AN ABSTRACT OF THE THESIS OF

Jessica M. Cortell for the degree of Master of Science in Horticulture presented on August 6, 1996. Title: Effect of Floricane Number on Primocane Growth, Yield Components, and Cold Hardiness in 'Marion' Trailing Blackberry.

Abstract approved:

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In spring of 1993 and 1994, mature 'Marion' (*Rubus* sp.) plants were pruned to 0, 4, 8, and 12 floricanes. An additional treatment of 0 floricanes with early (30 cm) primocane pruning was included. Primocane growth was measured from emergence in April until growth cessation at the end of October. Yield component analysis was completed after harvest during the first season and in the following season. Dry weight partitioning was determined in summer and winter. During the winter, cold hardiness of primocanes was determined by controlled freezing.

In 1993, plants without floricanes produced more primocanes with a greater total length and showed a trend toward a greater number and length of primocane branches at the end of the season. In 1993, internode length was significantly reduced in plants with 0 or 4 floricanes compared to plants with 8 or 12 canes. In 1994, there were no significant differences in primocane growth among treatments. Primocane growth in all

treatments occurred in flushes with plants without floricanes having a significantly higher absolute growth rate (AGR) on 5 dates compared to plants with floricanes in 1993. In 1994, there was no treatment effect on AGR over the season; however, plants without floricanes still had a greater primocane AGR than plants with floricanes on six dates before fruit harvest. During both years, there were approximately 5-7 peaks in AGR throughout the season. When comparing primocane growth at three phenological stages in 1993, plants with no floricanes had a significantly higher AGR during fruit production and from harvest to growth cessation than plants with floricanes. In 1994, plants with no floricanes had the highest rate of growth before bloom and a trend towards higher AGR during fruit production. After fruit production, there were no differences in AGR between the treatments in 1994. Plants with floricanes produced a second flush of primocanes while plants with no floricanes produced only one flush. Primocane length (averaged for 4, 8, and 12 floricane plants) of the first flush was significantly different from the second flush at all dates during the season except for the final end of season measurement. In 1993, primocane topping at 30 cm tended to decrease primocane number and total length. In 1994, there were no significant effects of topping except for increased branch length. Plants without floricanes produced primocanes that were significantly more cold hardy (lower LT_{50}) in 1994 and 1995 than plants with floricanes. All treatments had greater hardiness in 1995 than in 1994.

In both 1993 and 1994, plants with four floricanes had significantly higher percent budbreak than plants with 12 floricanes. In 1993, plants with four floricanes also had significantly fewer nodes per cane, a shorter average cane length, reduced lateral length, and a lower number of branch canes compared to plants with 8 or 12 floricanes. In 1994, there were no variables affected by floricane number per plant other than percent budbreak. In 1993, there was no significant difference in yield between plants with 8 and 12 floricanes while plants with 4 floricanes had a lower yield. In 1994, yield per cane was significantly higher in plants with 4 floricanes compared to plants with 8 or 12 floricanes; yield per plant was not affected by floricane number. There were no significant treatment effects on berry weight in either year.

In summer of 1993, there was a trend for a decrease in primocane dry weight and a significant decrease in branch dry weight with an increase in floricane number. Total plant, fruit, floricane and lateral dry weight increased linearly with increasing floricane number. Results were similar for floricane components in the summer of 1994, however, there were no treatment effects on primocane or branch dry weight. There was also a positive linear relationship between crown dry weight and floricane number in 1994. By the winter of 1994 and 1995, there were no treatment effects on primocane or crown dry weight.

Plants without floricanes produced a significantly greater number of canes per plant than plants with floricanes in 1993 but not in 1994. Plants without floricanes produced primocanes that had a significantly lower percent budbreak the following year (1994) than plants with floricanes. There was a similar trend in 1995. Plants without floricanes had a higher number of nodes per branch and a greater average branch cane length than plants with 8 or 12 floricanes. Number of nodes per cane tended to decrease with increased floricane number per plant in 1994 and 1995. There was no significant treatment effect on fruit per lateral, berry weight or yield per plant in either 1994 or 1995. However, in 1994, plants without floricanes had the lowest yield per cane but the highest yield per meter of cane compared to plants with floricanes. Topping primocanes at 30 cm in 1993 had no significant effect on yield components the following season. The only variable significantly affected by pruning in 1994 was a reduction in fruit per lateral with primocane pruning.

'Marion' primocanes had a typical sigmoid growth curve similar to the growth pattern seen in red raspberry and other plants. Our findings of the emergence of two flushes of primocanes without primocane suppression and absolute growth rate occurring in peaks of growth throughout the season have not been previously reported in *Rubus.* Primocanes on plants with floricanes may have the ability to "catch up" to those on plants without floricanes after harvest as there were no differences in primocane dry weight by winter. In this study, we did not see an increase in yield in plants grown without floricanes the previous season as is generally found in 'Marion'. This may have been a result of winter training rather than primocanes being trained in the summer as they grew, a practice that improves light exposure to the canes. Yield compensation occurred through an increase in percent budbreak in plants with 4 floricanes compared to those with 8 or 12 canes.

Effect of Floricane Number on Primocane Growth, Yield Components, and Cold Hardiness in 'Marion' Trailing Blackberry.

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Jessica M. Cortell, Author

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In memory of my Father

Effect of Floricane Number on Primocane Growth, Yield Components and Cold Hardiness of 'Marion' Trailing Blackberry.

Introduction

The Pacific Northwest is a major growing region for trailing blackberry cultivars produced for processing. The most important cultivar is 'Marion' which accounts for 50% of the hectarage in Oregon (Strik, 1992). Although 'Marion' is a vigorous plant with high fruit quality, its production has been unstable due to its sensitivity to winter cold injury and concomitant fluctuations in yield (Bell et al., 1992). Two systems currently used commercially for 'Marion' are the annual (every year-EY) and biennial (alternate year-AY) production systems. The AY system in 'Marion' has been observed, in the field, to have greater cold hardiness (Sheets, 1987). In alternate year production 85% of the yield of the EY system is produced over a two year time period. AY production also has the added advantages of reduced labor, fertilizer and pesticide inputs, damage of primocanes during machine harvest is eliminated, and a less favorable environment for disease than in the EY system (Sheets, 1987). An increase in primocane number during the "off year" in the AY system was found with 'Marion' and other caneberry cultivars tested (Sheets et al., 1972). In 'Boysen', Nelson and Martin (1989) found plants grown in the AY system produced significantly higher yields, more canes, and smaller fruit than plants grown in the EY system. However, relatively little research has been done on the effect of the presence or absence of floricanes on primocane physiology and growth rates in blackberry.

There is interest in studying ways to increase the cold hardiness of 'Marion' because winter injury resulting in crop loss is a major factor limiting 'Marion' production (Strik, 1992). 'Marion' is the least hardy blackberry cultivar grown commercially in Oregon. Winter injury has resulted in fluctuating prices and unstable markets as well as direct crop loss (Conroy, 1967). The most recent serious freeze was in 1990 when the 'Marion' crop was reduced by 70% (Bell et al., 1992). Cold injury is usually associated with movement of arctic air masses into the region which cause a rapid drop in temperature. In 'Marion', the buds are the most susceptible to freeze injury. Although severe conditions can kill entire primocanes, more typical damage is reduced and erratic budbreak along the cane as well as stunted fruiting lateral growth (Bell et al., 1992). Poor budbreak in general, is another major concern with 'Marion. Although sometimes poor budbreak is a result of cold injury, in other cases, buds appear a healthy green but do not break.

Several cultural methods have been found to improve cold hardiness in 'Marion'. February training often reduces winter injury compared to August training, however, the latter is generally preferable because of higher budbreak and yield (Bell et al, 1995a; Sheets et al., 1972). Recent findings by Bell et al., (1995b) show improved cold hardiness in 'Marion' with late primocane suppression. The AY system in 'Marion' has been observed in the field to have greater cold hardiness than with EY production (Sheets, 1987). However more research is needed to understand the effect of the presence/absence of floricanes (as is found in AY and EY production) on the subsequent cold hardiness of primocanes.

EY and AY systems also provide a good model for studying plant physiology and partitioning. In red raspberry, new primocanes use reserves stored in the root system until a functional leaf biomass is established. However, in red raspberry, the root system is a strong sink and rapidly replenishes its store of reserve carbohydrate from photosynthates from floricanes and primocanes and continues to do so into the fall (Fernandez and Pritts, 1993, 1994, 1996; Whitney, 1982). Whitney (1982) found carbohydrate levels in the primocanes were high early in the spring, dropped to low concentrations in July, then returned to higher levels again by the end of the season. Fernandez and Pritts (1996) report that the large amount of carbohydrate reserves in the roots can be remobilized to floricanes during fruiting or stored for use the following year. Fruiting laterals on floricanes initially rely on carbohydrate reserves stored in the overwintered canes with later fruit development being supported by the adjacent fruiting lateral leaves (Whitney, 1982). Floricanes grow early in the season, with dry matter and macroelement uptake nearly complete by mid-summer. Floricane senescence occurs after mid-summer with concomitant dry matter and nutrient loss (Kowalenko, 1994). New primocanes of red raspberry begin to grow and take up macroelements later in the spring than floricanes and continue growth and uptake later into the fall (Kowalenko, 1994).

Although research in raspberry provides insights, different factors may play a role in the success of biennial production in trailing blackberries because they differ from red raspberry in growth habit and in the training system used. 'Marion' is more vigorous, has a trailing growth habit, numerous branch canes, and is more productive in the basal rather than the terminal cane section in contrast to raspberry (Bell et al., 1995a). Trailing blackberries, such as 'Marion', have a canopy where the floricanes are spatially separated from the primocanes in annual production because the floricanes are wrapped horizontally on trellis wires while the primocanes grow along the ground. This creates a different light microclimate than that found in red raspberry where vegetative and reproductive canes exist in the same vertical canopy.

'Marion' produces vigorous branch canes without pruning while red raspberry generally does not produce axillary branches on primocanes. The branch canes in 'Marion' have been found to be an important yield component (Bell et al., 1995a). Branch cane development is important in other *Rubus* species such as erect blackberry (Moore and Skirvin, 1990) and purple raspberry (Gundersheim and Pritts, 1991). In these crops, primocanes are summer pruned/tipped to stimulate branching.

This research was undertaken to develop a better understanding of the physiology of vegetative and reproductive cane growth as well as carbohydrate partitioning in 'Marion'. The specific objectives of this research were to determine the effect of floricane number and primocane pruning on primocane growth, dry weight partitioning, subsequent cold hardiness, yield components within the season, and yield components the following season.

Chapter 1

Review of Literature

Description of the trailing blackberry industry

The Pacific Northwest is the major growing region for trailing blackberry cultivars while upright and semi-erect cultivars are grown in other parts of the United States. Approximately 98% of the blackberry hectarage grown in Oregon is planted to trailing blackberry cultivars (Strik, 1992). The most commonly grown cultivar is 'Marion' which accounts for 50% of the hectarage grown in Oregon (Strik, 1992). The next two most popular cultivars are 'Thornless Evergreen' and 'Boysen' which accounted for 29% and 17% of the total hectarage in 1990, respectively (Strik, 1992).

Over 90% of the trailing blackberry crop in Oregon and Washington is for processing. Oregon produces 95% of the loganberries, 85% of the blackberries, and over 50% of the boysenberries used for commercial processing in the U. S. Oregon processors do a variety of packs with blackberries including IQF (individually quick frozen), straight or sugared frozen, canned, juices, purees and concentrates. These products are sold in an international market. In 1994, there were 2040 hectares of blackberries harvested with a value of $14.2 million. Of the total hectarage harvested, 1416 hectares were 'Marion' (Anonymous, 1995).

'Marion', released in 1956, was developed by the OSU/USDA cooperative breeding program, and was selected from a cross of 'Chehalem' and 'Olallie' made in 1945. It is thought to have 'Black Logan', 'Santiam', 'Young', and Himalaya in its parentage. 'Santiam' was a selection made from wild, native trailing blackberries (*Rubus ursinus*) and contributed to the superb flavor of 'Marion'. The use of 'Olallie' in the cross could have contributed to the relatively poor cold hardiness of 'Marion'.

'Marion' produces a medium sized (5.0g) dark red to black berry with a medium sized seed. Fruit harvest occurs from July 10- August 10. 'Marion' has been the favored berry for processing, over 'Thornless Evergreen' and 'Boysen', because of its good flavor and small seed size. Two other trailing blackberry cultivars grown commercially are 'Kotata' which has similar fruit quality to 'Marion' but is firmer and 'Waldo' a genetically thornless cultivar (Strik, 1992). However, 'Marion' is still preferred over these cultivars by the processing industry.

Primocane and root growth.

The following literature presented is from red raspberry research unless otherwise stated. 'Marion' has a growth habit similar to most *Rubus* species with a perennial crown and biennial canes. New primocanes emerge from buds on the crown and the base of floricanes and are vegetative for the first season (Waister et al., 1977). In red raspberry, the primocanes start emerging in April initially using carbohydrate reserves from the roots until leaf area is established. The rate of elongation is the primary determinant of final cane length (Jennings and Dale, 1982). Nodes are produced at a continual rate so the internode length varies according to changes in growth rate (Jennings and Dale, 1982). Primocanes of red raspberry have a three phase growth pattern with a linear increase up to peak first harvest, a leveling off during harvest, and another linear increase after harvest (Fernandez and Pritts, 1993). Whitney (1982) found carbohydrate levels in the primocanes were high early in the spring dropped to low concentrations in July then returned to higher levels again by the end of the season. Kowalenko (1994) found that primocanes began to grow later in the spring than floricanes and growth and macroelement uptake in primocanes continued later into the fall. Waister and Wright (1989) found that post-harvest primocane growth in red raspberry could account for as much as 25% of the total dry weight at the end of the season. In the fall growth ceases and in the case of trailing blackberries, rooting may occur at the cane tip.

Red raspberry roots were shown to experience an initial loss in dry weight during budbreak of floricanes and primocane emergence (Fernandez and Pritts, 1993). Roots had a significant increase in dry weight gain during the period that coincided with the onset of fruiting, followed by another loss during peak harvest (Fernandez and Pritts, 1993). Carbohydrate levels in roots were replenished by the end of the growing season. Fernandez and Pritts (1993, 1994, 1996) have found that raspberry roots are strong carbon sinks capable of maturing a crop of fruits when current photosynthates are inadequate.

Depending on the genotype, primary, secondary and tertiary buds may form at each primocane node; these generally do not break to produce fruiting laterals until the following season. Axillary buds of red raspberry do not usually break the first year. However, in 'Marion' and other blackberry cultivars these axillary buds on primocanes often break to produce branch canes.

Floricane growth and yield components

Fruit are usually produced on two-year-old canes called floricanes. Flower initiation takes place in late-summer through fall of the previous year in the axillary buds at the nodes of primocanes. In the spring, these buds break to produce fruiting laterals. The energy for initial growth of the laterals comes from reserves in the cane. Floricanes produce laterals early in the season, with dry matter and macroelement uptake nearly complete by mid-summer then senescence occurs with dry matter and nutrient loss in the form of leaves (Kowalenko, 1994). The laterals have three sections: a barren basal section, a middle with later developing flower buds, and a terminal with both fruit and flower buds (Dale and Topham, 1980). The number of fruit per lateral varies by genotype (Dale and Topham, 1980) and environmental factors (Jennings and McGregor, 1989). Flower initiation within the axillary buds occurs first in the apical section of the cane which terminates the differentiation of lateral nodes. Consequently, lateral length decreases from the base to tip of the cane (Dale, 1979). Flowering and fruiting generally occur first in terminal sections of the cane (Dale and Topham, 1980). In raspberry, the fruitfulness of the laterals decreases from the apical to the basal part of the cane (Crandall et al., 1974; Crandall et al., 1980). However, 'Marion' has been found to be more productive in the basal rather than the terminal section of cane (Bell et al., 1995a). In red raspberry, developing fruit obtain photosynthates produced by the floricane leaves (Whitney, 1982).

The final yield of a caneberry plant can be expressed as the product of yield per cane multiplied by the number of canes per unit area. In red raspberry, the minimum cane density required for maximum yield has been obtained with about 15 canes • m^{-1} in North America and Tasmania (Buszard, 1986; Clark, 1984; Crandall, 1980; Fejer, 1979; Orkney and Martin, 1980) while in Europe the optimal number has been found to be 8-12 • m^{-1} (Dale, 1989; Wood, 1960). With increasing cane density, there is usually a decrease in yield per cane as the canes have fewer laterals, fewer fruit per lateral and smaller fruit (Crandall et al., 1974). Optimal cane densities for the trailing blackberries has yet to be determined.

Individual cane can be broken into a number of yield components including: cane diameter, cane length, number of nodes per cane, number of laterals per cane, lateral length, number of fruit per lateral, and fruit weight. Increased cane diameter has been associated with increased yield in red raspberry (Lott, 1931). However, Crandall et al. (1974) found there was little effect of cane diameter because thicker canes had more berries per lateral but fewer laterals than thinner canes. Cane length has generally been found to a be a positive yield component in red raspberry (Darrow and Waldo, 1933; Strik and Cahn, 1996).

A strong positive correlation has been found between the number of nodes and the number of fruitful laterals per cane and yield (Dale and Daubeny, 1985; Hoover et al, 1988; Nehrbas and Pritts, 1988). Compensation for low budbreak can occur through increases in fruit weight (Gundersheim and Pritts, 1991; Kollanyi, 1988) and number of fruit per lateral (Waister and Barritt, 1980). The number of fruit per lateral is often determined by cane diameter and percent budbreak. In red raspberry, Waister and Barritt (1980) found 'Meeker' produced 68% of a normal crop with 50% of the buds removed. In another study, Moore (1994) found no significant difference in yield between disbudded plants (all primary buds removed) and plants with buds. Braun and Garth (1984) found no effect on productivity of the remaining buds with alternate bud removal, however, they found an increase in the productivity of lower fruitful nodes with removal of buds on the upper half of the cane in red raspberry. Fernandez and Pritts (1996) suggest that these plastic responses are due to the capacity of red raspberry to store large amounts of carbohydrates in the roots and to shift carbon partitioning to various plant parts depending on the current situation. In research on 'Marion', primary bud removal had no significant effect on yield per cane indicating 'Marion' has the capacity to compensate for primary bud damage (Bell et al., 1995a; Strik et al., 1996). August training in 'Marion' has also been found to result in a significantly higher percent budbreak and a greater number of fruit per lateral than February training (Bell et al., 1995a).

Fruit weight is usually positively correlated with yield (Dale and Daubeny, 1985; Freeman et al., 1989b; Hoover et al., 1988) but negatively correlated with bud number per cane (Gundersheim and Pritts, 1991). Fruit weight is determined by drupelet number and weight (Waister and Wright, 1989).

Branch canes are an important yield component in 'Marion' (Bell et al., 1995a), purple raspberry (Gundersheim and Pritts, 1991) and in erect blackberry cultivars (Moore and Skirvin, 1990). 'Royalty' purple raspberry plants with branch canes were estimated to produce 27% more fruit than those without branches at a given density (Gundersheim and Pritts, 1991). 'Marion' has numerous branch canes with the longest and most productive branch canes in the basal section (Bell et al., 1995a). In 'Marion', Sheets and Kangas (1972) found 57% of axillary buds on branch canes produced fruitful laterals.

Primocane suppression

One method of production used to increase yield in caneberries is primocane suppression or vigor control. Research on red raspberry found annual removal of the first flush of primocanes increased fruit yield by an average of 38% over a five year period (Lawson and Wiseman, 1983). The increased yield from primocane suppression came from increased fruit number, fruit weight, and number of cropping nodes per cane (Crandall et al., 1980; Dale, 1989; Lawson and Wiseman, 1983; Nehrbas and Pritts, 1988). In the first year of cane vigor control, increased yield was mainly a result of a higher number of berries per node (Dale, 1989). In other years, greater yield with primocane suppression was a result of more cropping nodes on shorter canes and an increased fruit number (Dale, 1989, Lawson and Wiseman, 1977). Increases in fruit number with primocane suppression occurred on longer lower laterals (Dale, 1977; Crandall et al. 1980; Nehrbas and Pritts, 1988). Bell et al. (1995a) studied the effect of date of primocane suppression on yield components of 'Marion' and found the highest yield per plant the following season on April-suppressed plants due to increased cane number and total main cane length.

Alternate-Year (AY) and Every-Year (EY) production

In a typical 'Marion' production system, plants are generally spaced at 2.4 m in rows 3.1 m apart. The canes are trained by weaving them around two wires (at 1.2 and 1.5 m high) in bundles containing several canes. In Oregon, 85% of the trailing blackberry hectarage is machine harvested. Canes are either summer- or winter -trained. Summer-training in August generally increases yield (Bell et al., 1995a; Bullock, 1961; Sheets et al., 1972) although summer-trained plants may be more susceptible to cold injury (Bell et al., 1992).

Trailing blackberries are either grown in every year (EY) or alternate year (AY) production systems. In the EY system, floricanes are trained onto the trellis while the primocanes grow along the ground. After fruit harvest, the old floricanes are removed and the current season's primocanes are trained in either August or February to produce the next season's crop. In this system, both vegetative and reproductive canes are present on the plant during the growing season and fruit are harvested every year.

In the AY system, all canes are removed in October so only new primocanes grow the following season (the "off year"). These primocanes are trained to the trellis throughout the summer and fruit the next year (the "on year"). After harvest, all canes are removed again. Consequently, fruit are harvested every other year. The AY system yields approximately 85% that of the EY system over a two year period (Sheets et al, 1975). In Oregon an average of 20 to 50% of the hectarage is grown in the AY system each year (Strik, 1992). As compared to EY production, the biennial or AY system also has the advantage of reducing labor costs, lowering fertilizer and pesticide inputs, eliminating damage to the primocanes during machine harvest, and providing a less favorable environment for disease (Sheets, 1987). Sheets (1987) also observed that AY plants appear to have greater cold hardiness than plants grown in EY production.

The most common system used for caneberries is EY production where fruit is harvested every year. In this system, there is competition for light, nutrients, and possibly assimilates because primocanes and floricanes are growing concurrently (Crandall et al. 1980; Dale, 1989; Nehrbas and Pritts, 1988; Vasilakakis and Dana, 1978; Williamson et al 1979; Wright and Waister, 1982a,b). Problems have been associated with EY production because primocanes shade the floricanes causing reduced yield (Wright and Waister, 1984) as well as interfering with machine harvest (Clark, 1984). Cormack and Waister (1976) reported that the catching devices on machine harvesters damaged the primocanes resulting in yield losses from physical damage and increased pathogen infections in the wounds.

The AY system is more extreme having a complete separation of the vegetative and reproductive phases by producing fruit in alternate years. Clark (1984) found the biennial system in red raspberry yielded 75% of the 2-year hand -harvested yield produced in the annual system. In the biennial system, greater yields came from increased primocane emergence with each having shorter internodes during the vegetative stage and increased fruit number and weight during the fruiting phase (Dale, 1989; Waister et al. 1980; Waister et al. 1977; Wright and Waister 1982b). Floricanes grown without competition from primocanes had greater productivity per node and larger fruit weight (Wright and Waister, 1982b). One problem found with AY production in red raspberry is a general decline in plant vigor over several years (Dalman, 1989; Freeman et al., 1989a). Sheets et al. (1972) also found an increase in primocane number during the "off year" in the alternate year system with 'Marion' and several other caneberry cultivars. One advantage of alternate year production in trailing blackberries is that canes in the "off year" can be trained by mid to late July which stimulates profuse lateral development (Sheets and Kangas, 1970). Early training may also be an advantage in AY production of 'Marion' because Bell et al. (1995a) found August-trained plants had longer main canes, a higher percent bud break, and a higher number of fruit per lateral compared to February-trained plants.

In both primocane suppression and AY production, increased yield is attributed to reduced competition for storage products in the spring and to changes in the light climate (Lawson and Wiseman, 1983; Waister and Wright, 1989). Crandall et al. (1974) related the number of flowers and fruit set to assimilate supply. Wright and Waister (1984) and

Nehrbas and Pritts (1988) found improved light regimes with primocane suppression and in AY production systems. The number of fruit per unit leaf area and per lateral node increased with increasing light exposure (Braun et al., 1989). Primocane growth caused most of the changes in light exposure and volume within the canopy (Braun et al., 1989). In red raspberry self-shading has been found to cause reduced fruit production on the basal cane section in EY production while in the AY system, fruit is evenly distributed along the cane (Wright and Waister, 1984). Although yield can be improved in the "on" year with the AY system for red raspberry it has not been adopted because of reduced

yield over a two year time period caused by high cane density and smaller fruit (Nehrbas and Pritts, 1988). Sullivan and Evans (1992) found an increase in yield per cane and a decrease in diameter over time with an AY system.

