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SUMMARY

Variation in fruit load, leaf area, and light exposure among almond spurs was used to evaluate whether or not spurs were autonomous with regard to Winter survival and return bloom. Fruiting was associated with reduced spur survival over the subsequent Winter and reduced return bloom in the subsequent year. This resulted in a tendency for individual spurs to bloom and bear fruit in alternate years. Survival was high among all non-fruiting spurs, but survival of fruiting spurs was positively related both to leaf area per spur and specific leaf weight (SLW; an indicator of light exposure). SLW was a much stronger correlate for spur survival than leaf area per spur. The likelihood of flowering varied positively with spur leaf area the previous season on both fruiting and non-fruiting spurs, but was not related to spur SLW. Localisation of leaf area and shading effects within individual spurs created spur sub-populations with differing tendencies toward alternate bearing. The likelihood of flowering on spurs was enhanced when branch-wide carbohydrate demand by fruit was eliminated by early fruit removal the previous season, suggesting that almond spurs are not entirely autonomous with regard to carbohydrate supply during floral initiation and development. Nevertheless, our data are consistent with a high degree of spur autonomy regarding Winter survival and return bloom, with each spur apparently being strongly influenced by the ability of its own leaves to meet its carbohydrate demands.

Rosette-like short shoots ("spurs") serve as the fundamental bearing units in almond, because mature almond trees bear a high percentage of fruit on these short shoots, with only a small percentage (fewer than 15%) of fruit borne laterally on long 1-year-old shoots (S. A. Weinbaum, unpublished data). Accordingly, the most important yield determinants for almond trees are: 1) the total number of living spurs per tree, as determined by the balance of annual renewal and mortality of spurs; 2) the average number of flowers per spur; and 3) the percentage of flowers that set fruit in the Spring. This study focused on Winter survival of spurs and spur flowering.

Carbohydrate availability affects flowering in fruit trees (Jackson and Palmer, 1977a,b), and photosynthesis-derived carbon probably varies widely among spurs (Johnson and Lakso, 1986a,b). Almond fruit are large and strong carbohydrate sinks (Hawker and Buttrose, 1980; Kramer and Kozlowski, 1979; Wardlaw, 1990) and, despite the potential up-regulation of photosynthesis in response to fruit carbohydrate demands (DeJong, 1986; Syvertsen *et al.*, 2003), fruiting increases the carbohydrate demand of a spur shoot relative to supply (Marquard, 1987). Differences in the balance of carbohydrate supply and demand of an individual shoot are expected to be of little consequence in highly integrated canopies, where carbohydrates flow freely among shoots. Under such circumstances, shoots having a high carbohydrate supply relative to demand would "share" carbohydrates with shoots having a low carbohydrate supply relative to demand, lessening (or eliminating) any differences in carbohydrate availability among shoots.

For many tree species, however, it appears that shoots, at least during certain parts of the year, are functionally "semi-autonomous" for carbon; that is, the carbon sinks on each shoot in the canopy are supplied primarily with carbon fixed by leaves on the same shoot (Sprugel *et al.*, 1991; Watson and Casper, 1984). The notion of branch or shoot semi-autonomy for carbon is supported by studies showing only limited movement of labelled carbon between shoots (Hasegawa *et al.*, 2003; Yamamoto, 2001), or an absence of negative effects on shoot growth or fruiting when shoot import of carbohydrates is blocked by means of phloem girdling (Hoch, 2005; Obeso, 1998). The highly localised effects often seen when shoot carbohydrate supply and demand are manipulated experimentally (e.g., by defoliation, shading, or fruit thinning of individual shoots) are also consistent with the carbon semi-autonomy of shoots (Henriksson, 2001; Marsal *et al.*, 2003; Ruohomäki *et al.*, 1997). Our understanding of the carbon dynamics of almond spur shoots in relation to

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yield determinants, such as spur survival over Winter, and flowering, is far from complete.

