of 'UC157'. In terms of growth, Sudjatmiko et al. (1997) showed there was difference between 'UC157' and 'Jersey Giant' in crown, shoot, and total weights at the beginning but similar at the final harvest. Although bud and bud cluster distribution were not clear in the current aeroponics experiment, results indicated potentially heavier fresh and dry weight in 'Jersey Giant' than 'UC157' although the difference was not significant (Table 5.5 and 5.6). A significantly greater plant height in 'Jersey Giant' than 'UC157' (Fig. 5.4) and tendency to be heavier weight with similar number of ferns indicated possible higher photosynthetic rate in 'Jersey Giant' cladophylls. This result was supported by Faville et al. (1999d) showing net photosynthetic rate of 'Jersey Giant' (3.0 μmol.m^{-2}.s^{-1}) was greater than 'UC157' (2.4 μmol.m^{-2}.s^{-1}).

Further research regarding bud clusters can help understanding the trend of aerial parts of asparagus during plant growth. Very few studies have observed asparagus bud growth in relation to their position on primary, secondary or tertiary bud clusters. Bigard (1973) suggested that asparagus plants with more tertiary buds would be likely to have higher potential production, whereas Nichols and Woolley (1985) indicated that spear size would be determined by bud size which would affect spear production. These findings however have not been thoroughly followed on the same individual plant, which is important because plant variation is substantial. Identifying potential production by estimating bud number and bud distribution on an asparagus crown at transplanting will be of benefit in selecting transplants for production evaluation.

A major objective for this Expt 7 was to study development of bud and bud cluster distribution on a seedling crown. Any increase or reduction in available buds with subsequent development for bud usage, such as spears and ferns, and cluster distribution within a period of crown development, may denote specific character of bud dynamics for a cultivar as found for example in *Carex flacca* and *Brachypodium pinnatum*, two chalk grassland perennials having different characters in bud dynamics and rhizome length (de Kroon and Knops, 1990).

As crowns develop under the ground, a simple technique for easy access for visual observation without destruction should be investigated. Aeroponics, a soilless culture, has been reported to be a tool for research in morphology (Zobel, 1989), physiology (Arzani et al., 1997; Jie and Kong, 1998; Gilmer et al., 2001) or even production (Lim and Lee, 1996; Lim, 1997; Giacomelli, 2002; Nichols and Christie, 2002) of a plant species. In this Expt 7, aeroponics was utilized to observe bud dynamics of asparagus seedling crowns. Apart from clean root and easily removed the seedlings from the system, in this Expt 7, the growth of green algae on the surface of the plants (precisely on the rhizome) caused difficulty in observing each plant. The buds and bud clusters tended to group together, making it difficult to classify axial, secondary or tertiary bud clusters. The technique of aeroponics tank needs to be modified to allow for rhizome spread and to allow control of misting only under rhizome, not over it. A hydroponics system was used as an alternative in Expt 8 to observe bud and cluster distribution and it is reported in Chapter 6.

5.5. CONCLUSIONS

Seedlings of 'Jersey Giant' were less sensitive than 'UC157' when exposed to 'drought stress' without nutrient solution misting for six minutes. Greater plant height, longer roots, and a tendency to have heavier fresh and dry weight, and higher ratio root:shoot dry weight were shown in 'Jersey Giant' than in 'UC157', but 'UC157' produced higher number of buds and roots. Similarity in fern number may come from the same number of bud clusters but discrimination amongst axial, secondary and tertiary bud clusters was not successful in aeroponics system so that the differences in yield between two cultivars could not be explained in terms of to bud and cluster distribution.

Following bud and cluster distribution in seedling development may give basic information that can indicate likely plant behaviour in field condition. Plant structure is complex in established plants than in seedlings. Differences in cultivar and management cultures should be taken into account when making comparison between seedlings and older plants.

CHAPTER 6

A NON-DESTRUCTIVE INVESTIGATION OF MORPHOLOGY AND PHYSIOLOGY OF *ASPARAGUS OFFICINALIS* L. SEEDLINGS: EFFECTS OF ELECTRICAL CONDUCTIVITY IN HYDROPONICS†

6.1. INTRODUCTION

Asparagus plants with high bud number and heavy root mass are expected to have bud availability for marketable spear production with enough support of carbohydrate from the root. Total bud number itself may not limit spear production, but the number of large sized buds determines marketable spears as demonstrated in Expt 3 and 4 (see Chapter 3). Marketable spears come from large buds located at the bases of bud clusters. This is supported from visual observation that buds at the base of a cluster are usually larger than subsequent buds, and spear size is assumed to be correlated with bud size (Blasberg, 1932; Nichols and Woolley, 1985).

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†Part of this chapter was presented orally in International Symposium for Growing Media and Hydroponics, Sweden, September 2001 and published in Acta Horticulture (in press) with authors and title:

Daningsih, E., David J. Woolley and Mike A. Nichols:
Changes in morpho-physiology of *Asparagus officinalis* L. at different electrical conductivities.

Furthermore, a concept developed from time trends of spear production during harvest (see Chapter 3) revealed that number of bud clusters and possibly the size of bud clusters will further determine marketable yield and time for maximum spear production. This concept is supported by the results from the studies conducted by Wardana et al. (1999) and Sudjatmiko et al. (1997).

To observe buds, bud clusters and their distribution on crowns of established plants in the field, however, is difficult due to complex field conditions and high variation amongst asparagus plants. Aeroponics, a soilless culture, was used in Expt 7 to overcome these difficulties, but there were limitations to the technique which compromised interpretation of results. The growth of green algae on the seedling crown and a tendency of a crown to produce a big clump of buds close together made it difficult to discern axial, secondary or tertiary bud clusters, relating to bud cluster distribution (see Chapter 5). The aeroponics technique required further modification for the observation of cluster development on asparagus crowns.

While morphological study can lead to an understanding of plant development, most studies of asparagus seedlings deal more with growth and carbohydrate partitioning (Benson and Takatori, 1980; Dufault and Greig, 1983; Sudjatmiko et al., 1997). Morphological studies on the development of fern and crown (defined as storage roots, rhizome and associated buds) of asparagus are very limited (Bigard, 1973; Robb, 1984; Duangpaeng et al., 2002). Detailed study of crown development, particularly on how buds are allocated to clusters and the relationship between storage root numbers and bud numbers, will give information for the development of predictive techniques for assessing future yield potential (Sudjatmiko, 1993). As storage roots and rhizomal buds are both underground organs, hydroponics – an alternative soilless culture - offers an ideal method for non-destructive continuous observation of the pattern of development. The use of plant seedlings may help to simplify the complexity of established plants and enhance the possibility of early detection of characteristics of cluster development on a crown that could be used for yield prediction. It can also be used to develop a quick tool for selection of plants where growth is limited by environmental condition such as water stress or nutrient deficiency.

When the plant is supplied with sufficient mineral nutrients and water, cytokinin together with auxin induce cell division and growth (Miller et al., 1955 in Miyazawa et al., 1999; Coenen and Lomax, 1997). Cytokinins have a side chain rich in carbon and hydrogen attached to the nitrogen protruding from the top of the purine ring (Salisbury and Ross, 1992); thus, cytokinin chemical structure is closely related to nitrogen. Bud production is strongly influenced by nitrogen level available to the plants (Salisbury and Ross, 1992). Following bud production, bud clusters may also develop, extending the rhizome and crown development. Nitrogen is the only macronutrient which may be present as an anion or a cation. Plant roots will release H^+ if cations are taken up more rapidly than anions, and the roots will release $HCO3^-$ and OH^- if anions are taken up more rapidly than cations (Willumsen, 1984). Increasing ammonium content up to 30% increased fresh weight of lettuce (Johnson and Moore, 1983; Ikeda and Osawa, 1984), but higher concentration adversely affected lettuce growth due to toxicity (Ikeda and Osawa, 1984).

Plant water uptake can be limited by high electrical conductivity (EC) of the nutrient solution used in hydroponics (Ehert and Ho, 1986) as a result of an increase in osmotic potential. At lower EC growth is reduced due to limitation in nutrient availability while at higher EC growth is reduced mainly due to water stress (low osmotic potential) (Heinen et al., 2002). The EC level causing stress in vegetable crops varies. In tomato an EC between 2 and 6 $mS.cm^{-1}$ did not reduce dry weight (Ehert and Ho, 1986). An EC of 4 $mS.cm^{-1}$ produced the highest leaf area, leaf area ratio and specific leaf area of sweet pepper (Tadesse et al., 1999) but in many vegetable crops this EC has reduced growth, development and yield (Huett, 1994).

Several asparagus growing areas are arid for at least part of the growing season and irrigation must be applied to maximize carbohydrate storage for subsequent spear production. Many cultivars of asparagus are reportedly to be drought tolerant, but yield may be severely depressed by water stress during critical times (Drost and Wilcox-Lee, 1990). Water stress is also reported to alter the number of roots, buds and shoots in asparagus (Drost and Wilcox-Lee, 1997a, b). Bud, stem and root development over the growing period of asparagus is crucial to the crown development that will eventually determine potential yield as a function of bud number and spear production.

Cultivar UC157 and Jersey Giant are two commonly grown hybrid-asparagus. Cultivar UC157 is tolerant of high temperature and tends to be faster growing (Wehner, 2003), but in many asparagus growing regions 'Jersey Giant' out yields 'UC157' (Faville et al., 1999d; Feibert et al., 1996; Bakka et al., 1999). These two cultivars would be expected to exhibit differential sensitivities to electrical conductivities in the growing medium.

This study was intended to provide more reliable evaluation of plant morphology and bud dynamics using two cultivars of *Asparagus officinalis* L. seedlings which have different size of spears and number of buds and are adapted to somewhat different environments, and to compare their sensitivity to water stress and nutrient stress as determined by conductivity of nutrient solution.

6.2. MATERIALS AND METHODS

6.2.1. Plant materials

Seeds of *Asparagus officinalis* L. 'Jersey Giant' and 'UC157' were germinated at 28°C in multi-single cell transplanting plug trays on 17 January 2000. The plants were transferred to hydroponics once they emerged from the peat based growing medium, having at least one root and only one spear on 1 February 2000 (Fig. 6.1). The plants were given 3 days at EC 1.4 $mS.cm^{-1}$ for acclimation to hydroponics environment. This EC level was suggested for use in asparagus by Hanger (1978). Any sick or dead plants were replaced during this time of adjustment.

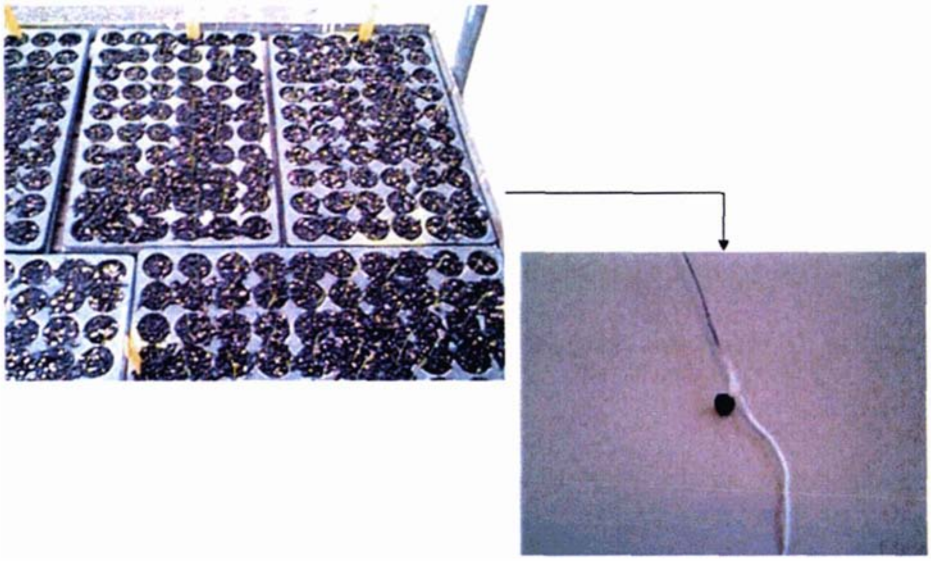


Figure 6.1 Asparagus seedlings at the stage with at least one root and only one stem when they were transferred from peat based medium growing environment in transplanting plug into hydroponics.

Temperature set points for heating and ventilating in the greenhouse were 15°C and 25°C, respectively. In addition, solution temperature was recorded daily. The greenhouse roof was covered with 40 % green shade cloth.

6.2.2. Hydroponics solution

Hydroponics solutions of different EC were obtained by mixing the four stock solutions modified from Cooper (1979) as described in Chapter 4. All levels of EC had the same amount of micronutrient but had an increased proportion of macronutrient as EC increased. Table 6.1 illustrates a guide to achieve the levels of EC from these four stock solutions into 5 liter of water.

Table 6.1 Expt 8: Proportion of hydroponics mixtures and the quantity (ml) of stock solutions added into 5 liter water for making up different levels of electrical conductivity.

Levels of EC ($mS.cm^{-1}$)	Proportions of main nutrient mixture				The amount (ml) added to 5 liter of water				Actual EC
	A	B	C	D	A	B	C	D	
1.4(Control)	1	1	1	1	35	35	35	35	1.43
2	1	1	1	1	60	60	60	60	2.11
4	2	2	1	1	130	130	65	65	4.09
6	3	3	1	1	219	219	73	73	6.20
8	4	4	1	1	300	300	75	75	7.91
10	5	5	1	1	440	440	88	88	10.19
12	6	6	1	1	516	516	86	86	12.17
14	7	7	1	1	560	560	80	80	13.85†

†Added into 5.5 liter of water

EC level was measured using a Conductivity meter (Hanna Inst, Model HI8633). A pH of 6.5 was maintained by adding 1% KOH or 10% sulphuric acid to balance pH during the experiment. The nutrient solutions were replaced bi-weekly to minimize imbalance in nutrients. Hydroponics tanks with a non-circulating nutrient system were placed on the concrete floor.

Hydroponics was non-circulating system supplied with continuous oxygen to each tank through two PVC tubes with diameter of 16 mm, creating air bubbles and water movement in nutrient solution. An aerostone was attached at the end of each PVC air tube to avoid contamination that could come from the air tube. The size of tanks was (86 x 62 x 15) cm^3.

6.2.3. Treatment and design of experiment: Experiment 8

The design was RCBD with split-plot arrangement. The main treatments were EC level and each EC level was split into two cultivars. Each EC level was assigned randomly to one tank equipped with two floating polystyrene Styrofoam platforms (34 x 60) cm^2, functioned as replication for each EC treatment. There were two rows; each was assigned randomly to each cultivar, on a floating polystyrene Styrofoam, with 8 holes in each row. The distance between rows was 10 cm, and 5.5 cm between two centers of its hole within a row. Total plants used in the experiment were 256, inserted through holes in polystyrene floats placed on the surface of hydroponics solutions (Fig. 6.2). One asparagus plant was anchored in each hole using a flexible wire similar to Chapter 5 so that the roots were exposed to nutrient solution (Fig. 6.2 A), but the crown was above the solution. Plants were subjected to eight levels of EC (1.4, 2, 4, 6, 8, 10, 12 and 14 $mS.cm^{-1}$). Plants were covered by perlite to minimize nutrient solution accumulation on the surface of the crown (Fig. 6.2 B).

