

Spur Fruit Set Is Negatively Related with Current-year Spur Leaf Area in Almond

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Abstract. Almond spurs are known to be the primary bearing unit in almond tree and are subject to alternate bearing. Fruits are a strong sink in bearing spurs and can influence spur leaf growth. At the same time the percent of flowers that set fruit on a spur (spur relative fruit set) could be influenced by the competition among multiple flowers/fruits borne on the same spur as well as by limited leaf area on the same spur. The aim of the present work was to investigate the relationship between current-year spur leaf area and spur absolute and relative fruit set. Approximately 2400 spurs were tagged and followed over 6 years and data concerning spur leaf area, number of flowers per spur, and number of fruits per spur were collected. Spur leaf area was reduced in fruiting spurs in comparison with non-fruiting spurs according to the number of fruits borne by each spur. This phenomenon contributes to spur alternate bearing because spur flowering and survival in the next year are a function of the leaf area in the current year. Relative fruit set in almond appears to be negatively associated with current-year spur leaf area. Competition among fruits on the same spur did not appear to influence spur relative fruit set.

Most perennial horticultural and forest tree species exhibit large annual fluctuations in fruit production that are often referred to as alternate bearing (Kelly and Sork, 2002; Monselise and Goldschmidt, 1982). In almond (*Prunus dulcis* Mill.), alternate bearing occurs at the spur level but not at the tree level, because only a fraction of the entire tree population of spurs bears fruits in a given year (Tombesi et al., 2011); however, it is still not clear why individual spurs alternate.

Different hypotheses on alternate bearing have been postulated for tree species. One hypothesis postulates that fruit and seeds are sources of hormones that may signal developing meristems to remain vegetative and not produce flowers for the year after a heavy fruit load (Chan and Cain, 1967; Hoad, 1978; Monselise and Goldschmidt, 1982). Some authors have specifically indicated that auxins (Hoad, 1978), gibberellins (Luckwill, 1970), or abscisic acid (Tamas et al., 1979) may be involved. However, hormones produced by seeds can also increase the sink strength of fruits and are not always linked to a direct inhibitory effect on the next year's flowering (Weinbaum et al., 2001).

Another hypothesis is that large fruit loads deplete carbohydrate and/or nutrient resources

that ultimately influence the development of floral buds. Kernels of pecans and pistachios are major assimilate sinks during the ripening process (Davis and Sparks, 1974; Spann et al., 2008) and depletion of carbohydrates (Rosecrance et al., 1998; Spann et al., 2008) and nutrients (Brown et al., 1995; Reidel et al., 2001) during the kernel fill period in nut crop species can negatively influence flower bud initiation, especially if kernel fill occurs simultaneously with the period of floral initiation. Floral initiation is reported to be strongly influenced by carbohydrate availability (Harley et al., 1942; Monselise and Goldschmidt, 1982; Reig et al., 2006).

In almond spurs (the main fruit bearing unit in almond trees), flower induction is related to the spur leaf area in the previous year and fruit bearing decreases the probability that a spur can bear flowers in the next year in comparison with spurs with similar leaf area that did not bear fruits in the previous year (Lampinen et al., 2011). Thus, fruit bearing appears to increase the amount of spur leaf area needed for flower induction, probably through depletion of carbohydrate reserves or through inhibition by fruit-associated hormones. Many studies have reported competition between reproductive activity and vegetative growth (i.e., shoot growth and/or leaf growth) when available resources are limited (Hasegawa et al., 2003; Kawamura and Takeda, 2006; Lovet Doust, 1989; Obeso, 2002; Reznik, 1985; Tuomi et al., 1983). Thus, on a spur basis, fruiting can compete not only with flower

induction, but also with leaf growth. Furthermore, considering that almond spurs have a high degree of semiautonomy for carbohydrates (Heerema, 2005) and that in many species the percent of flowers on a spur that produce fruit (spur relative fruit set) is largely influenced by spur light exposure and spur leaf area (Stephenson, 1981), relative fruit set could be limited in spurs bearing a large number of flowers. The aim of the present work was to investigate the relationship between current-year spur leaf area and spur absolute fruit set (number of nuts per spur) as well as spur relative fruit set (percent of flowers that set fruit).

