Research paper

Spur behaviour in almond trees: relationships between previous year spur leaf area, fruit bearing and mortality

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In mature almond (*Prunus dulcis*) orchards, the majority of crop is borne on spurs (short, proleptic shoots) that can live for several years and can produce from one to five fruits. Previous research has led to the hypothesis that spur longevity is related to spur light exposure, cropping and age. However, limited quantitative data are available to substantiate these hypotheses. The objective of this study was to determine spur characteristics that were most highly correlated with spur productivity and longevity in mature, bearing almond trees. Previous year spur leaf area was strongly related to spur viability and flowering; the greater the leaf area in the previous year, the higher the probability of spur survival into the next year and the higher the probability for the spur to bear one or more flowers. Previous year bearing also appeared to influence viability and return bloom, especially in spurs with low leaf area. These results suggest that spur source–sink balance is basic to the life cycle of almond spurs. Furthermore, the results are consistent with the hypothesis that spurs are semi-autonomous organs with respect to carbohydrate balance for much of the growing season. Finally, this information provides general thresholds for maintaining spur viability and productivity that will be useful for developing and evaluating tree training systems and orchard management practices.

Keywords: leaf area, specific leaf area, spur dynamics, spur mortality, spur productivity.

Introduction

Almond (*Prunus dulcis* [Mill.] DA Webb) is the most important fruit tree crop in California with more than 300,000 ha under cultivation (Tombesi et al. 2010). Almond yields depend on fruit number and kernel weight. Kernel weight is influenced by cultivar and factors such as irrigation management and total yield (Hill et al. 1987, Goldhamer and Viveros 2000). However, fruit number is the most important parameter that determines yield. Spurs are the main fruit-bearing shoot type in mature almond trees (Kester et al. 1996) and they generally remain viable for 3–5 years (Weinbaum and Spiegel-Roy 1985). Spurs initially grow vegetatively and after 1 or 2 years bear fruit. Eventually spurs weaken and die (Krueger et al. 1996). Esparza et al. (2001) reported that 66% of spurs die after 3 years. Factors that determine the number of spurs, their productivity

and longevity are therefore important for understanding the processes that influence cropping in almond orchards.

Previous year bearing seems to play a central role in bearing at the spur level. Fruit bearing can create a strong demand for carbohydrates in perennial fruit species (Marquard 1987) and can affect following year flowering (Jackson and Palmer 1977a, 1977b). Differences in carbohydrate availability among spurs have been reported in apple (Johnson and Lakso 1986a, 1986b) and, in some species, shoots appear to function as semi-autonomous organs (Watson and Casper 1984, Sprugel et al. 1991, Allen and Antos 1993, Heerema 2005). In perennial species there is substantial evidence that the carbohydrate balance of each shoot is influenced by sources and sinks located in the same shoot (Ruohomäki et al. 1997, Obeso 1998, Henriksson 2001, Yamamoto 2001, Hasegawa et al. 2003, Marsal et al. 2003, Hoch 2005).

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. (1991a) 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.

The objective of this study was to follow the behaviour of a large number of spurs, distributed throughout tree canopies, over multiple years to test the hypotheses presented by Polito et al. (2002) and Heerema et al. (2008). Specifically, the goal was to provide more information regarding factors influencing spur survival and cropping in almond and how they are integrated with the physiology of the tree. The aim of this work was to determine (i) mean spur longevity and factors related to spur mortality; (ii) 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 (iii) how bearing fruit one year influences spur viability and cropping potential the following year.

Material and methods

The 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 pollenizer rows of 'Monterey' (25%), and 'Wood Colony' (25%). The orchard was divided into six, equal-sized replicate blocks and 50 spurs were tagged on eight 'Nonpareil' trees within each of the six blocks. A total of 2400 spurs were marked with aluminium tags 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.

Leaf and fruit counts

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. Almond spurs tend to have alternating large and small leaves and this characteristic was useful for selecting adjacent similar spurs as described below. The length of the longest leaf on each tagged spur was also measured.

Adjacent spur sampling for leaf area and specific leaf area

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 8 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 within 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 area for tagged spurs that did not have adjacent spurs sampled (2003 and 2005) for leaf area measurement was estimated by developing regression equations 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 of locations within the canopy). Specific leaf area for these spurs was estimated by sampling a 1 cm^2 leaf disc from the largest leaf on the tagged spur. Leaves were then dried at 70 °C (OV-490A-3, Blue M Electric, Watertown, WI, USA) for ~48 h and weighed. Sigmascan Pro (Systat Software Inc., San Jose, CA, USA) image analysis software was used to count the number of leaves and calculate the leaf area for each spur from the digital photographs. Specific leaf area (leaf area per unit dry weight) was calculated from leaf area and leaf dry weight measurements.

