Root and Cane Pruning Affect Vegetative Development, Fruiting, and Dry-matter Accumulation of Grapevines

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Abstract. Dormant, 2-year-old, own-rooted ‘Chambourcin’ grapevines (*Vitis* sp.) were subjected to two levels of root pruning (none, two-thirds roots removed) and were subsequently trained with either one or two canes. Vines were destructively harvested at bloom and after harvest when dormant to determine the effect of stored reserves in the root and competition between shoots for these reserves on vine growth and berry development. Removing 78% of the root system reduced shoot elongation and leaf area more effectively than did increasing the number of shoots per vine from one to two. Root pruning reduced the elongation rate of shoots for 45 days after budbreak, whereas increasing the shoot number reduced the shoot elongation rate for only 20 days after budbreak. A positive linear relationship was observed between leaf area per shoot at bloom and the number of berries per single cluster. These results demonstrate the importance of 1) the roots as a source of reserves for the initial development of vegetative tissues in spring, and 2) the rapid development of leaf area on an individual shoot for high set of grape berries on that shoot.

Initial development of the leaf canopy of grapevines is determined by the number of shoots that grow in the spring and the delivery of reserves remobilized from storage tissues to those shoots (Winkler et al., 1974). A major objective of dormant pruning is to limit the number of shoots that develop, so that within-canopy shading is minimized. An additional objective is to limit the number of clusters that develop to the optimum number the vine can mature. As the number of buds that are retained after winter pruning is increased, growth of individual shoots is reduced, but development of the leaf canopy on the vine as a whole is more rapid, and light penetration into the canopy interior is reduced (Sommer et al., 1995). Shading within the canopy can reduce the yields of fruit per vine by reducing the number of berries that set on a cluster. A light reduction of only 8% during Stage 17 (Coombe, 1995), when flowers had separated in the inflorescence, reduced the set of berries on ‘Chardonnay’ vines (Ebadi et al., 1996).

The set of fruit on apple (*Malus × domestica* Borkh.) spurs is influenced by the rate of growth of the bourse shoot; rapid development reduces set (Quinlan, 1975). Apple fruitlets compete weakly for assimilates with developing shoots on the same spur (Hansen, 1970, 1971). The relationship between fruit set in grapevines and the rate of early-season

shoot growth has not been extensively studied.

In apple, the rate of growth of individual shoots can also be influenced by root pruning either during dormancy or after growth has resumed in the spring. Root pruning reduced shoot extension, leaf number and area, photosynthesis, and transpiration of apple trees (Geisler and Ferree, 1984). The effects of root pruning on growth of grapevines has not been extensively reported in the literature, but root pruning reduced the rate of shoot growth in proportion to the amount of root system removed in one study (Buttrose and Mullins, 1968), and enhanced the vigor of grapevines growing in a compacted soil (Van Zyl and Van Huyssteen, 1988). If root pruning increases the concentration of soluble carbohydrates in cane tissues at the end of the growing season, it may also increase the cold hardiness of the buds, since hardiness is positively correlated with the concentration of soluble carbohydrates in the canes (Wample and Bary, 1992).

We used root- and cane-pruning treatments, either alone or in combination, in order to test the hypotheses that 1) development of individual grapevine shoots is dependent on both the supply of stored reserves in the root tissues and competition between shoots for those reserves, 2) flower clusters compete weakly for carbohydrates with the shoot tip so that berry set will be reduced when early-season shoot growth is rapid, and 3) root pruning increases both the concentration of soluble carbohydrates in cane tissues and the cold hardiness of dormant buds.

Materials and Methods

One-year-old ‘Chambourcin’ vines growing on their own roots in 8-L nursery containers with a 1 soil : 1 peat : 1 perlite medium were

