Intra-canopy variability of fruit growth rate in peach trees grafted on rootstocks with different vigour-control capacity

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SUMMARY

The aim of the present research was to study intra-canopy variability in fruit growth under conditions of low fruit-tofruit competition in peach trees grafted on rootstocks with differing size-controlling capacity. The experiment was conducted on adult peach trees of two cultivars, each grafted on five rootstocks. Tree canopies were divided vertically into five layers. The diameter of 12 fruit per canopy layer was measured early in the growing season and at harvest. At harvest, the fresh weight of each selected fruit was also determined. After harvest, thirty shoots per tree bearing the selected fruit were harvested, and several parameters related to local carbon source availability, competition between vegetative and reproductive organs, vigour of the fruiting shoot, and position of the fruit on the fruiting shoot were measured. The results demonstrated that fruit variability within peach trees is very large, even when fruit-to-fruit competition is low. Fruit size at harvest decreased significantly and progressively from the top layers to the bottom layers of the canopy. Fruit growth was positively correlated with specific leaf weight, leaf area, and vigour of the fruiting shoot, and was negatively correlated with the vigour of current-season shoot growth on the fruiting shoot. However, the relative importance of each parameter depended on the cultivar. Rootstock affected the relationship between fruit growth and the measured parameters, and some rootstocks appeared to limit the maximum potential fruit growth rate. The measured parameters did not explain all the intra-canopy variability in fruit growth, suggesting that other factors also played a role. Interestingly, fruit size within 1 month of full bloom increased progressively from the top to the bottom of the canopy.

Several studies on peach trees have demonstrated that (Genard and Bruchou, 1993; Weibel, 1999) and in qualitative fruit characteristics (Forlani *et al.*, 2002; Lewallen and Marini, 2003). Similar results have also been reported for other fruit tree species (Crisosto *et al.*, 1997; Smith *et al.*, 1997; Broom *et al.*, 1998; Barry *et al.*, 2004).

A lack of understanding of the factors affecting the variability of peach fruit growth within the canopy limited the early sink-driven PEACH model (Grossman and DeJong, 1994) which partitioned carbon among compartments consisting of organ types (fruit, shoots, trunk, and roots) and ignored the intra-canopy variability of individual organs. The need for more detailed functional-structural models of plant growth, such as L-PEACH (Allen *et al.*, 2005), requires a better understanding of the factors that affect the growth of each organ within the plant. Indeed, in L-PEACH, each organ represents an elemental source or sink of carbohydrate, and individual calculations are made for each of them.

Fruit trees can be considered as a collection of semiautonomous, interacting growing organs (sinks) that compete for resources (Grossman and DeJong, 1994).

Fruit generally are considered to be very strong sinks for carbohydrates (Grossman and DeJong, 1995a). However, like all other tree organs, fruit are also subjected to a complex network of source-sink relationships that can decrease their growth below their genetically-determined maximum potential growth rate (Grossman and DeJong, 1995b). In particular, local source-sink relationships within the canopy may have important implications for fruit growth and quality, since branches have been demonstrated to be partially autonomous for carbohydrates (Marsal et al., 2003). Indeed, several authors have related the intra-canopy variability of peach fruit characteristics to the heterogeneity of light distribution within the canopy (Bible and Singha, 1993; Marini et al., 1993; Luchsinger et al., 2002; Lewallen and Marini, 2003). In addition to the availability of light inside the canopy compartment where the fruit are growing, other major factors related to source-sink relationships may affect fruit growth, such as: source proximity (Corelli-Grappadelli and Coston, 1991), leaf-to-fruit ratio (Wu et al., 2005), and competition with other growing fruit (Grossman and DeJong, 1995c) or with vigorously growing shoots (Caruso et al., 1997).

Previous studies (Pavel and DeJong, 1993; Grossman and DeJong, 1995b) calculated maximum potential fruit growth by thinning peach trees heavily, which minimised

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resource limitations to fruit growth due to fruit-to-fruit competition. However, Weibel (1999) reported that within-canopy variability in fruit size was still present in heavily-thinned peach trees, suggesting that local resource limitations due to fruit-to-fruit competition are not the only factors causing fruit size variability within the tree.

Size-controlling rootstocks decrease peach tree vigour by significantly reducing both the stem extension growth rate (i.e., producing stems with shorter internodes), and the number of watersprouts (Weibel et al., 2003). These rootstock effects may directly alter source-sink relationships within the tree by modifying both the amount of resources available (i.e., the size of the source located close to the growing fruit) and the strength of the competition among growing organs (i.e., fruit-to-fruit and fruit-tovegetative-organ competition). These effects appeared to be confirmed by studies that reported that rootstock significantly affected carbon partitioning between the reproductive and vegetative organs of peach trees (Caruso et al., 1997; Inglese et al., 2002). The competition between vegetative and reproductive organs has been reported to be stronger in trees grafted on dwarfing rootstocks than in trees on vigorous rootstocks, because a smaller carbon pool is available in dwarfed trees (Lliso et al., 2004). In addition, rootstock may modify the light distribution within the canopy, which can have a direct effect on light availability within the micro-environment where each fruit is growing (i.e., have an effect on locally available photosynthate). Similarly, scion cultivars with different vegetative and/or reproductive habits are expected to exhibit differences in their sourcesink relationships between reproductive and vegetative organs. Indeed, Scorza et al. (1986) reported dramatic differences in light distribution within the canopies of peach cultivars with different growth and reproductive habits. In addition, cultivars with different vegetative and reproductive growth habits are generally pruned differently, and pruning may also affect carbon partitioning as suggested by DeJong and Doyle (1984). These authors reported that minimally-pruned dwarf trees partitioned more dry matter to fruit compared to standard trees trained to an "open vase".