Return bloom assessment

The number of flowers produced on each tagged spur was counted in the spring of each year from 2002 through 2007. Multiple year records of previous year leaf area (PYLA; from an adjacent, similar spur as described earlier), previous year specific leaf area (PYSLA), previous year bearing, number of flowers in the current year and number of fruit in the current year were used to assess spur behaviour in relation to PYLA, PYLSA and previous year bearing. These analyses involved data from 6980 spurs spread over the 6 years.

Statistical analysis was carried out using linear regression (SAS statistical software, SAS Institute, Cary, NC, USA) to test the effect of each variable on viability and flowering. Relative frequencies of living/dead spurs were calculated per leaf area interval of 5 cm^2. A χ^2 test was used to test the differences in frequencies where possible. P value was set at 0.001.

Results

The number of spurs that were originally tagged in 2001 and that remained alive in successive years decreased over the 6 years of the study (Table 1). After 4 years, only 55.8% of the original tagged spurs were alive. During the first three seasons (i.e., until 2004) spurs died at an average rate of ~9% per year. After 2004, this mortality rate significantly increased ($P < 0.001$) to ~24% per year.

There was a broad range of spur PYLA and PYSLA represented in the sampled spur populations. Of the 6980 spur measurements over 6 years (Figure 1) the mean estimated PYLA was 32.4 ± 1.86 cm^2 and the median was 22.5 cm^2 with the majority of spurs having a total leaf area between 10 and 40 cm^2 (Figure 1a). Fifty-nine per cent of spurs had PYLA >20 cm^2 and 12.4% had PYLA >40 cm^2. The mean PYSLA was 199.61 ± 8.23 cm^2 g^{-1} and the median was 153.62 cm^2 g^{-1} (Figure 1b). The number of flowers that a spur produced in a given year was linearly related to PYLA but was not significantly related to PYSLA (Table 2).

The probability that a spur remained alive into the next season (number of spurs alive/total number of spurs per each PYLA interval) was correlated with the spur PYLA ($P < 0.001$)

and differed for bearing and non-bearing spurs (Figure 2a; Table 3). There was no correlation between the probable viability of non-bearing spurs and PYSLA (Figure 2b; Table 3). There were clear effects of fruit bearing on spur mortality in the following year. Bearing spurs with PYLA values <28 cm^2 were much more likely to die than non-bearing spurs with comparable leaf area (Figure 2a).

In addition to the probability of spur survival, the probability that a spur bore flowers was also correlated with spur PYLA ($P < 0.01$) (Figure 3; Table 4). The probability of flowering was
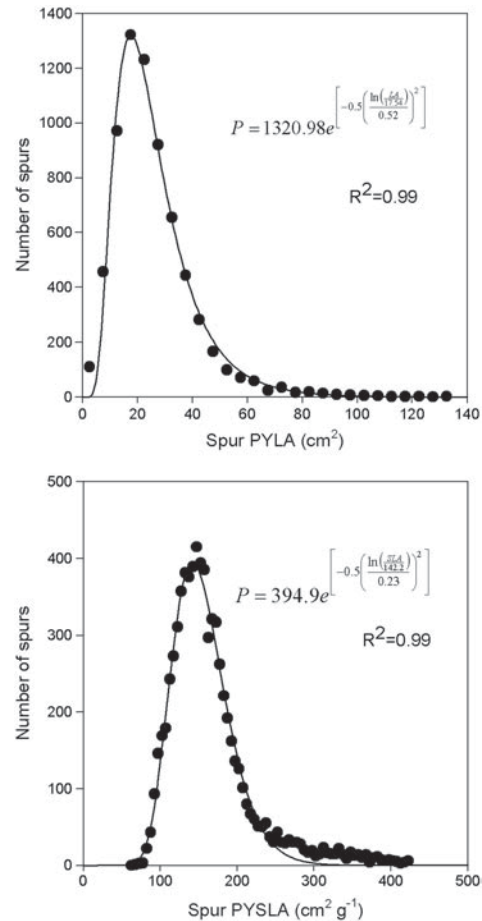

$$P = 1320.98 e^{\left[-0.5\left(\frac{\ln\left(\frac{PYLA}{17.6}\right)}{0.52}\right)^2\right]}$$

$$R^2 = 0.99$$

$$P = 394.9 e^{\left[-0.5\left(\frac{\ln\left(\frac{PYLA}{142.2}\right)}{0.23}\right)^2\right]}$$

$$R^2 = 0.99$$

Figure 1. Spur distributions with respect to their PYLA (cm^2) and PYSLA (cm^2 g^{-1}) ($n = 6890$).

