

Current-year and Subsequent-year Effects of Crop-load Manipulation and Epicormic-shoot Removal on Distribution of Long, Short and Epicormic Shoot Growth in *Prunus persica*

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• **Background and Aims** The distribution of canopy growth among different shoot types such as epicormic, long and short shoots is not well understood in the peach tree. In this experiment, the effects of crop load and early epicormic sprout removal on current and subsequent-year distribution of vegetative growth among epicormic, long and short shoots was investigated in *Prunus persica*.

• **Methods** Field trials were conducted in Winters, California, in 2003–2004. Crop load was manipulated with fruit thinning in 2003 to produce trees that were de-fruited, commercially thinned or full crop, and half of the trees in each cropping treatment had all current year epicormic sprouts removed at the time of fruit thinning. Yield was recorded and trunk and root carbohydrates were sampled to confirm the effect of 2003 crop load differences on tissue carbohydrate concentration. All current-season vegetative-shoot extension growth was harvested from half of the trees in each treatment in the autumn of 2003 and from the other half in the autumn of 2004. Epicormic, long and short shoots were separately evaluated for dry weight, node number and leaf-stem parameters.

• **Key Results** In 2003, long-shoot dry weight and node number were significantly affected by crop load; however, short-shoot dry weight and node number were not significantly affected. The 2003 crop-load treatments did not affect 2004 vegetative growth of any shoot type. Some re-growth of epicormic shoots followed early epicormic sprout removal: by the end of the 2003 season, trees in the early shoot-removal treatment had approximately one-third of the epicormic-shoot dry weight as unpruned trees.

• **Conclusions** Fruit thinning promoted distribution of growth similar to that of de-fruited trees. While thinning was effective in increasing fruit size, it exacerbated the problem of epicormic sprouting. Early epicormic sprout removal did not stimulate the excessive epicormic re-growth in the same or subsequent year relative to previously studied summer pruning methods.

Key words: Neof ormation, nodes, crop load, water sprout, pruning, epicormic shoot, long shoot, short shoot, carbohydrate, vegetative growth, shoot type, *Prunus persica*.

INTRODUCTION

In plants, vegetative growth provides photosynthate and sites for future reproductive growth. Understanding the physiology of vegetative growth is key to understanding cropping dynamics, and has important economic implications for food crops. In tree crops such as peach, canopy management is known to affect fruit quality parameters such as colour, sugar content, size and disease susceptibility (Crisosto *et al.*, 1997) as well as fruit number and yield (Bargioni *et al.*, 1985; DeJong *et al.*, 1999).

Peach tree canopies are composed of multiple shoot types, which can be categorized as long, short or epicormic. Long and short shoots, produced from the previous year's lateral and terminal buds, are primarily distinguished by length and node number. Short shoots, also called rosette shoots or spurs, are approx. 1 cm in length with few nodes, while long shoots, also called hangers, may approach 1 m in length and have more than 30 nodes. Previous work has shown that, in peach, the buds that will produce long and short shoots are visually indistinguishable at the time of bud break, and all have approximately

ten foliar organ primordia per bud (Gordon *et al.*, 2006a). However, short shoots cease growth when a number of preformed nodes has extended, while long shoots can continue growth by producing neof ormed nodes simultaneously with shoot elongation. Epicormic shoots, which in peach appear to be preventitious (D. Gordon, unpubl. res.), arise from dormant, latent buds formed prior to the previous growing season. These buds remain dormant in their first year and are gradually enveloped by bark. They remain latent at the level of the cambium awaiting a stimulus to grow, and can then produce vigorous neof ormed shoots (Kramer and Kozlowski, 1979).

Shoot type differences are of interest to peach growers because some types are more productive than others: long shoots being the most fruitful (Fournier *et al.*, 1998). Short shoots often do not set floral buds, though they can become net carbohydrate exporters early in the season and may support the growth of desirable long shoot growth as is the case in apple (Johnson and Lakso, 1986). Epicormic shoots also tend to produce relatively few flower buds (Büsgen and Münch, 1929; Yamashita, 1971). These undesirable shoots tend to congest the centre of the canopy, blocking light and preventing fruit coloration (Myers,

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1993; Tymoszuk, 1984). Vigorous shoots such as epicormic shoots are generally thought to take longer than less vigorous shoots to become carbohydrate exporters (Johnson and Lakso, 1986) and to contribute little carbohydrate to fruit growth (Tymoszuk, 1984; Mika, 1986), thus they are often removed with summer and/or dormant pruning (Gerdtz, 1987; Day *et al.*, 1989). Ideally for commercial fruit production, a high percentage of tree resources would be allocated to long shoots and a low percentage to epicormic shoots. For this reason, the study of the physiology of growth allocation and its effect on shoot populations in the canopy is of interest.

A high capacity for neof ormation, such as that noted in peach (Gordon *et al.*, 2006a), gives the canopy great plasticity in response to limb removal or breakage as well as current-year environmental conditions such as rainfall or temperature. This responsiveness of the canopy to manipulation and current conditions makes peach a good model to study the effects of management techniques such as summer pruning and crop load manipulation on the distribution of vegetative growth to short, long and epicormic shoots.

Summer pruning reduces the amount of carbon fixed by the canopy in proportion to the leaf area removed (Li *et al.*, 2003a, b) and is known to decrease vegetative vigour in the same and subsequent years with respect to unpruned trees (Mika, 1986). Summer pruning can also temporarily upset the root : shoot equilibrium of the tree, until canopy re-growth takes place, often within the season in young peach (Rom and Ferree, 1985). The effects of summer pruning on the distribution of current and subsequent year vegetative growth to short, long and epicormic shoots are not clear.

