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

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Abstract

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.

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).

48   Epicormic shoots (also known as 'water sprouts') arise from preventitious meristems

49   without undergoing a period of dormancy (Wilson, 2000; Costes et al., 2006). Epicormic shoots

50   are characterized by vigorous, upright growth stimulated by heavy pruning (Figure 1), branch

51   breaking, or drastic branch bending (Bussi et al 2011; DeJong et al., 2012). Heavy pruning which

52   is usual in many peach production systems often stimulates excessive epicormic growth which

53   necessitates further pruning to avoid negative impacts on fruit production. Epicormic peach

54   shoots tend to exhibit low correlative inhibition which results in many lateral sylleptic branches

55   (Figure 1, DeJong et al., 2012). Because lateral meristems have no preformed organs, epicormic

56   shoots are made entirely of neoformed growth (Fournier et al., 1997; Costes et al., 2006).

57   Epicormic shoots, in contrast to the determinate nature of proleptic shoots, tend to continue

58   growing until environmental conditions become unfavorable (DeJong and Doyle, 1985).

59   Physiological differences between proleptic and sylleptic shoots may have an effect on fruit

60   set. The ability of a flower bud to succeed from bud initiation through to bloom and fruit set is

61   dependent on environmental factors as well as endogenous factors such as hormonal signaling

62   and access to organic and mineral nutrient reserves (Feucht, 1982; DeJong, 1999; Loescher et al.,

63   1990). Floral bud growth during the summer season is limited; although flower buds begin to

64   differentiate in mid-summer of the year prior to bloom (late July-early August) (Tufts and

65   Morrow, 1925; Reinoso et al., 2002) and continue to develop through August and September (Gur,

66   1985). Flower buds are not fully developed by the onset of dormancy, and depend on

67   mobilization of stored carbohydrates to continue to development throughout the rest period

68   (Maurel et al., 2004; Reinoso et al., 2002; Luna et al., 1990). Bloom and fruit set depend on

69   carbohydrate and mineral nutrient reserves as well as bud development and growth that occurs

70   in the early spring before vegetative growth initiates and leaves become a net source of

71   carbohydrates (Loescher et al., 1990).

72   The ability of a developing organ to access assimilates during any growth phase depends

73   on the supply of carbohydrates as well as the amount of competition for resources from other

74   growing organs (DeJong, 1999). The distribution of resources is determined by the location of

75   carbohydrate sinks (i.e. reproductive organs, shoots, and roots) relative to carbohydrate sources

76   (i.e. mature leaves or storage organs) as well as relative 'sink strength' of each growing structure

77   (Pavel and DeJong, 1993; DeJong, 1999). Other factors may also be at play other than actual

78   amount of stored carbohydrate; Maurel et al. (2004) demonstrated a link between inadequate

79   chilling accumulation and subsequent carbohydrate limitation due to reduced storage

80   mobilization for vegetative buds.

81   Proleptic shoots finish extending by the end of June, before floral initiation and

82   differentiation occurs, while epicormic shoots continue to grow vigorously throughout the

83   growing season. Vigorous vegetative growth has been found to be antagonistic to flower bud

84   initiation in several temperate fruit trees (Guimond et al., 1998; Wilkie et al., 2008; Koutinas et

85   al., 2010). In some cases flushes of vegetative growth have been reported to have sufficient sink

86   strength to outcompete fruit (Quinlan and Preston, 1971).

87   There is limited direct evidence that there is a difference in fruit bud formation and fruit

88   set between proleptic shoots and sylleptic shoots borne on epicormic shoots. Yamashita et al.

89   (1971) reported that epicormic shoots produce fewer flower buds with lower fresh weight

90   compared to 'normal bearing shoots'. Results from attempts to develop new cropping systems

91   for peach in California which depended on sylleptic shoots on epicormic branches for fruit set

92   suggest that fruit set on sylleptic shoots borne on epicormic shoots may be lower than on

93   proleptic shoots (DeJong et al., 1999; Grossman and DeJong 1998). One such system was a peach

94   "Meadow Orchard" which removed shoots from alternating sides of the tree so epicormic growth

95 would set fruit on alternating sides annually (Erez, 1976). The other, known as the Cordon or

96 Salter System (Rogers, 1986), involved training vigorous first-year growth to bend towards the

97 ground to stimulate epicormic sprouts, which would then be managed for fruit production in

98 subsequent years. Trials of both systems in California were of limited success partially because

99 fruit production on epicormic shoots tended to be low (unpublished data). Understanding the

100 difference in fruit set patterns on sylleptic shoots on epicormic shoots compared to proleptic

101 shoots can inform in pruning decisions made by peach growers, as well as expand limited existing

102 knowledge of the potential implications of physiological differences between sylleptic and

103 proleptic shoots.

104   The overall goal of this study was to determine whether fruit production potential differs

105 between proleptic shoots, and sylleptic shoots borne on epicormic shoots, and if differences occur

106 among early and later maturing cultivars. Based on limited previous experiences and the fact

107 that proleptic shoots are formed earlier in the growing season prior to flower bud differentiation

108 than sylleptic shoots on epicormics, our hypothesis was that fruit set would be lower for sylleptic

109 shoots than proleptic shoots.

