



Tree Physiology 31, 1413–1421  
doi:10.1093/treephys/tpr119



## Research paper

# Relationships between spur- and orchard-level fruit bearing in almond (*Prunus dulcis*)

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Received September 14, 2011; accepted October 24, 2011; handling Editor Douglas Sprugel

Almond is often considered to be a moderately alternate-bearing species but historical yield data typically do not exhibit clear patterns of alternate bearing at the orchard level, while research has indicated that spurs (the main fruit bearing unit in almond trees) rarely produce fruit in two subsequent years. The objective of the present work was to analyze the bearing behavior of almond trees at both the orchard level and the individual spur level over multiple years to explain this apparent paradox. The 10-year yield patterns of three almond cultivars grown at three different sites within California were analyzed for tendencies of alternate bearing at the orchard level. At the individual spur level, data on spur viability, and number of flowers and fruits per spur were collected on 2400 individually tagged spurs that were observed over 6 years to characterize bearing at that level. At the orchard level one cultivar (Nonpareil) did exhibit a tendency for alternate bearing at one site (Kern) but other cultivars and sites did not. The orchard and the individual trees in which the spur population study was conducted showed tendencies for alternate bearing but the spur population did not. 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 alternate year bearing. However, from historical records, this would appear to be the exception rather than a normal circumstance. Therefore, almond should not be considered to be a strictly alternate-bearing species.

**Keywords:** alternate bearing, bearing fluctuations, fruit crops, spur viability.

## Introduction

Crop productivity in perennial, deciduous fruit trees is very sensitive to environmental conditions because most of these crops bloom during highly variable weather conditions in early spring (Moss et al. 1981, Monselise and Goldschmidt 1982, Lobell et al. 2007). Some models correlated bearing fluctuations to climatic variables that may influence some important physiological processes (Dorfman et al. 1988, Sparks 1996, Lobell et al. 2007, Tombesi et al. 2010). Pollination, fertilization and fruit set can be negatively influenced by multiple factors.

Spring frosts can kill flowers and/or fruitlets, excessive rain and cold temperatures can restrict pollinator movement (Corbet et al. 1993, Thorp 1996, Vicens and Bosch 2000) and increase flower and fruitlet diseases, high temperatures and dry winds can decrease flower longevity and the effective pollination period (Ortega et al. 2004). When weather conditions are optimal for pollination and fruit set, some species can set very heavy crops and then heavy crops can lead to decreased crops in the following year because bearing shoot growth and flower bud development for the next year overlap with the bearing of

a heavy crop in the current year. In some species, this can set up a cycle of repeated alternate bearing (Monselise and Goldschmidt 1982). When there is a distinct pattern of alternating years of high and low productivity, it is generally assumed that endogenous factors are involved and the phenomenon is referred to as alternate bearing. There are two main theories concerning the underlying endogenous causes of alternate bearing.

One theory is focused on the fact that fruit and seeds are thought to be sources of hormones that may signal developing meristems to remain vegetative and not produce flowers for the year subsequent to a heavy crop load (Chan and Cain 1967, Hoad 1978, Monselise and Goldschmidt 1982). Some authors have specifically indicated that auxins (Hoad 1978), gibberellins (Luckwill 1970) and abscisic acid (Tamas et al. 1979) may be involved. However, hormones produced by seeds can increase the sink strength of fruits and are not always linked to a direct inhibitory effect on following year flowering (Weinbaum et al. 2001).

The other theory is focused on the thought that large crop loads can deplete carbohydrate and/or nutrient resources that influence the development of floral buds for the next year. 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 crops 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). The two proposed underlying mechanisms involved in alternate bearing are not mutually exclusive and could act in concert under some circumstances.

Spurs (very short proleptic shoots) are the main bearing unit in mature almond trees (Kester et al. 1996). Their viability is influenced by parameters related to the CO<sub>2</sub> fixation, such as the spur leaf area (Polito et al. 2002, Heerema et al. 2008, Lampinen et al. 2011), water stress (Esparza et al. 2001), nutrient availability (Basile et al. 2003, Heerema 2005) and previous year bearing (Heerema et al. 2008, Lampinen et al. 2011). Fruit bearing in perennial fruit species can cause depletion of stored carbohydrates in shoots (Marquard 1987, Spann et al. 2008). Carbohydrate depletion appeared to strongly affect the following year flowering in apple (Jackson and Palmer 1977a, 1977b) and carbohydrate availability in individual apple spurs varied as a consequence of the balance between sources and sinks located in the spur itself (Johnson and Lakso 1986a, 1986b). Variations in carbohydrate availability among spurs suggest that branches and spurs function as semi-autonomous organs during most of the year except for early spring. (Watson and Casper 1984, Sprugel et al. 1991, Heerema 2005). This theory suggests that branches

are dependent on the tree for water and mineral nutrient supply but carbohydrate sinks located on an individual branch are largely supplied by the sources located on the same branch (except perhaps in the spring when stored carbohydrates are mobilized and come up from the trunk and roots in the xylem), making each branch a semi-autonomous system. Such a theory has been supported by many experiments (Ruohomäki et al. 1997, Obeso 1998, Henriksson 2001, Yamamoto 2001, Hasegawa et al. 2003, Marsal et al. 2003, Hoch 2005). Heerema (2005) suggested that almond spurs may also be considered as semi-autonomous organs.

