

Preformation in vegetative buds of *Prunus persica*: factors influencing number of leaf primordia in overwintering buds

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Summary We investigated the influence of bud position, cultivar, tree age, tree carbohydrate status, sampling date, drought and light exposure on the number of leaf primordia formed in dormant vegetative peach buds (*Prunus persica* (L.) Batsch) relative to the number of primordia formed after bud break (neofomed). During winter dormancy, vegetative peach buds from California and Italy were dissected and the number of leaf primordia recorded. Between leaf drop and bud break, the number of leaf primordia doubled from about five to about 10. Parent shoot length, number of nodes on the parent shoot, cross-sectional area of the parent shoot, bud position along the parent shoot and bud cross-sectional area were correlated with the number of leaf primordia. Previous season light exposure, drought and tree carbohydrate status did not affect the number of leaf primordia present. The number of leaf primordia differed significantly among peach varieties and tree ages at leaf drop, but not at bud break. Our results indicate that neofomation accounted for all shoot growth beyond about 10 nodes. The predominance of neofomed shoot growth in peach allows this species great plasticity in its response to current-season conditions.

Keywords: bud dissection, dormancy, growth habit, neofomation, nodes.

Introduction

The term “preformation” has been used to describe the formation of shoot organs within the dormant vegetative bud that will later give rise to a shoot. In mature trees of many species, including *Persea* spp., *Fraxinus pennsylvanica* Marsh., and *Juglans regia* L., all node units in the majority of shoots are formed before bud break (Hallé et al. 1978, Remphrey 1989, Thorp et al. 1994, Sabatier et al. 1995) and shoots cease elongation when the number of preformed nodes has been depleted. Other species, such as *Nothofagus* spp., *Larix laricina* (Du Roi) K. Koch and *Acer saccharum* Marsh., have a number of preformed node units present within the bud. However, shoot growth continues after the exhaustion of the preformed

units with the production of new nodes by the elongating shoot tip, a process termed neofomation (Steingraeber 1982, Remphrey and Powell 1984, Puntieri et al. 2000).

The relative extent of preformed and neofomed growth has been studied in only a few species, despite its importance in understanding the physiology of canopy growth. Information on this subject could assist in scheduling treatments such as fertilizer application, pruning or deficit irrigation in intensively managed orchard crops to achieve desired effects on vegetative growth. Early observers assigned *Prunus* spp. to the group of trees with partial neofomation (Priestley and Scott 1938). However, Brown et al. (1994) assumed that all peach leaves were preformed because most peach shoots apparently make a single smooth flush of spring growth. The preformed or neofomed nature of peach (*Prunus persica* (L.) Batsch) leaves has not been confirmed by bud dissection prior to bud break.

Peach is notable for its diversity of growth habits. Multiple forms have been bred and selected with the goal of creating cultivars that invest proportionately more resources in reproductive growth and are suitable for high-density planting. Compact trees produce a denser canopy than standard trees, because they have a higher percentage of lateral buds that form long shoots (Fideghelli et al. 1979, Scorza et al. 1984). It is unknown whether the observed differences in lateral shoot growth of compact peach and of standard peach are manifestations of different numbers of preformed leaf primordia.

Peach canopies tend to be moderately dense with a leaf area index greater than four and with considerable interior shading (Tworkoski and Scorza 2001). Trees typically form greater numbers of short shoots (< 1 cm length with few nodes) in the shady interior of the canopy and more vigorous long shoots in the exposed canopy exterior (up to 1 m in length with more than 30 nodes). It has been established that dormant peach buds can sense light (Erez 1977), but it is not known whether the difference in irradiance between the canopy interior and the canopy exterior affects the formation of leaf primordia in the developing buds. In *Larix laricina*, well-lit shoots at the top of the canopy have 50% more preformed needles than less

vigorous shoots at the bottom of the canopy (Remphrey and Powell 1984).

Tree age can affect the formation of leaf primordia in vegetative buds. In some species, such as *Fraxinus pennsylvanica*, trees produce buds with proportionately more scales and fewer leaf primordia as they age (Remphrey and Davidson 1994). Although young peach trees are noted for their vegetative vigor and tend to produce more long shoots and fewer short shoots compared to mature trees, it has not been determined if this difference is associated with the number of preformed leaf primordia in the vegetative buds.

