Root Pruning Effects on Growth and Yield of Red Raspberry

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Abstract. Annual production systems for red raspberry (*Rubus idaeus* L.) have been proposed for off-season production or for increasing crop diversity in warm winter climates. However, yields in these annual systems are low compared with annual yields in perennial production systems. The yield reduction may be from the root pruning that occurs during removal and shipment of the canes from the nursery. This would result in significant root loss and may decrease the availability of root carbohydrates for reproductive development. To investigate this, 'Cascade Delight' red raspberry plants were root pruned during dormancy, and growth and fruiting of these plants were compared with non root-pruned controls the next season. Dry weights of all organs except floricanes stems increased throughout the growing season; however, root pruning decreased root, floricanes lateral, and total fruit dry weight compared with no root pruning. The yield decrease observed in root-pruned plants was because of a decrease in flower and fruit number per cane compared with the control. Total carbohydrate concentration in roots of root-pruned and non root-pruned plants decreased significantly between pruning and budbreak; however, root carbohydrate concentration and content were always lower in root-pruned compared with non root-pruned plants. The lower root carbohydrate availability in root-pruned compared with non root-pruned plants during budbreak apparently limited flower bud formation/differentiation, resulting in decreased yield. These results suggest that yields in annual red raspberry production systems are limited because of the loss of root carbohydrates during removal from the nursery. Management practices that increase yield per plant (e.g., by ameliorating root loss) or increase yields per hectare (e.g., by increasing planting density) are needed to render the annual production system economically viable.

There is increasing interest in off-season production of raspberry, necessitating the need for new cropping systems. In subtropical areas, an annual production system has been examined (Darnell et al., 2006; Knight et al., 1996). This system uses prechilled, dormant, long-cane raspberry plants obtained from northern nurseries, thus eliminating problems associated with insufficient chilling and dormancy release. Plants are field-planted in January and fruit harvest occurs as early as March (Darnell et al., 2006; Knight et al., 1996). In this annual system, raspberry plants are removed after harvest and are replaced with new prechilled long-caness for the next season. Previous work has shown that yields in this annual system are less than yields observed in perennial red raspberry production systems (Alvarado-Raya et al., 2007; Darnell et al., 2006). This may be from disturbance of the root system during digging and shipment from the nursery, which can lead to significant root loss. This, in turn, can result in decreased root carbohydrate reserves and decreased yield.

Many studies have shown that root pruning in temperate crops affects shoot growth and yield. Dormant root pruning, such as

what occurs in the above described annual raspberry production system, reduces vegetative growth and fruit size in apple (Schupp and Ferree, 1987; 1989), grape (Ferree et al., 1999; Lee and Kang, 1997), and sweet cherry (Webster et al., 1997). This may be from removal of a large source of reserve carbohydrate in the roots that would normally be used to support vegetative or floral budbreak.

In raspberry, spring vegetative and reproductive growth are concomitant (Atkinson, 1973), and both need carbohydrate for production of new biomass. Primocanes also begin growth at this time and are an additional sink for root carbohydrates (Whitney, 1982). Root pruning could further exacerbate carbohydrate competition because root growth also increases after root pruning (Schupp et al., 1992), resulting in additional sink activity. Given this scenario and the low photosynthetic activity in floricanes leaves before bloom (Fernandez and Pritts, 1994), there is a high probability that roots of raspberry plants, especially in an annual production system, may be carbohydrate depleted by the beginning of bloom.

Root carbohydrate depletion before bloom would potentially decrease flower bud number (and therefore fruit number) and fruit size in raspberry. Flower bud initiation/differentiation in the lower portion of raspberry floricanes continues during early bloom (Williams, 1959; Qingwen and Jinjun, 1998),

and work with other fruit crops indicates that adequate carbohydrate supply is critical for this process (Darnell, 1991; Ooshiro and Anna, 1998). Therefore, the elimination of part of the root system during dormancy could decrease the carbohydrate reserves required for early floricanes lateral growth, including flower bud initiation and consequently, fruit number and yield.