Esparza *et al.* (2001) reported that spur mortality in almond was > 60% over a 3-year period and that the probability of spur survival from one year to the next declined with the number of fruit produced by a spur. Similarly, Reidel *et al.* (2004) found, in almond, that the estimated odds of dying before the subsequent Spring was 8.2-times higher for fruiting than for non-fruiting spurs, and also that the estimated odds of surviving fruiting spurs blooming in the subsequent Spring was only 17.9% that of non-fruiting spurs. Based on these previous studies, we hypothesised that Winter survival and return bloom of almond spurs would be affected by factors that would likely influence the spur-level balance of carbohydrate supply and demand, and thus the extent to which almond spurs function as carbon-autonomous units. We inferred spur carbohydrate demand from the number of fruit per spur, and inferred spur carbohydrate supply from spur leaf area and specific leaf weight [SLW; leaf dry weight (DW) per unit area]. SLW is a good indicator of relative leaf light exposure (Klein *et al.*, 1991a; Marini and Marini, 1983; Weinbaum *et al.*, 1989) and photosynthetic capacity (DeJong and Doyle, 1985; Niinemets *et al.*, 2004). Thus, we tested whether spur survival rates through Winter and return bloom in Spring would vary as a function of spur fruit load, leaf area, and SLW in the previous season.

MATERIALS AND METHODS
Effects of spur fruit load, leaf area, and specific leaf weight on spur survival and return bloom

Seven-year-old 'Nonpareil' almond trees, planted near Lost Hills, California (35° N; 119° W) were used in this experiment. On 7 May 2003, approx. 50 fruiting and 50 non-fruiting spurs, 2-years-old or older, were tagged throughout the canopies of each of nine uniform trees. Although some fruiting almond spurs can carry five or more fruit, typically, most have only one fruit. All fruiting spurs selected had only one fruit, in order to minimise variability among fruiting spurs.

The number of leaves per spur and the length of the longest spur leaf were recorded for each tagged single-fruited and non-fruiting spur on 7 May 2003. Leaf area per spur was estimated non-destructively for each tagged spur using a regression relationship of leaf area per spur to the product of leaf number per spur and the length of the longest spur leaf ($r^2 = 0.9137$; $P < 0.0001$) developed from leaves destructively sampled from similar spurs on adjacent trees. For this analysis, digital photographs were made of the destructively sampled leaves compressed under glass, and the areas of the leaves were measured using SigmaScanPro (SYSTAT, Richmond, CA, USA) image analysis software.

On 25 July 2003, three 0.3 cm^2 leaf discs (made using a hand-held paper punch) were collected from each tagged spur. The leaf discs were dried in an oven at 60°C and spur SLW was calculated as leaf disc DW per unit leaf disc area. The leaf areas of tagged spurs were assumed to be similar on 7 May and 25 July, because leaf expansion on spurs was complete by May, and only negligible leaf abscission occurred between these two dates (data not shown). Shortly before bud-break the following Spring

(12 February 2004), spur return bloom (the presence of at least one flower bud) and spur survival rates were recorded for the tagged spurs.

Statistical analyses were performed using SAS software (SAS Institute, Cary, NC, USA). Logistic regression (SAS Procedure Logistic and SAS Procedure Genmod) was used for statistical comparisons of percentage return bloom and survival.

Effects of spur fruit removal and partial spur defoliation on spur survival through the subsequent Winter

Spurs having either one or three fruit were selected on 16 adjacent 13-year-old 'Nonpareil' almond trees growing near Arbuckle, CA, (39° N; 122° W). Two fruit were removed from spurs with three fruit on 17 April 2003, (before the start of embryo development), or on 11 – 14 July 2003 (a few weeks before harvest). A partial defoliation treatment, consisting of removal of all but the largest spur leaf, was imposed on the same dates as the fruit removal treatments on spurs that originally had one fruit. Untreated three-fruited and single-fruited spurs served as the controls for these experiments. On average, approx. six spurs were tagged per treatment per tree. Spur survival was recorded on 24 June 2004. Spur survival rates were compared statistically using logistic regression (SAS Procedure Logistic and SAS Procedure Genmod). The effects of fruit removal and defoliation were analysed separately.

Effects of branch de-blossoming on subsequent season spur return bloom

Three adjacent 12-year-old 'Nonpareil' almond trees growing near Arbuckle, California were used in this experiment. Four, approx. 1.5 m-long, branches were selected in exposed peripheral positions in each of the tree canopies, and half were de-blossomed on 26 February 2002. The remaining branches served as untreated controls. The de-blossomed branches set no (or very few) fruit, while the untreated control branches had heavy fruit loads.