Cold hardiness

Although there is considerable literature on dormancy and cold hardiness of raspberry, little research is available on other *Rubus* species. Although there has been some research on erect blackberry cultivars, these are quite different from the trailing blackberries grown in the Pacific Northwest and consequently, the results may not be directly applicable. However, work with red raspberry and Eastern blackberry cultivars can provide insight into the cold hardiness of 'Marion' as the physiological processes are likely to be similar for *Rubus.*

The onset of dormancy is triggered by decreasing temperatures and shortening days in red raspberry (Brierley and Landon, 1946; Jennings, 1988; Mage, 1975). Dormancy is expressed by shoot elongation cessation and reduced water content of canes (Jennings et al., 1972: Jennings and Cormack, 1969). *Rubus* species then go through a rest period where they must be exposed to a given number of hours in a specific temperature range before growth can resume. The rest requirements are generally completed in mid -December in most raspberry producing regions (Brierley and Landon, 1946; Jennings et al., 1972). After rest, mild spells in winter can cause plants to lose hardiness making them more susceptible to injury by subsequent cold weather (Bailey, 1948; Brierley and Landon, 1946; Van Adrichem, 1970).

In 'Marion', the buds are the most susceptible to freeze injury (Bell et al., 1992) while cane tissue is most susceptible to injury in red raspberry (Brierley and Landon, 1946; Kraut et al., 1986). This is primarily due to phloem and cambial tissue damage. Phloem damage to lateral buds can result in laterals emerging but later collapsing under the demands of flowering and fruiting (Moore and Brown, 1971). The relative hardiness of buds and xylem parenchyma compared to phloem and cambial tissues is due to the ability of these tissues to supercool (Warmund and George, 1989: Warmund et al., 1988). Buds on terminal sections of red raspberry break rest earlier than buds on other sections of cane and are consequently more susceptible to midwinter or early spring injury (Jennings et al., 1972; Mage, 1975). Although severe conditions can kill entire primocanes, more typical damage on 'Marion' is lower and erratic budbreak along the cane as well as stunted fruiting lateral growth (Bell et al., 1995b).

Chapter 2

Effect of floricane number in 'Marion' trailing blackberry. I. Primocane growth and cold hardiness

Abstract

In spring of 1993 and 1994, mature 'Marion' (*Rubus* sp.) were pruned to 0, 4, 8, and 12 floricanes per plant. An additional treatment of 0 floricanes with early (30 cm) primocane topping/pruning was included. Primocane growth was measured from emergence in April until growth cessation at the end of October. In January 1994 and 1995, cold hardiness was evaluated by controlled freezing. In 1993, plants without floricanes had a greater number of primocanes with increased total length and a trend towards greater branch number and length at the end of the season. In 1993, internode length was significantly reduced for plants with 0 or 4 floricanes compared to plants with 8 or 12 canes. In 1994, there were no significant differences in primocane growth. In all treatments, the absolute growth rate (AGR) of primocanes occurred in flushes with plants having no floricanes having 5 peaks of growth that were significantly greater than those in plants with floricanes in 1993. In 1994, there was no treatment effect on AGR over the season and the peaks were not as distinct. However, plants without floricanes still had a greater primocane growth rate than plants with floricanes on six dates before fruit harvest. When comparing primocane growth at three phenological stages in 1993, plants with no floricanes had a significantly higher total growth per day during fruit production and from

harvest to growth cessation. In 1994, plants with no floricanes had the highest rate of growth before bloom and a trend towards greater growth during fruit production. After fruit production, there were no differences in growth rate between the treatments in 1994. Plants with floricanes produced a second flush of primocanes while plants with no floricanes produced only one flush of primocanes. By the end of the season there was no significant difference in length of primocanes from the first flush and second flush. In 1993, primocane topping at 30 cm tended to decrease primocane number and total length. In 1994, there were no significant effects except that topping increased branch length. Plants without floricanes produced primocanes that were significantly more cold hardy (lower LT_{50}) in 1994 and 1995 than plants with floricanes. Although many of our results were similar to findings in red raspberry, the emergence of two flushes of primocanes without primocane suppression and absolute growth per day occurring in rapid flushes of growth throughout the season have not been previously reported.

Introduction

The Pacific Northwest is a major growing region for trailing blackberry cultivars produced for processing. The most important cultivar is 'Marion' which accounts for 50% of the hectarage in Oregon (Strik, 1992). Although 'Marion' is a vigorous plant with high fruit quality, its production has been unstable due to its sensitivity to winter cold injury and concomitant fluctuations in yield (Bell et al., 1992). Recent findings by Bell et al., (1995b) show improved cold hardiness in 'Marion' with late primocane suppression.

Two other systems currently used commercially for 'Marion' are the every year (EY) and alternate year (AY) production systems.

There is interest in studying ways to increase the cold hardiness of 'Marion' because winter injury resulting in crop loss is a major factor limiting 'Marion' production (Strik, 1992). 'Marion' is the least hardy blackberry cultivar grown commercially in Oregon. Winter injury has resulted in fluctuating prices and unstable markets as well as direct crop loss (Conroy, 1967). The most recent serious freeze was in 1990 when the 'Marion' crop was reduced by 70% (Bell et al., 1992). Cold injury is usually associated with movement of arctic air masses into the region which cause a rapid drop in temperature. In 'Marion', the buds are the most susceptible to freeze injury. Although severe conditions can kill entire primocanes, more typical damage is reduced and erratic budbreak along the cane as well as stunted fruiting lateral growth (Bell et al., 1992). Poor budbreak in general, is another major concern with 'Marion. Although sometimes poor budbreak is a result of cold injury, in other cases, the buds appear a healthy green but do not break.

'Marion' grown in the AY system has been observed in the field to have greater cold hardiness (Sheets, 1987). In AY production, 85% of the yield of the EY system is produced over a two year time period. AY production also has the added advantages of reduced labor, fertilizer and pesticide inputs, damage to the primocanes during machine harvest, and disease pressure (Sheets, 1987). An increase in primocanes during the "off year" in the alternate-year (AY) system was found in 'Marion' and other berry cultivars tested (Sheets et al., 1972). In 'Boysen', Nelson and Martin (1989) found plants grown in the AY system produced significantly higher yields, more canes, and smaller fruit than plants grown in the EY system. However, relatively little research has been done on the effect of altering the floricane number on primocane physiology and growth.

Many scientists have documented competition between primocanes and floricanes in studying annual and biennial production systems of red raspberry (Crandall et al. 1980; Nehrbas and Pritts, 1988; Vasilakakis and Dana, 1978; Williamson et al 1979; Wright and Waister, 1982 a, b). In annual production, the vegetative primocanes grow concurrently with the reproductive floricanes during fruit production. In red raspberry, primocanes shade the floricanes reducing fruitfulness (Wright and Waister, 1984) and interfere with harvest (Clark, 1984).

In the biennial system, only primocanes grow in the “off” year and fruit the following “on” year. This separates the vegetative and reproductive phases of growth and is consequently a good model for studying source/sink relationships. Research in red raspberry has shown that in the absence of floricanes more primocanes are produced with reduced internode length and cane height (Waister et al., 1977; Wright and Waister 1982a). Consequently, there was a higher yield the following season due to a greater number of primocanes and nodes per cane (Wright and Waister, 1982a). Waister et al. (1977) also found that when primocanes were removed during floricane growth and production there was an increase in bud fruitfulness and fruit weight. In AY production in red raspberry, yield increases were from greater yield per cane when cane density treatments were imposed (Clark, 1984). Clark (1984) found that the AY system yielded about 75% as much as the traditional every- year (EY) system over a two year time period. The increase in primocane number and reduction in internode length of primocanes in biennial production have been attributed to reduced competition for storage products in the spring (Crandall et al., 1974) and to improvements in the light environment (Lawson and Wiseman, 1983; Waister and Wright, 1989).

Primocanes of red raspberry have a three phase growth pattern with a linear increase up to peak first harvest, a leveling off during harvest, and another linear increase after harvest (Fernandez and Pritts, 1993). Whitney (1982) found carbohydrate levels in the primocanes were high early in the spring, dropped to low concentrations in July, then returned to higher levels again by the end of the season. Waister and Wright (1989) found that post-harvest primocane growth in red raspberry could account for as much as 25% of the total dry weight at the end of the season. Research on primocane growth in relationship to fruit production has not been studied in trailing blackberry cultivars such as 'Marion'.

Although research on biennial production has led to a greater understanding of the biology of red raspberry, different factors may play a role in the success of biennial production in trailing blackberries because they differ from red raspberry in growth habit and in the training system used. This is evidenced by the fact that biennial production is not a commercial practice in red raspberry but is in trailing blackberry. 'Marion' is more vigorous, has a trailing growth habit, numerous branch canes, and is more productive in the basal rather than the terminal cane section in contrast to raspberry (Bell et al., 1995a). Trailing blackberries, such as 'Marion', have a canopy where the floricanes are spatially separated from the primocanes in annual production because the floricanes are wrapped horizontally on trellis wires while the primocanes grow along the ground. This creates a different light microclimate than that found in red raspberry where vegetative and reproductive canes exist in the same vertical canopy.

'Marion' primocanes produce vigorous branch canes without pruning while red raspberry generally does not produce axillary branch canes. The branch canes in 'Marion' have been found to be an important yield component (Bell et al., 1995a). Branch cane development is important in other *Rubus* species such as erect blackberry (Moore and Skirvin, 1990) and purple raspberry (Gundersheim and Pritts, 1991). In these crops, primocanes are summer pruned/tipped to stimulate branching. However, the effect of primocane pruning on growth and yield of trailing blackberry has not been researched to date.

This research was undertaken to develop a better understanding of the physiology of vegetative and reproductive cane growth and carbohydrate partitioning in 'Marion' as affected by the reproductive component (number of floricanes). The specific objectives of this project were to determine the effect of floricane number and primocane pruning on primocane growth and subsequent cold hardiness. The effect of floricane number and primocane pruning on yield components in the same season, yield components in the following year, and dry weight partitioning are presented in Chapter 3.

Materials and Methods

A eight-year old planting of 'Marion' blackberry on a latourell loam soil at the North Willamette Research and Extension Center, Aurora, Ore. was used. Plants were spaced 2.4 m within rows spaced 3.1 m apart. The trellis consisted of two horizontal wires at 1.2 and 1.5 m. Weed management, irrigation, and fertilization followed standard commercial practice. No primocane suppression was done on any treatment plants. In 1993 and 1994, plants were pruned to establish treatments of 0, 4, 8, and 12 floricanes per plant. Excess canes on each plant were counted and removed at ground level. An additional treatment was included with zero floricanes and early primocane pruning or tipping at 30 cm. The plants used in 1993 had fruited in 1992 while plants used in 1994 did not fruit in 1993. Floricanes were trained to the trellis in February. The experimental design was completely randomized with five replicates of three plants per plot.

Primocane growth measurements. Primocane growth measurements were done on one plant in each replicate. The third primocane to emerge was labeled for individual cane measurements. The length, number of nodes, number of branch canes, and branch cane length were measured weekly in 1993 and weekly or biweekly in 1994 from April until November. On each date, the remaining canes on the plant were counted for number of main and branch canes, and measured for total main and branch cane length. In 1994, an additional cane from a second flush of growth was marked and measured independently.

Cold hardiness evaluation. In January 1994 and 1995, canes were randomly selected from treatment plants. Four node cane sections were then randomly selected after the extreme basal and apical cane sections were removed. The criterion used for selection was that each section had four healthy green buds. Five cane sections (totaling 20 buds) were selected for each temperature regime for each of the five treatments and five replications.

Cane sections were bundled in subsamples of five, wrapped in cheese cloth, misted with water and enclosed in aluminum foil to create freeze packs. Freeze packs were randomly assigned to five test temperatures of 4 (control), -5, -10, -15, -20 °C. In 1995, an additional temperature of -25 °C was added. The freezer packs were placed overnight in a programmable freezer (Forma Scientifica, Marietta, Ohio) at -2 °C and the following morning the temperature was lowered by 5 °C per hour. Temperature within freeze packs was monitored by thermocouples attached to a DAS 8 data acquisition and interface board. After the packs were removed at the designated temperature, they were placed in a 4 °C refrigerator to defrost. The following day, the basal end of each cane section was recut and placed in water to force budbreak at 25 °C.

After approximately two weeks, percent budbreak was determined. The buds were recorded as being dead, still green but no emerging lateral, or with an emerging lateral. Only buds that produced a lateral were used in calculating percent budbreak. The Spearman-Karber Method as described by Bittenbender and Howell (1974) was used to calculate the LT_{50} for each treatment.

Statistical Analysis. General trends in primocane growth were compared using repeated measures analysis (SAS Institute, 1988). Data for end of season primocane growth totals, dry weight partitioning, and cold hardiness were compared by analysis of variance to determine treatment differences. Means were compared using a Fisher's Protected LSD. Logarithmic transformation was used on primocane growth data to account for increasing variance throughout the season. Equations were fit to the log-transformed data using regression. Absolute growth rate (AGR) was calculated with the equation:

AGR =(growth 2- growth 1)/(date 2-date 1) =dL/dT

This is the change in growth (dL) in cm from measurement date 1 to date 2 divided by the number of days (dT). The primocane AGR was also calculated and compared with analysis of variance in three time periods: before bloom, during fruit production, and harvest to growth cessation. Relative growth rate (RGR) was not included because the relative amount of growth became small compared to the long canes already present.

Results

Primocane Growth. Although individual cane measurements were determined (Appendix 1 and 2), whole plant measurements are presented because they were less variable within a treatment. Years were compared using the end of the season primocane growth per plant data. There was a significant year effect on primocane number (P=.02), branch number (P=.0001), primocane length (P=.02), branch length (P=.0001), and total (main cane + branch canes) length (P=.0001). There was a year by floricane number interaction on total (main cane + branch canes) length (P=.04). Thus, years are presented separately.

Regression analysis indicated that the log of total (main + branch cane) primocane growth could be fit to a quadratic equation in both 1993 and 1994 (Table 2-1). Separate curves for main and branch primocane growth were fit to quadratic equations in 1993 (Table 2-2) and 1994 (data not shown). Although repeated measures analysis was done on log-transformed data, actual growth data are presented in figures to facilitate interpretation unless otherwise stated. Date as determined by repeated measures analysis had a significant effect on total primocane growth in 1993 (P=.0001) and 1994 (P=.0001)(Figure 2-1 and 2-2). Date was also significant for primocane (P=.0001) and branch (P=.0001) growth in 1993 (Figure 2-3 and 2-4). Floricane number had a significant effect on the log of primocane (P=.02), branch (P=.0008) and total (primocane + branch) growth (p=.005) in 1993. There was a trend for treatment differences in total (primocane + branch) growth in 1994 (P=.08) There were no date by treatment interactions for total primocane growth per plant in 1993 or 1994. There was a significant date by treatment interaction for branch growth in 1993 (P=.0001) (Fig. 2-4). Primocane and branch cane data for 1994 had similar trends and thus are not presented (see appendix).

In 1993, plants without floricanes produced a greater number of primocanes with a greater total length and a trend towards greater branch number and length at the end of the season than plants with floricanes (Table 2-3). However, no linear relationship (by

Table 2-1. Equations for logarithmic transformed data for total (main + branch cane) primocane growth in 1993 and 1994.

Treatment Number of floricanes	intercept	x	x^2	r^2
1993				
0	-3.58	.098	$-2.0X10^{-4}$	.97
4	-2.80	.088	$-1.6X10^{-4}$	.97
8	-3.09	.089	$-1.6X10^{-4}$	.94
12	-2.57	.834	$-1.5X10^{-4}$	.96
1994				
0	-3.64	.10	$-1.9X10^{-4}$	.96
4	-4.12	.01	$-1.8X10^{-4}$	.98
8	-3.97	.01	$-1.7X10^{-4}$	.98
12	-3.84	.09	$-1.6X10^{-4}$	.99

Table 2-2. Equations for logarithmic transformed data for main and branch primocane growth in 1993.

Treatment Number of floricanes	intercept	x	x^2	r^2
primocane growth				
0	-3.16	.094	$-1.8X10^{-4}$	.95
4	-2.09	.082	$-1.5X10^{-4}$	.92
8	-3.03	.090	$-1.7X10^{-4}$	.94
12	-2.47	.084	$-1.6X10^{-4}$	.94
branch growth				
0	-13.16	.16	$-3.0X10^{-4}$	.93
4	-17.33	.19	$-3.0X10^{-4}$	.88
8	-12.31	.01	$-2.0X10^{-4}$	.81
12	-14.45	.14	$-2.0X10^{-4}$	.89

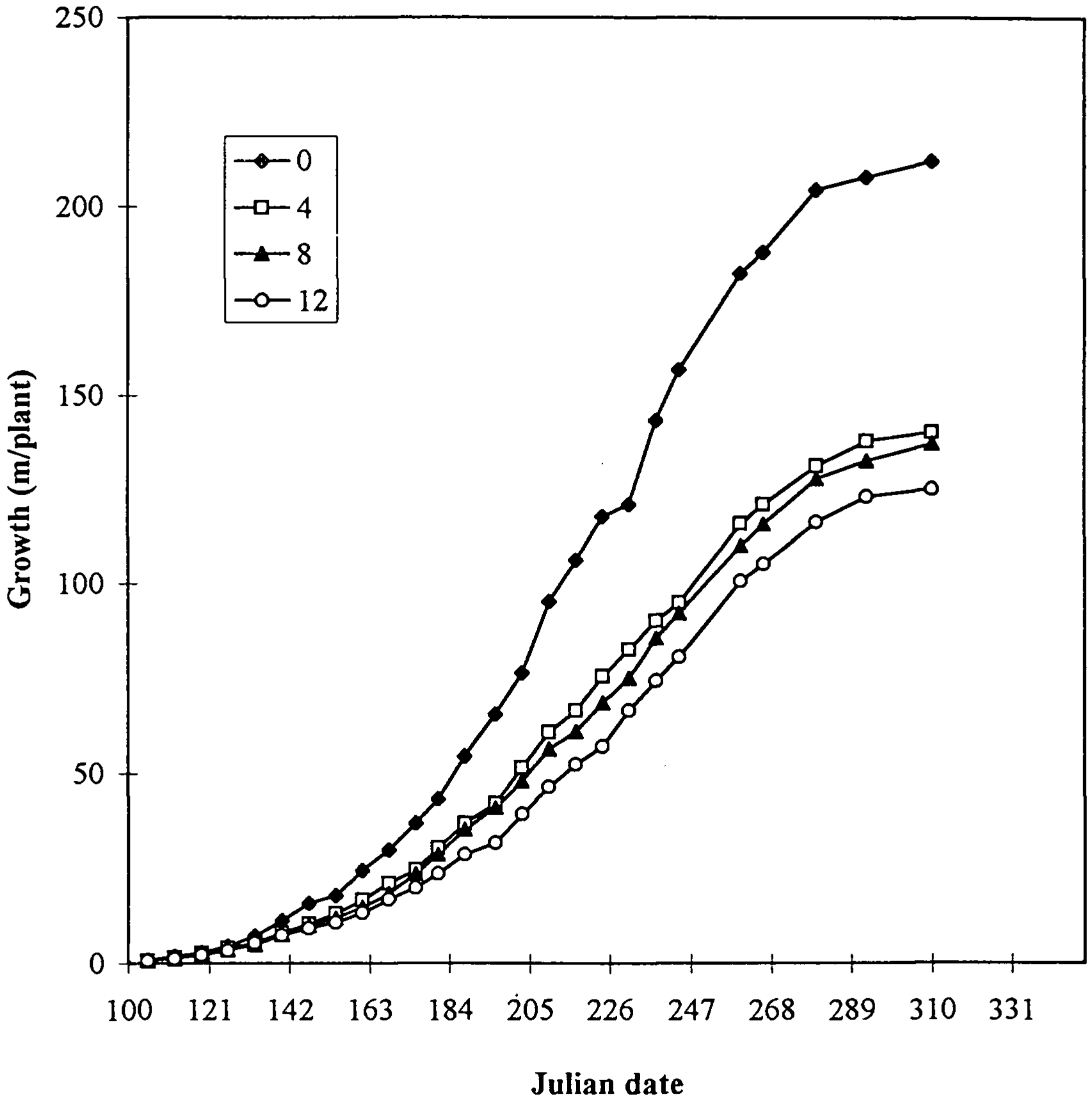


Figure 2-1. Effect of floricane number on total (main + branch canes) primocane growth per plant in 1993.

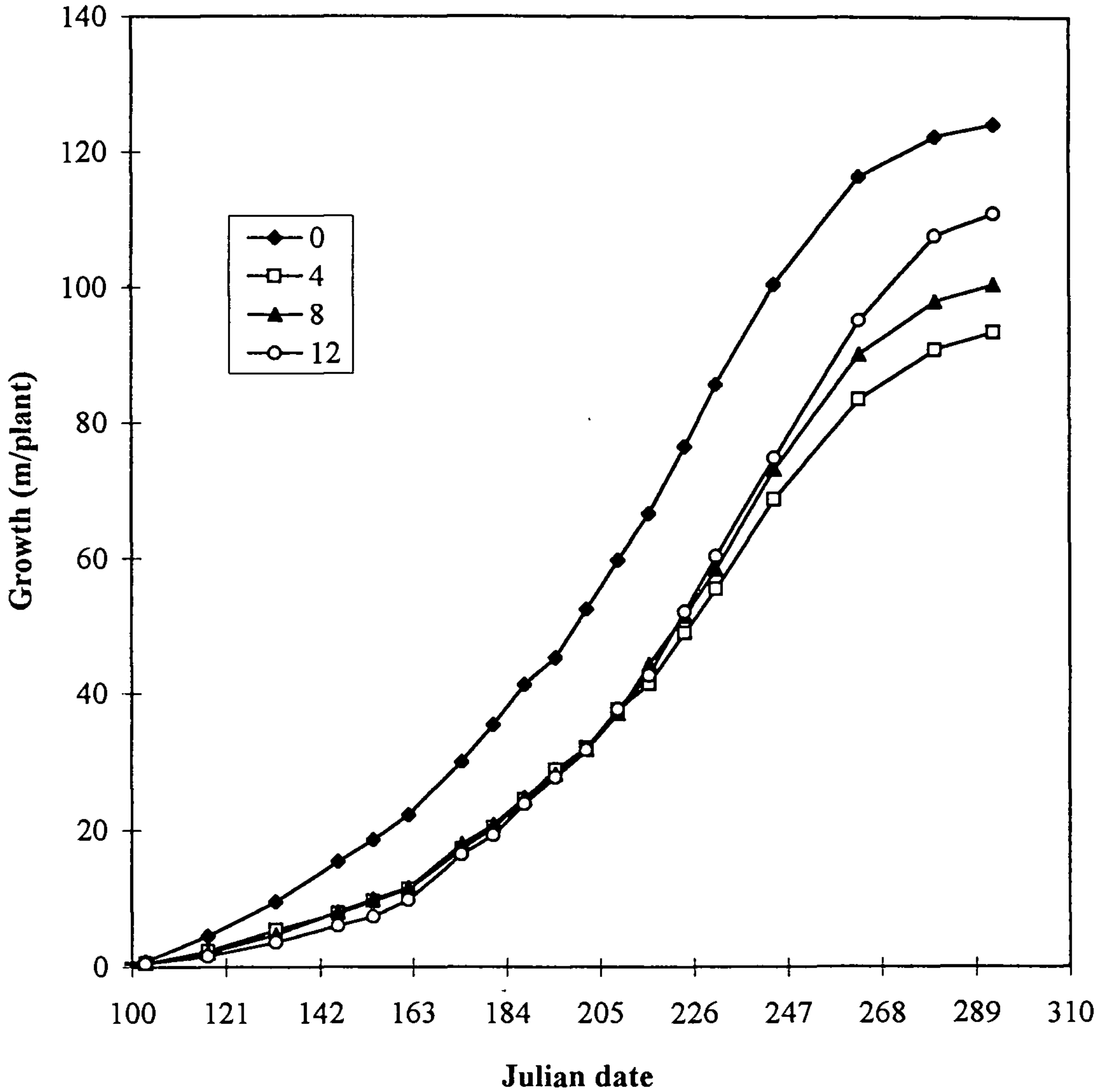


Figure 2-2. Effect of floricane number on total (main + branch canes) primocane growth per plant in 1994.

