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Effect of Floricane Number in 'Marion' Trailing Blackberry. I. Primocane Growth and Cold Hardiness

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ABSTRACT. **In Spring 1993 and 1994, mature trailing 'Marion' blackberries (*Rubus* L. subgenus *Rubus* Watson) were pruned to 0, 4, 8, and 12 floricanes/plant. An additional treatment of 0 floricanes with early (30 cm) primocane topping and pruning was included. Primocane length was measured from emergence in April until growth cessation at the end of October on individual canes and for the whole plant. In January 1994 and 1995, cane cold hardiness was evaluated by controlled freezing. In 1993, plants without floricanes produced more primocanes and branches with an increased total length at the end of the season than plants with floricanes. However, there were no significant differences in primocane length among treatments in 1994. In all treatments, the absolute growth rate (AGR), on a length basis, of primocanes occurred in flushes of rapid growth followed by slower growth throughout the season. Plants without floricanes had a significantly greater AGR than plants with floricanes on five dates in 1993. In 1994, there was no effect of floricane number per plant on AGR of primocanes over the season and the growth peaks were not as distinct. When comparing primocane elongation rate at three phenological stages in 1993, plants with no floricanes had a significantly higher total primocane growth per day during fruit production and from harvest to length cessation. The following year, plants with no floricanes had the highest rate of growth before bloom and a trend toward greater growth during fruit production. After fruit production, there were no differences in AGR between the treatments. Plants with floricanes produced a second flush of primocanes, while plants with no floricanes produced only one flush of primocanes. Primocane length of the first flush (averaged for 4-, 8-, and 12-floricane plants) was significantly different from the second flush at all dates during the season except for the final end of season measurement date. Primocanes pruned at 30 cm did not produce significantly more branches than unpruned primocanes on plants without floricanes. Plants without floricanes produced primocanes that were significantly more cold hardy (lower LT_{50}) in 1994 and 1995 than plants with floricanes.**

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). '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): in one year, the 'Marion' crop was reduced by 70% (Bell et al., 1992). In 'Marion', the buds are the plant part 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'. Sometimes this is a result of cold injury, in other cases some buds appear healthy green but do not break. Recent findings by Bell et al. (1995b) show improved cold hardiness in 'Marion' with late primocane suppression.

Two production systems currently used commercially for 'Marion' are every year (EY) and alternate year (AY) production. In annual or EY production, the vegetative primocanes grow concurrently with the reproductive floricanes during fruit production. In the biennial or AY system, only primocanes grow in the "off" year and fruit the following "on" year. This separates the vegetative and reproductive phases of growth and, consequently, is a good model for studying source–sink relationships. 'Marion' primocanes grown in the AY system have been observed in the field to have greater cold hardiness than those in the EY system (Sheets, 1987). In AY production, 85% of the yield of the EY system is produced over a 2-year period. AY production also has the advantages of reducing labor, fertilizer, and pesticide inputs; eliminating damage to the primocanes during machine harvest; and providing a less-favorable environment for disease over the EY system (Sheets, 1987). An increase in primocane number during the "off" year in the AY system was found in 'Marion' and other caneberry cultivars (Sheets et al., 1972). Nelson and Martin (1989) found that 'Boysen' 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 floricane number on primocane physiology and growth.

Many scientists have documented competition between primocanes and floricanes in red raspberry (Crandall et al., 1980; Nehrbas and Pritts, 1988; Vasilakakis and Dana, 1978; Williamson et al., 1979; Wright and Waister, 1982 a, 1982b). 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, fruit yield the following season was higher due to a greater number of primocanes and nodes per cane (Wright and Waister, 1982b). Clark (1984) found in raspberry that the AY system yielded ≈75% as much as the traditional EY system over a 2-year 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

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harvest, and another linear increase after harvest (Fernandez and Pritts, 1993). Whitney (1982) found that carbohydrate levels in the primocanes were high early in the spring, dropped to low concentrations in July, then returned to higher levels by the end of the season. Waister and Wright (1989) found that postharvest primocane growth in red raspberry could account for as much as 25% of the total dry mass 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. 'Marion' is more vigorous, has a trailing growth habit, produces numerous primocane branch canes, and is more productive in the basal rather than the terminal cane section in contrast to raspberry (Bell et al., 1995a). 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), where primocanes are topped or pruned. However, the effect of primocane pruning on growth and yield of trailing blackberry has not been researched to date.