Table 1. Number of living, retagged and dead almond spurs, relative mean LA and SLA, and return bloom by year. Frequencies of dead/alive spurs were separated by the χ^2 test. Means were separated by Tukey's test. Different letters indicate significant differences with $P < 0.01$.

Year	Alive spurs (n)	Retagged spurs (n)	Dead spurs (n)	Dead spurs (%)	SLA (cm^2/g)	LA (cm^2)	Return bloom (%)
2001	2400	0	0	0	132.58 ± 0.62f	19.21 ± 0.19e	–
2002	1887	344	125	5.21b	142.36 ± 5.78e	21.93 ± 0.94d	5.52
2003	2086	65	202	9.05b	149.60 ± 1.74d	23.06 ± 0.65d	10.97
2004	2106	70	165	7.67b	213.57 ± 1.68a	26.76 ± 0.31c	12.18
2005	1746	13	486	22.33a	167.34 ± 1.89b	33.01 ± 0.79a	6.91
2006	1895	0	365	20.75a	156.11 ± 0.63c	29.89 ± 0.56b	10.98
2007	1371	0	524	27.65a	–	–	3.39

Table 2. Coefficients ($y = ax + b$), R^2 values and P values of linear regressions between PYLA, PYSLA and number of flowers in the following year, and percentage mortality. Statistical significance of R^2 differences was determined by the t-test as described by Sokal and Rohlf (1969) ($n = 6980$).

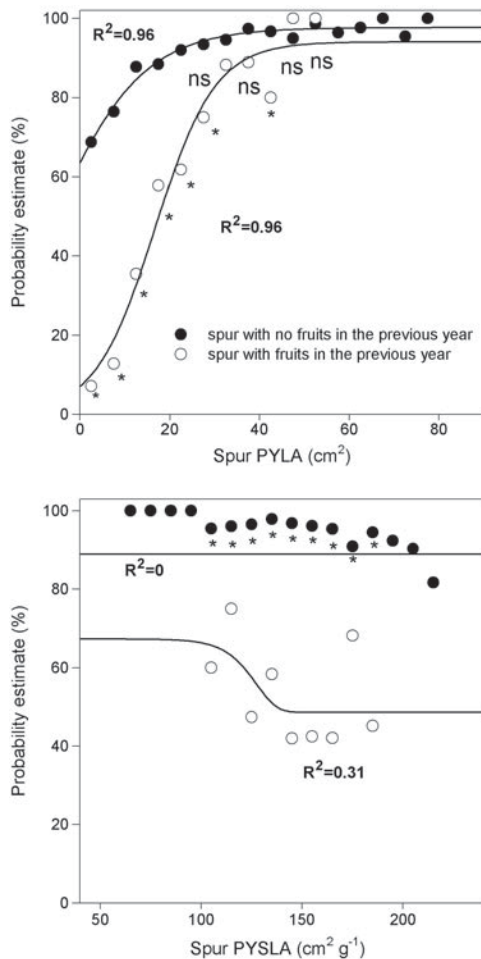| y	x	a	b	R^2	$P < 0.0001$
Number of flowers	PYLA	0.00049	0.63	0.0037	*
	PYSLA	−0.00003	0.65	0.0002	Ns
Mortality	PYLA	0.00005	0.83	0.0004	Ns
	PYSLA	−0.00001	0.84	0.0002	Ns

Figure 2. Probability estimation (%) of spur survival after bearing and not bearing fruit in the previous year in relation to frequency classes of spur PYLA (cm^2) (upper panel) and spur PYSLA (cm^2 g^{-1}) (lower panel). Frequencies per each class were tested by χ^2; *indicate significant differences at $P < 0.001$. Regression equations and coefficients are reported in Table 3.

