



How does peach fruit set on sylleptic shoots borne on epicormics compare with fruit set on proleptic shoots?

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Summary

Proleptic and epicormic shoots on peach (*Prunus persica*) have different growth characteristics that have management implications for peach production. Proleptic shoots arise from buds after a dormant period, and are made up mostly of preformed nodes and organs which exist in dormant buds and extend after bud-break. Epicormic shoots (also known as ‘water sprouts’) arise from preventitious meristems without the formation of a bud and are characterized by vigorous, upright growth. They are usually stimulated by heavy pruning, branch breaking, or drastic branch bending and exhibit low correlative inhibition which results in many lateral sylleptic shoots. Because lateral meristems that form sylleptic shoots have no preformed organs, sylleptic shoots are made entirely of neo-formed growth. Epicormic shoots, in contrast to the determinate nature of proleptic shoots, continue growing until environmental conditions become unfavorable; however this study indicates that sylleptic shoots on epicormic shoots appear to be limited to similar numbers of nodes as proleptic shoots even though they may grow as late as 180 days after bud-break. Both proleptic, and sylleptic shoots borne on epicormic shoots, have flower buds but it is not clear if the flower buds on both types of shoots are equally capable of setting fruit. The objective of this research was to compare flowering and fruit set on proleptic and sylleptic shoots on four different peach cultivars with different times of fruit maturity. Differences in flower bud density, flowering, initial fruit set and final fruit set were observed between shoot types and among cultivars. Flower bud density was higher on proleptic shoots than sylleptic shoots on all cultivars and there was greater flower bud drop prior to bloom on sylleptic shoots of three of the cultivars. Initial percent fruit set of buds that flowered was very high (>80%) on both shoot types of all cultivars but percent final fruit set was higher on sylleptic shoots of two of the cultivars. On average, proleptic shoots of a specific cultivar bore more fruit per shoot than sylleptic shoots of the same cultivar and the two earliest maturing cultivars tended to bear more fruit per respective shoot type than the two later maturing cultivars.

Keywords

flowering, neoformation, bud fate, fruit drop, carbohydrate competition

Significance of this study

What is already known on this subject?

- Most peach production systems focus of fruit production on proleptic shoots because they are assumed to be inherently more productive than sylleptic shoots borne on water sprouts (epicormics shoots).

What are the new findings?

- This research shows that sylleptic shoots borne on water sprouts can be nearly as productive as proleptic shoots on four peach cultivars that differ in their time of fruit maturity.

What is the expected impact on horticulture?

- The research has implications for pruning practices, especially with regard to vigorous trees that produce a lot of water sprouts.

Introduction

Proleptic and epicormic shoots have different growth characteristics and management implications for peach (*Prunus persica* (L.) Batsch) production. Proleptic shoots are considered the main fruiting wood for peach production. These arise from buds which have undergone a dormant period, and can be made up both preformed and neo-formed nodes and organs (Figure 1). Preformed nodes/organs exist in dormant buds and grow out in spring after bud-break (Wilson, 2000; Gordon et al., 2006a). In most peach cultivars proleptic shoots show strong correlative inhibition and do not give rise to many lateral branches (DeJong et al., 2012). In peach the phyllochron (the time elapsed between successive leaf emergence that is used to quantify the rate at which shoots produce new nodes) is relatively consistent at approximately 2–3 days during the growing season and is not significantly affected by temperature or solar radiation (Davidson et al., 2015). Medium and long proleptic shoots generally have fewer than 34 nodes, which means that they cease adding new nodes after approximately 60–100 days after bud break in late May or June (DeJong et al., 2012).

Epicormic shoots (also known as ‘water sprouts’) arise from preventitious meristems without undergoing a period of dormancy (Wilson, 2000; Costes et al., 2006). Epicormic shoots are characterized by vigorous, upright growth stimulated by heavy pruning (Figure 1), branch breaking, or drastic branch bending (Bussi et al., 2011; DeJong et al., 2012). Heavy pruning which is usual in many peach production systems often stimulates excessive epicormic growth which necessitates further pruning to avoid negative impacts on