The objectives of this project were to determine the effect of floricane number and primocane pruning on primocane growth and subsequent cold hardiness of 'Marion' blackberry. The effect of floricane number on yield components in the same season and in the following year, and on dry mass partitioning are presented in Cortell and Strik (1997).

Materials and Methods

An 8-year-old planting of 'Marion' blackberry on a latourell loam soil at the North Willamette Research and Extension Center, Aurora, Oreg., 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. In February 1993 and 1994, plants were pruned to establish treatments of 0, 4, 8, and 12 floricanes/plant and floricanes were trained to the trellis. Excess canes on each plant were counted and removed at ground level. An additional treatment was included with 0 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. The experimental design was completely randomized with five replications of three plants per plot.

PRIMOCANE GROWTH MEASUREMENTS. Primocane growth was measured on one plant in each replicate. The third primocane to emerge was labeled for individual cane measurements. The length of the main cane, 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 main and branch canes on the plant were counted and measured for total length. In 1994, an additional cane from a second flush of growth was marked and measured independently for one plant in each replication.

COLD HARDINESS EVALUATION. In January 1994 and 1995, canes were randomly selected from treatment plants. Four-node cane sections were chosen 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 randomly selected for each temperature regime for each of the five treatments and five replications.

Cane sections were bundled in subsamples of five, wrapped in cheesecloth, 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, and –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/h. Temperature within freezer packs was monitored by thermocouples attached to a DAS 8 data acquisition and interface board (Metra Byte Corp., Taunton, Mass.). 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 ≈2 weeks, percent budbreak was determined. The buds were recorded as being dead, still green but with 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 temperature at which 50% budbreak occurred (LT_{50}) for each treatment.

STATISTICAL ANALYSIS. General trends in primocane growth

Fig. 1. Effect of floricane number on total (main + branch canes) primocane length per plant in 1993.

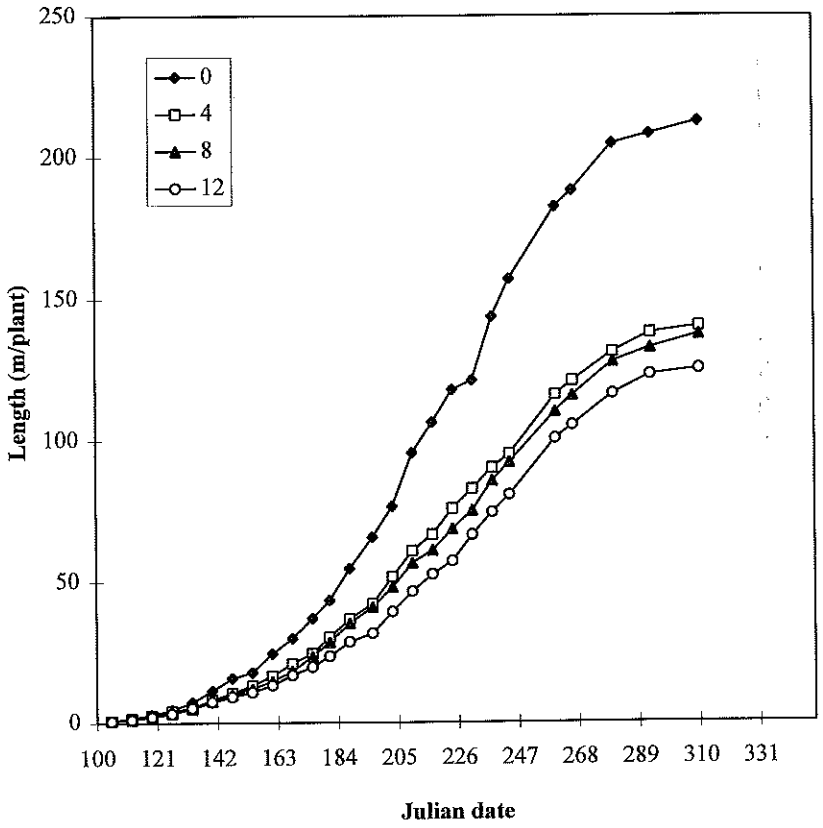


Table 1. Equations for logarithmic transformed data for total (main + branch cane) primocane length in 1993 and 1994.