Environmental conditions can influence the formation of leaf primordia in developing buds. The differentiation of peach floral buds begins in late summer (Tufts and Morrow 1925, Raseira and Moore 1986, Reinoso et al. 2002) at which time only bud scale primordia are present in all buds. The following season's leaf primordia are subsequently produced in buds that remain vegetative. Loiseau et al. (2001, 2002) reported that the development of young primordia in vegetative peach buds was influenced by temperature during dormancy: relatively warm temperatures caused the youngest primordia to cease growing, moderate temperatures encouraged differentiation into scales and cool, but non-freezing temperatures, favored the production of leaf primordia. Remphrey and Davidson (1994) found fewer preformed leaf primordia in a clone of *F. pennsylvanica* at a site with a severe winter than at a site with a milder winter. Deficit irrigation during floral bud development can affect the following year's floral quality and yield in peach and almond (Handley and Johnson 2000, Lamp et al. 2001), but it is not known if drought affects vegetative bud development and leaf primordium formation in peach.

Crop load and maturation date can affect tree carbohydrate reserves during bud development. Carbohydrate status during bud development can affect organ formation in buds. In late-maturing peach cultivars, fruit develops rapidly during late summer and competes with, and delays the growth of, simultaneously developing organs in floral buds (H. Johnson, personal communication, University of California, Davis, CA).

There have been no studies to determine if fruit development during late summer competes with, and delays, leaf primordium formation in vegetative buds, although it is known that high crop loads can significantly decrease the diameter of floral buds (H. Johnson, personal communication). Peach floral buds are thought to have a greater sink strength than vegetative buds (Bonhomme et al. 1999) and their presence at the same node could, therefore, affect vegetative bud development through competition for carbohydrates. Factors such as shoot length, diameter and position may also affect parent shoot carbohydrate status and the number of preformed leaf primordia in vegetative buds.

Many studies have shown that *Prunus* floral buds continue development during dormancy (Tufts and Morrow 1925, Feng et al. 1974, Reinoso et al. 2002), but there are conflicting reports on the activity of vegetative peach apices during the dormant period. Loiseau et al. (2002) concluded that organogenesis continued steadily throughout the winter, whereas Luna et al. (1991) reported that vegetative buds were "almost com-

pletely developed by midsummer–early autumn and remained in a resting state until the end of the winter."

The objective of this project was to assess the extent of leaf preformation in dormant vegetative buds of *P. persica* as affected by bud position within the canopy, cultivar, tree age, tree carbohydrate status, date, local light exposure and drought.

Materials and methods

Experiment 1: bud dissections across canopies

On February 27, 2003, two shoots of the previous year's growth were excised from each of five 13-year-old peach trees (cv. 'O'Henry') growing in the Wolfskill Experimental Orchard in Winters, CA, USA. The trees were trained to the Kearney Agricultural Center perpendicular-V system (KAC-V) (DeJong et al. 1995) with 1.8 m within-row and 5.2 m between-row spacing. The orchard was managed for commercial production. Shoots were selected from the top, the bottom, the inside and the outside of the canopy. Shoot angle of insertion, length of shoot and number of nodes on the shoot were recorded. The cut ends of the shoots were placed in a bucket containing a 5% sucrose solution to which a drop of bleach was added. The bucket of shoots was wrapped in plastic and stored at 5 °C for no more than 5 days before the buds were dissected.

Before dissection, we recorded the position of each lateral or terminal bud ($n = 93$) along the parent shoot (most basal bud = 1), shoot diameter at that node, basal diameter of the bud and the floral or vegetative character of other buds present at the same node. When multiple buds were present at one node, only the most central vegetative bud was dissected. Buds were dissected with the aid of a stereo-microscope. Fragments of fine razor blades were used to remove bud scales and cataphylls to reveal the underlying primordial leaves and stipules. Leaf primordia were individually removed and counted until the apical meristem was fully exposed. Groups of swellings along the margin of each meristematic dome that had a characteristic stipule-leaf-stipule form were counted as single leaf primordia. Relationships between the number of primordia per bud and shoot characteristics were examined by multiple regression analysis.