On 21 August 2002, about 30 non-fruiting spurs were tagged on each of the selected branches. The number of leaves, and the length of the longest leaf on each tagged spur were recorded. Ninety spurs, similar to the tagged spurs elsewhere in the canopies of the same trees, were destructively sampled on 21 August 2002. Digital photographs were made of the leaves sampled destructively and leaf areas were measured using Sigma Scan Pro (SYSTAT) image analysis software. The regression relationship ($r^2 = 0.8826$; $P < 0.0001$) of the product of spur leaf number and length of the longest spur leaf to the actual spur leaf area of destructively sampled spurs was used to non-destructively estimate

TABLE I

The relationship of 'Nonpareil' almond spur fruiting status in 2003 to spur Winter survival and return bloom in Spring 2004

Spur fruiting status (2003)	Spur survival (%) (2004)	Return bloom (%)[z] (2004)	Flower buds per spur (2004)[y]
Single-Fruited	86.5	18.9	1.67 ± 0.10
Non-Fruiting	99.2	56.6	1.92 ± 0.06

[z]Return bloom was the percentage of surviving spurs with at least one flower bud on 12 February 2004.
[y]Data are means ± standard error.

TABLE II
The relationship between leaf area and subsequent winter survival of single-fruited and non-fruiting spurs

Spur fruiting status (2003)	Spur leaf area in 2003 (mg cm^{-2})^z	Number of spurs	Spur survival (%) (2004)
Single-Fruited	0–18	117	77.8
	18–30	189	87.8
	30–42	66	95.5
Non-Fruiting	0–18	77	98.7
	18–30	174	98.9
	30–42	109	100

^{z}Leaf area was estimated on 7 May 2003, using the regression relationship between spur leaf area and the product of spur leaf number and length of the longest spur leaf ($r^2 = 0.9137$; $P < 0.0001$).

TABLE III
The relationship between specific leaf weight (SLW) and subsequent Winter survival of single-fruited and non-fruiting spurs

Spur fruiting status (2003)	Spur SLW in 2003 (mg cm^{-2})^z	Number of spurs	Spur survival (%) (2004)
Single-Fruited	0–8	121	68.6
	8–10	160	92.5
	10–12	100	98.0
Non-Fruiting	0–8	90	97.8
	8–10	178	99.4
	10–12	100	100

^{z}Specific leaf weight, leaf dry weight per unit leaf area, is a reliable indicator of relative leaf light exposure and was measured on 25 July 2003.

the leaf areas of the tagged spurs. The numbers of flower buds were recorded for each of the tagged spurs in the following Spring (8 February 2003).

Statistical comparisons of return bloom for non-fruiting spurs on de-blossomed and untreated control branches were made using logistic regression (SAS Procedure Logistic and SAS Procedure Genmod).

RESULTS
Effects of spur fruit load, leaf area, and specific leaf weight on subsequent spur survival

Nearly 100% of non-fruiting spurs survived the Winter period, while the percentage survival of single-fruited spurs was 86.5% (Table I). The estimated probability of survival (Π_S) for non-fruiting and single-fruited spurs into 2004, in relation to spur leaf area and SLW in 2003, indicated that the Π_S of non-fruiting spurs was highest for those spurs with high leaf areas and/or specific leaf weights (Figure 1). However, even those non-fruiting spurs with the lowest SLW values or leaf areas had a Π_S of approx. 0.95 (Figure 1).

Both spur leaf area and SLW were significantly related to the subsequent survival of single-fruited spurs ($P < 0.05$; Table II, Table III; and Table IV). The interaction between SLW and leaf area on spur survival was not significant ($P > 0.05$), and thus was not considered. Single-fruited spur Π_S was 0.98 for spurs with the highest leaf areas (57.4 cm^2), decreasing to 0.84 for spurs with the lowest leaf areas (3.3 cm^2; Figure 1A). Spur SLW had a more pronounced effect on subsequent survival of single-fruited spurs than did spur leaf area (Table IV; Figure 1). Within the range of SLW on tagged single-fruited spurs, Π_S dropped off rapidly from 0.99 for spurs with the highest SLW (12.6 mg cm^{-2}), to only 0.22 for spurs with the lowest SLW values (3.5 mg cm^{-2}; Figure 1B).