Floricanes (no.)	Variable[z] r ($m \cdot d^{-1}$)	K (m/plant)
	1993	
0	0.036	224.59
4	0.033	150.26
8	0.032	149.49
12	0.032	139.20
Contrast		
0 vs. others	NS	***
	1994	
0	0.032	138.46
4	0.032	98.79
8	0.033	106.72
12	0.034	119.98
Contrast		
0 vs. others	NS	NS

[z]Abbreviations: r = intrinsic rate of increase; K = asymptote or carrying capacity for logistic growth curve (Hunt, 1982).
NS,***Nonsignificant or significant at $P < 0.001$, respectively.

were compared using repeated measures analysis (SAS Institute, Cary, N.C.). Data for end of season primocane growth components and cold hardiness were analyzed by linear regression with contrasts used for treatment comparisons. Primocane length data were analyzed by nonlinear regression (SAS Institute, 1988). The logistic growth curve was fit to the data with the growth curve descriptors for each treatment; r = the intrinsic rate of increase and K = the asymptote or carrying capacity, compared by analysis of variance and contrasts (Hunt, 1982). Absolute growth rate (AGR) was calculated with the following equation:

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

where dL = the change in length and dT = the number of days. AGR also was calculated and compared by analysis of variance for three time periods: before bloom, during fruit production, and harvest to length cessation.

Results and Discussion

Primocane growth. Although individual cane measurements were determined, whole-plant results are presented because they were less variable within a treatment. Years were compared using the end of the season primocane growth data. There was a significant year effect on primocane number ($P = 0.02$), branch number ($P = 0.0001$), primocane length ($P = 0.02$), branch length ($P = 0.0001$), and total (main cane + branch canes) length ($P = 0.0001$). There was a year × floricane number interaction on total length ($P = 0.04$). Thus, the results are presented separately by year. The significant year effects may have been due to an unusually wet Summer 1993 compared to the more typical warm and dry Summer =1994 (data not shown). In red raspberry, soil temperature and water were found to have a major influence on vegetative components (Privé et al., 1993).

Nonlinear regression showed that floricane number per plant had a significant effect on the total primocane length in 1993 (Fig. 1; Table 1, K). Plants with no floricanes produced a greater total primocane length than those with 4, 8, or 12 floricanes in 1993 (Table 1). There was a trend ($P < 0.06$) for the early season growth rate (Table 1, r) to be greater in plants without floricanes. However, there was no significant effect of floricane number on total length in 1994 (Table 1).

In 1993, plants without floricanes produced more primocanes with a greater total length than plants with floricanes (Table 2). These results are comparable to findings in red raspberry where primocane dry mass in biennial plots (no floricanes) was found to

Table 2. Effect of floricane number per plant on end of season total primocane growth in 'Marion'.

Floricane (no.)	Primocanes (no.)	Internode length (cm)	Main cane length/plant (m)	Branch canes (no.)	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
r^2	0.27	0.11	0.28	0.27	0.45	0.59
Significance	*	NS	*	*	**	***
Contrast						
0 vs. 4, 8, 12	**	NS	***	*	**	***
4 vs. 8, 12	NS	NS	NS	NS	*	NS
8 vs. 12	NS	NS	NS	NS	NS	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
r^2	0.02	0.02	0.03	0.01	0	0.02
Significance	NS	NS	NS	NS	NS	NS
Contrast						
0 vs. 4, 8, 12	NS	NS	NS	NS	NS	NS
4 vs. 8, 12	NS	NS	NS	NS	NS	NS
8 vs. 12	NS	NS	NS	NS	NS	NS

