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# Preformation in vegetative buds of pistachio (*Pistacia vera*): relationship to shoot morphology, crown structure and rootstock vigor

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**Summary** Effects of rootstock, shoot carbohydrate status, crop load and crown position on the number of preformed leaf primordia in the dormant terminal and lateral buds of mature and immature 'Kerman' pistachio (*Pistacia vera* L.) trees were investigated to determine if rootstock vigor is associated with greater shoot preformation. There was no significant variation in preformation related to the factors studied, suggesting strong genetic control of preformation in 'Kerman' pistachio. The growth differences observed among trees on different rootstocks were associated with greater stimulation of neoformed growth in trees on the more vigorous rootstocks. However, most annual extension growth in mature tree crowns was preformed, contrasting with the relatively high rate of neoformation found in young tree crowns. Large amounts of neoformed growth in young trees may allow the trees to become established quickly and secure resources, whereas predominantly preformed growth in mature trees may allow for continued crown expansion without outgrowing available resources. We hypothesized that the stimulation of neoformed growth by the more vigorous rootstocks is associated with greater resource uptake or transport, or both. Understanding the source of variation in shoot extension growth on different rootstocks has important implications for orchard management practices.

*Keywords: bud dissection, crown development, leaf primordia, neoformation, shoot extension growth.*

## Introduction

Shoots of temperate deciduous trees are formed by fixed or free growth. Fixed growth arises from the elongation of preformed metamers from a bud following dormancy or a rest period (Kozlowski and Pallardy 1997). These preformed metamers consist of a greatly reduced internode and node with an embryonic leaf that are initiated and remain in a quiescent state in the dormant bud until bud break. Free growth arises from the simultaneous initiation and extension of new (neoformed) metamers without bud formation or an intervening rest period (Pollard and Logan 1974). A shoot elongated during an uninterrupted period of growth, on a temperate deciduous tree, may be composed entirely of preformed metamers, or a combination of preformed and neoformed metamers. The number of preformed metamers and proportion of preformed to neoformed metamers for a given shoot may be dependent on species, shoot morphology, parent shoot position or other endogenous and exogenous factors (Remphrey and Powell 1984, Puntieri et al 2000, Sabatier and Barthélémy 2001, Puntieri et al 2002, Sabatier et al. 2003). Shoots composed entirely of preformed metamers have been referred to as "short" shoots and may have internodes of only 1–2 mm as in *Ginko* or *Prunus*, or as long as 1–2 cm as in striped maple (*Acer pennsylvanicum* L.) (Kozlowski and Pallardy 1997).

A detailed knowledge of the origin of growth units and the relationship between preformation and final shoot morphology is particularly important to understanding tree crown architecture (Costes et al. 1992, De Reffye and Houllier 1997). This information is also useful for developing crop models based on biological data (Remphrey and Powell 1984, Prusinkiewicz et al. 1994). In addition, such knowledge may be useful in developing pruning and management strategies and identifying limitations to manipulating trees in horticultural or forestry settings.

Detailed studies of bud structure have been performed on many temperate deciduous species, including *Fraxinus* spp., *Ginkgo biloba* L., *Populus* spp., *Quercus petraea* (Matt.) Liebl., *Nothofagus* spp., *Acer saccharum* Marsh., *Juglans regia* L. and peach (*Prunus persica* L. (Batsch.)) (Critchfield 1960, 1970, Gill 1971, Steingraeber 1982, Remphrey and Davidson 1994*b,* Fontaine et al. 1999, Puntieri et al. 2000, 2002, Souza et al. 2000, Sabatier and Barthélémy 2001, Gordon et al. 2006). These studies have focused on understanding the effects of crown location, bud position along a shoot, plant ontogeny, genotype, environmental conditions and year of formation on the number of metamers preformed in a bud. Remphrey (1989) showed that preformation in mature *Fraxinus pennsylvanica* Marsh. trees is relatively uniform within a tree and that growth differences among shoots are primarily a result of differences in internode length. However, others have shown that preformation can vary within a crown and in some species is correlated with parent shoot size and vigor, as well as position along the parent shoot and in the crown (Gill 1971, Baxter and Cannell 1978, Remphrey and Powell 1984, Puntieri et al. 2000, 2002), with larger shoots having larger buds with more preformed metamers. Remphrey and Davidson (1994*b*) speculated that data on preformation provide an indication of how current-year resources are allocated and ultimately translated into crown architecture differences; however, the only study in which tree or shoot resource status relative to preformation were measured showed no correlation (Gordon et al. 2006).