Crop load is another factor that influences the resources available for growth, particularly carbohydrates (Grossman and DeJong, 1995b; Li *et al.*, 2003b). Maturing fruits constitute a strong sink for photosynthate, particularly during the last stage of fruit growth (DeJong and Grossman, 1995) and heavy cropping has been shown to reduce vegetative growth (DeJong *et al.*, 1987; Berman and DeJong, 2003) as well as starch concentrations in vegetative tissues (Monselise and Goldschmidt, 1982; Berman and DeJong, 2003). Previous work supports the role of carbohydrate availability in promoting epicormic shoot initiation (Gordon *et al.*, 2006b), but the effect of carbohydrate availability on the distribution of vegetative growth among shoot types is not well understood.

The objective of this research was to examine the effect of tissue carbohydrate concentration on canopy architecture: specifically, how crop load manipulation and early epicormic sprout removal affect the amount of dry weight, number of nodes, and properties of leaves and stems produced by epicormic, long and short shoots in the canopies of mature peach trees.

MATERIALS AND METHODS

This experiment was initiated in April 2003 using 72 13-year-old peach trees ('O'Henry' grafted on 'Lovell' rootstock) located in Wolfskill Experimental Orchard near

Winters, California (38°32'N, 121°58'W). The trees were trained to the 'Kearney Agricultural Center perpendicular-V system' (DeJong *et al.*, 1995) with two scaffold branches per tree trained perpendicular to the tree row, with a 1.8-m within-row and 5.2-m between-row spacing (1055 trees ha⁻¹). The soil was a Yolo clay loam. The orchard was managed for commercial production, including application of fertilizer and pesticides, and was irrigated weekly with micro-sprinklers to replace 100 % crop evapotranspiration (ET_C) through harvest and then at 80 % ET_C after harvest using CIMIS data (California Irrigation Management Information System, <http://www.cimis.water.ca.gov/>). Mean monthly temperatures in 2003 were April 12.2 °C, May 18.7 °C, June 23.3 °C, July 26.4 °C, August 23.6 °C and September 22.8 °C. Mean monthly temperatures in 2004 were April 16.9 °C, May 19.5 °C, June 22.9 °C, July 24.1 °C, August 24.0 °C and September 22.1 °C.

Three north-south-orientated rows of trees were assigned to a combination of pruning and cropping treatments, within a randomized complete block design. Blocks were divided along a potential north-south gradient in soil quality due to grading of the orchard. Trees had either all epicormic sprouts removed once early in the season ('Removal' or R), or all epicormic shoots were left on the trees ('No removal' or N). The same trees either had all fruit removed ('De-fruited' or D), were thinned to approximately half of the crop load ('Thinned' or T), or were left with the natural crop load ('Full crop' or F). One tree with each combination of pruning and crop-load treatment (RD, RT, RF, ND, NT, NF) was present in each of the 12 blocks.

Initial measurements of trunk diameter were made on 18 April 2003 and trunk cross-sectional area (TCSA) was calculated. Thinning and pruning treatments were performed by hand on 15-16 April 2003. The fruit were harvested on 11 August 2003. Total fresh weight (f. wt) of the fruit produced by each tree was recorded as well as the number of fruit per tree, and mean f. wt per fruit was calculated.

In December 2003, samples for carbohydrate analysis were taken from six de-fruited and six full-crop trees in the epicormic sprout removal treatment in order to assess the effect of crop-load treatments on carbohydrate concentrations in perennial vegetative tissues. A cork borer was used to punch a 1-cm-diameter disc of bark including all tissue layers external to the vascular cambium. Four bark samples per tree were taken from the lower trunk. A drill with a spade bit was used to remove the most recent several years of xylem tissue in the same four places where bark samples were taken. Root samples were collected from a depth of 15-30 cm, within 1 m of the trunk, at the four cardinal points. Four 10-cm lengths of current year roots of 0.5-1.0 cm diameter were taken per tree. All samples were dried at 60 °C for 2 d, weighed and ground to pass through a 40-mesh sieve, and analysed for non-structural carbohydrate (NSC) at the Division of Agriculture and Natural Resources' analytical laboratory at the University of California at Davis by standard methods (Smith, 1969). Starch was hydrolysed

with amyloglucosidase, and high-performance liquid chromatography was performed for quantifying glucose, sucrose and fructose using a fast carbohydrate column (HPAP; Bio-Rad Laboratories, Hercules, CA, USA). Concentrations of glucose, sucrose and fructose were summed to give an estimate of NSC, and should reflect a large percentage of the NSC available.

Vegetative shoot growth was harvested from the trees in odd-numbered blocks (1, 3, 5, 7, 9 and 11) on 9–12 September 2003, after most shoots had stopped growing but about 1 month earlier than natural leaf fall. All current year (2003) vegetative growth was removed by hand, first epicormic shoots, then long shoots and then short shoots. The total dry weight (d. wt) of each shoot type was determined separately and a representative sub-sample taken for dry mass calculations. In half of the blocks, the sub-samples were dried at 60 °C for 1–2 weeks and the resulting d. wt was used to estimate the total d. wt of that shoot in the canopy. In the other blocks, additional data on leaf and stem properties were taken prior to drying the sub-samples. In these blocks, leaf and stem material was dried and weighed separately, and leaf number, leaf area, leaf d. wt, primary stem length, sylleptic growth length, stem number and stem d. wt were recorded. From these data, specific leaf weight (SLW, in mg cm^{-2}), mean area per leaf, specific stem weight (SSW, in mg cm^{-1}), mean length per shoot, mean length of sylleptic shoot growth, and mean internode length were calculated for the sub-samples of each shoot type. Each shoot type's contribution to total leaf area per tree and total number of nodes per tree was estimated using sub-sample data and sample f. wt.