NS,*,**,***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

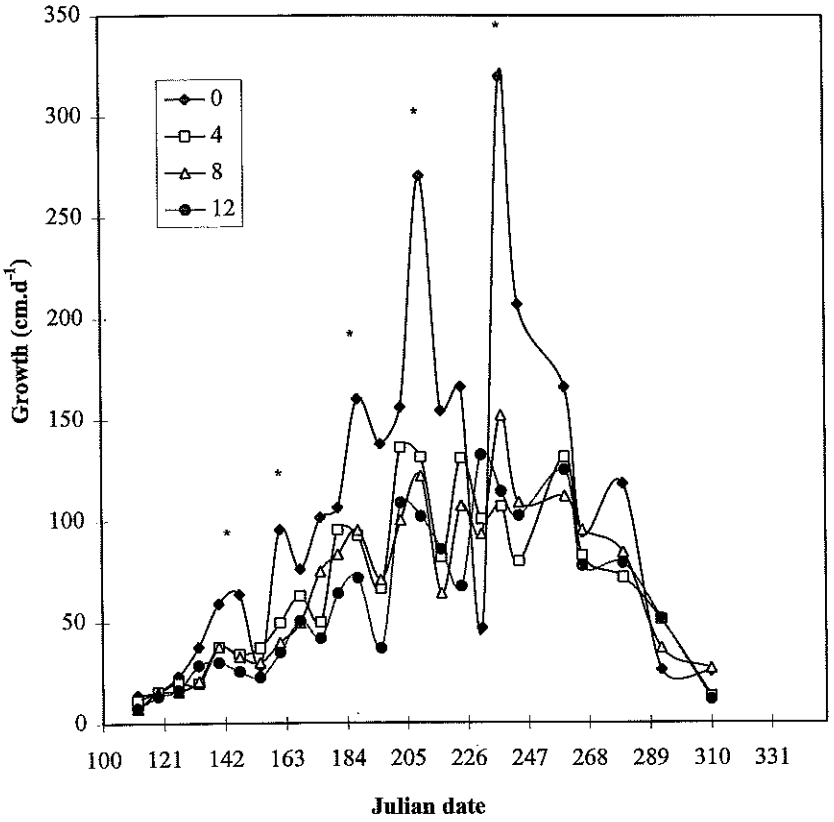


Fig. 2. Effect of floricane number on absolute growth rate (AGR) of primocanes per plant in 1993. Stars denote significant treatment effects at that date ($P < 0.05$).

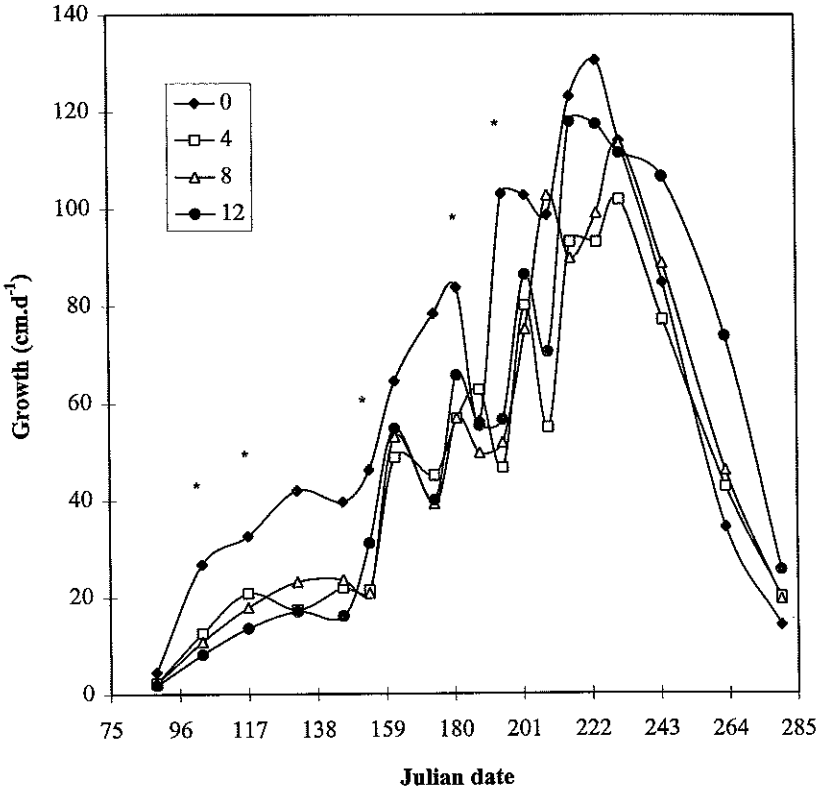
exceed annual plots throughout the season because of a greater number of canes (Wright and Waister, 1982a; Waister and Wright, 1989). Sheets and Kangas (1970) also found that more canes were produced in the "off" year of AY production in 'Marion' blackberry. Wright and Waister (1982a) suggested that the increased emergence of primocanes in red raspberry could be due to removal of apical dominance exerted by the floricanes or competition in spring for stored reserves in the roots. Research in red raspberry also has shown that, in the absence of floricanes, primocanes are produced with a reduced internode length (Waister et al., 1977; Wright and Waister, 1982a). However, in our study, floricane number had no significant effect on internode length of 'Marion' (Table 2).