Pistachio (*Pistacia vera* L.) offers a unique system in which to study preformation because in mature trees most of the lateral buds become floral, leaving only the terminal and one or two distal lateral buds, which frequently remain dormant, to produce vegetative growth (Crane and Iwakiri 1981). Therefore, most shoots are born from terminal buds, resulting in a tree with a relatively open crown. Also, the California pistachio industry is almost entirely based on a single clonal female cultivar, ‘Kerman’, that is budded onto seedling rootstocks that are produced through controlled pollination (Ferguson et al. 2005). These rootstocks greatly influence the size and yield of mature trees (Ferguson et al. 1998). Additionally, the more vigorous rootstocks (PGI and UCB) produce trees with numerous long, leafy shoots in the uppermost portion of the crown (Spann 2006), resulting in a crown structure unfavorable for horticultural production. Given that the scion population is genetically uniform, the opportunity exists to study rootstock effects on preformation. Furthermore, the horticultural training of pistachio results in trees with uniform populations of shoots because trees are pruned annually to develop the desired crown structure and, once mature, to maintain their size and renew the fruiting wood. Thus, regardless of the tree axis, the shoot population on a mature tree is highly uniform in both chronological as well as physiological age. This uniformity allows for the study of crown position effects on preformation without other confounding factors (e.g., axis, physiological age, etc.).

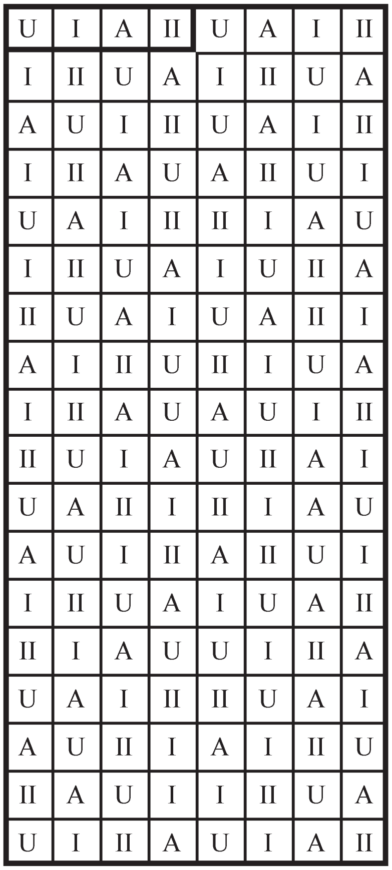
The alternate bearing habit of pistachio (i.e., a high yielding “on” year followed by a low yielding “off” year) reportedly causes trees to have significantly different carbohydrate reserves depending on their cropping status (Rosecrance et al. 1998). This presents the opportunity to study the effects of tree carbohydrate status on preformation and to see if differences in preformation can account for the reported greater shoot length of off-year trees compared with on-year trees (Weinbaum et al. 1994, Brown et al. 1995, Rosecrance et al. 1996, Picchioni et al. 1997).

The objectives of this study were to: (1) determine the number of preformed metamers within the terminal and lateral buds of young (non-bearing) trees; (2) determine the number of preformed metamers within the terminal buds of mature pistachio trees on different rootstocks with varying crop loads; (3) investigate the relationship of shoot carbohydrate content and preformation within mature trees; and (4) determine if the growth differences of trees on different rootstocks is the result of differences in preformation or neoformation, or both.

## Materials and methods

### *Plant material*

All experiments on mature trees were conducted in a pistachio rootstock trial block (Ferguson et al. 1998) at the University of California, Kearney Agricultural Center, Parlier, California (36.6° N, 119.5° W). The block was planted in February 1989 with 1-year-old nursery seedlings that were field budded to *P. vera* ‘Kerman’ after planting. There were 20 rows of 18 trees spaced 5 m apart within rows and 6 m between rows. The trees were planted in a randomized complete block design with 90 blocks, each block spanned four rows and contained one tree of each of four rootstocks (Figure 1). At the time these experiments began, the trees were 13 years old and considered ma-



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|---|---|---|---|---|---|---|---|
| U | I | A | II | U | A | I | II |
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| I | II | A | U | A | II | U | I |
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| A | U | II | I | A | I | II | U |
| II | A | U | I | I | II | U | A |
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Figure 1. Diagram of eight rows of the pistachio rootstock trial planted in February 1989 at the University of California Kearney Agricultural Center where trees were selected for this study. The rootstocks represented are *Pistacia atlantica* (A), *P. integerrima* ‘Pioneer Gold I’ (I) and *P. atlantica* × *P. integerrima* ‘UC Berkeley I’ (U). ‘Pioneer Gold II’ (II) was not used in our study. The heavy lines in the upper left-hand corner highlight one block of the randomized complete block design, the entire planting contained 90 blocks.

ture, shading 70–75% of the orchard floor at midday. Before and during the experiments, the trees received standard horticultural care typical of commercial production, including dormant pruning, irrigation, fertilization and pest control (see Ferguson et al. 2005).