Other than the treatment pruning on 15 April 2003, no green pruning was done in 2003. The only dormant pruning in the winter of 2003–2004 was the removal of some epicormic sprouts from the 'N' treatment to make the number of epicormic sprouts comparable to those within the 'R' treatment prior to the 2004 growing season. No green pruning was performed in 2004. Crop load was not adjusted in 2004, leaving all trees with a full crop load. Unusually high temperatures during the 2004 bloom period (maximum daily temperature above 25 °C for 15 consecutive days) caused very high fruit set in 2004. Branches broke under the heavy crop in three trees, one each from the ND, NT and RT treatments, which were dropped from the experiment.

Vegetative shoot growth was harvested from the trees in even numbered blocks (2, 4, 6, 8, 10 and 12) on 5–12 October 2004, as above, removing all current-year growth separately by shoot type. Data were recorded and calculations performed as above, with d. wt recorded for all blocks and additional leaf and stem properties recorded for half of the blocks.

Within each year, the amount of current-year growth expressed as d. wt and number of nodes was evaluated with a two-factor ANOVA (crop-level treatment and epicormic sprout-removal treatment). TCSA was included as a covariate. Leaf and stem properties were also evaluated with an ANOVA, as was tissue NSC. The Tukey test was used to detect significant differences between treatment means (5 %). Statistical Analysis Systems software version

9.1 (SAS Institute Inc., Cary, NC, USA) was used for all statistical analyses.

RESULTS

Crop load

The fruit thinning treatment reduced the number of fruit per tree and mass of fruit per tree by similar amounts in the two pruning treatments relative to the fully cropped trees (treatments NT and RT vs. NF and RF) in 2003. Relative to the full crop treatments, the number of fruit in the thinned treatments was reduced on average by 60 % in the NT treatment and 57 % in the RT treatment (Fig. 1A). Correspondingly, thinning decreased the total fresh weight of fruit produced per tree by an average of 34 % in the NT

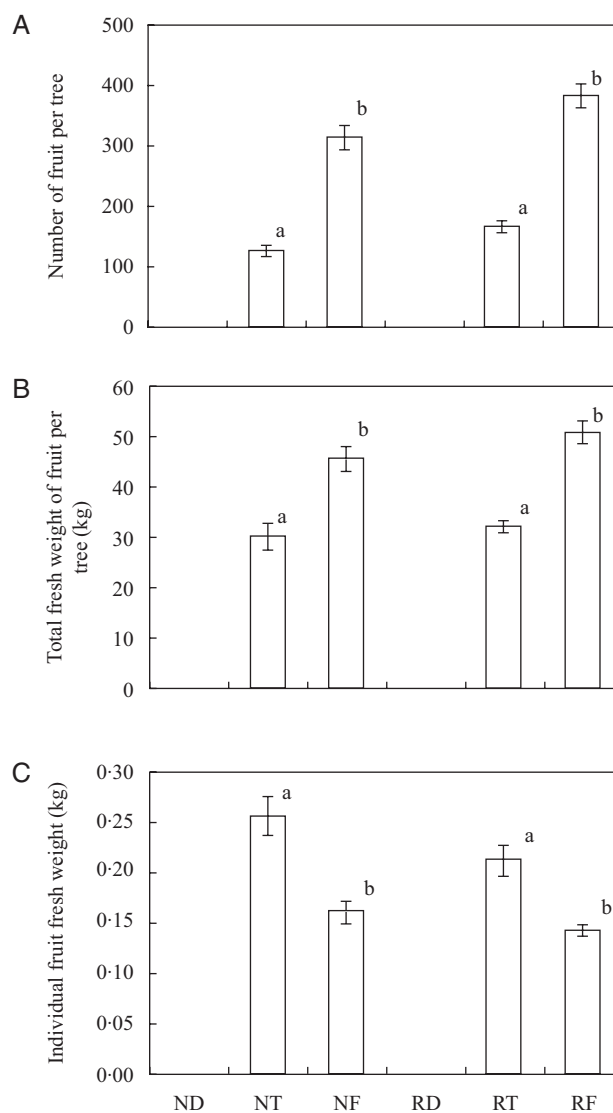


FIG. 1 Mean number of fruits per tree (A), mean total fresh weight of fruit produced per tree (B), and mean fresh weight per fruit (C) across thinning and epicormic sprout removal treatments. The same letters indicate the lack of significance of the difference between N and R pruning treatment means (Tukey, 5 %). Bars indicate s.e.

TABLE 1. Non-structural carbohydrate content (glucose + starch, fructose, sucrose and total) as percentage dry weight of bark, wood and root tissues of peach trees following crop load manipulation

Crop load	Tissue sampled	Glucose + starch	± s.e.	Fructose	± s.e.	Sucrose*	± s.e.	Total	± s.e.
No crop	Bark	4.5	0.37	1.4	0.10	1.0	0.08	6.9	0.31
	Wood	5.5	0.26	0.9	0.08	NA		6.4	0.32
	Root	11.4	0.41	1.0	0.16	0.6	0.15	13.0	0.39
Full crop	Bark	3.7	0.23	1.2	0.12	0.8	0.08	5.7	0.25
	Wood	3.9	0.28	1.0	0.09	NA		4.9	0.30
	Root	9.1	1.36	1.0	0.14	0.5	0.08	10.6	1.31

* NA, Data not available, below detectable threshold of 0.02 %.

treatment and 37 % in the RT treatment (Fig. 1B). Thinning increased the mean weight of individual fruits by 56 % in the NT treatment and 50 % in the RT treatment compared to the NF and RF treatments, respectively (Fig. 1C). Mean number of fruit per tree, mean total fresh weight of fruit per tree, and mean individual fruit fresh weight were not significantly different between N and R thinned treatments, nor between N and R full crop treatments.