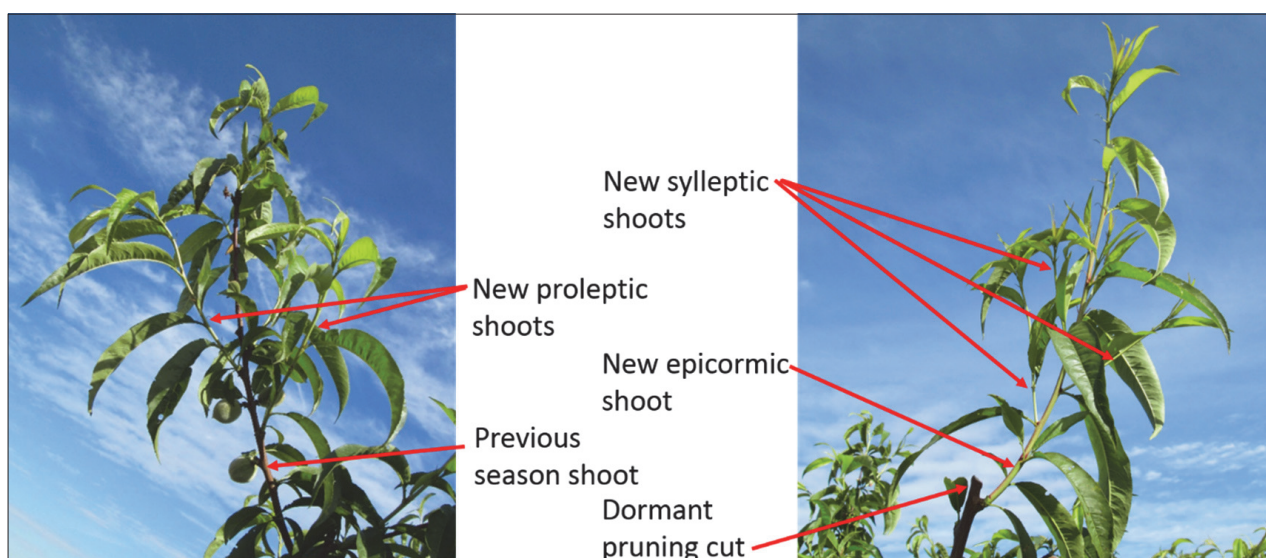


FIGURE 1. Photographs comparing origins of proleptic shoots on a previous year shoot after a period of dormancy vs. sylleptic shoots borne on a rapidly growing epicormic shoot that was stimulated by a dormant pruning cut. This study evaluated the flowering and fruit behavior of these two types of shoots in the season following their initial development.

fruit production. Epicormic peach shoots tend to exhibit low correlative inhibition which results in many lateral sylleptic branches (Figure 1; DeJong et al., 2012). Because lateral meristems have no preformed organs, epicormic shoots are made entirely of neofirmed growth (Fournier et al., 1997; Costes et al., 2006). Epicormic shoots, in contrast to the determinate nature of proleptic shoots, tend to continue growing until environmental conditions become unfavorable (DeJong and Doyle, 1985).

Physiological differences between proleptic and sylleptic shoots may have an effect on fruit set. The ability of a flower bud to succeed from bud initiation through to bloom and fruit set is dependent on environmental factors as well as endogenous factors such as hormonal signaling and access to organic and mineral nutrient reserves (Feucht, 1982; DeJong, 1999; Loescher et al., 1990). Floral bud growth during the summer season is limited; although flower buds begin to differentiate in mid-summer of the year prior to bloom (late July–early August) (Tufts and Morrow, 1925; Reinoso et al., 2002) and continue to develop through August and September (Gur, 1985). Flower buds are not fully developed by the onset of dormancy, and depend on mobilization of stored carbohydrates to continue to development throughout the rest period (Maurel et al., 2004; Reinoso et al., 2002; Luna et al., 1990). Bloom and fruit set depend on carbohydrate and mineral nutrient reserves as well as bud development and growth that occurs in the early spring before vegetative growth initiates and leaves become a net source of carbohydrates (Loescher et al., 1990).

The ability of a developing organ to access assimilates during any growth phase depends on the supply of carbohydrates as well as the amount of competition for resources from other growing organs (DeJong, 1999). The distribution of resources is determined by the location of carbohydrate sinks (i.e., reproductive organs, shoots, and roots) relative to carbohydrate sources (i.e., mature leaves or storage organs) as well as relative ‘sink strength’ of each growing structure (Pavel and DeJong, 1993; DeJong, 1999). Other factors may also be at play other than actual amount of stored carbohydrate; Maurel et al. (2004) demonstrated a link between

inadequate chilling accumulation and subsequent carbohydrate limitation due to reduced storage mobilization for vegetative buds.

Proleptic shoots finish extending by the end of June, before floral initiation and differentiation occurs, while epicormic shoots continue to grow vigorously throughout the growing season. Vigorous vegetative growth has been found to be antagonistic to flower bud initiation in several temperate fruit trees (Guimond et al., 1998; Wilkie et al., 2008; Koutinas et al., 2010). In some cases flushes of vegetative growth have been reported to have sufficient sink strength to outcompete fruit (Quinlan and Preston, 1971).

There is limited direct evidence that there is a difference in fruit bud formation and fruit set between proleptic shoots and sylleptic shoots borne on epicormic shoots. Yamashita et al. (1971) reported that epicormic shoots produce fewer flower buds with lower fresh weight compared to ‘normal bearing shoots’. Results from attempts to develop new cropping systems for peach in California which depended on sylleptic shoots on epicormic branches for fruit set suggest that fruit set on sylleptic shoots borne on epicormic shoots may be lower than on proleptic shoots (DeJong et al., 1999; Grossman and DeJong, 1998). One such system was a peach ‘Meadow Orchard’ which removed shoots from alternating sides of the tree so epicormic growth would set fruit on alternating sides annually (Erez, 1976). The other, known as the Cordon or Salter System (Rogers, 1986), involved training vigorous first-year growth to bend towards the ground to stimulate epicormic sprouts, which would then be managed for fruit production in subsequent years. Trials of both systems in California were of limited success partially because fruit production on epicormic shoots tended to be low (unpublished data). Understanding the difference in fruit set patterns on sylleptic shoots on epicormic shoots compared to proleptic shoots can inform pruning decisions made by peach growers, as well as expand limited existing knowledge of the potential implications of physiological differences between sylleptic and proleptic shoots.