Individual spurs of almond (Lampinen et al. 2011), walnut (Klein et al. 1991) and apple (Chan and Cain 1967, Luckwill 1970) rarely produce fruit in two consecutive years. In almond, bearing spurs had a lower probability of survival the year after bearing than non-bearing spurs especially if they had low leaf area in the bearing year. Flowering and bearing appeared to be related to previous season spur leaf area and fruiting status (Lampinen et al. 2011). However, the bearing patterns of whole trees do not always reflect the pattern exhibited by individual spurs and may be influenced by environment and other factors (Monselise and Goldschmidt 1982).

On an orchard level almond, like other species that show alternate bearing tendencies on a spur level, can be considered to be an alternate-bearing crop (Krueger et al. 1996). However, Monselise and Goldschmidt (1982) did not include it among alternate-bearing fruit tree species and Dorfman et al. (1988) reported that previous year crops exercised a small effect on following year crops compared with environmental factors such as rainfall during the month when almonds bloom.

These reports at the orchard and macro-area scales (Monselise and Goldschmidt 1982, Dorfman et al. 1988) are in contradiction with data reported at the spur level (Heerema et al. 2008, Lampinen et al. 2011).

The aims of the present work were to: (i) assess the degree of alternate bearing exhibited by the 'Nonpareil', 'Carmel' and 'Butte' almond cultivars (the most important cultivars produced in California) in three contrasting locations and orchard situations where pollination problems should have been minimal over a period of 10 years; (ii) assess the yield behavior of 'Nonpareil' in a specific orchard and the degree of alternate bearing exhibited by a small population of trees within that orchard as well as the bearing patterns of a large population of individual spurs on those trees over a 6-year period; and (iii) explain contradictions between apparent alternate-bearing patterns at the orchard, tree and spur scales.

## Materials and methods

In the present work, fruit-bearing data were analyzed at the multiple orchard/sites, in an individual orchard site where a spur population study was conducted, on individual trees on which

the spur population study was conducted and on the individual spur scale. At the orchard scale annual kernel yield data were collected from experimental regional variety trial orchards (Lampinen et al. 2002) located near Chico, in the northern Sacramento Valley (Chico site); Manteca in the northern end of the San Joaquin Valley (Delta site); and Shafter in the southern end of the San Joaquin Valley (Kern site). These orchards were planted in 1993 to evaluate 34 different almond cultivars. For this study only data from three of the most important Californian cultivars (Nonpareil, Butte and Carmel) were considered. Trees were planted at densities of 158, 185 and 213 trees per hectare at the Chico, Delta and Kern sites, respectively. The Butte and Carmel cultivars were planted in single rows of 20–25 trees, alternating with rows of the standard cultivars, 'Nonpareil' or 'Mission', for cross-pollination and data normalization purposes. Fruits were harvested at commercial maturity and kernel yield data were recorded for whole rows of a given cultivar. Kernel yields per hectare for each cultivar were calculated from mean tree kernel yields and tree densities per hectare.

Spur-bearing behavior was analyzed on trees of a 59 hectare orchard located in Kern County that was planted in 1996. Tree spacing was 7.3 m between and 6.4 m within rows (215 trees per hectare). Cultivar composition was 50% 'Nonpareil' with 25% 'Monterey' and 25% 'Wood Colony' as pollenizers (rows of 'Nonpareil' trees were planted with alternating rows of the pollenizer cultivars). Individual spurs were tagged on randomly selected 'Nonpareil' trees within the 59 hectare orchard (avoiding border trees). A total of 2400 spurs were tagged with aluminum tags in late March and early April 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 ~2–3 m. If tags were lost they were replaced at comparable locations to the original tags during the first 4 years of the study. 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). 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).

Bienniality and alternate-bearing intensity indices were calculated to evaluate the degree of alternate bearing in the regional variety trial orchards as described by Monselise and Goldschmidt (1982). Statistical analyses were carried out with SAS statistical software (SAS Institute, Cary, NC, USA) using linear regression to test the effect of variables on each other. A *t*-test as described by Sokal and Rohlf (1969) was used to test  $R^2$  of regressions (*P* value was set at 0.05).