The aim of the present study was to improve our understanding of the intra-canopy parameters that decrease fruit growth rate below its maximum potential, causing within-tree variability in fruit size at harvest. With this objective, we hypothesised that local (i.e., very close to the growing fruit), within-canopy factors directly affect fruit growth. In addition, we hypothesised that the rootstock may alter the relationship between fruit growth and local parameters, and that rootstock effects may be different for cultivars with different vegetative and reproductive habits. Therefore, the present research focussed on within-tree variability in the fruit growth rate of heavily-thinned trees of two cultivars with different reproductive and vegetative habits: a fresh market freestone peach cultivar ('Flavorcrest'), and a processing clingstone cultivar ('Loadel'), grafted on five rootstocks with differing sizecontrolling potential.

MATERIALS AND METHODS

Plant material and orchard management

The experiment was conducted at the Kearney Agricultural Center of the University of California (Parlier, CA, USA) in 2000. Measurements were taken on two peach cultivars, 'Flavorcrest' (an early-maturing yellow-fleshed cultivar) and 'Loadel' (an early-maturing clingstone processing cultivar) grafted on five rootstocks with different size-controlling potential: a vigorous control [Nemaguard (Prunus persica × P. davidiana hybrid)]; three intermediate vigour rootstocks [K119-50 (Prunus salicina × P. dulcis hybrid), P30-135 (Prunus salicina \times P. persica hybrid), and Hiawatha (openpollinated seedling of a Prunus besseyi \times P. salicina hybrid)]; and a semi-dwarfing rootstock [K146-43 (*Prunus salicina* \times *P. persica* hybrid)]. Trees were planted in 1996 and trained to a KAC-perpendicular V system (DeJong et al., 1994) in a North-South orientation. Planting distances for Nemaguard and P30-135 rootstocks were 4.88 m \times 1.98 m (corresponding to a planting density of 1,035 trees ha⁻¹), while trees on K119-50, Hiawatha and K146-43 were spaced 4.88 m \times 1.83 m apart (corresponding to a planting density of 1,120 tree ha⁻¹). Trees were planted according to a randomised complete block design with four replicates and five trees per rootstock plot per replicate.

Routine horticultural care was provided to trees according to commercial protocols for fruit production (LaRue and Johnson, 1989). Flood irrigation was provided to trees in the amount necessary to replace 100% of the computed evapotranspiration throughout the growing season. A 2 m-wide herbicide-treated strip was maintained in the tree rows, to control weed growth. The space between rows was planted with a grass cover crop and mowed regularly. At the beginning of the experiment, four homogeneous trees (one in each block) were selected for each cultivar/rootstock combination (i.e., a total of 40 trees). Full bloom occurred on 7 March 2000. On 5 April 2000, selected trees were thinned heavily, leaving only one fruit on each fruiting shoot.

Canopy layer and fruit sample selection

Tree canopies were divided vertically into five hypothetical canopy layers. Each canopy layer included a part of both main scaffolds of the perpendicular-V. Twelve fruit within each canopy layer were selected at random and tagged (i.e., six fruit on each scaffold; giving a total of 60 fruit per tree).

Fruit growth and harvest

The diameters of the selected fruit were measured with a digital caliper at the beginning of the experiment (5 April 2000) and at harvest time. Harvest was split into two pickings for 'Flavorcrest' trees (15 and 19 June 2000) and into three pickings for 'Loadel' trees (29 June, 3 July, and 10 July 2000). On each picking date, fruit were harvested using the surface ground colour as a maturity index according to Delwiche and Baumgardner (1985). In addition, the untagged fruit harvested on each picking date were also counted and weighed.

Vegetative parameters

On 5 March 2000, the trunk circumference of each selected tree was measured 20 cm above the ground and

the trunk cross-sectional area (TCSA) was computed assuming each trunk was circular. Crop load was calculated both by the number of fruit per tree, and by normalising the number of fruit per tree by the TCSA. Also the fruit yield per tree was normalised by the TCSA.

After fruit harvest, half of the shoots bearing the selected fruit were removed from the tree (i.e., six shoots per canopy layer; 30 shoots per tree). The following measurements were taken on these shoots: total shoot length, the distance between the base of the shoot and the point where the selected fruit was attached, the distance between the point where the fruit was attached and the terminal end of the shoot, the number of currentseason lateral shoots, the total length of current-season shoots, the fresh weight (FW) of current-season shoots, the total number of leaves, total leaf FW, and total leaf dry weight (DW; leaves were weighed after being ovendried at 60°C to constant weight). Fruiting shoots shorter than 10 cm were considered spurs, whereas the others were considered hangers. In addition, 15 leaves were sampled from each shoot, and their FW, DW and leaf areas were measured to calculate the specific leaf weight (SLW) for each fruiting shoot. Leaf area was measured with a leaf area meter (Li-COR 3200; Li-COR, Lincoln, NE, USA). SLW data were used to convert the total leaf DW data measured on each selected shoot into total leaf area per fruiting shoot. In addition "percent of maximum specific leaf weight" values were calculated by dividing each SLW datum point by the maximum SLW value measured on each tree.