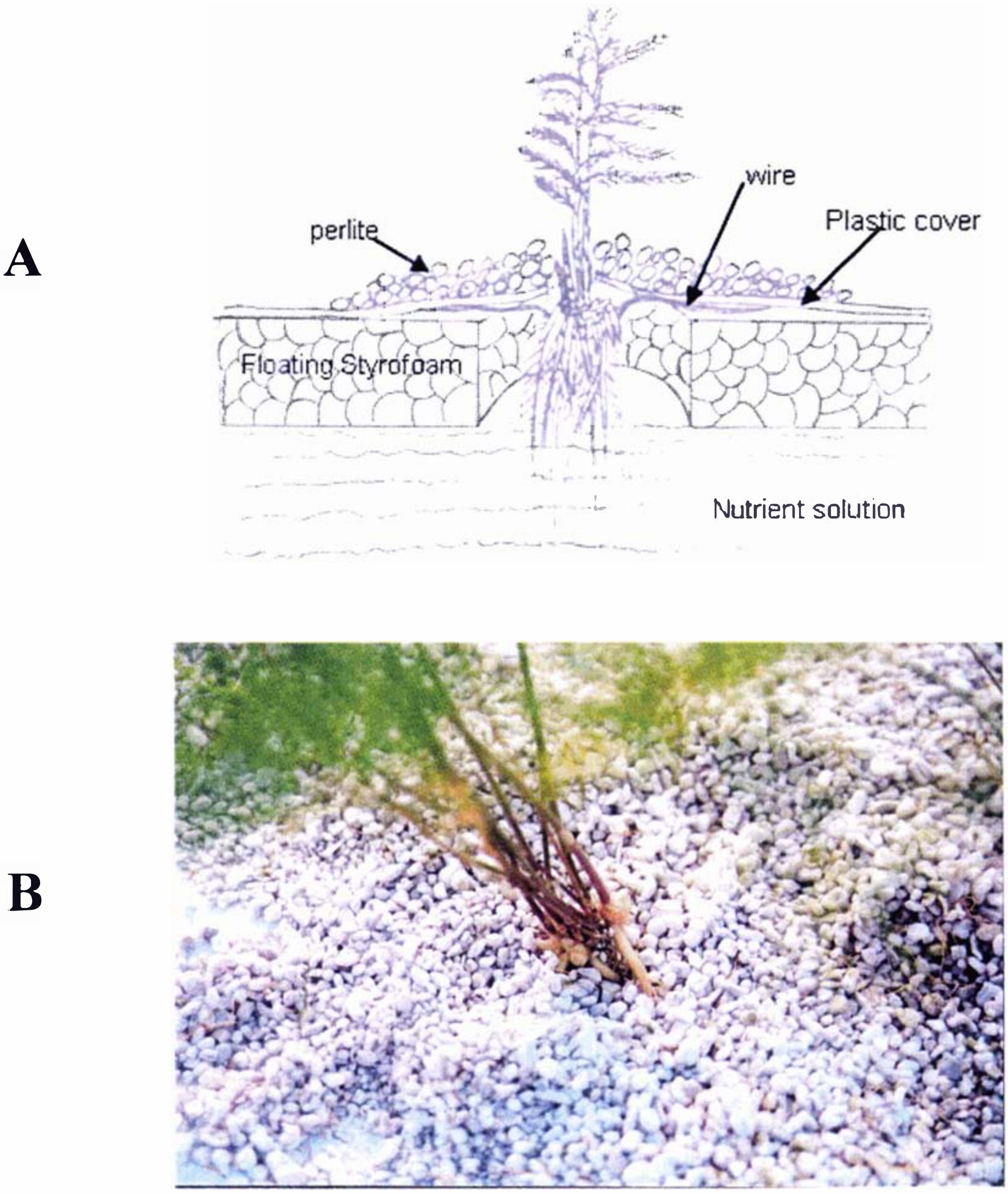


Figure 6.2 Diagram of a polystyrene float showing how an asparagus plant was anchored on a wire (A) and perlite was used to cover the exposed surface of the asparagus crown in hydroponics experiment (B).

6.2.4. Measurements

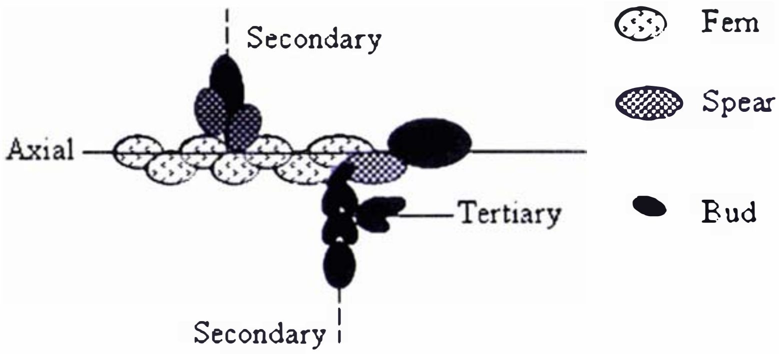
The crown of each plant was mapped weekly, recording the position and number of buds, spears, and ferns with developed cladophylls. Total shoot number was calculated by adding spear and fern together. The total bud numbers were the sum of fern, spear and non-elongated buds together. Plant height was measured from the base at the rhizome to the top of the highest fern whereas longest root was measured from the basal rhizome to the longest tip of the root. Buds, bud clusters and crown development of seedlings were measured and mapped on a weekly basis for 15 weeks started from 4 February 2000, followed by extracting chlorophyll at the end of the experiment and measured one week later. Plants were removed from the hydroponics system for measurements. Ratios of root to total bud number, root to shoot number, root to bud number, and root to shoot dry weight of asparagus were also calculated by dividing the root by those components. Chlorophyll content, fern water potential, and shoot and root dry weight were measured at the end of experiment.

6.2.4.1. Crown morphology

A branching scheme for bud cluster direction was used as described by Bigard (1973). The first bud cluster is defined as axial from which secondary or tertiary bud clusters may emerge (Fig. 6.3).

The number of buds and bud clusters were justified from the map drawn for each observation. Buds in a cluster alternate on the cluster axis (see Fig 6.3 A and B). An extra bud at any particular angle of this cluster is considered to be a potential new cluster.

A



B

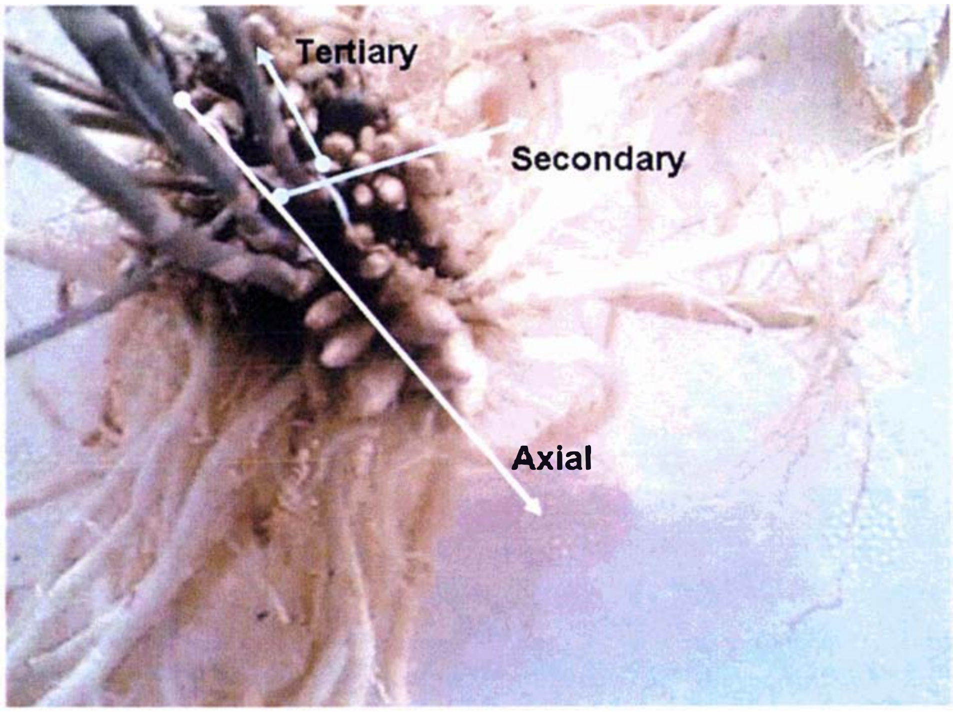


Figure 6.3 Expt 8: Diagram of branching scheme for bud clusters adapted from Bigard (1973) (A) and an example of cluster direction on a asparagus crown (B). In these seedling plants the basal buds are not necessarily the longest.

6.2.4.2. Chlorophyll content and fern water potential.

Chlorophyll was estimated as described by Witham et al. (1986). Eight grams of cladophylls from four plants at random in each cultivar in each treatment were extracted in 80% acetone in scintillation vials. The samples were shaken at 2°C for one week in the dark room before measurement of absorbance at λ of 663, 652, 645 and 640 nm in a spectrophotometer (Hitachi Model type U-2000).

Ferns (stem with cladophylls) were cut three centimetres from the surface of the crown and fern water potential was measured using a Scholander pressure bomb between 11 am and 3 pm.

6.2.4.3. Root and shoot dry weight.

Dry weight measurements of roots and shoots were recorded after drying in the oven for three days at 80°C.

6.2.5. Statistical analyses

After testing normal distribution and homogeneity of residuals, data were analysed using Proc GLM in SAS (SAS Version 8.2, 1999-2001) for testing the effect of treatments, cultivar and their interaction using split plot in RCBD in each week. Quadratic models using proc REG in SAS were fitted to dry weight, the number of buds, total buds, and roots, and plant height to estimate the response of the asparagus seedlings to different level of EC at the final week. Plants were grouped, based on their morphological and physiological characteristics using Cluster Analysis (CA) and the results were further compared using Principal Component Analysis (PCA). The variables included for the CA and PCA were the number of buds, spears, ferns, and roots, the number of secondary and tertiary bud clusters, shoot and root dry weight, amount of chlorophyll a, chlorophyll b and total chlorophyll, fern water potential, plant height, and longest root length.

6.3. RESULTS

The performance of plants in EC 6 $mS.cm^{-1}$ was very poor, and inconsistent with EC 4 and EC 8 $mS.cm^{-1}$ in terms of growth parameters and premature senescence. All plants from this treatment were omitted from data analysis.

There were significant interactions between cultivar and treatment effects at the end of the experiment on fern and ratio of root to shoot number (Table 6.2). Significant differences occurred between cultivars in bud, total bud, root number, ratio of root to shoot number, root dry weight and the amount of chlorophyll a, b, and c. In addition, the effect of EC significantly affected the number of roots, longest root length, plant height, ratio of root to shoot number, root dry weight, shoot dry weight, ratio of root to shoot dry weight, fern water potential and amount of chlorophyll.

6.3.1. Morphological measurements

Interactions of EC and cultivars were significant for fern number ($P = 0.0125$) and ratio of root to shoot number ($P = 0.0486$) at the end of experiment (Table 6.2).

In all levels of EC except at EC 2 and 4 $mS.cm^{-1}$, fern number of 'Jersey Giant' was lower than that of 'UC157' whereas ratio of root to total shoot number was lower than that of 'UC157' at EC 4 $mS.cm^{-1}$.

Table 6.2 Expt 8: Fern number and ratio of root to total shoot (spear + fern) number due to the effect of EC level and cultivar interaction on *Asparagus officinalis* L. at the end (week 15) of experiment in hydroponics in the greenhouse.

EC Level	Fern number		Ratio of root to total shoot number	
	Jersey Giant	UC157	Jersey Giant	UC157
1.4	6.63	7.25	2.14	2.16
2	9.25	9.0	2.02	2.87
4	13	7.63	1.88	3.64
8	8.08	8.38	2.04	3.52
10	6.13	9.88	2.41	2.90
12	2.17	5.5	2.16	1.29
14	5.00	7.30	2.11	1.53
s.e.d	3.9552		0.1630	

Cultivar influenced bud number ($P = 0.0015$) (Fig. 6.4 A), total buds ($P = 0.0055$) (Fig. 6.4 E), and root number ($P = 0.0003$) (Fig. 6.4 F) at the end of experiment. Cultivar 'UC157' produced more roots than 'Jersey Giant' as indicated by the difference in root number throughout the experiment (Fig. 6.4. F). The bud numbers differed significantly between the two cultivars from the eighth week to the end of the experiment (Fig. 6.4. A). Differences between the cultivars were detected in the number of total buds from week 10 onward (Fig. 6.4 E). Fern number were similar except at week 5 (Fig. 6.4 C), and spear numbers were different at week 11 and 13 (Fig. 6.4 B), resulting in differences between cultivars in total shoot number (Fig. 6.4 D).

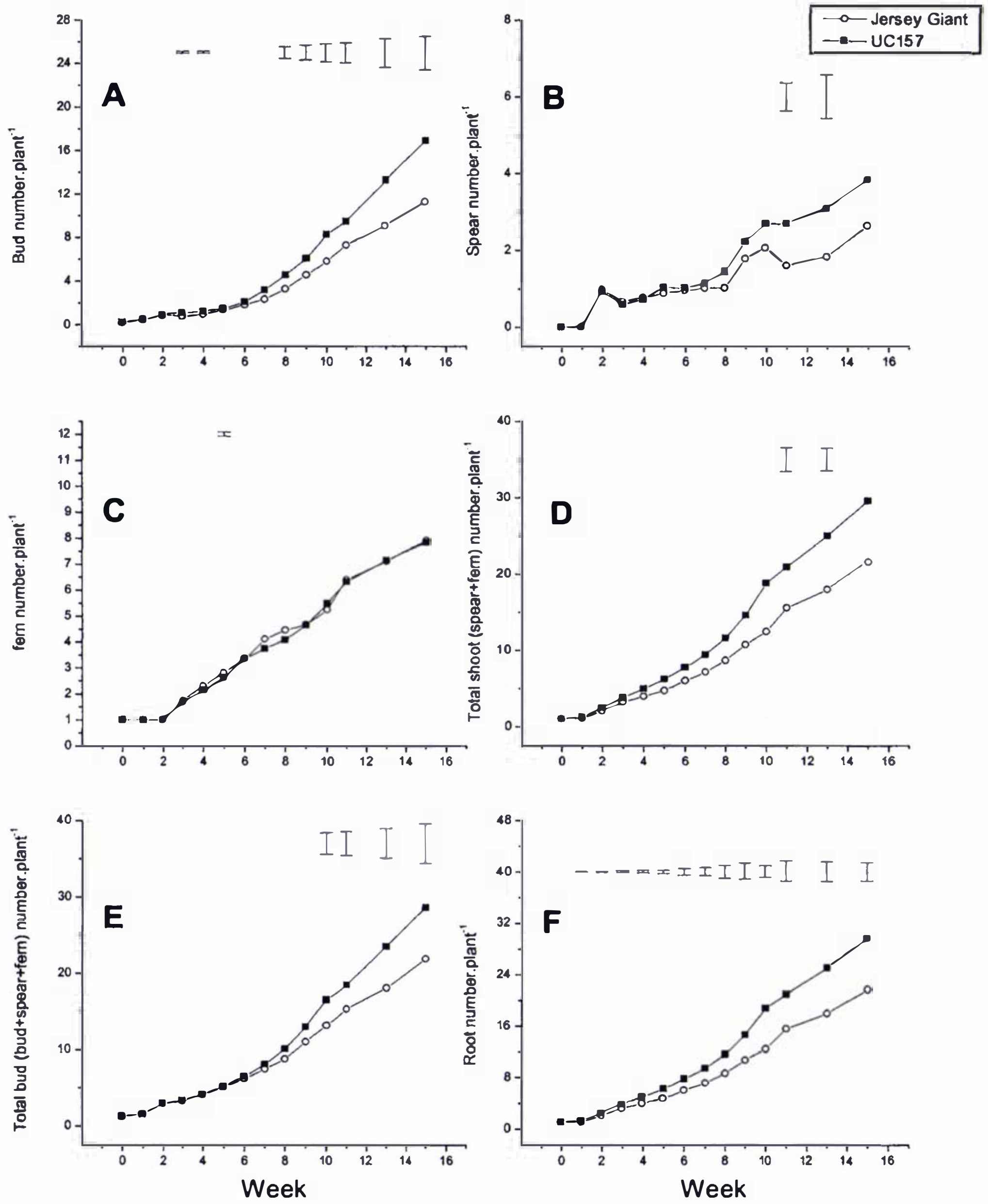


Figure 6.4 Expt 8: The number of buds (A), spears (B), ferns (C), shoot or total of spear and fern (D) and total buds or additional of bud, spear, and fern (E) and root (F) in two *Asparagus officinalis* L cultivars grown in hydroponics. Vertical bars indicate $LSD_{0.05}$.