## Results

Orchard kernel yields at the three regional variety trial sites generally increased over time but varied considerably in each

of the 10 years of the study (Figure 1). 'Nonpareil' tended to follow an approximate biennial bearing cycle except in some years, such as 2000–2001 and 2003–2004 for Chico, 2000–2001 and 2004–2005 for Delta and 2001–2002 for Kern site, but this trend was not consistent for all years or sites. Kernel yields of the 'Butte' and 'Carmel' cultivars were more consistent over the time considered and exhibited lesser trends toward biennial bearing than 'Nonpareil' (Table 1). Indices describing alternate bearing varied depending on the site. The Chico site (the northernmost one) generally had lower bienniality and intensity indices than the other two sites (Table 1).

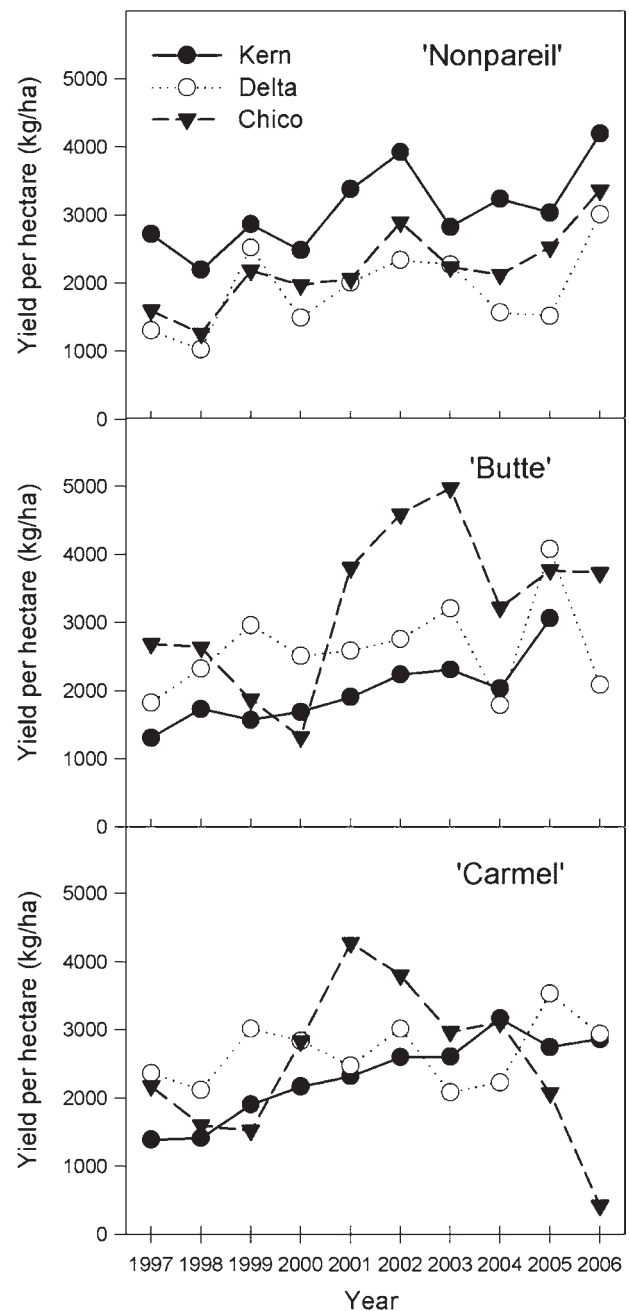


Figure 1. Yield (kernel kg ha<sup>-1</sup>) trend from 1997 to 2006 in Chico, Delta and Kern orchards for 'Nonpareil', 'Butte' and 'Carmel'.

Table 1. Calculated bienniality and intensity indices (see Monselise and Goldschmidt 1982) based on yield records for the 'Nonpareil', 'Carmel' and 'Butte' cultivars located in the three orchard locations (Kern, Delta and Chico) over 10 years (1997–2006).