Experiment 2: bud dissections across cultivar, tree age and dissection date

At 50% leaf drop in 2003 and at 50% bud break in 2004, shoots were collected for bud dissection from 1- and 10-year-old trees of six peach varieties from the collection at the Istituto Sperimentale per la Frutticoltura in Rome, Italy. Varieties were selected to include diversity of canopy architectural types and of harvest dates: dwarf ('Nano 91.14'), columnar ('Pillar 542'), compact ('Compact Redhaven'), weeping ('Nettarina pendula'), early-maturing ('MayGlo' nectarine) and late-maturing ('August Red' nectarine). Leaf drop and bud break dates depended on variety—50% leaf drop occurred between October 23 and November 12 and 50% bud break occurred between

February 10 and March 30. Shoots from three 10-year-old trees and four 1-year-old trees of each variety were analyzed. Four shoots from each 10-year-old tree were collected per variety—one horizontal and one vertical shoot was taken from the top and from the bottom of the canopy of each tree. Two buds per shoot were dissected (one near the basal end of the shoot and one near the apical end) for a total of 24 buds per variety per dissection date. Three shoots, from the top, the middle and the bottom of the canopy, were taken from each 1-year-old tree per variety. Four buds along each of these shoots were dissected for a total of 24 buds per variety per dissection date.

All collected shoots were immediately wrapped in damp paper, placed in plastic bags and stored in a refrigerator for 48 h before analysis. Various bud and parent shoot characteristics were recorded before dissection of selected lateral buds, including shoot length, number of nodes on the shoot, bud position along the parent shoot (most basal bud = 1), shoot diameter at that node, basal diameter of the bud and floral or vegetative character of other buds clustered at the same node. Buds were dissected as described for Experiment 1 and the number of leaf primordia per bud was recorded.

Effects of tree age and dissection date on the number of leaf primordia per bud were evaluated by analysis of variance (ANOVA). Variation within dissection dates was evaluated by weighted ANOVAs. Effects of bud group, shoot height in the canopy and shoot insertion angle on the number of primordia per bud were evaluated separately. We calculated the Pearson correlation coefficient for the relationship between the number of leaf primordia per bud and parent shoot length, number of nodes per shoot, shoot cross-sectional area (CSA) at the node from which the bud was taken, bud position along the shoot and bud basal CSA for each combination of variety, tree age and dissection date. Relationships between the number of leaf primordia and bud position along parent shoot were analyzed separately for the leaf drop and bud break dissections.

Experiment 3: bud dissections and light exposure

In August 2002, hours of daily light exposure were estimated for selected leaves of 10- to 12-year-old peach trees (cv. 'O'Henry') located at Wolfskill Experimental Orchard based on the dry mass of punched discs of leaf lamina tissue. Three discs (60.5 mm² each) were punched from each of two adjacent leaves near the midpoint of each shoot, taking care to avoid the midrib and major veins. The punched leaves remained attached to the tree. Discs were initially held in a cooler and later dried at 60 °C for 2 days and weighed. The duration of leaf exposure to a photosynthetic photon flux (PPF) greater than 100 µm⁻² s⁻¹ was estimated from the relationship between leaf dry mass per unit area and current season light exposure in *P. persica* (Rosati et al. 2000). Because Rosati et al. (2000) used whole leaves rather than leaf discs, we plotted a regression between mass per area of whole leaves and mass per area of punched discs from which to estimate the light exposure of discs from their dry mass ($r^2 = 0.965$).

In November 2002, sample size was dramatically reduced by accidental pruning. In December, the remaining vegetative buds at nodes for which 2002 leaf light exposure had been estimated were dissected. On 10 short shoots, the single terminal bud was dissected ($n = 10$). On 10 long shoots, vegetative buds were dissected at the three to five nodes nearest to the leaves for which irradiance had been estimated ($n = 43$).

Experiment 4: bud dissections across irrigation treatments

Two-year-old peach trees (cv. 'Autumn Flame') were grown in the Teaching Orchard of the University of California, CA, Davis during the 2002 growing season. Two rows of 56 trees, oriented north–south, were designated for the experiment. The southern half of each row was sprinkler irrigated between late May and early November, whereas the northern half of each row served as the non-irrigated control. There was no natural rainfall between late May and early November. Midday stem water potential (Ψ_{snd}) of trees in each treatment was assessed weekly between May 22 and August 21 with a pressure chamber (Scholander et al. 1965). One bagged leaf per tree from each of 3–5 randomly selected trees per treatment was used to estimate the treatment mean Ψ_{snd} (Fulton et al. 2001).