Effects of spur fruit load, leaf area, and specific leaf weight on spur return bloom

The probability that spurs would have at least one flower bud in the Spring was significantly ($P < 0.05$) related to spur fruiting status the previous-season (Table I; Table VII) and leaf area (Table V; Table VII), but not
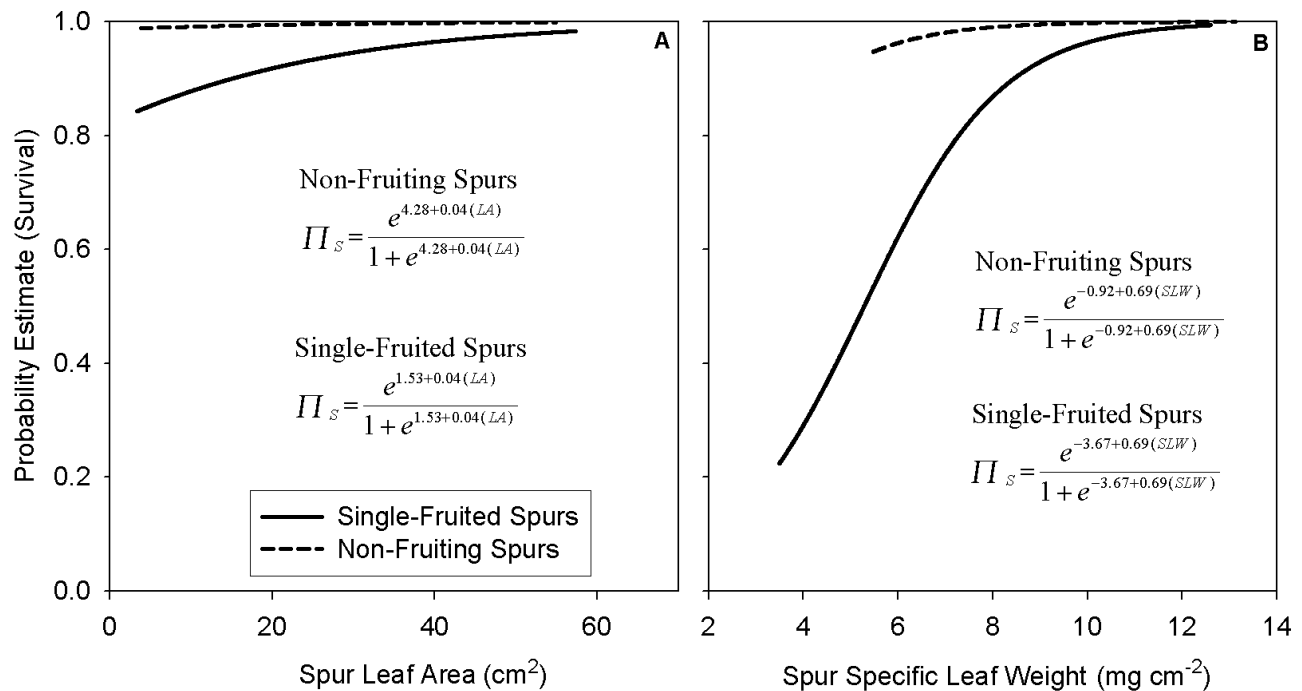

Non-Fruiting Spurs
$$\Pi_S = \frac{e^{4.28+0.04(LA)}}{1+e^{4.28+0.04(LA)}}$$

Single-Fruited Spurs
$$\Pi_S = \frac{e^{1.53+0.04(LA)}}{1+e^{1.53+0.04(LA)}}$$

Non-Fruiting Spurs
$$\Pi_S = \frac{e^{-0.92+0.69(SLW)}}{1+e^{-0.92+0.69(SLW)}}$$

Single-Fruited Spurs
$$\Pi_S = \frac{e^{-3.67+0.69(SLW)}}{1+e^{-3.67+0.69(SLW)}}$$

FIG. 1
The estimated probability (Π_S) of spur survival through 12 February 2004, modelled on (Panel A) the leaf area data (LA, on 7 May 2003, controlling for specific leaf weight) shown in Table II or (Panel B) the specific leaf weight data (SLW, on 25 July 2003, controlling for leaf area) shown in Table III. Leaf area was estimated non-destructively on 7 May 2003 using a regression equation for spur leaf area and the product of the length of the longest spur leaf and the number of spur leaves ($r^2 = 0.9137$; $P < 0.0001$).