110 **MATERIALS AND METHODS**

111 **Plant material**

112   The experiment was performed in 2016 in a semi-commercial peach (*Prunus Persica* L.

113 Batsch) orchard located at the University of California's Wolfskill Experimental Orchards in

114 Winters (lat. 38° 30' N, long. 121° 58' W), California, USA. Four cultivars were selected for the

115 study with different maturity: "Lorrie May" (early maturing) on Controller™ 9 rootstock,

116 "Flavorcrest" (early maturing), "Elegant Lady" (early-mid maturing) and "O'Henry" (mid-late

117 maturing) on 'Nemaguard' rootstock. One north-south oriented row located in the middle of each

118   cultivar orchard was selected for the study. Trees were pruned during the winter of 2015 to

119   maintain their KAC-V-training system (DeJong et al., 1994), but water sprouts (epicormic shoots)

120   were not removed from the trees located in the row selected for the study. In February 2016, 40

121   long proleptic shoots and 20 epicormic shoots (water sprouts) were selected and tagged from 10

122   different trees for each cultivar for observation. Three sylleptic shoots with the longest length

123   were selected and tagged on each tagged epicormic shoot. Each proleptic and sylleptic shoot was

124   assigned an individual identification number and the shoots were individually monitored to

125   determine their number of nodes and flower buds prior to bloom, the number of actual flowers

126   that bloomed and the number of fruits that set, 30 days after bloom and after physiological fruit

127   drop ("June drop").

128   **Number of nodes, number of flowers and fruits per shoot**

129   All nodes and flower buds on all shoots were counted at the end of dormancy on February

130   18, 2016. The numbers of flowers on each shoot were counted at full bloom (February 27). On

131   March 29, one month after full bloom, the numbers of fruitlets were counted to determine the

132   percentage of initial fruit set. The numbers of remaining fruits were counted on May 10 to

133   determine percent fruit set after physiological fruit drop ("June drop"). Percent fruit set was

134   calculated in relationship to the number of flower buds ("potential flowers") and the number of

135   flowers which actually bloomed ("actual flowers").

136   **Data analysis**

137   The effect of shoot type (proleptic vs. sylleptic) and cultivar on the quantitative variables

138   was evaluated by analysis of variance (ANOVA) when variables met the assumption of normality.

139   Otherwise the Wilcoxon-Mann-Whitney test was used. Statistical significance was established at

140   P < 0.05. Tukey's HSD test was applied for separation of the least square means that differed

141   significantly. All analyses were performed using the R software (R version 3.2.4 Revised).

142   **RESULTS**

143   **Shoot structural characteristics**

144   The mean maximum node number of both shoot types on all four cultivars was 35 or less

145   and sylleptic shoots on average had modestly fewer nodes than proleptic shoots of the same

146   cultivars (Table 1).

147   All shoots were composed of similar node types (blind, vegetative with or without floral

148   buds and floral only) (Figure 2). Proleptic shoots had more nodes with central vegetative buds

149   with associated floral buds than sylleptic shoots in all the cultivars although differences were not

150   statistically significant in 'Flavorcrest' (Figure 2C). However, proleptic shoots had fewer non-

151   floral (vegetative) nodes than sylleptic shoots in 'Lorrie May' and 'Flavorcrest', and the earlier

152   maturing cultivars tended to have more floral nodes than the later maturing 'O'Henry' cultivar

153   (Figure 2B).

154   **Flower Bud Density and Percent Bloom**

155   There were significant differences among cultivars in flower bud density on proleptic and

156   sylleptic shoots, with 'Lorrie May' having the highest and 'O'Henry' the lowest on both shoot types

157   (Table 2). There were no significant differences between percent bloom across cultivars on

158   proleptic shoots. On sylleptic shoots, 'Elegant Lady' had significantly higher percent bloom than

159   the other three cultivars (Table 2).

160   **Initial Fruit Set**

161   *Across cultivars.*

162   Fruit set was very high in all cultivars and shoot types (Figure 3). There were no significant

163   differences in initial fruit set on proleptic shoots among cultivars. There were significant

164   differences among cultivars in fruit set of potential and actual flowers on sylleptic shoots (Figure

165   3). Considering potential flowers, 'Elegant Lady' had the highest mean fruit set on sylleptic shoots

166   while 'Lorrie May', 'O'Henry' and 'Flavorcrest' had significantly lower fruit set than 'Elegant Lady'

167   (Figure 3C).

168   Considering actual flowers, 'Elegant Lady' again had the highest fruit set on sylleptics,

169   significantly higher than 'O'Henry' and 'Flavorcrest' but not 'Lorrie May' (Figure 3A).

170   *Within cultivars.*

171   There were also significant differences between proleptic and sylleptic shoots in fruit set

172   with both potential and actual flowers (Figure 3). Proleptic shoots had significantly higher fruit

173   set compared to sylleptic shoots for 'Lorrie May', 'Flavorcrest' and 'O'Henry' considering potential

174   flowers, but differences were not significant for 'Elegant Lady' (Figure 3C). Only 'Flavorcrest' had

175   a significant difference between shoot types on actual flowers, with proleptic shoots having a

176   higher fruit set than sylleptic shoots (Figure 3A).