Tissue carbohydrate concentration

Because the starch fraction was hydrolysed to glucose, the glucose fraction accounted for the vast majority of carbohydrates quantified in bark, xylem and root tissue (Table 1). Crop load did not significantly affect the concentration of fructose or sucrose in any of the tissues sampled. Crop load did not significantly affect the concentration of glucose + starch in sampled bark or root tissue, but did significantly affect glucose + starch in wood ($P = 0.002$). The total measured non-structural carbohydrate (NSC) concentration (fructose + sucrose + glucose + starch) in fully cropped trees differed from

de-fruited trees in the xylem and bark tissue ($P = 0.007$ and $P = 0.014$, respectively) but not in roots.

Vegetative growth in 2003

No significant block effect was present in 2003 (Table 2). Significantly less total-canopy shoot d. wt was produced by full-crop trees than by thinned and de-fruited trees ($P < 0.0001$; Fig. 2A). Thinned trees did not produce significantly less canopy d. wt than de-fruited trees. Trees with early season epicormic sprout removal had significantly less total shoot d. wt at the end of the season than unpruned trees ($P = 0.028$; Fig. 2A). In all treatments, leaves and stems each accounted for approximately half of the total harvested canopy d. wt. Across all treatments, short shoots accounted for 4–10 % of harvested canopy d. wt, long shoots accounted for 56–80 % of harvested canopy d. wt, and epicormic shoots accounted for 12–39 % of harvested canopy d. wt (Fig. 2B). Relatively more harvested canopy d. wt was due to long shoots than epicormic shoots in the R compared with N treatments. Early season removal of epicormic sprouts resulted in production of about one-third of the epicormic d. wt of the unpruned treatment (Fig. 2C). Production of long and

TABLE 2. Results of the 2003 analysis of variance of factors affecting dry weight and number of nodes of epicormic, long and short shoots

Source	d.f.	Epicormic shoots		Long shoots		Short shoots	
		Mean square	F-value	Mean square	F-value	Mean square	F-value
Dry weight							
Epicormic removal	1	21.41	20.48**	1.75	2.23	0.003	0.24
Crop load	2	4.42	4.23*	11.77	15.04**	0.024	2.34
Removal × crop	2	2.50	2.40	1.75	2.23	0.004	0.43
TCSA	1	6.42	6.14*	8.91	11.39**	0.000	0
Block	5	1.39	1.14	0.89	1.14	0.025	2.45
Error	24	1.05		0.78		0.010	
Nodes							
Epicormic removal	1	20633427	6.78*	367329	0.21	275398	0.34
Crop load	2	5106103	1.68	21928382	12.26**	112296	0.14
Removal × crop	2	182864	0.06	1210072	0.68	539445	0.67
TCSA	1	4791105	1.57	5778020	3.23	30672	0.04
Block	2	3360437	1.10	2993492	1.67	1731232	2.15
Error	9	3045241		1789111		803503	

* and **, P-values at 0.05 and 0.01 levels of significance, respectively.

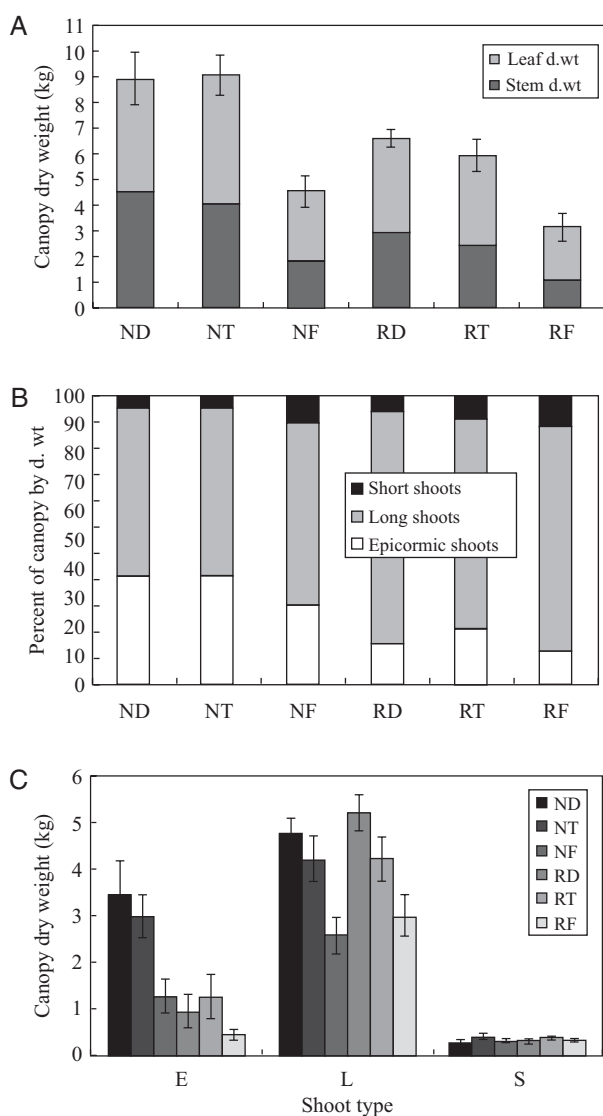


FIG. 2. (A) Mean 2003 canopy dry weight by treatment, showing proportion from stems and leaves. (B) Percentage of total 2003 canopy dry weight from each shoot type, for each treatment. ND, No sprout removal, de-fruited; NT, no sprout removal, thinned; NF, no sprout removal, full crop; RD, sprout removal, de-fruited; RT, sprout removal, thinned; RF, sprout removal, full crop. (C) Total dry weight of 2003 canopy, by shoot type and by treatment. E, Epicormic shoots; L, long shoots; S, short shoots. Bars indicate s.e.

epicormic shoot dry mass was inversely related to crop load ($P = 0.027$ and $P < 0.0001$, respectively), but short shoot d. wt was not significantly affected. Mean d. wt produced as short shoots was remarkably constant across all treatments, at about 0.5 kg (Fig. 2C). Production of long and short shoot d. wt was not significantly affected by the removal of epicormic shoots (Table 2). TCSA had a significant positive effect on d. wt of epicormic and long shoots produced, but did not affect short shoot d. wt.