In December 2002, one long shoot was removed from each of eight trees per treatment. Five dormant adjacent vegetative lateral buds were dissected from the middle of each shoot. The number of hairy green cataphylls present was recorded in addition to the number of hairless leaf primordia. The significance of treatment differences in the numbers of leaf primordia, green cataphylls and total organs (leaf primordia and green cataphylls) per tree were assessed by Tukey's test.

Experiment 5: bud dissections and crop load

In April 2003, crop load treatments were imposed on 12-year-old peach trees (cv. 'O'Henry') at the Wolfskill Experimental Orchard. Trees were in a uniform block trained to the KAC-V system and had been managed for commercial production before the experiment. Twelve trees were completely defruited and twelve trees were left unthinned.

In December 2003, carbohydrate samples were taken from six defruited and six unthinned trees to assess the effect of crop load treatments on tree carbohydrate status. A 1-cm diameter disc of bark including all tissue layers external to the vascular cambium was punched with a tree corer. Four bark samples per tree were taken from the lower trunk. A drill with a spade 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 two days, weighed and ground to pass a 40-mesh sieve and analyzed for nonstructural carbohydrate (NSC) by standard methods (Smith 1969) at the DANR analytical laboratory at the University of California at Davis. Starch was hydrolyzed with amyloglucosidase and high performance liquid chromatography (HPLC) was performed for glucose, sucrose and fructose using a fast carbohydrate col-

umn (HPAP, Bio-Rad Laboratories, Hercules, CA). Concentrations of glucose, sucrose and fructose were summed to give an estimate of NSC.

In December 2003, two current-year shoots, one from the middle of the canopy and one from the lower canopy, were selected from each of six trees per treatment. The buds were dissected as described previously and the numbers of leaf primordia and cataphylls were recorded.

Results

Experiment 1: canopy position

The number of primordia per bud from shoots taken from throughout the canopies of five 'O'Henry' peach trees ranged from 8 to 14 (Figure 1). The mean number (\pm standard deviation (SD)) of leaf primordia per vegetative bud was 10.59 ± 1.17 . Multiple regression analysis with forward addition, backward elimination or Mallows's C(p) (Mallows 1973) generated models with relatively high (>0.8) coefficients of determination (R^2), but no single best model emerged.

Experiment 2: cultivar, tree age and dissection date

The number of leaf primordia roughly doubled between leaf drop and bud break ($P < 0.0001$) (Table 1). The effects of cultivar and age, sampling date by cultivar and sampling date by age interactions were also highly significant ($P < 0.001$), although the variation in number of leaf primordia explained by these factors was small compared to the difference between sampling dates.

At leaf drop, both cultivar and tree age had highly significant ($P = 0.0044$ and < 0.0001 , respectively) effects on the number of primordia per bud, and there was a significant ($P = 0.023$) age by cultivar interaction. At bud break, age, cultivar and age by cultivar interactions were not significant.

The presence or absence of other floral or vegetative buds at the same node as the dissected vegetative bud had no significant effect on the number of leaf primordia within the dissected bud. For mature trees, neither parent shoot height in the canopy (low or high), nor the angle of the shoot (horizontal or vertical) significantly affected the number of leaf primordia within the dissected bud.

Combining measurements for all cultivars, tree ages and sampling dates indicated that parent shoot and bud characteristics significantly affected leaf primordium number. Parent shoot length and number of nodes, bud position along the parent shoot and bud CSA were highly significant ($P < 0.01$), as was the parent shoot CSA ($P < 0.05$).

Taking the 24 combinations of cultivar, tree age and sampling date separately, the length of the parent shoot was significantly ($P < 0.05$) correlated with number of leaf primordia within the bud in six of the groups (Table 2). The total number of nodes on the parent shoot was significantly ($P < 0.05$) correlated with number of leaf primordia in five of the groups, all of which were young trees. The CSA of the parent shoot at a bud node was significantly ($P < 0.05$) correlated with number of

leaf primordia within that bud in two of the groups. A bud's position along the length of the parent shoot was significantly ($P < 0.05$) correlated with the number of leaf primordia in seven of the groups. The basal CSA of a bud was significantly ($P < 0.05$) correlated with number of leaf primordia in 14 of the groups.