Fruit were divided into 11 fresh-weight classes, which were defined as follows: class 1 (70-95 g), class 2 (95-120 g), class 3 (120-145 g), class 4 (145-170 g), class 5 (170-195 g), class 6 (195-220 g), class 7 (220-245 g), class 8 (245-270 g), class 9 (270-295 g), class 10 (295-320 g), and class 11 (320-345 g).

Statistical analyses

All statistical analyses were performed with SPSS software (SPSS Inc., Chicago, IL, USA). Two-way ANOVAs were used to study the significance of cultivar (C), rootstock (R), and C × R interaction effects on the number of fruit per tree, fruit yield per tree, TCSA, crop load (number of fruit cm⁻² TCSA), and the fruit yield cm⁻² TCSA, (P = 0.05). Four-way ANOVAs were used to study the significance of the effects of cultivar, rootstock, block (B), canopy layer (L), and all interactions on SLW, initial fruit diameter, and absolute fruit growth rate. Finally, a five-way ANOVA was used to study the significance of the effects of cultivar, rootstock, block, canopy-layer, fruiting-shoot-type (F), and all interactions on fruit FW at harvest. Tukey's HSD (P = 0.05) was used to perform mean separations.

Two (one for each cultivar) separate multiple regression analyses, between absolute growth rate and the parameters measured for each fruiting shoot, were performed using backward elimination as a stepwise procedure for variable selection. The backward elimination procedure started with all of the predictors in the model and, at each step, the variable that was least significant (i.e., the one with the least significant P value) was eliminated and the model was refitted. The elimination procedure was repeated until all the

remaining variables had individual P values less than 0.10. Multiple regression analyses were applied only on fruit grown on hangers, because we hypothesised that short lateral fruiting shoots were characterised by less branch autonomy, and therefore fruit growth on them was more affected by factors external to the fruiting shoot. Multiple regression analyses were performed on mean values calculated for the different parameters for each canopy layer of each tree (i.e., each analysis was performed on a total of 100 complete sets of parameters). The accuracy of the multiple regression models in predicting absolute fruit growth rate (AGR) were evaluated by calculating the following statistics: r^2 (calculated for estimated-AGR vs. measured-AGR with linear regression analysis); the root mean square error of prediction (RMSEP); the standard deviation ratio (SDR); the model bias; and the significance of the difference of the model bias from zero (i.e., the null hypothesis of the model bias equal to zero was tested with paired-samples t-tests). The RMSEP was measured, as reported by Peirs et al. (2003), as follows:

$$RMSEP = \sqrt{\frac{\sum_{i=1}^{n} (AGR_{i}^{'} - AGR_{i})^{2}}{n}}$$

where AGR_i and AGR_i are the estimated and measured AGR values for the *i*th fruit, respectively.

The SDR was calculated according to McGlone and Kawano (1998), with the following equation:

$$SDR = \frac{SD}{RMSEP}$$

where *SD* is the standard deviation of the measured data and *RMSEP* is the root mean square error of prediction. The model bias was measure as follows:

$$bias = \frac{\sum_{i=1}^{n} (AGR_{i}' - AGR_{i})^{2}}{n}$$

RESULTS

Trunk cross-sectional area, crop load and yield

Both cultivar (C) and rootstock (R) significantly affected the TCSA. 'Flavorcrest' trees grafted on K146-43 had significantly smaller TCSA values than those grafted on the other rootstocks (Table I). The TCSAs of 'Loadel' trees grafted on Nemaguard were significantly greater than trees on K146-43, whereas 'Loadel' trees on the other rootstocks had intermediate TCSA values (Table I).

Crop load was significantly affected by rootstock. Crop load did not differ significantly among 'Flavorcrest' trees grafted on the different rootstocks (Table I), and ranged between 98.8 (on Hiawatha) to 157.8 fruit per tree (on Nemaguard), or between 1.3 - 3.8 fruit tree⁻¹ cm⁻² TCSA. 'Loadel' trees on Nemaguard had larger numbers of fruit per tree than trees on P30-135, Hiawatha, or K146-43 (Table I). The effects of cultivar and rootstock were non-significant when crop loads were normalised by TCSA (Table I).

Cm TCSA in Flavorcrest and Loader peach trees grafted on Nemagaura, 130-155, K117-50, Huwana, 07 K140-45 rootstocks						
Cultivar	Rootstock	TCSA (cm ²)	No of fruit/tree	No of fruit cm ⁻² TCSA	Total yield (kg/tree)	Total yield/ TCSA (kg cm ⁻²)
'Flavorcrest'	Nemaguard P30-135	114.8a ^z 88.8a	157.8a 149.3a	1.4a 1.9a	29.6a 29.1a	0.26a 0.38a
	K119-50	81.5a	148.5a	2.0a	31.0a	0.41a
	K146-43	81.0a 33.1b	98.8a 116.0a	1.3a 3.8a	21.2a 19.1a	0.29a 0.63a
'Loadel'	Nemaguard	75.5a	215.0a	2.9a	38.3a	0.51a
	P30-135	57.6ab	107.5b	2.0a	19.8b	0.37a
	K119-50	55.4ab	135.8ab	2.6a	24.4b	0.47a
	Hiawatha	58.5ab	91.3b	1.6a	15.8b	0.28a
	K146-43	35.7b	106.3b	3.0a	17.0b	0.48a

TABLE I Trunk cross-sectional area (TCSA), number of fruit per tree, number of fruit per tree cm⁻² TCSA, total fruit yield per tree, and total fruit yield per tree cm⁻² TCSA in 'Flavorcrest' and 'Loadel' peach trees grafted on Nemaguard, P30-135, K119-50, Hiawatha, or K146-43 rootstocks

^ZFor each cultivar, mean separation within columns by Tukey's HSD (P = 0.05). Values followed by a different lower-case letter are significantly different.