	Bienniality index (%)			Intensity index (%)		
	Kern	Delta	Chico	Kern	Delta	Chico
'Nonpareil'	77%	66.7	44.4	10.7	17.4	11.2
'Carmel'	55.6	66.7	22.2%	14.4	19.7	8.2
'Butte'	44.4	55.6	44.4	17.1	19.8	12.2
'Nonpareil' spurs	75			16.5		

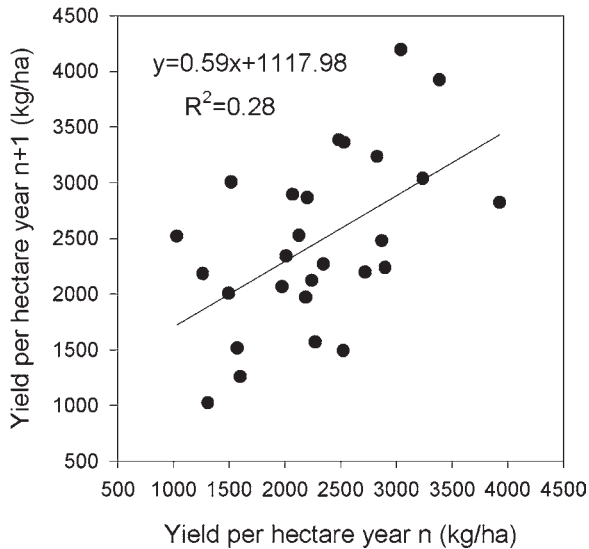


Figure 2. Correlation between yield (kernel kg) per hectare in year  $n$  and yield per hectare in year  $n + 1$  of 'Nonpareil' in the three orchards considered in Figure 1.

In the regional variety trial orchards, kernel yield per hectare in the previous year had no relationship to kernel yield in the next year (Figure 2). The slope of the relationship between kernel yield in year  $n$  and year  $n + 1$  was positive, contrary to what would be expected if alternate bearing was significant.

In the orchard where the spur population study was carried out, the orchard kernel yield tended to alternate over the 6 years of the study but one cycle out of five (2003–2004) did not exhibit a classical alternate-bearing pattern (Figure 3a). There was a clear alternating pattern in the trees in which spurs were tagged for the spur population study (Figure 3b). In two cycles out of five the trend was opposite to the one observed for the whole orchard (Figure 3a). A comparison of yearly individual tree kernel yields relative to their 6-year mean kernel yields indicated that in any given year (except for 2003) there were individual trees that produced kernel yields that were both above and below their 6-year-mean kernel yields (Figure 3c).

In the spur population study, the total numbers of flowers produced by all the tagged spurs were fairly constant over the first 3 years of the study and then increased, and again were