trained to a single upright shoot in 1996. The vines were moved into storage at 4 °C in Nov. 1996 and removed from storage on 11 Jan. 1997. The medium was removed from 48 plants, shaking all soil from the roots. The root system was pruned from each of 24 vines by removing two of every three roots where they originated on the shank. The roots were pruned from an additional six vines in the same way and these vines were then destructively harvested, separating the tissues into roots removed, roots retained, trunk and cane tissues. Data from these vines demonstrated that 78% of the roots were removed in root pruning. All vines were repotted in the same medium and returned to cold storage until 3 Feb. 1997 when they were moved into a greenhouse. Fertilizer (3 g per plant of Osmocote 14–7–13; Scotts-Sierra Hort Products, Marysville, Ohio) was applied once and vines received water as required. All 48 vines were pruned to five buds on a single cane at the time of root pruning and were then pruned again when the emerging shoots were ≈2 cm in length to leave either one or two actively growing shoots. Twenty-four vines were destructively harvested at bloom (18 Apr. 1997) and the remaining 24 vines harvested while dormant 1 month after fruit harvest (3 Dec. 1997). At the bloom and dormant harvests, vines were separated into root, shank, cane, and shoot tissues, which were frozen immediately in liquid nitrogen and stored at –20 °C pending analysis for dry weight and nonstructural carbohydrates. Vines were arranged in a 2 × 2 factorial design with two levels of root pruning (none, two-thirds roots removed) and two levels of cane pruning (one shoot, two shoots) with six replicates.

Nondestructive measurements of leaf and shoot growth, flower number and berry set, and leaf photosynthesis were made on the 24 dormant vines harvested at the end of the season. The width of each leaf was measured every 2 d from 10 until 35 d after budbreak (bloom). A calibration curve of leaf width vs. area was derived from a sample of 200 leaves taken from own-rooted ‘Chambourcin’ vines of the same age growing in the same greenhouse. The area of individual leaves was estimated nondestructively using the regression equation developed for the relationship between leaf width and area:

$$A = -0.006032 \times (w) + 0.006739 \times (w)^2 - 0.000003809 \times (w)^3$$

where w = lamina width; $R^2 = 0.99$. A second-order polynomial function was used to describe the increase in leaf area per vine up until bloom. Shoot length was measured every 2 d until bloom, and weekly thereafter until shoot growth ceased 70 d after budbreak. Cluster number was reduced to one per shoot prior to bloom, and the number of flowers and berries on each cluster was counted before cap fall (3 Apr. 1997) and at harvest (1 July 1997), respectively. Berry set was calculated as the number of berries per 100 flowers. Photosynthesis was measured under saturating light conditions (Poni et al., 1993) at bloom (8 Apr. 1997), veraison (28 May 1997), and harvest (1 July 1997) on the leaf opposite each cluster with

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a portable photosynthesis unit (model LCA2; Analytical Development Co., Hoddesdon, England). Air flow rate was regulated at 300 mL·min⁻¹ and ambient CO₂ concentration was monitored periodically during each series of measurements. Chlorophyll was extracted from three leaf discs taken from the leaf opposite the cluster (2.4 cm² total area) at bloom using *N,N*-dimethyl-formamide according to Moran (1982). Total chlorophyll content was expressed on both an area and a fresh-weight basis, and the ratio of chlorophyll a to chlorophyll b calculated according to Moran (1982). Soluble solids, pH, and titratable acidity were determined for fruit juice at harvest. Four weeks after harvest (1 Aug. 1997), plants were returned to cold storage (4 °C) to induce dormancy. The cold hardiness of dormant buds was determined by measuring the low temperature exotherms (LTEs) of four buds per vine after 100 d in cold storage (Nov. 1997) according to the method of Wolf and Pool (1987).

Weights of tissues collected at bloom and at the end of the season were measured gravimetrically. Tissues were freeze-dried and ground to pass a 2-mm mesh screen prior to analyses for nonstructural carbohydrates. Soluble sugars in 100 mg tissue were extracted three times (7.5 + 3.0 + 3.0 mL) in hot (70 °C) 80% ethanol in a shaking water bath. The combined extracts were partitioned in 7 mL water and 7 mL chloroform and the aqueous phase taken to dryness in vacuo at 40 °C. After evaporation the residue was resuspended in 7 mL deionized water and passed over a polyvinylpyrrolidone (PVPP) column. Soluble sugars were quantified using the phenol-sulfuric acid method (Dubois et al., 1956). Glucose was used as the standard and sugars were expressed on a percent dry-weight basis. The pellet remaining after ethanol extraction was boiled for 2 h in 5 mL of a 0.1 N sodium acetate buffer (pH 5), cooled to room temperature, then incubated with 11.5 U amyloglucosidase (EC 3.2.1.3) and 11.5 U isoamylase (EC 3.2.1.68) in a shaking water bath for 24 h at 55 °C. After incubation, a 1-mL aliquot was removed, made up to 80% with cold ethanol and centrifuged to remove proteins. The glucose liberated by starch digestion was quantified using the phenol-sulfuric acid method (Dubois et al., 1956). Glucose was the standard and starch was expressed on a percent dry-weight basis. Statistical analyses of the data were performed using regres-

sion and generalized linear model procedures in the SAS statistical package (SAS Institute, 1989).