TABLE IV

Logistic regression statistics[†] for type III analysis of the effects of spur fruiting status, leaf area[z] and specific leaf weight[y] in 2003 on whether or not spurs survived until 12 February, 2004

Effect[x]	Degrees of freedom	Wald Chi-Square	$P >$ Chi-Square
Spur fruiting status	1	43.79	< 0.0001
Spur leaf area	1	5.37	0.0205
Spur specific leaf weight	1	34.32	< 0.0001
Tree	8	16.71	0.0333

[z]Leaf area was estimated non-destructively on 7 May 2003, using the regression relationship of spur leaf area on that date to the product of spur leaf number and the length of the longest spur leaf ($r^2 = 0.9137$; $P < 0.0001$).
[y]Specific leaf weight was leaf dry weight per unit leaf area, and was measured on 25 July 2003.
[x]The model was selected by backward elimination of non-significant interactions.
[†]Data are shown in Table II and Table III.

SLW (Table VI; Table VII). Non-fruiting spurs were three-times more likely than single-fruited spurs to have flower buds the next Spring (Table I). The predicted probabilities of having at least one flower bud (Π_{RB}) were modelled on the data shown in Table II and Table III (Figure 2A). Among non-fruiting spurs, Π_{RB} declined dramatically with declining spur leaf area [i.e., Π_{RB} values were 0.99, 0.57 and 0.04 for high (55.0 cm^2), median (25.2 cm^2) and low (3.8 cm^2) leaf areas, respectively; Figure 2A]. At the highest leaf area (57.4 cm^2), the return bloom of single-fruited spurs was almost 100% (Π_{RB} = 0.97; Figure 2A). Similar to non-fruiting spurs, the Π_{RB} for single-fruited spurs declined with declining previous-season spur leaf area; but, to attain any given Π_{RB} value, single-fruited spurs required approx. 12 cm^2 more leaf area than did non-fruiting spurs (Figure 2A).

Effects of spur fruit removal and partial spur defoliation on spur survival through the subsequent Winter

Removal of immature fruit increased spur survival until the next season. Spurs bearing three fruit had a survival rate of 4.8%, compared with 62.8% survival for single-fruited spurs (Table VIII). When the fruit number per spur was reduced from three to one in mid-July (a few weeks before harvest), spur survival rates increased significantly ($P < 0.05$) to 25.3% (Table VII). The increase in spur survival rates of three-fruited spurs, from which two fruit had been removed in mid-April (shortly before embryo growth began), compared to spurs given the same treatment in mid-July, was not statistically significant ($P > 0.05$; Table VIII). Single-fruited spurs had

TABLE V

The relationship between leaf area and return bloom of single-fruited and non-fruiting spurs

Spur fruiting status (2003)	Spur leaf area (mg cm^{-2})[z] in 2003	Number of spurs	Return bloom (%)[y] (2004)
Single-Fruited	0–18	91	1.1
	18–30	166	15.1
	30–42	63	44.4
Non-Fruiting	0–18	76	14.5
	18–30	172	54.7
	30–42	109	81.7

[z]Leaf area was estimated on 7 May 2003, using the regression relationship between spur leaf area and the product of spur leaf number and length of the longest spur leaf ($r^2 = 0.9137$; $P < 0.0001$).
[y]Return bloom was the percentage of surviving spurs with at least one flower bud on 12 February 2004.

TABLE VI

The relationship between specific leaf weight (SLW) and return bloom of single-fruited and non-fruiting spurs

Spur fruiting status (2003)	Spur SLW in 2003 (mg cm^{-2})[z]	Number of spurs	Return bloom (%)[y] (2004)
Single-Fruited	0–8	83	9.6
	8–10	148	15.5
	10–12	98	29.6
Non-Fruiting	0–8	88	50.0
	8–10	177	55.9
	10–12	100	62.0

[z]SLW, leaf dry weight per unit leaf area, is a reliable indicator of relative leaf light exposure and was measured on 25 July 2003.
[y]Percentage of spurs with at least one flower bud in Spring 2004.

significantly ($P < 0.05$) higher survival rates than three-fruited spurs with two fruit removed either in mid-April or mid-July (Table VIII).