During the spring of 2002, 18 trees, six trees on each of three rootstocks, *P. atlantica* Desf. (Atl), *P. integerrima* Stew. selection Pioneer Gold I (PGI) and *P. atlantica* × *P. integerrima* selection UC Berkeley I (UCB), were selected for uniformity within a rootstock from within eight contiguous rows of the block. Based on the bearing history of this block, 2002 was considered an on-year. Three of the six trees on each rootstock were randomly selected and the immature fruiting rachises removed from them on June 10, 2002 to produce off trees in an otherwise on-year. Aside from this manipulation, the trees continued to receive standard horticultural care typical of commercial production.

Young trees on PGI rootstock were selected in a commercial orchard in the winter of 2004–2005. Twenty adjacent, uniform 2-year-old trees were selected from within one row of an orchard near Hanford, California (36.3° N, 119.6° W). In a second orchard, near Lost Hills, California (35.6° N, 119.7° W), twenty 5-year-old trees were selected from within two adjacent rows of the orchard. In both cases, the trees were managed according to standard commercial horticultural practices.

### *Experiment 1: bud dissection and the relationship of bud content to shoot growth*

For the mature trees, between August 28 and 30, 2002, just before nut harvest (September 9), 10 pairs of shoots were selected from the lower, middle and upper one-third of the crown of each tree on each rootstock × cropping status combination. Shoots were paired based on similarity in length, diameter, lack of lateral branching, crop load where applicable and position in the crown. Following selection, one shoot of each pair was removed. The shoot removed included the current-season growth (2002) and subtending 1-year-old wood (from 2001). The terminal bud was removed from each harvested shoot and placed in 70% ethanol for later dissection. The remaining tissue was immediately placed on ice in a cooler and taken to the laboratory. The shoot tissue was divided into current-season wood, 1-year-old wood, leaves, fruit and rachises, and each tissue was dried at 60 °C to constant mass and ground to pass a 40-mesh (0.60 mm) screen. The ground tissue was sent to the Division of Agriculture and Natural Resources Analytical Lab at the University of California, Davis campus for total nonstructural carbohydrate determination by enzymatic hydrolysis and HPLC analysis (ANR Analytical Lab 2006). The same procedures were followed on January 22, 2003 for the second shoot of each pair.

The excised terminal bud from each shoot was dissected with the aid of a dissecting microscope to determine the number of preformed metamers in each bud. For each bud, the bud scales (cataphylls) were removed to expose the green embryonic leaves. Embryonic leaves were distinguished from the bud scales by the presence of well-defined leaflet primordia and a dense covering of long tangled hairs. Undifferentiated organs (usually one to two per bud) surrounding the meristematic dome were assumed to be leaf primordia and were included in the embryonic leaf totals. The number of embryonic leaves (hereafter referred to as primordia) was recorded for each bud at each sampling time.

To understand how the number of primordia found in the dormant terminal buds related to the number of nodes of shoots that grew from buds similar to those dissected, 20 stems were tagged in fully exposed locations in the top of the crown of three trees that had not been used in previous experiments on each of the three rootstocks from the same block on March 25, 2004 (about 2 weeks before bud break). To minimize possible crown position and microclimate effects on shoot growth, all tagged stems (both within and between trees) were similar in sun exposure, height in the crown, length of previous-season's growth and lack of lateral branching on 1-year-old wood. During the 2004 growing season, the length and number of nodes of the shoots that grew from the terminal buds of the tagged shoots were recorded at about weekly intervals from bud break (April 6) until crown extension growth stopped (late August). Measurements were repeated on 20 different shoots (dormant pruning precluded the use of the same shoots) on the same trees in 2005, beginning on April 7.