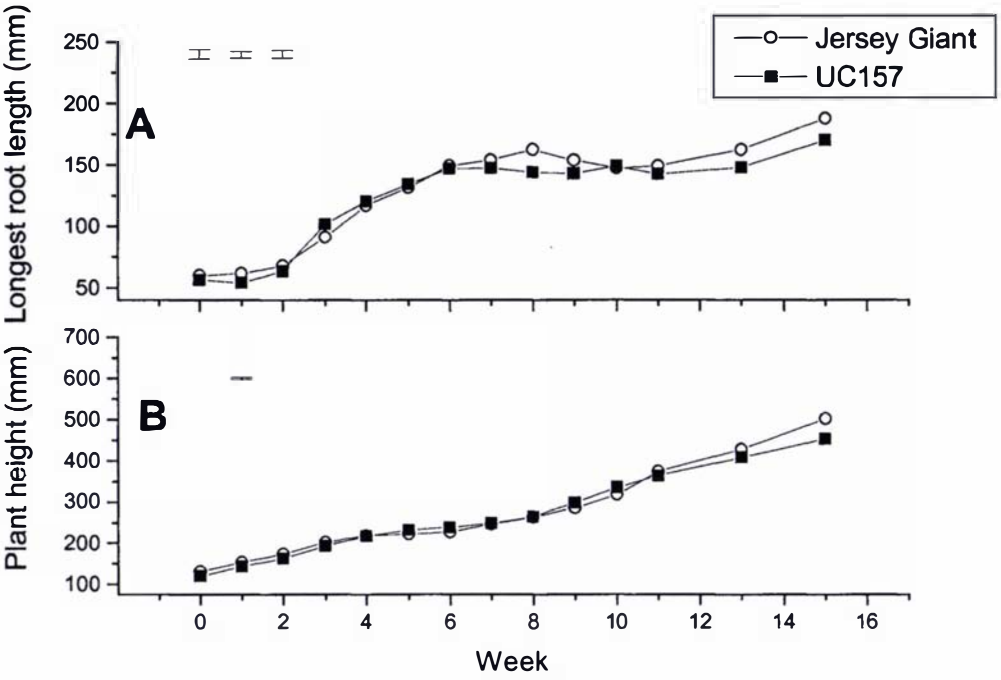


Figure 6.5 Expt 8: The length of the longest root (A) and plant height (B) in two *Asparagus officinalis* L. cultivars grown in hydroponics. Vertical bars indicate $LSD_{0.05}$.

The length of longest root in each cultivar was very similar; after 10 weeks 'Jersey Giant' had a slightly longer root length than 'UC157' but this was not significantly different (Fig. 6.5 B). Significant differences between longest root and plant height (Fig. 6.5 B) occurred early in the experiment.

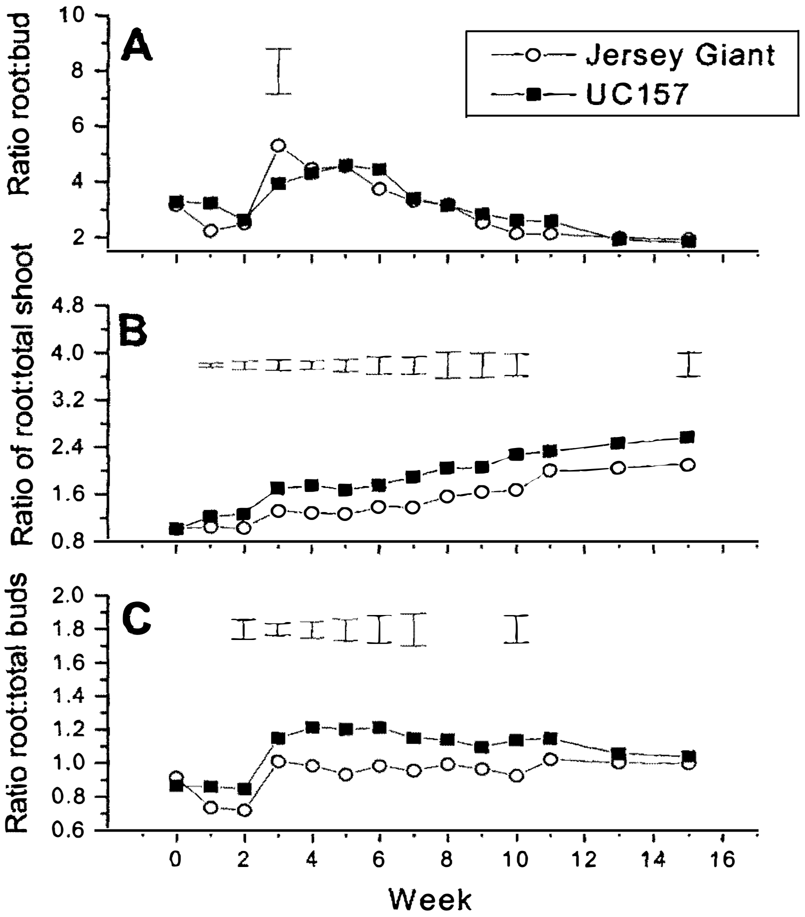


Figure 6.6 Expt 8: Time course of ratio of root to bud number (A), to shoot (spears + ferns) number (B), and total bud number (bud + spear + fern) (C) in two *Asparagus officinalis* L cultivars grown in hydroponics. Vertical bars indicate $LSD_{0.05}$.

Ratios of root to bud number were not significantly different between cultivars except at week 3 (Fig. 6.6 A). The ratio of root number to total shoot number in 'UC157' was significantly higher than in 'Jersey Giant' except at weeks 11 and 13 (Fig. 6.6 B). The ratios of root to total shoot number were 2.56 and 2.10 for 'UC157' and 'Jersey Giant', respectively at the end of experiment. Similarly, ratios of root to total bud number were significantly different between two cultivars from week 2 to 7 and week 10 (Fig. 6.6 C).

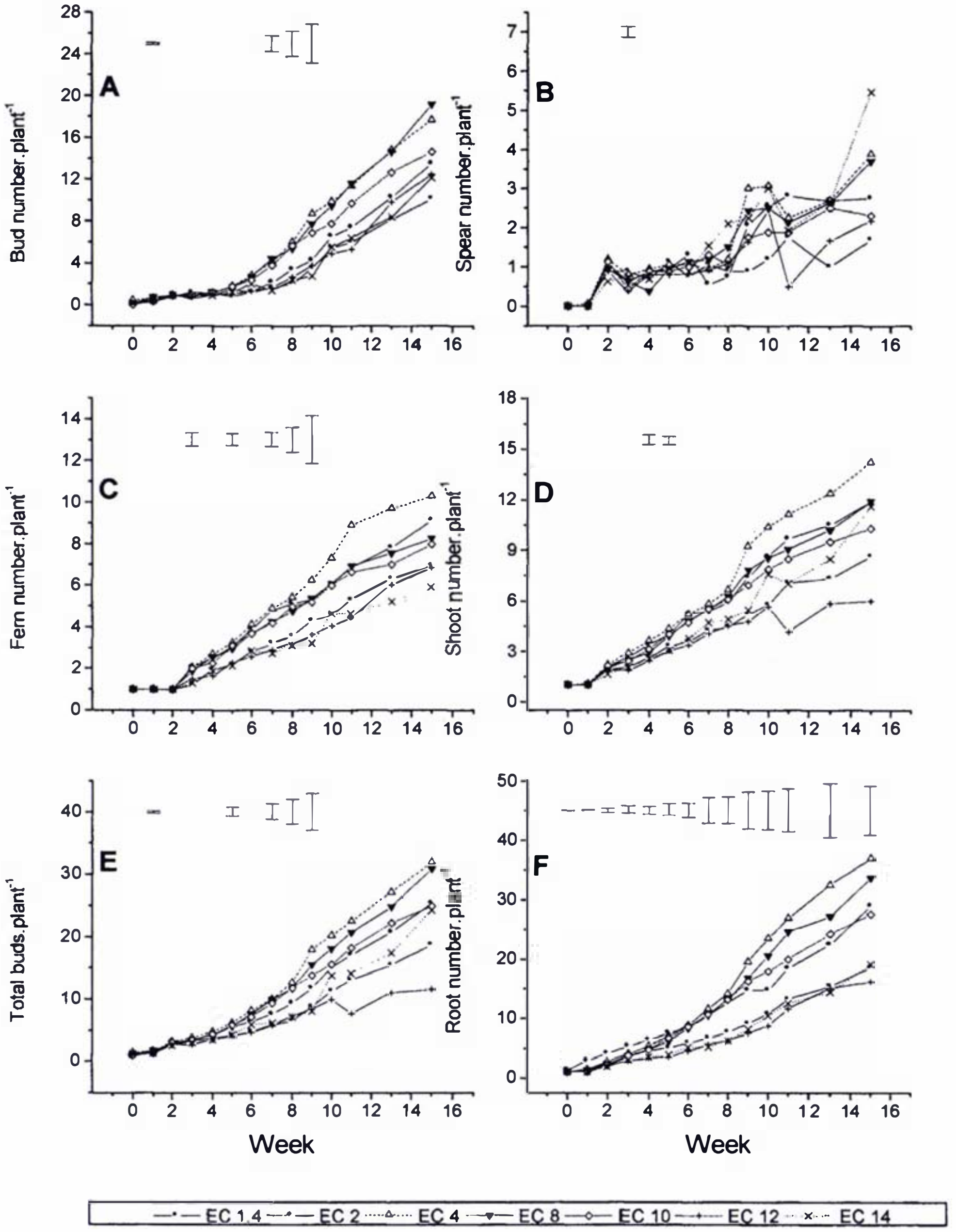


Figure 6.7 Expt 8: The effect of EC treatment on the number of buds (A), spears (B), ferns (C), shoots (spear+fern) (D) and total buds (bud+spear+fern) (E) and roots (F) in two *Asparagus officinalis* L cultivars grown in hydroponics. Vertical bars indicate $LSD_{0.05}$.

Root numbers were affected by EC throughout the experiment (Fig. 6.7 F). Plants under EC 4 and 8 mS.cm^{-1} not only formed more roots (Fig. 6.7.F) than any other level of EC but also produced more buds (Fig. 6.7 A), ferns (Fig. 6.7 C), and total buds (bud + spear + fern) (Fig. 6.7 E) even though the effect was not significant in the final week for ferns and total buds. Spear number was not influenced by EC except at week 3 (Fig. 6.7 B). At EC 14 mS.cm^{-1}, 65% of 'Jersey Giant' plants and 43% of 'UC157' plants died by the end of the experiment, and the apparent increase in spear number per plant under EC 14 mS.cm^{-1} at week 15 relates only to surviving plants. Treatment EC 4 and 8 mS.cm^{-1} produced the greatest bud number (Fig. 6.7. A), total bud number (Fig. 6.7. E.) and root number (Fig. 6.7. F).

At the end of the experiment, bud number, total bud number and root number also increased as EC level increased from 1.4 to 8 mS.cm^{-1}, but reduced as EC level increased above 8 mS.cm^{-1}. Quadratic fitting was appropriate to estimate the optimal EC level for the highest response of the plants (Fig. 6.8). The estimates of highest bud number for 'UC157' and 'Jersey Giant' were 7.6 mS.cm^{-1} and 5 mS.cm^{-1} and the quadratic models fitted 60.32% and 40% of data variation, respectively.

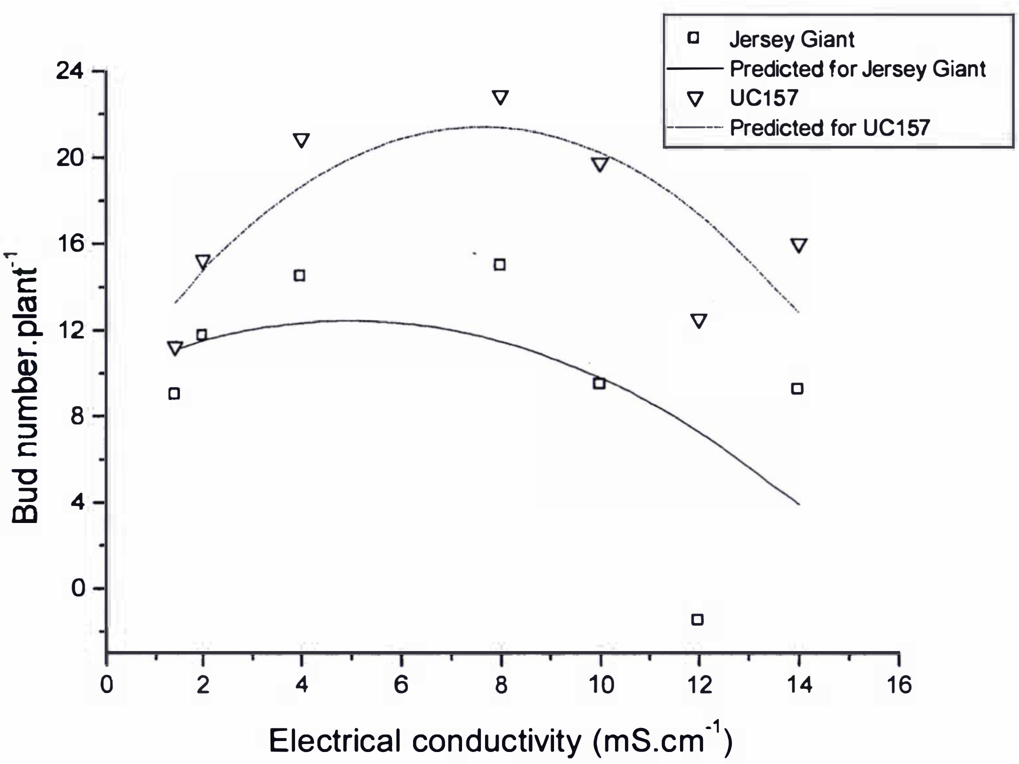


Figure 6.8 Expt 8: Effect of EC treatments on quadratic curve estimates of bud number at the end of the experiment of asparagus seedlings grown in hydroponics.

Quadratic analyses to estimate highest total bud (bud + spear + fern) number for each individual cultivar only fitted for less than 40% of data variation. The estimates of total bud number were at EC 4.9 and 8.1 mS.cm^{-1} for 'Jersey Giant' and 'UC157', respectively (Fig. 6.9).