Rootstock significantly affected the total yield per tree (expressed as kg fruit per tree, or as kg fruit per tree cm⁻² TCSA). Total fruit yields from 'Flavorcrest' trees on Nemaguard were significantly greater than on the other rootstocks. The effects of cultivar and rootstock were non-significant when the total fruit yield per tree was normalised by TCSA (Table I).

Within-canopy variability of fruit size at harvest

Cultivar, rootstock, and canopy layer (L) significantly affected fruit size at harvest (Table II; Figures 1–4), whereas fruit size was not significantly affected by the type of fruiting shoot (F; hangers or spurs). The $C \times R$, $C \times F$, and $R \times L \times F$ interactions also significantly affected fruit FW at harvest. Similarly, C, R, L and C \times R significantly affected AGR (Figure 3; Figure 4).

Independent of cultivar, trees on K146-43 had the smallest mean fruit size. 'Flavorcrest' trees on K119-50 and Hiawatha had larger fruit than those on the other rootstocks (Table II), whereas the mean fruit size from 'Loadel' trees was largest for those on P30-135 (Table II).

Individual fruit size varied greatly within trees, in all cultivar-rootstock combinations (Table II). Size variability in 'Flavorcrest' fruit was greatest in trees grafted on P30-135 (226 g total range), intermediate in trees on Nemaguard, K119-50, and Hiawatha (203, 204, and 191 g total range, respectively), and least in trees grafted on K146-43 (164 g total range; Table II). In 'Loadel' trees, fruit size variability was greatest in trees on Nemaguard and K119-50 (211 and 218 g total range, respectively), intermediate in trees on P30-135 and Hiawatha (187 and 186 g total range, respectively), and least in trees grafted on K146-43 (169 g total range; Table II).

The size of fruit grown on hangers exhibited significant variability in all cultivar-rootstock combinations (Figure 1; Figure 2). Independent of cultivar, trees on Nemaguard produced a large variability in fruit size; between fruit size classes 1 and 9 for 'Flavorcrest' trees grafted on Nemaguard, and between size classes 1 and 8 for 'Loadel' trees on Nemaguard. Fruit size in 'Flavorcrest' trees on K146-43 ranged between size classes 2 and 8. In general, 'Loadel' trees had a lower overall variability in fruit sizes (i.e., only between class 1 and class 8) compared to 'Flavorcrest' trees. 'Loadel' trees on K146-43, and on P30-135, had ranges of fruit sizes between class 1 and 7, and between class 2 and 8, respectively.

Fruit FW at harvest differed significantly between the different canopy layers of trees in all cultivar-rootstock combinations (Figure 3; Figure 4). In general, fruit FW at harvest, and accordingly also absolute fruit growth rate, was highest in the top layers and decreased progressively towards the bottom layers of the canopy (Figure 3; Figure 4). The steepness of these gradients was affected by the cultivar-rootstock combination (Figure 3; Figure 4). These within-canopy gradients were evident in all 'Flavorcrest' trees, independent of rootstock, even though the width of the gradient changed with rootstock (Figure 3). Gradients in fruit FW and in absolute fruit growth rate within 'Loadel' trees were more evident in trees grafted on Nemaguard and P30-135, than in trees on K119-50, Hiawatha or K146-43 (Figure 4).

Initial fruit size was significantly affected by C, R and L, whereas the effects of the block, and of all the other interactions between factors, were non-significant. Independent of cultivar-rootstock combination, initial fruit size also differed significantly among canopy layers (Figure 3; Figure 4), with the largest fruit located in the bottom layers. Initial fruit size decreased progressively from the bottom to the top layers of the canopy.

Multiple regression analysis extracted a significant model for each cultivar (with an r^2 of 0.305 and 0.386 for 'Flavorcrest' and 'Loadel', respectively; Table III). According to the model extracted for 'Flavorcrest', AGR was positively correlated with SLW, and with the total leaf area of the hanger, and negatively correlated with initial fruit diameter and the FW of current season shoots. In this model, the standardised coefficients were highest for the "current-season shoot FW" and "specific leaf weight" variables. In the model extracted for 'Loadel', AGR was positively correlated with SLW and

TABLE II	
Mean fresh fruit weight and range of variation in fresh fruit we	ight in
Flavorcrest' and 'Loadel' peach trees grafted on Nemaguard, P3	0-135,
V110 50 Higwatha on V146 42 restated	

	·Flavor	crest'	'Loadel'		
Rootstock	Fresh weight (g/fruit)	Range (min–max) (g/fruit)	Fresh weight (g/fruit)	Range (min–max) (g/fruit)	
Nemaguard P30-135 K119-50 Hiawatha K146-43	185c ^z 207b 218a 220a 166d	76–274 95–321 112–316 129–320 99–263	174b 185a 174b 174b 155c	71–282 96–283 78–296 86–272 70–239	

^ZMean separation within columns by Tukey's HSD (P = 0.05). Values followed by a different lower-case letter are significantly different.







FIG. 3

Relationship between percentage of maximum specific leaf weight (SLW) and fresh fruit weight at harvest, initial fruit diameter, and absolute fruit growth rate (AGR) measured for each of five canopy layers (Top, Mid-top, Mid, Mid-bottom, Bottom) in 'Flavorcrest' trees grafted on Nemaguard, P30-135, K119-50, Hiawatha, or K146-43 rootstock. Percentage of maximum SLW values were calculated by dividing each SLW value by the maximum SLW value measured for the same tree from which the sample was collected.