### *Experiment 2: preformation and shoot development in young trees*

At the time the young trees were selected (winter 2004–2005), two similar shoots (based on the criteria described previously for mature trees) were identified. Because of the horticultural training performed on these trees, all of the shoots that grew in a given season arose from a similar axis; e.g., all current-season shoots on the 2-year-old trees at the time of selection were third-order shoots. One of the selected shoots from each tree was removed in its entirety at the time of selection and the terminal and lateral buds were dissected as previously described. The position of lateral buds relative to the terminal bud was recorded. On shoots from 5-year-old trees, some lateral buds were floral and, therefore, excluded from the final data analysis. The second shoot, a sister shoot to the one destructively harvested, on each tree was tagged so that lateral and terminal shoot growth data from buds similar to those dissected could be collected following the growing season (spring–summer 2005).

On January 23, 2006, all of the lateral shoot growth, as well as the growth from the terminal bud, that occurred during the 2005 growing season was measured for each of the intact tagged shoots on the 2-year-old trees (now 3-years-old). The length and number of nodes of all terminal and lateral shoots and their node position along the parent shoot were recorded. Buds that did not grow were noted. Whether a bud that did not grow was dormant or dead was not determined. The 5-year-old trees were mistakenly pruned by the grower so no terminal or lateral shoot length data could be collected.

### *Data analysis*

Effects of rootstock and crop load on the number of preformed primordia and shoot carbohydrate concentration for mature trees were evaluated by analysis of variance. Mean separation for the number of preformed primordia and shoot carbohydrate concentration (mature trees only) for mature and young trees was performed at $\alpha = 0.05$ by Duncan's multiple range test. Analysis of variance was used to test the effects of rootstock and shoot type on the number of nodes per shoot and shoot length for young trees. Mean separation for the number of nodes per shoot and shoot length was performed at $\alpha = 0.05$ by Duncan's multiple range test for mature trees. Node position effects on the probability of bud break in young trees were investigated by linear regression.

## Results

### *Mature trees*

In mature pistachio trees there were no differences in the number of primordia per bud based on crown position (8.0 ± 0.8, 8.6 ± 0.9 and 8.9 ± 1.1 primordia (mean ± SD) per bud for lower, middle and upper positions, respectively); therefore, the presented data represent pooled values across crown positions. The terminal bud contained between seven and eight primordia just before nut harvest (August 2002) and the number increased by approximately one between harvest and the late dormant season (January 2003, Table 1). The number of primordia was similar for buds from trees on different rootstocks and different crop cycles regardless of the dissection time. In August 2002, just before harvest, the on-year trees had significantly lower carbohydrate concentrations in both the current-season (2002 wood) and 1-year-old (2001 wood) wood of trees on all rootstocks compared with the off-year trees (Table 1). However, by the late dormant season (January 2003) these differences had diminished.

The length of shoot growth produced from terminal buds on mature trees was quite variable, with the shortest shoots being less than 10 cm long and the longest shoots approaching a meter in some years (Table 2, Figure 2). The longest shoots measured were found to have considerable neoformed growth as evidenced by their greater number of nodes compared with the number of metamers preformed in dormant terminal buds (Tables 1 and 2). Thus, there were two distinct shoot types in the crown: those composed entirely of preformed metamers and those composed of both preformed and neoformed metamers.

Table 1. Number of leaf primordia in the terminal buds of shoots from 'Kerman' pistachio trees on three rootstocks and two crop loads (on-year = high-yielding and off-year = low-yielding) at two dissection times, and carbohydrate concentrations of the current-season (2002) and 1-year-old (2001) wood subtending the dissected buds. Different letters indicate significant differences within columns ($P \le 0.05$). Abbreviations: Atl, *Pistacia atlantica*; PGI, *P. integerrima* selection Pioneer Gold I; and UCB, *P. atlantica* × *P. integerrima* selection UC Berkeley I.

| Rootstock | Crop year | August 2002 | | | January 2003 | | |
|---|---|---|---|---|---|---|---|
| | | No. of primordia (mean ± SD) | Total nonstructural carbohydrates (mg Glu equivalents $g^{-1}$ DW) | | No. of primordia (mean ± SD) | Total nonstructural carbohydrates (mg Glu equivalents $g^{-1}$ DW) | |
| | | | 2002 Wood | 2001 Wood | | 2002 Wood | 2001 Wood |
| Atl | On- | 7.5 ± 0.9 a | 114.3 d | 89.3 c | 8.3 ± 1.1 a | 100.0 bc | 78.0 b |
| | Off- | 7.7 ± 0.7 a | 144.3 ab | 137.3 a | 8.4 ± 1.0 a | 102.5 abc | 103.0 a |
| PGI | On- | 7.8 ± 1.0 a | 137.7 bc | 107.3 bc | 8.3 ± 1.2 a | 115.0 ab | 94.0 ab |
| | Off- | 7.5 ± 0.8 a | 157.0 a | 132.7 a | 8.4 ± 0.7 a | 119.0 a | 83.0 ab |
| UCB | On- | 7.9 ± 1.0 a | 123.0 cd | 96.3 c | 8.5 ± 1.0 a | 112.5 abc | 84.0 ab |
| | Off- | 7.7 ± 0.7 a | 157.5 a | 120.0 ab | 8.8 ± 0.9 a | 94.0 c | 83.5 ab |