Materials and Methods

A 59-ha orchard that was planted in 1996 and located in Kern County, CA, was chosen for the study. Tree spacing was 7.3 m between and 6.4 m within rows. Cultivar composition was 50% 'Nonpareil' with 25% 'Monterey' and 25% 'Wood Colony' as pollenizers [rows of 'Nonpareil' trees planted with alternating rows of the pollenizer cultivars to avoid pollen supply limitation (Dag et al., 2000)]. Spurs were tagged on 48 'Nonpareil' (blooms in mid-February and is the most cultivated almond cultivar in California) trees randomly distributed across the orchard. A total of 2400 spurs were tagged with aluminium tags in late March and early Apr. 2001. The tags were placed on young spurs spanning from the most shaded portion of the canopy (near the trunk) to the more exposed, outer canopy positions at a height of ≈ 2 to 3 m. If tags were lost they were replaced at comparable locations to the original tags during the first 4 years of the study. Results reported in this study are based on data collected over 6 years (2002–07). The dynamics of annual leaf growth, flowering, fruitfulness, and spur mortality were quantified using annual assessments of tagged spurs (for more details on tagged spur populations, see Lampinen et al., 2011). In particular, for measuring spur leaf area, the following protocol was used: an adjacent, similar spur from a nearby location (but not so near as to be a direct influence on the tagged spur) with a similar light exposure was sampled for leaf area and specific leaf area analysis in July each year from 2001 to 2006. In 2001, 2002, 2004, and 2006, the adjacent spurs were sampled on all 48 trees, but in 2003 and 2005, these samples were only taken from eight of the 48 trees. Similar spurs were selected based on number and size of leaves, leaf length (visual comparison), and number of nuts present. Sampled leaves were wrapped in moist cloth and placed in a plastic bag and kept under refrigeration until leaf areas were measured. Leaf area was assessed by taking a digital photograph (Coolpix 900; Nikon, Tokyo, Japan) of all of the leaves on each adjacent sampled spur. Leaf areas for tagged spurs that did not have adjacent spurs sampled (2003 and 2005) for leaf area measurements were estimated by developing a regression equation relating the length of the longest leaf on each spur to the leaf area of spurs (using an independent sample of 400 spurs from a range

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of locations within the canopy). Sigmascan Pro (Systat Software Inc., San Jose, CA) image analysis software was used to count the number of leaves and calculate the leaf area for each spur from digital photographs. To assess the correlation between current-year spur leaf area and spur absolute fruit set in the current year, only spurs for which leaf area data were available (5195 spurs) were used for analysis (from 2002 to 2006). To assess the correlation between current-year spur leaf area and spur relative fruit set in the current year, only spurs that bore at least one flower were considered and for which leaf area data were available; thus, data of 1920 spurs were used for analysis (from 2002 to 2006). Retagged spurs were excluded in the studied sample. Spur relative fruit set was calculated as the number of fruits borne on each spur divided per the number of flowers borne on the same spur using a sample of 4354 spurs (those that bore at least one flower excluding retagged spurs from 2002 to 2007).

Statistical analysis was carried out using SAS (SAS statistical software; SAS Institute, Cary, NC). Means were analyzed by one-way analysis of variance (ANOVA) with significance level set at 0.05. Means were then separated by Tukey's *w*-procedure at $P = 0.05$. Regressions were performed by Sigmaplot 8.0 (Systat Software Inc., San Jose, CA) and R^2 significance was assessed by ANOVA.

Results

Total spur leaf area and number of leaves per spur in the current year varied in conjunction with the number of fruits borne per spur in the current year (Fig. 1). Spur leaf area of spurs that bore one, two, three, and four fruits was decreased by 15%, 59%, 68%, and 84%, respectively, compared with spurs that bore no fruits.

Current-year spur leaf area was negatively related to spur relative fruit set ($R^2 = 0.57$, $P < 0.001$) (Fig. 2). Relative fruit set varied significantly among years ($P < 0.001$) but did not vary among spurs bearing different numbers of flowers ($P > 0.05$) (Fig. 3). Relative fruit set variation among years was between 18.4% in 2005 and 35.9% in 2004. In 2003, 2004, 2005, and 2007 spur relative fruit set per spur appeared to be independent of the number of flowers borne by each spur; there was no statistical difference between the mean spur relative fruit set on spurs bearing variable numbers of flowers (Tukey test $P > 0.05$). However, in 2002, spurs bearing five flowers had significantly ($P < 0.05$) lower relative fruit set than spurs bearing fewer numbers of flowers and in 2006, spurs with three flowers had the lowest relative fruit set.