Additionally, root pruning may also affect cane yield by decreasing fruit size. Fernandez and Pritts (1996) found that the maximum demand for assimilates in red raspberry is at the onset of fruiting while primocanes, roots, and fruits are all growing. In an annual cropping system, the elimination of part of the root system and the consequent intensive root regeneration (Schupp et al., 1992) during the high sink activity of the raspberry plant could decrease carbohydrate availability for the developing fruit.

The hypothesis tested in the present experiment was that low yields observed in an annual red raspberry production system are because of dormant root pruning that occurs during removal from the nursery, and a resultant decrease in root carbohydrate availability for floricanes during budbreak and early bloom. Our objectives were to assess the effect of dormant root pruning on plant carbohydrate allocation, fruit number, fruit size, and overall yield.

Materials and Methods

Plant material. Dormant bare-root long canes (≈ 1.5 m) of the summer bearing red raspberry 'Cascade Delight' were purchased from a nursery in the Pacific northwestern United States in mid-January 2004. Roots were wrapped in damp cypress sawdust and canes were placed in a dark walk-in cooler at 7 °C for 1320 h.

On 11 March 2004, canes were potted in black polyethylene containers (36.7 L capacity; Olympia™ C4000; Nursery Supplies, Fairless Hills, PA) containing a mixture of coir, perlite, and peat (1:3:1) and were placed outdoors. Plants were hand-watered as needed and were fertilized weekly with a water-soluble fertilizer (20N–8.8P–16.6K; J.R. Peters, Allentown, PA) at a rate of 0.6 g N/plant.

Canes were allowed to fruit during the season, and fruits were harvested when ripe. All primocanes in the container were allowed to grow throughout the season, and only floricanes were pruned at the media level after fruit harvest.

In December 2004, 24 plants were selected for the experiment. Two primocanes per plant were selected based on uniform height and vigor, and the rest were pruned at the media level. Half of the plants were root pruned in early December. Root pruning was performed with a sharp machete, and roots were pruned to a $12 \times 12 \times 12$ cm³ volume, removing $\approx 45\%$ of the root dry weight. After root pruning, four root-pruned and four non root-pruned plants were separated into roots and canes (now referred to as floricanes) and fresh weights measured. Plant tissues were

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dried at 80 °C until constant weight and dry weights were recorded. The remaining plants were placed in a dark walk-in cooler and chilled for 1220 h at 7 °C. On 31 January 2005, chilled canes were moved to a heated polyethylene tunnel greenhouse. Greenhouse temperatures averaged 22 °C/15 °C day/night, and light intensity ranged from 1000 to 1500 photosynthetic photon flux. Canes were hand-watered as needed and were fertilized as described above.

At floricane lateral budbreak in early March, four root-pruned and four non root-pruned plants were harvested, separated into roots, the floricane, floricane laterals, and primocanes, and were processed as described above. Three new primocanes were allowed to grow on the remaining plants, and these plants were grown through the end of fruit harvest. Bumble bees (*Bombus impatiens*) were released at the beginning of bloom in early April to improve pollination. Flowers and fruits were counted and fruits were hand-harvested at pink and red color stages, weighed, and dried at 80 °C until constant weight or kept frozen at -20 °C for fruit quality analysis. Each plant was harvested individually at the end of fruit harvest. Plants were divided and processed as described above.

Fruit quality analysis. Fruits used for quality measurements were homogenized in a mortar and pestle and were filtered through three layers of cheesecloth. Juice was centrifuged for 20 min at 2000 g_n and the supernatant was decanted. Fruit-soluble solids were determined with a refractometer (Atago PR-101; Tokyo). Total titratable acidity was determined as a percentage of citric acid by diluting 6 mL of the supernatant with 50 mL of distilled water and titrating with 0.1 N NaOH to a final pH of 8.2. Milliliters of NaOH were recorded and titratable acidity (as citric acid equivalents) was calculated as described by Garner et al. (2003) with a millequivalent factor of 0.064 for citric acid.