The overall goal of this study was to determine whether fruit production potential differs between proleptic shoots,

and sylleptic shoots borne on epicormic shoots, and if differences occur among early and later maturing cultivars. Based on limited previous experiences and the fact that proleptic shoots are formed earlier in the growing season prior to flower bud differentiation than sylleptic shoots on epicormics, our hypothesis was that fruit set would be lower for sylleptic shoots than proleptic shoots.

Materials and methods

Plant material

The experiment was performed in 2016 in a semi-commercial peach (*Prunus persica* L. Batsch) orchard located at the University of California's Wolfskill Experimental Orchards in Winters (lat. 38°30'N, long. 121°58'W), California, USA. Four cultivars were selected for the study with different timings of fruit maturity: 'Lorrie May' (early maturing) on Controller™ 9 rootstock, 'Flavorcrest' (early maturing), 'Elegant Lady' (early-mid maturing) and 'O'Henry' (mid-late maturing) on 'Nemaguard' rootstock. One north-south oriented row located in the middle of each cultivar orchard was

selected for the study. Trees were pruned during the winter of 2015 to maintain their KAC-V-training system (DeJong et al., 1994), but water sprouts (epicormic shoots) were not removed from the trees located in the row selected for the study. In February 2016, 40 long proleptic shoots and 20 epicormic shoots (water sprouts) were selected and tagged from 10 different trees for each cultivar for observation. Three sylleptic shoots with the longest length were selected and tagged on each tagged epicormic shoot. Each proleptic and sylleptic shoot was assigned an individual identification number and the shoots were individually monitored to determine their number of nodes and flower buds prior to bloom, the number of actual flowers that bloomed and the number of fruits that set, 30 days after bloom and after physiological fruit drop ("June drop").

Number of nodes, number of flowers and fruits per shoot

All nodes and flower buds on all shoots were counted at the end of dormancy on February 18, 2016. The numbers of flowers on each shoot were counted at full bloom (February 27).