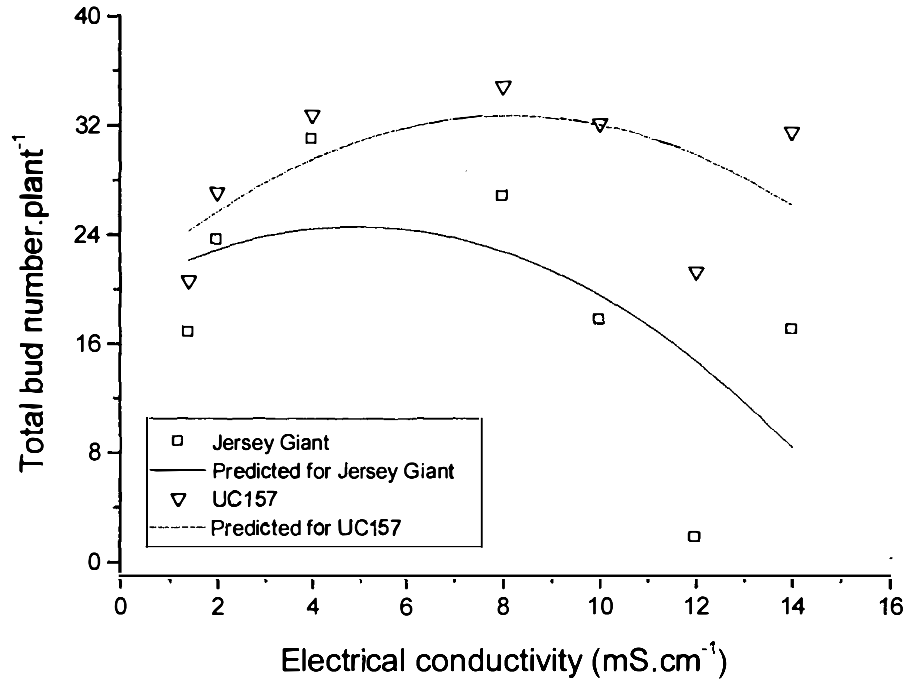


Figure 6.9 Expt 8: Effect of EC treatments on quadratic curve estimates of total bud (bud + spear + fern) number at the end of the experiment of asparagus seedlings grown in hydroponics.

The highest root numbers could be estimated at EC 5.7 and 6.5 mS.cm^{-1} for 'Jersey Giant' and 'UC157', respectively (Fig. 6.10). Both models explained more than 50% of the data variation.

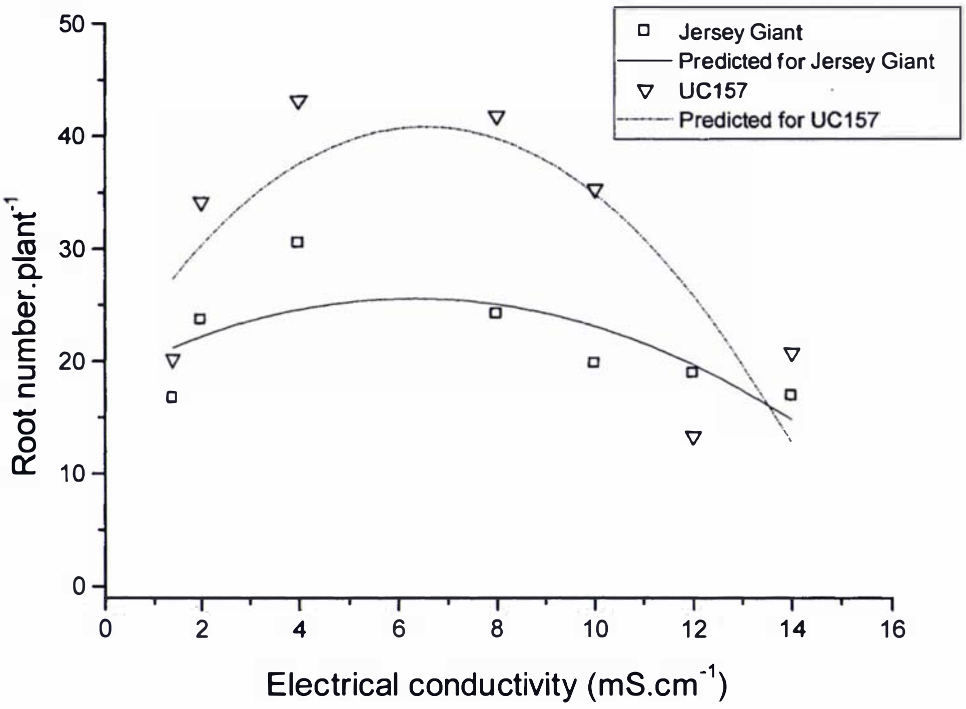


Figure 6.10 Expt 8: Effect of EC treatment on quadratic curve estimates of root number at the end of the experiment of asparagus seedlings grown in hydroponics.

EC influenced plant height throughout and the length of longest root from week 3 to week 9 and week 15 (Figure 6.11 A and B). Longest root length was shortest under lowest EC (1.4 mS.cm^{-1}) and higher EC (12 and 14 mS.cm^{-1}) whereas it was the longest under EC 8 and 4 mS.cm^{-1} (Fig 6.11 A). Higher EC at 12 and 14 mS.cm^{-1} also reduced plant height significantly. The plant height was greatest at EC 4 followed by EC 8, 2 and 1.4 mS.cm^{-1} (Figure 6.11 B).

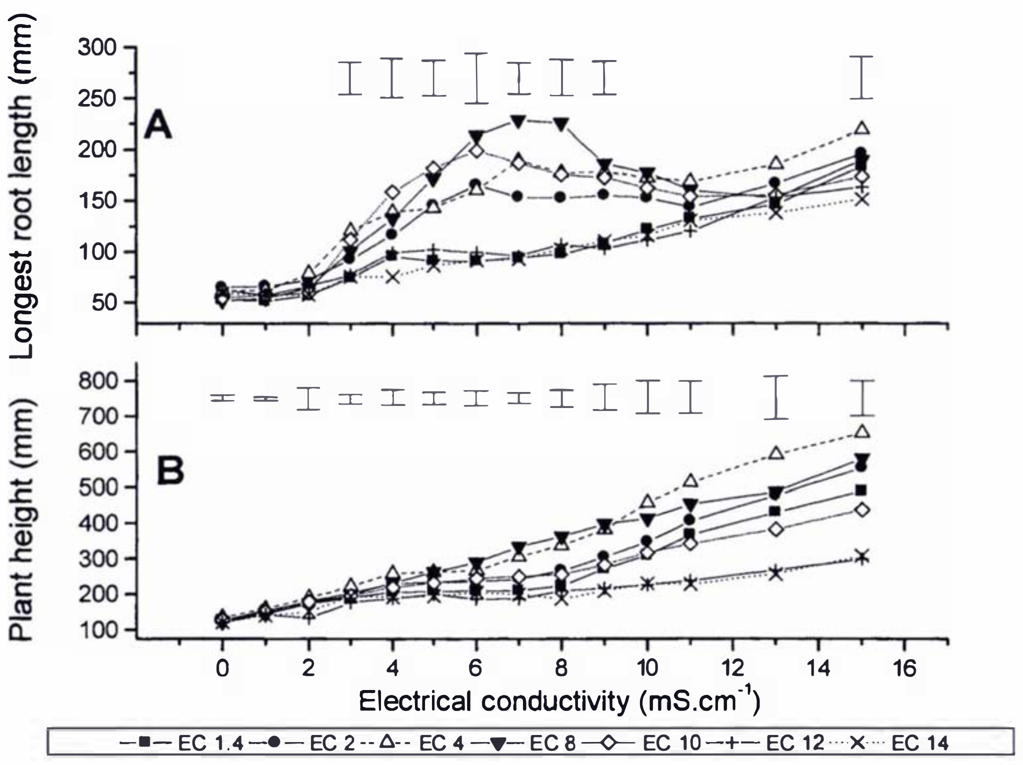


Figure 6.11Expt 8: Effect of EC treatments on plant height (A) and longest length of the root in two *Asparagus officinalis* L cultivars grown in hydroponics. Vertical bars indicate LSD$_{0.05}$.

Estimates of maximum plant height for 'Jersey Giant' and 'UC157' were 4.6 and 5.0 mS.cm^{-1} (Fig. 6.12). The estimates based on the models which accounted for more than 75% of data variation. The plant height declined extremely at EC 12 and 14 mS.cm^{-1} for both cultivars.

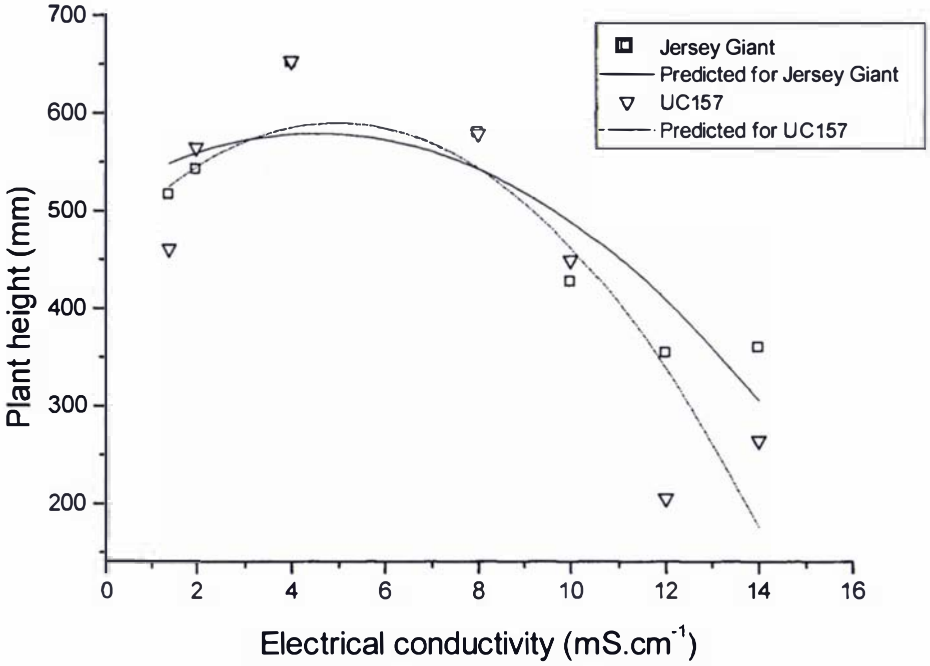


Figure 6.12 Expt 8: Effect of EC treatment on quadratic curve estimates of plant height at the end of the experiment of asparagus seedlings grown in hydroponics at different level of EC.

The effects of EC on the ratio of root to bud number and ratio of roots to total buds was significant only at week ten (Fig. 6.13 A and C) and on the ratio of root to shoot number at weeks 1, 10 and 15 (Fig. 6.13 B).

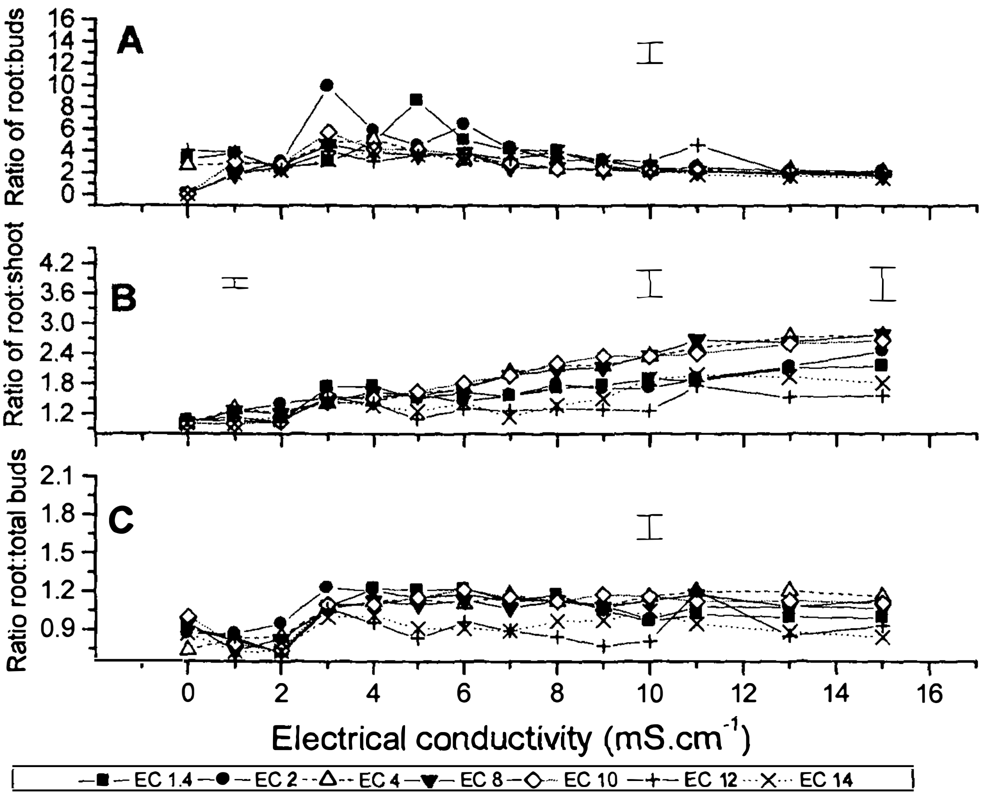


Figure 6.13 Expt 8: Effect of EC treatment on ratio of root to bud number (A), to shoot (spear and fern) number (B), and total bud (bud, spear and fern) number (C) in two *Asparagus officinalis* L cultivars grown in hydroponics. Vertical bars indicate $LSD_{0.05}$.

6.3.1.1. *Bud clusters*

There was a general trend that average numbers of bud clusters were similar between 2 and 10 mS.cm^{-1} and reduced thereafter (Table 6.3). EC 2, 4, 8, and 10 mS.cm^{-1}

produced average bud clusters of 8.5, 7.5, 9.5, and 8.5, respectively. EC 1.4, 12 and 14 mS.cm^{-1} produced bud clusters of 4.5, 4, and 5.5, respectively.

Table 6.3 Expt 8: Number of bud clusters and position on rhizomes of *Asparagus officinalis* L. at the end (week 15) of experiment in hydroponics experiment in the green house.

EC level	Cultivar	Axial†	Secondary†	Tertiary†	Total
1.4	Jersey Giant	1	4	0	5
	UC157	1	3	0	4
2.0	Jersey Giant	1	6	1	8
	UC157	1	6	2	9
4.0	Jersey Giant	1	5	1	7
	UC157	1	6	1	8
8.0	Jersey Giant	1	5	1	7
	UC157	1	6	3	10
10.0	Jersey Giant	1	3	2	6
	UC157	1	7	3	11
12	Jersey Giant	1	4	0	5
	UC157	1	2	0	3
14	Jersey Giant	1	3	0	4
	UC157	1	6	0	7

†Refers to Figure 6.3

Increases in bud number and total bud number per crown between EC 4 and 10 mS.cm^{-1} reflected the increase in both numbers of secondary and tertiary bud clusters (Table 6.3) and the number of bud per cluster (Table 6.4). At lowest EC (1.4 mS.cm^{-1}) and high EC (12 and 14 mS.cm^{-1}), there was no tertiary bud clusters (Table 6.3 and 6.4).

Table 6.4 Expt 8: Range of bud and total bud number for each bud cluster at different positions on *Asparagus officinalis* L. crown at the end (week 15) of experiment in hydroponics experiment in the green house.

EC level	Cultivar	Range of bud number per cluster						Total per crown	
		Axial		Secondary		Tertiary			
		Bud	Total bud†	Bud	Total bud†	Bud	Total bud†	Bud	Total bud†
1.4	Jersey Giant	2-4	7-11	1-6	1-7	0	0	3-10	8-18
	UC157	2-5	6-11	2-6	2-7	0	0	4-11	8-18
2.0	Jersey Giant	2-4	9-12	1-5	1-6	1	1	4-10	11-19
	UC157	2-6	9-17	1-6	1-9	1-5	1-5	4-17	11-31
4.0	Jersey Giant	2-4	9-15	1-5	1-10	2-4	3-7	5-13	13-32
	UC157	3-6	11-15	1-6	1-10	1-4	1-5	5-16	13-30
8.0	Jersey Giant	0-5	4-14	1-5	1-9	1-4	1-4	2-14	6-27
	UC157	0-5	4-14	1-8	1-10	1-7	1-7	2-20	6-31
10.0	Jersey Giant	0-6	6-12	1-6	1-8	1-2	1-2	2-14	8-22
	UC157	0-5	6-12	1-6	1-9	1-3	1-4	2-14	8-25
12	Jersey Giant	2-4	4-11	0-4	1-6	0	0	2-8	5-17
	UC157	2-2	2-10	1-3	2-4	0	0	3-5	4-14
14	Jersey Giant	2-2	6-9	1-6	1-6	0	0	3-8	7-15
	UC157	0-3	7-11	1-4	1-6	0	0	1-7	8-17

†Total bud = buds + spears + ferns

Although the bud size was not measured, visual observation suggested that bud size increased toward the apex of a cluster (see Fig. 6.3 B). This is different from established plants in which the buds at the base of a cluster are usually larger than the buds at the subsequent position toward the apex of a cluster.