Table 2. Mean number of nodes per shoot for short shoots (composed entirely of preformed metamers) and long shoots (composed of preformed and neoformed metamers) of 'Kerman' pistachio trees on three rootstocks in 2004 and 2005. Different letters indicate significant differences within a column ($P \le 0.05$). Abbreviations: Atl, *Pistacia atlantica*; PGI, *P. integerrima* selection Pioneer Gold I; and UCB, *P. atlantica* × *P. integerrima* selection UC Berkeley I.

| Rootstock | Shoot type | 2004 | | 2005 | |
|---|---|---|---|---|---|
| | | No. of nodes per shoot (mean ± SD) | Shoot length (cm, mean ± SD) | No. of nodes per shoot (mean ± SD) | Shoot length (cm, mean ± SD) |
| Atl | Short | 8.0 ± 1.2 c | 14.9 ± 6.7 c | 7.9 ± 0.7 b | 6.6 ± 2.4 b |
| | Long | 13.8 ± 5.3 bc | 31.9 ± 15.8 bc | 15.3 ± 6.9 a | 33.3 ± 18.1 a |
| PGI | Short | 7.9 ± 0.9 c | 19.0 ± 11.1 c | 8.0 ± 0.8 b | 8.5 ± 3.5 b |
| | Long | 24.6 ± 13.6 a | 58.6 ± 33.0 a | 14.7 ± 7.1 a | 29.7 ± 18.7 a |
| UCB | Short | 8.3 ± 0.8 c | 14.6 ± 5.9 c | 8.4 ± 0.8 b | 8.1 ± 2.4 b |
| | Long | 18.8 ± 11.7b | 44.5 ± 30.1 ab | 12.8 ± 3.2 a | 25.7 ± 11.2 a |

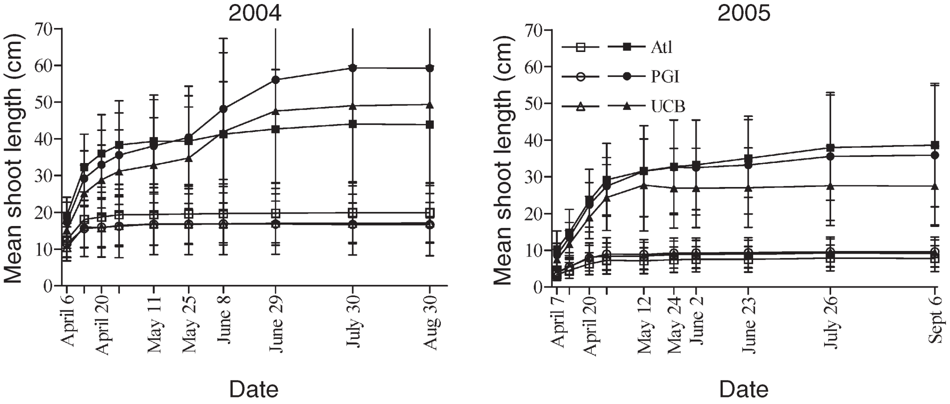

Figure 2. Mean (± SD) length of short shoots (composed only of preformed metamers, open symbols) and long shoots (composed of preformed and neoformed metamers, closed symbols) measured at about weekly intervals beginning at bud break for 'Kerman' pistachio trees on three different rootstocks in two years. Data are from 20 parent buds that were tagged in the top of the crowns of three trees of each rootstock during the dormant season before the year of measurement. The selected buds were similar to those that were dissected (see Table 1). Abbreviations: Atl, *Pistacia atlantica*; PGI, *P. integerrima* selection Pioneer Gold I; and UCB, *P. atlantica* × *P. integerrima* selection UC Berkeley I.