The fewest number of nodes were produced on full-crop trees, significantly less than in the other two crop-load treatments ($P = 0.001$) (Fig. 3A). Trees with early season epicormic sprout removal had significantly fewer total

nodes at the end of the season than unpruned trees ($P = 0.011$). Though a higher absolute number of nodes were produced on thinned trees than on de-fruited trees, the difference was not significant. Across all treatments, short shoots accounted for 16–29%, long shoots for 48–68%, and epicormic shoots for 8–33% of total canopy nodes (Fig. 3B). Thinned trees produced more nodes on epicormic sprouts than did de-fruited trees though the difference was not significant (Fig. 3C). Crop load affected the number of nodes produced by long shoots ($P = 0.003$) but did not significantly affect the number of nodes produced by epicormic or short shoots. The number of nodes produced by short shoots did not differ significantly among treatments (Fig. 3C). TCSA did not have a significant effect on the number of nodes produced by any shoot type (Table 2).

Generally, across treatments, the majority of the total canopy leaf area was born on long shoots (data not shown). Total leaf area produced by epicormic shoots was significantly reduced by the epicormic shoot removal treatment ($P = 0.023$), but long and short shoot leaf areas were not affected. Leaf size and SLW of short shoots were lower than leaves of long or epicormic shoots. Area per leaf and SLW were not significantly affected by pruning or thinning treatments for any of the shoot types. Epicormic shoots had greater SSW and shoot length than long shoots, which in turn had greater SSW and shoot length than short shoots. SSW was significantly related to crop treatment and initial TCSA in epicormic shoots ($P = 0.006$ and $P = 0.018$, respectively) and to crop treatment in long shoots ($P = 0.002$), though it was not significantly affected in short shoots. For epicormic and short shoots, shoot length and sylleptic growth were not affected by pruning or thinning treatments; however, shoot length and sylleptic growth in long shoots significantly decreased with increasing crop load ($P = 0.039$ and $P = 0.002$, respectively). Mean sylleptic growth was higher in epicormic shoots than long and short shoots. Mean internode length was not significantly affected by crop or pruning treatments in any shoot type.

Vegetative growth in 2004

No significant block effect was present in 2004 (Table 3). Less vegetative growth was observed in 2004 than in 2003 (Figs 2A and 4A). Neither the 2003 crop load nor the 2003 pruning treatments significantly affected total harvested canopy d. wt in 2004 (Fig. 4A). Leaves constituted a larger portion of total shoot d. wt than stems, approx. 4 : 1 or 3 : 1 (Fig. 4A). Across all treatments, short shoots accounted for 31–44%, long shoots for 55–67% and epicormic shoots for 0.3–1.3% of total canopy d. wt (Fig. 4B). The d. wt produced as epicormic, long and short shoots did not differ among previous-year crop-load or pruning treatments. Epicormic shoot production was negligible in all previous year crop load and pruning treatments (Fig. 4C). TCSA had a significant positive effect on the d. wt of short shoots produced, but did not affect the d. wt of epicormic and long shoots (Table 3).

