

Spur dynamics: the key to understanding cropping in almond trees

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Abstract

The majority of the crop in mature almond (*Prunus dulcis*) orchards is borne on short, proleptic shoots called spurs. Spur dynamics were studied in commercial almond orchards in two experiments; in 1995-1998 and again in 2001-2006. In the first experiment 2185 spurs were initially tagged and in the second experiment 2400 spurs were tagged and followed for the duration of the experiments. The first experiment involved trees in three different late season water stress treatments and in the second experiment the tagged spurs were on trees in four irrigation/nutrient regime treatments. The primary lessons learned from both experiments involved insights into the dynamics of individual and collective spur behaviors over multiple years. In both studies less than 20% of the tagged spurs bore fruit in a given year and significant numbers of spurs died each year (5-27%) after the trees reached full productive maturity. On average, fewer than 10% of the spurs flowered in two sequential years. Spur productivity and mortality in a given year was positively and negatively correlated with previous year spur leaf area, respectively. Spur fruiting tended to increase chances of subsequent spur death. Both decreased subsequent year flowering and increased chances of spur death after fruiting appeared to be linked to a negative effect of spur fruiting on the development of leaf area of fruiting spurs. Decreased leaf area on fruiting spurs appeared to be caused by competition for resources between simultaneously developing fruit and vegetative growth (leaves) shortly after bud-break in spring. This was exacerbated in almonds because flowers came out prior to vegetative growth and developing fruit subtended spur extension and leaf growth. Alternate bearing was apparently not a major problem at the whole tree or orchard level in highly productive orchards, in spite of strong tendencies for alternate bearing among individual spurs, because of an overall spur population dynamic in which a majority of spurs do not bear fruit in any given year and thus accumulate critical amounts of leaf area and are available to flower and set fruit in subsequent years. Interestingly, spur death and turnover was greater in the orchard treatments that received more water and nutrients, presumably because of increased internal canopy shading. Based on this research it is clear that successful management of almond orchards should be focused on maintenance of dynamic populations of healthy spurs. It appears inevitable that a significant percentage of spurs die each year and thus growers must insure that modest amounts of vegetative shoot growth occur each year to provide renewal sites for new spurs to replace dead spurs but excessive growth can increase the rate of spur death by the promotion of internal canopy shading. Thus, it appears that excesses should be avoided in almond orchards as in life.

Keywords: flowering, fruit set, spur mortality, alternate bearing, *Prunus dulcis*

INTRODUCTION

Spurs are the main fruit-bearing shoot type in mature almond trees (Kester et al., 1996) and understanding the factors and processes that influence spur productivity (flowering and fruit set), spur longevity and mortality is the key to understanding cropping potential and behavior in mature almond orchards. Spurs are short proleptic shoots that are produced laterally on longer almond shoots and initially grow vegetatively and after



1 or 2 years produce lateral solitary flower buds that can bear fruit.

In perennial species there is substantial evidence that the carbohydrate balance of each shoot is influenced by sources and sinks located within the same shoot (Yamamoto, 2001; Hasegawa et al., 2003; Marsal et al., 2003; Hoch, 2005). Differences in carbohydrate availability among spurs have been reported in apple (Johnson and Lakso, 1986a, b) and, in some species, shoots appear to function as semi-autonomous organs (Watson and Casper, 1984; Sprugel et al., 1991). Heerema (2005) has asserted that this is also the case with almond spurs.

Prior reports stated that almond spurs generally remain viable for 3-5 years (Weinbaum and Spiegel-Roy, 1985) but there was little data available on the rate of individual spur mortality or the factors that led to spur death. Factors that determine the spur longevity are important for understanding the processes that influence cropping in almond orchards and can inform optimization of orchard management for sustained productivity.

It is known that fruit bearing can create a strong demand for carbohydrate in perennial fruit species (Marquard, 1987) and can affect following year flowering (Jackson and Palmer, 1977a, b). Thus, previous year bearing seems to play a central role in fruit bearing at the spur level in many species but quantitative data on this phenomenon was previously not available for almond.