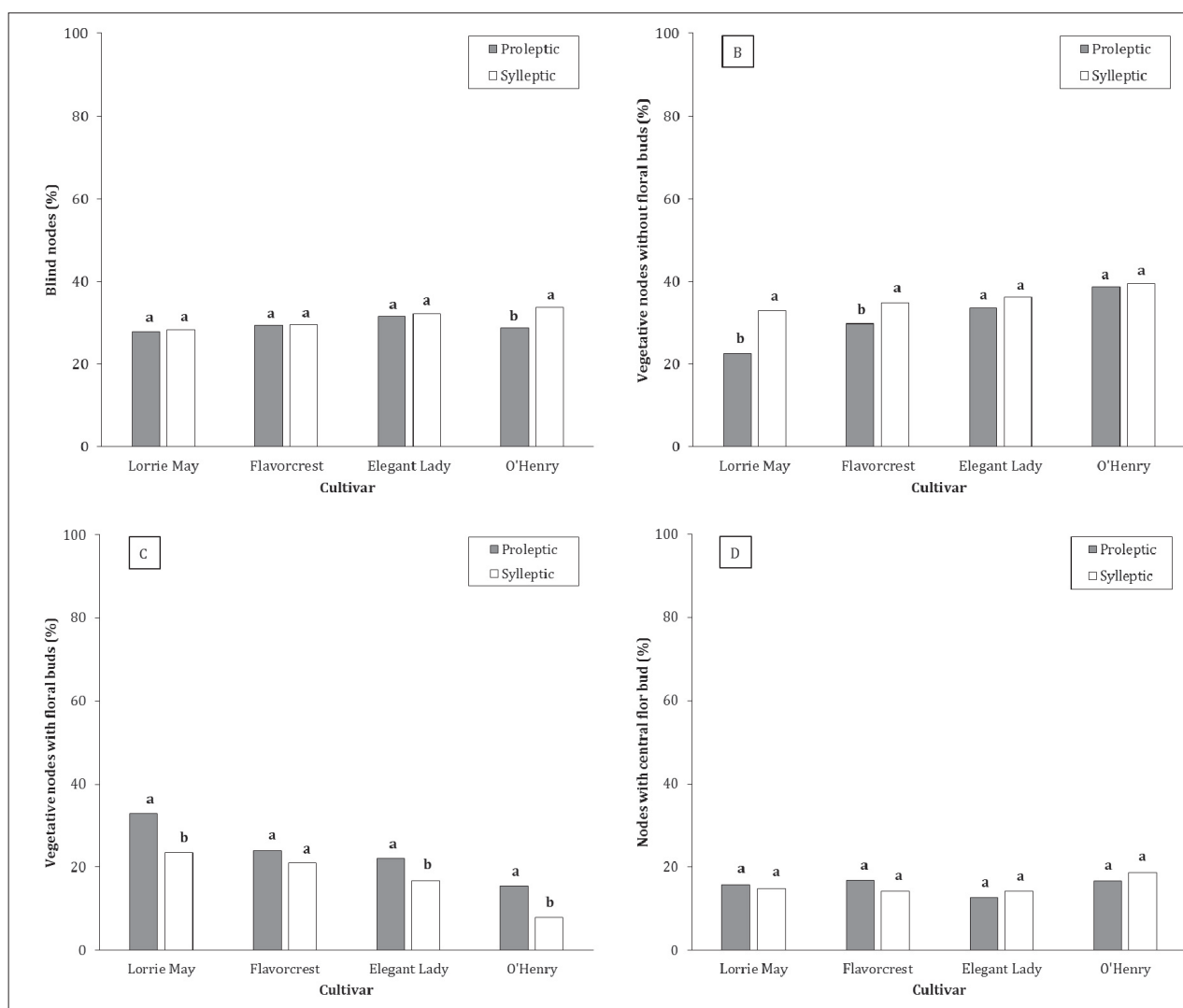


FIGURE 2. Relative frequency (% of total nodes on a shoot) of the occurrence nodes with specific lateral bud categories on proleptic and sylleptic shoots of four peach cultivars. Node categories were: (A) blind (only latent buds present); (B) central vegetative with no floral buds; (C) central vegetative with one or two associated lateral floral buds; and (D) central floral bud. Significant differences between shoot types are indicated by different letters ($p \leq 0.05$, ANOVA and Tukey's HSD test for 'Lorrie May', 'Flavorcrest' and 'Elegant Lady', and $p \leq 0.05$, Wilcoxon-Mann-Whitney test for 'O'Henry' cultivar).

TABLE 1. Mean (\pm SE) number of nodes for the tagged proleptic and sylleptic shoots on each of four cultivars.

Shoot		Cultivar			
		'Lorrie May'	'Flavorcrest'	'Elegant Lady'	'O'Henry'
Proleptic ¹	Mean	32.5 ^a	33.7 ^a	35.1 ^a	28.6 ^b
	SE	\pm 0.87	\pm 1.08	\pm 0.82	\pm 1.02
Sylleptic ²	Mean	27.9 ^b	31.6 ^a	29.8 ^a	23.0 ^b
	SE	\pm 0.60	\pm 0.73	\pm 0.59	\pm 0.47

¹ Different letters means significant differences between cultivars according to ANOVA and Tukey's HSD test ($P \leq 0.05$).

² Different letters means significant differences between cultivars according to Wilcoxon-Mann-Whitney test ($P \leq 0.05$).

On March 29, one month after full bloom, the numbers of fruitlets were counted to determine the percentage of initial fruit set. The numbers of remaining fruits were counted on May 10 to determine percent fruit set after physiological fruit drop ("June drop"). Percent fruit set was calculated in relationship to the number of flower buds ("potential flowers") and the number of flowers which actually bloomed ("actual flowers").

Data analysis

The effect of shoot type (proleptic vs. sylleptic) and cultivar on the quantitative variables was evaluated by analysis of variance (ANOVA) when variables met the assumption of normality. Otherwise the Wilcoxon-Mann-Whitney test was used. Statistical significance was established at $P < 0.05$. Tukey's HSD test was applied for separation of the least square means that differed significantly. All analyses were performed using the R software (R version 3.2.4 Revised).

Results

Shoot structural characteristics

The mean maximum node number of both shoot types on all four cultivars was 35 or less and sylleptic shoots on average had modestly fewer nodes than proleptic shoots of the same cultivars (Table 1).

All shoots were composed of similar node types (blind, vegetative with or without floral buds and floral only) (Figure 2). Proleptic shoots had more nodes with central vegetative buds with associated floral buds than sylleptic shoots in all the cultivars although differences were not statistically significant in 'Flavorcrest' (Figure 2C). However, proleptic shoots had fewer non-floral (vegetative) nodes than sylleptic shoots in 'Lorrie May' and 'Flavorcrest', and the earlier ma-

turing cultivars tended to have more floral nodes than the later maturing 'O'Henry' cultivar (Figure 2B).

Flower bud density and percent bloom

There were significant differences among cultivars in flower bud density on proleptic and sylleptic shoots, with 'Lorrie May' having the highest and 'O'Henry' the lowest on both shoot types (Table 2). There were no significant differences between percent bloom across cultivars on proleptic shoots. On sylleptic shoots, 'Elegant Lady' had significantly higher percent bloom than the other three cultivars (Table 2).

Initial fruit set

Across cultivars

Fruit set was very high in all cultivars and shoot types (Figure 3). There were no significant differences in initial fruit set on proleptic shoots among cultivars. There were significant differences among cultivars in fruit set of potential and actual flowers on sylleptic shoots (Figure 3). Considering potential flowers, 'Elegant Lady' had the highest mean fruit set on sylleptic shoots while 'Lorrie May', 'O'Henry' and 'Flavorcrest' had significantly lower fruit set than 'Elegant Lady' (Figure 3C).

Considering actual flowers, 'Elegant Lady' again had the highest fruit set on sylleptics, significantly higher than 'O'Henry' and 'Flavorcrest' but not 'Lorrie May' (Figure 3A).

Within cultivars

There were also significant differences between proleptic and sylleptic shoots in fruit set with both potential and actual flowers (Figure 3). Proleptic shoots had significantly higher fruit set compared to sylleptic shoots for 'Lorrie May', 'Flavorcrest' and 'O'Henry' considering potential flowers, but

TABLE 2. Mean (\pm SE) of flower bud density (# flower buds/total # buds) and % bloom was compared across cultivars within each shoot type. Per cent bloom was also compared within each cultivar.