At leaf drop, there was a significant increase in the number of leaf primordia per bud acropetally along the parent shoot ($P = 0.012$). Additionally, there was a barely significant increasing and then decreasing gradient in the number of leaf primordia per bud along the parent shoot ($P = 0.049$), with the maximum number of leaf primordia at 58% of total shoot length. At bud break, neither positional gradient was significant.

Averaging the variance components for the 24 combinations of cultivar, tree age and sampling date, tree-level factors were responsible for 9.3%, shoot-level factors for 21.8% and bud-level factors for 68.9% of the total variation.

Experiment 3: light exposure

Estimated daily irradiance ranged from 0.1 to 10.7 h at PPF $> 100 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the selected leaves. Estimated daily light exposure was not correlated with the number of organs or organ primordia in the vegetative buds closest to the sampled leaf. For both long and short shoots, the number of leaf primordia and the total number of organs were not correlated with estimated light exposure of the nearby leaves.

Experiment 4: drought

Midday stem water potentials were significantly higher in irrigated than in non-irrigated trees after the second week of June (data not shown). Before then, mean Ψ_{sdm} values of the irrigated and non-irrigated trees were within 0.1 MPa. From the second week of June until the end of August, mean Ψ_{sdm} of the irrigated trees was between -0.86 and -1.25 MPa, whereas Ψ_{sdm} of the non-irrigated trees declined steadily from -1.12 to -2.24 MPa. Non-irrigated trees exhibited symptoms consistent with severe drought stress, including reduced leaf size and premature cessation of growth (data not shown).

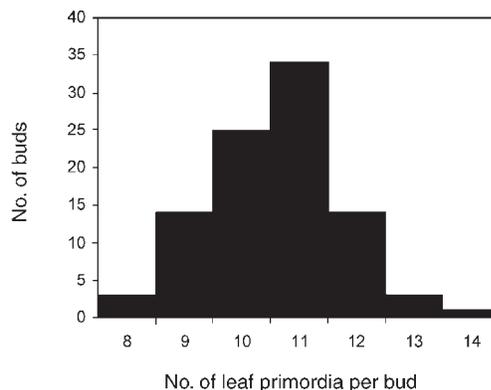


Figure 1. Frequency distribution of leaf primordium number per bud in the canopies of five cv. 'O'Henry' peach trees in February 2003.

Table 1. Effects of peach variety, tree age and sampling date on mean (\pm standard error (SE)) number of leaf primordia per bud.

Cultivar	Mean no. leaf primordia \pm SE at leaf drop (October–November)		Mean no. leaf primordia \pm SE at bud break (February–March)	
	1-year-old trees	10-year-old trees	1-year-old trees	10-year-old trees
Early-maturing cultivar (‘MayGlo’)	5.85 \pm 0.19	5.40 \pm 0.13	9.56 \pm 0.32	9.31 \pm 0.15
Late-maturing cultivar (‘August Red’)	5.42 \pm 0.19	4.46 \pm 0.11	9.60 \pm 0.18	9.56 \pm 0.26
Genetic dwarf (‘Nano 91.14’)	5.04 \pm 0.17	5.06 \pm 0.17	9.00 \pm 0.24	9.27 \pm 0.22
Weeping growth habit (‘Nettarina pendula’)	5.67 \pm 0.12	5.21 \pm 0.14	10.13 \pm 0.36	10.71 \pm 0.24
Columnar growth habit (‘Pillar 542’)	5.71 \pm 0.18	4.52 \pm 0.09	9.71 \pm 0.27	10.00 \pm 0.21
Compact growth habit (‘Compact Redhaven’)	5.73 \pm 0.12	5.00 \pm 0.12	9.58 \pm 0.18	9.25 \pm 0.23

In mid-December, the mean (\pm standard error (SE)) number of preformed leaf primordia per lateral vegetative bud of irrigated trees was 5.05 (\pm 0.18), versus 5.25 (\pm 0.15) in non-irrigated trees. Although irrigation had no significant effect on the number of leaf primordia, irrigated trees produced significantly more green cataphylls than non-irrigated trees

and, thus, a greater total number of organs ($P < 0.001$; $P = 0.003$) (Figure 2).

Experiment 5: tree carbohydrate status

Crop removal significantly increased the NSC concentration of recently formed xylem and bark tissue ($P = 0.007$; $P =$

Table 2. Pearson coefficients for correlations of numbers of leaf primordia with shoot and bud characteristics in cultivars of 1- and 10-year-old peach trees. Measurements were made at leaf drop and bud break. Abbreviation: CSA = cross-sectional area. Asterisks indicate significance levels: * = $P < 0.05$; ** = $P < 0.01$ and ns = not significant.