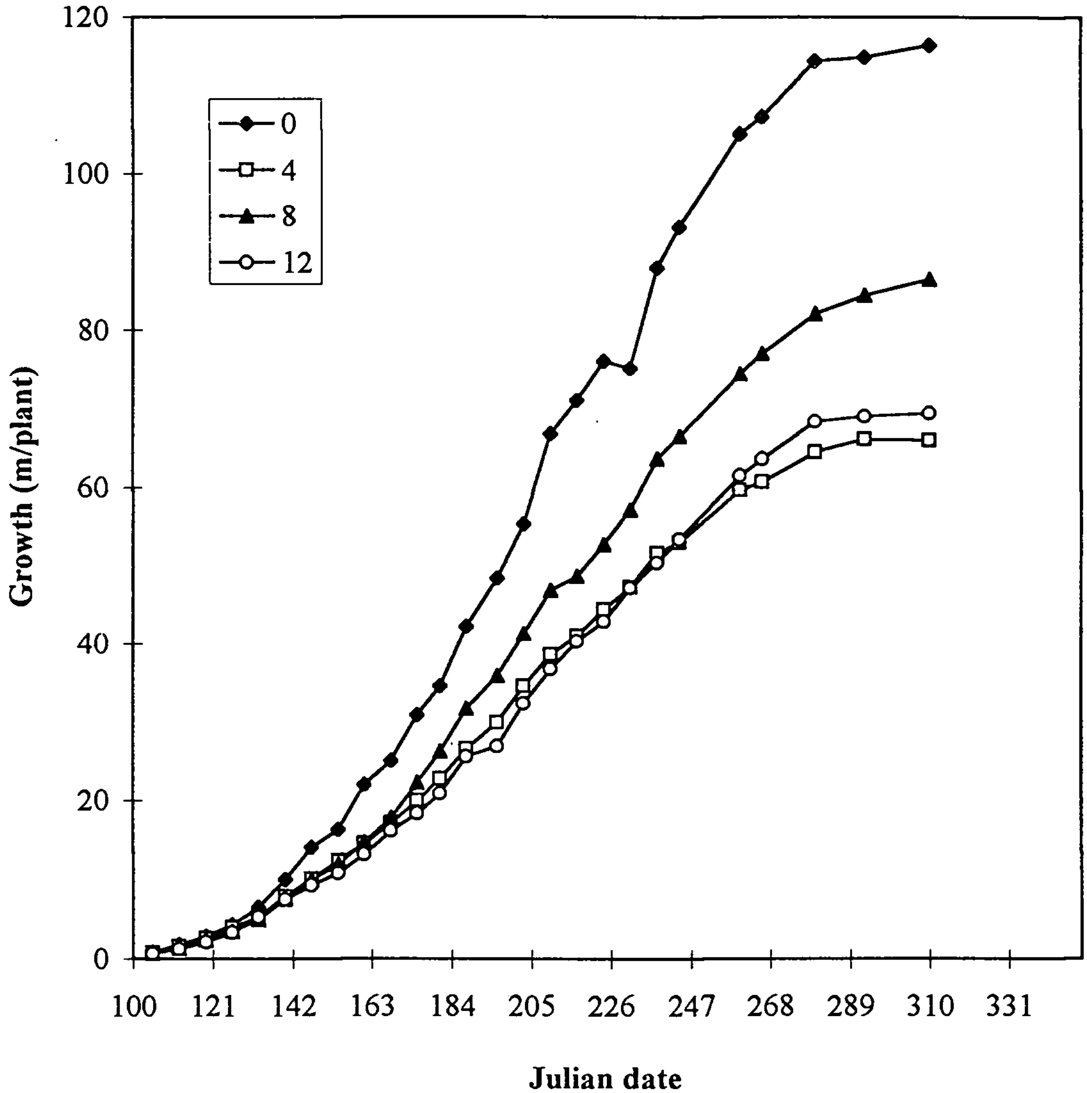


Figure 2-3. Effect of floricane number on primocane growth per plant in 1993.

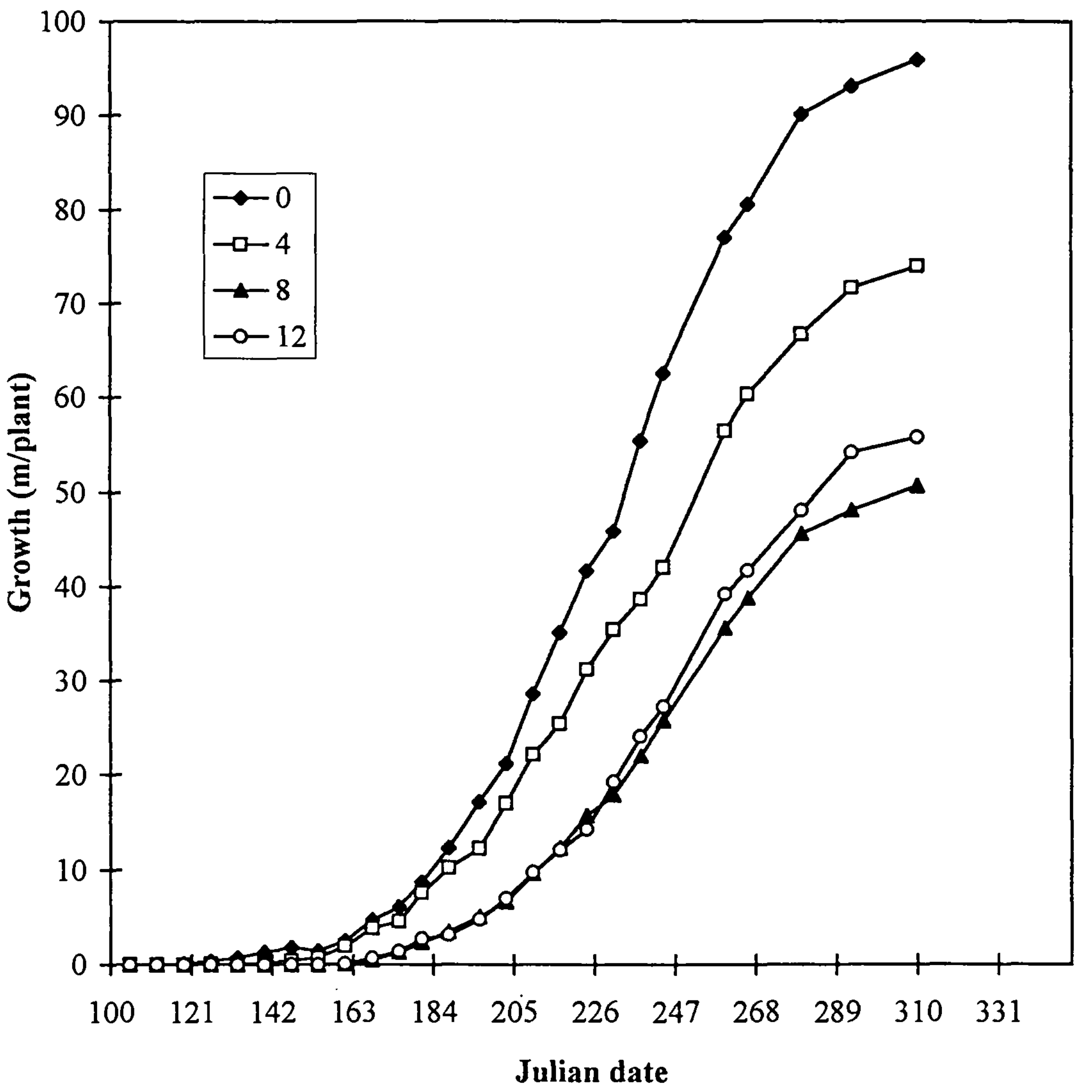


Figure 2-4. Effect of floricane number on primocane branch growth per plant in 1993.

Table 2-3. Effect of floricane number per plant on end of season total primocane growth.

No. of floricanes	No. of primocanes	Internode length (mm)	Main cane length/plant (m)	No. of branch canes	Branch cane length (m)	Total primocane length (m)
1993						
0	20.8	6.22	116.41	39.0	95.96	212.37
4	13.0	6.31	65.90	31.4	74.13	140.03
8	15.4	7.00	86.47	26.8	50.65	137.12
12	12.4	6.95	69.35	27.0	55.76	125.12
LSD[z]	5.38	.43	24.16	10.77	23.96	26.60
Significance[y]	*	**	**	NS	**	**
1994						
0	16.2	6.35	84.42	20.0	39.81	124.23
4	10.8	6.57	57.94	18.0	35.31	93.25
8	13.0	7.72	64.84	20.0	35.53	100.37
12	14.0	6.62	71.75	18.6	39.18	110.93
LSD[z]	5.69	1.4	33.23	9.48	25.32	29.10
Significance[y]	NS	NS	NS	NS	NS	NS

[z]Mean separation by Fisher's Protected LSD.
[y]NS, *, ** Nonsignificant or significant at $P<0.05$ or <0.01, respectively.

regression analysis) was found for floricane number on any growth component. There were no significant differences in primocane and branch number and length between plants with 4, 8, or 12 floricanes. In 1993, internode length was significantly reduced in plants with 0 or 4 floricanes compared to plants with 8 or 12 floricanes. There were no significant end of season treatment effects on primocane growth in 1994 (Table 2-3).

Absolute growth rate. There was a significant date (P=.0001) and date by treatment interaction (P=.0001) for the AGR of total primocane growth in 1993 (Figure 2-5), while in 1994 there was only a significant date effect (P=.0001) (Figure 2-6).
In all treatments, primocane growth occurred in flushes with plants having from 5-7 peak growth periods. Plants no floricanes having 5 peaks that were significantly greater than those plants with floricanes in 1993. In 1994, there was no treatment effect on AGR over the season and the peaks were not as distinct (Figure 2-6). However, plants without floricanes had a greater primocane growth rate than plants with floricanes on six dates before fruit harvest (Figure 2-6).

When comparing primocane growth at three phenological stages in 1993, plants with no floricanes had significantly higher primocane growth per day from bloom to harvest and from harvest to growth cessation for total (primocane + branch) growth per day (P=.0001) (Figure 2-7). In 1993, analysis of variance indicated a significant time period effect (P=.0001) and an interaction between time period and floricane number (P=.0002) (Figure 2-7). In 1994, plants with no floricanes had the highest rate of primocane growth before bloom (P=.006) and a trend towards greater growth during fruit

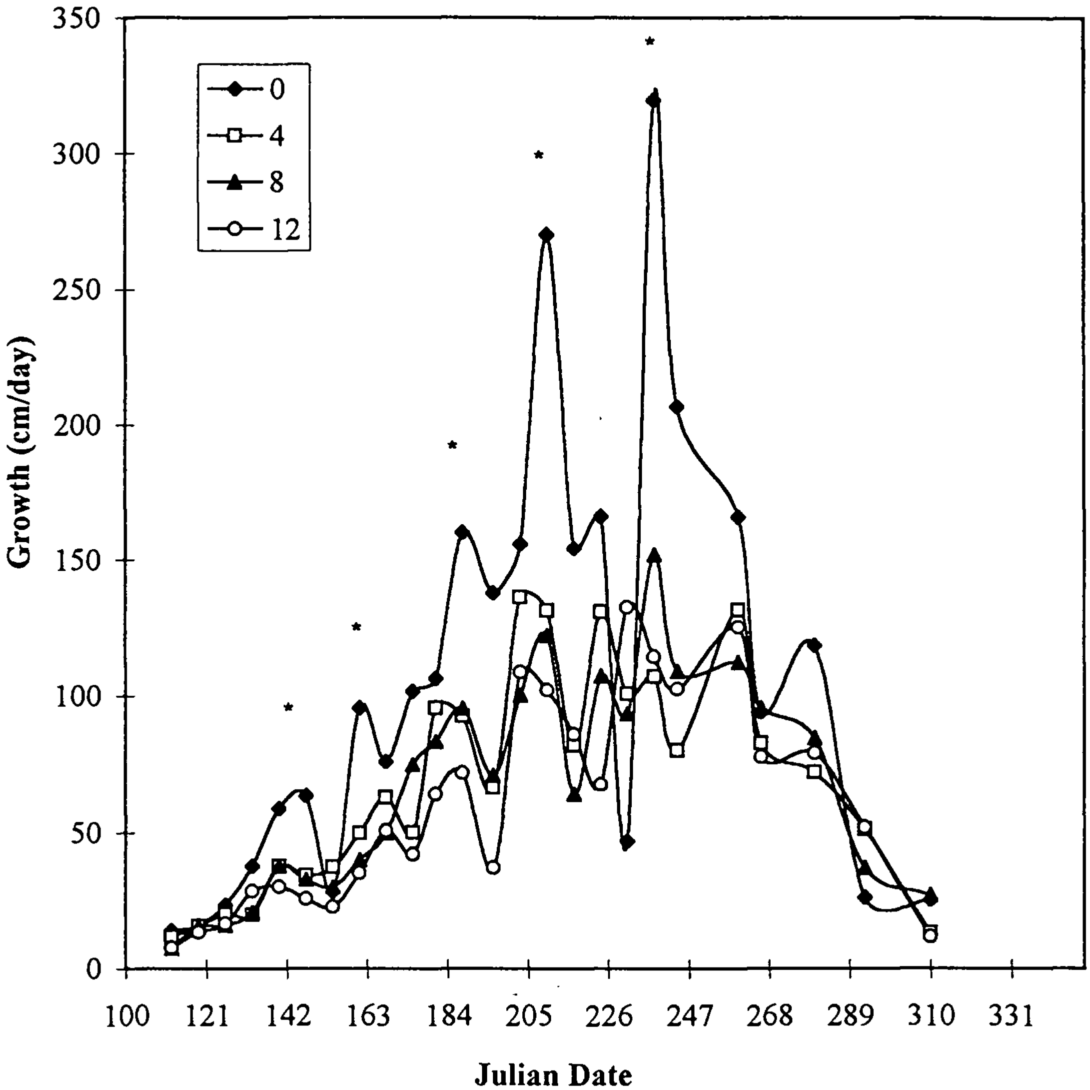


Figure 2-5. Effect of floricane number on absolute growth rate(AGR) of primocanes per plant in 1993. Stars denote significant treatment effects at that date (P<0.05).

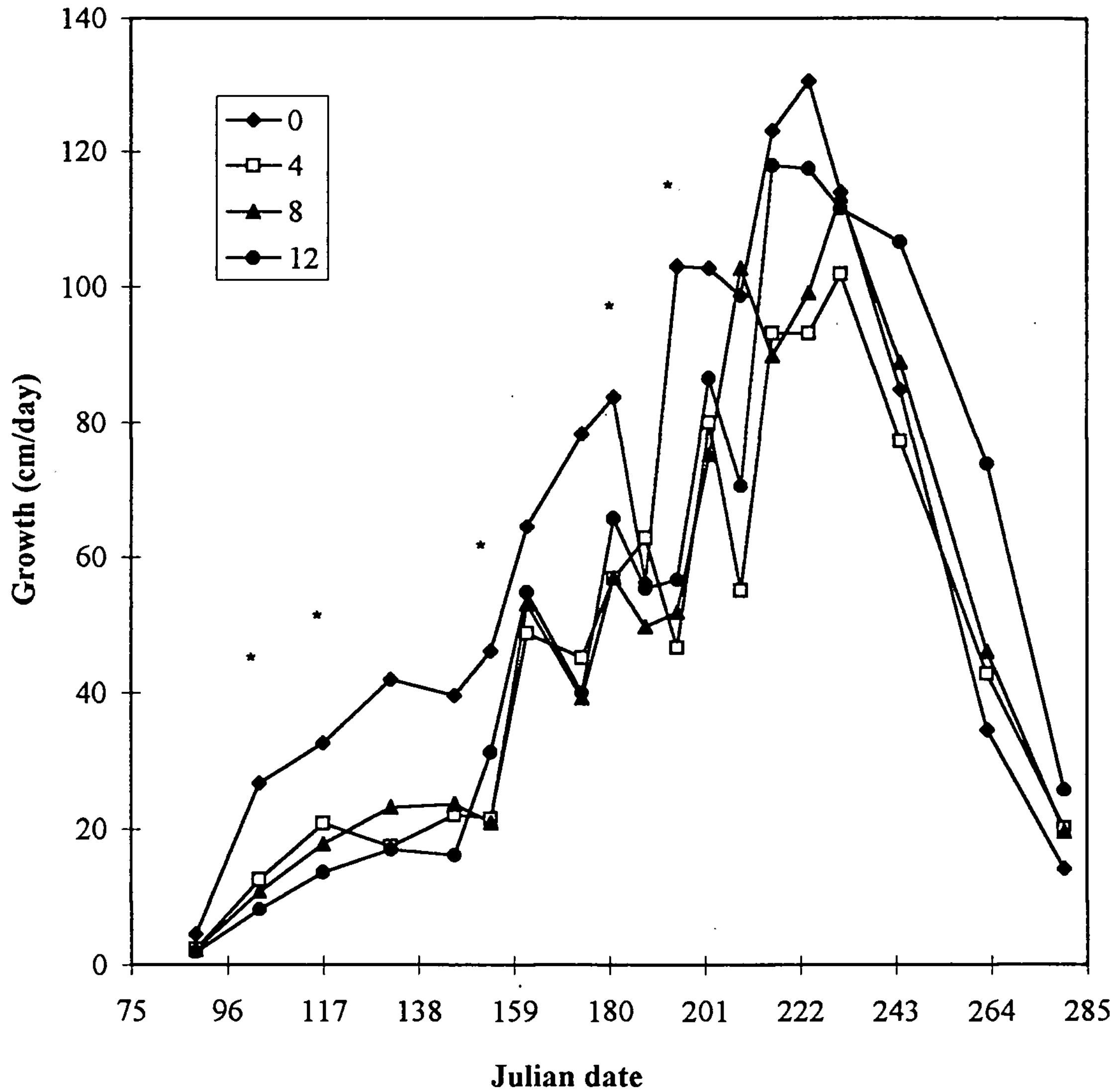


Figure 2-6. Effect of floricane number on absolute growth rate (AGR) of primocanes per plant in 1994. Stars denote significant treatment effects at that date (P<0.05).

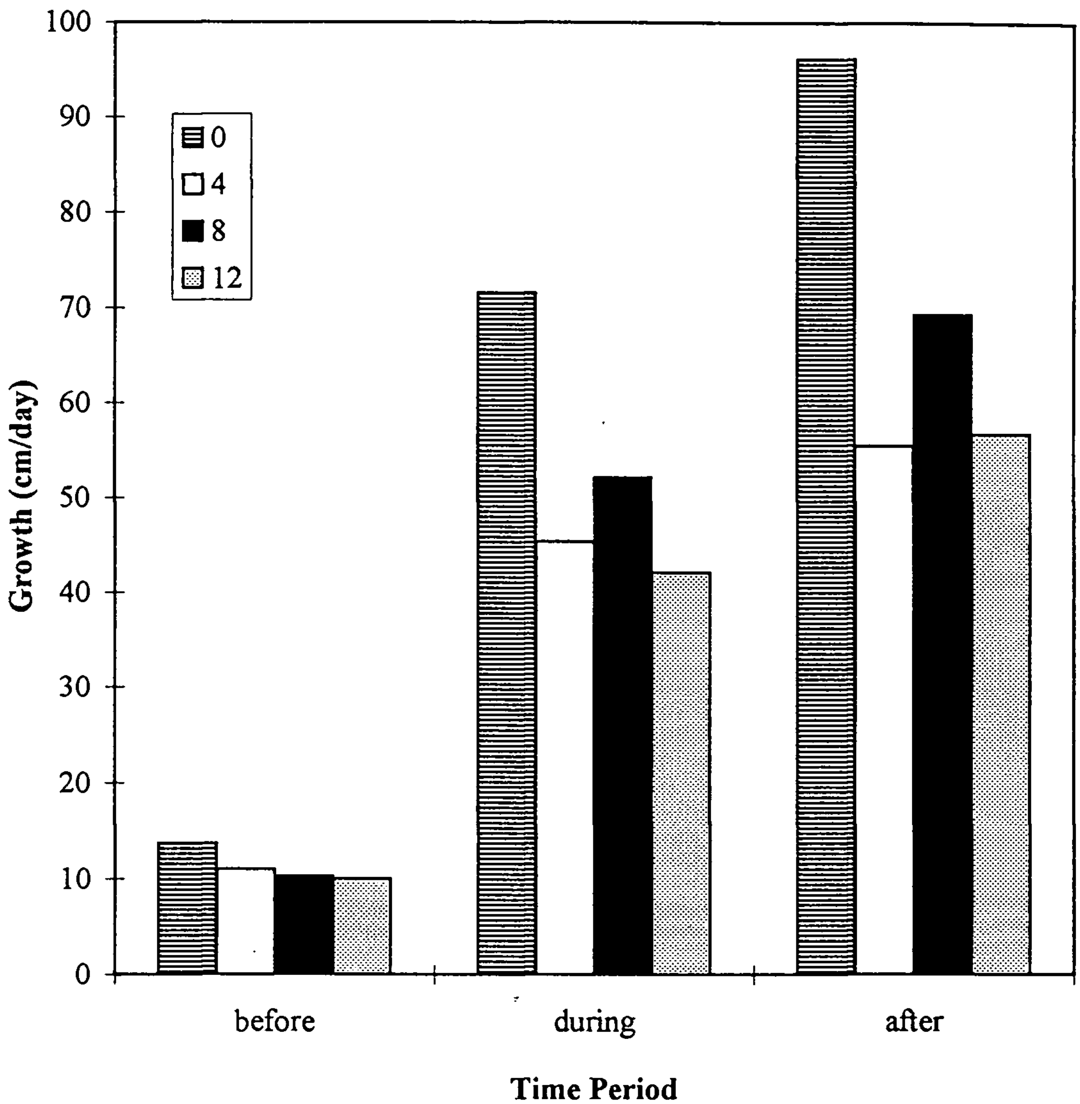


Figure 2-7. Effect of floricane number on absolute growth rate (AGR) of primocanes per plant during three time periods ("before" bloom, bloom to the end of harvest= "during", and end of harvest to growth cessation= "after") in 1993.

production (P=.07) (Figure 2-8). After fruit production, there were no differences in growth rate among treatments (Figure 2-8). In 1994, there was a significant time period effect on primocane growth rate (P=.0001).

Comparison of the first and second flush of primocane growth. Plants with floricanes produced a second flush of primocanes while plants with no floricanes produced only one flush of primocanes. Primocane length (averaged for 4, 8, and 12 floricane plants, as there were no significant differences among the treatments) of the first flush was significantly different from the second flush at all dates during the season except for the final end of season measurement date (Figure 2-9).

Primocane Pruning. End of season results for the primocane pruning experiment in 1993 showed trends for a decrease in primocane number (P=.07) and total length (P=.06) with tipping at 30 cm. In 1994, there were no significant effects except for branch length (Table 2-4).

Cold Hardiness Evaluation. There was a significant year effect on cold hardiness and a year by floricane number interaction. All treatments had greater hardiness in 1995 than in 1994 (Figure 2-10). Plants without floricanes produced primocanes that were significantly more cold hardy (lower LT_{50}) in 1994 and 1995 (Figure 2-10). However, there was no linear relationship (regression analysis) between LT_{50} and the number of floricanes per plant because of the similarity of primocane hardiness on plants that had 4, 8, or 12 floricanes.

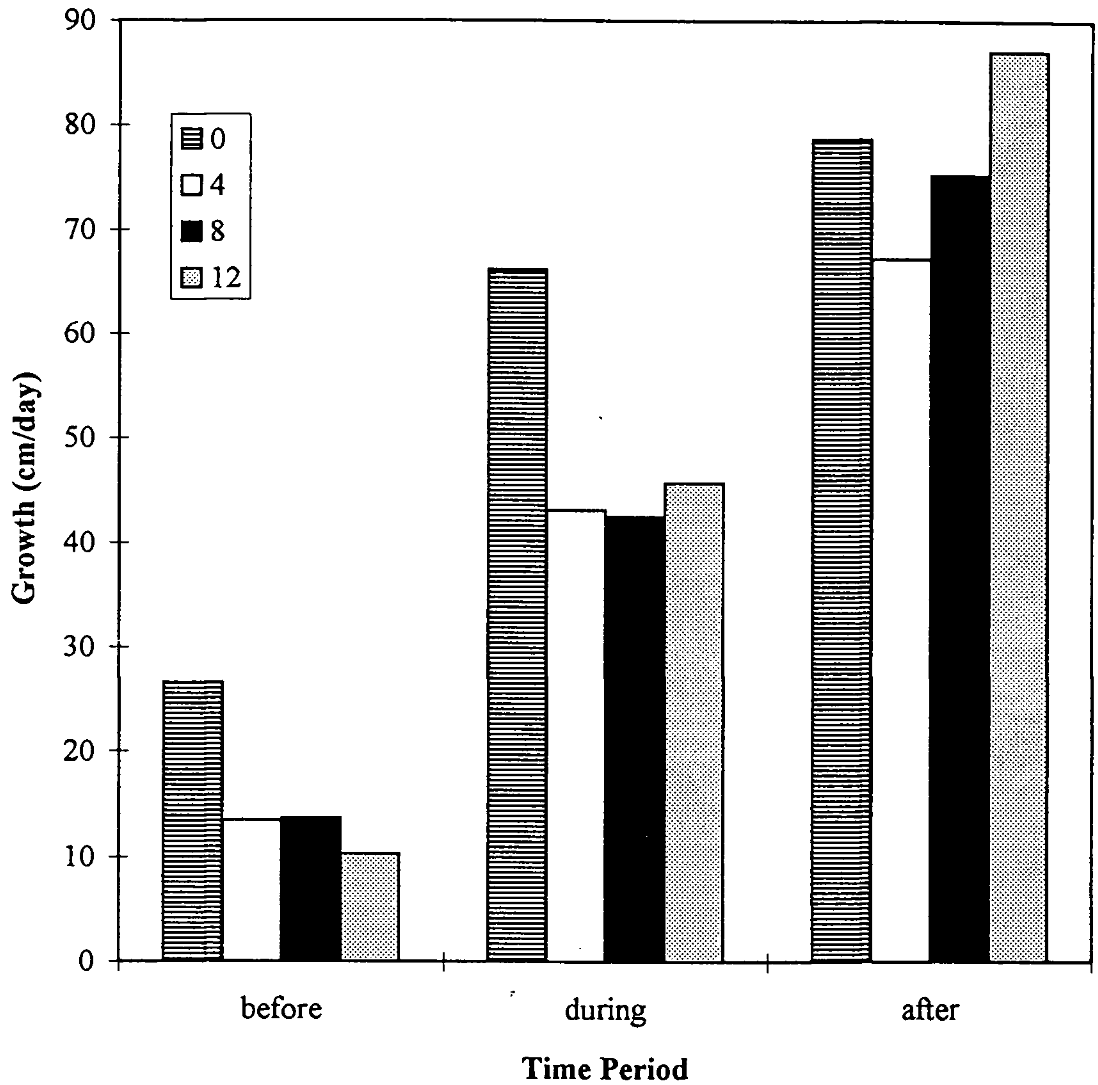


Figure 2-8. Effect of floricane number on absolute growth rate (AGR) of primocanes per plant during three time periods("before" bloom, bloom to the end of harvest= "during", and end of harvest to growth cessation= "after") in 1994.