6.3.2. Physiological measurement

Chlorophyll a, b and total chlorophyll differed with both EC and cultivar (Table 6.5). Chlorophyll a, b, and total chlorophyll were highest at EC 8 mS.cm^{-1}, and all variables were higher for 'Jersey Giant' than 'UC157'.

Table 6.5 Expt 8: Chlorophyll content (mg/g fresh weight) of *Asparagus officinalis* L. at the end (week 15) of experiment affected by electrical conductivity.

Variables	Chlorophyll-a	Chlorophyll-b	Total chlorophyll
Level of EC			
1.4	0.933bc	0.346bc	1.279bc
2	1.106ab	0.376ab	1.481ab
4	1.079abc	0.377ab	1.455ab
8	1.279a	0.459a	1.739a
10	1.281a	0.426ab	1.706a
12	1.015abc	0.333bc	1.347abc
14	0.772c	0.272c	1.043c
Cultivars			
'Jersey Giant'	1.161 A	0.398 A	1.558 A
'UC157'	0.998 B	0.352 B	1.350 B

Means within a column with different letters are significantly different ($P \leq 0.05$).

Root and shoot dry weights were highest at EC 4 mS.cm^{-1} (Table 6.6). However, the highest root to shoot dry weight ratios occurred in plants under EC 12 and 14 mS.cm^{-1} followed by 1.4 mS.cm^{-1}. Root dry weight was significantly higher in 'Jersey Giant' than 'UC157'. Fern water potential increased as EC increased to 8 mS.cm^{-1} and levelled off thereafter.

Table 6.6 Expt 8: Effect of cultivars and electrical conductivities on root and shoot dry weight, ratio root to shoot dry weight, fern water potential of *Asparagus officinalis* L. at the end (week 15) of experiment.

Variables	Root dry weight (gr)	Shoot dry weight (gr)	Root:shoot dry weight	Fern water potential (-MPa)
Level of EC				
1.4	1.30bc	0.69c	1.98b	0.41c
2	2.46abc	1.89abc	1.51cd	0.30c
4	3.41a	2.93a	1.18d	0.60b
8	2.96ab	2.40ab	1.35cd	0.73ab
10	2.01abc	1.38bc	1.58c	0.70ab
12	1.9abc	0.83c	2.50a	0.75a
14	0.96c	0.45c	2.57a	0.81a
Cultivars				
'Jersey Giant'	2.46 A	1.71 A	1.68 A	0.55 A
'UC157'	2.16 B	1.76 A	1.51 A	0.56 A

Means within a column with different letters are significantly different ($P \leq 0.05$).

Further statistical analysis using quadratic curve fitting showed that the heaviest shoot dry weight could be estimated at EC 6.4 and 6.5 mS.cm^{-1}, for 'Jersey Giant' and 'UC157', respectively. These models explained 65 % of data variation (Fig. 6.14).

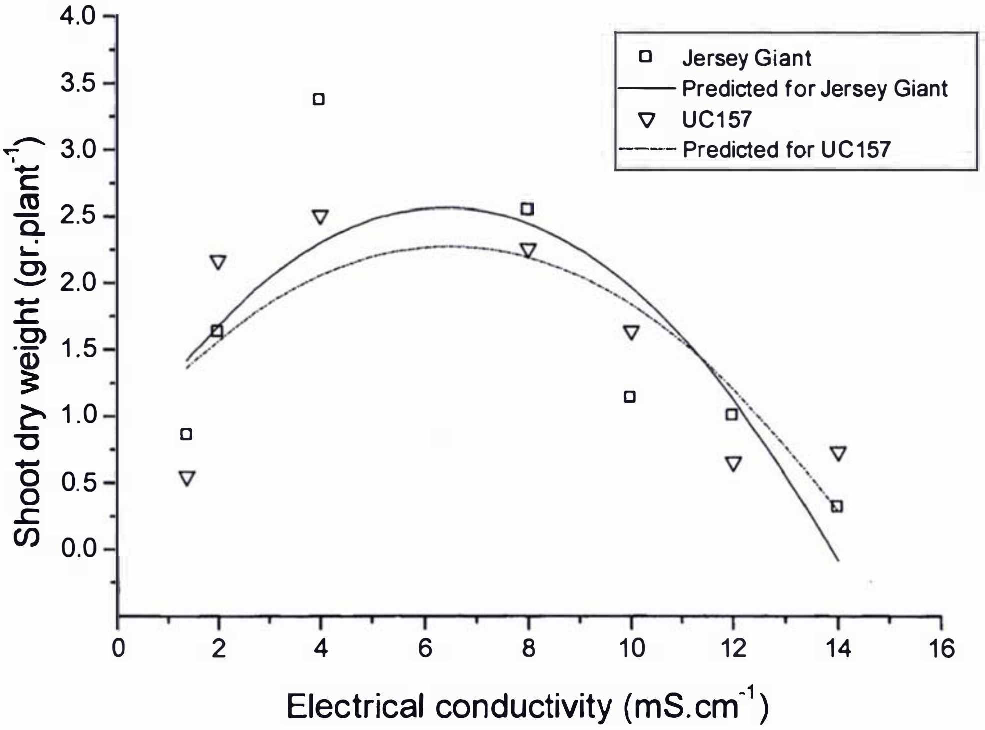


Figure 6.14 Expt 8: Effect of EC treatment on quadratic curve estimates of shoot dry weight at the end of the experiment of asparagus seedlings grown in hydroponics at different level of EC.

Similarly, the heaviest root dry weight was estimated at EC 6.8 and 6.5 mS.cm^{-1} for 'Jersey Giant' and 'UC157', respectively (Fig 6.15).

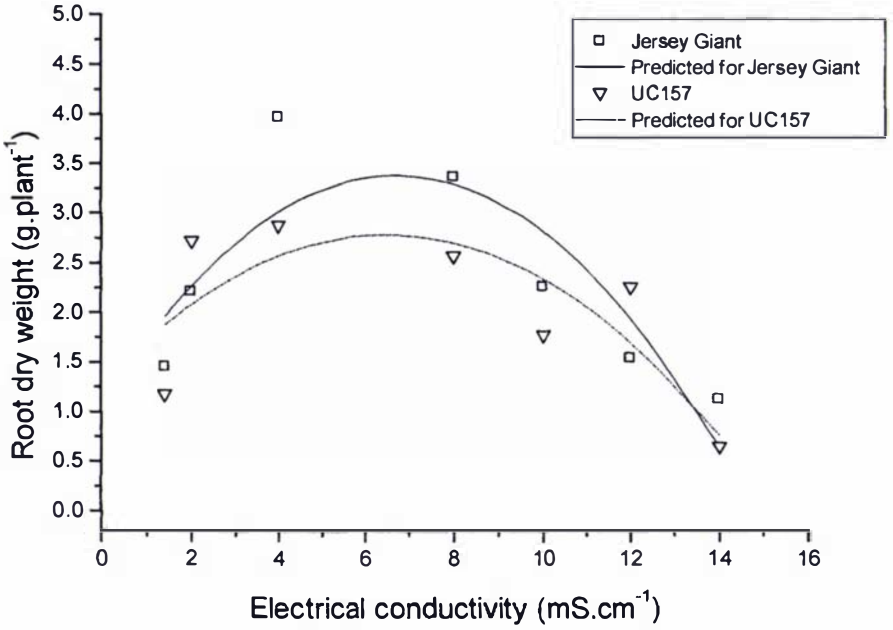


Figure 6.15 Expt 8: Effect of EC treatment on quadratic curve estimates of root dry weight at the end of the experiment of asparagus seedlings grown in hydroponics at different level of EC.

6.3.3. Cluster analysis

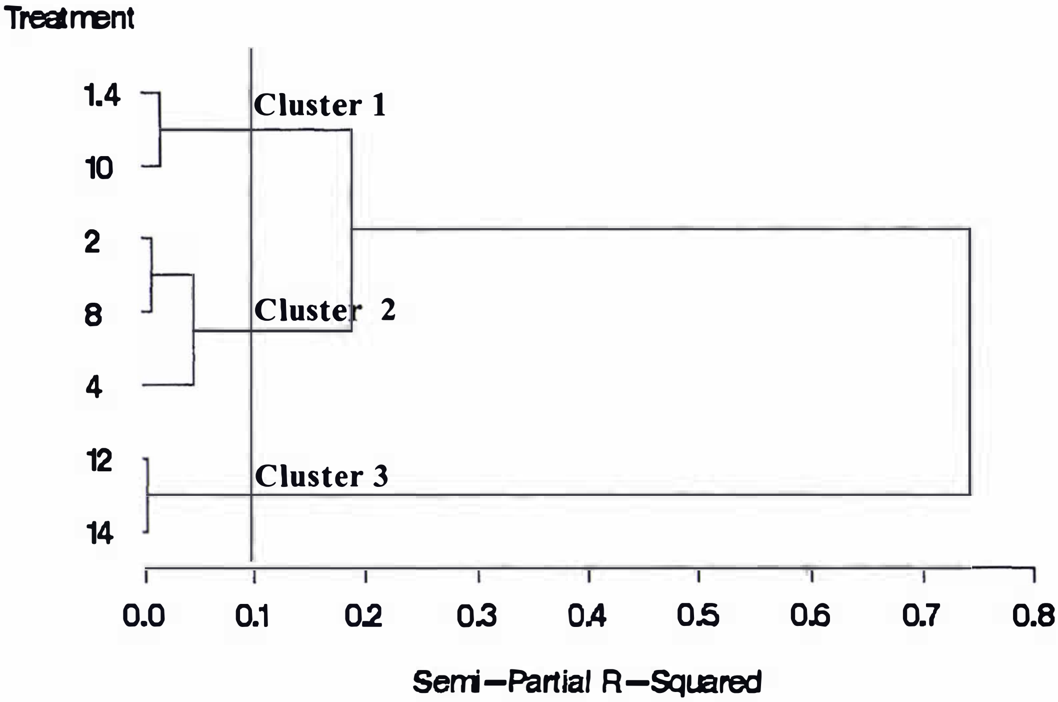


Figure 6.16 Expt 8: Morphology-physiology grouping of asparagus seedlings influenced by different electrical conductivity.

The Ward Method of Cluster Analysis distinguished three morphological-physiological clusters at different EC (Fig. 6.16). Plants in EC 2, 4, 8 mS.cm^{-1} were grouped into one cluster and could be combined with a group comprising plants in EC 1.4 and 10 mS.cm^{-1} to make up a higher cluster. The third cluster was made up from plants in EC 12 and 14 mS.cm^{-1}.

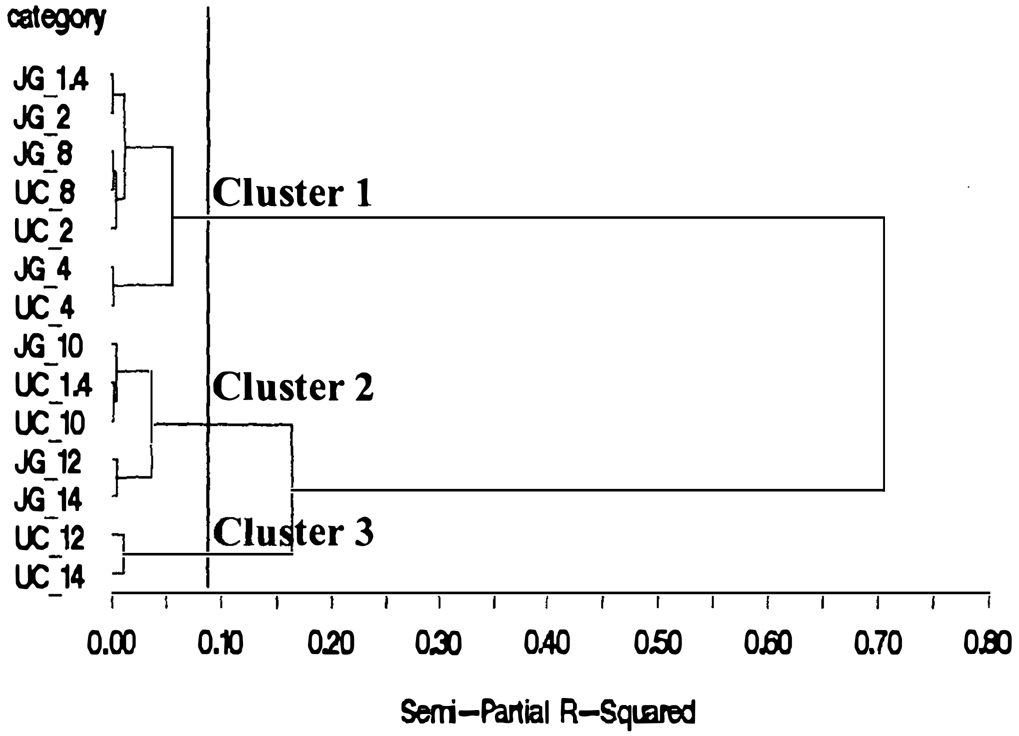


Figure 6.17 Expt 8: Morphology-physiology grouping of asparagus influenced by different electrical conductivity in two different varieties of asparagus seedlings grown in hydroponics. UC = 'UC157'; JG = 'Jersey Giant'.

The second dendrogram (Fig. 6.17) produced from cluster analysis based on cultivars and EC levels also separated three major clusters. 'Jersey Giant' under EC 1.4 mS.cm^{-1}, and 'UC157' and 'Jersey Giant' under EC 2, 4, and 8 mS.cm^{-1} formed a cluster. The second cluster comprised 'Jersey Giant' under 10, 12, 14 mS.cm^{-1} and 'UC157' under 1.4 and 10 mS.cm^{-1}. The extreme EC treatments (12 and 14 mS.cm^{-1}) for 'UC157' were grouped together as a third cluster.

6.3.4. Principal component analysis

Three principal components (PCs) together explained 83.3% of the total variation (data not shown). The eigenvalues of these three PCs were all more than one. The eigenvalues of the other PCs were much smaller than one and contributed only 16% in explaining the total variation. The coefficients of the three main PCs are given in the Table 6.5. The coefficients of variables in PC1 were slightly dominated (ranging from 0.29 to 0.36) by shoot and root dry weight, root number and plant height. This first component explained 42.60% of total variation.

Table 6.7 Expt 8: Coefficient of principal components influencing morpho-physiology of two different varieties of asparagus seedlings grown at different level of electrical conductivity in hydroponics.

Variables	Prin1 (PC1)	Prin2 (PC2)	Prin3 (PC3)
bud number	0.206452	0.365585	0.217781
spear number	-0.068955	0.450623	0.069174
fern number	0.291684	0.127743	-0.265755
root number	0.310654	0.270146	0.081257
secondary bud cluster	-0.014883	0.428206	0.077497
tertiary bud cluster	0.237498	0.180687	0.324114
shoot dry weight	0.365794	0.167036	-0.0664
root dry weight	0.343608	0.038823	-0.01557
chlorophyll-a	0.267951	-0.331799	0.268294
total chlorophyll	0.274856	-0.326945	0.266088
fern water potential	-0.10875	0.128637	0.582964
chlorophyll-b	0.292154	-0.306778	0.25542
plant height	0.365286	0.027075	-0.193147
longest root length	0.29083	-0.014002	-0.411916

The second component, accounting for 25.9% of total variation, was dominated by positive values for spear number (0.45) and number of secondary bud cluster (0.43) and to a lesser extents by negative values for all chlorophyll components (-0.33 to -0.30). Finally the third component, explaining 14.78% of the total variation, was dominated positively by fern water potential (0.58) and negatively by longest root length (-0.41).