>80% for previously non-bearing spurs with PYLA values over >45 cm^2. The probability of flowering on spurs that bore fruits in the previous year was so low that it could not be related to PYLA. The probability of different numbers of flowers occurring on a spur was also significantly related to the spur PYLA ($P < 0.01$) (Figure 3; Table 4). The probability of spurs having two or fewer flowers peaked at PYLA values around 40 cm^2 and the probability of having three or more flowers per spur increased to >50% when PYLA was >50 cm^2 (Figure 3).

Discussion

Spur mortality rate changed dramatically over the years of this study. Spur mortality in the first 3 years of this study was significantly less than reported for the same almond cultivar by Esparza et al. (2001) (i.e., > 20%/year), but the increased mortality after 2004 was similar to the previously published values. The increased mortality rate after 2004 may have been related to increasing canopy age as the trees began to fill their allotted space since the orchard was relatively young (5 years) at the beginning of the study. Alternatively, a heavy crop in 2004 (89% greater than in the previous year) may have caused an increase in subsequent spur mortality. Previous research has documented that alternate bearing of spurs is common in fruit and nut trees (apples, Chan and Cain 1967; pear, Weinbaum et al. 2001; walnuts, Klein et al. 1991a; plum, Couranjou 1989). However, there have been few studies of the effect of cropping on spur mortality or of specific characteristics of spurs in one year that relate to spur viability and productivity in the next.

Klein et al. (1991b) reported that there was high variability in leaf light exposure in walnut tree canopies and that the spurs located in the interior part of the canopy were capable of surviving even though exposed to low light flux densities for most of the day. However, more shaded spurs had lower viability and fruit bearing (Klein et al. 1991a). Polito et al. (2002) reported that PYLA of almond spurs was related to spur bearing behaviour the following year and Heerema et al. (2008) reported that PYSLA affected almond spur viability and flowering in the next year. Based on their findings, Heerema et al. (2008) asserted that almond spurs function semi-autonomously with regard to source–sink behaviour for at least the latter part of the growing season based on the assumption that the measurements of the leaf characteristics reflect general photosynthetic source activity and spur fruit load represents dominant sink activity. However, their study was conducted on two contrasting spur populations (exposed and shaded) over 2 years on relatively few spurs and other 'carry-over' effects from one year to the next may have affected the outcome. If their hypothesis is correct, then spur productivity and mortality in any one year should be a function of a combination of spur leaf characteristics and spur fruit load in the previous year. Data presented in Figures 3 and 4 are consistent with this expectation.

Contrary to the results of Heerema et al. (2008), in the present study, PYLA was more indicative of subsequent year fruitfulness and mortality than was a measure of leaf thickness (PYSLA). This may have been because the sample used in the present work was more representative of a range of intra-canopy

Table 3. Formulae and regression parameters for the curves in Figure 2. Pr is the estimated probability (%), PYLA is the spur previous year leaf area (cm²) and PYSLA is the spur previous year specific leaf area (cm² g⁻¹). Statistical significance of R^2 differences was determined by the t-test as described by Sokal and Rohlf (1969).

	R^2	Formula	$P < 0.001$	n
No fruits previous year	0.96	$Pr = a/(1 + \exp(-(PYLA - x_0)/b))$	*	16
Fruits previous year	0.96	$Pr = a/(1 + \exp(-(PYLA - x_0)/b))$	*	11
No fruits previous year	0	$Pr = a/(1 + \exp(-(PYSLA - x_0)/b))$	Ns	16
Fruits previous year	0.31	$Pr = y_0 + a/(1 + \exp(-(PYSLA - x_0)/b))^c$	Ns	9

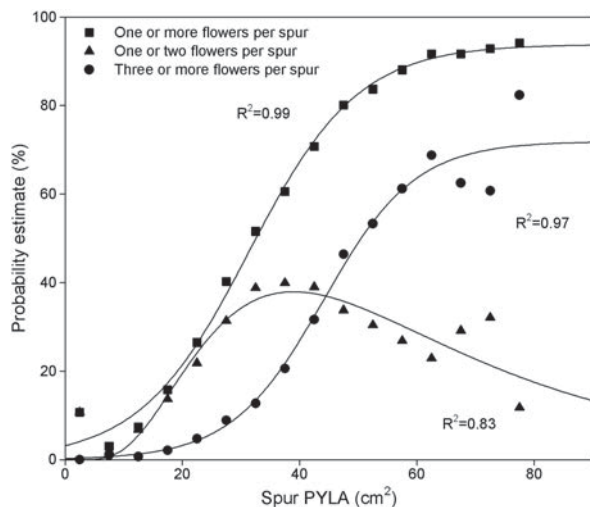|	a	b	x_0	c	y_0
No fruits previous year	97.68	10.11	−6.31		
Fruits previous year	94.06	6.68	16.73		
No fruits previous year	88.94	11527.55	−383886		
Fruits previous year	18.69	−9.12	145.68	7.39	48.59