177   **Final Fruit Set**

178   *Across cultivars.*

179   There were significant differences among cultivars in final fruit set on proleptic shoots

180   (Figure 3B, 3D). 'Lorrie May' and 'O'Henry' had the lowest final proleptic fruit set considering

181   potential flowers, significantly lower than 'Elegant Lady'. 'Flavorcrest' was significantly higher

182   than all other cultivars (Figure 3D). Final fruit set based on actual flowers had the same statistical

183   groupings as potential flowers.

184   There were significant differences on sylleptic shoots as well (Figure 3B, 3D). Considering

185   potential flowers, 'Flavorcrest' had the highest final fruit set on sylleptics, but not significantly

186   higher than 'O'Henry'. 'Lorrie May' and 'Elegant Lady' had significantly lower final fruit sets

187   compared to Flavorcrest (Figure 3D). Differences were similar considering actual flowers.

188   'Flavorcrest' had significantly higher final fruit set than 'O'Henry' and 'Elegant Lady', but not

189   significantly different than 'Lorrie May' (Figure 3B).

190   ***Within cultivars.***

191   There were significant final fruit set differences between proleptic and sylleptic shoots for

192   some cultivars (Figure 3B, 3D) ($p < 0.05$). 'Lorrie May' and 'O'Henry' sylleptic shoots had

193   significantly higher final fruit set than proleptic shoots based on both potential and actual flower

194   counts. 'Elegant Lady' did not show significant differences between shoot types based on

195   potential or actual flower counts. 'Flavorcrest' did not show significant differences considering

196   actual flowers, but fruit set was significantly lower on sylleptic shoots than on proleptic shoots

197   based on potential flower counts.

198   **Percent Fruit Drop**

199   ***Across cultivars***

200   There were significant differences in percent fruit drop across cultivars (Figure 4). 'Lorrie

201   May' and 'O'Henry' had the highest percent fruit drop from proleptic shoots, significantly higher

202   than 'Elegant Lady', which was significantly higher than 'Flavorcrest'. For sylleptic shoots,

203   'Elegant Lady' had the highest fruit drop, not significantly higher than 'O'Henry', but significantly

204   higher than 'Lorrie May' and 'Flavorcrest'.

205   ***Within cultivars***

206   Proleptic shoots had significantly higher percent fruit drop compared to sylleptic shoots

207   for 'Lorrie May' and 'O'Henry', but there were no significant differences between shoot types for

208   'Elegant Lady' or 'Flavorcrest' (Figure 4).

209   **DISCUSSION**

210   **Shoot structural characteristics**

211   The overall structure of proleptic and sylleptic shoots was more similar than expected. Both

212   shoot types had similar mean shoot lengths (Table 1) and nodal composition (Figure 2). Detailed

213   analysis of shoot structures of both shoot types on all four cultivars support the idea that both

214   shoot types are determinate and likely largely under strong genetic control in peach trees

215   (unpublished data).

216   **Flower development**

217   The presence of fruit can have an inhibitory effect on the number of flowers developed in

218   peach and apple as a result of hormonal control (Reig et al., 2006; Buszard and Schwabe, 1995;

219   Goldschmidt et al., 1997). Of the varieties observed in this study, 'Elegant Lady' and 'O'Henry'

220   would have the greatest likelihood of fruit development and floral initiation overlap since flower

221   buds are initiated in late July or August of the year prior to bloom (Tufts and Morrow, 1925;

222   Reinoso et al., 2002) and fruit of these cultivars mature in July and August, respectively. The

223   flower bud density data are partially consistent with the idea that the presence of fruit during

224 flower bud initiation may have been a factor in determining floral density (Table 2). However

225 Reig et al. (2006) reported that commercial fruit thinning in peach tends to minimize this effect.

226   Proleptic and sylleptic percent bloom was similar across all four cultivars except for

227 'Elegant Lady' which had significantly higher sylleptic percent bloom (Table 2). Comparing shoot

228 types within cultivars, 'Lorrie May' and 'Flavorcrest' had significantly higher proleptic percent

229 bloom compared to sylleptic shoots (Table 2). Environmental conditions in addition to

230 carbohydrate availability are both important in determining bud break capacity in spring. Bud

231 break in peach is determined by chilling accumulation during the dormant period and subsequent

232 heat accumulation in spring (Erez et al., 1990). The bud break and growth capacity of epicormic

233 shoots (Gordon et al., 2006b) and lateral vegetative buds (Maurel et al., 2004) have been shown

234 to be limited by availability of nonstructural carbohydrates in peach trees. Maurel et al., (2004)

235 demonstrated a potential link between chilling and adequate mobilization and availability of

236 stored carbohydrates during dormancy. The potential for direct competition between floral and

237 vegetative buds during 'dormancy' is unexplored, but vegetative buds have the potential to act as

238 relatively strong sinks during 'dormancy' (Maurel et al., 2004). Cultivars may differ in the amount

239 and/or timing of resource mobilization to developing flower buds.