6.4. DISCUSSION

6.4.1. Cultivar effects

Throughout the experiment, cultivar 'UC157' produced higher root number (Fig. 6.4 F) than 'Jersey Giant' and higher root to shoot ratio except at week 11 and 13 (Fig.6.6). A greater bud number (Fig. 6.4 A) together with greater total bud number (Fig. 6.4 E) within the last four measurements in Expt 8 suggests that 'UC157' should have a higher potential yield, from the function of bud number and root number, than 'Jersey Giant'. However, with mature plants 'Jersey Giant' is the higher yielding cultivar in most conditions (Cueto and Lesnick, 1999; Nichols and Fisher, 1999). A higher amount of chlorophyll in 'Jersey Giant' (Table 6.5) with tendency for higher plant height (Fig. 6.5 B) and higher root dry weight (Table 6.6) suggested that 'Jersey Giant' has a potentially more active photosynthetic system and was more effective in storing assimilate in the root. This result agreed with Expt 7 using aeroponics.

Although chlorophyll levels do not normally correlate very well with photosynthetic rate asparagus is one of the few crops in which chlorophyll, photosynthetic rate and final yield are well correlated (Faville et al., 1999a,b,d; Bay and Kelly, 1999). A slightly higher root:shoot dry weight of 'Jersey Giant', but not significantly different from 'UC157' was another indication that 'Jersey Giant' developed root mass heavier than 'UC157'. Here the root mass, defined as root dry weight, was related to total buds and resulted in greater root weight per bud in 'Jersey Giant' than 'UC157' (Table 6.8). Stancanelli and Falavigna (1990) indicated that the ratio of root weight:total bud number of seedlings can be related to yield performance of established asparagus in the field.

Table 6.8 Expt 8: Ratio of root to different components of asparagus plants from two different cultivars grown at different level of electrical conductivity in hydroponics.

Cultivar	Root:total bud number	Root:shoot number	Root:bud number	Root:shoot dry weight	Root dry weight:total bud number
Jersey Giant	0.99a	2.10b	1.92a	1.68a	0.11a
UC157	1.04a	2.56a	1.81a	1.51a	0.08a

Means within a column with different letters are significantly different ($P \leq 0.05$).

In this Expt 8, heavier root mass in terms of dry weight, but fewer root number in 'Jersey Giant' implied the average of roots was heavier in 'Jersey Giant' than in 'UC157'. Longest root length may associate with the heavier roots but not precisely as a function of root mass. Longest root length has been used more as indicator for adaptation to water stress (Schmidhalter et al., 1998; Price et al., 2002; Matsui and Singh, 2003) as it was shown in Expt 8, influenced by EC treatments and their relationship to water potential (Section 6.4.3).

Bigards (1973) suggested that potential yield would be likely to increase if the crown had more tertiary bud clusters. Bud number and total bud number did not affect spear production as much as the number of bud clusters, as demonstrated in a concept developed in Chapter 3 and supported by the notion that asparagus spear production is influenced by correlative inhibition (Nichols and Woolley, 1985) and as described in Chapter 4. In Expt 8, a higher numbers of buds and total buds in 'UC157' did not indicate that 'UC157' had higher growth in terms of root dry weight than 'Jersey Giant' (Table 6.6). However, data derived from continuous visual mapping (Table 6.3) showed that 'UC157' had 5.1 and 1.2, whilst 'Jersey Giant' had 4.3 and 0.71 secondary and tertiary clusters, respectively. Thus, bud cluster information suggest that 'UC157' may have a higher production potential than 'Jersey Giant', in contrast to the conclusion drew earlier for comparison of photosynthetic activity and root storage capability. These conflicting results in regards to potential production may be due to the effects of EC, and may be influenced more by the interrelationship amongst factors of morphology and physiology of the plants as indicated by cluster analysis (Fig. 6.17) and principal components analysis (Table 6.7) (See section 6.4.3).

6.4.2. The effects of electrical conductivity (EC)

An increase of EC up to 8 mS.cm^{-1} affected not only numbers of secondary and tertiary clusters but also other morphological and physiological factors, resulted in quadratic trends for both cultivars (Fig. 6.8-6.10, 6.12, 6.14-6.15). An EC of four significantly increased root number (Fig. 6.7 F), plant height (Fig. 6.11), and had tendency to promote higher fern and shoot number (Fig 6.7 C and D) compared to other electrical conductivities. In contrast, an EC of 8, as well as 4 mS.cm^{-1} was effective in stimulating root production (Fig. 6.7 F) and bud production (Fig. 6.7 A and C), at least until week eight when the root reached the bottom of the container (Fig. 6.11). A range of EC between 2.0 – 2.5 mS.cm^{-1} was suggested for hydroponics in some horticultural crops such as tomato but nowadays an EC between 3.0 and 4.5 has been recommended in some crops since some quality attributes can be achieved better at this range of EC, such as in tomato (Auerswald et al., 1999), or thyme (Udagawa, 1995).However, an increase of nutrient solution EC by adding macronutrient in soilless culture can also cause physiological disorders such as blossom end rot of tomato (Adam, 1994).

As EC increased, the availability of nutrient increased since proportions of macronutrients in the solution were multiplied (Table 6.1). The increase of macronutrients implied an increase in nitrogen which has been reported to have wide range of plant developmental effects that are attributed to the influence of hormonal factors (Pilbeam and Kirkby, 1990) and bud growth (Nigam and McIntyre, 1976; Waters et al., 1990). But in this Expt 8, an increase of nitrogen is confounded with EC level and not isolated as a main factor affecting morphological and physiological crowns. In Expt 8, more secondary and tertiary bud clusters were produced within the optimal range of EC level between 4 to 8 $mS.cm^{-1}$ (Table 6.3 and 6.4), and no tertiary bud cluster at EC level of 1.4 possibly because of insufficient nutrient for asparagus growth, and at EC level of 12, and 14 $mS.cm^{-1}$ due to low water potential caused by high concentration of nutrient. Fern water potential decreased with increasing EC but effects on growth were quite small except at the highest EC's (Table 6.6). Osmotic potential was not measured in these experiments but the change in water potential of the tissue, together with the small effect on growth suggest that the plants osmotically adjusted. That the production of buds is as effective at EC 8 as EC 4 $mS.cm^{-1}$ is surprising as Drost and Wilcox-Lee (1990, 1997a,b) found that bud production was quite sensitive to water stress. Interrelationships amongst morphological and physiological factors could be used to explain the conflicting results from one to another measurement in univariate analysis. Multivariate analysis enables one to understand the relationship between many factors determining potential production in asparagus.

6.4.3. Multivariate analysis of morphological and physiological factors in determining potential production

Whilst univariate analysis of single factor in morphology or physiology showed conflicting results in regard to potential production, multivariate analyses were used to show a series of interlinked factors in morphology and physiology to explain plant responses to the treatment. Multivariate analysis using Cluster Analysis (CA) indicated there were different responses of the two cultivars to EC, indicating some interaction between cultivar and EC level (Fig. 6.17) at the extreme EC level and general responses to EC level (Fig. 6.16).

Cluster analysis based on EC level (Fig. 6.16) reinforced the results of univariate analysis in quadratic responses. Figure 6.16 illustrates a simple application of cluster analysis with mild stress brought about by lack of nutrients (EC 1.4 $mS.cm^{-1}$) or low water stress (EC 10 $mS.cm^{-1}$) forming cluster one, EC 2, 4, and 8 $mS.cm^{-1}$, with an optimum at 4 $mS.cm^{-1}$ being grouped as cluster two, and the severest treatments from water stress being cluster three (EC 12 and 14 $mS.cm^{-1}$). These results agreed with recent experiment in tomato (Heinen et al., 2002). At lower EC growth is reduced due to limitation in nutrient availability while at higher EC growth is reduced mainly due to water stress (low osmotic potential). In Expt 8, although univariate analysis did not show any significant cultivar/treatment interaction, the value of pooling all variables is shown in the more complex example of cluster analysis illustrated in Figure 6.17. At high EC, 'UC157' formed a separate cluster (cluster 3), 'Jersey Giant' dominated at low EC as a sub cluster of cluster one, and both cultivars were grouped together at intermediate EC's, particularly EC4. The widely separated grouping of EC1.4 suggests that comparisons at low nutrient levels may reveal significant cultivar differences. However, none of the parameters used in Cluster Analysis showed any difference between two cultivars at EC 1.4, 12 and 14 $mS.cm^{-1}$ when univariate analysis was run. The grouping in Cluster Analysis is based on similarity and dissimilarity amongst groups of measured variables, not on individual measurement as in univariate analyses.

Based on principal component analysis most of the variation was due to effects on plant size (PC1 representing 42.6% of the variation), as may be expected as cell expansion and cell division are the processes most sensitive to the relatively mild stresses indicated by the water potential measurements. Here the plant size strongly determined the plants in the group at optimum growth. Interestingly PC2, representing 25.9% of the variation, was mainly attributable to bud and spear number and number of secondary bud clusters, together with chlorophyll levels. The plants within optimum growth range had developed more secondary bud clusters (Table 6.3 and 6.4) which could result in higher potential spear numbers due to less influence of correlative inhibition amongst bud clusters (Nichols and Woolley, 1985). Similarly, chlorophyll content was high in this range of optimal growth (Table 6.5). Instead of single factor such as producing many bud clusters (Bigard, 1973), large buds (Nichols and Woolley, 1985) and high fern chlorophyll levels (Faville et al., 1999a, d), the second component in PCA in this experiment found an incorporation of bud development and photosynthetic capacity likely to affect potential production in high yielding cultivars.

The results from multivariate analysis reinforced the importance of plant size along with high bud clusters and chlorophyll level for potential high production. It is only in the third component (PC3) that fern water potential (0.5829) and longest root length (-0.4119) were dominant. Therefore, these results explained that there are other factors contributing to the capability of the plants producing optimal growth under low water potential between EC 4 to 8 $mS.cm^{-1}$, indicating a highly versatile adaptation in asparagus.

From Expt 8, it is found that potential production of asparagus can be determined largely by plant size and bud dynamics in terms of bud and cluster development which is associated with photosynthetic capacity. These responses were cultivar dependant and subject to change when the plants are exposed to stress. The adjustment to different environments in Expt 8, however, is based on seedlings rather than established plants. A database and comparative study between seedlings and established plants is needed to build the prediction of potential production in a cultivar and further assess what is limiting yield both amongst cultivar and in different environments.

6.5. SUMMARY

Similar root:shoot ratios but higher photosynthetic rates in 'Jersey Giant' indicate that this cultivar should potentially be more productive than 'UC157'. However, 'Jersey Giant' may be limited by the number of buds available to form spears, especially in deep well-drained soil suited to the deep root-systems that can develop in 'Jersey Giant'. Although 'UC157' produces many buds, yield of high quality spears may still be limited by bud size as many produced have small diameters.

Morpho-physiology of asparagus 'Jersey Giant' and 'UC157' could be modified by Electrical Conductivity (EC) of nutrient solution. Three asparagus clusters were identified based on the changes of morpho-physiology regardless of different cultivars. The largest plants were found in the group with EC's 2, 4, and 8 $mS.cm^{-1}$ and followed by the group with EC's 1.4 and 10 $mS.cm^{-1}$. The third group consisted of the plants with EC's 12 and 14 $mS.cm^{-1}$. Grouping was, however, slightly different at the extreme level when the combinations between cultivars and EC's treatments were analysed for cluster analysis indicating different adaptation of each cultivar to different environment. Cultivar Jersey Giant with EC's 1.4, 2, 4, and 8 $mS.cm^{-1}$ grouped together with 'UC157' with EC's 2, 4, 8 $mS.cm^{-1}$. The second cluster consisted of 'Jersey Giant' with EC's 10, 12 and 14 $mS.cm^{-1}$ together with 'UC157' with EC's 1.4 and 10 $mS.cm^{-1}$. The third cluster only comprised for 'UC157' at EC's 12 and 14 $mS.cm^{-1}$. Change of dry weight, chlorophyll content, and fern potential suggested that the asparagus adjusted osmotically. It is the number of secondary and tertiary bud clusters that determine the development of cluster distribution and most likely influence spear production in terms of t_{max} and time trend of spear harvest, as described in Chapter 3.

CHAPTER 7

GENERAL DISCUSSION AND CONCLUSIONS

7.1. INTRODUCTION

In this thesis eight experiments were aimed at studying interrelationships between the dynamics of bud number and aggregation during plant development and subsequent spear growth, in relation to storage carbohydrate and yield. Asparagus yield can be improved by the production of more spears in a given time and/ or by increasing harvest duration, provided adequate supplies of buds and carbohydrate are available. There appears to be consumer demand for a longer harvest season but lengthening harvest is constrained by social factors and the need to build up sufficient carbohydrate and large buds for the following season. The research reported in this thesis explored, in particular, the possible importance of bud dynamics as an important factor determining asparagus yield.

The results of Expt. 3, 4, 5, 6 indicated that increases in both number of bud clusters and number of medium to large sized buds will potentially extend harvest duration or increase spear production in a given harvest period and therefore increase yield. Observations on increase in bud number during the harvest season, both in greenhouse (Expt 4) and field (Expt. 5) studies provided new information on bud dynamics, supporting the importance of buds as a limiting factor for yield in terms of the number of buds of adequate size for developing marketable spears. In addition crown size, which reflects photosynthate storage and release from the roots, influenced potential yield (Expt. 1, 2, 4, 8). Thus there is involvement of two processes, bud dynamics and photoassimilate supply, which together dictate harvest intensity and duration (Fig. 7.1). How effective these processes are in influencing yield will depend also upon the ability of specific genotypes to adapt to their environment. These general interrelationships are illustrated in Fig. 7.1.

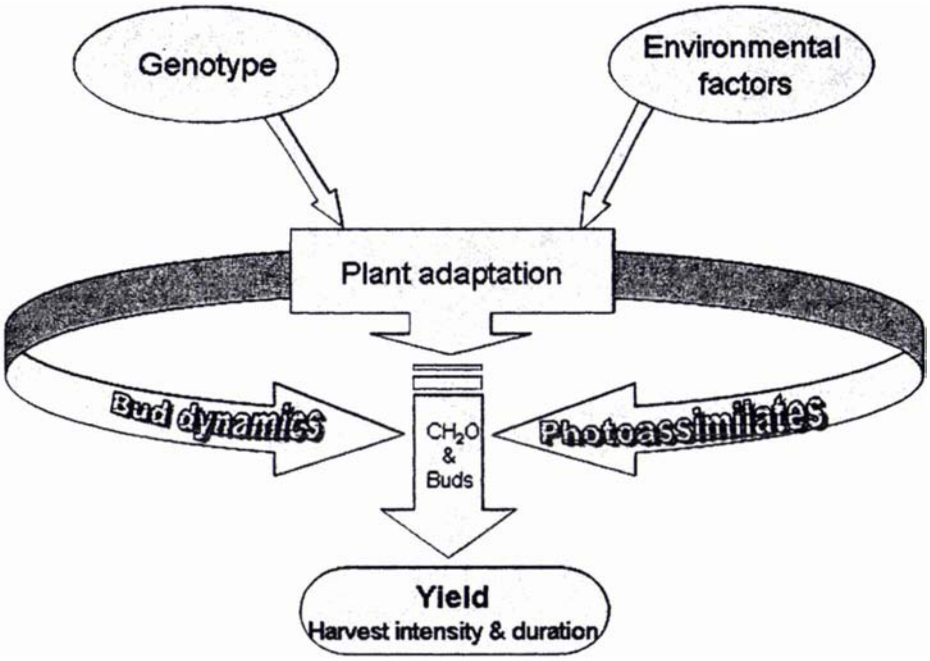


Figure 7.1 Factors influencing the capacity to be high yielding. CH_2O = carbohydrate

One of the key points for producing high yield within a narrow window of production during spring and early summer is to have an adequate number of medium and large sized buds available and a large root mass containing substantial carbohydrate reserve. These internal factors may be influenced by daylength and temperature changes, and can be modified by nutrition and water availability as external factors (Fig. 7.2). In addition fern development and cladophyll structure influence the supply of assimilate for root storage and subsequent release during spear formation. All of these factors may be subject to genotypic variation.