Partial spur defoliation (i.e., removal of all but the largest spur leaf) treatments significantly reduced the survival of single-fruited spurs through the subsequent Winter, especially when defoliation occurred early in the season. As mentioned previously, untreated single-fruited spur survival was 62.8% (Table IX). Partial spur defoliation in mid-July significantly ($P < 0.05$) reduced the survival of single-fruited spurs to 34.1% (Table IX). The survival of single-fruited spurs partially defoliated in mid-April was 25.3%, significantly ($P < 0.05$) lower than that of spurs that received the same treatment in mid-July (Table IX).

Effects of branch de-blossoming on subsequent season spur return bloom

In non-fruiting spurs, leaf areas were positively related to spur likelihood of return bloom, regardless of the fruiting status of the branch (Table X). The main effect of branch fruiting status on non-fruiting spur return bloom percentage was not significant ($P > 0.05$), but the interactive effect of branch fruiting status and spur leaf area on non-fruiting spur return bloom percentage was significant ($P < 0.05$; Table XI). At leaf areas ≤ 18 cm^2, non-fruiting spurs on both fruiting and non-fruiting branches exhibited ≤ 10% return bloom (Table X). Percentage return bloom increased with increasing spur leaf area more rapidly for non-fruiting spurs on non-fruiting branches than for non-fruiting spurs on fruiting branches (Table X). On non-fruiting branches, return

TABLE VII

Logistic regression statistics[†] for type III analysis of the effects of spur fruiting status, leaf area[z], and specific leaf weight[y] in 2003 on whether or not spurs had at least one flower bud on 12 February 2004

Effect[x]	Degrees of freedom	Wald Chi-Square	$P >$ Chi-Square
Spur fruiting status	1	120.26	< 0.0001
Spur leaf area	1	157.96	< 0.0001
Spur specific leaf weight	1	0.02	0.9007
Tree	8	34.37	< 0.0001
Spur fruiting status × Tree	8	20.84	0.0076

[z]Leaf area was estimated non-destructively on 7 May 2003, using the regression relationship of spur leaf area on that date to the product of spur leaf number and length of the longest spur leaf ($r^2 = 0.9137$; $P < 0.0001$).
[y]Specific leaf weight was leaf dry weight per unit leaf area and was measured from leaf hole punches sampled on 25 July 2003.
[x]The model was selected by backward elimination of insignificant interactions.
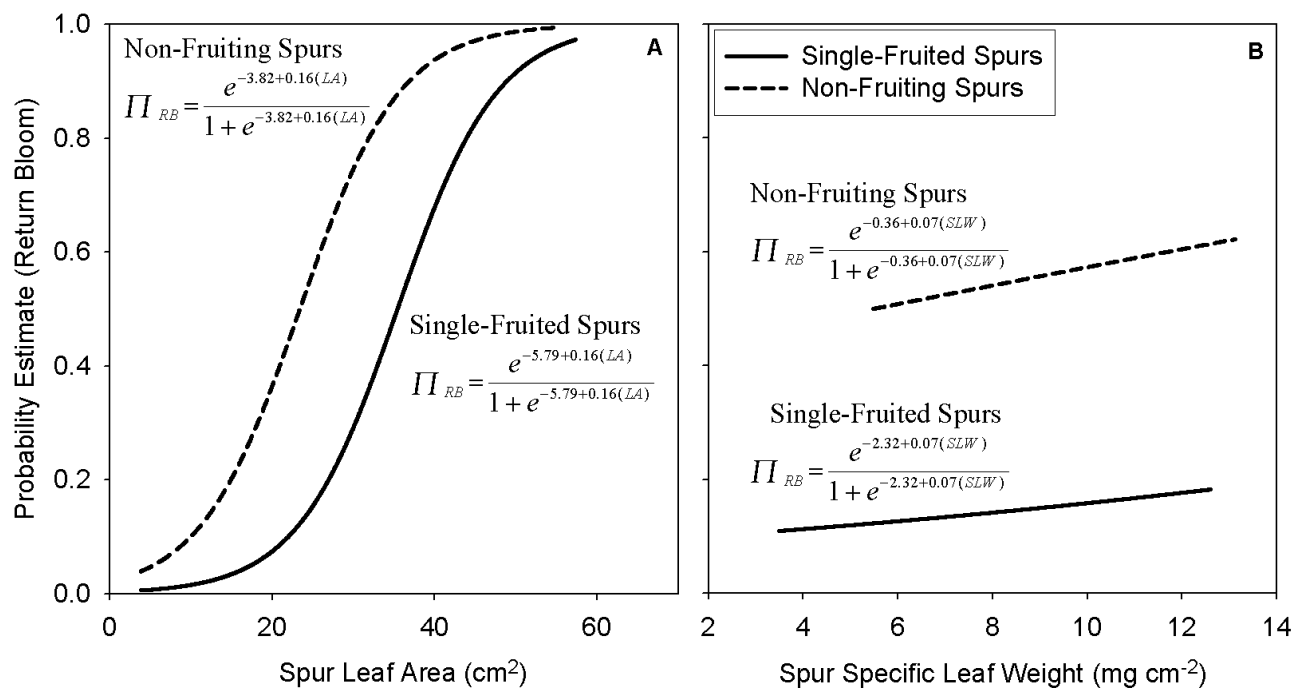[†]Data are shown in Table V and Table VI.