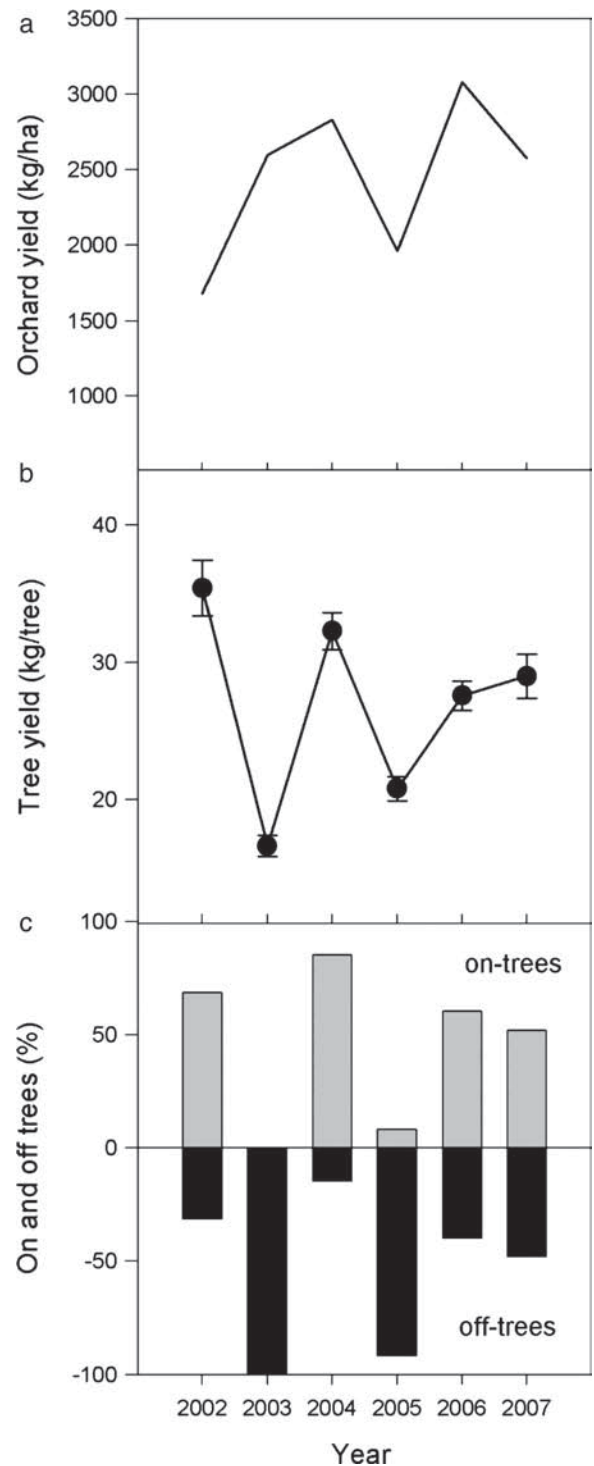


Figure 3. Orchard yield (kernel kg ha<sup>-1</sup>) (a), mean tree yield (kernel kg tree<sup>-1</sup>) of trees ( $n = 48$ ) where spurs were tagged (b) and percent of trees above (on-trees) and below (off-trees) their own mean yield over 6 years (c). Error bars in (b) represent the calculated standard error for the 48 trees considered.

fairly constant over the second 3 years (Figure 4). Thus, no clear alternating flower production pattern was apparent. On the other hand, the total number of fruit produced on those same tagged spurs did have an alternating trend indicating that

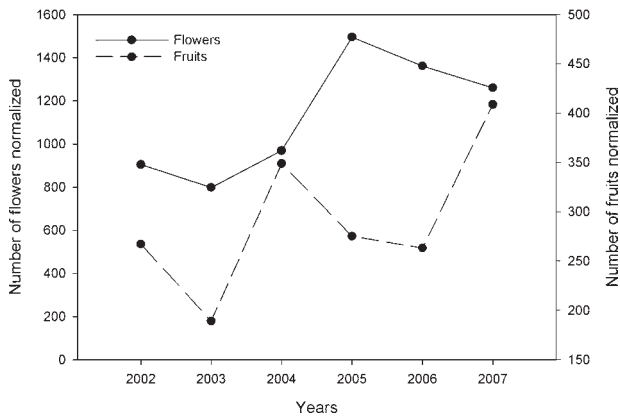


Figure 4. Number of flowers and fruits normalized to the lowest number of spurs still tagged in the study (1371 spurs in 2007).

a biennial cycle of bearing may have been involved. However, there were no consistent, significant relationships between fruits per spur in year  $n$  and the flowers per spur in year  $n + 1$  ( $P = 0.22$ ) or fruits per spur in year  $n + 1$  ( $P = 0.56$ ) (Figure 5). However, analysis at the individual spur level indicated that very few spurs flowered after producing fruit in the previous year (Figure 6). Over 5 years, an average of 8.89% of individual spurs produced flowers and only 3.47% bore fruit after bearing fruit in the previous year. Individual spur return bloom after bearing varied between 3.38% in 2006 and 12.18% in 2003. Return fruit bearing after bearing fruit the previous year varied between 1.36% in 2006 and 7.11% in 2003.

Among the population of tagged spurs, the number of flowering spurs, bearing spurs and dead spurs after bearing varied among years (Figure 7). The number of non-flowering spurs in

any given year was always greater than the number of flowering spurs, bearing spurs or dead spurs. The number of spurs that died in a given year was always less than the number of spurs in the other categories (Table 2). On average, 7% of the total tagged spur population died in each year of the 5-year study while 35.3 and 14.25% of the tagged spurs flowered and bore fruit, respectively.

## Discussion

Even though it is commonly believed that almond is an alternate-bearing crop with heavy crops in one year competing with the crop of the following year (Krueger et al. 1996), Monselise and Goldschmidt (1982) did not list it as a typical alternate-bearing crop in their review. This study clearly indicates why there is confusion about whether almond is an alternate-bearing crop. In the regional variety trial orchards 'Nonpareil' tended to alternate bear at some sites but this was not consistent among sites or cultivars. The mean kernel yields for the population of individual trees over 6 years in the individual orchard did show a clear alternate bearing tendency but the tendency appeared to dampen over time and in all but 1 year there were trees in the same population of trees that produced both above and below their 6-year mean kernel yields. As previous research clearly indicated (Lampinen et al. 2011) individual bearing spurs exhibited a strong tendency to not bear in two consecutive years but the spur population data did not indicate strong alternate-bearing tendencies.