Results and Discussion

Root pruning reduced root, shoot, and total dry weight at bloom and in the dormant season, while shoot number had no influence on dry-weight distribution (Table 1). Total dry weight of vines immediately after root pruning was 18.4 vs. 23.7 g for nonpruned vines. At bloom, total dry weight had increased 11% and 21% in root-pruned and nonpruned vines, respectively; at final harvest, the total dry weight had increased 172% and 210%, respectively (Table 1). Current assimilates were translocated to the roots before bloom, as indicated by the net increase in dry weights of roots on both root-pruned and nonpruned vines recorded at bloom. Partitioning of assimilated carbon to the root system was greater in root-pruned vines. After the growing season, the weight of nonpruned roots was 358% greater than at bloom, while the weight of pruned roots had increased 809%. Since sink strength is a combination of sink size and sink activity, the reduction in shoot elongation rate in root-pruned vines could be the result of both a reduction in stored carbohydrates in the roots ("size") and competition of the pruned roots for the remaining stored carbohydrates ("activity").

The shoot elongation rate declined during the first 25 d after budbreak, then increased until ≈35 d (bloom), followed by a steady decline until the end of the season (Fig. 1A). The initial reduction in shoot elongation coincided with the period of rapid cluster elongation immediately prior to bloom. Both an increase in shoot number and root pruning significantly reduced the rate of shoot elongation when measurement began 10 d after budbreak. The effect of shoot number on shoot elongation rate had disappeared by bloom. The effects of root pruning were evident 6 weeks after budbreak, but were nonsignificant at the end of the growing season as rate of elongation declined.

Total shoot elongation was inhibited more by root pruning than by restricting shoot number (Fig. 1B). The effect of shoot number was significant only on vines that were not root-pruned; shoots on two-shoot vines were 22% longer following root pruning, but those on one-shoot vines were only 8% longer.

The rate of leaf area increase per vine during the period between budbreak and bloom was 13 and 31 cm² per day on root-pruned vines with one and two shoots, respectively, and 34 and 63 cm² per day for nonpruned vines with one and two shoots, respectively. Root pruning reduced the rate of leaf area increase per vine ($P \leq 0.001$) by inhibiting the expansion of individual leaves, but did not affect the rate of their appearance (data not shown). These data suggest that removal of stored reserves by root pruning inhibited shoot development to a greater extent than did increasing competition between developing shoots by increasing the number of shoots per vine from one to two.

The number of berries per cluster was significantly reduced by both root pruning and by increasing the shoot (and cluster) number per vine ($P \leq 0.05$) (Table 2). Root pruning reduced the number of berries per cluster by 29%. Increasing the number of shoots and clusters per vine from one to two reduced the number of berries per cluster 34%. Even considering the reduction in berry number per cluster, vines with a single cluster on each of two shoots produced more berries than did vines with a single shoot and cluster. Treatment effects on berry number may be related to their effects on leaf area per shoot, or perhaps to competition between clusters on the same vine for available assimilates. Berry number per cluster was positively correlated with leaf area per shoot at bloom (Fig. 2). These data support the suggestion by Candolfi-Vasconcelos and Koblet (1990) that final crop yield varies with the existing assimilating surface during the first period of berry growth.

Rates of photosynthesis were highest when measured at bloom, and declined as the season progressed, reaching ≈40% of the bloom rate at harvest (Table 3). Interaction between root pruning and shoot number per vine was significant for the rate of leaf photosynthesis at bloom and at veraison. Increasing the number of shoots per vine increased in the rate of photosynthesis in root-pruned vines, but decreased it in nonpruned vines. Increased rates of photosynthesis on root-pruned vines with increasing shoot number; i.e., with reduced leaf area of individual shoots, is consistent with the vines' response to defoliation treatments (Hofacker, 1978). The lower rate of photosynthesis in the nonpruned vines with two shoots vs. those with one shoot may be due

Table 1. Effects of root pruning and shoot number on dry weight (g) of 'Chambourcin' grapevine tissues.