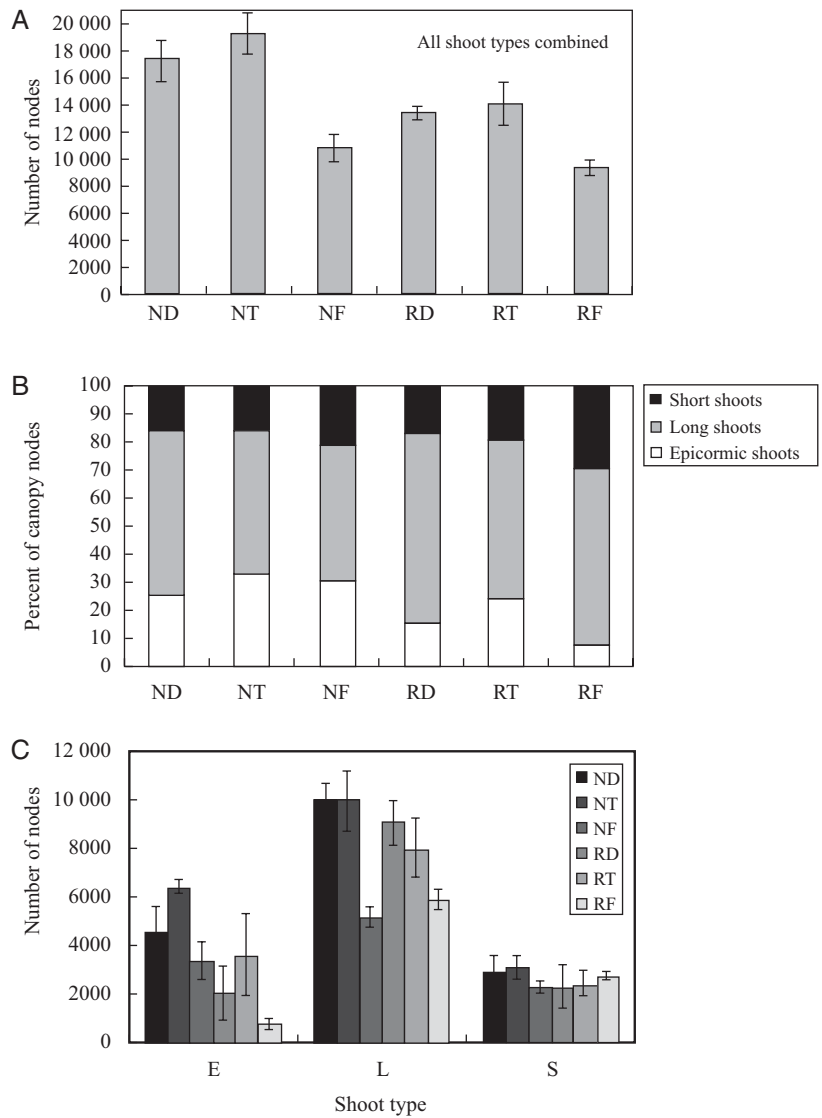


FIG. 3. (A) Mean number of nodes in 2003 canopy by treatment. (B) Percentage of total number of nodes in 2003 canopy from each shoot type, for each treatment. ND, No sprout removal, de-fruited; NT, no sprout removal, thinned; NF, no sprout removal, full crop; RD, sprout removal, de-fruited; RT, sprout removal, thinned; RF, sprout removal, full crop. (C) Total number of nodes in 2003 canopy, by shoot type and by treatment. E, Epicormic shoots; L, long shoots; S, short shoots. Bars indicate s.e.

Across all treatments, short shoots accounted for 42–67 %, long shoots for 33–57 %, and epicormic shoots for 0.2–1.1 % of total canopy nodes (Fig. 5B). The number of nodes produced on epicormic, long and short shoots did not differ among crop load or pruning treatments. TCSA had a significant positive effect on the number of nodes produced by long shoots but did not affect short- or epicormic-shoot node number (Table 3).

In all treatments, canopy leaf area was produced chiefly by long and short shoots, with little leaf area present on epicormic growth (data not shown). Epicormic and long shoot leaves were larger than short shoot leaves. SLW was highest in long shoots and lowest in short shoots. SSW was higher in long shoots than in epicormic and short shoots. Mean shoot length was greatest in epicormic shoots and least in short shoots. Sylleptic growth was very

low in 2004, and there were no significant differences among the shoot types. Mean internode length was longest in epicormic shoots and least in short shoots. There were no significant differences due to previous year pruning or thinning treatments for any of the shoots types for any of the variables measured: canopy leaf area, area per leaf, SLW, SSW, shoot length, sylleptic growth or internode length.

DISCUSSION

Effect of 2003 crop load on 2003 distribution of d. wt and nodes to shoot types

Total d. wt of current-year shoots in the canopy responded to current-year crop load as in previous studies of peach

TABLE 3. Results of the 2004 analysis of variance of factors affecting dry weight and number of nodes of epicormic, long and short shoots

Source	d.f.	Epicormic shoots		Long shoots		Short shoots	
		Mean square	F-value	Mean square	F-value	Mean square	F-value
Dry weight							
Epicormic removal	1	0.000	1.01	0.134	0.55	0.038	0.54
Crop load	2	0.000	0.89	0.499	2.04	0.025	0.35
Removal × crop	2	0.000	0.97	0.038	0.15	0.100	1.43
TCSA	1	0.000	0.00	0.643	2.62	0.388	5.55*
Block	5	0.000	0.51	0.539	2.2	0.079	1.13
Error	21	0.000				0.070	
	19			0.245			
Nodes							
Epicormic removal	1	2670	0.88	393	0	3271659	0.47
Crop load	2	1363	0.45	3272123	4.54	202223	0.03
Removal × crop	2	1807	0.59	2933230	4.07	7510427	1.07
TCSA	1	3972	1.30	5167053	7.17*	8460124	1.2
Block	2	973	0.32	3678724	5.11	2388590	0.34
Error	7	3045				7034994	
	5			720504			

* *P*-value at 0.05 level of significance.

vegetative growth (DeJong *et al.*, 1987; Grossman and DeJong, 1995b): decreased vegetative d. wt was observed in full-crop trees (Fig. 2A). The effect of crop load on distribution of resources to different shoot types varied with shoot type.

Actively growing long-shoot meristems appeared to be sensitive to crop load, probably as related to the effects of crop load on tissue carbohydrate concentration, as indicated by bark and xylem NSC content at the end of the season (Table 1). The reduction in long-shoot d. wt and node number in response to a full crop load (Figs 2C and 3C) demonstrated the apparent sensitivity of neo-formed growth to competition for carbohydrates during the spring growth period.

Additionally, the meristems of epicormic shoots appeared to be sensitive to tissue carbohydrate concentration. The suppression of current year epicormic growth, both d. wt and node number, in response to full crop load (Figs 2C and 3C) confirms the results of earlier work (Gordon *et al.*, 2006b) that suggested a link between epicormic bud break/epicormic shoot growth and tissue carbohydrate concentration. It is noteworthy that a full crop load was required for suppression of epicormic growth: in thinned trees producing approximately two-thirds of full crop (by f. wt; Fig. 1) suppression of epicormic growth was not evident.

The remarkable consistency in total d. wt of short shoots among all treatments (Fig. 2C) apparently indicates that their fate was committed prior to the date of fruit thinning. Several workers have suggested that competition for carbohydrate between primary (apical) and secondary (cambial) growth of shoots results in an increased number of short shoots (Barnola and Crabbé, 1993; Costes *et al.*, 2000). Such competition would be expected to be more severe in the presence of a high crop load. The results of the current experiment indicate that any effect of crop load on intra-shoot competition would occur in the very early

season in peach, in this case prior to mid-April. Short shoots constituted a relatively smaller portion of total canopy d. wt with decreasing crop load (Fig. 2B), apparently because the extra carbohydrate available in low-crop trees was invested in additional long shoot or epicormic growth. It is interesting that a relative increase in availability of carbohydrate potentially available in de-fruited trees after 15 April did not cause the short-shoot apical meristems to continue or recommence growth though they are capable of doing so under some conditions (D. Gordon, unpubl. res.).