While high kernel yields of 'Nonpareil' almond trees tended to be followed by low crop yields in several 2-year sequences over the 10-year period of the regional variety trial orchard

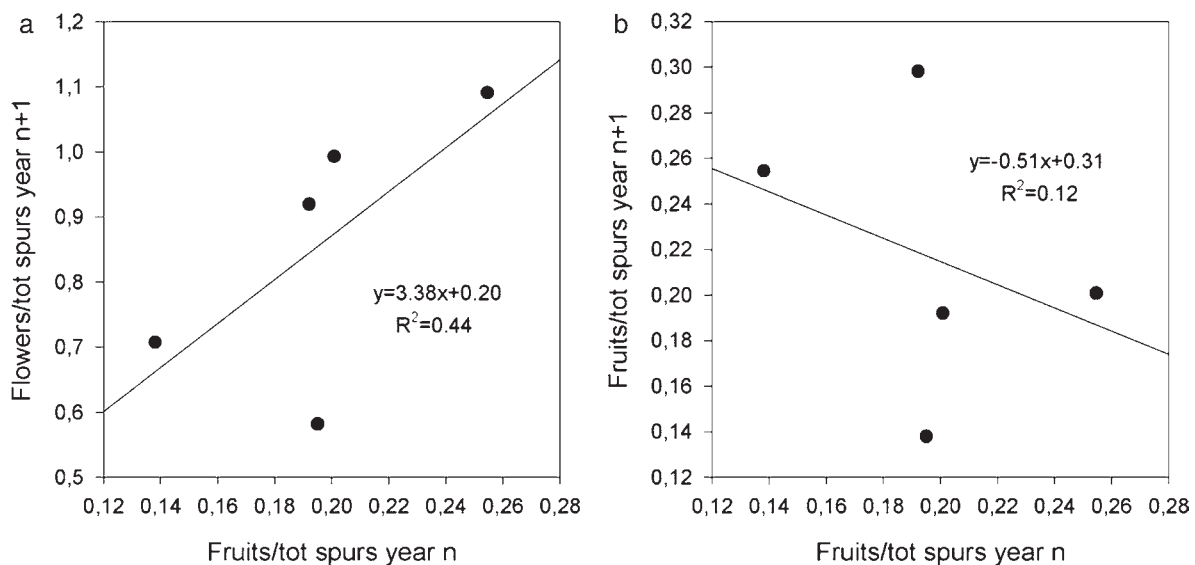


Figure 5. Relationship between fruits per total spurs in the previous year and flowers per total spurs in the next year ( $P = 0.22$  ns) (a) and fruits per total spurs in the previous year and fruits per total spurs in the next year ( $P = 0.56$  ns) (b).  $R^2$  statistical analysis was carried out by  $t$ -test as described by Sokal and Rohlf (1969).

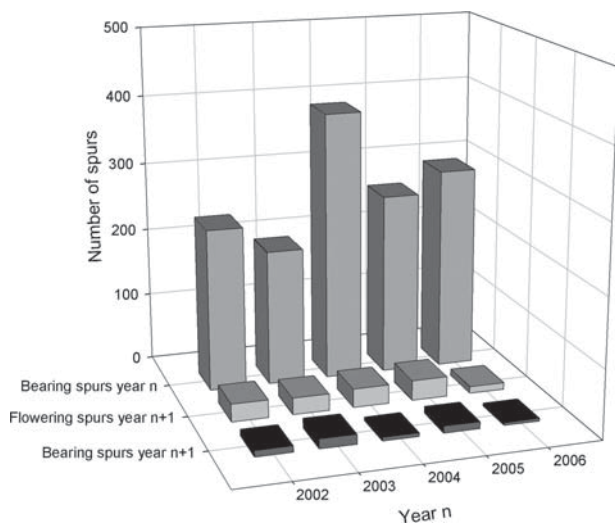


Figure 6. Number of bearing spurs in the year  $n$  and return bloom and fruit bearing in the subsequent year.

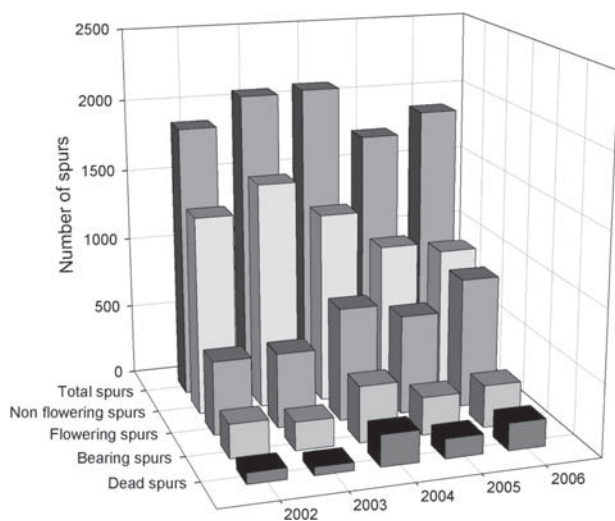


Figure 7. Population description over 5 years. Number of total spurs, non-flowering spurs, flowering spurs, bearing spurs and dead spurs in the following year after bearing.

Table 2. Total number of tagged spurs and percentage of tagged spurs that were flowering, bearing or died each year.