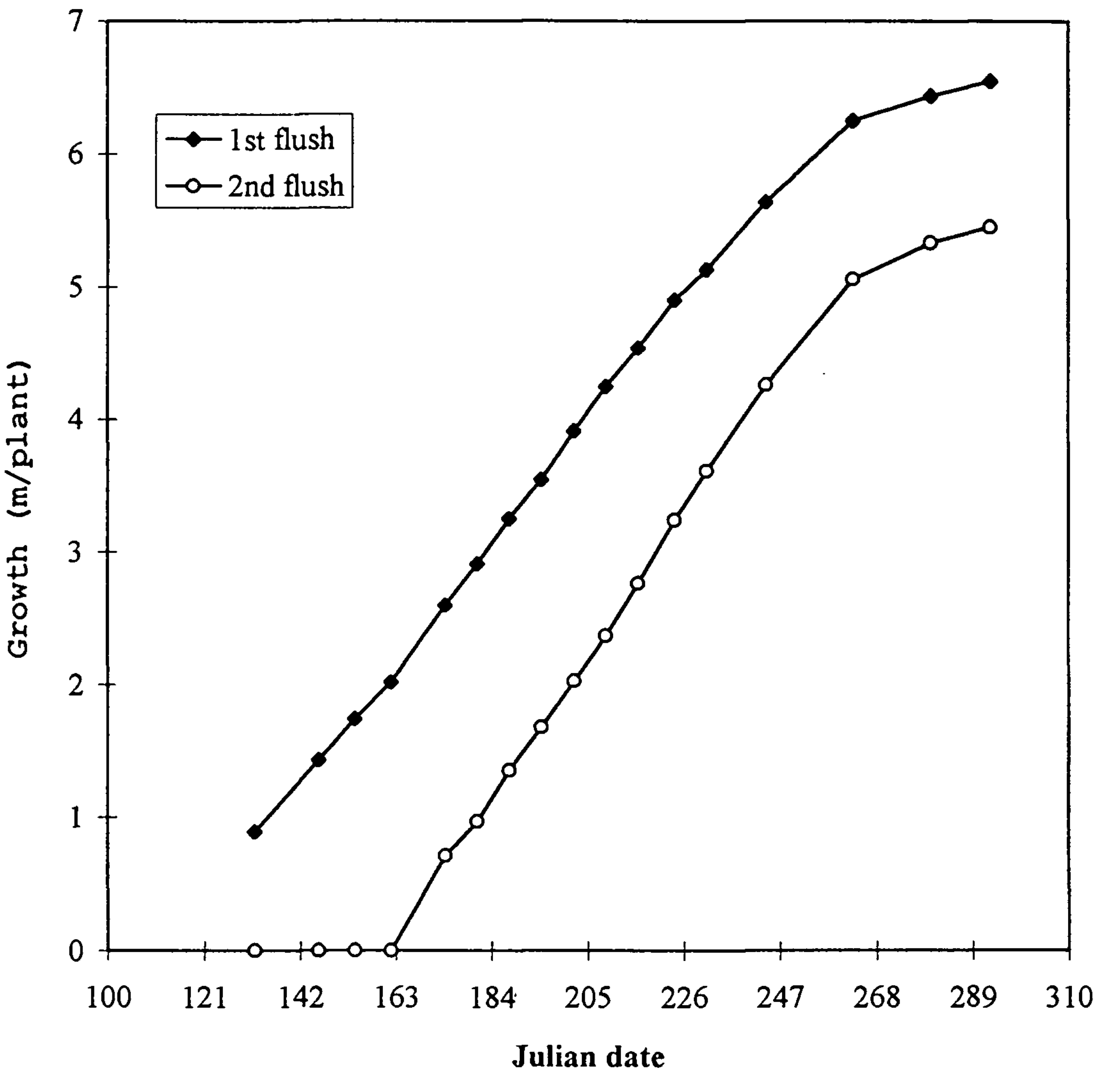


Figure 2-9. Growth of the first and second flush of individual primocanes averaged for the 4, 8, and 12 floricane treatments (floricane treatments were not significantly different) in 1994.

Table 2-4. Effect of primocane pruning (tipping at 30 cm) on subsequent primocane growth

Treatment	No. of Primocanes/ plant	Internode length (mm)	Main cane length/ plant (m)	No. of branches/ plant	Branch length/ plant (m)	Total primocane length/plant (m)
1993						
Pruned	13.8	6.13	60.02	37.0	102.96	176.99
Unpruned	19.8	6.22	109.20	37.4	90.65	212.37
Significance[z]	NS	NS	**	NS	NS	NS
1994						
Pruned	15.2	6.14	61.54	21.4	65.92	141.79
Unpruned	14.2	6.28	78.09	16.8	34:67	124.23
Significance[z]	NS	NS	NS	NS	*	NS

[z]Mean comparison by t-test. NS, *, ** Nonsignificant or significant at P < or =0.05 or 0.01, respectively.

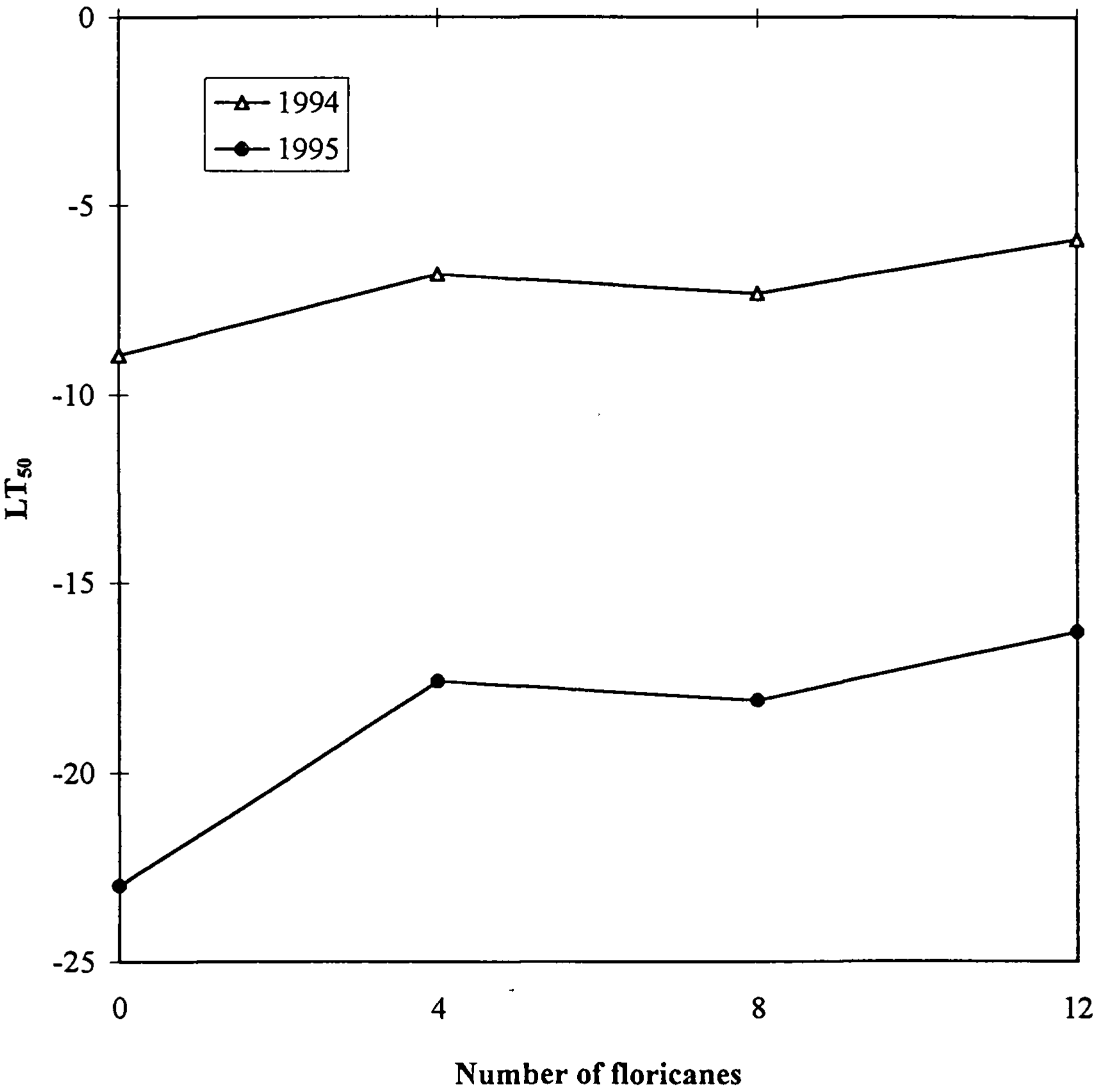


Figure 2-10. Effect of floricane number on subsequent cold hardiness (LT_{50}) of primocanes in 1994 and 1995.

Discussion

Primocane growth. In 1993, all plants produced longer primocanes than in 1994 (Figure 2-1 and Figure 2-2) possibly because it was an unusually wet summer in 1993 compared to the more typical warm and dry summer of 1994 (appendix). In red raspberry, soil temperature and water were found to have a major influence on vegetative components (Privé et al., 1993). In 1993, plants without floricanes produced a greater number and length of primocanes than those with floricanes. These results are similar to findings on red raspberry by (Wright and Waister 1982 a, b) and results found in 'Marion' (Sheets and Kangas, 1970). In red raspberry, primocane dry weight in biennial plots was found to exceed annual plots throughout the season because of a greater number of canes (Waister and Wright, 1989). Wright and Waister (1982a) suggested the increased emergence of primocanes could be due to removal of apical dominance exerted by the floricanes or competition in spring for stored reserves in the roots. This may also be the case in this study with 'Marion'.

There were few differences in primocane growth between the floricane treatments (4, 8, and 12) perhaps due to the low yields in 1993 which did not provide a strong competitive reproductive sink (Chapter 3). In 1994, yields were higher but treatment effects may not have been as pronounced because of high variability in the planting as evidenced by original cane number per plant (data not shown) and crown dry weight data (Chapter 3). Yield compensation occurring in response to the reduction in floricane number also reduced differences between the treatment levels (or "sink") of floricanes

(Chapter 3) again helping to explain the lack of differences in primocane growth for plants with varying numbers of floricanes.

Waister and Wright (1989) found that post-harvest primocane growth in red raspberry could account for as much as 25% of the total dry weight at the end of the season. In this study, 58 and 66% of the total increase in primocane length of 'Marion' occurred after harvest in 1993 and 1994, respectively. The primocanes appeared to have a similar three phase growth curve to red raspberry (Fernandez and Pritts, 1993) although a leveling off during harvest as they found was less pronounced in this study. Fernandez and Pritts (1993) suggested that the reduction in primocane growth during fruit development may have been caused by competition from the roots for photosynthate. In our comparison of the absolute growth rate during the three periods of growth during the season the AGR was highest in plants with no floricanes in all periods (Figure 2-7), however, the growth rates of all treatments were similar after harvest in 1994 (Figure 2-8), possibly because of reduced competition by the spent floricanes or because of higher original vigor in plants with floricane treatments. Measurements on changes in root dry weight were not made in this experiment.

Flushes of Growth. There were approximately 5 flushes of primocane growth throughout the season in 1993 and 1994 (Figures 2-5 and 2-6). This has not been reported in red raspberry nor previously in blackberry and was likely observed due to the high number of non-destructive sampling dates. The flushes of growth were not as apparent in 1994, perhaps as a result of biweekly instead of weekly sampling in the early and late season. One possible explanation is that this was in response to the biweekly irrigation schedule since red raspberry's vegetative growth has been found to be responsive to soil moisture content (Privé et al., 1993). However, this was not apparent from looking at weather data and 1993 was a very wet summer where it was unlikely the plants experienced water stress. Consequently, the reasons for the flushes of growth are not understood.

Primocane emergence in flushes. The occurrence of two flushes of primocanes on plants with floricanes has not been documented previously in red raspberry or blackberry (without primocane suppression). In this study, the second flush occurred during the green/red fruit stage. Primocanes that emerged in the second flush apparently had a higher growth rate as there was no significant difference in length between the two flushes by the end of the season. The emergence of a second flush was surprising considering that in red raspberry assimilate demand is greatest during the development of red fruit (Cameron et al., 1993; Klauer et al., 1992). However, it has also been found that the root system of red raspberry is also a strong sink (Fernandez and Pritts, 1993, 1994, 1996). Consequently, it is possible that the leaf area of floricane laterals as well as primocanes function as sources and replenish carbohydrate levels in the root system and crown thus supporting a second flush of primocane growth. If this was the case, then plants without floricanes had a reduced source supplying carbohydrates to the root system and crown which could explain why these plants did not produce a second flush of primocanes. This would need to be substantiated with source/sink limiting experiments or ^{14}C labeling studies.

Branching Habit. In both 1993 and 1994, plants without floricanes produced primocanes that tended to branch naturally early in the season, producing strong basal branches. These basal branch canes have been found to be an important yield component in 'Marion' (Bell et al., 1995a). Branch canes are also important in purple raspberry (Gundersheim and Pritts, 1991) and erect blackberry (Moore and Skirvin, 1990) where primocanes are topped to encourage branching. Plants with floricanes also had considerable branching during the season but branching generally occurred in response to damaged cane tips creating smaller lateral branches in the apical section.

The increase in naturally occurring branching in plants with no floricanes could be due to better light exposure in the absence of floricanes, greater availability of carbohydrates early in the season, or hormonal responses. Summer training has been found to increase branch growth and budbreak the following spring compared to winter training, probably due to better light exposure to buds (Bell et al., 1995a; Sheets et al., 1972). Light exposure has been found to increase percent bud break and the number of fruit per lateral in red raspberry (Braun et al., 1989) and in 'Marion' (Bell et al., 1995a).

The zero floricane, pruning treatment did not necessarily increase branching much over growing the primocanes without shading and competition from floricanes (0 floricane, unpruned). The lack of differences in the pruned and unpruned treatment suggest that 'Marion' can be stimulated to produce lateral branch canes in response to more than one factor. Although no significant treatment effects were found, some possible disadvantages of the pruning treatment were that the canes were more difficult to manage, were more dense causing more self thinning, increased shading of buds, and increased disease pressure. This was especially a problem in 1993, a wet year, when there was a serious outbreak of orange rust on the canes. The effect of pruning or topping primocanes in the presence of floricanes or at a greater height, as is done in erect blackberry (Moore and Skirvin, 1990) was not studied here.

Cold hardiness. Although the reason for increased cold hardiness in plants grown without floricanes is not understood, our research agrees with observations noted by (Sheets, 1987). Bell and workers (1995b) found increased hardiness with later primocane suppression(primocanes then grow in absence of floricanes). Carbohydrates are thought to play a role in cold hardiness but Bell et al. (1995b) did not find a relationship between carbohydrate levels and hardiness in 'Marion' blackberry.

<u>Summary</u>

Our results with 'Marion' were similar to findings in biennial red raspberry research (Waister et al., 1977; Waister et al., 1980; Wright and Waister, 1982b) as in the first year we found a greater number of primocanes on plants without floricanes and these primocanes had a reduced internode length. Generally 'Marion' has increased yield in biennial production (Nelson and Martin, 1989), but in this study, plants in AY production did not have a greater yield the following year than those with floricanes due to reduced budbreak (Chapter 3).

Several findings in our research on 'Marion' have not been previously reported in red raspberry. One of these was the emergence of two naturally occurring flushes (separated by 1-2 months) of primocanes in plants with floricanes. This may explain why primocane suppression in 'Marion' is such a successful practice. because the plant naturally sent up two flushes of canes. It would be interesting to study whether this occurs in other *Rubus* species as well.

Secondly, both primocanes and branches, on an individual (appendix) and a whole plant basis, grew in several flushes of growth throughout the season. Further research on the factors influencing these dynamics in growth could help in understanding blackberry physiology. It would also be interesting to see if primocanes of other *Rubus* species also grow in flushes.

The natural branching from basal primocane buds that occurred on plants without floricanes may have been in response to greater availability of assimilates or improved light conditions compared to plants with floricanes. In our findings, the primocane pruning treatment did not appear to have any advantages over unpruned canes; however, pruning at a higher height as is done in semi-erect blackberries may have beneficial effects. Further research on carbohydrate partitioning and light interception in AY and EY systems could help explain the branching patterns in 'Marion'.

Although this research provides considerable information on 'Marion' primocane growth, additional studies could add more detail to our current understanding of blackberry physiology. This research could provide a foundation on which to develop new studies such as using radio-labeled C^{14} to trace movement of photoassimilates in primocanes, floricanes and roots. These types of experiments could be used to explore the dynamics of primocane growth in relationship to fruit production and root growth, investigate the partitioning of resources in the occurrence of two flushes of growth, and possibly provide information on changes in absolute growth rate during the season. Other studies, such as to research the light environment in the canopy and LAR measurements in EY and AY systems could be useful. Exploring factors that stimulate branching in 'Marion' as well as studying other primocane pruning techniques could be helpful in developing alternative productions systems.

Literature cited

Bell, N., E. Nelson, B. Strik, and L. Martin. 1992. Assessment of winter injury to berry crops in Oregon, 1991. Agr Expt. Sta. Spec. Rpt. 902, Oregon State Univ.

Bell, N., B. Strik and L.W. Martin. 1995a. Effect of primocane suppression date on 'Marion' trailing blackberry. I. Yield Components. J. Amer. Soc. Hort. Sci. 120 (1):21-24.

Bell, N.C., B.C. Strik and L.W. Martin. 1995b. Effect of primocane suppression date on 'Marion' trailing blackberry. II. Cold Hardiness. J. Amer. Soc. Hort. Sci. 120 (1):25-27.

Bittenbender, H.C. and G.S. Howell Jr. 1974. Adaptation of the Spearman-Karber method for estimating the T_{50} of cold stressed flower buds. J. Amer. Soc. Hort. Sci. 99(2):187-190.

Braun, J.W., J.K.L. Garth and C. A. Brun. 1989. Distribution of foliage and fruit in association with light microclimate in the red raspberry canopy. J. of Hort. Sci. 64(5):565-572.

Cameron, J.S., S.F. Klauer, and C. Chen. 1993. Developmental and environmental influences on the photosynthetic biology of red raspberry (*Rubus idaeus* L.) Acta Hort. 352:113-121.

Clark, R. J. 1984. Biennial cropping, an alternative production system for red raspberries (*Rubus idaeus* L.). Sci Hort. 24:315-321.

Crandall, P.C., D.F. Allmendinger, J.D. Chamberlain, and K.A. Biderbost. 1974. Influence of cane number and diameter, irrigation, and carbohydrate reserves on the fruit number of red raspberries. J. Amer. Soc. Hort. Sci. 99:524-526.

Crandall, P.C., J.D. Chamberlain, and J.K.L. Garth. 1980. The effects of primocane suppression on growth, yield, and chemical composition of red raspberries. J.Amer. Soc. Hort. Sci. 99:524-526.

Fernandez, G.E. and M.P. Pritts. 1993. Growth and source- sink relationships in 'Titan' red raspberry. Acta Hort. 352:151-157.

Fernandez, G.E. and M.P. Pritts. 1994. Growth, carbon acquisition and source-sink relationships in 'Titan' red raspberry. Acta Hort. 325:151-157.

Fernandez, G.E., and M. P. Pritts. 1996. Carbon supply reduction has a minimal influence on current year's red raspberry (*Rubus idaeus* L.) fruit production. J. Amer. Soc. Hort. Sci. 121(3):473-477.

Gundersheim, N.A., and M. P. Pritts. 1991. Pruning practices affect yield, yield components, and their distribution in 'Royalty' purple raspberry. J. Amer. Soc. Hort. Sci. 116:390-395.

Klauer, S.F., C. Chen, and J.S. Cameron. 1992. Diurnal photosynthesis and starch deposition in leaves of fruiting and deflowered red raspberry canes. HortScience. 27:654.

Lawson, H.M., and J.S. Wiseman. 1983. Techniques for the control of cane vigor in red raspberry in Scotland: Effects of timing and frequency of cane removal treatments on growth and yield in cv Glen Cova. J. Hort. Sci. 58:247-260.

Moore, J. N. and R.M. Skirvin. 1990. Blackberry Management, p. 214-244. In: G.J. Galletta and D.G. Himelrick (eds.). Small fruit crop management. Prentice Hall, Englewood Cliffs, N. J.

Nehrbas, S.R. and M.P. Pritts. 1988. Effect of pruning system on yield components of two summer- bearing raspberry cultivars. J. Amer. Soc. Hort. Soc. 113:314-321.

Nelson, E. and L.W. Martin. 1989. Comparison of four training systems in alternate-year (AY) and Every-year (EY). Proc. Ore. Hort. Soc. 80:174-176.

Privé, J.P., J. A. Sullivan, J.T.A. Proctor and O.B. Allen. 1993. Climate influences vegetative and reproductive components of primocane-fruiting red raspberry cultivars. J. Amer. Soc. Hort. Sci. 118(3):393-399.

SAS Institute Inc. 1988. SAS/STAT user's guide. release 6.03. SAS Inst., Cary, N.C.

Sheets, W. A. 1987. Alternate-year (AY) training is for real. Or. Hort. Soc. 78:179-182.

Sheets, W.A. and K.F. Kangas. 1970. Progress report on A-Y production of caneberries. Proc Ore. Hort. Soc. 61:91-92.

Sheets, W.A., R.M. Bullock, and R. Garren. 1972. Effects of plant density, training, and pruning on blackberry yield. J. Amer. Soc. Hort. Sci. 97(2):262-264.

Strik, B.C. 1992. Blackberry cultivars and production trends in the Pacific Northwest. Fruit Var. J. 46:202-206.

Vasilakakis, M.D. and M.N. Dana. 1978. Influence of primocane inflorescence removal on number of inflorescences and suckers in 'Heritage' red raspberry. HortScience. 13:700-701.

Waister, P.D., M. R. Cormack, and W.A. Sheets. 1977. Competition between fruiting and vegetative phases in the red raspberry. J. of Hort. Sci. 52:75-85.

Waister, P.D. and C.. Wright. 1989. Dry matter partitioning in cane fruits, P. 51-61. In: C.J. Wright (eds.). Manipulation of fruiting. Butterworths, Boston,

Whitney, G.C. 1982. The productivity and carbohydrate economy of a developing stand of *Rubus idaeus*. Can. J. Bot. 60:2697-2703.

Williamson, B., H.M. Lawson, J.A.T Woodford, A.J. Hargreaves, J.S. Wiseman, and S.C. Gordon. 1979. Vigour control, an integrated approach to cane, pest, and disease management in red raspberry (*Rubus idaeus*). Ann Appl. Biol. 92:359-368.

Wright, C.J. and P.D. Waister. 1984. Light interception and fruiting cane architecture in the red raspberry grown under annual and biennial management systems. J. of Hort. Sci. 59(3):395-402.

Wright C.J. and P.D. Waister. 1982a. Within-plant competition in red raspberry. I. Primocane growth. J. of Hort. Sci. 57(4):437-442.

Wright C.J. and P.D. Waister. 1982b. Within-plant competition in red raspberry. II. Fruiting cane growth. J. of Hort. Sci. 57(4):443-448.