Tree age/description	Measurement time	Shoot length	No. of nodes per shoot	Shoot CSA at bud node	Bud position on shoot	Basal CSA of bud
<i>One-year-old trees</i>						
Early-maturing cultivar (‘MayGlo’)	Leaf drop	0.3917 ns	0.3080 ns	0.1896 ns	0.4304 *	0.5725 **
	Bud break	0.2295 ns	0.1340 ns	-0.0915 ns	0.6454 **	0.7441 **
Late-maturing cultivar (‘August Red’)	Leaf drop	-0.4409 *	-0.4724 *	-0.2349 ns	0.0836 ns	0.4377 *
	Bud break	0.1801 ns	0.1322 ns	0.2387 ns	0.0739 ns	0.1752 ns
Genetic dwarf (‘Nano 91.14’)	Leaf drop	0.6557 **	0.6499 **	0.3121 ns	0.6204 **	0.4849 *
	Bud break	0.3748 ns	0.3976 ns	0.2608 ns	0.4316 *	0.5515 **
Weeping growth habit (‘Nettarina pendula’)	Leaf drop	-0.1129 ns	0.0974 ns	0.2390 ns	0.0132 ns	-0.1284 ns
	Bud break	0.6873 **	0.5990 **	0.5335 **	0.3022 ns	0.7693 **
Columnar growth habit (‘Pillar 542’)	Leaf drop	-0.4234 *	-0.5162 **	0.2907 ns	-0.2702 ns	0.1927 ns
	Bud break	0.1374 ns	0.0874 ns	-0.1300 ns	0.0883 ns	0.8925 **
Compact growth habit (‘Compact Redhaven’)	Leaf drop	0.3193 ns	0.4128 *	0.0476 ns	0.4825 *	0.4639 *
	Bud break	0.2561 ns	0.1018 ns	0.2557 ns	0.1319 ns	0.6500 **
<i>Ten-year-old trees</i>						
Early-maturing cultivar (‘MayGlo’)	Leaf drop	0.4105 *	0.1672 ns	-0.3224 ns	0.4769 *	0.2676 ns
	Bud break	0.2960 ns	0.2604 ns	0.1017 ns	0.2066 ns	0.0560 ns
Late maturing cultivar (‘August Red’)	Leaf drop	-0.0178 ns	0.2980 ns	0.0463 ns	0.9950 ns	-0.0095 ns
	Bud break	0.4179 *	0.1599 ns	0.1833 ns	0.0376 ns	0.5852 **
Genetic dwarf (‘Nano 91.14’)	Leaf drop	0.2181 ns	0.2518 ns	-0.0459 ns	0.4864 *	-0.2058 ns
	Bud break	-0.0380 ns	-0.1140 ns	-0.0961 ns	0.3871 ns	0.2817 ns
Weeping growth habit (‘Nettarina pendula’)	Leaf drop	-0.4912 ns	0.3625 ns	-0.1876 ns	0.3988 ns	0.1224 ns
	Bud break	0.2680 ns	0.1779 ns	0.1361 ns	-0.0532 ns	0.6862 **
Columnar growth habit (‘Pillar 542’)	Leaf drop	0.2674 ns	0.1084 ns	0.1908 ns	0.0652 ns	0.5500 **
	Bud break	0.3229 ns	0.0856 ns	-0.1504 ns	0.2370 ns	0.6384 **
Compact growth habit (‘Compact Redhaven’)	Leaf drop	-0.1325 ns	-0.0497 ns	-0.1553 ns	0.0607 ns	-0.0616 ns
	Bud break	0.3715 ns	0.3825 ns	0.4331 *	-0.0612 ns	0.8040 **

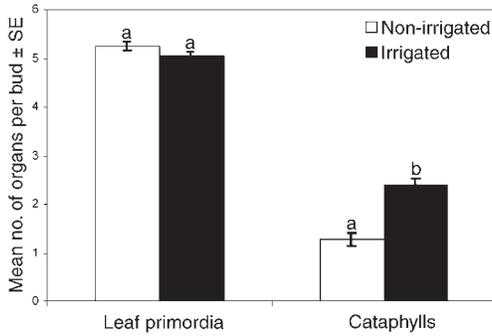


Figure 2. Number of leaf primordia and cataphylls in buds of cv. 'Autumn Flame' peach trees grown in irrigated and non-irrigated treatments. Buds were dissected in December 2002. Means followed by different letters indicate significant differences between the non-irrigated and irrigated treatments (Tukey's test, 5%). Abbreviation: SE = standard error.