Spur light exposure varies depending on the position within the canopy and influences leaf thickness and nitrogen content (DeJong and Doyle, 1985; Weinbaum et al., 1989; Kull and Niinemets, 1993; Rosati et al., 2000). Nitrogen content per leaf area of exposed leaves is higher than in shaded leaves while nitrogen per unit mass is relatively stable because of the increased leaf mass of exposed leaves (Rosati et al., 2000). Modification of the light environment during the season results in an apparent reallocation of N from shaded leaves to more sunlit leaves and this may help to maintain high levels of canopy photosynthesis (DeJong and Doyle, 1985; DeJong et al., 1989; Rosati et al., 1999). Since leaf thickness reflects the light environment of leaves within a tree canopy, leaf area per unit mass and/or leaf nitrogen per unit leaf area measurements reflect natural integrated light exposure of leaves or spurs in orchard canopies (DeJong and Doyle, 1985; Rosati et al., 2000). Klein et al. (1991) used these measurements to study the influence of shading on spur viability and bearing in walnut tree canopies. Similarly, in almond the number of floral buds on a spur has been reported to be related to the spur leaf area (Polito et al., 2002). Furthermore, Heerema et al. (2008) found that winter survival and return bloom of almond spurs were related to both spur specific leaf area and spur leaf area. Based on these results, Heerema et al. (2008) asserted that spurs have a high degree of carbon autonomy and that spur survival and return bloom are closely related to the spur carbon economy. However, these almond studies focused on limited spur populations from contrasting sunlit and shaded portions of the canopy and only followed the spurs for 2 years.

Spur dynamics (flowering, fruit set, productivity, longevity and mortality in association with spur bearing, spur leaf area and leaf N content of large populations of individual spurs) were studied in two experiments. A preliminary spur dynamics experiment involved following large populations of spurs in mature almond trees over three years and was part of a larger study involving multiple-year effects of water stress treatments on almond tree productivity. The primary lessons from the spur dynamics part of that study were that only 20-25% of spurs produced fruit in any given year and more than 60% of tagged spurs died after 3 years (Esparza et al., 2001a, b).

A second, larger spur dynamics experiment was initiated in 2001 with the express objectives of determining (a) mean spur longevity and factors related to spur mortality; (b) how spur leaf characteristics that may reflect relative light exposure and carbohydrate balance (leaf area, specific leaf area) influence spur survival and cropping potential; and (c) how bearing fruit one year influences spur viability and cropping potential the following year (Lampinen et al., 2011).

The goal of this paper is to review the findings of both studies related to spur productivity and spur population dynamics to provide a comprehensive understanding of

almond spur behavior and its implications for orchard management practices.

MATERIALS AND METHODS

The preliminary experiment was initiated during summer 1995, in an almond (*Prunus dulcis* grafted on *Prunus persica* L. Batsch 'Nemaguard' rootstock) orchard in the southern San Joaquin Valley at the Paramount Farming Company, Shafter, CA (35°N, 117°E). The experiment was initiated in a 7-year-old, high-yielding orchard. The almond cultivars included rows of 'Nonpareil' (50%), planted alternately with pollinizer rows of 'Monterey' (25%) and 'Price' (25%). Monitored yield determinants included flowering, fruit set, and mortality of individually tagged spurs. On July 27, 1995, 15-20 individual successive spurs along each of 8 branches (4 branches tree⁻¹) per irrigation replicate (total of 2185 spurs) were selected. On each branch, every fifth spur was tagged to facilitate record keeping. Tagged spurs were distributed evenly among the irrigation treatments. Fruiting status and number of fruits per spur were recorded in 1995, before the initiation of the irrigation treatments. Flower counts on individually tagged spurs were made a few days before bloom in February of 1996, 1997 and 1998. Final fruit set was recorded after fruitlet drop each year during the first week of May (Kester and Griggs, 1959).

The main spur dynamics study was done in a 59-ha orchard, planted in 1996, at 7.3 m between and 6.4 m within rows. The orchard planting was rows of 'Nonpareil' (50%) alternating with pollinizer rows of 'Monterey' (25%), and 'Wood Colony' (25%). The orchard was divided into 6, equal-sized replicate blocks and 50 spurs were tagged on 8 'Nonpareil' trees within each of the 6 blocks. A total of 2400 spurs were tagged in late March and early April 2001. Twelve spurs were selected on each of the north-east and north-west quadrants of individual trees and 13 spurs were selected on each of the south-east and south-west quadrants of the same trees. Tagged spurs were located at positions ranging from shaded (near the trunk) to exposed (on the periphery) portions of the canopy at a height of ~1-3.5 m. During the first 4 years of the study, lost tags or dead spurs were replaced with spurs in close proximity with similar light exposure to the original tagged spurs.