Chapter 3

Effect of floricane number in 'Marion' trailing blackberry. II. Yield components and dry mass partitioning

Abstract

In spring, 1993 and 1994, mature 'Marion' trailing blackberries were pruned to 0, 4, 8, and 12 floricanes. In both 1993 and 1994, plants with four floricanes had a significantly higher percent budbreak than plants with 12 floricanes. In 1993, plants with four floricanes also had fewer nodes per cane, a shorter average cane and lateral length, and fewer branch canes than plants with 8 or 12 floricanes. In 1994, other than percent budbreak, there were no variables affected by floricane number per plant. In 1993, there was no significant difference in yield between plants with 8 or 12 floricanes, while plants with 4 floricanes had a lower yield. In 1994, yield per cane was higher for plants with 4 floricanes compared to plants with 8 or 12 floricanes; yield per plant was not affected by floricane number. There were no significant treatment effects on berry weight in either year. In the summer of 1993, there was a trend for decreasing primocane dry weight with a higher floricane number and a significant decrease in branch dry weight with increasing numbers of floricanes. Total plant, fruit, floricane and lateral dry weight increased linearly with floricane number. Results were similar in the summer of 1994, except there were no treatment effects on primocane or branch dry weight and there was a significant

linear increase in crown dry weight with floricane number. By the winter of 1994 and 1995, there were no treatment effects on primocane or crown dry weight. Plants without floricanes produced more primocanes per plant than plants with floricanes in 1993 but not in 1994. Plants without floricanes produced primocanes that had a significantly lower percent budbreak the following year (1994) than plants with floricanes. There was a similar trend in 1995. Primocanes from plants without floricanes had more nodes per branch and a greater average branch cane length than plants with 8 or 12 floricanes the previous season. The number of nodes per cane tended to decrease with increased floricane number per plant in 1994 and 1995. There was no significant treatment effect on fruit per lateral, berry weight or yield per plant in either 1994 or 1995. However, in 1994, plants without floricanes the previous year, had the lowest yield per cane but the highest yield per meter of cane compared to plants with floricanes. Topping primocanes at 30 cm in 1993 had no significant effect on yield components the following season. The only variable significantly affected by pruning in 1994 was fruit per lateral with the primocane pruning treatment having fewer fruit per lateral. There were differences in primocane dry weight among treatments after harvest in 1993 but by mid-winter there were no differences in either 1994 or 1995. Although plants grown without floricanes in 1993 had more primocanes, these canes had a lower percent budbreak the following season. This was perhaps a result of primocanes not being trained as they grew, a practice that improves light exposure to the buds. "Marion' blackberry can compensate for reduced floricane number through an increase in percent budbreak on remaining canes.

Introduction

'Marion', trailing blackberry (*Rubus* sp.) is the most important trailing blackberry cultivar grown for processing in Oregon accounting for 50% of the hectarage in the state (Strik, 1992). Two of the major production problems for 'Marion' are low bud break and relatively poor cold hardiness. Low bud break may be a result of numerous factors including winter injury, disease problems, poor light exposure, and intracane competition for resources. Susceptibility to winter injury resulting in erratic bud break is one of the major production problems in 'Marion' causing an unstable market (Bell et al., 1992). Production systems have been found to affect bud break and cold hardiness in 'Marion' (Bell et al., 1992, 1995 a, b).

The most common system for caneberries is annual production where vegetative and reproductive canes grow simultaneously within the same canopy. Another system used commercially for 'Marion' is biennial or alternate year (AY) production where there is a complete separation of the vegetative and reproductive phases. In 'Marion', the AY system produces 70-90% as much as the annual or every year (EY) system over a two year time period (Strik, 1992). Alternate-year production is used commercially for 20-55% of the hectarage in Oregon (Strik, 1992). One advantage of the AY system is reduced production costs through lower labor requirements, fertilizer inputs and pesticide use while achieving comparable yields (Burt et al., 1979, Sheets, 1987). The AY system also eliminates primocane damage that occurs during mechanical harvest in the EY system and primocanes can be trained to the trellis during the summer (Sheets, 1987). Summer training has been found to stimulate cane growth, improve light exposure and provide a less favorable environment for disease pathogens compared to winter training which is often done in EY production (Bell et al., 1995a, Sheets and Kangas, 1970). The AY system is thought to be more winter hardy (Sheets, 1987) and also allows for more flexibility in production during years when 'Marion' is damaged by cold weather.

Competition between vegetative and fruiting canes has been studied most extensively in red raspberry with the use of annual and biennial systems to modify sinks and sources. Clark (1984) found the biennial system yielded 75% of the 2-year hand-harvested annual system. In the biennial system, greater yield resulted from increased primocane emergence, each with a shorter internode length during the previous season's vegetative stage (Dale, 1989; Sullivan and Evans, 1992; Waister et al. 1977; Waister et al. 1980; Wright and Waister 1982b). Nehrbas and Pritts, (1988) found alternate year mowing increased cane number per plant but reduced the number of fruitful laterals per cane, flower number per lateral, and berry weight. Also, floricanes grown without competition from primocanes had greater productivity per node and greater fruit weight (Clark, 1984; Wright and Waister, 1982b). These changes in primocane growth in biennial production have been attributed to reduced competition for storage reserves in the spring (Crandall et al., 1974) and to improvements in the light environment (Lawson and Wiseman, 1983; Waister and Wright, 1989).

New primocanes use reserves stored in the root system until a functional leaf biomass is established. However, in red raspberry, the root system is a strong sink and rapidly replenishes its store of reserve carbohydrate from photosynthates from floricanes and primocanes and continues to do so into the fall (Fernandez and Pritts, 1993, 1994, 1996; Whitney, 1982). Whitney (1982) found carbohydrate levels in the primocanes were high early in the spring dropped to low concentrations in July then returned to higher levels again by the end of the season. Fernandez and Pritts (1996) report that the large amounts of carbohydrate reserves in the roots can be remobilized to floricanes during fruiting or stored for use the following year. Fruiting laterals on floricanes initially rely on carbohydrate reserves stored in the overwintered canes with later fruit development being supported by the adjacent fruiting lateral leaves (Whitney, 1982). Floricanes grow early in the season, with dry matter and macroelement uptake nearly complete by mid-summer. Floricane senescence occurs after mid-summer with concomitant dry matter and nutrient loss (Kowalenko, 1994). New primocanes of red raspberry begin to grow and take up macroelements later in the spring than floricanes and continue growth and uptake later into the fall (Kowalenko, 1994).

In red raspberry, the minimum cane density required for maximum yield was found to be about 15 canes • m^{-1} in North America and Tasmania (Buszard, 1986; Clark, 1984; Crandall, 1980; Fejer, 1979; Orkney and Martin, 1980) while in Europe the optimal number has been found to be 8-12 • m^{-1} (Dale, 1989; Wood, 1960). With increasing cane density, there is usually a decrease in yield per cane as the canes have fewer laterals, fewer fruit per lateral and smaller fruit (Crandall et al., 1974). Optimal cane density for the trailing blackberries has yet to be determined.

Research on biennial production has led to a greater understanding of the biology of red raspberry even though biennial production is not a commercial practice. However, in 'Marion', alternate year production is practiced and is thought to improve winter hardiness and budbreak the following spring although the physiology is not well understood. Although raspberry research provides insights, different factors may play a role in the success of biennial production in trailing blackberries because they differ from red raspberry in growth habit and in the training system used. 'Marion' is more vigorous, has a trailing growth habit, numerous branch canes, and is more productive in the basal rather than the terminal cane section in contrast to raspberry (Bell et al., 1995a). Trailing blackberries such as 'Marion' have a canopy where the floricanes are spatially separated from the primocanes in annual production because the floricanes are wrapped horizontally on trellis wires while the primocanes grow along the ground. This creates a different light microclimate than that found in red raspberry where vegetative and reproductive canes exist in the same vertical canopy.

'Marion' also differs from red raspberry in that primocanes produce vigorous branch canes while red raspberry primocanes generally do not have axillary branch canes. Branch canes in 'Marion' have been found to be an important yield component (Bell et al., 1995a). Branch cane development is important in other *Rubus* species such as erect blackberry (Moore and Skirvin, 1990) and purple raspberry (Gundersheim and Pritts, 1991) where primocanes are pruned or topped to stimulate branching.

This research was undertaken to develop a better understanding of the physiology of vegetative and reproductive cane growth and carbohydrate partitioning in 'Marion'. Differing levels of the reproductive sink were established by manipulating the number of floricanes per plant. The specific objectives of this research were to determine the effect of floricane number and primocane pruning on yield components in the same season, yield components in the following year, and dry weight partitioning. The effect of floricane number and primocane pruning on primocane growth and subsequent cold hardiness are presented in Chapter 2.

Materials and Methods

An eight-year old planting of 'Marion' blackberry on a latourell loam soil at the North Willamette Research and Extension Center, Aurora, OR was used. Plants were spaced 2.4 m within rows spaced 3.1 m apart. The trellis consisted of two horizontal wires at 1.2 and 1.5 m. Weed management, irrigation, and fertilization followed standard commercial practice. No primocane suppression was done on any treatments. In 1993 and 1994, plants were pruned to establish treatments of 0, 4, 8, and 12 floricanes per plant. Excess canes on each plant were counted and removed at ground level. An additional treatment was included with zero floricanes and early primocane pruning at 30 cm. The plants studied in 1993 had fruited in 1992 while plants used in 1994 did not fruit in 1993. Floricane training was done in February. The experimental design was completely randomized with five replicates of three plants per plot.

Yield component analysis. On plants with 4, 8, and 12 floricanes, fruit harvest was from July 7-August 2 in 1993 and from June 27 to July 21, 1994. Total yield per plant was measured at each picking date. A randomly selected 25 berry sample was used to obtain average fruit weight per treatment on each harvest date.

After fruit harvest, floricanes were carefully unwrapped from the training wires. In 1993 and 1994, the year of the floricane number treatment, four canes were randomly selected from one plant in each plot for yield component analysis. The canes were divided into basal and mid sections of 150 cm each and an apical section of the remaining cane length. Branch canes were separated from the main cane. Cane diameter was measured 30 cm from the base of the main cane and on each branch cane. Yield component data collected on each of the main cane sections and on each branch cane included number of nodes, nodes with a lateral, nodes with a fruitful lateral and fruiting sites, and lateral and main cane length. Yield component data were also collected the year after treatment establishment (1994 and 1995) to follow the primocanes through their complete life cycle. Six canes per treatment plant including the pruned and unpruned plants grown without floricanes the previous season, were randomly selected for yield component analysis in the second year. Yield data were collected as described previously.

Dry weight partitioning. On a separate plant in each treatment plot, fruit were weighed to obtain yield and a subsample was dried to a constant weight at 40 C to determine dry weight. Immediately following fruit harvest in late July in 1993 and 1994, one plant per plot was partitioned into floricanes, laterals, primocanes, primocane branches, and crown tissues. Samples were dried to constant weight at 40 C (or to a constant weight) and then weighed. Dry weight partitioning of primocanes and crown was also determined in February of 1994 and 1995

Data analysis. Yield per plant, percent fruitful budbreak, number of fruit per lateral, average lateral length and internode length were calculated. In the first season, yield per cane was calculated using yield data and cane number in the original treatment (i.e. 4, 8, or 12 floricanes per plant). Yield per meter of cane was calculated in the second season using the previous season's final primocane length. The effect of year and floricane number on yield components were determined using analysis of variance (SAS, 1988) with mean separation using Fisher's Protected LSD. A T-test comparison was performed on the 0 floricane pruned and unpruned treatments. Regression analysis was used to determine treatment effects on the second year's yield components and on dry weight partitioning.

Results

Effect of floricane number on yield components in the year of floricane pruning. There was a significant year effect on the number of nodes per cane (P=.0001), average cane length (P=.0001), and percent budbreak (P=.0001). There was a year by treatment interaction for number of nodes per cane (P=.05)

In both 1993 and 1994, plants with four floricanes had significantly higher percent budbreak than plants with 12 floricanes (Table 3-1). In 1993, plants with four floricanes also had significantly fewer nodes per cane, a shorter average cane length, reduced lateral length, and fewer branch canes compared to plants with 8 or 12 floricanes. In 1994, other than percent budbreak, there were no variables affected by floricane number per plant (Table 3-1). In 1993, there was no significant difference in yield between plants with 8 and 12 floricanes while plants with 4 floricanes had a lower yield (Table 3-2). In 1994,

Table 3-1. Effect of floricane number on total (main + branch canes) and branch yield components in the year of floricane pruning.

No. of floricanes	No. nodes/cane	Budbreak (%)	No. fruit/ lateral	Average lateral length (cm)	Average cane length (m)	No. branches/ cane	Average branch length (m)
1993							
4	37.4	50	5.49	32.52	2.32	.3	.54
8	62.0	43	5.53	38.91	3.87	1.1	.69
12	63.4	40	5.23	35.55	3.55	.9	.74
LSD[Z]	14.1	8	1.96	5.13	.93	.6	.59
Significance[Y]	**	*	NS	*	**	*	NS
1994							
4	226.6	24	7.21	38.3	14.61	2.8	3.61
8	158.9	19	6.98	33.9	10.49	1.5	3.40
12	242.8	17	7.43	37.4	15.90	2.9	3.40
LSD[Z]	94.9	5	1.23	6.5	6.43	1.7	.81
Significance[Y]	NS	*	NS	NS	NS	NS	NS

[Z]Mean separation by Fisher's Protected LSD.
[Y]NS, *, ** Nonsignificant or significant at P<0.05 or <0.01, respectively.

Table 3-2. Effect of floricane number on yield during the year of floricane pruning.

Treatment	Yield/plant (kg)	Yield/cane (kg)	Berry weight average (g)	Berry weight above[Z] (g)	Berry weight below[Z] (g)
1993					
4	1.7	.42	4.01	3.63	4.16
8	4.7	.59	4.58	4.32	4.79
12	6.9	.57	4.60	4.30	4.88
LSD[Y]	2.4	.29	.88	1.07	.70
Significance[X]	**	NS	NS	NS	NS
1994					
4	7.48	1.87	5.08	--	--
8	7.82	.98	4.96	--	--
12	11.08	.92	5.19	--	--
LSD[Y]	3.33	.53	.35	--	--
Significance[X]	NS	**	NS	--	--

[z]Berry weight data were collected separately from above and below the lower training wire in 1993 to assess possible cold injury effects.
[Y]Mean separation by Fisher's Protected LSD.
[x]NS, *, ** Nonsignificant or significant at $P<0.05$ or <0.01, respectively.

yield per cane was significantly higher in plants with 4 floricanes compared to plants with 8 or 12 floricanes; yield per plant was not affected by floricane number (Table 3-2). There were no significant treatment effects on berry weight in either year, although berries from the tips of canes (above the trellis wire) were of lower weight than those from the basal portion of canes (Table 3-2).

Dry weight partitioning. There was a significant year effect in the summer of 1993 and 1994 on the dry weight components: crown (P=.0001), primocane (P=.001), floricane (P=.0001), lateral (P=.0001), fruit (P=.0001) and total (P=.0001) tissues. There was also a significant year by floricane number interaction for crown (P=.004), primocane (P=.01), floricane (P=.0001), lateral (P=.004), and total (P=.0001) dry weight. In the winter of 1994 and 1995, there was a significant year effect on crown dry weight (P=.004).

In the summer of 1993, there was a trend for decreasing primocane dry weight with increasing numbers of floricanes and a significant decrease in branch dry weight with increasing numbers of floricanes (Fig. 3-1, Table 3-3). Total plant, fruit, floricane and lateral dry weight showed a significant linear increase with floricane number (Fig. 3-1, Table 3-3). Results were similar in the summer of 1994 except there were no treatment effects on primocane or branch dry weight (Fig. 3-2, Table 3-3). However, in the summer of 1994, there was a significant increase in crown dry weight with increasing floricane number (Fig. 3-2, Table 3-3). By the winter of 1994 and 1995, there were no treatment differences in primocane or crown dry weight (Fig. 3-3 and 3-4, Table 3-3).

Effect of floricane number on the following year's yield components. There was a significant year effect on yield (P=.0001), number of nodes per cane (P=.0001), average

Table 3-3. Linear regression equations for dry weight partitioning

Tissue component	**Equation**[Z]	r^2	**P-value**
1993 summer			
Crown	$y = .23x + 0.42$	-.06	NS
Primocane	$y = -.12x + 1.55$	.11	NS
Branch	$y = -.16x + 0.88$	.55	.0002
Floricane	$y = .27x - 0.54$	.83	.0001
Lateral	$y = .34x - 0.63$	.75	.0001
Fruit	$y = .33x - 0.64$	.78	.0001
Total	$y = .66x + 1.04$	.54	.0002
1994 summer			
Crown	$y = .18x + 0.06$	.43	.001
Primocane	$y = .09x + 0.85$	.03	NS
Branch	$y = .12x + 0.42$	.05	NS
Floricane	$y = .56x - 0.97$	.85	.0001
Lateral	$y = .66x - 1.23$	.86	.0001
Fruit	$y = .44x - 0.72$	.81	.0001
Total	$y = 1.88x - 1.58$	.89	.0001
1994 winter			
Crown	$y = .04x + 0.39$	.23	NS
Primocane	$y = -.17x + 2.87$	-.20	NS
Total	$y = -.14x + 3.26$	-.31	NS
1995 winter			
Crown	$y = .11x + 0.31$	.58	NS
Primocane	$y = -.02x + 1.84$	-.48	NS
Total	$y = .08x + 2.15$	-.37	NS

[Z] y = dry weight of component indicated (kg/plant); x = number of floricanes/plant.

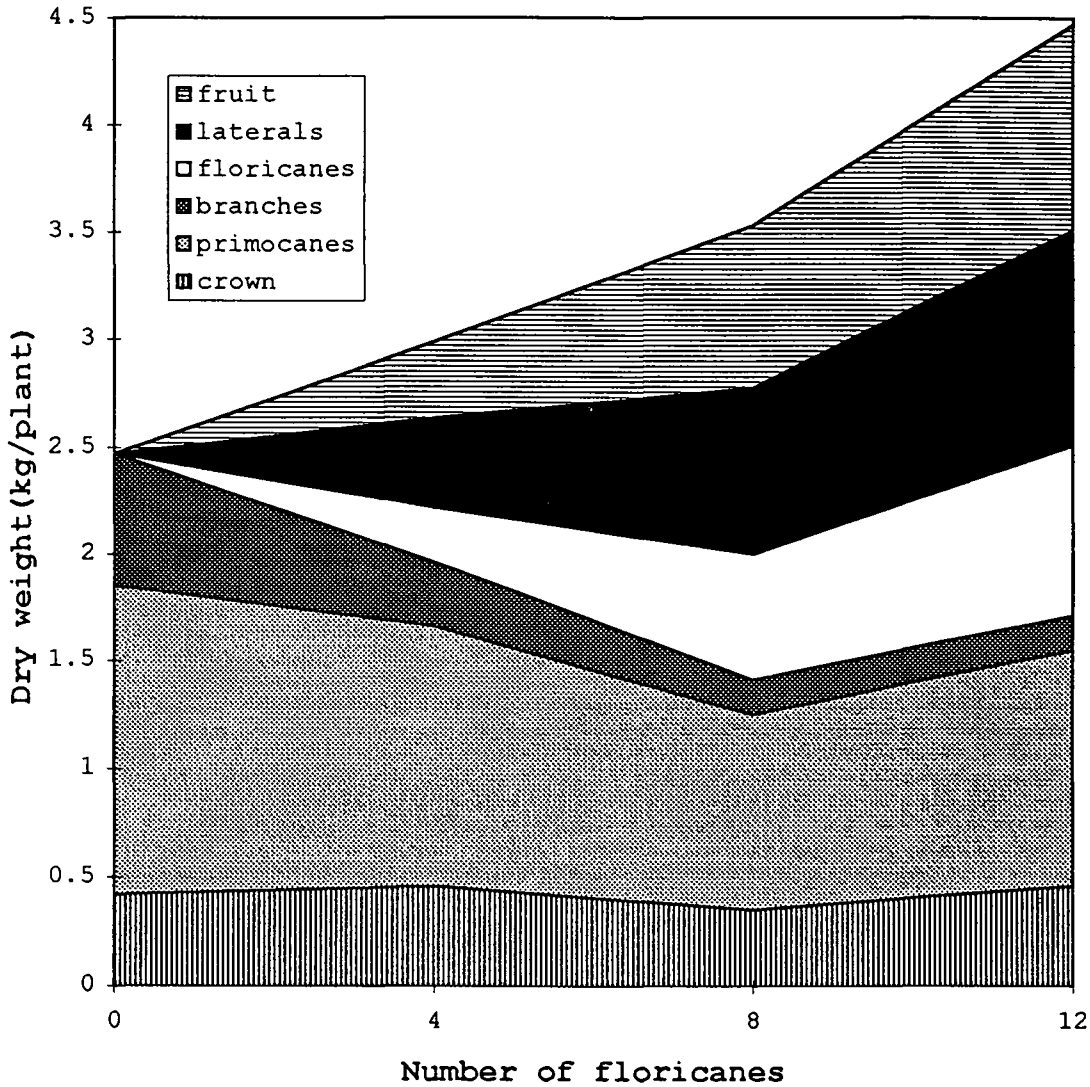


Figure 3-1. Effect of floricane number on summer dry weight partitioning in 1993.

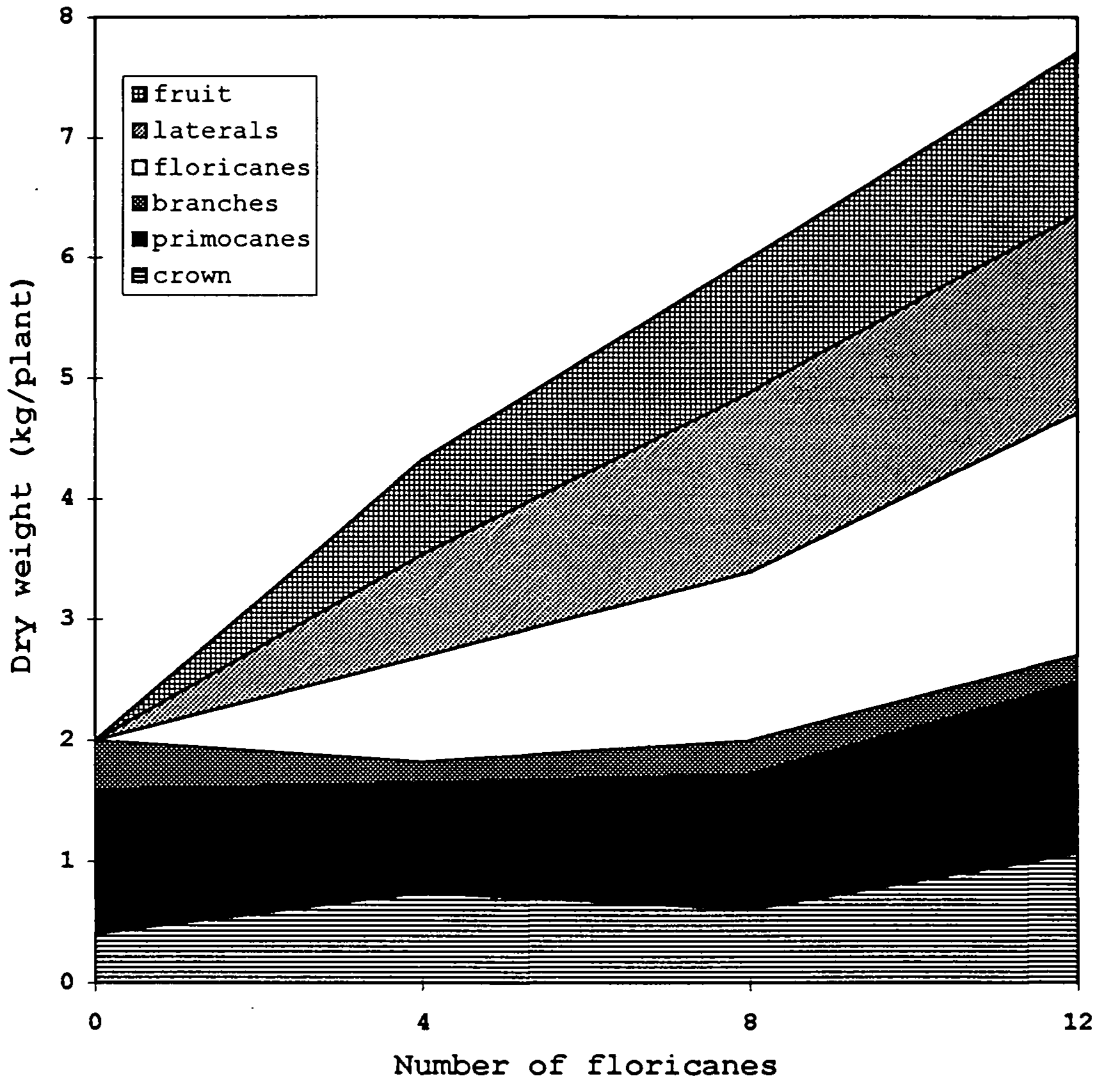


Figure 3-2. Effect of floricane number on summer dry weight partitioning in 1994.