0.014) but not of roots (Figure 3). The treatment was also without effect on the number of leaf primordia or the total number of organ primordia present in dormant buds in December.

Discussion

Capacity for preformation and neof ormation

At bud break, all trees examined had about 10 preformed leaf primordia per vegetative bud. In intensively pruned and managed crop trees, like the ones sampled, shoots with additional neof ormed growth are abundant. Because shoots with 80 or 100 nodes can be found in vigorous peach canopies (author's unpublished data), neof ormed growth must account for up to 90% of the nodes on these shoots. This demonstrates a higher capacity for neof ormation in peach than has been reported in *Acer saccharum* and *Nothofagus dombeyi* (Mirb.) Blume, which produce up to 60 and 30% neof ormed units, respec-

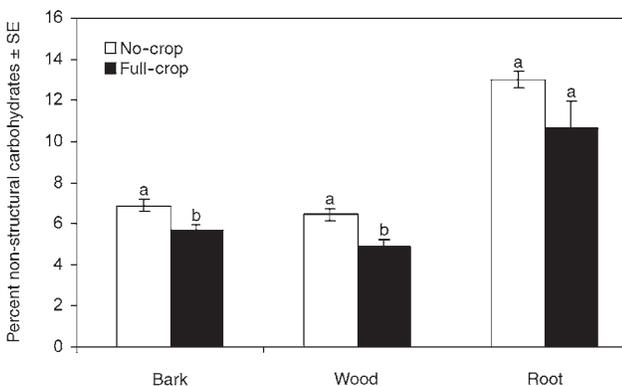


Figure 3. Non-structural carbohydrate concentrations (sum of starch, sucrose, glucose and fructose concentrations) of bark, wood and root tissue in full-crop and no-crop cv. 'O'Henry' peach trees. Samples were taken in December 2003. Means followed by different letters indicate significant differences between the no-crop and full-crop treatments (Tukey's test, 5%). Abbreviation: SE = standard error.

tively (Steingraeber 1982, Puntieri et al. 2002a). Species with a high capacity for neof ormation exhibit high plasticity in adapting to current-season conditions relative to species in which preformation predominates (Puntieri et al. 2002b).

Peach canopies contain shoots with less than 10 leaves, including an abundance of short shoots with four to six leaves, which raises the question of the fate of the remaining preformed leaves. Whether some abort during development, a process termed premature senescence (Richards and Larson 1981), or whether they change developmental course to form bud scales rather than leaves (Loiseau et al. 2001) is unclear.

Organogenesis during dormancy

The approximate doubling in number of leaf primordia between leaf drop and bud break indicates high organogenic activity during dormancy. This contradicts the assertion by Luna et al. (1991) that vegetative peach buds are almost completely developed by autumn and supports the findings of Loiseau et al. (2001) that thermally regulated morphogenesis in peach vegetative buds continues from November through March. According to the calculations of organogenic rate in dormant peach buds made by Loiseau et al. (2001), 1–3 new primordia per month could be expected, depending on temperature (Loiseau et al. 2002). Our results from bud dissections at Italian and Californian sites all fall within this range (5–6 primordia were formed over 4–5 months) and were similar at both sites, as would be expected given the similarity between sites in the length and severity of the winter.

Based on the combined results over several years from the three orchards, we infer that leaf primordium formation and development occurred continuously throughout the dormant period (Figure 4). We made an additional measurement in January 2005 by dissecting buds from the same 'O'Henry' trees using the same technique as described for Experiment 1. The new value fell directly on the regression line predicted by the data from Experiments 1 through 5, which supports the inference that development is continuous during dormancy. Although the data are equivocal in that the comparison was made across cultivars, ages, years and continents, it is clear that leaf