Effect of 2003 crop load on 2003 leaf and stem properties

The lack of effect of crop load or early epicormic sprout pruning on SLW and canopy and individual leaf area indicates that in this experiment these treatments apparently had minimal effects on canopy light conditions, since canopy light conditions are known to affect leaf area and SLW (Rosati *et al.*, 2000). Berman and DeJong (2003) found significantly greater total canopy leaf area in de-fruited trees but the trees used in that experiment were young and had not completely filled their space. General observations in the literature about the lesser SLW and smaller leaf size present on short shoots were supported by these data, across all treatments.

Some stem properties, however, were affected by crop load, in ways that may help shed light on canopy carbohydrate dynamics. Stem mass increases much more than leaf mass in the mid- and late season (Grossman and DeJong, 1998). The length and sylleptic growth of epicormic shoots were not sensitive to crop load, though length and sylleptic growth of long shoots were. This may be due to the location of the epicormic shoots in the canopy – by definition they arise only on older, non-fruiting wood – which places epicormic shoots further away from fruiting sinks than long shoots. This physical arrangement puts

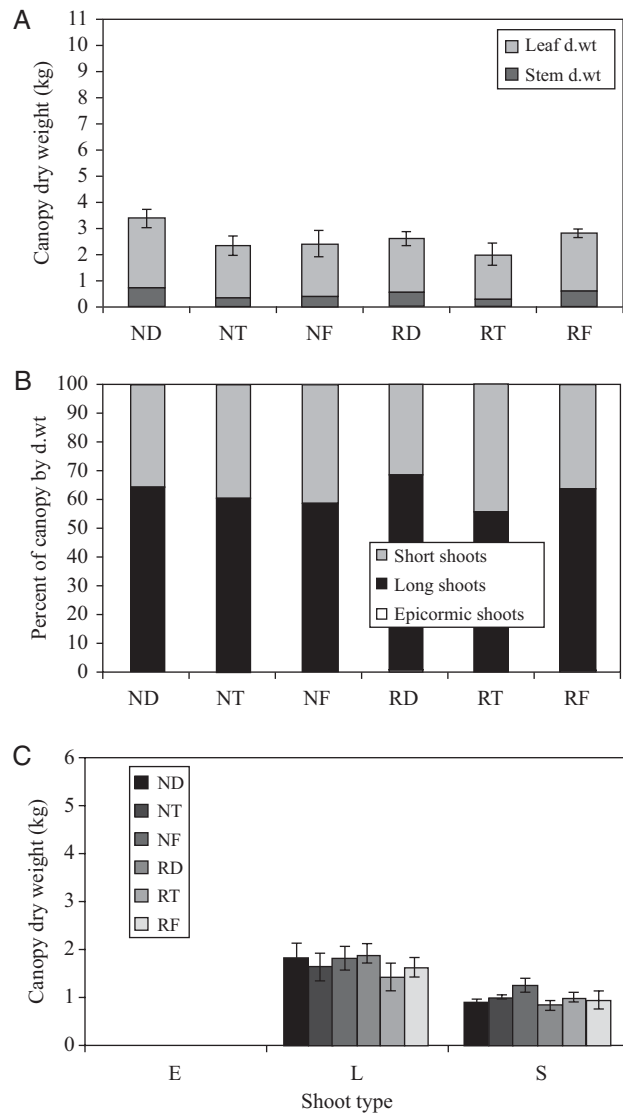


FIG. 4. (A) Mean 2004 canopy dry weight by treatment, showing proportion from stems and leaves. (B). Percentage of total 2004 canopy dry weight from each shoot type, for each treatment. ND, No sprout removal, de-fruited; NT, no sprout removal, thinned; NF, no sprout removal, full crop; RD, sprout removal, de-fruited; RT, sprout removal, thinned; RF, sprout removal, full crop. (C) Total dry weight of 2004 canopy, by shoot type and by treatment. E, Epicormic shoots; L, long shoots; S, short shoots. Bars indicate s.e.

syllaptic and apical growth of epicormic shoots less in competition with the growing fruit during the time when syllaptic and apical growth happens. This supports growth models that include distance as a factor in sink-source relationships (DeJong, 1999; Allen *et al.*, 2005).

It has been proposed that primary growth is out-competed by secondary growth some time during the season when shoot elongation ceases and diameter increases (Costes *et al.*, 2000). At this point in the season, competition for carbohydrate may intensify as the stage III fruit are growing rapidly (DeJong and Grossman, 1995). The effect of crop load on epicormic SSW noted in this experiment supports the importance of considering shifts