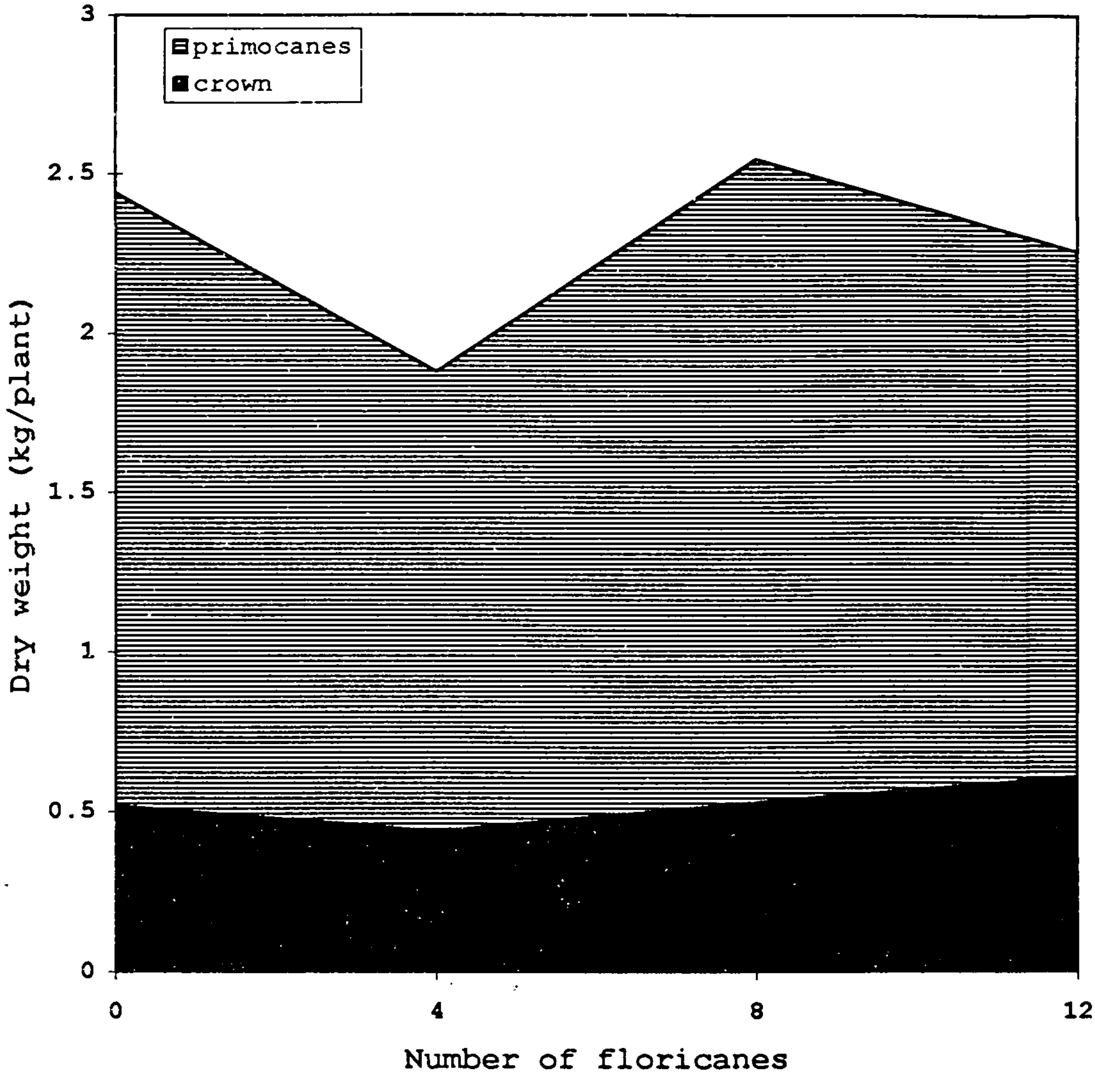


Figure 3-2. Effect of floricane number on summer dry weight partitioning in 1994.

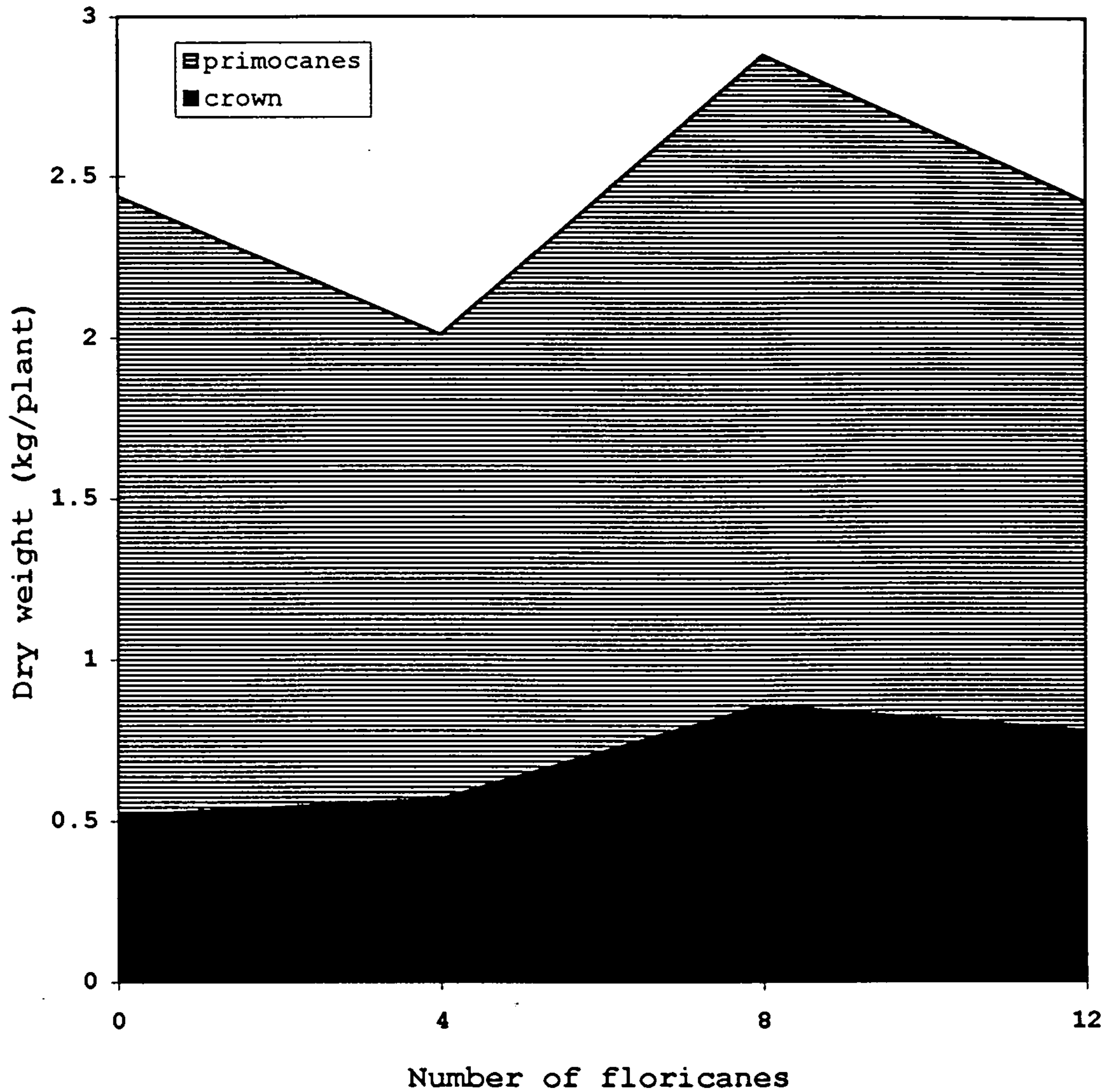


Figure 3-4. Effect of floricane number on winter dry weight partitioning in 1995.

cane length (P=.0002), and on percent budbreak (P=.0001). There were significant year by treatment interactions for berry weight (P=.02), and percent budbreak (P=.0002). Plants without floricanes produced a significantly greater number of canes per plant than plants with floricanes in 1993 but not in 1994 (Table 4 and Chapter 2). Plants without floricanes produced primocanes that had a significantly lower percent budbreak the following year (1994) than plants with floricanes (Table 3-4). There was a similar trend in 1995 (Table 3-4). Plants without floricanes had a significantly higher number of nodes per branch and a greater average branch cane length than plants with 8 or 12 floricanes (Table 3-4). Number of nodes per cane tended to decrease with increased floricane number per plant in 1994 and 1995. There was no treatment effect on fruit per lateral. There was no significant treatment effect on yield per plant in either 1994 or 1995 (Table 3-5). However, in 1994, plants without floricanes had the lowest yield per cane but the highest yield per meter of cane compared to plants with floricanes (Table 3-5). There was no significant treatment effect on berry weight in either 1994 or 1995 (Table 3-5). In 1994, regression analysis showed no linear relationship between any yield components and the floricane number per plant (data not shown), because there were few differences among the plants with 4, 8, and 12 floricanes. In 1995, there was a significant linear relationship between number of nodes per cane and of floricanes the previous season (P=.008). There was a negative correlation between number of nodes and budbreak in 1995 (r=-.49; P=.03) and a similar trend in 1994(r=-.43; P=.06).

Table 3-4. Effect of floricane number on total (main cane + branch) and branch cane yield components the following season.

No of floricanes applied in 1993 or 1994	No. of canes/ plant	No. nodes/ cane	Budbreak (%)	No. fruit/ lateral	average cane length (cm)	No. branches/ cane	No. nodes/ branch	average branch cane length (m)
1994								
0	20.8	188.8	19	7.30	11.71	1.7	55.3	3.50
4	13.0	184.8	27	6.98	11.28	1.9	53.6	3.22
8	15.4	124.6	32	6.97	8.39	1.1	36.9	2.30
12	12.4	147.6	30	7.18	9.67	1.8	38.0	2.24
LSD[z]	5.38	58.05	5	1.71	3.45	.7	15.4	1.08
Significance[y]	*	NS	**	NS	NS	NS	*	*
1995								
0	13.0	112.2	36	8.48	7.14	--	--	--
4	9.6	108.2	42	9.48	7.13	--	--	--
8	12.2	100.3	39	9.58	7.72	--	--	--
12	12.4	95.3	38	9.22	6.27	--	--	--
LSD[z]	5.24	38.8	4	1.20	3.02	--	--	--
Significance[y]	NS	NS	*	NS	NS	--	--	--

[z] Mean separation by Fisher's Protected LSD.
[y] NS, *, ** Nonsignificant or significant at $P<0.05$ or <0.01, respectively.

Table 3-5. Effect of floricane number on the following season's yield.

No. of floricanes applied in 1993 or 1994	yield/plant (kg)	yield/cane (kg)	yield/ meter (kg)	berry weight (g)
1994				
0	17.08	.84	.13	5.44
4	15.09	1.19	.12	5.10
8	18.16	1.18	.11	5.31
12	14.52	1.27	.08	5.27
LSD[z]	3.24	.33	.03	.30
Significance[y]	NS	*	*	NS
1995				
0	9.17	.70	.10	4.18
4	10.28	1.10	.16	4.65
8	11.93	1.08	.14	4.44
12	9.97	.89	.14	4.59
LSD[z]	2.96	.43	.04	.43
Significance[y]	NS	NS	NS	NS

[z] Mean separation by Fisher's Protected LSD.
[y] NS, *, ** Nonsignificant or significant at $P<0.05$ or <0.01, respectively.

In relating the yield components to the previous season's primocane growth, there was a positive correlation between yield and primocane number (r=.57; P=.008) and length (r=.56; P=.01) in 1993/1994. Percent budbreak was negatively correlated with number and length of primocanes (r=-.4; P=.03 and r=-.68 and P=.02, respectively) and branches (r=-.68; P=.001 and r=-.84; P=.0001, respectively). In 1994/1995, the number of nodes was positively correlated with an primocane number (r=.57; P=.008) primocane length (r=.56; P=.01), branch length (r=.53; P=.02) and total length (r=.80; P=.0001). Berry weight was negatively correlated with primocane number (r=-.51; P=.02) and length (r=-.48; P=.03) in 1994/1995.

Effect of primocane pruning on yield components. Topping primocanes at 30 cm in 1993 had no significant effect on yield components the following season (Table 3-6). The only variable significantly affected by pruning in 1994 was fruit per lateral with the primocane pruning treatment having fewer fruit per lateral (Table 3-7). There were no significant treatment effects on yield or berry weight in 1994 or 1995 (Table 3-8).

Discussion

Effect of floricane number on yield components. The establishment of treatments consisting of different numbers of floricanes per plant was used to determine the effect on primocane growth (Chapter 2) and to evaluate the effect of cane number on yield components. In this research, the ability of 'Marion' to compensate for the removal of canes was apparent. Yield compensation occurred through a higher percent budbreak in plants with 4 floricanes compared to plants with 8 or 12 floricanes. This agrees with

Table 3-6. Effect of primocane pruning on branch yield components, 1994.

No. of floricanes applied 1993	No. branches/ cane	No. nodes/ branch	No. fruit/ lateral	Budbreak (%)	Average branch length (cm)	Cane diameter (mm)	Internode length (cm)
+ pruning	3.05	60.08	6.09	19	3.71	6.50	6.13
- pruning	3.28	55.33	6.27	25	3.50	6.09	6.22
Significance[z]	NS	NS	NS	NS	NS	NS	NS

[z]Mean comparison by T-test. NS Nonsignificant.

Table 3-7. Effect of primocane pruning on branch yield components, 1995.

No. of floricanes applied 1994	No. of canes/ plant	No. nodes/ cane	No. fruit/ lateral	Budbreak (%)	Average cane length (m)
+ pruning	14.8	133.94	7.64	31	8.25
- pruning	14.0	108.88	8.48	37	6.91
Significance[z]	NS	NS	*	NS	NS

[z]Mean comparison by T-test. NS, * Nonsignificant or significant at $P<0.05$.

Table 3-8. Effect of primocane pruning on yield the following season.

No. of floricanes applied in 1993 or 1994	Yield (kg)	Yield/cane (kg)	Yield/meter (kg)	Berry weight (g)
1994				
+ pruning	13.66	1.03	.08	4.39
- pruning	17.08	.84	.08	4.76
Significance[z]	NS	NS	NS	NS
1995				
+ pruning	8.92	.69	.08	3.68
- pruning	9.17	.68	.10	4.19
Significance[z]	NS	NS	NS	NS

[z] Mean comparison by t-test. NS Nonsignificant.

findings by Bell et al. (1995a) that 'Marion' has the ability to compensate for lost buds by increasing production at remaining nodes. This potential for increased budbreak could be related to the normally low percentage, approximately 41 percent budbreak typically found in 'Marion' (Bell et al., 1995a). In another study, primary bud removal in 'Marion' had no significant effect on yield per cane, showing 'Marion' has the capacity to compensate for primary bud damage (Strik et al., 1996). In red raspberry, Waister and Barritt (1980) found 'Meeker' produced 68% of a normal crop with 50% of the buds removed. In another study, Moore (1994) found no significant difference in yield between disbudded plants (all primary buds removed) and non-disbudded plants. Compensation for low budbreak can occur through increases in fruit size (Gundersheim and Pritts, 1991) and number of fruit per lateral (Waister and Barritt, 1980) in red raspberry. Fernandez and Pritts (1996) suggest that these plastic responses are due to the capacity of red raspberry to store large amounts of carbohydrates in the roots and to shift carbon partitioning to various plant parts depending on the current situation. In this case, compensation for low cane number per plant through increased fruit weight or number of fruit per lateral was not apparent in 'Marion'.

In 1993, all plants were affected by winter injury as evidenced by low yields, cane dieback, stunted laterals in the terminal cane sections, and reduced berry weight. This type of damage in 'Marion' has been reported previously by Bell et al.(1992) who observed reduced, erratic budbreak along the canes in addition to stunted laterals. This type of injury could be due to damage to the phloem and cambial tissues at the bud base causing laterals to emerge and extend normally, then later to collapse under the demands of flowering and fruiting which overwhelms the vascular system (Moore and Brown, 1971). In this research, plants with 4 floricanes appeared to be most severely affected by cold injury as they had a reduced number of nodes per cane, a shorter average cane length, and fewer branch canes; data were not collected on dead, winter injured sections of cane. However, all plants exhibited some compensation through increased production in the basal cane section. In other compensation research in red raspberry, Braun and Garth (1984) found no effect of alternate bud removal on productivity of the remaining buds, however, they found an increase in the productivity of lower fruitful nodes with removal of buds on the upper half of the cane.

In both 1993 and 1994, there were no differences in the yield among the 4, 8, and 12 floricane treatments due to compensation through increased percent budbreak at lower floricane numbers. This could explain why plants with different numbers of floricanes did not have significant differences in primocane growth (Chapter 2).

Effect of floricane number on dry weight partitioning. In the summer of 1993, primocane branch dry weight increased with a reduction in floricane number while there was similar trend for primocane dry weight. This is similar to findings in red raspberry where primocane dry weight in biennial plots exceeded that of annual plots throughout the season because of a greater number of canes (Waister and Wright, 1989). However, in the summer of 1994, there were no significant differences in primocane dry weight which might be explained by the high variability in original cane number in the planting before experiment establishment. These dry weight results agree with the primocane length measurements made throughout the summer in 1993 and 1994 (Chapter 2). The positive correlation between crown and total dry weight suggests that plants with healthy crowns have the ability to produce more primocane dry weight regardless of the number of floricanes. It was interesting to find in this research that there were no differences in primocane dry weight by mid-winter suggesting plants with floricanes have the ability to "catch up" after harvest (Chapter 2). Waister and Wright (1989) found that post-harvest primocane growth in red raspberry could account for as much as 25% of the total dry weight at the end of the season.

There was a positive linear relationship between dry weight of reproductive components and number of floricanes (Table 3-3). However, in many cases, plants with fewer floricanes compensated by increased budbreak as discussed previously. In our research, there did not appear to be a limit on total biomass that could be produced with up to 12 floricanes. Thus, 'Marion' appears sufficiently vigorous to support more than 12 canes per plant without decreased yield. In red raspberry, the minimum cane density required for maximum yield was found to be about 15 canes • m^{-1} in North America and Tasmania (Buszard, 1986; ; Clark, 1984; Crandall, 1980; Fejer, 1979; Orkney and Martin, 1980) while in Europe the optimal number has been found to be 8-12 • m^{-1} (Dale, 1989; Wood, 1960).

Effect of floricane number on the following season's yield. Yield components were done during the season after treatment establishment to determine the effect of changing the reproductive sink in the previous season on subsequent yield. The low yield of the AY plants (0 floricanes the previous season) in this experiment was contrary to findings that 'Marion' generally produces 70-90% of the two -year yield in the "on year"

(Strik, 1992). In red raspberry, the biennial system was also found to produce a higher yield in the "on" year (Clark, 1984; Waister et al., 1977; Wright and Waister, 1982b). Wright and Waister (1982b) found an increase in number of nodes as well as the number of nodes that produced fruitful laterals in biennial red raspberry production. In our findings, plants with no floricanes produced primocanes with more nodes, but fewer nodes produced fruiting laterals. Berry weight was not affected by floricane number in this study. This is similar to findings on biennial raspberry production by Waister et al. (1977) and Wright and Waister (1982b). Plants with no floricanes the previous year tended to have the lowest yield per cane. These results are in contrast to Wright and Waister's (1982b) findings of higher yield per cane with biennial production of red raspberry.

The reduction in percent budbreak and low yield per cane in plants with no floricanes in this study could have been from the poor light exposure and air flow resulting from February training. Plants are often February-trained in annual production, however, in alternate year (AY) production, primocanes are generally trained onto the trellis as they grow allowing for good light exposure to the buds. Sheets and Kangas (1970) found that canes trained by mid-to late-July had profuse lateral development resulting from stimulation of the axillary buds. Bell et al. (1995a) found August-trained plants had longer main canes, a higher percent budbreak, and a higher number of fruit per lateral than February-trained plants. This may explain why, in this study, AY production did not show increased yield in the "on" year.

Another reason for the low percent budbreak in plants grown without floricanes the previous season could have been intracane competition for carbohydrates. 'Marion' is more vigorous than red raspberry, producing a tremendous amount of cane (about 10 m per cane or 100 to 212 m per plant; Chapter 2) which is generally not tipped. It is possible that ‘Marion’ cannot support such a high number of potentially fruitful nodes per cane as was found on the plants grown without floricanes. This was supported in 1994 by negative correlations between budbreak and primocane and branch number. Percent budbreak was also generally negatively correlated with total cane length and node number in 1994 and 1995. As mentioned previously, compensation through increased percent budbreak has been documented by Bell et al. (1995a) showing that ‘Marion’ is “plastic” in its ability to compensate for lost buds by increasing production at remaining nodes.

Some of the differences in response to biennial production in red raspberry and ‘Marion’ could be related to differences in the trellis system used and the growth habit of the plants. For example, one of the benefits of biennial production in red raspberry is that the floricanes are not shaded by the primocanes. Shading of the floricanes by the primocanes has been attributed to reduced yield on the basal cane section (Braun et al., 1989; Wright and Waister, 1984). However, in ‘Marion’, the primocanes grow along the ground and do not shade the floricanes. Consequently, any increases in yield occurring during the fruiting stage when plants are grown without primocanes would be more likely from reduced competition for resources rather than from shading. In ‘Marion’, the primocanes can benefit from the removal of floricanes because this reduces shading caused by the floricanes thus creating a better light environment. Therefore, primocanes in the “off” year in AY production produced canes with a shorter internode length as well as with more branch canes as was seen in 1993 (Chapter 2). However, in our findings, there were no differences in primocane growth in 1994 (Chapter 2). Thus, it is not surprising that there was no significant effect of floricane number on yield the following season (1995). In 1994, the lack of treatment effects could have been in part due to high variability in the planting as evidenced by the significant differences in original cane number per plant and summer crown dry weight. It is also possible that training time is a key factor in the success of AY production in 'Marion'.

Effect of primocane pruning on branching and yield components. Primocane pruning had relatively little effect on yield components the following season because plants with no floricanes and without pruning also had increased branching. In all treatments, primocanes branched later in the season from tip damage, but plants without floricanes tended to have greater natural branching earlier in the season producing branch canes of increased length. Bell et al. (1995a) found the longest and most productive branch canes in the basal cane section in research on primocane suppression. The improved light conditions or carbohydrate availability for primocane growth in the AY system may have stimulated greater branching from basal buds. Sheets and Kangas (1970) observed axillary branching increased with good light conditions from August primocane training. The lack of differences in the pruned and unpruned treatment suggest that 'Marion' can be stimulated to produce lateral branch canes in response to more than one factor. Although primocane pruning is a successful practice in erect and semi-erect blackberry cultivars (Moore and Skirvin, 1990), pruning to 30 cm in our study did not look promising for 'Marion'. However, pruning at a higher height, as is done in the erect blackberries, may be a practice worth investigating.

Summary

'Marion' blackberry produced a greater number of primocanes when grown without floricanes (Chapter 2). This is similar to findings in biennial production of red raspberry (Waister et al., 1977; Waister et al., 1980; Wright and Waister, 1982b). In this study, primocanes growing in the absence of floricanes had more nodes from a reduced internode length rather than from increased cane length. Generally 'Marion' has increased yield in biennial production, however, in this study, this was not found due to reduced bud break. The reduction in budbreak could have been caused by delaying training until February (not a commercial practice in AY production) resulting in canes having poor air circulation and light exposure throughout the fall and winter causing premature loss of leaves and increased disease pressure. 'Marion' can compensate for missing buds or fewer canes through increased percent budbreak to produce a greater number of fruitful laterals. This differs from the increased fruitfulness per node seen in raspberry (Gundersheim and Pritts, 1991; Waister and Barritt, 1980). The stimulation of natural branching of basal cane buds on primocanes that occurred when plants were grown without floricanes may have been in response to greater availability of assimilates or improved light conditions compared to plants with floricanes. In our findings, the primocane pruning treatment did not appear to have any advantages over unpruned canes. Further research on the role of root growth in relationship to primocane and floricane growth could be useful in understanding the dynamics of carbon partitioning in 'Marion'.

Literature cited

Bell, N., E. Nelson, B. Strik, and L. Martin. 1992. Assessment of winter injury to berry crops in Oregon, 1991. Agr Expt. Sta. Spec. Rpt. 902, Oregon State Univ.

Bell, N.C., B.C. Strik and L.W. Martin. 1995a. Effect of primocane suppression date on 'Marion' trailing blackberry. I. Yield components. J. Amer. Soc. Hort. Sci. 120:21-24.

Bell, N.C., B.C. Strik and L.W. Martin. 1995b. Effect of primocane suppression date on 'Marion' trailing blackberry. II. Cold hardiness. J. Amer. Soc. Hort. Sci. 120:25-27.

Braun, J.W., and J.K.L. Garth. 1984. Intracane yield compensation in the red raspberry. J. Amer Hort. Sci. 109:526-530.

Braun, J.W., J.K.L. Garth, and C.A. Brun. 1989. Distribution of foliage and fruit in association with light microclimate in the red raspberry canopy. J. Hort. Sci. 64:565-572.