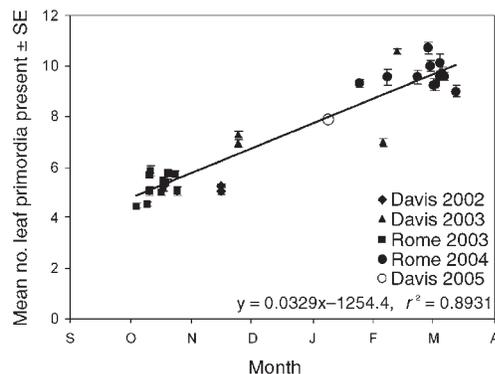


Figure 4. The relationship between time of year and mean number of leaf primordia per bud across all experiments in California and Italy over the years 2002–2004. Abbreviation: SE = standard error.

primordium development is not confined to the latter half of dormancy, as is floral bud development (Feng et al. 1974, Wang and Faust 1987, Faust et al. 1997).

If the development of leaf primordia in peach vegetative buds is continuous throughout the dormant season, *P. persica* appears to display growth intermediate between Hallé's definitions of preformation and neoformation. According to Hallé et al. (1978), preformation is "the formation of a large part of a shoot in the primordial state with a period of rest prior to expansion" and neoformation is "the continued extension of primordia immediately after they are initiated without any intervening period of rest." The vegetative peach apex appears not to experience a true rest period, although at the whole-tree level the plants experience dormancy as part of the annual cycle of growth.

Preformation and bud and shoot characteristics

Although the effect of bud position along the parent shoot was significant, there was little difference in the number of primordia at leaf drop despite the difference in the amount of time the buds had to form. The axillary buds that formed on the proximal end of the shoot in May reached leaf drop with about the same number of leaf primordia as axillary buds on the distal end of the shoot that formed later in the growing season. This is similar to the pattern found in peach flower buds—floral induction is completed uniformly within a single canopy, although the onset of induction varies widely within the population of buds (Li et al. 1989).

A gradient in the number of preformed leaf primordia in buds along the parent shoot was less evident in peach than in *Juglans regia* (Sabatier and Barthélémy 2001) and *Nothofagus dombeyi* (Puntieri et al. 2000). In peach, the number of leaf primordia was closely related to the basal CSA of the bud.

Preformation and architectural diversity of peach canopies

Despite a significant difference in the numbers of leaf primordia between peach varieties at leaf drop, the difference was not responsible for the architectural diversity in the peach tree canopies. The 1–1.5 additional leaf primordia present in the breaking buds of the variety with the largest number of primordia (weeping) relative to the variety with the lowest number of primordia (dwarf) was not significantly different and appears unrelated to the large difference in the characteristic forms of weeping and dwarf canopies. Other factors, such as the variation in the capacity for neoformed growth (Brown et al. 1994) and in the numbers of lateral buds that break (Tworokski and Scorza 2001), are more likely to be responsible for differences in canopy architecture between peach varieties with genetically compact, dwarf, pillar, weeping and standard growth habits.

Preformation and tree carbohydrate status

Local competition between vegetative and floral buds clustered at a single node had no effect on the number of leaf primordia in the vegetative buds, even though evidence of tree-level competition was mixed. The highly significant differences noted at leaf drop between early- and late-ripening

cultivars indicate that late-season tree carbohydrate status may affect early leaf primordium development, even though the lack of a significant difference at bud break suggests that some "catching up" occurred during dormancy.

Effects of light and drought on preformation

The lack of a significant effect of the previous year's light exposure on the number of preformed leaf primordia in lateral buds of long shoots or terminal buds of short shoots may indicate that irradiance is not a significant factor regulating vegetative bud development above a threshold value. Alternatively, it may reflect the inexactitude of the technique used to estimate light exposure. However, in another experiment (author's unpublished results) peach buds from the well-exposed upper canopy and buds from the shadier lower canopy did not differ significantly in number of primordia.

Drought had no significant effect on the number of leaf primordia in buds dissected in December. However, it is possible that water stress delayed bud development during late summer, but that autumn rains allowed the development of buds of drought treated trees to catch up with that of buds of irrigated trees by the time of the December sampling.

Conclusion

In conclusion, peach trees in a Mediterranean climate arrive at bud break with about 10 leaf primordia per vegetative bud, half of which were formed during the dormant period. The mean number of primordia per bud may vary slightly with cultivar and tree age, but it is relatively constant throughout a canopy and between individual trees growing under the same management system. Neoformation accounted for the majority of leaves formed, indicating that vegetative growth in peach is highly dependent on current season conditions.

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