The dynamics of annual growth, flowering, fruitfulness and spur mortality were quantified annually. The number of fruit and leaves per tagged spur were counted and the number of large and small leaves per spur noted. The length of the longest leaf on each tagged spur was also measured. 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. (For additional sampling details see Lampinen et al. 2011)

RESULTS

The results for the spur dynamics aspects of the preliminary study have been reported by Esparza et al. (2001a) and the other aspects of that study were reported by Klein et al. (2001) and Esparza et al. (2001b). The primary lessons from the spur dynamics part of that study were that 40-60% of the tagged spurs flowered in any given years and flowering was more effected by year than by water stress treatment and only 20-25% of spurs produced fruit in any given year. In addition, approximately 20% of tagged spurs died the first year followed by an additional 25% the next year and approximately 15% the next year so that more than 60% died after 3 years (Esparza et al., 2001). Perhaps the most important result of this study was an increased awareness of the importance of spur dynamics in understanding cropping dynamics in mature almond orchards and the need for understanding factors that determine spur flowering, fruit set, longevity and mortality.

The fundamental aspects of almond spur dynamics (year to year spur survival/mortality and spur flowering as a function of previous year leaf area (PYLA) per spur were established in a paper by Lampinen et al. (2011). This paper established that both spur flowering and survival were strongly associated with PYLA and previous year fruitfulness. A substantial portion of the spur population had a leaf area of less than 20 cm² and these spurs had a less than 60% likelihood of survival to the next year if they bore a fruit

whereas spurs that had a leaf area of $>20 \text{ cm}^2$ and did not bear fruit had a $>90\%$ likelihood of survival. Flowering was clearly related to PYLA and spurs with $<40 \text{ cm}^2$ PYLA were much less likely to produce flowers, and spurs with higher PYLA were more likely to produce multiple flowers. Return bloom on spurs that bore fruit the previous year was 11% or less in all but one year of the study. Per cent spur mortality was less than reported in the preliminary during the first three years of the study (5-9%) but was similar to the previous study in the last three years of the study (20-27%) and was apparently related to tree age and overall canopy size relative to the allotted space for the trees.

A follow-up paper from the same spur dynamics study analyzed spur dynamics in association with the potential for alternate bearing in almond (Tombesi et al., 2011). Almond is not thought to be a severe alternate bearing species but there have been reports of tendencies for lighter crops following years of heavy bearing in some years. This paper answers the question as to why almond orchards are not strongly alternate bearing even though almond spurs tend not to bear fruit and flower in sequential years. The minor tendency of almond toward alternate bearing can apparently be explained by the fact that only a relatively small percentage of the total tagged spur population bore fruit in any given year and therefore while individual fruiting spurs exhibited a high level of non-bearing after fruiting the previous year, the spurs that did produce fruit in any year generally did not constitute enough of the total spur population to exhibit alternate bearing at the whole population level. Our results suggest that annual bearing fluctuations in almond are probably mainly due to year-to-year variations of parameters affecting fruit set and that high rates of fruit set in a given year may involve a larger-than-normal percentage of a spur population in fruit bearing. This would limit the size of the spur population available for flowering in the subsequent year and could cause and tendency toward heavy crop years followed by lighter crop years or especially a lighter crop year after two heavy crop years. However, in general, almond should not be considered to be a strongly alternate-bearing species.

A third paper closed the circle on providing an understanding of why almond spurs have a strong tendency toward non-sequential bearing in consecutive years (Tombesi et al., 2015). This analysis focused on the relationships between spur fruit bearing and spur leaf area in the same year. The study showed that spur leaf area was reduced in fruiting spurs in comparison with non-fruiting spurs according to the number of fruits borne by each spur, i.e., more fruits per spur led to less spur leaf area. This phenomenon apparently contributes to non-sequential year bearing because spur flowering and survival in the next year are a function of the leaf area in the current year. Current-year spur leaf area appeared to be negatively associated with relative fruit set but competition among fruits on the same spur did not appear to influence spur relative fruit set.

A final paper analyzed the relative importance of the number of flowers per tree vs. relative fruit set in almond trees (Tombesi et al., 2016). Previous aspects of the spur dynamics study emphasized the factors that influence spur flowering and mortality and spur numbers, however, the total number of flowering spurs on a tree may be of limited significance if greater relative fruit set of the flowers can compensate for decreased flower numbers in the orchard. Thus, understanding the relative impact of flower number and relative fruit set on almond tree yield is essential for understanding the key factors controlling almond tree productivity. In addition to collecting all the spur population and behavior data kernel yield of the individual trees with tagged spurs and the kernel yield of the orchard containing those trees were also recorded for 6 years (2002-2007).