Carbohydrate analysis. Soluble sugars and starch in roots, floricanes (laterals, cane, and fruits), and primocanes (when present) were measured. Dried tissue was ground and passed through a 20 mesh screen (1.27 mm mesh). Soluble sugars were determined by extracting 50 mg of ground tissue in 2 mL of 80% ethanol (1:100 w/v). Tissue was shaken for 20 min on an orbital shaker (Model 361; Fisher Scientific, Pittsburgh, PA). Extracts were centrifuged at 2270 g_n for 10 min. After decanting the supernatant, the remaining pellet was re-extracted twice in 1 mL of 80% ethanol (1:100 w/v). Supernatants were combined, final volume was measured, and aliquots were used for total sugar analysis. Pigment was removed by mixing 35 mg of activated charcoal and centrifuging at 14,900 g_n for 4 min. Percentage recovery was estimated by using ¹⁴C-sucrose as an external standard. Soluble sugars were determined by the phenol-sulfuric acid colorimetric procedure (Chaplin and Kennedy, 1994) using glucose as a standard and correcting for percentage of recovery.

Tissue starch content was determined by suspending the insoluble pellet in 2.0 mL of

0.2 N KOH and boiling for 30 min. The pellet was cooled and adjusted to a pH of 4.5 with 1.0 mL of 1 M acetic acid. *Rhizopus amyloglucosidase* (50 units) and α -amylase (10 units; Sigma Chemical Co., St. Louis MO) in 0.2 M calcium acetate buffer (pH 4.5) were added to each sample. After enzyme addition, samples were incubated at 37 °C for 24 h while shaking in a constant temperature bath (Magni Whirl; Blue M, Blue Island, IL). After incubation, samples were centrifuged at 2270 g_n for 10 min and the supernatant was decanted, measured, and aliquots were used for sugar analysis. Supernatant pigment was removed by mixing 35 mg of activated charcoal and centrifuging at 14,900 g_n for 4 min. Percentage of recovery was estimated by using ¹⁴C-sucrose as an external standard. Glucose obtained from starch hydrolysis was quantified by the phenol-sulfuric acid method (Chaplin and Kennedy, 1994) using glucose as standard and correcting for percentage of recovery.

Experimental design. The two root treatments and three plant developmental stages (harvest dates) were analyzed as a 2 × 3 factorial for carbohydrate concentration, carbohydrate content, and dry weight allocation. Treatments were distributed in the greenhouse in a randomized complete block design. There were four replications per treatment with single-plant experimental units. Yield components, photosynthesis, and fruit quality were analyzed as one-way randomized complete block design. Data were analyzed with the GLM procedure of SAS (SAS Institute, Cary, NC).

Results

Root pruning significantly decreased dry weight partitioning to fruit compared with no root pruning (Table 1). Root dry weight also decreased as a result of root pruning, as did floricane lateral dry weight. There were no effects of root pruning on floricane stem or primocane dry weight. There were no significant interactions between root pruning treatments and plant developmental stage (plant harvest) on dry weight of any organ.

Dry weight of all organs except floricane stems increased significantly between budbreak and the end of fruit harvest (Table 2). This resulted in a 5-fold increase in total plant dry weight by the end of harvest.

Root pruning decreased the number of flowers per cane compared with the non root-pruned canes, whereas percentage of fruit set and fruit size were unaffected (Table 3). The reduction in flower number per cane from root pruning resulted in significantly fewer fruits per cane and lower yields. The fruit harvest period in non root-pruned plants was delayed by ≈9 d compared with fruit harvest in root-pruned plants (data not shown), possibly because of the increased fruit load in the non root-pruned plants. Fruit quality was unaffected by root pruning (data not shown). Fruit-soluble solids averaged 9.8% and titratable acidity averaged 2.5% for both treatments.

There were no significant interactions between root pruning treatments and plant developmental stage on carbohydrate concentration or content, thus only main effects are

Table 1. Effect of dormant root pruning on dry weight allocation at the end of fruit harvest in 'Cascade Delight' red raspberry.