As described by Kozlowski and Pallardy (1997), these shoots are referred to as short and long shoots, respectively. Long shoots had a greater duration of growth because of the production of neoformed metamers, and had a higher growth rate at the beginning of the season compared with short shoots, based on the initial slopes of the growth curves (Figure 2).

### *Young trees*

The terminal buds of shoots on 2-year-old and 5-year-old trees contained significantly more primordia than any lateral bud on the same shoot (Table 3). The most distal lateral bud tended to have more primordia than subsequent lateral buds of the shoot on trees of both ages, although this difference was not significant. Following the most distal lateral bud on a shoot, subsequent lateral buds were highly consistent in the number of preformed metamers they contained; therefore, for clarity, data are presented only for every fifth bud along a shoot rather than for all 45 nodes. The most proximal buds on shoots on both 2- and 5-year-old trees tended to have the fewest primordia. Shoots that grew from buds on sister shoots in similar positions to those dissected tended to have a similar number of nodes to the number of primordia preformed in the dormant buds (Table 3). However, the shoots that grew from terminal buds and the most distal lateral bud had greater numbers of nodes than were preformed, indicating the presence of neoformation at these positions.

For lateral buds on 2-year-old trees, the most distal buds had the highest probability of growing the season after the bud was produced (Figure 3A). There was a linear decline in the probability that a bud would grow from node positions 1 through 10 (distal to proximal). The probability of a lateral bud growing from node positions >10 was random, ranging from 0.2 to 0.7. The mean length of the lateral shoot produced at each node position for these shoots is shown in Figure 3B. The terminal bud produced the longest shoot on average. Similar to the probability data, lateral shoot length generally decreased from node 1

Table 3. Number of leaf primordia in terminal and lateral buds of shoots from dormant 2-year-old and 5-year-old 'Kerman' pistachio trees on PGI (*P. integerrima* selection Pioneer Gold I) rootstock and the number of nodes per shoot that grew on sister shoots from buds in the same position as those dissected (2-year-old trees only). Data are the means of 20 buds or shoots (2-year-old) and 10 buds (5-year-old) at each node position. Different letters indicate significant differences within columns ($P \leq 0.05$). Abbreviation: ND = no data collected.

| Node position (distal to proximal) | 2-Year-old shoots | | 5-Year-old shoots |
|---|---|---|---|
| | No. of leaf primordia (mean ± SD) | No. of nodes per shoot (mean ± SD) | No. of leaf primordia (mean ± SD) |
| Terminal | 8.5 ± 0.5 a | 25.6 ± 15.7 a | 9.3 ± 0.5 a |
| 1 | 7.1 ± 0.3 b | 13.3 ±13.9 b | 7.1 ± 1.1 b |
| 5 | 6.6 ± 0.6 bc | 6.9 ± 1.2 b | 6.1 ± 1.1 bc |
| 10 | 6.4 ± 0.8 cd | 6.4 ± 0.5 b | 5.7 ± 1.2 c |
| 15 | 6.4 ± 0.5 cd | 7.6 ± 3.0 b | 6.3 ± 0.9 bc |
| 20 | 6.4 ± 0.6 cde | 6.8 ± 0.4 b | 6.0 ± 0.0 bc |
| 25 | 6.3 ± 0.7 cde | 6.4 ± 0.5 b | 5.0 ± 1.4 c |
| 30 | 6.4 ± 0.5 cd | 6.6 ± 0.5 b | 6.1 ± 0.7 bc |
| 35 | 6.1 ± 0.7 cde | 6.1 ± 0.9 b | 5.5 ± 1.1 c |
| 40 | 5.8 ± 0.6 df | 6.0 ± 0.8 b | ND |
| 45 | 5.6 ± 0.5 ef | 5.3 ± 0.5 b | ND |