Discussion

Developing fruits are strong resource sinks. In almond spurs, fruit bearing can be associated with spur death in the subsequent year (Lampinen et al., 2011). In this study, fruit bearing decreased spur leaf area and number of leaves per spur in the same year (Fig. 1).

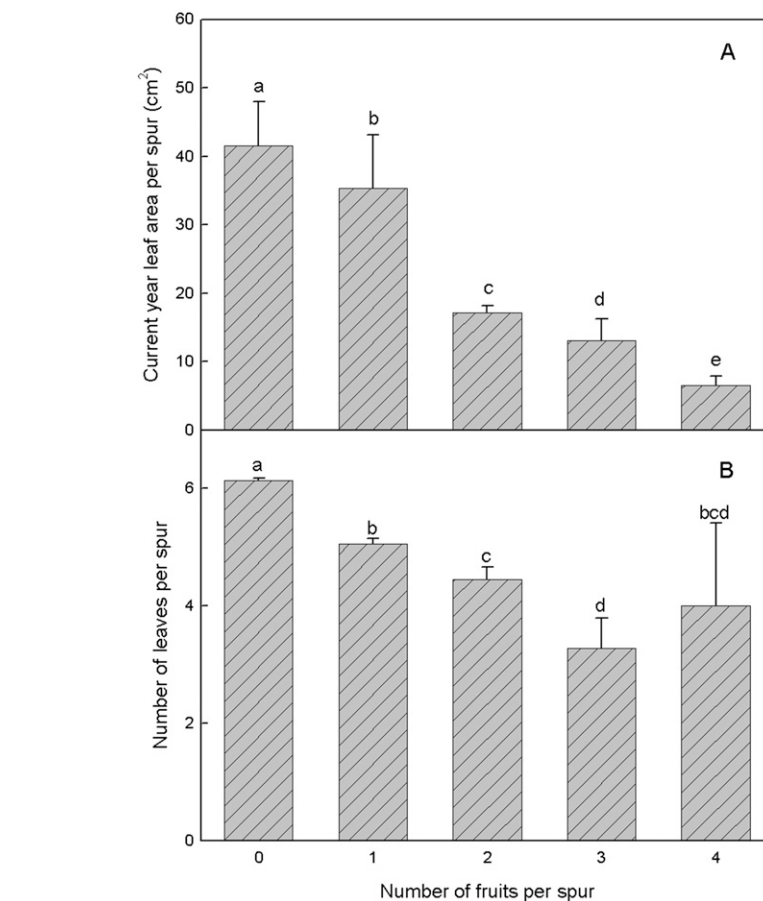


Fig. 1. Mean spur leaf area (cm²) (A) and number of leaves per spur (B) in flowering spurs with zero, one, two, three, and four fruits from 2002 to 2006. Error bars represent SE (0 fruit $n = 4424$; 1 fruit $n = 580$; 2 fruits $n = 158$; 3 fruits $n = 25$; 4 fruits $n = 8$). Bars with different letters are different at $P < 0.05$ (Tukey's test).

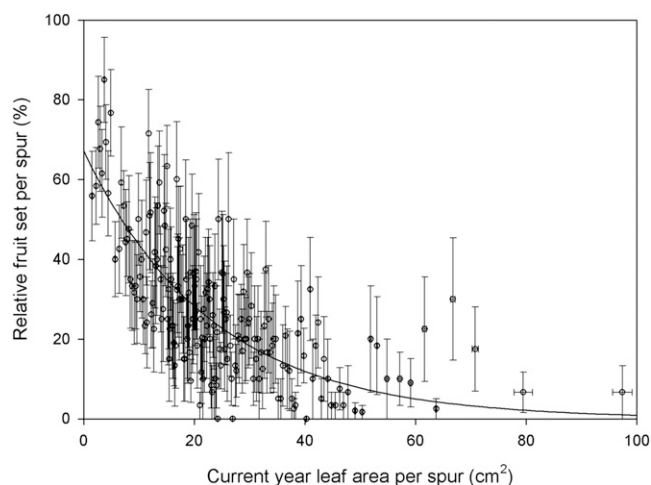


Fig. 2. Relationship between mean spur relative fruit set (%) and spur leaf area in the current year (cm²) ($R^2 = 0.57$, $P < 0.001$). Each value is the mean of 10 spurs grouped by class of leaf area from 2002 to 2006. Error bars represent \pm SE.