Burt, J.G., K.N. Brown, and T.L. Cross. 1979. Enterprise cost study for Marion blackberries. Ore State Univ. Ext. Ser. Special Rep. 792.

Buszard, D.J.I. 1986. The effect of management system on winter survival and yield of raspberry in Quebec. Acta Hort. 183:175-182.

Clark, R.J. 1984. Biennial cropping, an alternative production system for red raspberries (*Rubus idaeus* L.). Scientia Hort. 24:315-321.

Crandall, P.C. 1980. Twenty years of red raspberry research in southwestern Washington State. Acta Hort. 112:53-59.

Crandall, P.C., D.F. Allmendinger, J.D. Chamberlain, and K.A. Biderbost. 1974. Influence of cane number and diameter, irrigation, and carbohydrate reserves on the fruit number of red raspberries. J. Amer. Soc. Hort. Sci. 99:524-526.

Dale, A. 1989. Productivity in red raspberry. Hort. Reviews. 199:185-228.

Fejer, S.O. 1979. Note on the effects of cane density in red raspberry. Gartenbauwissenschaft. 44:136-137.

Fernandez, G. and M. P. Pritts. 1993. Growth and source-sink relationships in 'Titan' red raspberry. Acta Hort. 352:151-157.

Fernandez, G.E. and M.P. Pritts. 1994. Growth, carbon acquisition and source-sink relationships in 'Titan' red raspberry. Acta Hort. 325:151-157.

Fernandez, G.E. and M.P. Pritts. 1996. Carbon supply reduction has minimal influence on current year's red raspberry (*Rubus idaeus* L.) fruit production. J. Amer. Soc. Hort. Sci. 121(3):473-477.

Gundersheim, N.A., and M. P. Pritts. 1991. Pruning practices affect yield, yield components, and their distribution in 'Royalty' purple raspberry. J. Amer. Soc. Hort. Sci. 116:390-395.

Kowalenko, C.G. 1994. Growing season dry matter and macroelement accumulations in Willamette red raspberry and related soil-extractable macroelement measurements. Can J Plant Sci. 74(3):565-571.

Lawson, H.M., and J.S. Wiseman. 1983. Techniques for the control of cane vigor in red raspberry in Scotland: Effects of timing and frequency of cane removal treatments on growth and yield in cv Glen Cova. J. Hort. Sci. 58:247-260.

Moore, P.P. 1994. Yield compensation of red raspberry following primary bud removal. HortScience, Vol. 29:701.

Moore, J.N. and G.R. Brown. 1971. Susceptibility of blackberry and blueberry cultivars to winter injury. Fruit Var. Hort. Digest 25:31-32.

Moore, J. N. and R.M. Skirvin. 1990. Blackberry Management, p. 214-244. In: G.J. Galletta and D.G. Himelrick (eds.). Small fruit crop management. Prentice Hall, Englewood Cliffs, N. J.

Nehrbas, S.R. and M.P. Pritts. 1988. Effect of pruning system on yield components of two summer- bearing raspberry cultivars. J. Amer. Soc. Hort. Soc. 113:314-321.

Orkney, G.D. and L.W. Martin. 1980. Fruiting potential and flower truss characteristics of select 'Willamette' red raspberry canes. Acta Hort. 112:191-193.

SAS Institute Inc. 1988. SAS/STAT user's guide. release 6.03. SAS Inst., Cary, N.C.

Sheets, W.A. and K.F. Kangas. 1970. Progress report on A-Y production of caneberries. Proc. Ore. Hort. Soc. 61:91-92.

Sheets, W. A. 1987. Alternate-year (AY) training is for real. Proc. Or. Hort. Soc. 78:179-182.

Strik, B.C. 1992. Blackberry cultivars and production trends in the Pacific Northwest. Fruit Var. J. 46:202-206.

Strik, B.C., H. Cahn, N. Bell, J. Cortell and J. Mann. 1996. What we've learned about 'Marion' blackberry, potential alternative production systems. Proc. Ore. Hort. Soc. 87 (in press).

Sullivan, J.A. and W.D. Evans. 1992. Comparison of conventional and alternate-row pruning in four raspberry cultivars. J. Hort. Sci. 67:375-380.

Waister, P.D. and B.H. Barritt. 1980. Compensation in fruit numbers following loss of lateral buds in the red raspberry. Hort Res. 20:25-31.

Waister, P.D., M. R. Cormack and W.A. Sheets. 1977. Competition between fruiting and vegetative phases in the red raspberry. J. Hort. Sci. 52:75-85.

Waister, P.D., C.J. Wright and M.R. Cormack. 1980. Potential yield in red raspberry as influenced by interaction between genotype and cultural methods. Acta Hort. 112:273-283.

Waister, P.D., and C.J. Wright. 1989. Dry matter partitioning in cane fruits. p. 51-61. In: C.J. Wright (ed.). Manipulation of fruiting. Butterworths, Boston, MA.

Whitney, G.C. 1982. The productivity and carbohydrate economy of a developing stand of *Rubus idaeus*. Can. J. Bot. 60:2697-2703.

Wood, C.A. 1960. Commercial raspberry: the integration of cultural factors. Sci Hort. 14:97-103.

Wright, C.J. and P.D. Waister. 1984. Light interception and fruiting cane architecture in the red raspberry grown under annual and biennial management systems. J. Hort. Sci. 59(3):395-402.

Wright C.J. and P.D. Waister. 1982a. Within-plant competition in red raspberry. I. Primocane growth. J. Hort. Sci. 57(4):437-442.

Wright C.J. and P.D. Waister. 1982b. Within-plant competition in red raspberry. II. Fruiting cane growth. J. Hort. Sci. 57(4):443-448.

Conclusions

Our research on 'Marion' trailing blackberry has many similarities yet some key differences to findings in red raspberry. This research contributes to the current understanding of 'Marion' physiology and provides a backbone for further research. The following is a summary of our findings and ideas for future research.

In 'Marion', we had similar findings to biennial red raspberry research (Waister et al., 1977; Waister et al., 1980; Wright and Waister, 1982b) as we found a greater number of primocanes on plants without floricanes and these primocanes had a reduced internode length. Generally 'Marion' has increased yield in biennial production (Nelson and Martin, 1989), but in this study, plants in AY production did not have a greater yield than those in EY production due to reduced budbreak. The reduction in budbreak observed may have been caused by delaying training until February (not a commercial practice in AY production) resulting in canes having poor air circulation and light exposure throughout the fall and winter causing premature loss of leaves and increased disease pressure.

We found 'Marion' can compensate for fewer canes through increased percent budbreak to produce a greater number of fruitful laterals. This agrees with other research on the ability of 'Marion' to compensate for lost or damamged buds (Bell et al., 1995a and Strik et al., 1996). In contrast, compensation found in red raspberry is usually through increased fruitfulness per node (Gundersheim and Pritts, 1991; Waister and Barritt, 1980).

Several findings in our research on 'Marion' have not been previously reported in red raspberry. One of these was the emergence of two flushes of primocanes without the use of primocane suppression. This may explain why primocane suppression in 'Marion' is a successful practice because the plants naturally sent up two flushes of canes separated by 1-2 months. It would be interesting to study whether this occurs in other *Rubus* species as well.

In addition, we found that both primocanes and branches, on an individual and a whole plant basis, grew in several flushes of growth throughout the season. This pattern was probably observed due to the numerous length measurements taken throughout the season compared to dry weight sampling techniques used in other studies. Further research on the factors influencing these dynamics in growth could help in understanding blackberry physiology. It would also be interesting to see if this pattern of growth flushes throughout the season is typical of other *Rubus* species.

Stimulation of natural branching of basal primocane buds occurring on plants without floricanes may have been in response to greater availability of assimilates or improved light conditions compared to plants with floricanes. In our findings, the primocane pruning treatment did not appear to have any advantages over unpruned canes, however, pruning at a higher height may have beneficial effects. Further research on carbohydrate partitioning and light interception in AY and EY systems could help explain the branching phenomenon in 'Marion'.

Although this research provides information on 'Marion' growth, partitioning of resources and yield components, additional studies could add more detail to our current understanding of blackberry physiology. This study could provide a foundation on which to develop new studies such as using radio-labeled C^{14} to trace movement of photoassimilates in primocanes, floricanes and roots. These types of experiments could be used to explore the dynamics of primocane growth in relation to fruit production and root growth, investigate the partitioning of resources in the occurrence of two flushes of growth, and possibly provide information on changes in absolute growth rate during the season. Other studies, such as to research the upper limit for cane density in 'Marion', light interception of the canopy and LAR measurements in EY and AY systems could be useful. Exploring factors that stimulate branching in 'Marion' as well as studying other primocane pruning techniques could be helpful in developing alternative production systems.

Bibliography

Anonymous. 1995. Berry crops summary. Ore. Agr. Stat. Serv., Portland, OR.

Bailey, J.S. 1948. A study of the rest period in red raspberries. Proc. Amer. Soc. Hort. Sci. 52:265-270.

Bell , N., E. Nelson, B. Strik, and L. Martin. 1992. Assessment of winter injury to berry crops in Oregon 1991. Oregon State University. Ag. Exp. Sta. Spec. Rep. # 902.

Bell, N., B. Strik, and L. Martin. 1995a. Effect of primocane suppression date on 'Marion' trailing blackberry. I. Yield Components. J. Amer. Soc. Hort. Sci. 120 (1):21-24.

Bell, N.C., B.C. Strik and L.W. Martin. 1995b. Effect of primocane suppression date on 'Marion' trailing blackberry. II. Cold Hardiness. J. Amer. Soc. Hort. Sci. 120 (1):25-27.

Bittenbender, H.C. and G.S. Howell Jr. 1974. Adaptation of the Spearman-Karber method for estimating the T_{50} of cold stressed flower buds. J. Amer. Soc. Hort. Sci. 99(2):187-190.

Braun, J.W., and J.K.L. Garth. 1984. Intracane yield compensation in the red raspberry. J. Am Hort. Sci. 109:526-530.

Braun, J. W., J.K.L. Garth, and C.A. Brun. 1989. Distribution of foliage and fruit in association with light microclimate in the red raspberry. J. Hort. Sci. 64:565-572.

Brierley, W.G., and R.H. Landon. 1946. Some relationships between rest period, rate of hardening, loss of cold resistance and winter injury in the Latham raspberry. Proc. Or. Hort. Soc. 71:97-100.

Bullock, R.M. 1961. Spacing, timing, training trials on caneberries at the North Willamette Branch experiment Station. Proc. Or. St. Hort. Soc. 53:97-99.

Burt, J.G., K.N. Brown, and T.L. Cross. 1979. Enterprise cost study for Marion blackberries. Ore State Univ. Ext. Ser. Special Rep. 792.

Buszard, D.J.I. 1986. The effect of management system on winter survival and yield of raspberries in Qubec. Acta Hort. 183:175-182.

Cameron, J.S., S.F. Klauer, and C. Chen. 1993. Developmental and environmental influences on the photosynthetic biology of red raspberry (*Rubus idaeus* L.) Acta Hort. 352:113-121.

Clark, R.J. 1984. Biennial cropping, an alternative production system for red raspberries (*Rubus idaeus* L.). Sci Hort. 24:315-321.

Conroy, B. 1967. The caneberry market situation-today, 1968, and the future. Proc. Or. Hort Soc. 59:105-109.

Crandall, P.C. 1980. Twenty years of red raspberry research in southwestern Washington State. Acta Hort. 112:53-59.

Crandall, P.C., J.D. Chamberlain , and J.K.L. Garth. 1980. The effects of chemical primocane suppression on growth, yield, and chemical composition of red raspberries. J. Amer. Soc. Hort. Sci. 105:194-196.

Crandall, P.C., D.F. Allmendinger, J.D. Chamberlain, and K.A. Biderbost. 1974. Influence of cane number and diameter, irrigation, and carbohydrate reserves on the fruit number of red raspberries. J. Amer. Soc. Hort. Sci. 99:524-526.

Dale, A. 1977. Yield responses to cane vigor control. Scot. Hort. Res. Inst. Assn., Bull. 13:12-18.

Dale, A. 1979. Varietal differences in the relationships between some characteristics of red raspberry fruiting laterals and their position on the cane. J. Hort. Sci. 54:257-265.

Dale, A. 1989. Productivity in red raspberry. Horticultural Reviews. 199:185-228.

Dale, A., and H. A. Daubeny. 1985. Genotype-environment interactions involving British and Pacific Northwest red raspberry cultivars. HortScience. 20:68-69.

Dale, A., and H. A. Daubeny. 1987. Flower-bud initiation in red raspberry (*Rubus* L.) in two environments. Crop Res. 27:61-66.

Dale, A. and P. B. Topham. 1980. Fruiting structure of the red raspberry: multivariate analysis of lateral characteristics. J. Hort. Sci. 55:397-408.

Dalman, P. 1989. Within-plant competition and carbohydrate economy in the red raspberry. Acta Hort. 262:269-277.

Darrow, G.M. and G.F. Waldo. 1933. Raspberry and blackberry cane measurements. Proc. Amer. Soc. Hort. Soc. 30:269-274.

Fejer, S.O. 1979. Note on the effect of cane density in red raspberry. Gartenbauwissenschaft 44:136-137.

Fernandez, G. and M. P. Pritts. 1993. Growth and source-sink relationships in 'Titan' red raspberry. Acta Hort. 352:151-157.

Fernandez, G.E. and M.P. Pritts. 1994. Growth, carbon acquisition and source-sink relationships in 'Titan' red raspberry. Acta Hort. 325:151-157.

Fernandez, G.E. and M.P. Pritts. 1996. Carbon supply reduction has minimal influence on current year's red raspberry (Rubus idaeus L.) fruit production. J. Amer. Soc. Hort. Sci. 121(3):473-477.

Freeman, J.A., V.R. Brookes and H.A. Daubeny. 1989. Effect of continual primocane removal on several raspberry cultivars. Acta Hort. 262:341-344.

Freeman, J.A., G.W. Eaton, T.E. Baumann, H. A. Daubeny, and A. Dale. 1989. Primocane removal enhances yield components of raspberries. J. Amer. Soc. Hort. Sci. 116:390-395.

Gundersheim, N.A., and M. Pritts. 1991. Pruning practices affect yield, yield components, and their distribution in "Royalty' purple raspberry. J. Amer. Soc. Hort. Sci. 116:390-395.

Hoover, E., J. Luby, D. Bedford, and M. Pritts. 1988. Vegetative and reproductive yield components of primocane fruiting red raspberries. J. Amer. Hort. Soc. Sci. 113:824-826.

Jennings, D.L. 1988. Raspberries and blackberries: Their breeding, diseases and growth. Academic Press, New York.

Jennings, D.L., E. Carmichael, and J.J. Costin. 1972. Variation in the time of acclimation of raspberry canes in Scotland and Ireland and its significance for hardiness. Hort. Res. 12:187-200.

Jennings, D.L., and M.R. Cormack. 1969. Factors affecting the water content and dormancy of overwintering raspberry canes. Hort Res. 9:18-25.

Jennings, D.L., and A. Dale. 1982. Variation in growth habit of red raspberries with particular reference to cane height and node production. J. Hort. Sci. 57:197-204.

Jennings, D.L., and G.R. McGregor. 1989. Some genetic factors that control the number and size of raspberry fruits produced on the raspberry cane, p. 315-327. In: C.J. Wright (eds.). Manipulation of fruiting. Butterworths, Boston.

Klauer, S.F., C. Chen, and J.S. Cameron. 1992. Diurnal photosynthesis and starch deposition in leaves of fruiting and deflowered red raspberry canes. HortScience. 27:654.

Kollanyi, L. 1988. Effect of the extent of pruning on the yield of raspberries and on the mass of the berries. Acta Agronomica Hungarica 37:227-231.

Kowalenko, C.G. 1994. Growing season dry matter and macroelement accumulations in Willamette red raspberry and related soil-extractable macroelement measurements. Can J. Plant Sci. 74(3):565-571.

Kraut, J.L., C.S. Walsh, and E.N. Ashworth. 1986. Acclimation and winter hardiness patterns in the eastern thornless blackberry. J. Amer. Soc. Hort. Sci. 111:313-315.

Lawson, H.M., and J.S. Wiseman. 1983. Techniques for the control of cane vigor in red raspberry in Scotland: Effects of timing and frequency of cane removal treatments on growth and yield in cv Glen Cova. J. Hort. Sci. 58:247-260.

Lawson, H.M., and J.S. Wiseman. 1977. Management factors in cane vigor. Bull. Scot. Hort. Res. Inst. Assn., Bull. 13:2-11.

Lott, R.V. 1931. Raspberry investigations: a preliminary study of the fruiting habit of the red raspberry -*Rubus strigosus.* Colo Agr. Expt. Sta. Bull. 367.

Mage, F. 1975. Dormancy in buds of red raspberry. Meldinger fra Norges landbrukshogskole # 85.

Moore, P.P. 1994. Yield compensation of red raspberry following primary bud removal. HortScience, Vol. 29:701.

Moore, J.N. and G.R. Brown. 1971. Susceptibility of blackberry and blueberry cultivars to winter injury. Fruit Var. Hort. Digest 25:31-32.

Moore, J. N. and R.M. Skirvin. 1990. Blackberry Management, p. 214-244. In: G.J. Galletta and D.G. Himelrick (eds.). Small fruit crop management. Prentice Hall, Englewood Cliffs, N. J.

Nehrbas, S.R. and M.P. Pritts. 1988. Effect of pruning system on yield components of two summer- bearing raspberry cultivars. J. Amer. Soc. Hort. Soc. 113:314-321.

Nelson, E. and L.W. Martin. 1989. Comparison of four training systems in alternate-year (AY) and Every-year (EY). Proc. Ore. Hort. Soc. 80:174-176.

Orkney, G.D. and L.W. Martin. 1980. Fruiting potential and flower truss characteristics of select 'Willamette' red raspberry canes. Acta Hort. 112:195-203.

Prive', J.P., J. A. Sullivan, J.T.A. Proctor and O.B. Allen. 1993. Climate influences vegetative and reproductive components of primocane-fruiting red raspberry cultivars. J. Amer. Soc. Hort. Sci. 118(3):393-399.

SAS Institute Inc. 1988. SAS/STAT user's guide. release 6.03. SAS Inst., Cary, N.C.

Sheets, W. A. 1987. Alternate-year (AY) training is for real. Or. Hort. Soc. 78:179-182.

Sheets, W.A., R.M. Bullock, and R.Garren, Jr. 1972. Effects of plant density, training, and pruning on blackberry yield. J. Amer. Soc. Hort. Sci. 97:262-264.

Sheets, W.A. and K.F. Kangas. 1970. Progress report on A-Y production of caneberries. Proc Ore. Hort. Soc. 61:91-92.

Sheets, W.A. and K.F. Kangas. 1972. Chemical pruning of blackberries with dinoseb. Proc. Or. Hort. Soc. 63:118-119.

Sheets, W.A., T.L. Nelson, and A.G. Nelson. 1975. Alternate-year production of Thornless Evergreen blackberries: technical and economic feasibility. Oregon State University. Ag. Exp. Sta. Bull. #620.

Strik, B.C. 1992. Blackberry cultivars and production trends in the Pacific Northwest. Fruit Var. J. 46:202-206.

Strik, B.C., and H. Cahn. 1996. Raspberry cane management for high yields; effect of cane density, pruning, and training on machine harvest efficiency and yield. Proc 38th Ann. Grower's Short Course and Trade Show. Ministry of Ag., Fisheries, and Food. BC., Canada. 61-63.

Strik, B.C., H. Cahn, N. Bell, J. Cortell and J. Mann. 1996. What we've learned about 'Marion' blackberry, potential alternative production systems. Proc. Ore. Hort. Soc. 87 (in press).

Sullivan, J.A. and W.D. Evans. 1992. Comparison of conventional and alternate-row pruning in four raspberry cultivars. J. of Hort. Sci. 67:375-380.

Van Adrichem, M.C.J. 1970. Assessment of winterhardiness in red raspberries. Can. J. Plant. Sci. 50:181-187.

Vasilakakis, M.D. and M.N. Dana. 1978. Influence of primocane inflorescence removal on number of inflorescences and suckers in 'Heritage' red raspberry. HortScience 13:700-701.

Waister, P.D., and B.H. Barritt. 1980. Compensation in fruit numbers following loss of lateral buds in the red raspberry. Hort Res. 20:25-31.

Waister, P.D., M. R. Cormack and W.A. Sheets. 1977. Competition between fruiting and vegetative phases in the red raspberry. J. of Hort. Sci. 52:75-85.

Waister, P.D., and C.J. Wright. 1989. Dry matter partitioning in cane fruits. p. 51-61. In: C.J. Wright (eds.). Manipulation of fruiting. Butterworths, Boston, MA.

Waister, P.D., and C.J. Wright, and M.R. Cormack. 1980. Potential yield in red raspberry as influenced by interaction between genotypes and cultural methods. Acta Hort. 112:273-283.

Warmund, M.R., and M.F. George. 1989. Freezing avoidance by supercooling in floral buds and canes of 'Shawnee' blackberry. Acta Hort. 262:333-340.

Warmund, M.R, M.F. George, and B.G. Cumbie. 1988. Supercooling in 'Darrow' blackberry buds. J. Amer. Soc. Hort. Sci. 113:418-422.

Whitney, G.C. 1982. The productivity and carbohydrate economy of a developing stand of *Rubus idaeus*. Can. J. Bot. 60:2697-2703.

Williamson, B., H.M. Lawson, J.A.T. Woodford, A.J. Hargreaves, J.S. Wiseman and S.C. Gordon. 1979. Vigour control, an integrated approach to cane, pest, and disease management in red raspberry (*Rubus idaeus*). Ann. Applied Biol. 92:359-368.

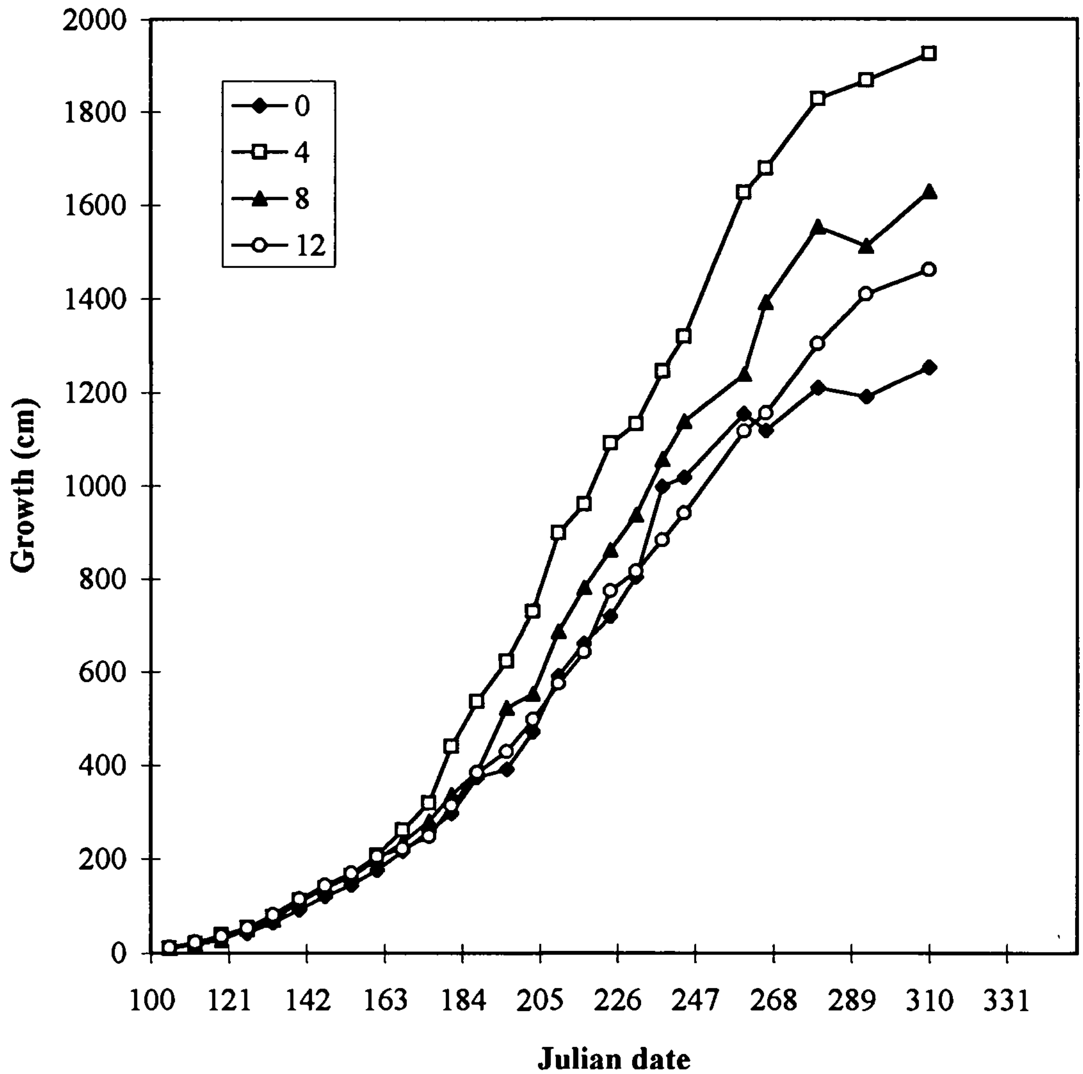
Wood, C.A. 1960. Commercial raspberry growing: the integration of cultural factors. Sci. Hort. 14:97-103.