Relationship between percentage of maximum specific leaf weight (SLW) and fresh fruit weight at harvest, initial fruit diameter, and absolute fruit growth rate (AGR) measured for each of five canopy layers (Top, Mid-top, Mid, Mid-bottom, Bottom) in 'Loadel' trees grafted on Nemaguard, P30-135, K119-50, Hiawatha, or K146-43 rootstock. Percentage of maximum SLW values were calculated by dividing each SLW value by the maximum SLW value measured for the same tree from which the sample was collected.

		jor riavorcresi	ana Loadei peach i	rees		
	Coefficient					
	'Flavorcrest' ^Y			'Loadel' ^Z		
Predictor	В	β	Sig.	В	β	Sig.
Constant	+0.617	_	0.001	+0.514	_	0.001
Initial fruit diameter	-0.007	-0.149	0.091	-0.005	-0.182	0.041
Current-season shoot FW	-0.002	-0.616	0.035			
Specific leaf weight	+0.033	+0.454	0.001	+0.024	+0.411	0.001
Total leaf area	+0.002	+0.001	0.007			
Fruiting shoot FW	_	_	_	+4.96E-4	+0.226	0.012

TABLE III Unstandardised (B) and standardised (β) coefficients and significance of the coefficients for each predictor of the multiple regression models extracted for 'Flavorcrest' and 'Loadel' peach trees

^YThe model calculated for 'Flavorcrest' was highly significant (P < 0.0001) and had $r^2 = 0.305$.

^zThe model calculated for 'Loadel' was highly significant (P < 0.0001) and had $r^2 = 0.386$.

with the FW of the fruiting shoot, and negatively correlated with initial fruit diameter. The standardised coefficient of the "specific leaf weight" variable was the highest in the 'Loadel' model. Both models fitted the data well, as suggested by the low RMSEP values (0.0486 and 0.0349 mm d⁻¹ for 'Flavorcrest' and 'Loadel', respectively), the low (and non-significantly different from zero) model bias (-0.0002 and 0.0001 mm d⁻¹ for 'Flavorcrest' and 'Loadel', respectively), and the high SDR values (1.20 and 1.28 for 'Flavorcrest' and 'Loadel', respectively; Table IV).

Each model had a different fit, depending on the rootstock (Figure 5; Figure 6; Table IV). The 'Flavorcrest' model best fitted the data from trees on K119-50 (r^2 = 0.614; P < 0.0001), and also fitted data from trees on Nemaguard ($r^2 = 0.483$; P = 0.0021) and on Hiawatha (r^2 = 0.437; P = 0.0015) (Figure 5). Indeed, although in 'Flavorcrest' trees on K119-50, the model tended to slightly, but significantly, underestimate AGR (as suggested by the negative and significant value of the model bias), the slope of the linear regression equation was highest and the intercept lowest (Figure 5), the RMSEP was fairly low, and the SDR relatively high (Table IV). The worst fit of the 'Flavorcrest' model occurred for trees grafted on K146-43 (Table IV; Figure 5; $r^2 = 0.296$; P = 0.02). This model tended to overestimate AGR, as suggested by the significant positive model bias of 0.0606 mm d^{-1} , across the whole data range (Figure 5). In addition, the slope of the estimated AGR vs. measured AGR linear regression equation was low (0.308) and the intercept was high (0.546). The r^2 was low (0.296), the RMSEP was relatively large (0.0702 mm d⁻¹), and the SDR was fairly low (0.61; Table IV). The ability of the 'Flavorcrest' model to predict AGR values of trees on Nemaguard, P30-135, or Hiawatha was intermediate (Table IV; Figure 5).

The 'Loadel' model best fitted the data from trees grafted on P30-135 ($r^2 = 0.597$; P < 0.0001) and on Nemaguard ($r^2 = 0.560$; P = 0.0001; Figure 6). The 'Loadel' model also fitted the fruit growth of trees grafted on K146-43 ($r^2 = 0.469$; P = 0.0009), whereas the fitting of data from trees on K119-50 was poorer (r^2 = 0.213; P = 0.04) than trees on Nemaguard, P30-135, or K146-43 (Figure 6). The 'Loadel' model did not significantly fit the fruit growth data in trees grafted on Hiawatha (Figure 6). The 'Loadel' model predicted fruit AGR in trees grafted on P30-135 fairly accurately. For these data, the slope and the intercept of the estimated AGR vs. measured AGR linear regression equation were relatively high and low, respectively (besides the relatively high r^2), the RMSEP was fairly low, the SDR relatively high, and the bias non-significantly different from zero (Table IV; Figure 6). The fit of the 'Loadel' model for fruit AGR was lowest in trees grafted on Hiawatha and K146-43, and intermediate in trees on Nemaguard and K119-50 (Table IV; Figure 6).