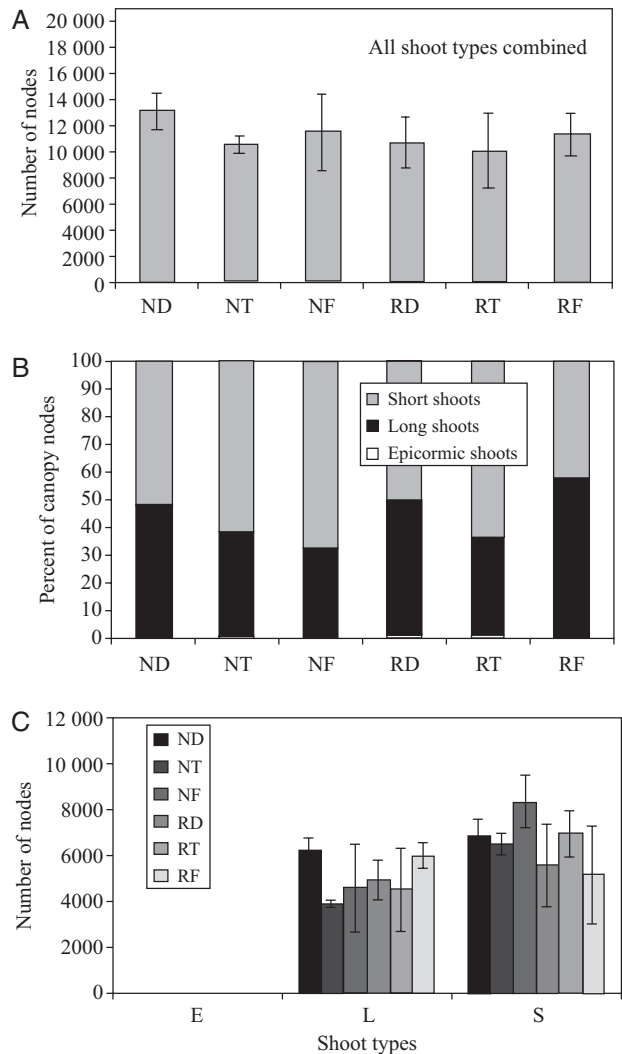


FIG. 5. (A) Mean number of nodes in 2004 canopy by treatment. (B) Percentage of total number of nodes in 2004 canopy from each shoot type, for each treatment. ND, No sprout removal, de-fruited; NT, no sprout removal, thinned; NF, no sprout removal, full crop; RD, sprout removal, de-fruited; RT, sprout removal, thinned; RF, sprout removal, full crop. (C) Total number of nodes in 2004 canopy, by shoot type and by treatment. E, Epicormic shoots; L, long shoots; S, short shoots. Bars indicate s.e.

in sink priority and strength throughout the season (DeJong and Grossman, 1994; Grossman and DeJong, 1995a). Also implied is a shift in the level of autonomy experienced by an epicormic branch though the growing season, despite the greater distances to fruit than typically experienced by other branch types (Marsal *et al.*, 2003).

Effect of 2003 and 2004 crop loads on 2004 distribution of d. wt and nodes to shoot types

Though effects of the previous-year crop load on current-year shoot growth have been reported in apple (Rogers and Booth, 1964; Palmer, 1992), they were not

evident in this experiment in peach. Despite the fact that trees under 2003 full-crop or no-crop treatments started the 2004 season with significantly different NSC reserves in xylem and bark tissue (Fig. 1), 2004 growth distribution was very similar for all shoot types for both d. wt (Fig. 4C) and node number (Fig. 5C).

One possible explanation is that the effect of an unusually heavy 2004 crop load may have overpowered any effects of pruning or thinning treatments in the preceding year. However, if the heavy crop were solely responsible, behaviour similar if not more extreme compared with the full crop in 2003 would have been expected in all 2004 trees. Relative to the 2003 full crop, production of epicormic shoots of the 2004 trees approached zero, the short shoots more than doubled, and the long shoots decreased slightly (Figs 2C and 4C), indicating that something other than crop load may have been responsible.

Alternatively, the fact that the trees were virtually unpruned in the 2003–2004 dormant season probably altered the type of vegetative response that occurred in 2004 so that it is not typical of many previous horticultural studies related to this subject. As the 2004 data indicates, epicormic shoot growth in peach trees appears to be almost solely a response to pruning. Previous research has shown a strong stimulation of epicormic shoot growth by dormant pruning in black birch and red maple (Wilson, 1992). Comparison of 2003 and 2004 long-shoot node-number data (Figs 3 and 5) also indicates that dormant pruning probably has a strong stimulatory effect on long shoot growth. Thus the virtual absence of pruning between years also may have removed a stimulus for manifesting differential growth due to the previous-year crop load or spring pruning. This indicates that natural shoot growth-control phenomena such as apical dominance or apical control (Brown *et al.*, 1967) may have stronger influence on canopy development under unpruned conditions than differences in carbohydrate availability.

Effect of epicormic sprout removal treatment

In the literature there are mixed reports regarding the effect of summer pruning on fruit size and yield (Brown and Harris, 1958; Day *et al.*, 1989; Kappel and Bouthillier, 1995; Li *et al.*, 2003a). Day *et al.* (1989) found an increase in size of early maturing nectarines with pre-harvest water sprout removal that was not mirrored here, with earlier sprout removal. The slightly smaller average size per fruit noted in the R treatment is probably due to the slightly higher number of fruit per tree (DeJong and Grossman, 1995), rather than a direct effect of epicormic shoot removal on fruit size.

Most of the flexibility in the vegetative response to epicormic pruning was evident in increased long-shoot growth, though the response was not statistically significant due to large tree-to-tree variation. It is possible that epicormic removal may slightly increase the amount of productive and desirable hanger growth in the canopy, but this should be investigated further, possibly using younger, more uniform trees.

Trees with all epicormic shoots removed in the spring did experience some epicormic re-sprouting, but it was limited to only one-third of what unpruned trees had by the end of the season. This supports earlier work indicating that green pruning of epicormic shoots in April appears to minimize epicormic re-growth both in peach and other species (Wignall *et al.*, 1985; Gordon *et al.*, 2006b) compared with other times of the year. It is interesting to note that the green pruning of epicormic shoots from thinned trees was equivalent in epicormic-suppression value to leaving trees with a full crop.

CONCLUSIONS

In summary, crop load impacted the distribution of growth to shoot types in the peach canopy, with high crop load lessening the d. wt allocated to epicormic and long shoots. It appears that fruit thinning promotes distribution of shoot growth similar to that of de-fruited trees, and, while effective in increasing fruit size, contributes to the problem of excess vegetative vigour in peach, particularly epicormic sprouting. Although early epicormic sprout removal increased the relative proportion of long and short shoots in the canopy, it did not affect the distribution of d. wt to long and short shoots. It appears that early epicormic sprout removal does not stimulate the excessive epicormic re-growth in the same or subsequent year relative to other previously studied summer pruning methods.

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