Treatment	Dry wt (g)					
	Root	Floricane laterals	Floricane stem	Primocane	Fruits	Total ^z
Root-pruned	148.3 ^y	37.1	25.6	313.9	36.5	561.0
Non root-pruned	208.6	86.6	37.0	268.4	67.8	668.7
P-value	0.03	0.005	0.32	0.48	0.0001	0.0001

^zTotal is the sum of root, floricane laterals, floricane stem, primocane, and fruit dry weights.

^yMean separation by *t* test at the indicated P-value (n = 4). Means were determined for root-pruned versus non root-pruned plants after fruit harvest (9 June to 16 July 2005) so that fruit dry weight and total plant dry weight could be included.

Table 2. Main effects of plant developmental stage on dry weight allocation in 'Cascade Delight' red raspberry.

Developmental stage ^c	Dry wt (g)					
	Root	Floricane laterals	Floricane stem	Primocane	Fruits	Total
Pruning	76.2b ^y	ND ^x	36.9	ND	ND	137.5b
Budbreak	61.6b	8.0b	29.1	5.2b	ND	116.0b
Fruit harvest	178.4a	61.2a	31.3	291.1a	52.2	614.9a
P-value	0.0003	0.001	0.61	0.0005	—	0.0002

^zPlants were harvested at root pruning (11–16 Dec. 2004), budbreak (11 Mar. 2005), and after fruit harvest (9 June to 16 July 2005).

^yLeast significant mean separation by Tukey at the indicated P-value (n = 8).

^xND = no data available.

Table 3. Effect of dormant root pruning on yield components in 'Cascade Delight' red raspberry.

Treatment	Flowers/cane	Fruit/cane	Fruit set (%)	Yield/cane (g FW)	Fruit size (g)
Root-pruned	146.0 ^z	85.3	60.3	380.4	4.32
Non root-pruned	284.8	148.8	51.4	658.9	4.46
P-value	0.04	0.0006	0.70	0.01	0.64

^zMean separation by *t* test at the indicated P-value (n = 4).

shown. Total carbohydrate (soluble sugars + starch) concentration was significantly lower in roots of root-pruned plants compared with non root-pruned plants (Table 4). On the other hand, total carbohydrate concentration in primocanes of root-pruned plants was significantly higher than primocanes of non root-pruned plants. There was no effect of root pruning on total carbohydrate concentration in the floricanes or floricanes laterals. Root pruning also decreased total carbohydrate content in roots and floricanes compared with non root-pruned plants (Table 5); however, carbohydrate content in floricanes laterals and primocanes was similar between treatments.

Carbohydrate concentrations in roots and floricanes laterals changed significantly as the season progressed. Soluble sugar concentration decreased in roots between the time of root pruning (mid-December) and budbreak (mid-March; Table 4). Root-soluble sugar concentrations then increased between budbreak and fruit harvest, at which time they were similar to concentrations at the time of root pruning. Soluble sugar concentrations in floricanes laterals decreased from budbreak through the end of fruiting. Soluble sugar concentration in floricanes stems and primocanes were similar at all harvest dates.

Starch concentration and total carbohydrate concentration (soluble sugars + starch) in roots decreased significantly between root pruning and budbreak, before increasing at the end of fruit harvest (Table 4). Starch concentrations in floricanes laterals increased between budbreak and the end of fruit harvest. However, total carbohydrate concentra-

tion in floricanes laterals was similar between budbreak and the end of fruit harvest. Starch and total carbohydrate concentrations in floricanes stems and primocanes were similar at all harvest dates, although primocane starch concentration at the end of fruit harvest was higher than at budbreak at $P = 0.06$.

In general, the pattern of developmental changes in root-soluble sugar, starch, and total carbohydrate content was similar to the pattern observed for root carbohydrate concentrations, although statistical separation among means differed because of dry weight differences (Table 5). Soluble sugar, starch, and total carbohydrate content in floricanes laterals and primocanes increased significantly between budbreak and fruit harvest (because of increases in dry weights), whereas floricanes stems exhibited little change in total carbohydrate content during this period.