DISCUSSION

Tree vigour

As reported previously (DeJong *et al.*, 2004) rootstock significantly affected tree vigour in both scion cultivars,

Root mean square error of prediction (RMSEP), r², standard deviation ratio (SDR), model bias, and probability of the difference of model bias from zero calculated for the two multiple regression models on 'Flavorcrest' and 'Loadel' trees^{a,b}

	Rootstock	<i>r</i> ²	$\begin{array}{c} \mathbf{RMSEP} \\ (\mathbf{mm} \ \mathbf{d}^{-1}) \end{array}$		Model bias	
Cultivar				SDR	Bias value (mm d ⁻¹)	Probability
'Flavorcrest'	Nemaguard P30-135 K119-50 Hiawatha K146-43	0.483 0.335 0.614 0.437 0.296	0.0310 0.0424 0.0319 0.0556 0.0702	1.37 1.22 1.38 0.87 0.61	+0.0081 -0.0097 -0.0174 -0.0429 +0.0606 +0.0606	0.252 0.320 0.010 0.001 0.001
Total 'Flavorcrest'		0.305	0.0486	1.20	-0.0002	0.962
'Loadel'	Nemaguard P30-135 K119-50 Hiawatha K146-43	0.559 0.597 0.213 0.044 0.469	0.0356 0.0268 0.0343 0.0405 0.0358	1.39 1.60 1.15 0.96 1.06	-0.0092 -0.0021 -0.0008 -0.0115 +0.0235	0.260 0.736 0.925 0.213 0.001
Total 'Loadel'		0.386	0.0349	1.28	+0.0001	0.999

^aFor more details, see Table III.

^bAll statistics were calculated for the relationships between estimated and measured absolute fruit growth rate (for more details see Table III, Figure 5 and Figure 6) both by pooling all the data from each cultivar independent of rootstock (Total 'Flavorcrest' and Total 'Loadel'), and by keeping the data from the twelve cultivar-rootstock combinations separate.





as demonstrated by the significant differences in TCSA among trees grafted on the different rootstocks (Table I). K146-43 substantially controlled peach tree size, while Hiawatha, K119-50, and P30-135 appeared to be rootstocks with intermediate size-controlling capacity.

Crop load and fruit yield

The number of fruit per tree was not different in 'Flavorcrest' trees on the different rootstocks, whereas 'Loadel' trees on Nemaguard had significantly more fruit than trees on P30-135, Hiawatha, or K146-43. However, no significant effect of rootstock was detected when crop load was normalised by TCSA (Table I). Therefore, crop load was fairly homogenous among the trees of each cultivar grafted on the different rootstocks. The crop load of all trees can be considered to be below the threshold of four fruit cm⁻² TCSA reported by Inglese et al. (2002) for crop load affecting fruit FW at harvest. In addition, the trees used in this experiment had substantially lower crop loads than commerciallythinned trees located in the same experimental plot. Commercially-thinned 'Flavorcrest' trees grafted on Nemaguard, P30-135, K119-50, Hiawatha, or K146-43 had 421 ± 14 , 422 ± 19 , 435 ± 28 , 302 ± 23 , and 271 ± 17 fruit tree⁻¹, respectively. Commercially-thinned 'Loadel' trees grafted on Nemaguard, P30-135, K119-50, Hiawatha, or K146-43 had 398 ± 14 , 318 ± 11 , 292 ± 16 , 271 ± 11 , and 278 ± 27 fruit tree⁻¹, respectively (DeJong et al., 2001).

Furthermore, the heavy thinning applied to the trees used in this experiment had a dramatic effect on fruit size compared to commercially-thinned trees. Commerciallythinned 'Flavorcrest' trees grafted on Nemaguard, P30-135, K119-50, Hiawatha, or K146-43 had average fruit sizes of 129 ± 5 , 120 ± 4 , 121 ± 4 , 123 ± 6 , and 101 ± 3 g fruit⁻¹, respectively. Commercially-thinned 'Loadel' trees grafted on Nemaguard, P30-135, K119-50, Hiawatha, or K146-43 had average fruit sizes of $133 \pm 3, 135 \pm 3, 132 \pm$ 6, 125 \pm 3, and 116 \pm 4 g fruit⁻¹, respectively (DeJong et al., 2001). However, a low crop load was not sufficient to guarantee maximum fruit growth, because fruit distribution within the canopy also apparently affected fruit growth. Indeed, Marsal et al. (2003) reported that fruit DW was lower when fruit were distributed in clumps on hangers, compared to when fruit were distributed evenly within the canopy. Inglese et al. (2002) thinned trees according to a fertility index (number of fruit/shoot length), whereas in the present experiment only one fruit was left on each fruiting shoot, to avoid fruit-to-fruit competition and to minimise transportlimitation effects due to distance from source (DeJong and Grossman, 1995). Therefore, in the present study, it was assumed that fruit growth was not limited by fruitto-fruit competition, because of the combined effects of low crop load, and the even fruit distribution within the canopy.

Total yield per tree was similar in 'Flavorcrest' trees on the different rootstocks, whereas 'Loadel' trees on Nemaguard exhibited higher yields per tree than on the other rootstocks. However, as for crop load, differences between rootstocks for either cultivar were not significant when yield was normalised by TCSA. With both cultivars, trees on Nemaguard appeared to have later fruit maturity. Almost half of the total 'Flavorcrest' yield was harvested at the second picking, and two-thirds of the 'Loadel' yield was harvested at the second and third pickings. Previous studies also reported significant effects of peach rootstock on the earliness of fruit ripening (Forlani and Di Vaio, 1992). In the present study, earliness of fruit ripening appeared to be negatively correlated with rootstock vigour in 'Flavorcrest' trees, but this was not the case for 'Loadel' trees.