Figure 3. Probability estimation (%) of spur having one or more flowers per spur, one or two flowers per spur or three or more flowers per spur after not bearing in the previous year in relation to frequency classes of spur PYLA (cm²). Regression equations and coefficients are reported in Table 4.

variability and a large number of the tagged spurs were exposed to low to intermediate amounts of light that are typical in mature nut tree canopies (Klein et al. 1991b). In the present study, tagged spurs represented positional gradients within the almond tree canopies whereas Heerema et al. (2008) selected spurs to represent the most exposed, outer regions of the canopies contrasted with more shaded internal regions. In the current study, 80% of spurs had SLA >125 cm² g⁻¹ and therefore would have been part of the more shaded category of leaves sampled by Heerema et al. (2008). In the present study, PYLA appeared to represent the vitality of spurs and correlated well with spur viability in shaded conditions after both bearing and not bearing.

An increase in spur PYLA corresponded to an increase in the probability that a spur would be alive the following year. However, fruit bearing decreased the probability of spur survival, especially in those spurs with low PYLA. Spurs with PYLA >28 cm² were apparently able to accumulate enough carbohydrates to both support fruit growth and store carbohydrate for initiating vegetative growth the following year but the probability of survival decreased dramatically when bearing spurs had <28 cm² of leaf area. To determine the relationship between spur PYLA and return bloom, we correlated spur PYLA with the relative number of spurs blooming in the following year (blooming spurs/total number of spurs) per specific PYLA interval. Spur flowering was closely related to spur PYLA and thus, presumably, resource availability in the previous year. Thus PYLA appeared to be a good indicator for predicting the number of flowers per spur in the following year. Previous year spur bearing almost totally shut down flowering in the year following bearing (in the 6 years of the study only 116 of 1384 tagged bearing spurs bore flowers after bearing fruit in the previous year) so it was not possible to reliably evaluate whether previous year fruit bearing also influenced number of flowers per spur. However, spur PYLA was positively related to the number of flowers produced per spur among spurs that did not bear fruit the previous year (data not shown). Survival of non-bearing as well as bearing spurs into the next year was almost certain when spur PYLA was > 20 cm². Spurs with PYLAs >50 cm² had > 80% probability of producing at least one flower if the spur did not bear in the previous year. These data confirm assertions by Polito et al. (2002) and Heerema et al. (2008) that spur carbon supply–demand balance strongly influences spur viability and flowering.

In conclusion, spur longevity in almond was not governed by a determinant cycle (vegetative growth, bearing and death) but rather appears to be related to factors that can have a strong influence on the balance between sources and sinks: when the

Table 4. Formulae and regression parameters for the curves in Figure 3. Pr is the estimated probability (%); PYLA is the spur previous year leaf area (cm^2). Statistical significance of R^2 differences was determined by the t-test as described by Sokal and Rohlf (1969) ($n = 6980$).

	a	b	x_0	R^2	Formula	$P < 0.001$	n
One or more flowers per spur	90.05	8.76	30.32	0.99	$Pr = a/(1 + \exp(-(PYLA - x_0)/b))$	*	11
One or two flowers	37.95	0.57	38.99	0.83	$Pr = a \times \exp(-0.5 \times (\ln(PYLA/x_0)/b)^2)$	*	16
Three or more flowers	71.89	7.83	44.03	0.97	$Pr = a/(1 + \exp(-(PYLA - x_0)/b))$	*	16

sources are insufficient to fulfil the sink requirements, spur death occurs. The main parameters associated with spur longevity in a well-managed orchard appear to be light exposure, leaf area and fruit bearing. Behaviour of individual spurs in a given year can be predicted by considering their PYLA and previous year fruit production. This work provides useful information for understanding factors governing almond tree productivity, and the definition of PYLA thresholds may provide a useful approach for assessing excessive canopy shading associated with specific tree training systems and crop management practices.

Acknowledgments

Funding

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