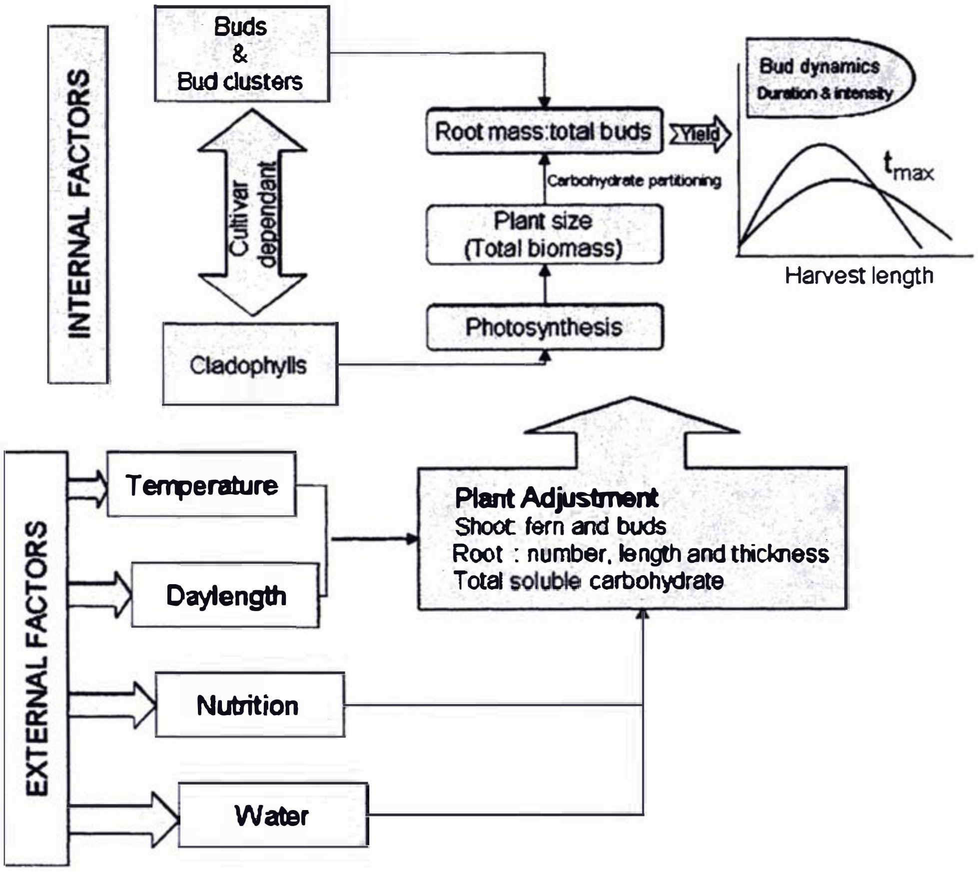


Figure 7.2 Internal and external factors with potential for increasing yield and lengthening harvest related to bud dynamics in asparagus. t_{max} = the time of maximum production.

In order to structure an evaluation of the results from the eight experiments, this general discussion is set out as follows:

1. Internal Factors
   - Cladophylls and photosynthesis in relation to carbohydrate partitioning and plant size
   - Buds and bud clusters
   - Ratio of root mass:total buds

- Bud dynamics, yield and harvest duration

2. External Factors
    - Daylength and temperature effects on plant growth
    - Nutrition and water effects on plant morphology and physiology.
3. Application
    - Practical implications of the above principles
4. Conclusions

7.2. INTERNAL FACTORS

7.2.1.1. Cladophylls and photosynthesis in relation to carbohydrate partitioning and plant size

Root:shoot dry weight ratio increased as pot size enlarged (Fig. 2.12) and as EC increased up to 8 mS.cm^{-2} (Table 6.6). Significant increases of root:shoot dry weight ratio indicate carbohydrate partitioning favouring roots rather than shoots. However, increase of root weight was not necessarily associated with an increase in root number (Fig. 2.10), indicating that increases in weight were due to increases in root length, as visual observation showed (Fig. 2.27). In larger pot sizes, it seems that the plants did not proliferate root number, but rather increased root exploring space by increasing root length.

This was not the case when nutrient concentration was raised. Root weight increased with the increase of EC from 2 to 8 mS.cm^{-2} (Table 6.6), and there was a parallel increase in root number (Fig. 6.7). Thus root number as well as root weight can be controlled through the nutrient supply to the plant. In this study, EC between 4 and 8 $mS.cm^{-2}$ was found to maximize asparagus growth in hydroponics.

The increase of root and shoot dry weight (Table 6.6) was correlated with an increase of chlorophyll content of cladophylls (Table 6.5) although this relationship is not necessarily causal. Asparagus unlike many other crops produces yield indirectly from photosynthesis. The photosynthate is stored into the roots, and later is released as a carbohydrate reserve supply for spear development. Asparagus has been reported as one of the few crops showing a positive causal correlation between photosynthesis and yield (Bai and Kelly, 1999; Guo et al., 2002). Increase in chlorophyll content correlated with the increase of the light-saturated rate of photosynthesis, $A_{sat,}$ (Faville et al., 1999b, d), and assimilate supply for investment in larger plant size and therefore heavier crown weight as has been shown in Expt 8. Increase in root weight and number is very critical since the increase of root number will most likely be linked to increase in bud number (Sudjatmiko, 1993). However, an increase of root weight because of root elongation may not increase bud numbers in proportion to weight (Expt 1).

In Expt 4 it was shown that growing small spears will take more energy than growing an equivalent dry weight of large spears. This is supported by the results of spear number (Table 3.15 – 3.18) and TSC concentration in the root amongst different cultivars (Fig. 3.33). Although total spear number was different between cultivars, the number of quality 1 spears was similar amongst cultivars. The numbers of spears were affected by cultivar only in spear quality 2 and 3. Cultivar ‘UC157’ demanded more carbohydrate in terms of TSC concentration than other cultivars (Fig. 3.33), although total spear yield was similar to ‘Apollo’ and ‘Atlas’ (Table 3.7). The difference lay in spear quality 3 where ‘UC157’ was significantly higher spear number than the other cultivars. Producing more small spears appeared to require more carbohydrate than producing a similar weight of fewer, large spears. It is acknowledge that this interpretation is based on evidence from studies involving limited control of bud population, and in the absence of weekly measures of carbohydrate reserves and root mass is unknown. Further understanding requires estimation of the energy demands of spear development from buds of different size. The ideas are dealt with more detail in section 7.4.

7.2.1.2. Buds and bud clusters

The number of buds of adequate size for quality spear development may be a yield limiting factor beside carbohydrate availability in the roots. Bud number has not generally been thought to be a limiting factor in asparagus yield since buds always appear to be available. However, in the current study, the limited number of large and medium buds affected the total yield especially marketable yield in some cultivars (Table 3.7 – 3.10 and Table 3.15 – 3.18). Large and medium sized buds mostly develop into marketable spears, and in this thesis spear diameter was the main determinant of spear quality, as was shown in the comparison between spear quality based on spear diameter only and that based on both spear diameter and head tightness (Table 3.25).

In Expt 8, increase of plant weight was accompanied by increase of buds and bud clusters as EC increased to 8 $mS.cm^{-2}$ (Table 6.3 and 6.4). The effect of crown size on spear diameter can be seen in aeroponic study in Expt 6, which showed that small crowns had only quality 5 spears (< 4 mm in diameter) whereas in large crowns, some spears were included in quality 2 (7 < 9 mm in diameter).

There were genotype variations in bud size and bud number, as has been shown in Expt 8. Cultivar 'Jersey giant' has been reported to have large diameter spears which come from large buds, as spear size is correlated with bud size (Blasberg, 1932; Nicholls and Woolley, 1985). On the other hand, 'UC157' produces many spears of small diameter, as shown in Expt 4 (Table 3.17). Compared to 'Atlas' and 'Apollo' in Expt 4, 'UC157' produced the highest number of spears, but had the highest number of quality 3 spears, which indicated that carbohydrate reserve was used up to grow non-marketable spears. In this case, marketable yield was limited by the availability of adequate sized buds for marketable spears.

7.2.1.3. Ratio of root mass:total buds

The results from this current study indicated the importance of root mass:total bud ratio as a possible limiting factor for yield in well-grown asparagus. This ratio, unlike root:shoot ratio in terms of number or dry weight, carries information on two potential limiting factors in determining yield, namely carbohydrate availability, implied from the root mass TSC concentration, and the number of buds. Very little information is available regarding the ratio of root mass to total buds. Study on four-month old plants in Expt 1 indicated that large crowns provided a lower number of buds per unit root mass (higher ratio of root mass:total buds) than small and medium crowns. As root mass increases yield will tend to increase but bud number may not increase in proportion (Expt 1); therefore, potential yield becomes limited by buds. Thus a study of bud dynamics becomes important.

7.2.1.4. Bud dynamics, yield and harvest duration

Lengthening harvest duration increases the number of spears produced, but spear quality may decline severely because of smaller spear diameter, open head, and reduction in TSC concentration in the spears (Expt 4). A maximum total marketable yield per week was defined as when large and medium-large buds reached their t_{max}, on a Gaussian curve of production versus time (Fig. 3.22-3.25 and Fig. 3.27-3.29).

Total bud number was not found to be a limiting factor in Expt 4 and 5, partly because "new" buds were developing through the harvest period. Approximately 16 % of the new buds contributed to spear yield in the current harvest (Expt 5), 68 % were dormant until the following summer and contributed 18 % to total buds at that time. The rest of the new buds appeared to develop into ferns during the summer period. There was a substantial increase of bud number (Fig. 3.42), but only 56 % of the buds were viable for potential yield. The rest appeared to die or to remain dormant. Large and medium large buds most likely to become marketable spears were located at the base of a cluster, and bud size slowly declined toward the apex of a cluster, as visual observation showed in established plants in Expt 4 and Expt 6.

Asparagus spear growth is affected by correlative inhibition, the degree of inhibition depending upon the crown size and carbohydrate availability (Expt 4). Buds in small crowns had not only longer period of correlative inhibition than those in large crowns (Table 4.13) but also a tendency to have slower elongation rate in terms of RSGR (Table 4.10). Furthermore, when a small crown had more bud clusters, the period of correlative inhibition was longer too (Table 4.10). These responses were not evident in large crowns, emphasizing the importance of large crown size for determining high potential yield.

Thus plant size, bud clusters, bud number per cluster and correlative inhibition will determine duration and intensity of harvest. A shorter period of correlative inhibition was observed in large crowns than small crowns (Expt 6). The increase of bud number will take up more carbohydrate regardless of the size of buds, as shown amongst genotypes in Expt 4 (Fig. 3.34, Table 3.15). For example, similar initial TSC between 'Atlas' and 'UC157' resulted in lower final TSC concentration in 'UC157' than 'Atlas' whereas total harvested spear number was higher in 'UC157' than in 'Atlas'. The different spear number was due to many more small spears harvested in 'UC157'.

Number of bud per cluster and number of cluster vary widely among crowns. Expt 1 and 6 showed that large crowns had potentially higher yielding than small crowns. This variability, and its potential for influencing spear yielded, is illustrated in Fig. 7.3 for four hypothesized patterns of bud development. These examples assume large uniformed crown size.

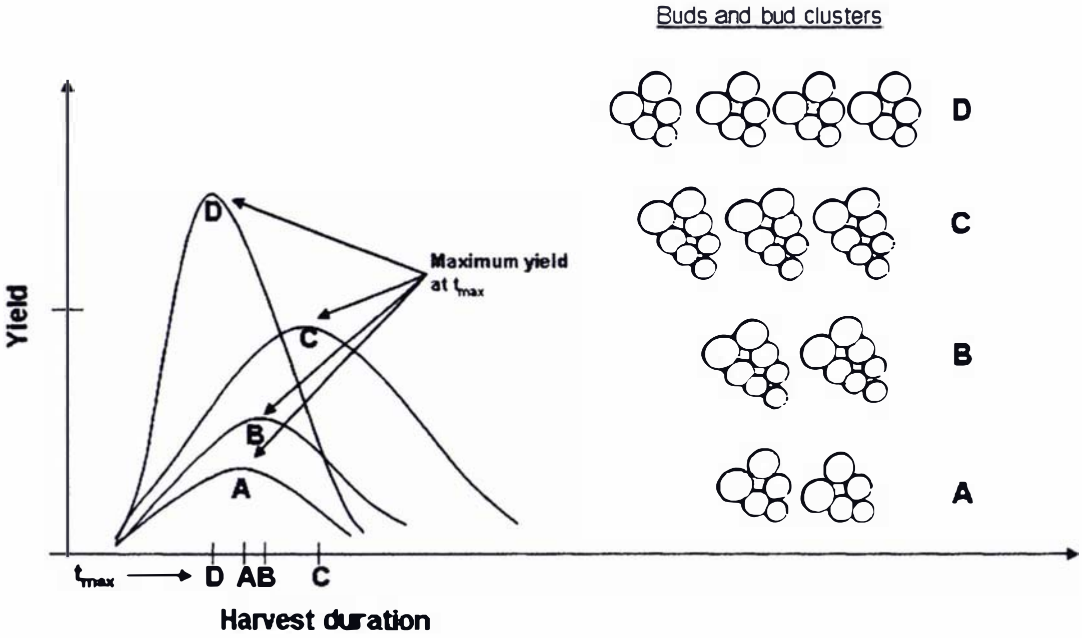


Figure 7.3 Differences in t_{max}, maximum and total yield and harvest period under four patterns of buds and bud clusters with different cluster size (see text)

1. Low total bud number and few bud clusters with small cluster size (Pattern A).

Root mass:total bud ratio will be high as has been shown in Expt 1 (Table 2.8), implying low availability of bud number per unit root mass. Carbohydrate availability is assured. Size of marketable spears however will be limited. Yield at t_{max} will be low with short harvest duration since only few bud clusters are available, causing long time for the buds to develop due to correlative inhibition within a bud cluster.

2. High total bud number and few bud clusters with large cluster size on a large crown (Pattern B)

   Root mass:total bud ratio will be lower than in pattern A, but carbohydrate in the storage roots will still be sufficient to support spear growth. T_{max} will be equivalent to pattern A or slightly later, but yield at t_{max} will be higher and the harvest duration will be longer since there are more buds per cluster that can be harvested in sequence.

3. High total bud number and large bud clusters with large cluster size (Pattern C)

   Root mass:total bud ratio will be lower than patterns A and B, but carbohydrate availability is still adequate to support spear development. T_{max} will be earlier than in patterns A and B, since many more buds from different bud clusters can develop within the same time. Correlative inhibition presumably does not exist amongst clusters, indicated by similar spear elongation in large crowns even with many more clusters (Table 4.10). Compared to A and B, pattern C will be expected to have larger total yield, having high yield at t_{max} and longer harvest duration than B.

4. High total bud number and large number of clusters with small cluster size (Pattern D)

This is possibly the arrangement of buds and bud clusters suitable for production of early, high yields. Spears are produced earlier, resulting in earlier t_{max} than pattern C, due to many more bud clusters, and harvest duration is more compact than patterns C. Yield at t_{max} will be higher than scheme C, but total production can be equivalent to pattern C.

In general Patterns C and D are desirable since they will give highest total yield but different effects on harvest duration. Pattern C provides longer harvest whilst D may produce higher yield at early harvest (Fig 7.3).

These are the main patterns for yield trends within harvest duration with differences in bud number and bud cluster size. There will be more complex patterns of combinations of different in bud numbers and bud cluster sizes.