These data are consistent with those reviewed by Obeso (2002) on other tree species in which seed bearing decreased organ survival and/or vegetative growth. In horticultural tree species, the competition of vegetative growth with fruits is a well-known phenomenon (Minchin et al., 2010; Pavel and DeJong,

1993), but from a horticultural point of view, attention is often focused on the detrimental effects of vegetative growth on fruit development (Lopez and DeJong, 2007; McFadyen et al., 2011). Our results indicate that in fruit-bearing spurs, fruits not only interfere with flower induction processes to decrease

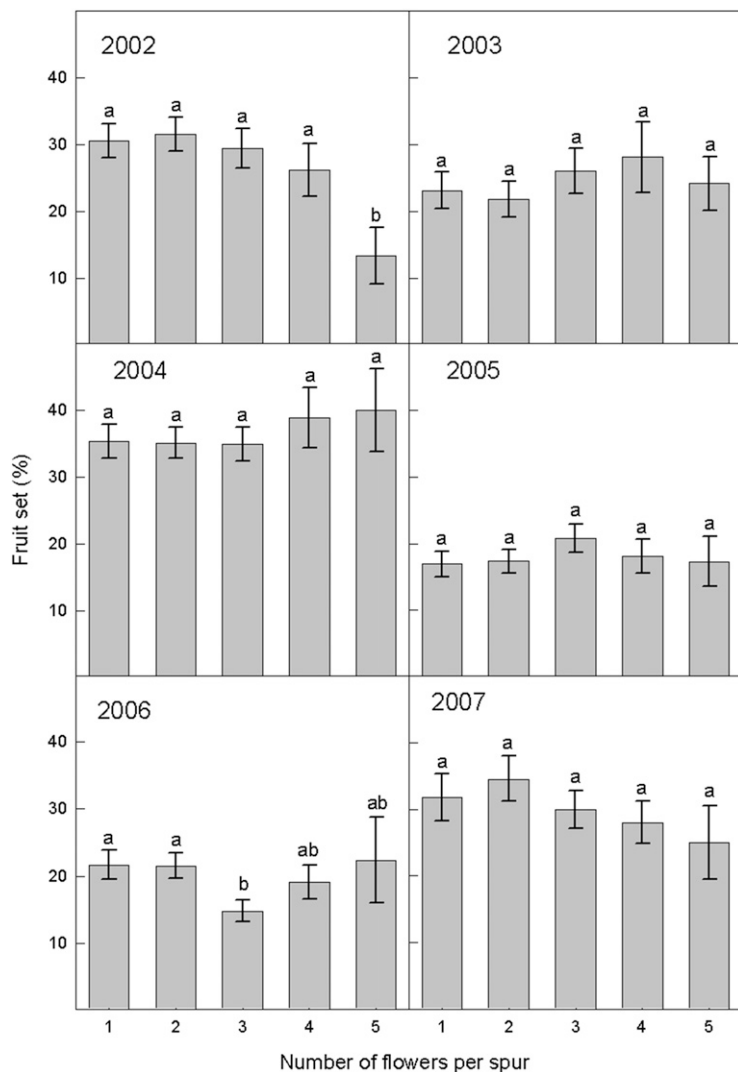


Fig. 3. Mean relative fruit set in spurs bearing one, two, three, four, and five flowers from 2002 to 2007 \pm SE. Bars with different letters are different at $P < 0.05$ (Tukey's test).

spur flowering in the next year (Lampinen et al., 2011) and also compete with leaf development on the same spur in the same year. This competition may ultimately reduce probability of survival and return bloom because both return bloom and spur survival are linked to previous-year leaf area (Lampinen et al., 2011). An alternative explanation could be that one or more bioregulators produced by developing fruit are inhibitory to floral processes occurring in axillary buds and therefore result in no flowering the next year but are stimulatory to developmental processes associated with the vegetative state. However, the negative correlation between spur fruit number and spur leaf number and/or spur leaf area support the carbon limitation hypothesis. In this experiment, vegetative activity of fruiting spurs was decreased in comparison with non-fruiting spurs.