Discussion

Dormant root pruning significantly decreased root dry weight and root carbohydrate concentration compared with no root pruning. The decrease in root dry weight and carbohydrate concentration reduced total carbohydrate content in root-pruned compared with non root-pruned plants. The decrease in root dry weight after root pruning was expected, because $\approx 45\%$ of the total root dry weight was removed at pruning. The concomitant decrease in root total carbohydrate (sugar + starch) concentration may have been from effects on the source-sink dynamics between floricanes laterals and roots. Because

root carbohydrates are the main source of carbon for floricanes during budbreak (Fernandez and Pritts, 1994), removal of 45% of the root system would reduce the available carbon supply. This would limit the amount of carbohydrate available to support floricanes budbreak and early lateral growth, resulting in the observed reduction in floricanes lateral biomass. This, in turn, would limit the total amount of photosynthate produced by the floricanes leaves. Previous work has shown that floricanes leaves serve as a carbohydrate source for roots as soon as they become photosynthetically competent (Fernandez and Pritts, 1993; Whitney, 1982), which can occur as early as bloom (Alvarado-Raya et al., 2007). Thus, the reduction in floricanes lateral leaf biomass and the resultant decrease in carbohydrate production via current photosynthesis would limit the ability of floricanes to supply sufficient carbohydrates to roots, and may have contributed to the decreased root carbohydrate concentration observed in root-pruned compared with non root-pruned plants.

Root carbohydrate concentration may also have been affected more directly by root pruning if rapid root regrowth occurred after root pruning, as reported for other fruit crops (Poni et al., 1992; Schupp et al., 1992). Rapid root growth would use carbohydrate reserves stored in the remaining root, resulting in a decrease in total root carbohydrate concentration. However, because total root dry weight and therefore total sink size of roots was less in root-pruned compared with non root-pruned plants, the increased sink activity

Table 4. Main effects of dormant root pruning and plant developmental stage on carbohydrate concentration of 'Cascade Delight' red raspberry.

Root treatment	Glucose equivalents ($\mu\text{g}\cdot\text{mg}^{-1}$ dry wt)											
	Root			Floricanes stem			Floricanes laterals			Primocanes		
	Sol. sugar	Starch	Total	Sol. sugar	Starch	Total	Sol. sugar	Starch	Total	Sol. sugar	Starch	Total
Root-pruned	13.9 ^z	46.0	58.9	22.3	34.6	57.0	65.0	29.1	94.1	40.0	31.8	71.9
Non root-pruned	19.7	53.2	72.9	19.3	34.4	53.7	61.4	33.4	94.7	26.7	26.2	53.0
<i>P</i> -value	0.17	0.16	0.03	0.41	0.98	0.76	0.51	0.37	0.93	0.09	0.36	0.04
Developmental stage ^y												
Pruning	22.2a ^x	49.8a	72.0a	21.0	44.7	65.7	—	—	—	—	—	—
Budbreak	6.9b	35.9b	42.8b	26.2	21.0	47.2	60.6	21.0	81.6	36.1	21.1	54.1
Fruit harvest	21.3a	63.1a	84.4a	15.2	37.8	53.0	43.2	43.2	86.5	30.6	37.0	67.6
<i>P</i> -value	0.02	0.01	0.001	0.14	0.12	0.39	0.001	0.04	0.68	0.46	0.06	0.22

^zMean separation by *t* test at the indicated *P*-value ($n = 12$).

^yPlants were harvested at root pruning (11–16 Dec. 2004), budbreak (11 Mar. 2005), and after fruit harvest (9 June to 16 July 2005).

^xLeast significant mean separation by Tukey at the indicated *P* value ($n = 8$).

Table 5. Main effects of dormant root pruning and plant developmental stage on carbohydrate content of 'Cascade Delight' red raspberry.