240   Fruit set considering the number of flower buds (potential flowers) was affected strongly

241 by percent bloom, but also encompassed differences that occurred between bloom and fruit set

242 on actual flowers. There were no significant differences in percent bloom (Table 2) or initial fruit

243 set (Figure 3) on proleptic shoots across cultivars. Within sylleptic shoots, 'Elegant Lady' had a

244 significantly higher initial fruit set (potential flowers), reflecting the pattern of percent bloom

245 data. However, the other three cultivars were further statistically differentiated considering

246 initial fruit set (potential flowers) (Figure 3) as compared to percent bloom (Table 2). This

247 differentiation was related to significant differences found between sylleptic fruit set from actual

248 flowers (Figure 3), suggesting that there were cultivar differences determining initial fruit set

249 after bloom as well as floral bud bloom capacity. Calculated fruit set considering potential flowers

250 illustrated the additive effects of these cultivar differences.

251 **Fruit set and Fruit Drop**

252 As hypothesized, our data suggest that fruit set on sylleptic and proleptic shoots can differ

253 significantly (Figure 3). However, contrary to our expectations, those differences were not

254 consistent across cultivars or shoot types. Where significant differences were found between

255 initial sylleptic and proleptic fruit set, as expected, sylleptic shoots always set less fruit. After fruit

256 drop, however, those differences were not always maintained. For two cultivars ('Lorrie May'

257 and 'O'Henry'), the pattern was reversed; sylleptic shoots ended up with a significantly higher %

258 fruit set than proleptic shoots after fruit drop (Figure 3). Only 'Flavorcrest' maintained

259 significantly higher proleptic fruit set, and 'Elegant Lady' showed no significant difference before

260 or after fruit drop. Forming hypotheses about why this may occur was difficult, as the factors that

261 influence flower bud development and fruit set are complex and occur over a period of months.

262 Environmental factors, in addition to endogenous factors such as the amount and availability of

263 stored carbohydrate, affect potential fruit growth from bud initiation to bloom (Feucht, 1982).

264 The very high overall fruit set experienced in this study (Figure 3) suggests that environmental

265 factors were nearly ideal for fruit set in the year of the study, offering an interesting opportunity

266 to gain insight into how fruit set differed based on endogenous factors.

267 Resource limitation is an important determining factor for fruit set in perennial (Hill-

268 Cottingham and Williams, 1967; Stephenson, 1981) as well as annual crops (Nightingale and

269 Farnham 1936, Leopold and Scott 1952). In peach trees, carbohydrate reserves are depleted by

270 flowers, developing fruit, and early vegetative growth to an annual minimum before the canopy

271   matures into becoming a net carbohydrate source (Loescher et al., 1990; Gordon et al., 2006b;

272   DaSilva et al., 2014). Competition with other flowers and developing fruits may be an important

273   factor in carbohydrate limitations affecting fruit set, which become increasingly important after

274   initial fruit set occurs. Abortion of undamaged juvenile fruit ('physiological fruit drop' or 'June

275   drop' in peach) is common among flowering plants, and it is most often due to competition for

276   limited resources (Stephenson, 1981). In general, the more fruit that are initially set, the more

277   juvenile fruits will be aborted (Stephenson, 1981).

278   Based on the concept of increasing competition for carbohydrates with increasing bloom

279   and fruit set, it may be expected that higher percent bloom would lead to lower percent initial

280   fruit set from actual flowers due to competition between flowers. However, our data do not

281   suggest that this is the case consistently across cultivars or shoot types. 'Elegant Lady', for

282   example, had the highest percent bloom (Table 2) as well as initial fruit set from actual flowers

283   (Figure 3A) while 'Lorrie May' and 'Flavorcrest' both showed significantly lower percent sylleptic

284   bloom compared to bloom on proleptic shoots (Table 2). However, 'Lorrie May' and 'O'Henry'

285   fruit set based on actual flowers, did not differ between shoot types (Figure 3).

286   Considering the transition between initial and final fruit set, our data suggest that direct

287   competition between initially set fruits may be important in determining percent fruit drop.

288   However, again, this trend was not observed consistently across cultivars or shoot types. Sylleptic

289   fruit drop data (Figure 4) suggested that percent sylleptic fruit drop increased with increasing

290   initial sylleptic fruit set (potential flowers) (Figure 3C, 3D). 'Elegant Lady' had the highest initial

291   fruit set as well as the highest percent fruit drop, 'Lorrie May' and 'O'Henry' intermediate, and

292   'Flavorcrest' the lowest. These data are in agreement with the argument for increasing

293   carbohydrate competition with increasing number of fruits as a major factor determining fruit

294   set (Stephenson, 1981). Some of the results comparing shoot types within cultivars, also support

295   this hypothesis. On 'Lorrie May', sylleptic shoots initially set significantly fewer fruit than

296   proleptic shoots (Figure 3C), and experienced a significantly higher percent fruit drop (Figure 4).

297   'Elegant Lady' had equivalent initial fruit set between shoot types (Figure 3C) and equivalent

298   percent fruit drop (Figure 4).