Shoot type	Cultivar			
	'Lorrie May'	'Flavorcrest'	'Elegant Lady'	'O'Henry'
Proleptic				
Flower bud density	69.7% \pm 0.02 ^a	51.9% \pm 0.02 ^b	44.2% \pm 0.02 ^{bc}	39.3% \pm 0.02 ^c
% bloom	89.8% \pm 0.02 ^a	91.7% \pm 0.02 ^a	94.9% \pm 0.02 ^a	91.0% \pm 0.02 ^a
Sylleptic				
Flower bud density	51.9% \pm 0.02 ^a	40.2% \pm 0.02 ^{ab}	40.2% \pm 0.02 ^b	29.9% \pm 0.02 ^c
% bloom	80.2% \pm 0.02 ^b	80.7% \pm 0.02 ^b	94.9% \pm 0.02 ^a	85.6% \pm 0.02 ^b
Proleptic/Sylleptic				
% bloom	$p = 0.001$ ^{ab}	$p = 0.003$ ^{ab}	$p = 0.97$ ^{aa}	$p = 0.171$ ^{aa}

Data were evaluated using a one-way ANOVA with Tukey's HSD post-hoc test. Different letters indicate significant differences (Tukey's HSD $p < 0.05$).

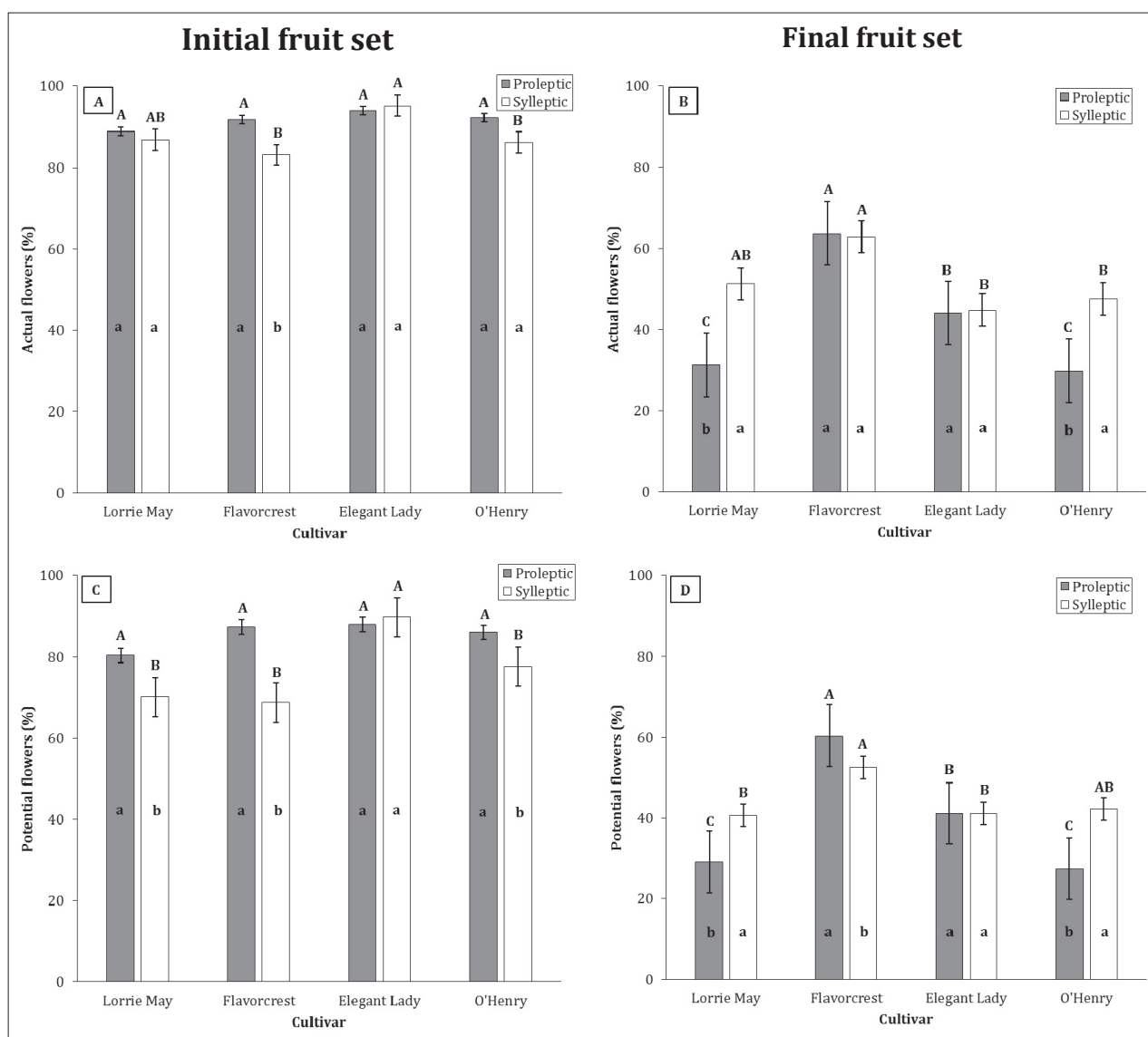


FIGURE 3. Mean percent fruit set prior to spring fruit drop (initial fruit set, A and C) and after spring fruit drop (final fruit set, B and D). Percent fruit set was calculated using number of floral buds (potential flowers) and number of flowers at full bloom (actual flowers). Capital letters above bars show differences across cultivars within that shoot type; different letters indicate significant differences (ANOVA, Tukey’s HSD, $p < 0.05$). Lower-case letters inside of bars show differences between shoot types within a cultivar; different letters indicate significant differences (ANOVA, Tukey’s HSD, $p < 0.05$). Error bars indicate standard errors.

differences were not significant for ‘Elegant Lady’ (Figure 3C). Only ‘Flavorcrest’ had a significant difference between shoot types on actual flowers, with proleptic shoots having a higher fruit set than sylleptic shoots (Figure 3A).