Root treatment	Glucose equivalents (g/organ)											
	Root			Floricanes stem			Floricanes laterals			Primocanes		
	Sol. sugar	Starch	Total	Sol. sugar	Starch	Total	Sol. sugar	Starch	Total	Sol. sugar	Starch	Total
Root-pruned	1.18 ^z	4.30	5.48	0.55	0.56	1.10	1.19	0.66	1.85	5.16	7.20	8.96
Non root-pruned	2.45	7.55	9.99	0.67	1.43	2.10	1.83	1.71	3.54	3.31	4.06	5.69
<i>P</i> -value	0.11	0.07	0.05	0.54	0.02	0.03	0.14	0.21	0.11	0.50	0.20	0.47
Developmental stage ^y												
Pruning	1.83 b ^x	3.91 b	5.74 b	0.68	1.59 a	2.28	—	—	—	—	—	—
Budbreak	0.65 b	2.27 b	2.93 b	0.63	0.42 b	1.05	0.24	0.08	0.32	0.23	0.12	0.36
Fruit harvest	2.96 a	11.58 a	14.54 a	0.51	0.97 ab	1.48	2.64	2.98	5.62	9.47	11.14	20.62
<i>P</i> -value	0.04	0.001	0.001	0.75	0.05	0.11	0.001	0.02	0.002	0.03	0.002	0.004

^zMean separation by *t* test at the indicated *P* value ($n = 12$).

^yPlants were harvested at root pruning (11–16 Dec. 2004), budbreak (11 Mar. 2005), and after fruit harvest (9 June to 16 July 2005).

^xLeast significant mean separation by Tukey at the indicated *P* value ($n = 8$).

from root regrowth may not have resulted in an increase in the total sink demand of the roots. In fact, it is likely that even with rapid root regrowth in response to root pruning, the total root sink demand in root-pruned plants was lower compared with non root-pruned plants. Because primocanes are a major source of carbohydrates for roots after roots have transitioned from sources to sinks (Alvarado et al., 2007; Fernandez and Pritts, 1993), this scenario would also explain the increase in primocane carbohydrate concentration in root-pruned compared with non root-pruned plants. This increase in primocane carbohydrate concentration did not translate into a significant increase in primocane carbohydrate content, possibly because primocane dry weights of root-pruned and non root-pruned plants were similar.

Concomitant with the decrease in root total carbohydrate concentration in root-pruned compared with non root-pruned plants was a significant decrease in yield. The negative impact of root pruning on yield was the result of a reduction in flowers per cane and consequently a reduction in fruits per cane. Individual fruit weight was unaffected. Flower bud formation occurs in the lower part of red raspberry canes as late as spring, just before budbreak (Williams, 1959). Additionally, pistils and anthers in flower buds throughout the cane continue differentiation through spring (Qingwen and Jinjun, 1998). Initiation and differentiation of flowers in raspberry require carbohydrate (Crandall et al., 1974), as found in other crops (Darnell, 1991; Ooshiro and Anna 1998) and because of the lack of photosynthetic leaves during flower differentiation, carbohydrate requirements must be supplied by reserves from the previous year. Whitney (1982) reported that red raspberry root dry weight decreased at budbreak and suggested that assimilates from the root were mobilized to the floricanes and primocanes during this time. Our experiment confirms this; demonstrating that total carbohydrate concentration in roots of root-pruned and non root-pruned plants decreased significantly between pruning and budbreak. However, the lower root carbohydrate availability in root-pruned compared with non root-pruned plants during budbreak apparently limited flower bud formation/differentiation, resulting in decreased yield.

Following the decrease in root total carbohydrate concentration between pruning and budbreak, a significant increase in root carbohydrate concentrations to levels observed at pruning was observed. This was accompanied by a significant increase in root dry

weight, and consequently, root carbohydrate content, between budbreak and fruit harvest. This further supports the idea that roots transitioned from source to sink sometime between lateral budbreak and fruit harvest and agrees with previous work in perennial (Fernandez and Pritts, 1993, 1994; Oliveira et al., 2007) and annual raspberry production systems (Alvarado-Raya et al., 2007).

In conclusion, the combined reduction in root dry weight and carbohydrate concentration resulted in a marked reduction in the total amount of root carbohydrate available for flowering and fruiting, and thus is consistent with the hypothesis that dormant root pruning reduces the supply of root carbohydrates, resulting in decreased yields in red raspberry. This has important implications for the feasibility of an annual raspberry production system. The reduction in yield could be off-set by increasing planting density, as long as light did not become limiting. Further work is necessary to determine the feasibility of this production system.

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