Main effect means ^z	Bloom					Dormant				
	Root	Shank	Cane	Shoot	Total	Root	Shank	Cane-2 ^y	Cane	Total
Root pruning										
Nonpruned	10.4	10.5	2.7	5.1	28.6	47.6	19.0	6.6	15.4	88.6
Pruned	2.2	12.6	3.4	2.2	20.4	20.0	15.5	5.9	8.6	50.0
	***	NS	NS	*	**	***	NS	NS	***	***
Shoot number										
One shoot	6.6	12.1	2.5	4.0	25.1	34.7	16.8	5.1	13.1	69.7
Two shoots	6.0	11.1	3.6	3.3	24.0	32.8	17.8	7.4	10.9	68.9
	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

^zNo interactions between root pruning and shoot number were significant.

^yTwo-year-old canes.

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

to an increase in cluster number per vine. The chlorophyll content of leaves, expressed on a leaf area basis, was reduced by reducing the number of shoots per vine from two to one.

The reduced rates of shoot elongation and leaf area expansion resulting from root pruning might be explained by short-term water stress, as was reported for apples (Giesler and Ferree, 1984; Schupp and Ferree, 1990). However, this response was observed in apple trees that were root-pruned when foliage was present and shoots were actively transpiring. In the present study, the rate of leaf transpiration at bloom was reduced 8% by root pruning ($P \leq 0.05$), indicating that these vines may have been under a mild water stress up to that time. Buttrose and Mullins (1968) found no evidence that shoots on root-pruned grapevines suffered from inadequate water supply. We were able to collect xylem exudate from nonpruned vines at budbreak, whereas root-pruned vines yielded no exudate, suggesting that root pressures were much lower in these vines, and presumably delivery of solutes normally carried in the xylem sap to developing tissues was reduced.

Treatment effects on fruit quality at harvest were minor. Fruit from vines with a single shoot had a higher soluble solids concentration than did those to vines from two shoots, while fruit from root-pruned vines had higher titratable acidity than did those from vines that were not root pruned (data not shown). These effects are probably related to the effects of the treatments on the leaf area per cluster, which was greater in vines with a single shoot than in those with two shoots, and in nonpruned vines than in root-pruned vines (data not shown).

Soluble carbohydrates accounted for $\approx 4\%$ of the dry weight in root and cane tissues both at bloom and in dormant vines (data not shown). At bloom, root tissues from vines with two shoots had a significantly higher soluble carbohydrate concentration than did those from vines with only a single shoot; however, all other differences in soluble carbohydrates and starch among treatments were nonsignificant. The increase in soluble carbohydrates in root tissues at bloom may have indicated that more of the newly assimilated carbon from the larger leaf area on these vines was being translocated to the roots. The starch content of root tissues increased at the end of the growing season from $\approx 2.2\%$ on a dry-weight basis at bloom to $>8\%$. Cane tissues had a lower starch content than did root tissues throughout the experiment. Defoliation treatments (Hunter et al., 1995) and delayed harvest (Wample and Bary, 1992) also had no effect on the concentration of nonstructural carbohydrates in grapevine root tissues. These data suggest that newly assimilated carbon was translocated to the roots and utilized for new root growth rather than stored as starch. Winter hardiness, as determined by the low temperature exotherms of dormant buds when frozen, were not affected by treatment. All buds were killed at a temperature of about -12°C .

Removing 78% of the dry weight of the root system from dormant 'Chambourcin' grapevines reduced the leaf area per vine by

Fig. 1. Effects of root pruning and shoot number per vine on (A) shoot elongation rates and (B) shoot length per vine in 'Chambourcin' grapevines. Error bars represent LSD_{0.05}. Arrow indicates time of bloom.

Table 2. Effects of root pruning and shoot number on vegetative development and productivity of 'Chambourcin' grapevines.

	Shoot elongation rate ^a (mm·d ⁻¹)	Leaf area/ vine at bloom (cm ²)	Flowers/ cluster	Berries/ cluster	Berry set (berries/ 100 flowers)
Main effect means ^b					
Root pruning					
Unpruned	17.0	1840	367	69	21
Pruned	8.1	893	352	49	17
	***	***	NS	*	NS
Shoot number					
One shoot	15.5	1206	368	71	23
Two shoots	9.6	1526	351	47	15
	**	**	NS	*	NS

^aDuring the period from budbreak to bloom.