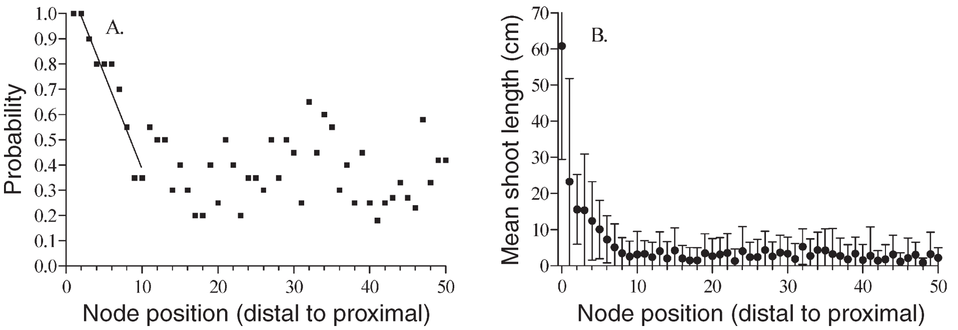

Figure 3. The probability that a lateral bud along a parent shoot on a 2-year-old tree grew the season after it was formed (A), and the mean (± SD) length of the shoots that grew at each node position (B). The relationship for node positions 1–10 is described by $y = -0.07545x + 0.4015$, $r^2 = 0.9178$, $P < 0.0001$. There was no relationship for node positions 11–50, $r^2 = 0.007515$, $P = 0.5948$.

through 10 (distal to proximal), followed by a leveling off of shoot lengths for the remaining nodes.

## Discussion

The growth habits of pistachio trees grown on the three commercially available rootstocks in California, Atl, PGI and UCB, have been observed to differ greatly (Ferguson et al. 2005). Trees on what are generally considered to be the more vigorous rootstocks, PGI and UCB, produce large amounts of vegetative growth, primarily in the top of the crown. Such growth is undesirable because it tends to be weak and hangs down into the orchard rows, making management and harvesting difficult. For these reasons, growers typically remove these shoots from the crown by pruning during the dormant season. Because of these pruning practices the shoots that grow the following season arise from the remaining shorter, sturdier shoots. Understanding why some of these shorter shoots give rise to another short, sturdy shoot whereas others produce a long, weak shoot has the potential to improve the management of pistachio orchards and increase our understanding of the basic biology of the tree.

We found little variation in the number of preformed nodes in the terminal buds of shoots on mature trees even though the buds were sampled from different height positions in the crown. In addition, there was no influence of rootstock on preformation, either in mean number of primordia per bud or in the variation within a tree. Thorp et al. (1994) reported similar findings for *Persea* spp. growing on several different rootstocks. The number of preformed nodes in the 'Kerman' pistachio cultivar was similar to the number of leaves per shoot reported for 'Bronte' pistachio (from 8.7 to 10.8; Crane and Nelson 1972), suggesting a similar degree of preformation in that cultivar.

Although there were significant differences in shoot carbohydrate status between the on-year and off-year trees at the August dissection time, there were no differences in the number of primordia preformed at this time, indicating that preformation was not delayed by the strong demand for carbon by the developing nuts. Similarly, Heerema (2005) and Gordon et al. (2006) found that preformation in almond (*Prunus dulcis* (Mill.) D.A. Webb) and peach, respectively, was unaffected by tree carbohydrate status. Furthermore, Gordon et al. (2006) showed that nearly half of the preformation in peach took place during the dormant season when no current photosynthates were available. However, significant relationships have been found between parent shoot size and preformation in peach (Gordon et al. 2006) and other species (Gill 1971, Baxter and Cannell 1978, Remphrey and Powell 1984), leading to the suggestion that preformation can be influenced by current-year resources (Remphrey and Davidson 1994*b*). Our data suggest that preformation in pistachio had a low carbon demand and was unaffected by shoot and tree carbohydrate status; furthermore, the data did not support the hypothesis that preformation is strongly influenced by current-year resources.

The variation in shoot length within the long shoots was considerable and primarily a result of variability in the number of neoformed nodes produced by each shoot. In contrast, the variation in shoot length within the short shoots was caused by differences in internode length, presumably a result of varying environmental conditions both within the crown and between years, because these shoots all had similar numbers of nodes. Remphrey and Davidson (1994*b*) found similar year-to-year and crown position variation in *Fraxinus pennsylvanica.* The between-year variation that we observed for both long and short shoots was likely associated with the unusually cool spring of 2005, which probably limited internode elongation of short shoots and neoformed node initiation of long shoots. Despite this year-to-year variation, the relative differences between short and long shoots were present in both years.

In addition to their greater length, long shoots had a higher growth rate as seen by comparing the slopes of the growth curves for long and short shoots in Figure 3, as well as a greater duration of growth. Similarly, shoots with neoformed growth in *F. pennsylvanica* have both a higher growth rate and greater growth duration (Remphrey and Davidson 1994*a*). In our study, the rate of extension of long shoots varied during the growing season, particularly in 2004, although no long shoots were observed to stop and then resume growth within the same season, as is the case in rhythmic growth.