Year	Total number of spurs	Flowering spurs (%)	Bearing spurs (%)	Dead spurs (%)
2002	1887	27.13	12.56	4.08
2003	2086	24.83	9.44	2.73
2004	2106	37.27	18.57	10.35
2005	1746	39.46	15.12	7.85
2006	1895	47.81	15.57	9.97
Mean		35.30	14.25	7.00

comparison study, especially at the Kern site (Figure 1), it was not as strong at the two other sites. This was supported by the higher bienniality index value for the Kern site compared with the Delta and Chico sites (Table 1). The positive correlation between 'Nonpareil' kernel yields of orchards from all sites in 1 year and kernel yields of the same orchards in the subsequent year (Figure 2) indicates that 'Nonpareil' kernel yield of a given orchard in any 1 year was more a characteristic of the orchard itself than the kernel yield of the orchard in the previous year. These positive kernel yield trends could be explained by annual canopy growth which progressively increased the amount of light intercepted by the canopies and potentially the number of available fruiting positions (spurs) (Hill et al. 1987; Lampinen et al., 2011). The orchard kernel yield data and bienniality indices for the 'Butte' and 'Carmel' cultivars indicated even less tendency toward alternate bearing than 'Nonpareil'. This is interesting since Lamp et al. (2001) reported that in 'Nonpareil', flower bud differentiation occurs after 90% hull-split whereas in 'Butte' and 'Carmel' it occurs during or before hull-split. Thus it might be expected that 'Nonpareil' would be less predisposed to alternate bearing than 'Butte' and 'Carmel' because flower bud differentiation does not coincide with periods of rapid growth and fruit carbohydrate accumulation. Our data indicate the opposite, with 'Butte' and 'Carmel' having less tendency toward alternate bearing at the orchard level than 'Nonpareil'. This may indicate that the fruit differentiation process is sensitive to depletion of stored carbohydrates that may occur during the final rapid phase of fruit growth as has been suggested for pistachio (Spann et al. 2008).

Orchard yields are the sum of single tree yields. Fruit yield patterns in the same orchard at two different levels (orchard and single tree) were different in some years (Figure 3) probably due to the different on – off year cycles of individual trees which if synchronized would accentuate on- and off-bearing years. Such behavior is consistent with the behaviors described for apple by Davis (1957) who emphasized that the behavior of individual trees and their components must be studied to understand alternate bearing at the orchard level.

Single tree and branch yields depend on spur population behavior. Spurs are the most important bearing structure in almond trees (Kester et al. 1996). When the flowering and bearing patterns of a large population of spurs in mature 'Nonpareil' almond trees were considered, there was no consistent relationship between the number of spurs in the tagged spur population that bore fruits in one year and the number of flowers and fruits in the tagged spur population in the next year (Figure 4). In general, there was a tendency for the number of flowers present in year  $n + 1$  to be positively related to the number of fruits present in the population in year  $n$ . Interestingly, the case was opposite for fruits in year  $n + 1$  and fruits in year  $n$  but neither relationship was statistically significant (Figure 5a and b). It may be worthwhile to study these types of relationships further because if they were significant it

would indicate that, at the spur population level, crop loads in one year may not negatively influence flower numbers the next year but the quality of the flowers produced may be decreased. Our data are consistent with data previously reported for pear (Weinbaum et al. 2001) but contrast with data reported for 'Spencer Seedless' apple (Chan and Cain 1967) where seeds in year  $n$  apparently caused hormonal inhibition of flowering in year  $n + 1$ . Considering such data from the point of view of carbohydrate depletion caused by the previous crop, our data are consistent with a recent report by Bustan et al. (2011) in which there was no consistent relationship between carbohydrate reserves and on- and off-years of olive production. Our data are also consistent with those reported for pecan in which neither root nor shoot N, K or non-structural carbohydrate concentrations appeared to be closely related to alternate bearing (Rohla et al. 2007; Smith et al. 2007).

On the other hand, individual spurs were subject to strong tendencies to not fruit in two consecutive years. The number of spurs that bore in the previous year and returned to bloom in the next one was very low (Figure 6) and only 14% of those that did produce flowers bore fruits. Furthermore, an average of 7% of the total spur population died subsequent to fruit bearing (Figure 7). Lampinen et al. (2011) reported that spur viability and flowering in a given year is strongly associated with previous leaf area and if the spur did or did not bear fruit in the previous year. Based on the bearing dynamics of individual spurs over a two-year, bearing/non-bearing cycle, it would seem likely that almond trees should exhibit a strong tendency toward alternate bearing. However, strong alternate bearing was not apparent at the spur population level.