^bNo interactions between root pruning and shoot number were significant.

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

Fig. 2. Relationship between leaf area per shoot at bloom and berry number per cluster at harvest in 'Chambourcin' grapevines. Vertical and horizontal bars represent $\pm$ SE ($R^2 = 0.91$, $P = 0.04$).

30%. Shoot elongation rates of root-pruned vines were reduced for the first 50 d after budbreak. Root pruning reduced growth of individual shoots to a greater extent than did increasing the number of shoots per vine from one to two. Increasing the shoot number per vine reduced shoot elongation rates; however, this was true only during the first 20 d after budbreak. The number of berries per cluster was positively related to leaf area per shoot at bloom, suggesting a positive relationship between vegetative development and fruiting for grapevines. This relationship explains the reduction in berry number per cluster measured in minimal-pruned vines (McCarthy and Ciriaco, 1990), which carry as many as five times the number of shoots as do cane-pruned vines (Sommer et al., 1995).

Root dry mass increased between budbreak and bloom, suggesting that roots were an important sink for current assimilates as early as bloom. In a previous experiment we reported a decline in root weight for the first 3 weeks following budbreak, and that root mass had not recovered to the level it had been at budbreak even 10 weeks after growth had resumed (McArtney and Ferree, 1999). The difference in carbon partitioning between these two studies might be explained by the age of the vines. Vines in the present study were only

2 years old, so roots were still growing rapidly. The previous study used older, container-grown vines that would have had better established root systems.

The increase in dry weight of roots, when expressed on a percentage basis, was greater on root-pruned vines than on nonpruned vines. The soluble carbohydrate concentration of root tissues at bloom was higher for vines with two shoots than for those with only one, but this was the only time we found a treatment difference in nonstructural carbohydrates. This increase might have been due to increased translocation of newly assimilated carbon from vines with two shoots, since these also had a greater leaf area per vine than did vines with only one shoot. However, according to this hypothesis we would also expect higher soluble carbohydrate concentrations in roots of nonpruned vines since leaf area per vine was reduced more by root pruning than was shoot number.

Neither root pruning nor the number of shoots per vine had any effect on cold hardiness of the buds. This was not surprising since the large differences in vegetative development due to treatments did not influence the concentration of nonstructural carbohydrates in canes. Wample and Bary (1992) reported a positive relationship between soluble carbo-

hydrates and primary bud cold hardiness for grapevines. Differences in leaf area per vine due to the treatments were probably not translated into differences in the starch content of the various tissues because of the age of the vines. Since the vines used in this study were only in their second season of growth, assimilated carbon was utilized for the growth of various tissues, especially roots, and did not accumulate in storage tissues as starch.

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Table 3. Effects of root pruning and shoot number on leaf photosynthesis, transpiration, and chlorophyll concentration at bloom, veraison, and harvest of 'Chambourcin' grapevine tissues.

Treatments		Photosynthesis (CO_2 , $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)			Leaf transpiration (H_2O , $\text{g}\cdot\text{cm}^{-2}\cdot\text{s}^{-1}$)			Chlorophyll		
		Bloom	Veraison	Harvest	Bloom	Veraison	Harvest	$\mu\text{g}\cdot\text{cm}^{-2}$	$\text{mg}\cdot\text{g}^{-1}$ fresh wt	Ratio a : b
Nonpruned	1	12.1	5.6	5.1	6.6	2.2	7.5	43.0	3.3	3.5
	2	10.5	4.9	5.1	6.1	2.1	6.4	41.8	3.2	3.4
Root pruned	1	9.7	4.5	5.7	5.5	1.8	8.3	44.2	3.4	3.4
	2	11.2	5.6	6.2	6.2	2.2	7.8	39.8	3.1	3.4
Significance										
Root pruning		NS	NS	NS	*	NS	*	NS	NS	NS
Shoot number		NS	NS	NS	NS	NS	*	*	NS	NS
Interaction		**	*	NS	*	NS	NS	NS	NS	NS

NS, *, ** Nonsignificant or significant at $P \leq 0.05$ or 0.01 , respectively.

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