Final fruit set

Across cultivars

There were significant differences among cultivars in final fruit set on proleptic shoots (Figures 3B and 3D). ‘Lorrie May’ and ‘O’Henry’ had the lowest final proleptic fruit set considering potential flowers, significantly lower than ‘Elegant Lady’. ‘Flavorcrest’ was significantly higher than all other cultivars (Figure 3D). Final fruit set based on actual flowers had the same statistical groupings as potential flowers.

There were significant differences on sylleptic shoots as well (Figures 3B and 3D). Considering potential flowers,

‘Flavorcrest’ had the highest final fruit set on sylleptics, but not significantly higher than ‘O’Henry’. ‘Lorrie May’ and ‘Elegant Lady’ had significantly lower final fruit sets compared to Flavorcrest (Figure 3D). Differences were similar considering actual flowers. ‘Flavorcrest’ had significantly higher final fruit set than ‘O’Henry’ and ‘Elegant Lady’, but not significantly different than ‘Lorrie May’ (Figure 3B).

Within cultivars

There were significant final fruit set differences between proleptic and sylleptic shoots for some cultivars (Figures 3B and 3D) ($p < 0.05$). ‘Lorrie May’ and ‘O’Henry’ sylleptic shoots had significantly higher final fruit set than proleptic shoots based on both potential and actual flower counts. ‘Elegant Lady’ did not show significant differences between shoot types based on potential or actual flower counts. ‘Flavorcrest’ did not show significant differences considering actual flow-

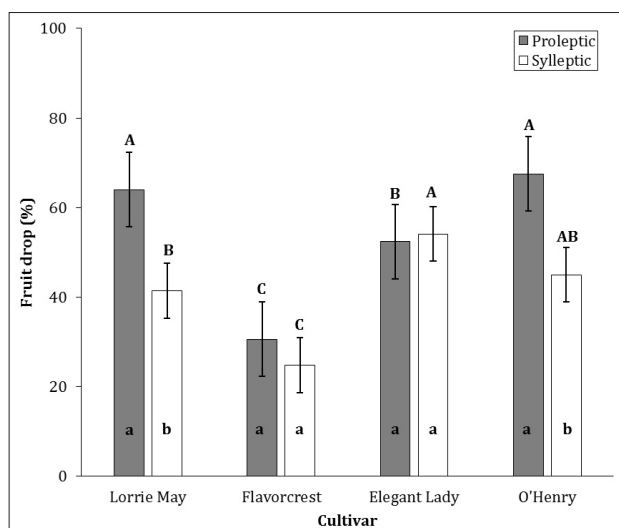


FIGURE 4. Mean percent fruit drop across and within cultivars. Letters above bars indicate differences across cultivars within that shoot type. Lower-case letters inside of bars indicates differences between shoot types within a cultivar. Different letters indicate significant differences (ANOVA, Tukey's HSD post-hoc test, significance level $p < 0.05$).

ers, but fruit set was significantly lower on sylleptic shoots than on proleptic shoots based on potential flower counts.

Percent fruit drop

Across cultivars

There were significant differences in percent fruit drop across cultivars (Figure 4). 'Lorrie May' and 'O'Henry' had the highest percent fruit drop from proleptic shoots, significantly higher than 'Elegant Lady', which was significantly higher than 'Flavorcrest'. For sylleptic shoots, 'Elegant Lady' had the highest fruit drop, not significantly higher than 'O'Henry', but significantly higher than 'Lorrie May' and 'Flavorcrest'.

Within cultivars

Proleptic shoots had significantly higher percent fruit drop compared to sylleptic shoots for 'Lorrie May' and 'O'Henry', but there were no significant differences between shoot types for 'Elegant Lady' or 'Flavorcrest' (Figure 4).

Discussion

Shoot structural characteristics

The overall structure of proleptic and sylleptic shoots was more similar than expected. Both shoot types had similar mean shoot lengths (Table 1) and nodal composition (Figure 2). Detailed analysis of shoot structures of both shoot types on all four cultivars support the idea that both shoot types are determinate and likely largely under strong genetic control in peach trees (unpublished data).

Flower development

The presence of fruit can have an inhibitory effect on the number of flowers developed in peach and apple as a result of hormonal control (Reig et al., 2006; Buszard and Schwabe, 1995; Goldschmidt et al., 1997). Of the varieties observed in this study, 'Elegant Lady' and 'O'Henry' would have the

greatest likelihood of fruit development and floral initiation overlap since flower buds are initiated in late July or August of the year prior to bloom (Tufts and Morrow, 1925; Reinoso et al., 2002) and fruit of these cultivars mature in July and August, respectively. The flower bud density data are partially consistent with the idea that the presence of fruit during flower bud initiation may have been a factor in determining floral density (Table 2). However, Reig et al. (2006) reported that commercial fruit thinning in peach tends to minimize this effect.