299   Proleptic shoot fruit drop, however, did not appear to follow the same pattern; there were

300   significant differences among cultivars for percent fruit drop from proleptic shoots (Fig 4) despite

301   a lack of differences in initial fruit set (Fig 3). For 'Flavorcrest' significantly higher fruit set on

302   sylleptic shoots compared to proleptic shoots (Fig 3) did not correspond to significantly higher

303   percent sylleptic fruit drop (Fig 4). Comparison of shoot types on 'O'Henry', also seemed to

304   contradict the increasing fruit set/increasing carbohydrate competition hypothesis for

305   determining fruit drop; sylleptic and proleptic shoots showed significant differences in percent

306   fruit drop despite a lack of significant differences in initial fruit set. These differences in fruit drop

307   behavior between sylleptic and proleptic shoots may reflect differences in carbon storage with

308   respect to these two different types of shoots. Proleptic shoots have a longer time to develop

309   storage tissue since they begin their growth and complete development earlier in the previous

310   season (DeJong et al. 1987).

311   Final fruit set patterns (Figure 3B, 3D) were distinctly different from patterns observed in

312   initial fruit set (Figure 3A, 3C). Final fruit set (Figure 3B, 3D), of course, was strongly influenced

313   by the percent fruit drop (Figure 4). However, percent fruit drop was difficult to explain given

314   percent bloom (Table 2) and initial fruit set (Figure 3A, 3C) data. It may be that endogenous

315   conditions which determined initial cultivar differences in fruit set differed from factors that

316   controlled final fruit set. This may have been due to cultivar differences in the amount or location

317   of carbohydrate reserves, systematic differences in shoot light exposure or leaf characteristics of

318   the two types of shoots, or some differences in how those resources were allocated (Corelli-

319   Grappadelli et al, 1996). When a young fruit is about to abscise, growth-promoting hormones are

320   replaced by increasing concentrations of the growth-inhibiting hormones such as abscisic acid

321   and ethylene (Bollard, 1970; Nitsch, 1970). The inability of a young fruit to acquire sufficient

322   resources for growth is thought to trigger the production of growth-inhibiting hormones (Nitsch,

323   1970; Addicott and Lynch, 1955). Genetic differences which result in differential patterns of

324   hormone production during fruit development, whether as a differential response to direct

325   competition or otherwise, could affect fruit set and development. Differences in carbohydrate

326   assimilation efficiency (amount of carbon used for respiration as opposed to dry matter

327   accumulation) of different cultivars may also affect percent fruit drop. DeJong and Walton (1989)

328   found that carbon demand for respiration is highest during early fruit development, and that

329   respiration requirements were significantly higher in an early-ripening peach cultivar as

330   compared to a later maturing cultivar. Genetic differences related to harvest date may be

331   important in determining degree of spring fruit drop.

332   Substantial differences in temporal separation between major growth phases across

333   cultivars affect whole-tree carbohydrate dynamics during the growing season (DeJong and Doyle,

334   1985). It is unclear what effect these differences may have on bloom or fruit set the following

335   season based on existing evidence or data from the present study. However, it may be that

336   cultivars differ in the amount, location, or ability to mobilize stored carbohydrates.

337   Differences in whole-tree carbohydrate dynamics have been shown to affect current season

338   yield. Early peach cultivars like 'Lorrie May' and 'Flavorcrest' (June harvest) do not temporally

339   separate peak fruit carbohydrate demand from peak shoot extension which negatively affects

340   yield potential (DeJong et al., 1987; Grossman and DeJong, 1995). For later cultivars such as

341   'O'Henry', the major sinks at the beginning of the season are shoots and roots, which are

342   interrupted temporarily by fruit ripening, and resume growth after harvest (Grossman and

343   DeJong, 1995; Berman and DeJong, 2003). Late-ripening fruits can have a much higher carbon

344   demand compared to early varieties; fruit acts as a carbohydrate sink throughout the season and

345   can reach higher dry weight per fruit in addition to higher requirements for maintenance

346   respiration (DeJong and Walton, 1989). The period of maximum carbon demand occurs during

347   ripening in the late summer, which is a critical time for building carbohydrate reserves (Loescher

348   et al., 1990; Barbaroux and Breda, 2002; Wong et al., 2003).

349   **CONCLUSION**

350   Data from this study show that while structurally similar, significant differences between

351   sylleptic and proleptic fruit set can occur within and across cultivars. Furthermore, it appears

352   that sylleptic shoot fruit set is determined more by factors affecting bloom and initial fruit set,

353   and there were cultivar differences in fruit drop on both sylleptic and proleptic shoots.

354   The results of this study are of interest from the perspectives of peach orchard

355   management and breeding. Sylleptic shoots on epicormic growth can contribute significantly to

356   yields. Thus they should be managed by orchardists, similar to proleptic shoots, which are usually

357   considered to be the primary fruit bearing shoots in peach production systems. Data from this

358   study suggest that some varieties may have a higher potential for epicormic-sylleptic fruit set

359   than others. If there are attempts at developing peach orchard systems that rely heavily on fruit

360   set on epicormic growth (Erez, 1976; Rogers, 1986), cultivar comparisons should be included in

361   such trials. Furthermore, cultivar differences in the propensity to set fruit on both proleptic and

362   sylleptic shoots may be valuable in peach breeding efforts for selecting genotypes with specific

363   fruit set characteristics as a potential avenue for mitigating expensive, hand-thinning costs.