In other tree crops, fruit set is related to light exposure and current-year leaf area. In apple, spur fruit set is positively related to the number of leaves per spur (Proctor and Palmer, 1991) and light availability during the young fruitlet stage (Byers et al., 1991; Corelli Grappadelli et al., 1994). This implies that

apple spur fruit set is dependent on current-season carbon assimilation of adjacent spur leaves (Proctor and Palmer, 1991; Wünsche et al., 1996). A similar relationship has been reported in citrus (Iglesias et al., 2003). Thus, it may seem reasonable that in almond, spur leaf area in the current year would be positively correlated with spur fruit set in the same year. However, in our experiment with almond, there was a negative relationship between spur leaf area and fruit set in the current year.

An explanation for these contrasting behaviors likely resides in differences in the phenological development of the various species. With citrus (an evergreen species), flowers are borne on new shoots produced before flowering and new leaves are already present and functioning when flowers open (Iglesias et al., 2003). Similarly, apple flowers are borne terminally on spurs that grow vegetatively and functional leaves are produced before the time when flowers open (Fleckinger, 1948). With almond, flower buds are produced laterally on shoots or spurs, and the flower buds open before the production of new leaves borne on new terminal or lateral extensions of the shoot or spur (Felipe, 1977; Kester et al., 1996).

Therefore, with both citrus and apple, substantial new functional leaf area is present on the bearing unit before flowering, but, with almond, new functional leaf area develops after flowering. Furthermore, with both apple and citrus, flower buds and fruits grow on the current season's vegetative growth and currently active leaves either subtend (apple) or alternate with the flowers on the same axis (citrus). With almond spurs, flowers are borne laterally on previous-season growth and new leaves are produced on new terminal growth of the spur (Felipe, 1977). Thus, newly active leaves are distal rather than proximal (or in alternating positions) with the flowers and fruit.

These developmental differences between species may not only relate to their apparent differences in behavior with regard to spur leaf area and fruit set, but they are probably involved in the apparent competition between the number of fruits per spur and spur leaf area (Fig. 1). Because almond flower pollination occurs before significant leaf development, and fruits are attached in a proximal position relative to new leaves appearing on new growth at the distal end of spurs, the flowers and developing fruitlets probably have greater access to recently mobilized carbohydrates moving up from the lower parts of the tree during spring (Oliveira and Priestley, 1988). This may also involve earlier development of vascular tissue into flowers and fruitlets compared with new leaves as well as positional differences between the two types of organs (Westwood et al., 1967).

In apple, flower thinning has been reported to cause increases in relative fruit set (Martin et al., 1961; Quinlan and Preston, 1968). Similar results have been reported in almond (Socias I Company et al., 2004). However, in our experiments, relative fruit set per spur was negatively correlated with current-year spur leaf area (Fig. 2) and relative fruit set per spur was not correlated with the number of flowers borne on each spur (Fig. 3). These data suggest that very little competition for fruit set occurred among flowers borne on the same spur. These data are consistent with those reported by Kester and Griggs (1959) who described an overall decrease of absolute fruit set in response to deblossoming practices. Thus, spur alternate bearing appears to be primarily explained by the combined effects of the reduction of spur leaf area caused by fruit bearing and the fact that high rates of flowering and fruiting only occur on spurs with large amounts of leaf area per spur in the previous year (Lampinen et al., 2011). Thus, reduced leaf area in the bearing year is apparently not sufficient to support bud flower induction and contemporary fruit bearing. Finally, relative fruit set in almond did not appear to be influenced by current-year spur leaf area or by competition among fruits on the same spur. However, these results cannot rule out a possible contribution of bioregulators to the inhibition of next year's flowering.

In conclusion, this research provides additional insight into the nature of spur semiautonomy in fruit bearing in tree species

like almond. Although there is ample evidence that spurs function in a semiautonomous manner with respect to the potential of leaves of individual spurs to function as a source for carbohydrates affecting development of the next year's flower buds in the summer and fall (Heerema, 2005; Lampinen et al., 2011; Tombesi et al., 2011), the present research indicates that almond spurs are not semiautonomous with respect to supplying ample carbohydrates to support both fruit set and new leaf development in the spring. This behavior is clearly different from what has been reported for apple (Lauri et al., 1996; Proctor and Palmer, 1991) and citrus (Iglesias et al., 2003; Mehouchi et al., 2000). This study highlights the need to understand the importance of bearing habit and developmental details involving the proximity and timing of various organs on spurs when trying to understand how they function. It also provides greater insight into the relationship between fruit and foliage of alternate-bearing almond spurs. However, future studies on the relative importance of "competition" and "inhibition" are needed to further clarify spur alternate bearing in almond.

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