Plants without floricanes also produced many primocane branches that were longer than on plants with floricanes in 1993 (Table 2). Plants in which all floricanes were removed produced primocanes that tended to branch naturally (without a pruning treatment) 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. Primocanes of plants with 4, 8, or 12 floricanes also showed 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. In 'Marion', 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 budbreak and the number of fruit per lateral in 'Marion' (Bell et al., 1995a) and in red raspberry (Braun et al., 1989).

Although a significant linear relationship was found for floricane number on most growth component data in 1993, there were no significant differences among plants with 4, 8, or 12 floricanes for most components (Table 2). The lack of significant differences among plants with floricanes was perhaps due to the low yields in 1993, which did not provide a strong competitive reproductive sink (Cortell and Strik, 1997). Yield compensation occurring in response to the reduction in floricane number also reduced differences between the treatment levels (or sink) of floricanes (Cortell and Strik, 1997), again helping to explain the lack of differences in primocane growth for plants with varying numbers of floricanes. There were no significant treatment effects at the end of the season for primocane growth components in 1994 (Table 2). The lack of significant results may have been because of high variability in the original cane number per plant before treatment establishment (data not shown) and significant differences in crown dry mass data (Cortell and Strik, 1997).

Fig. 3. Effect of floricane number on absolute growth rate (AGR) of primocanes per plant in 1994. Stars denote significant treatment effects at that date ($P < 0.05$).



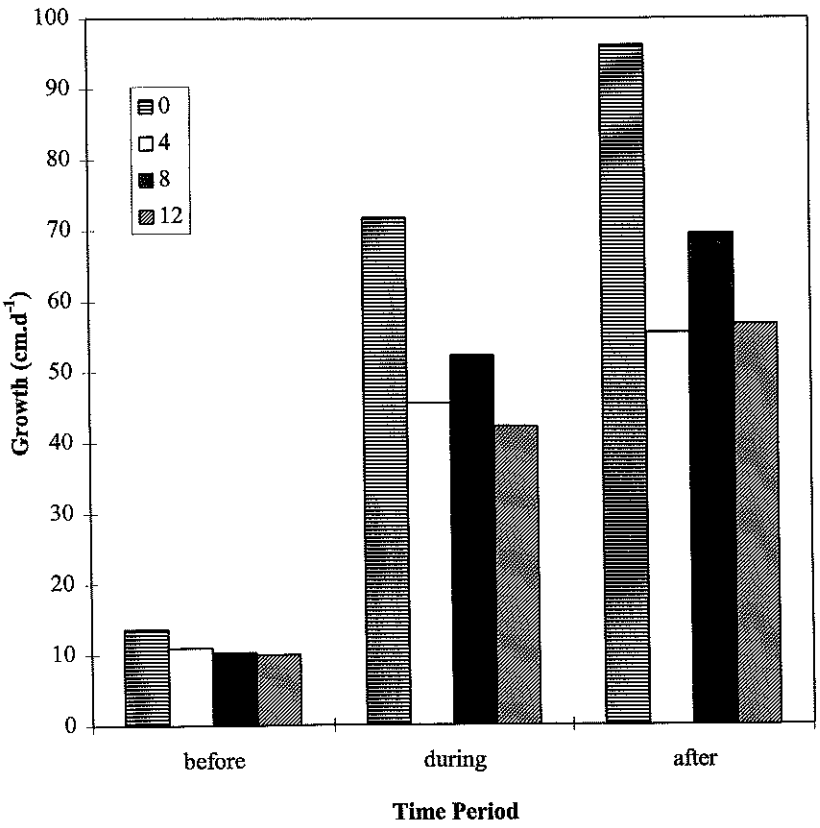


Fig. 4. Effect of floricane number on absolute growth rate (AGR) of primocanes per plant during three time periods ("before" bloom, bloom to the end of harvest = "during", and end of harvest to length cessation = "after") in 1993.