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Tables

Table 1. Mean (±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	± 0.87	± 1.08	± 0.82	± 1.02
Sylleptic[2]	Mean	27.9 [b]	31.6 [a]	29.8 [a]	23.0 [b]
	SE	± 0.60	± 0.73	± 0.59	± 0.47

[1]Different letters means significant differences between cultivars according to ANOVA and Tukey's HSD test (P≤0.05).
[2]Different letters means significant differences between cultivars according to Wilcoxon-Mann-Whitney test (P≤0.05).

Table 2. Mean (± 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%±0.02 [a]	51.9%±0.02 [b]	44.2% ±0.02 [bc]	39.3%±0.02 [c]
% bloom	89.8%±0.02 [a]	91.7%±0.02 [a]	94.9%±0.02 [a]	91.0%±0.02 [a]
Sylleptic				
Flower bud density	51.9%±0.02 [a]	40.2%±0.02 [ab]	40.2%±0.02 [b]	29.9%±0.02 [c]
% bloom	80.2%±0.02 [b]	80.7%±0.02 [b]	94.9%±0.02 [a]	85.6%±0.02 [b]
Proleptic/Sylleptic				
% bloom	p =0.001 [a/b]	p=0.003 [a/b]	p=0.97 [a/a]	p=0.171 [a/a]

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).

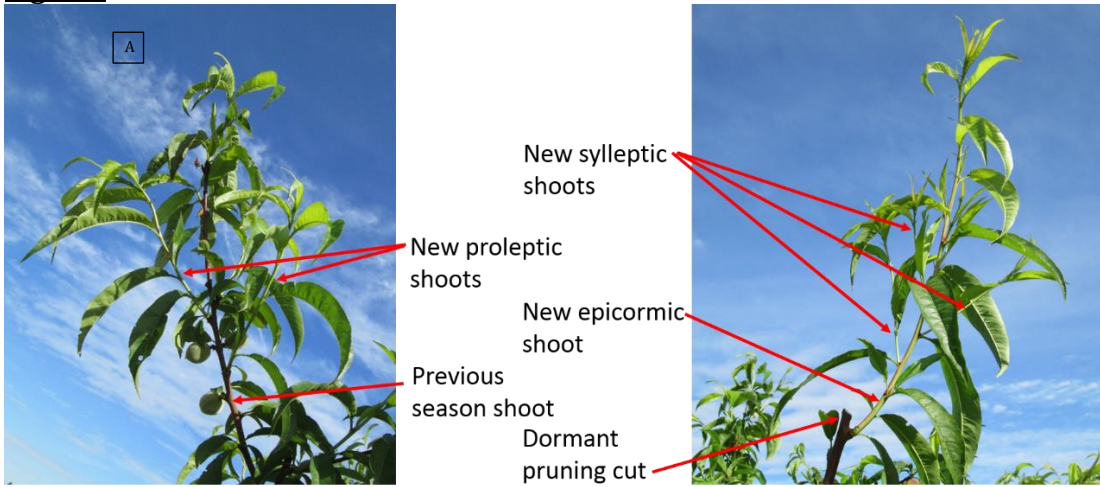495 **Figures**

496
497 Figure 1. Photographs comparing origins of proleptic shoots on a previous year shoot after a
498 period of dormancy vs sylleptic shoots borne on a rapidly growing epicormic shoot that was
499 stimulated by a dormant pruning cut. This study evaluated the flowering and fruit behavior of
500 these two types of shoots in the season following their initial development.