Proleptic and sylleptic percent bloom was similar across all four cultivars except for 'Elegant Lady' which had significantly higher sylleptic percent bloom (Table 2). Comparing shoot types within cultivars, 'Lorrie May' and 'Flavorcrest' had significantly higher proleptic percent bloom compared to sylleptic shoots (Table 2). Environmental conditions in addition to carbohydrate availability are both important in determining bud break capacity in spring. Bud break in peach is determined by chilling accumulation during the dormant period and subsequent heat accumulation in spring (Erez et al., 1990). The bud break and growth capacity of epicormic shoots (Gordon et al., 2006b) and lateral vegetative buds (Maurel et al., 2004) have been shown to be limited by availability of nonstructural carbohydrates in peach trees. Maurel et al. (2004) demonstrated a potential link between chilling and adequate mobilization and availability of stored carbohydrates during dormancy. The potential for direct competition between floral and vegetative buds during 'dormancy' is unexplored, but vegetative buds have the potential to act as relatively strong sinks during 'dormancy' (Maurel et al., 2004). Cultivars may differ in the amount and/or timing of resource mobilization to developing flower buds.

Fruit set considering the number of flower buds (potential flowers) was affected strongly by percent bloom, but also encompassed differences that occurred between bloom and fruit set on actual flowers. There were no significant differences in percent bloom (Table 2) or initial fruit set (Figure 3) on proleptic shoots across cultivars. Within sylleptic shoots, 'Elegant Lady' had a significantly higher initial fruit set (potential flowers), reflecting the pattern of percent bloom data. However, the other three cultivars were further statistically differentiated considering initial fruit set (potential flowers) (Figure 3) as compared to percent bloom (Table 2). This differentiation was related to significant differences found between sylleptic fruit set from actual flowers (Figure 3), suggesting that there were cultivar differences determining initial fruit set after bloom as well as floral bud bloom capacity. Calculated fruit set considering potential flowers illustrated the additive effects of these cultivar differences.

Fruit set and fruit drop

As hypothesized, our data suggest that fruit set on sylleptic and proleptic shoots can differ significantly (Figure 3). However, contrary to our expectations, those differences were not consistent across cultivars or shoot types. Where significant differences were found between initial sylleptic and proleptic fruit set, as expected, sylleptic shoots always set less fruit. After fruit drop, however, those differences were not always maintained. For two cultivars ('Lorrie May' and 'O'Henry'), the pattern was reversed; sylleptic shoots ended up with a significantly higher % fruit set than proleptic shoots after fruit drop (Figure 3). Only 'Flavorcrest' maintained significantly higher proleptic fruit set, and 'Elegant Lady' showed no significant difference before or after fruit drop. Forming hypotheses about why this may occur was dif-

difficult, as the factors that influence flower bud development and fruit set are complex and occur over a period of months. Environmental factors, in addition to endogenous factors such as the amount and availability of stored carbohydrate, affect potential fruit growth from bud initiation to bloom (Feucht, 1982). The very high overall fruit set experienced in this study (Figure 3) suggests that environmental factors were nearly ideal for fruit set in the year of the study, offering an interesting opportunity to gain insight into how fruit set differed based on endogenous factors.

Resource limitation is an important determining factor for fruit set in perennial (Hill-Cottingham and Williams, 1967; Stephenson, 1981) as well as annual crops (Nightingale and Farnham, 1936; Leopold and Scott, 1952). In peach trees, carbohydrate reserves are depleted by flowers, developing fruit, and early vegetative growth to an annual minimum before the canopy matures into becoming a net carbohydrate source (Loescher et al., 1990; Gordon et al., 2006b; DaSilva et al., 2014). Competition with other flowers and developing fruits may be an important factor in carbohydrate limitations affecting fruit set, which become increasingly important after initial fruit set occurs. Abortion of undamaged juvenile fruit (“physiological fruit drop” or “June drop” in peach) is common among flowering plants, and it is most often due to competition for limited resources (Stephenson, 1981). In general, the more fruit that are initially set, the more juvenile fruits will be aborted (Stephenson, 1981).

Based on the concept of increasing competition for carbohydrates with increasing bloom and fruit set, it may be expected that higher percent bloom would lead to lower percent initial fruit set from actual flowers due to competition between flowers. However, our data do not suggest that this is the case consistently across cultivars or shoot types. ‘Elegant Lady’, for example, had the highest percent bloom (Table 2) as well as initial fruit set from actual flowers (Figure 3A) while ‘Lorrie May’ and ‘Flavorcrest’ both showed significantly lower percent sylleptic bloom compared to bloom on proleptic shoots (Table 2). However, ‘Lorrie May’ and ‘O’Henry’ fruit set based on actual flowers, did not differ between shoot types (Figure 3).

Considering the transition between initial and final fruit set, our data suggest that direct competition between initially set fruits may be important in determining percent fruit drop. However, again, this trend was not observed consistently across cultivars or shoot types. Sylleptic fruit drop data (Figure 4) suggested that percent sylleptic fruit drop increased with increasing initial sylleptic fruit set (potential flowers) (Figures 3C and 3D). ‘Elegant Lady’ had the highest initial fruit set as well as the highest percent fruit drop, ‘Lorrie May’ and ‘O’Henry’ intermediate, and ‘Flavorcrest’ the lowest. These data are in agreement with the argument for increasing carbohydrate competition with increasing number of fruits as a major factor determining fruit set (Stephenson, 1981). Some of the results comparing shoot types within cultivars, also support this hypothesis. On ‘Lorrie May’, sylleptic shoots initially set significantly fewer fruit than proleptic shoots (Figure 3C), and experienced a significantly lower percent fruit drop (Figure 4). ‘Elegant Lady’ had equivalent initial fruit set between shoot types (Figure 3C) and equivalent percent fruit drop (Figure 4).