End-of-season results for the primocane pruning experiment in 1993 showed trends for a decrease in primocane number ($P = 0.07$) and total length ($P = 0.06$), with tipping at 30 cm. In 1994, primocane pruning resulted in a significant increase in branch cane length ($P = 0.05$) (data not shown). The lack of differences in branch length in 1993 suggest that 'Marion' may be stimulated to produce lateral branch canes in response to other factors besides pruning. Although no significant treatment effects were found, some possible disadvantages of the pruning treatment were that the canes had greater self-thinning, increased shading of buds, and increased disease pressure. The effect of pruning or topping primocanes in the presence of floricanes or at a greater length, as is done in erect blackberry (Moore and Skirvin, 1990), was not studied here.

AGR. The AGR per plant varied with time ($P = 0.0001$), and there was a time × treatment interaction ($P = 0.0001$) in 1993 (Fig. 2), while in 1994 there was only a significant time effect ($P = 0.0001$) (Fig. 3). In all treatments in 1993, primocane growth occurred in flushes, with plants in the 0-floricane treatment having five dates where primocane elongation was significantly greater than in plants with floricanes. This has not been reported in blackberry or red raspberry, and was likely observed due to frequent and repeated measurement of cane length during the growing season. In 1994, there was no treatment effect on AGR over the season, and the peaks were not as distinct (Fig. 3). However, plants without floricanes had a greater primocane growth rate than plants with floricanes on five dates before fruit harvest (Fig. 3). 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 for flushes of cane growth is that this was in response to the weekly 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 and irrigation scheduling data (data not shown), and 1993 was a very wet summer and it is unlikely that the plants experienced water stress. Consequently, the reasons for flushes of growth occurring in primocanes are not understood.

AGR was compared at three phenological time periods: from primocane emergence to bloom, bloom to end of harvest, and end of harvest to length cessation. In 1993, plants in the 0-floricane treatment had a significantly higher primocane elongation per day from bloom to harvest and from harvest to length cessation for total (primocane + branch) growth per day ($P = 0.0001$) compared to those treatments with floricanes (Fig. 4). Analysis of variance indicated a significant time period effect in 1993 and 1994 ($P = 0.0001$) and a time period × floricane number interaction in 1994 ($P = 0.0002$). In 1994, plants with no floricanes had the highest rate of elongation before bloom ($P = 0.006$) compared to those with floricanes (Fig. 5). There were no differences in the elongation rate among treatments

Fig. 5. 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 length cessation = "after") in 1994.