The number of nuts borne by individual trees was significantly correlated with the number of nuts borne by the tagged spur populations in those trees. Thus the spur sample was relatively representative of the spur population of the trees. Whole tree yield was not correlated with mean relative fruit set measured on tree spur populations. Instead, tree yields were more closely correlated with flower density on the tagged spur population. Thus, while relative fruit set is obviously important, it was not the primary yield limiting factor in this orchard and increased relative fruit set when floral densities were low did not compensate for lower numbers of flowers. There were significant correlations between spur

flower density and tree yield over years; for individual years, the relationship was significant in 4 of the 6 years of our experiment. On the other hand, the relationships between tree relative fruit set and tree yield were not significant in any of the 6 years of the experiment.

DISCUSSION

These spur dynamics studies provide insights into the dynamic behavior of almond spurs; the factors that determine their productivity, longevity and mortality and their importance to overall tree and orchard productivity. Spur survival and productivity in a given year is clearly a function of spur leaf area the previous year (Lampinen et al., 2011) while spur leaf area in the year that a spur bears fruit is reduced by the apparent competition between the growing fruit and leaf growth (Tombesi et al., 2015). The reduced leaf area of fruiting spurs dramatically decreases the likelihood of the spur flowering the following year so previously bearing spurs either “rest” or die the subsequent year (Lampinen et al., 2011), likely depending on the light exposure during that year. Previous research in several species has shown that specific leaf area (an indicator of leaf thickness) is strongly related to leaf light exposure (DeJong and Doyle, 1985; Rosati et al., 2000) and can be used as a proxy for indicating leaf light exposure in tree canopies. In the spur dynamics study, spur leaf area of non-bearing spurs was strongly correlated with specific leaf area (Figure 1). This provides key evidence for the importance of spur light exposure in determining the life history and bearing cycle of individual spurs.

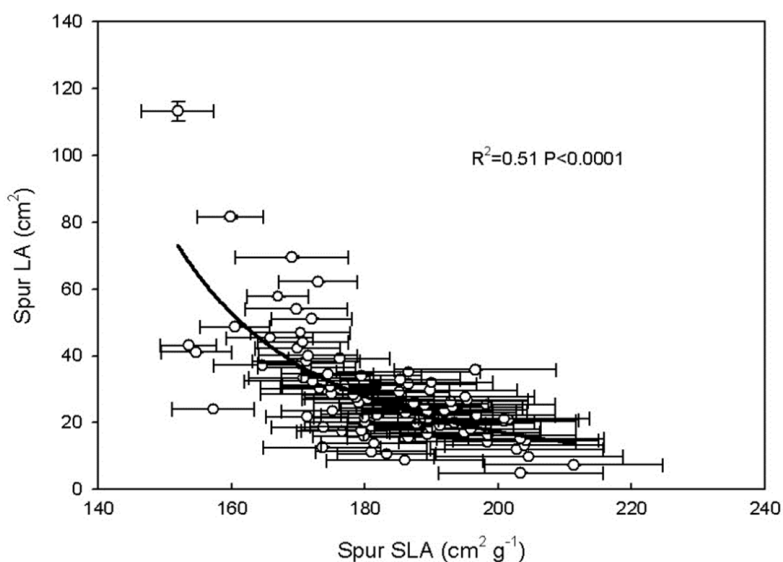


Figure 1. The relationship between individual spur leaf area and the specific leaf area of leaves on individual spurs for spurs measured over the 6 years of the spur dynamics study. Each circle is the mean of 88 spurs with the horizontal lines showing the standard deviation around those points.

A conceptual model of the life history and bearing cycle of almond spurs is summarized in Figure 2. A large, mature, bearing almond tree has a large population of active spurs (as many as 100,000). The majority of these spurs are >2 years old but there are some new spurs that are just beginning to produce flowers. The new spurs and the spurs that are in the more sun-lit positions in the canopy that had >20 cm² of leaf area and are capable of flowering. Less than 40% of those spurs that flowered will produce fruit and those that don't produce can be viewed as being part of a resting population that may or may not flower the next year, depending on their light exposure and subsequent leaf area development. Spurs that produce fruit in the current year will likely develop small leaves and not bear fruit the subsequent year and those in shaded positions in that year will likely die.