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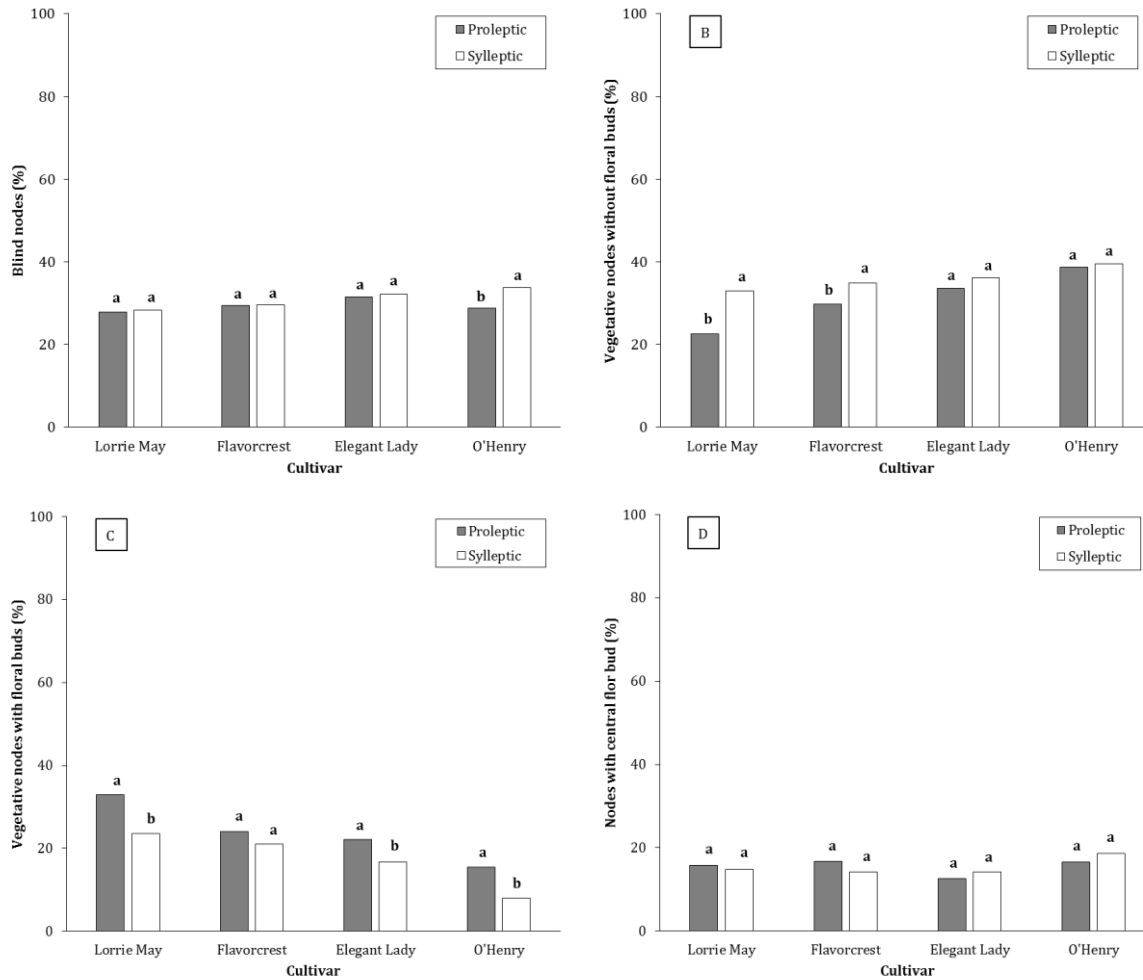
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503 Figure 2. Relative frequency (% of total nodes on a shoot) of the occurrence nodes with specific
504   lateral bud categories on proleptic and sylleptic shoots of four peach cultivars. Node
505   categories were: (A) blind (only latent buds present),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

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Initial fruit set **Final fruit set**

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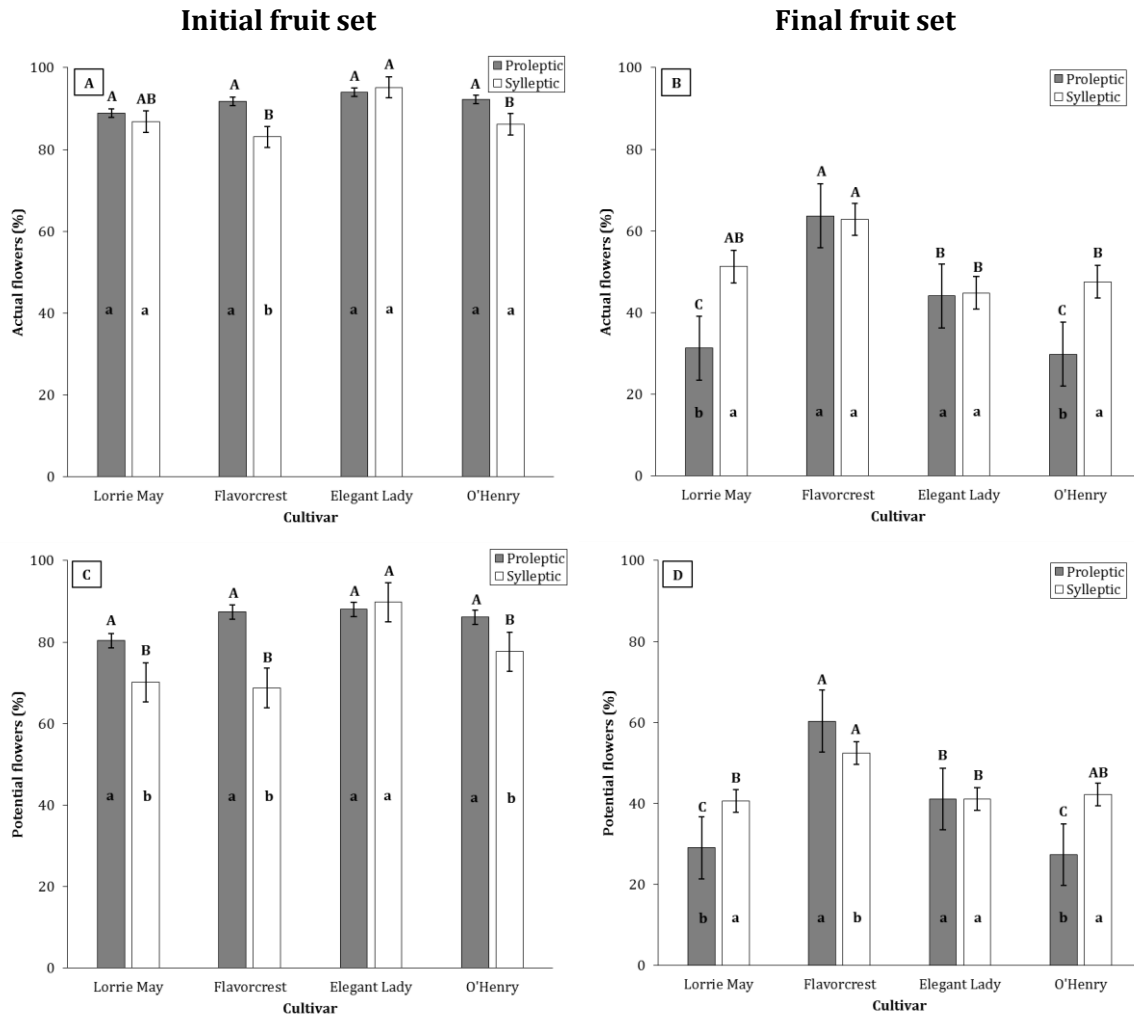
Figure 3. Mean percent fruit set prior to spring fruit drop (initial fruit set, A and C) and after spring
fruit drop (final fruit set, B and D). Percent fruit set was calculated using number of floral
buds (potential flowers) and number of flowers at full bloom (actual flowers). Capital
letters above 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.