Rootstock affected fruit size at harvest

Rootstock significantly affected mean fruit size at harvest, in heavily-thinned trees. Therefore, it appears that rootstock limited the maximum potential fruit growth in this experiment. Trees of both cultivars on K146-43 had the lowest mean fruit size. This may have been related to the stronger competition between vegetative and reproductive growth in trees on sizecontrolling rootstocks compared to trees on more vigorous rootstocks, because of the limited carbon pool available in dwarfed trees (Lliso et al., 2004). Furthermore, peach trees grafted on size-controlling rootstocks have been demonstrated to experience mild water stress early in the growing season (Basile et al., 2003a), because of the relatively low hydraulic conductance of their root systems (Basile et al., 2003b; Solari et al., 2006). Peach fruit are especially sensitive to water stress during growth stages I and III, whereas they are considered less sensitive during pit hardening (stage II; Chalmers et al., 1981; 1983). Girona et al. (2004) reported that mild water stress during stage I caused a decrease in fruit growth, because of an apparent limitation in carbon source. These authors hypothesised that the effect of water stress during stage I on early shoot growth may account for this source limitation. Weibel (1999) showed that most of the difference in shoot growth between trees grafted on the sizecontrolling K146-43, and trees on Nemaguard, occurred very early in the growing season. These early differences in shoot growth were later correlated with differences in tree water status (Basile et al., 2003a). Therefore, it appears plausible that the negative effect on fruit size of the size-controlling rootstock K146-43 is correlated with carbon source limitation, due to mild water stress early in the growing season, or perhaps to a direct effect of a slightly lower water status on the rate of fruit expansion. In the present study, trees were heavily-thinned. Girona et al. (2004) reported that the negative effect of water stress on fruit growth during stage I was more evident in low-to-moderately thinned trees, because the higher crop loads amplified the effects of carbon source limitation.

Variability in fruit growth rate

Although fruit were grown with little fruit-to-fruit competition, there was a large variability in individual fruit size at harvest (Table II; Figure 1; Figure 2). This observation confirmed results reported previously by Weibel (1999). Rootstock appeared to affect the range of variability in fruit size, which appeared to be larger in both 'Flavorcrest' and 'Loadel' trees on vigorous (Nemaguard) or semi-vigorous (P30-135 and K119-50) rootstocks, than in trees on the more size-controlling rootstock (K146-43). This difference may have been related to the negative effect that the size-controlling K146-43 rootstock had on the maximum rates of fruit growth.

In the present study, trees were heavily-thinned and the fruit were evenly distributed, therefore factors other than fruit-to-fruit competition caused the fruit to grow below their maximum potential growth rate. We hypothesised that factors related to the canopy compartment in which each fruit was growing affected fruit growth. The parameters we considered attempted to take into account local carbon source availability (i.e., light distribution, total leaf area), competition between vegetative and reproductive organs (i.e., number of current-year shoots, total length of current-year shoots), vigour of the fruiting shoot (i.e., basal diameter and FW of the fruiting shoot), and the position of the fruit on the fruiting shoot. Since it is unlikely that short, lateral fruiting shoots were autonomous for carbon (Lauri and Lespinasse, 1993), factors external to the fruiting spur were expected to affect fruit growth. For this reason short, lateral fruiting shoots were not considered in the multivariate analyses. Fruit growing on hangers exhibited high intra-canopy variability in all cultivarrootstock combinations (Figure 1; Figure 2).

Fruit position in the canopy was an important factor affecting fruit growth. In all cultivar-rootstock combinations, decreasing gradients in fruit size and in absolute fruit growth rate at harvest, were detected from the top to the bottom of the trees (Figure 3; Figure 4). Previous studies have reported similar gradients in fruit size in commercially-thinned peach trees (Forlani *et al.*, 2002; Farina *et al.*, 2005). In the present research, in some cases, fruit size was large in the top layers, then decreased dramatically in the lower layers. Similar patterns were previously reported in 'Elegant Lady' peach trees trained to a perpendicular-Y (Farina *et al.*, 2005) and, in the same experiment, the authors reported that fruit size decreased linearly from top to bottom in trees trained to a "delayed vase".

Light distribution within the canopy has been demonstrated to be an important factor determining variability in fruit growth and fruit quality (Bible and Singha, 1993; Marini et al., 1993; Myers, 1993; Luchsinger et al., 2002; Lewallen and Marini, 2003). In the present study, light intensity was not measured around the fruit during the season, but SLW was measured after fruit harvest for each fruiting shoot selected. SLW has been positively correlated with the amount of photosynthetically active radiation intercepted by the leaf in several fruit species (Weinbaum et al., 1989; Marini and Sowers, 1990; Li and Lakso, 2004). In addition, SLW is highly correlated with leaf photosynthetic capacity (Marini and Marini, 1983), leaf nitrogen per unit leaf area (Weinbaum *et al.*, 1989; Rosati et al., 2000), and daily carbon assimilation (Rosati et al. 1999). In the present study, gradients of decreasing SLW (from the top to the bottom of the tree) were detected in both cultivars, and differences in SLW could explain part of the within-canopy variability in fruit growth rates. Absolute fruit growth rate was positively correlated with SLW (Table III). In addition, the growth of 'Flavorcrest' fruit was also positively correlated with total leaf area on the fruiting shoot (Table III). This result confirmed the importance of an adequate local leaf-to-fruit ratio for

fruit growth, as reported previously (Wu *et al.*, 2005). Therefore, part of the variability in fruit growth appeared to be related to C-source limitation due to the low light intensity reaching leaves very close to the fruit, to the low photosynthetic capacity of these leaves, and/or to an insufficient area of leaves.