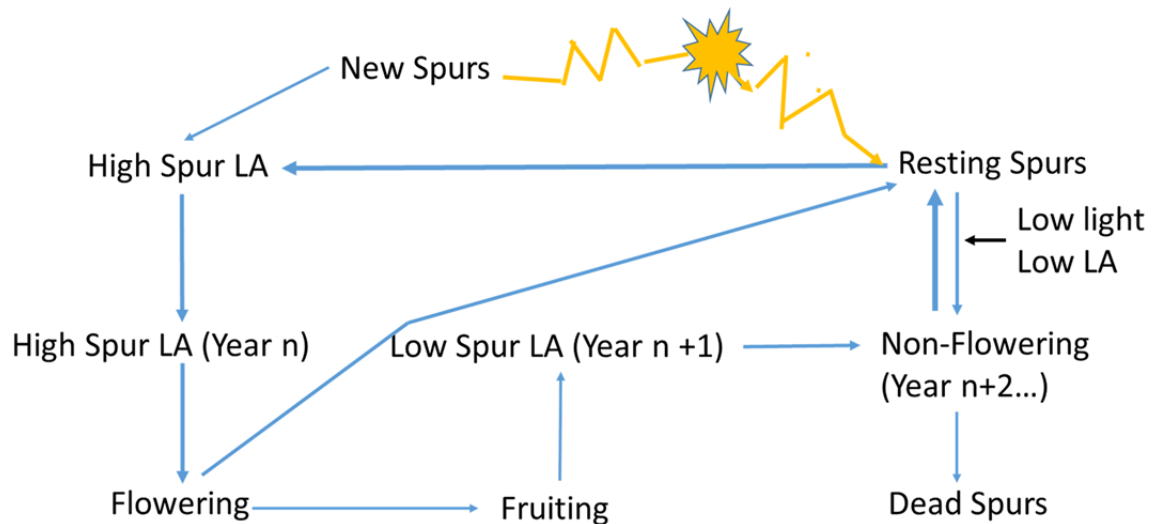


Figure 2. A schematic conceptual model of the life history and bearing cycle of almond spurs. Each tree has a large population of spurs, many of which are non-bearing (resting) and some of those develop large enough leaf area (in the presence of adequate light to develop flower buds for the subsequent year). Those spurs flower the subsequent year and a portion of those also produce fruit. If they don't produce fruit they are part of the resting population that may flower the following year if conditions are right. If they do produce fruit they will have reduced leaf area the following year and likely will not flower the next year and the most shaded ones die in subsequent years. Some spur death occurs in most years and the new replacement spurs must be continually added to the total population to maintain production.

Since spur productivity appears to be highly dependent on spur light exposure and there is a finite amount of light available in any given orchard, this model of the bearing cycle of spurs helps explain the strong dependence to sustained almond yields on orchard canopy light exposure that has been reported by Lampinen et al. (2012). Spurs require leaf area which is developed in exposed areas of the canopy to be fruitful, in addition to the direct requirement of light-dependent production of photosynthates for supplying carbohydrates required to grow fruit. Field experience has indicated that high water and nutrient supplies to trees can provide short term gains in almond productivity but not high sustained productivity over multiple years. This is apparently due to the fact that high levels of irrigation and nutrient supplies tend to create more shade within almond tree canopies, thus increasing the shaded spur population and hastening spur death. On the other, hand lack of water and nutrients, in addition to directly affecting fruit growth, can reduce shoot growth and thus lead to inadequate production of new shoots to provide locations for new spurs to replace the proportion of spurs that inevitably die in any given year. This suggests that after a canopy has reached a desired level of canopy cover, it is probably best to moderate water and nitrogen applications.

Analysis of almond tree productivity through the lens of studying spur population dynamics has provided useful insights into understanding factors controlling sustained productivity of almond orchards. These insights have provided answers as to why almond orchards are not strongly alternate bearing while individual spurs rarely fruit in consecutive years. They also provide greater understanding of the limits to achieving high sustained productivity by simply increasing management inputs. The importance of new shoot growth for the maintenance of healthy spur populations and sustained productivity have also been clarified. It may be interesting to conduct similar studies on other types of fruit tree species to gain a broader understanding of the diversity of spur (or functional bearing unit) dynamics strategies employed by other fruit and nut tree crops.

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