Proleptic shoot fruit drop, however, did not appear to follow the same pattern; there were significant differences among cultivars for percent fruit drop from proleptic shoots (Figure 4) despite a lack of differences in initial fruit set (Figure 3). For ‘Flavorcrest’ significantly higher fruit set on

sylleptic shoots compared to proleptic shoots (Figure 3) did not correspond to significantly higher percent sylleptic fruit drop (Figure 4). Comparison of shoot types on ‘O’Henry’, also seemed to contradict the increasing fruit set/increasing carbohydrate competition hypothesis for determining fruit drop; sylleptic and proleptic shoots showed significant differences in percent fruit drop despite a lack of significant differences in initial fruit set. These differences in fruit drop behavior between sylleptic and proleptic shoots may reflect differences in carbon storage with respect to these two different types of shoots. Proleptic shoots have a longer time to develop storage tissue since they begin their growth and complete development earlier in the previous season (DeJong et al., 1987).

Final fruit set patterns (Figures 3B and 3D) were distinctly different from patterns observed in initial fruit set (Figures 3A and 3C). Final fruit set (Figures 3B and 3D), of course, was strongly influenced by the percent fruit drop (Figure 4). However, percent fruit drop was difficult to explain given percent bloom (Table 2) and initial fruit set (Figures 3A and 3C) data. It may be that endogenous conditions which determined initial cultivar differences in fruit set differed from factors that controlled final fruit set. This may have been due to cultivar differences in the amount or location of carbohydrate reserves, systematic differences in shoot light exposure or leaf characteristics of the two types of shoots, or some differences in how those resources were allocated (Corelli-Grappadelli et al., 1996). When a young fruit is about to abscise, growth-promoting hormones are replaced by increasing concentrations of the growth-inhibiting hormones such as abscisic acid and ethylene (Bollard, 1970; Nitsch, 1970). The inability of a young fruit to acquire sufficient resources for growth is thought to trigger the production of growth-inhibiting hormones (Nitsch, 1970; Addicott and Lynch, 1955). Genetic differences which result in differential patterns of hormone production during fruit development, whether as a differential response to direct competition or otherwise, could affect fruit set and development. Differences in carbohydrate assimilation efficiency (amount of carbon used for respiration as opposed to dry matter accumulation) of different cultivars may also affect percent fruit drop. DeJong and Walton (1989) found that carbon demand for respiration is highest during early fruit development, and that respiration requirements were significantly higher in an early-ripening peach cultivar as compared to a later maturing cultivar. Genetic differences related to harvest date may be important in determining degree of spring fruit drop.

Substantial differences in temporal separation between major growth phases across cultivars affect whole-tree carbohydrate dynamics during the growing season (DeJong and Doyle, 1985). It is unclear what effect these differences may have on bloom or fruit set the following season based on existing evidence or data from the present study. However, it may be that cultivars differ in the amount, location, or ability to mobilize stored carbohydrates.

Differences in whole-tree carbohydrate dynamics have been shown to affect current season yield. Early peach cultivars like ‘Lorrie May’ and ‘Flavorcrest’ (June harvest) do not temporally separate peak fruit carbohydrate demand from peak shoot extension which negatively affects yield potential (DeJong et al., 1987; Grossman and DeJong, 1995). For later cultivars such as ‘O’Henry’, the major sinks at the beginning of the season are shoots and roots, which are interrupted temporarily by fruit ripening, and resume growth after harvest (Grossman and DeJong, 1995; Berman and DeJong,

2003). Late-ripening fruits can have a much higher carbon demand compared to early varieties; fruit acts as a carbohydrate sink throughout the season and can reach higher dry weight per fruit in addition to higher requirements for maintenance respiration (DeJong and Walton, 1989). The period of maximum carbon demand occurs during ripening in the late summer, which is a critical time for building carbohydrate reserves (Loescher et al., 1990; Barbaroux and Breda, 2002; Wong et al., 2003).

Conclusion

Data from this study show that while structurally similar, significant differences between sylleptic and proleptic fruit set can occur within and across cultivars. Furthermore, it appears that sylleptic shoot fruit set is determined more by factors affecting bloom and initial fruit set, and there were cultivar differences in fruit drop on both sylleptic and proleptic shoots.

The results of this study are of interest from the perspectives of peach orchard management and breeding. Sylleptic shoots on epicormic growth can contribute significantly to yields. Thus they should be managed by orchardists, similar to proleptic shoots, which are usually considered to be the primary fruit bearing shoots in peach production systems. Data from this study suggest that some varieties may have a higher potential for epicormic-sylleptic fruit set than others. If there are attempts at developing peach orchard systems that rely heavily on fruit set on epicormic growth (Erez, 1976; Rogers, 1986), cultivar comparisons should be included in such trials. Furthermore, cultivar differences in the propensity to set fruit on both proleptic and sylleptic shoots may be valuable in peach breeding efforts for selecting genotypes with specific fruit set characteristics as a potential avenue for mitigating expensive, hand-thinning costs.

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