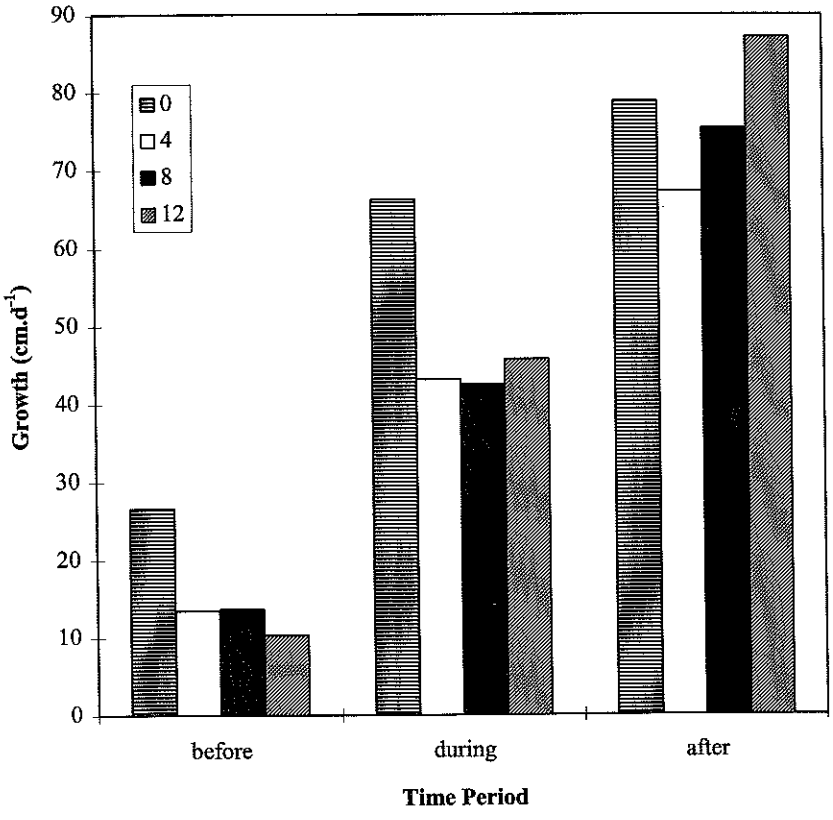


Table 3. Effect of floricane number on subsequent cold hardiness (LT_{50}) of primocanes in 1994 and 1995 (°C).

	Floricanes (no.)						Contrast
Hardiness	0	4	8	12	r^2	Significance	0 vs. 4, 8, 12
				1994			
LT_{50}	–8.95	–6.80	–7.30	–5.85	0.39	**	**
				1995			
LT_{50}	–23.0	–17.6	–18.1	–16.3	0.54	***	***

,*Significant at $P < 0.01$ or 0.001, respectively.

after fruit harvest (Fig. 5). The similar growth rates of all treatments after harvest may have been due to reduced competition by the spent floricanes or because of higher original vigor in plants with floricane treatments. Fernandez and Pritts (1993) found that the primocane growth rate decreased during fruit production in red raspberry, although we did not document this in 'Marion'. They suggested that the reduction in primocane growth during fruit development may have been caused by competition from the roots for photosynthate. Roots were not recovered in this experiment. Waister and Wright (1989) found that postharvest primocane growth in red raspberry could account for as much as 25% of the total dry mass at the end of the season. In our study, 58% and 66% of the total increase in primocane length and 47% and 34% of the total dry mass (Cortell and Strik, 1997) in 'Marion' occurred after harvest in 1993 and 1994, respectively.

Comparison of the first and second flush of primocane growth. Plants with floricanes produced a second flush of primocanes, whereas those plants without 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 longer than the second flush at all dates during the season except for the final end-of-season measurement date ($P = 0.08$, data not shown). The second flush of primocanes emerged during the green-red fruit stage. Primocanes that emerged in the second flush therefore had a higher growth rate, as there was no significant difference in length between the two flushes by the end of the season. The occurrence of two flushes of primocanes on plants with floricanes has not been documented previously in blackberry (without primocane suppression) or red raspberry. The emergence of a second flush in our study 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, the root system of red raspberry is also a strong sink (Fernandez and Pritts, 1993, 1994, 1996). Consequently, it is possible in 'Marion' that the leaf area of floricane laterals as well as primocanes function as sources and replenish carbohydrate levels in the root system and, in turn, the crown can support a second flush of primocane growth. Plants without floricanes may have had a reduced source supplying carbohydrates to the root system and crown, perhaps explaining why these plants did not produce a second flush of primocanes.

Cold hardiness evaluation. Primocanes from all treatments had greater hardiness in 1995 than in 1994 (Table 3). This reduction in cold hardiness in 1994 was most likely because of warm weather preceding the evaluation, which caused the buds to start emerging. After fulfilling its rest requirement, 'Marion' has been found to lose hardiness after warm periods of weather (Bell et al., 1992b). Plants without floricanes produced primocanes that were significantly more cold hardy (lower LT_{50}) in 1994 and 1995 than those with floricanes (Table 3). Although the reason for increased cold hardiness in plants grown without floricanes is not understood, our research agrees with observations noted by Sheets (1987). In other research, Bell et al. (1995b) found increased hardiness with later primocane suppression (primocanes then grow in absence of floricanes). Carbohydrates are thought to be associated with cold hardiness, but Bell et al. (1995b) did not find a relationship between carbohydrate levels and hardiness in 'Marion' blackberry.

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