Wright, C.J. and P.D. Waister. 1984. Light interception and fruiting cane architecture in the red raspberry grown under annual and biennial management systems. J. of Hort. Sci. 59(3):395-402.

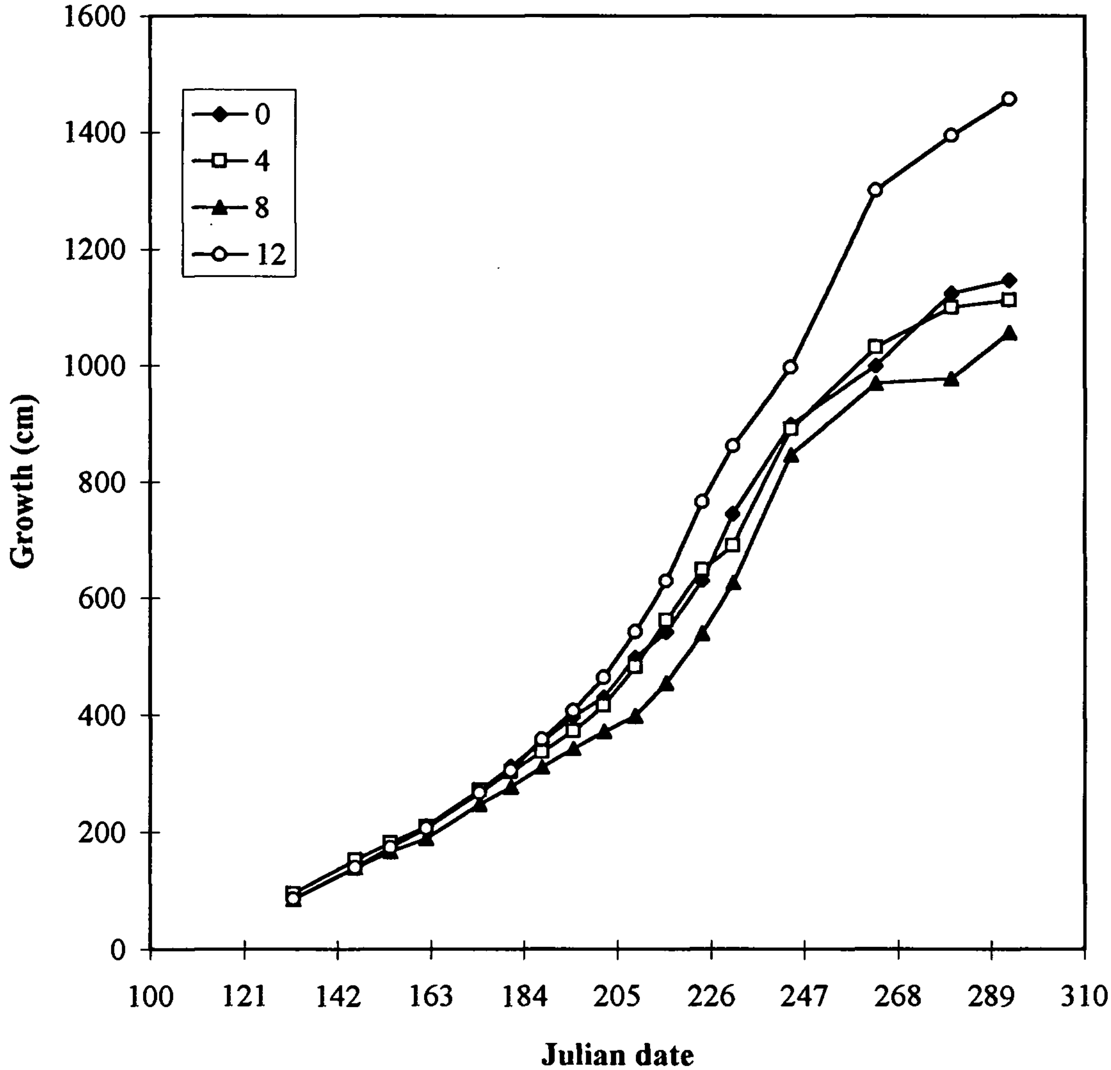
Wright C.J. and P.D. Waister. 1982. Within-plant competition in red raspberry. I. Primocane growth. J. of Hort. Sci. 57(4):437-442.

Wright C.J. and P.D. Waister. 1982. Within-plant competition in red raspberry. II. Fruiting cane growth. J. of Hort. Sci. 57(4):443-448.

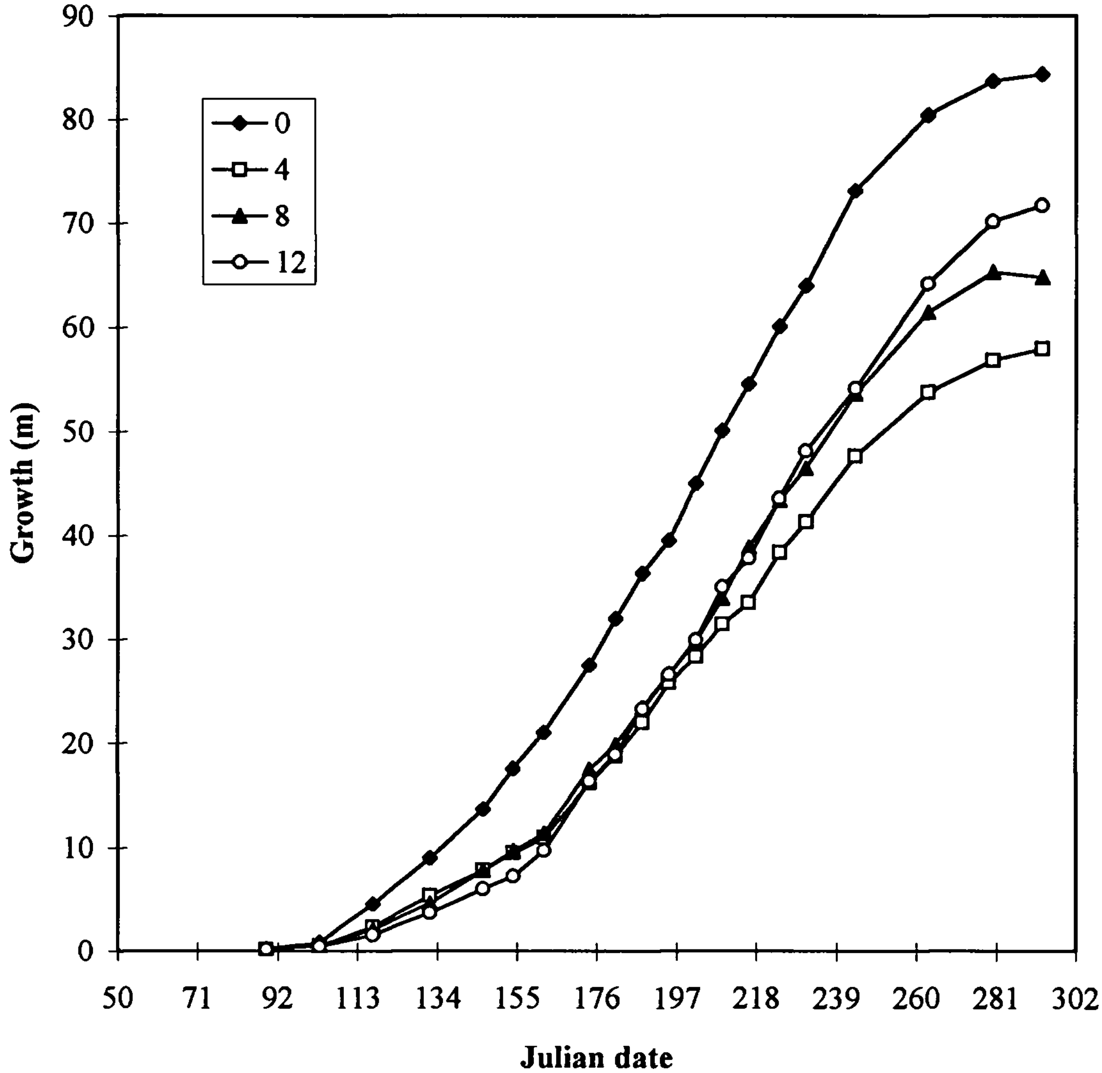
Appendix



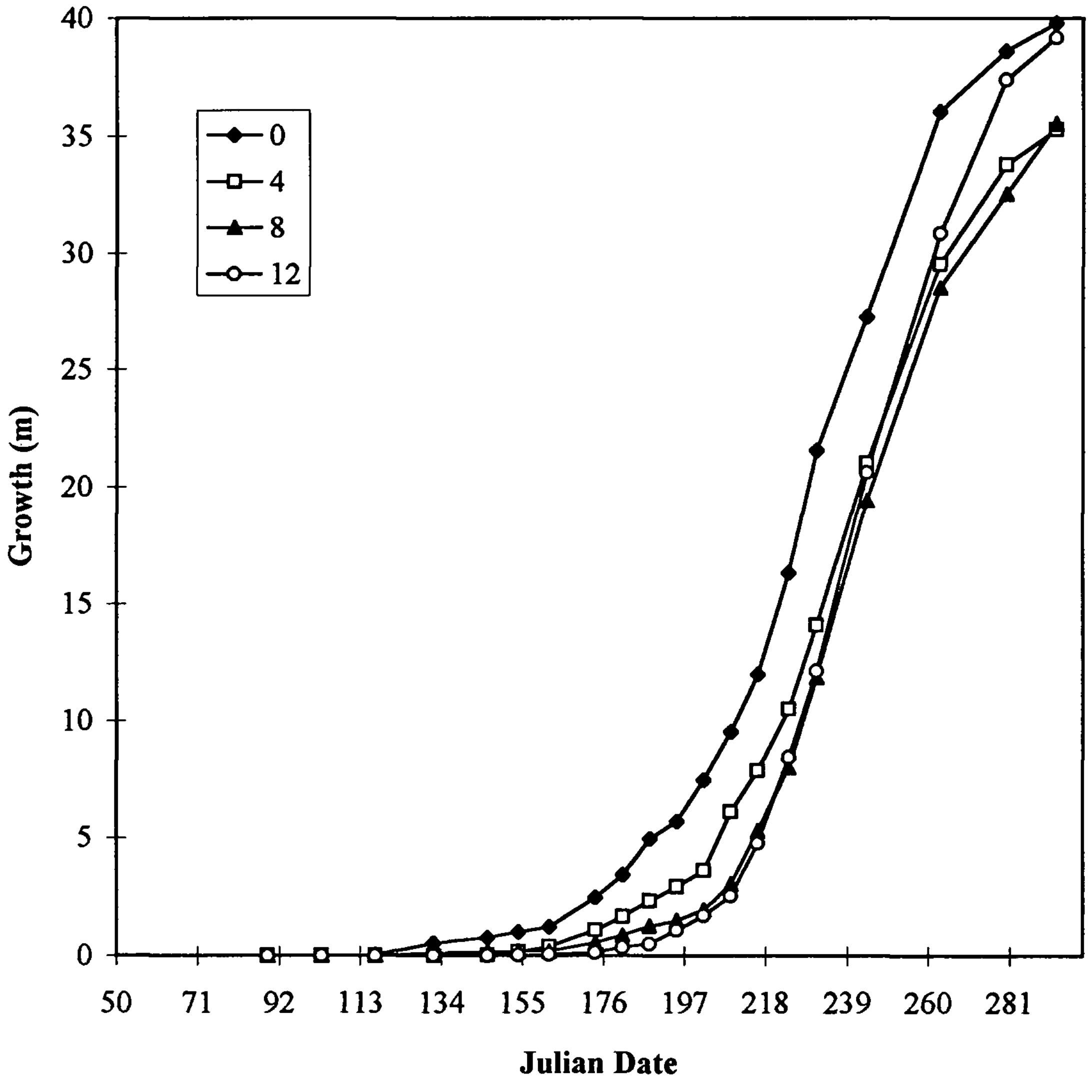
Appendix 1. Effect of floricane number on total (main + branch canes) primocane growth per cane in 1993.



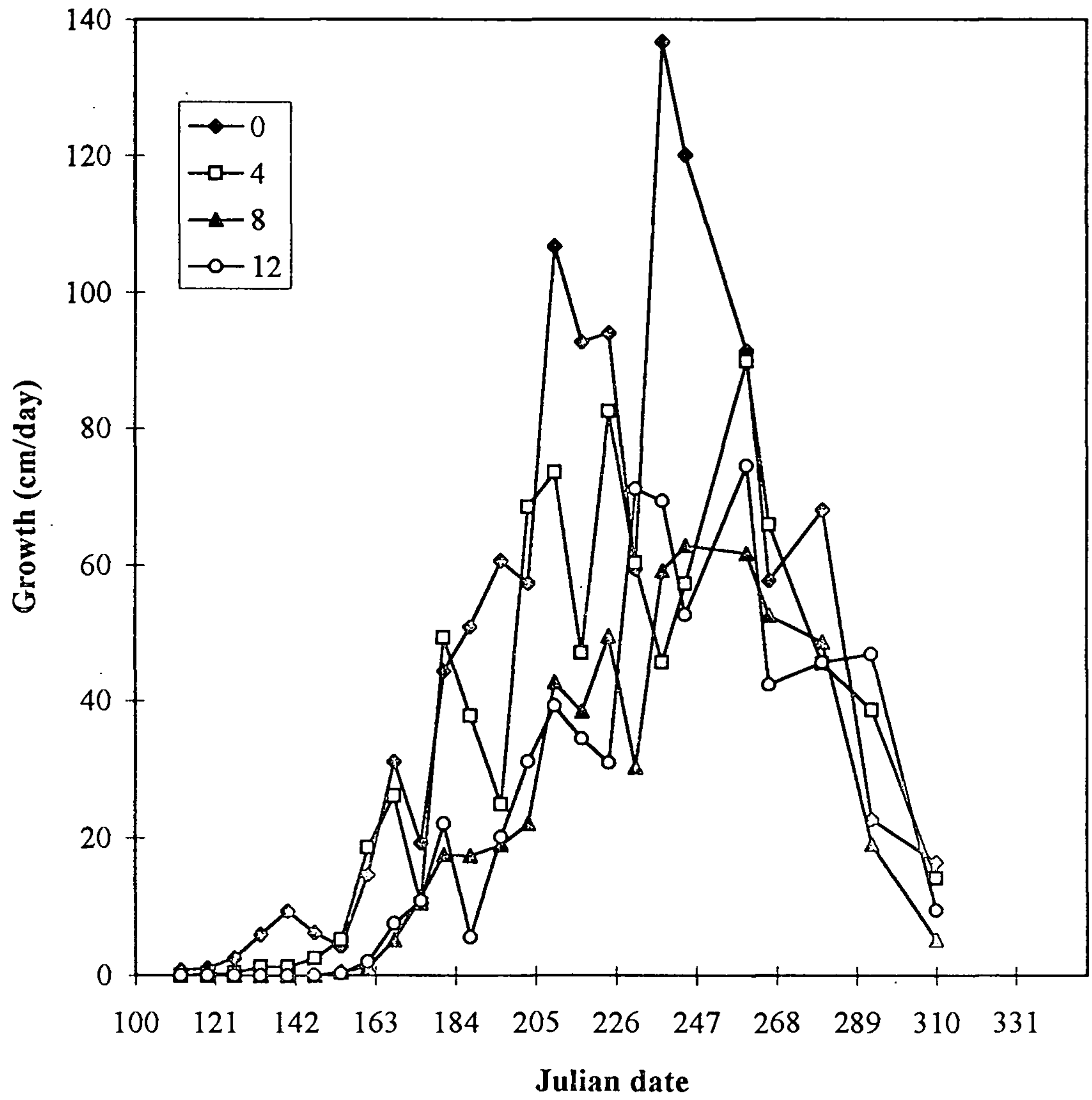
Appendix 2. Effect of floricane number on total (main + branch canes) primocane growth per cane in 1994.



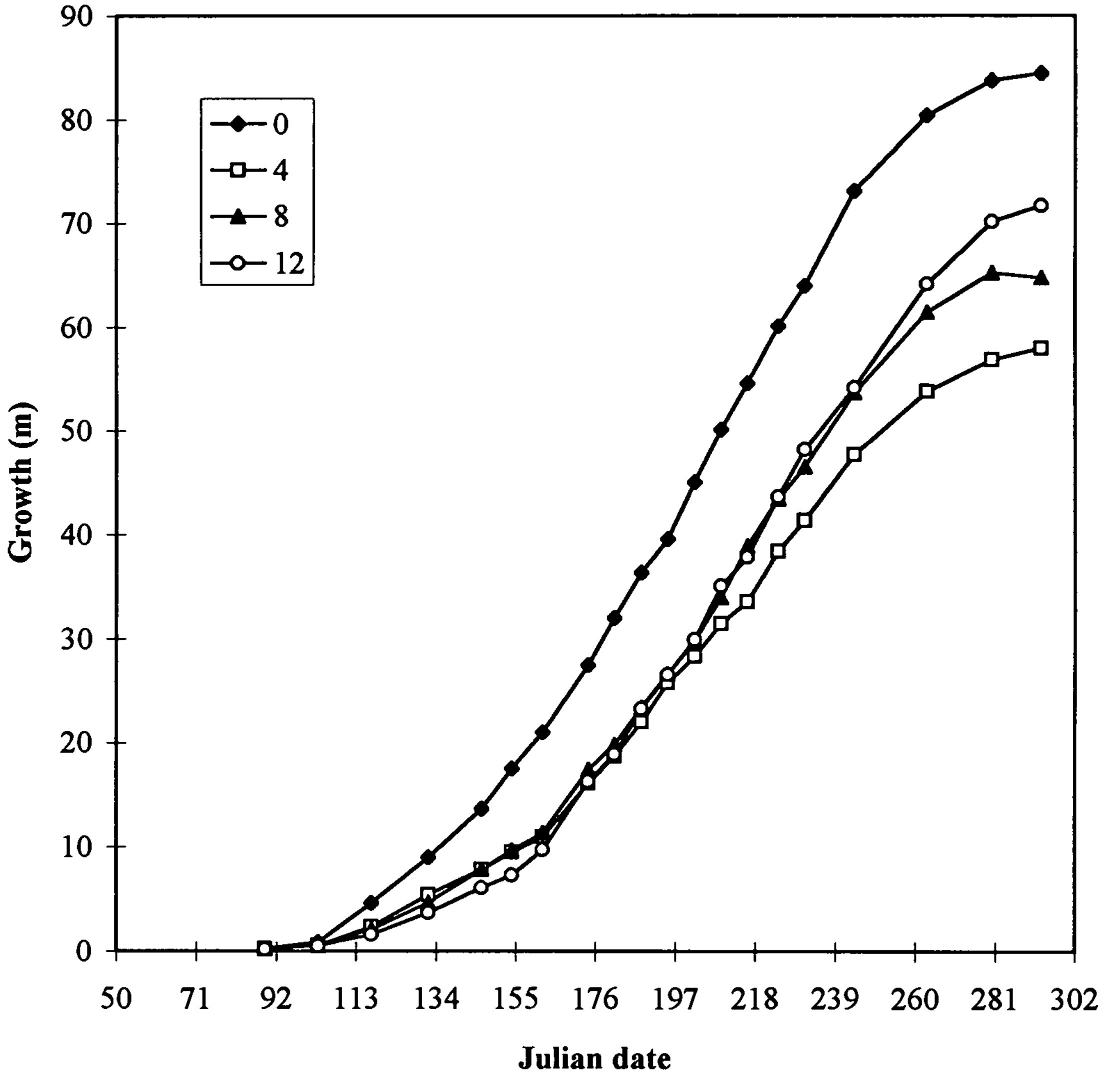
Appendix 3. Effect of floricane number on primocane growth per plant in 1994.



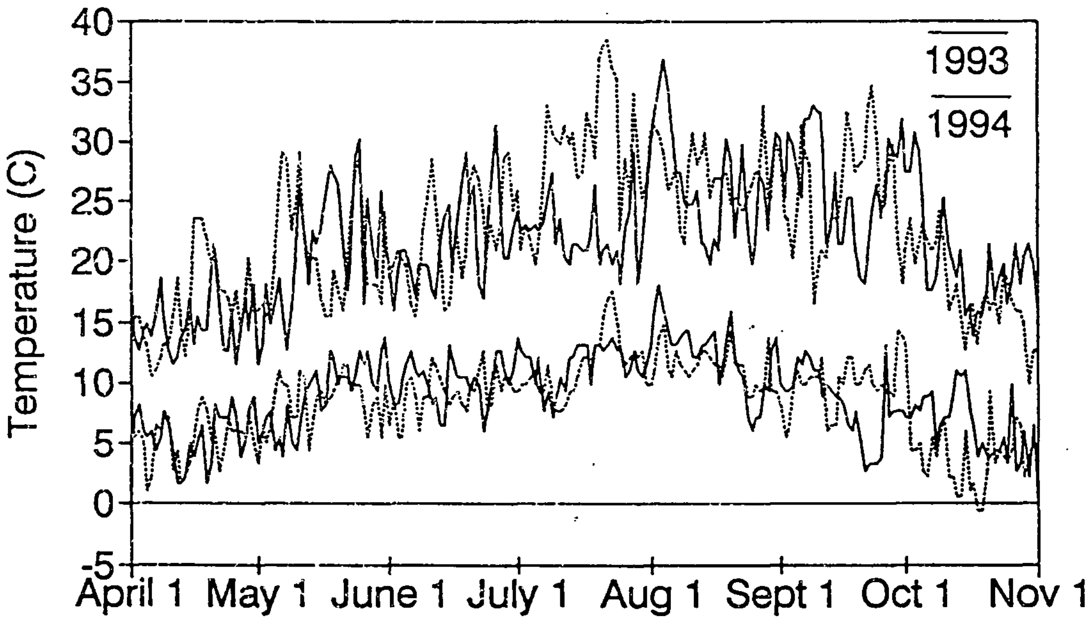
Appendix 4. Effect of floricane number on primocane branch growth per plant in 1994.



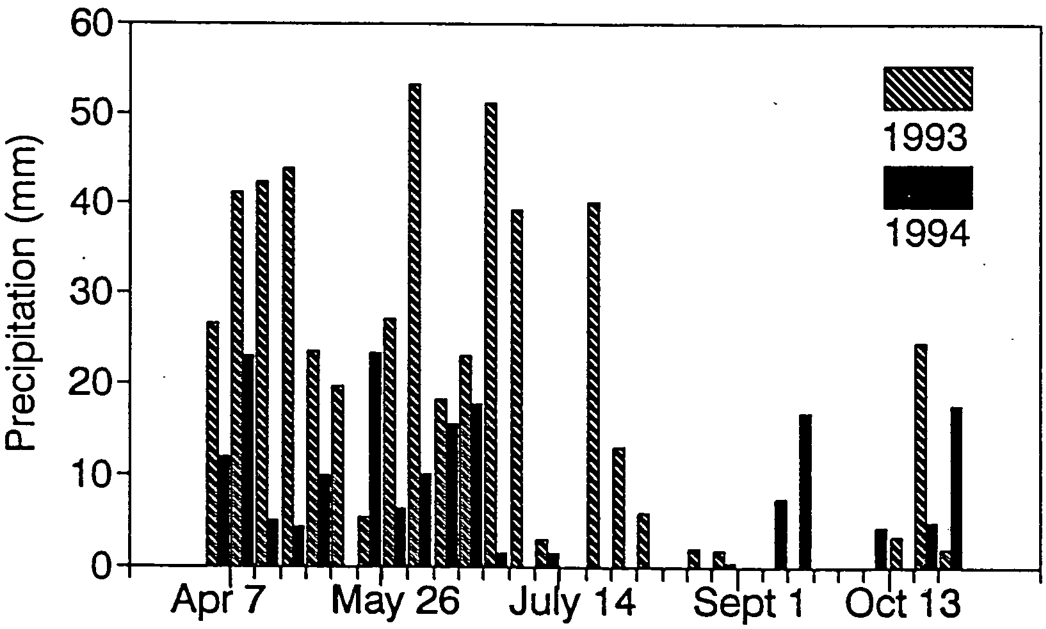
Appendix 5. Effect of floricane number on absolute growth rate (AGR) of primocane branches per plant in 1993.



Appendix 6. Effect of floricane number on absolute growth rate (AGR) of primocane branches per plant in 1994.



Appendix 7. Maximum and minimum temperatures in 1993 and 1994 at the North Willamette Research and Extension Center in Aurora, Ore.



Appendix 8. Precipitation in 1993 and 1994 at the North Willamette Research and Extension Center in Aurora, Ore.