Absolute fruit growth rate in 'Flavorcrest' was negatively correlated with the FW of current season shoots grown on the fruiting shoot (Table III). Therefore, it appeared that competition between vegetative and reproductive growth may occur at the fruiting shoot level. The model calculated for 'Loadel' trees did not indicate any significant correlation between AGR and the FW of the current season shoots, indicating that, in 'Loadel', competition between shoot and fruit growth was not relevant. 'Flavorcrest' trees are generally Winterand Summer-pruned more severely than 'Loadel' trees (DeJong et al., 2004), because of differences in the production habit between these cultivars. Summer- and Winter-pruning affects shoot growth in peach trees in the next growing season (Marini, 1985); therefore fruit growing on 'Flavorcrest' trees may have experienced a stronger competition with vegetative growth than fruit on 'Loadel' trees. On the other hand, fruit growth rate was positively correlated with shoot FW in 'Loadel' trees, indicating that, in these trees, fruit growth was enhanced on vigorous fruiting shoots.

Sink-strength is a positive function of sink-size (Farrar, 1993), and this relationship is in agreement with the fact that early peach fruit size has been reported to influence subsequent fruit growth (Davis and Davis, 1948; Wu et al., 2005). Early fruit size is affected not only by environmental factors (e.g., temperature) and sourcesink relationships for carbon and other resources occurring early in the growing season, but also by factors carried over from the previous year (i.e., factors affecting flower induction, the availability of storage carbohydrates and nutrients, etc.). In the present study, most parameters were measured immediately after fruit harvest, and therefore they could not account for the variability in fruit size observed early in the growing season. For these reasons, initial fruit size was inserted in both cultivarspecific multiple regression models, in order to take into account the variability induced by factors acting before the beginning of the experiment. Surprisingly, in both cultivars, AGR was negatively correlated with initial fruit size. This was apparently due to an opposite, within-tree gradient that initial fruit size exhibited, compared to final fruit size and AGR. Indeed, initial fruit size on the day of measurement increased significantly from the top to the bottom of the canopy in all cultivar-rootstock combinations (Figure 3; Figure 4). This result was unexpected. Possible explanations for these gradients in early fruit size may have been the heterogeneity of bloom time within the canopy, with bottom flowers opening before top flowers, as reported by Dann and Jerie (1988). Another hypothesis may be that flower induction progressed from the bottom to the top of the canopy during the previous season because of differences in vigour induced by the light distribution gradient. Alternatively, a progressively decreasing gradient in fruit-set from the top to the bottom of the canopy may cause stronger early fruit-to-fruit competition in the top compared to the bottom of the

canopy. George *et al.* (1996) reported that fruit set decreased from the top to the bottom of the canopy in persimmon trees. However, the data collected in the present experiment were not sufficient to test any of these hypotheses, and therefore more studies are needed to understand what affected early fruit size in peach trees. Regardless, initial fruit size explained only a small part of the total intra-canopy variability in fruit size, as suggested by the relatively small standardised coefficients calculated for this predictor in both models (Table III). This situation may be due to the large difference in fruit size between early season and harvest time.

The two multiple regression models fitted the fruit growth variability data for trees of both cultivars on Nemaguard fairly well (Table IV; Figure 5; Figure 6). However, rootstock appeared to affect the relationship between AGR and the measured parameters. Part of the lack of fit of the models regarding fruit growth variability in some cultivar-rootstock combinations may have been caused by the decrease in intra-canopy variability in fruit growth and light distribution induced by the rootstock. This appeared to be the case for 'Flavorcrest' trees grafted on K146-43 (Figure 1; Figure 3; Figure 5). In other cases, the cultivar-rootstock combination appeared to affect directly the relationship between the measured parameters. This seemed to be the case for 'Loadel' trees on K119-50, where light distribution within the canopy did not appear to exhibit a large gradient, but light seemed to be distributed less evenly through the canopy, as indicated by the low values of the percentage of maximum SLW measured in all the canopy layers (Figure 4). However, in most cases, trees on vigorous rootstocks had clearer intra-canopy variability in all the parameters measured, compared to trees on less vigorous

rootstocks. The models were able to account for only about 60% of the total variability in fruit growth in the best cases (i.e., in 'Flavorcrest' on K119-50; and in 'Loadel' on P30-135). Therefore, other factors not considered in the present study (e.g., within-canopy local nutrient availability, temperature gradients within the canopy, etc.) may also have played also a role in reducing the fruit growth rate below the maximum potential growth rate.

The present study confirmed that a large variability in individual fruit growth occurred within peach trees, even when fruit-to-fruit competition was minimised. Fruit size at harvest decreased progressively from the top to the bottom of the canopy. Local intra-canopy factors were positively (e.g., light distribution within the canopy, leaf area on the fruiting shoot, and fruiting shoot vigour) or negatively (e.g., vigour of current-season shoot growth on the fruiting shoot) correlated with the growth of individual fruit. The rootstock modified the relationship between fruit growth and local intra-canopy factors. In addition, the significant effect of rootstock on fruit growth in heavily-thinned trees indicated that rootstock may limit the maximum potential growth rate of fruit. This relationship was particularly evident for the size-controlling rootstock K146-43. The difference between cultivars, in parameters that explained intracanopy fruit growth variability, suggested that, in different cultivars, the same factors may be of different relative importance. The measured parameters did not explain all the intra-canopy variability in fruit growth, suggesting that other factors also played a role. Interestingly a decreasing gradient in early fruit size was detected from the top to the bottom of the canopy, but the data collected in the present experiment were not designed to explain this gradient.

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