This paradox can be explained by the fact that a relatively small percentage of the total spur population bore fruit in any given year (Figure 7). While individual spurs rarely bore fruit in two consecutive years, the bearing population in any year represented only a fraction of total spurs and there were always many more spurs that did not bear in a previous year than did. On average, ~6% of the tagged spur population died each year (Figure 6) while an average of 14.25% of the spur population bore fruit each year and would likely not fruit the following year. Thus, on average, tree yield in a given year was dependent on the size of the population of non-bearing spurs that were present the previous year (year  $n - 1$ ), the percentage of those spurs that produced flowers (in year  $n$ ) and the weather/pollination conditions that influence the percent of those flowers that set fruit (in year  $n$ ). Such conclusions are consistent with what was reported for apple by Davis (1957), who stated that alternate bearing can be at the branch (spur) level or the whole tree level, and whether it is at the whole tree level depends on the percentage of spurs that are alternate bearing. The tree data (Figure 3c) also indicate that alternate bearing at the orchard level is a function of the percentage of trees that are alternate bearing in the orchard population.

Collectively this study indicates that to understand bearing patterns in fruit and nut orchards strong emphasis needs to be placed on population studies of trees within orchards and bearing units within trees. This notion is contrary to traditional yield analysis approaches for annual crops that concentrate on the growth and yield behavior of individual plants and assume that populations of similar plants all behave similarly (Milthorpe and Moorby 1974). If this is true it means that in addition to understanding the physiological behavior of individual trees, to understand yield behaviors of orchards we must also understand the population dynamics of trees in an orchard. There has been relatively little research in this area but attempts to apply precision agriculture techniques to orchard crops have come to similar conclusions (Rosenstock et al. 2010).

There are a few additional trends in the spur dynamics data presented in Figure 7 that are important to point out. One is that there was an increase in the rate of spur mortality in the third year of the study that appeared to continue in subsequent years (the average annual spur mortality in the last 3 years was 9.39% compared with an average of 3.40% in the first 2 years) (Table 2).

The data on spur mortality during the last 3 years of study may not reflect the average spur mortality of whole trees because the spur population being followed in this study was tagged when the trees were 6 years old and the orchard had only reached ~50% canopy cover (data not shown). As the orchard continued to increase in canopy cover, these positions most likely became increasingly shaded and this may be the reason for increasing mortality in the later years of the study.

This study indicates that in order to maintain a constant (or increasing) population of spurs with potential to bear fruits, between 4 and 10% of the spur population must be replaced each year when the orchard is fully mature. Thus, in order to maintain yields after reaching full orchard maturity it is important for trees to maintain enough vegetative growth to effectively replace dying fruiting positions each year. In apple, Butler (1917) suggested a direct relationship between vegetative growth and productiveness because the new growth should be regular and always sufficient to compensate for the decrease in fertility and death of the spurs on the older bearing wood. This is generally the reason why some pruning and orchard management is recommended to maintain orchard yields after trees have fully occupied their allotted space in the orchard (Krueger et al. 1996). It would be interesting to compare the effect of various orchard management practices on almond spur population dynamics.

While these data explain why almond trees do not strictly display alternate bearing, the data also indicate why some very heavy yield years can be followed by years with lighter yields. Yields are not only determined by the size of the spur population but also by the environmental and biological factors that influence effectiveness of pollination, fertilization and fruit set

in a given year. Normally <50% of almond flowers produce fruit (Kester and Griggs 1959) but it is conceivable that under ideal conditions this percentage can be much higher. If conditions are near ideal for pollination, fertilization and fruit set, a higher-than-normal percentage of the total spur population may be occupied with fruit production. This would mean that in a subsequent year a smaller percentage of the total spur population would flower and the total subsequent crop would be lower. However, the data in Figure 5a indicate that this may be the exception rather than the rule since the previous year cropping of the sampled spur population was negatively correlated with flower number of the same spur population in the next season in only one out of 6 years.

In conclusion, almond yields of specific orchards tend to fluctuate over the years but those fluctuations do not exhibit strong alternate bearing even though only a small fraction of individual spurs bear fruit in two sequential years. This is explained by the fact that only a small fraction of the total spur population bear fruit in any given year. This study also indicated that there can be large yield differences among trees in the same orchard and to fully understand yield behaviors of orchards it will be necessary to comprehend the causes of yield variations among trees in orchards as well as the bearing behavior of individual spurs and the development, growth and physiology of individual trees.

## Acknowledgments

We thank Dr P. Proietti for making this collaboration possible as well as Joe Connell (UCCE Butte County), Paul Verdegaal (UCCE San Joaquin County) and Mario Viveros (UCCE Kern County, emeritus) for data from the three regional variety trials.

## Funding

Research was supported by the Almond Board of California and in-kind support was provided by Chico State University, Delta College, and Paramount Farming, Inc.

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