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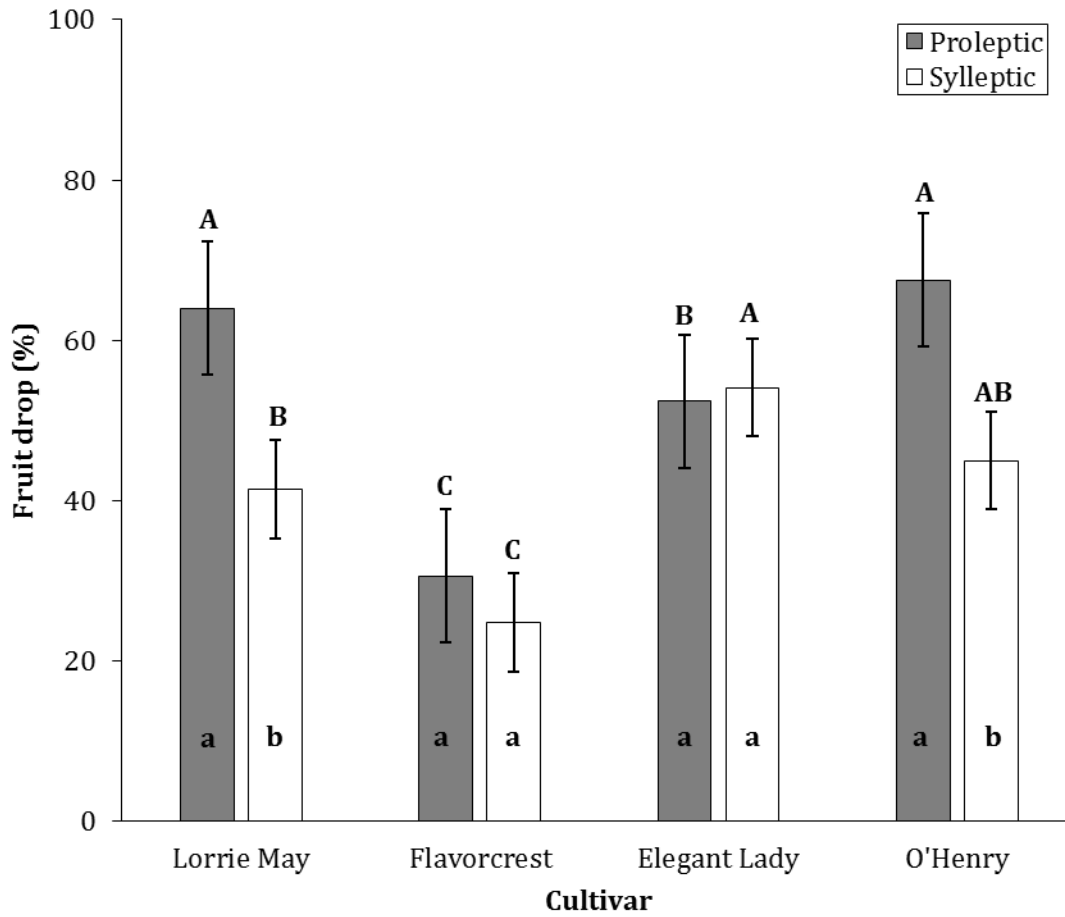
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526 Figure 4. Mean percent fruit drop across and within cultivars. Letters above bars indicate
527   differences across cultivars within that shoot type. Lower-case letters inside of bars
528   indicates differences between shoot types within a cultivar.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