At the whole-tree level, the majority of shoots in mature pistachio crowns are short shoots (Spann 2006). However, our finding that some rootstocks have the ability to stimulate neoformation demonstrates significant plasticity in crown development, indicating that crown structure in an orchard can be influenced by cultural practices to manage the plasticity to create and maintain a productive tree.

We found considerable differences in size and crown structure among pistachio trees grown on different rootstocks. Specifically, trees on the PGI and UCB rootstocks tended to produce significantly more long shoots in the uppermost portion of the crown compared with trees on Atl rootstock (Spann 2006). Additionally, rootstocks had some influence on the length of individual long shoots.

Because the experimental trees were growing in a commercial orchard, all of the long shoots from previous seasons were removed from the canopy by pruning. Thus, all of the long shoots that grew during the experiment, and consequently the buds that were dissected, arose from short shoots. Therefore, given that there was no variation in preformation among trees on different rootstocks and that all shoots arose from similar short shoots, the differences in growth among trees on the three rootstocks, commonly referred to as rootstock vigor, must have been the result of greater stimulation of neoformed growth in trees on the PGI and UCB rootstocks. A similar effect of rootstock has been reported for walnut (*Juglans regia* L.), where own-rooted trees produced only preformed growth (Sabatier and Barthélémy 2001), but trees grown on *J. hindsii* (Jeps.) Rehd. or *J. regia* × *J. hindsii* 'Paradox' rootstocks produced some neoformed (indeterminate second flush) growth (Ryugo and Ramos 1979). We hypothesize that the more vigorous rootstocks, PGI and UCB, have a greater capacity for resource acquisition or transport to the scion, or both, compared with Atl, thus stimulating the production of neoformed growth.

Regardless of rootstock or cultural practices, neoformation in mature pistachio trees was generally limited to shoots in the upper portion of the crown (authors' unpublished observations). A similar crown position limitation has been reported in *Betula papyrifera* Marsh. (MacDonald et al. 1984), although in that species long shoots were also distinguishable by greater preformation in the parent bud. In pistachio, buds producing long shoots and short shoots were indistinguishable based on preformation. The restriction of neoformation (i.e., long shoots) to the top of the crown indicated that, although the propensity for neoformation was influenced by rootstock, certain environmental conditions, positional influences or endogenous signals determine its occurrence within the crown.

Young pistachio trees appeared to have a greater propensity for neoformation than mature trees. None of the buds dissected from young trees contained more than 10 primordia; however, the parent shoots from which the buds were taken and a number of the lateral shoots that developed had as many as 50 nodes. It appears that neoformation plays an important role in developing the early structural framework of the pistachio tree, as MacDonald et al. (1984) concluded for *B. papyrifera*, but that in the mature tree the short shoots are responsible for maintaining the crown and producing the crop each season. This transition from considerable neoformed growth in the sapling stage to relatively little or none in the mature tree has been found in *Fraxinus pennsylvanica* as well (Remphrey 1989, Davidson and Remphrey 1994).

Pistachio has been described as having strong apical dominance (Crane and Iwakiri 1985). As defined by Brown et al. (1967) apical dominance in trees describes the suppression of lateral shoot growth along an actively growing shoot; i.e., the suppression of sylleptic branching. In contrast, apical control is used to describe a situation where the terminal shoot is able to outgrow the lateral branches after the year in which the buds were formed. In other words, the terminal shoot has control over proleptic lateral branches. Generally, trees with strong apical dominance have weak apical control (Harris 1983), as is the case in young pistachio trees. None of the shoots examined had lateral branching in the season that they grew, indicating strong apical dominance. However, as indicated by the high probability of the distal buds on young trees producing lateral branches the year after they were formed and the relatively long length of these branches, pistachio exhibited weak apical control. This growth habit appears to explain how the typical decurrent tree form of pistachio is formed.

In conclusion, the lack of rootstock or tree carbohydrate effects on preformation, along with the very limited variation in preformation as determined by dissection of buds from many crown positions, indicate that the number of preformed metamers is genetically fixed in terminal buds of 'Kerman' pistachio trees. However, the year-to-year variation in long and short shoot lengths as well as the restriction of long shoots to the top of the crown in mature trees indicates plasticity in shoot development. The large differences in tree size on different rootstocks previously reported and also observed in our study were not caused by variation in preformation, but by the stimulation of neoformed growth by rootstocks PGI and UCB compared with rootstock Atl. The potential for production of significant neoformed growth on some rootstocks emphasizes the importance of understanding structural growth processes when developing horticultural practices for training and managing trees.

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