7.3. EXTERNAL FACTORS

7.3.1. Daylength and temperature effects on plant growth

Temperature was not studied directly but may be important in relation to the daylength responses. As the season changes from early to mid summer, physical factors such as daylength are thought to influence switching of carbohydrate partitioning from the shoots to the roots (Sudjatmiko et al., 1997; Karno, 1999; Woolley et al., 1999; Woolley et al., 2002). Differences in the effects of a constant 13.5 h and 15 h daylength and gradual reduction of daylength from 15.5 to 12.0 h were not clearly distinguished in Expt 1 and Expt 2 which were conducted on seedlings and on six-month old plants respectively in growth chambers. Plants were not different in their assimilate partitioning in terms of root:shoot ratios in either number or dry weight (Fig. 2.17 – 2.18) when results were analyzed on a weekly basis. However, the allometric constants supported by the estimates of net photosynthetic rate indicated the possibility of different responses in some cultivars to daylength change (Fig. 2.19, 2.25 – 2.26) rather than constant long daylength (Fig. 2.8 – 2.9). Analysis of allometric relationships taking the whole duration of the experiment was clearly more effective rather than weekly analysis in defining plant responses to the change of daylength.

The effect of changing daylength on dry weight partitioning may not be a strong effect when the temperature is kept constant. Although Sudjatmiko et al., (1997) suggested that temperature may not have a large effect on the change in allometric constants, declining temperature together with daylength reduction has effected rapid changes in fructan storage in the roots of asparagus (Pressman et al., 1989), wheat (Gaudet et al., 2001) and many other plants (Pollock and Jones, 1979; Chatterton et al., 1989). The interaction of temperature and daylength changes has been noted as a major environmental determinant of plant phenology, adaptation and yield (Yan and Wallace, 1998). Thus the effect of temperature should be evaluated in conjunction with daylength reduction in the carbohydrate replenishment stage of asparagus.

7.3.2. Nutrition and water effects on plant morphology and physiology

Increasing electrical conductivity of the nutrient solution in Expt 8 increased the amounts of nutrient available but decreased water availability. Increasing EC up to 8 mS.cm^{-2} increased plant size, associated with increases in the number of buds and bud clusters (Table 6.3 and 6.4). An increase in bud numbers may be associated with an increase in nitrogen (Waters et al., 1990). Although the main effect of nitrogen was not isolated, the increase of macronutrient in EC implied increasing nitrogen availability. Asparagus grows best in NO_3^- dominated solutions, with maximum shoot and root growth occurring with NO_3^-:NH_4^+ mixtures containing 17 – 40 % of NH_4^+ (Follett and Douglas, 1987).

Nitrogen is usually applied every year in New Zealand at the end of harvest or pre-harvest (NZNAM, 1997). Providing nitrogen pre-harvest or during harvest as a split application may be beneficial in enhancing bud development since the development of unmapped buds occurred during the harvest period (Expt 4 and 5). However, to what extent the mapped buds may have grown during the harvest period is not known. Thus application of nitrogen fertilizer during early in the harvest season may influence the development of bud size and make it possible to increase the intensity or duration of harvest. Similarly, the application of nitrogen fertilizer in mid harvest season may accelerate bud size development in early summer and thus promote stronger fern establishment since the ferns would develop from larger buds. These nitrogen application regimes have not been studied previously, presumably because the results of Expt 4 and 5 are the first evidence that bud development continues through the harvest season (see section 7.2.1.4). However, Makus (1995) observed no increases in spear yield when supplemental nitrogen was applied either before or after the harvest season compared with crowns that received no supplemental nitrogen. Wilcox-Lee (1991) also concluded that neither the rate nor timing of nitrogen applications to asparagus had any impact on yields. There were possibilities why the application is not effective. The soil may have sufficient nitrogen availability and uptake in early spring is limited by temperature. Split application of nitrogen during the spring may give a different effect especially for bud development, depending on the nitrogen status of asparagus blocks. Slow release fertilizer could be more appropriate for field application as the soil temperature at the beginning of the spring is still low. The effectiveness of nutrient uptake by plants depends upon the temperature, for example Daskalaki and Burrage (1998) showed that the uptake of all nutrients in soilless culture increased sharply when root temperature was raised from 12° to 20°C.

The increase of EC up to 8 $mS.cm^{-2}$ also improved root length, which may be a benefit in terms of plant adjustment to drought. Water stress is a problem in some regions because asparagus can undergo dormancy when exposed to drought. Reduction in bud number and increase of bud death occurs when soil water potential is reduced (Drost and Wilcox-Lee, 1997a, b). This is an indication that asparagus, although it is considered a drought tolerant plant, as in many fructan storing species, is susceptible to severe drought. A severe reduction of bud and bud clusters was observed when asparagus plants were exposed to EC higher than 10 $mS.cm^{-2}$, conditions in which high concentration of nutrient created low water potential (Table 6.6).

Imbalance of nutrients at low nutrient levels (e.g. EC 1.4 $mS.cm^{-2}$) on the other hand, reduced growth in terms of fewer buds and bud clusters (Table 6.4) and lowered chlorophyll content (Table 6.5). These results suggest deprived plants may have fewer ferns with lower chlorophyll content, which may result in low net photosynthesis. Follett and Douglas (1987) found significant reduction in asparagus yield occurred with either 100% NO_3^- or 50% NH_4^+. Haynes and Goh (1978) stated that in the majority of species greatest growth and protein production occurs with a mixture of NO_3^- and NH_4^+, rather than nitrate alone. Varga et al. (2002) showed that the nitrogen imbalance under greenhouse conditions decreased shoot:root growth of corn and velvetleaf and caused stress condition and disorder of metabolic processes.

In Expt 8 asparagus plants showed a wide range of adjustment to EC. While in other crops EC 8 $mS.cm^{-2}$ reduced growth (Huett, 1994; Tadesse et al., 1999), optimum growth in asparagus occurred between 4 and 8 $mS.cm^{-2}$ despite similar fern water potential to plants at EC higher than 10 (Table 6.6). Results from multivariate cluster analysis (Fig. 6.17) emphasized this finding and suggest that asparagus could have osmotic adjustment. This mechanism to maintain turgor by osmotic adjustment is an important physiological adaptation for minimising the detrimental effects of water deficit (Morgan, 1980, Turner, 1990).

7.4. PRACTICAL IMPLICATIONS

Prolonged harvest under any of the four patterns can reduce root carbohydrate, resulting in reduced carbohydrate concentration. This effect will be more serious for small crowns than large crowns. Fern establishment will then rely on small buds and very low carbohydrate reserves resulting in poor growth and low carbohydrate storage for the following season. A practical decision to stop harvest at this time is based on an estimate of total soluble carbohydrate concentration from the selected roots. AspireNZ, a decision support system for managing storage carbohydrate, provides information on root TSC concentration taken from field samples (Wilson et al., 2002), but does not take into account root mass and thus total carbohydrate reserve.

The relationship between carbohydrate reserves and bud dynamics as yield-limiting factors in asparagus is described in Fig. 7.4 which illustrates the relationship between TSC concentration and spear development in the asparagus plants in Expt 4, and relates this to the limit of carbohydrate concentration set by AspireNZ. In making this comparison, however, the following conditions need to be borne in mind:

1. In the AspireNZ system samples are taken only from firm roots whilst in Expt 4 samples came from all roots, full, partially depleted, or empty. Thus in Expt 4 TSC declined to 20%, which may not be comparable with recommendation of the AspireNZ system (30 – 35 %).

2. The kinetics of reduction in TSC concentration during the harvest period in Expt 4 was derived from initial and final TSC concentrations; and a calculation based on weekly spear dry weight in Expt 4 and the results of Pressman et al. (1993) using weekly spear dry weight which indicated a crown respiration rate of about 30 % for warm temperatures.

3. T_{max}, time of maximum production was computed using Gaussian fitting for large and medium-large sized buds as indicators of marketable spears. T_{max} was used together with the height and width of the curve to define harvest intensity and duration.

4. Average values for TSC concentration of the roots depended on the proportion of new full, old full and old empty roots. TSC then depends on this average value and the root mass. Young plants may have TSC concentrations up to 65% but as plants get older TSC concentration tends to fall (D. J. Woolley, personal communication). In Exp 4 initial TSC concentration was approximately 500mg.g^{-1} or 50 % (Fig.3.32 and 3.34) but the plants had fully explored their containers which restricted root growth, as observed when the plants were re-potted at the beginning of the experiment. Thus Fig. 7.4 simply provides an illustration of the experimental protocol that should be followed for distinguishing between bud and carbohydrate limitation, but using fully non-restricted root systems, as would be the case for plants grown in a deep free-draining soil. It should be remembered that the original intention of the experiment was to use plants with similar root masses and then manipulate the relative demand for carbohydrate or buds by changing cutting height.

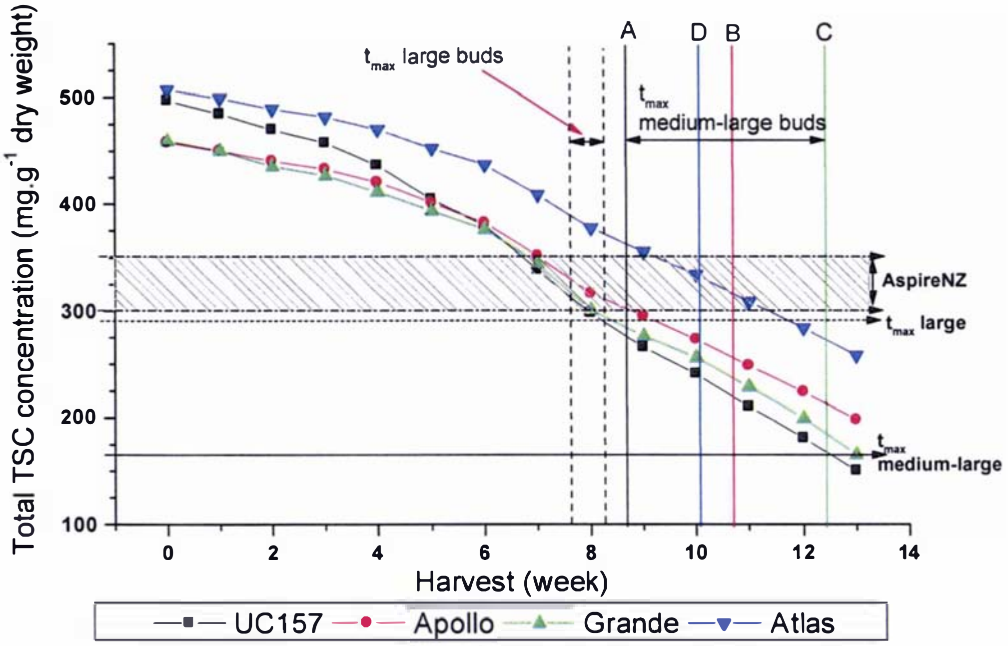


Figure 7.4 Relationship between total TSC concentration during harvest period and bud dynamics for large and medium-large sized buds in determining harvest intensity and period for different cultivars. t_{max},= the time of maximum production. Diameter for large buds and medium-large buds are > 9 mm and 7 < 9 mm, respectively. Shaded areas is the limit range of TSC concentration recommended by AspireNZ (a decision support system for managing root carbohydrate in asparagus). Letters associated with line color as indicated in symbol box indicated t_{max} for medium-large buds of different cultivars. A = UC157, B = Apollo, C = Grande, D = Atlas.

At the limit of TSC set by AspireNZ (350 mg.g^{-1} dry weight or 35 %), harvest duration was only 6.6 weeks which was 1 to 2.5 weeks earlier than when large buds reached their maximum production (t_{max} large) (Fig. 7.4). A termination of harvest at this time would lose considerably potential marketable yield, because harvest of available large buds could extend at least as far as week 8.2 (e.g. for 'Atlas'), a significant increase of marketable yield. In addition, plants with large root masses tend to have a lower TSC concentration (Personal communication – Dr. D.J. Woolley). A lower limit of TSC for stopping harvest should be considered and/or a more comprehensive root sampling method.

Potential yield is much higher since at this t_{max}, since large buds are still available. At the furthest range of t_{max} medium-large buds (C in Fig. 7.4), many more medium-large buds are still available to be harvested but large buds may be limited. By this time, TSC concentration was between 27 and 18 % (270 - 180 $mg.g^{-1}$) which was far below AspireNZ recommendation. However, care is needed in interpreting these results because the TSC concentration measured in Expt 4 and those used in AspireNZ recommendation clearly came from substantially different root samples. At this time, the comparison between the two methods has not been done, but the limit of TSC recommeded by AspireNZ is probably to a much lower concentration of TSCfrom the procedure adopted in Expt 4. Karno (1999) showed that TSC concentration in new full roots (42 %) was greater than in old full roots (35 %), and old empty roots (18%). Thus, if the TSC concentration limit recommended by AspireNZ is equivalent to TSC concentration achieved at t_{max} for medium-large spears, then marketable yield might be limited by the availability of large buds (Fig. 7.4). Further comparison between the two methods is needed either using field-grown plants from a deep, light soil or very deep containers. Additional measurement of root mass is also important since root mass will indicate of total carbohydrate content of a crown. Both in AspireNZ and in this current study, the root mass was not measured.

Applying the concept of bud dynamics from the different bud cluster patterns (Fig. 7.3), pattern D will produce a more intense harvest period of short duration and carbohydrate loss due to root respiration will be reduced.

It is often suggested that total bud number is not usually a limiting factor to yield, but the analysis of Fig. 7.4 shows clearly the circumstance in which the number of buds of adequate size for marketable spear sizes may set a limit to marketable yield.

7.5. CONCLUSIONS

From the above discussion the following conclusions may be drawn:

- Development of new buds continued throughout the period of spear harvest, and was not confined to the summer period. Approximately 16% of the new buds developed into spears during the current harvest and 13 % of the new buds developed into fern in the summer.

- Approximately 56% of the total buds were potentially productive but the rest of the buds were either dead or dormant. Fifty percent of the total buds for future yield were formed in the summer and the rest were dormant buds, either from previous harvest period or from the previous summer. This emphisizes the importance of bud dynamics in asparagus.

- Bud number can limit spear yield, at least in terms of the available number of adequately sized buds which develop into marketable spears. However, the relationship between bud size and final spear size requires further investigation

- Intensity and duration of harvest time was affected by different size of the buds and genotypes. Numbers of buds and bud clusters and different cluster size will largely determine the t_{max}, harvest intensity and duration.

- Correlative inhibition is a significant factor inhibiting the early growth of many spears. There is scope for investigating procedures to limit inhibiting effects; in particularly, correlative inhibition appears to be more serious in small than large crowns.

- Large crowns with many large bud clusters will encourage high spear yield and long harvest duration. However, large numbers of bud clusters with small cluster size will tend to result in shorter harvest duration. Bud number and bud size are influenced by plant genotypes. There is a need to investigate thoroughly the potential for influencing bud size and bud number through controlled use of fertilizer during the harvest period.

- Nine major shapes of spear elongation were identified based on their log forms of spear elongation. Only 43 % of spears demonstrated a clear exponential growth, which indicated that care must be taken in modelling spear development.

- An EC between 4 and 8 $mS.cm^{-2}$ is the optimum range of EC for asparagus growth in hydroponics. Some asparagus genotypes have the ability to adapt to a wide range of environmental conditions.

- The ratio of root mass:total bud number was found to be better indicator of yield potential than either root:shoot dry weight or root:shoot number ratio, because it provides a more objective index of energy source:sink relationships. The allometric constant of root to shoot dry weight provided a good indicator of environmental effects such as daylength on plant behaviour.

- Use of hydroponics and aeroponics technology provided a useful research tool for studying plant behaviour. However, it is recognized that care is necessary in extrapolating the results of these studies to field conditions.

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