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The estimated probability (Π_{RB}) for surviving spurs having at least one flower bud on 12 February 2004, modelled on (Panel A) the leaf area data (LA, on 7 May 2003, controlling for specific leaf weight) shown in Table V or (Panel B) the specific leaf weight data (SLW, on 25 July 2003, controlling for leaf area) shown in Table VI. Spur leaf area was estimated non-destructively on 7 May 2003 using a regression equation for spur leaf area and the product of the length of the longest spur leaf and the number of spur leaves ($r^2 = 0.9137$; $P < 0.0001$).

bloom was $\geq 90\%$ for spurs in the $30 - 42$ cm^2 leaf area category. On fruiting branches, return bloom was only 55% for spurs in the $30 - 42$ cm^2 leaf area category (Table X). Figure 3 shows the estimated probability for return bloom (Π_{RB}) modelled on the data from Table X.

DISCUSSION

Fruit and seeds are the most competitive of plant carbon sinks (Kramer and Kozlowski, 1979). In trees, fruiting has been associated with decreased current-season vegetative growth (Costes *et al.*, 2000; Maggs, 1963; Whiting and Lang, 2004), decreased subsequent-season flowering (Palmer *et al.*, 1991; Palmer, 1992; Wood, 1995), and decreased survival rates (Allen and Antos, 1993; Lovett Doust and Lovett Doust, 1988). In many tree genera, including oak (Sork *et al.*, 1993), beech (Hilton and Packham, 2003), pistachio, pecan and apple (Monselise and Goldschmidt, 1982), the effects of fruiting on growth and flowering often create an

"alternate bearing" or "masting" cycle in which the intensity of fruiting oscillates between very heavy 'On' seasons and very light 'Off' seasons.

Almond trees have only a mild tendency toward alternate bearing (USDA NASS, 2004). Nevertheless, our work shows that individual almond spurs have a strong tendency toward alternate bearing. That is, fruiting on a spur is associated with a reduced likelihood, for that spur, of surviving over Winter and blooming the next Spring (Table I). Since the fruiting status of a spur in the next season is contingent upon survival of that spur over Winter and production of at least one flower in the subsequent Spring, current-season spur fruiting dramatically reduced the potential of a spur for fruiting in the following season. Consistent with these results, Reidel *et al.* (2004), in almond, and Klein *et al.* (1991b), in Persian walnut [*Juglans regia* L., which also has a slight tendency toward alternate bearing (USDA NASS, 2004)], also showed that fruiting spurs had substantially lower Winter survival and return bloom rates than non-

TABLE VIII

The effect of fruit number per spur and fruit removal date in the 2003 growing season on spur survival rates over the subsequent Winter

Spur treatment	No. of surviving spurs	No. of dead spurs	Spur survival in 2004 (%)[x]
One fruit – no removal	59	35	62.8 a
Fruit removal in mid-April[z]	28	45	38.4 b
Fruit removal in mid-July[y]	23	68	25.3 b
Three fruit – no removal	4	79	4.8 c

[z]Three-fruited spurs with two fruit removed on 17 April 2003, before the initiation of embryo development.
[y]Three-fruited spurs with two fruit removed between 11–14 July 2003, a few weeks before harvest.
[x]Percentages accompanied by the same lower-case letter are not significantly different ($P < 0.05$) according to least squares means contrasts.

TABLE IX

The effect of partial defoliation in the 2003 growing season on mortality rates of single-fruited spurs over the subsequent Winter

Spur treatment	No. of surviving spurs	No. of dead spurs	Spur survival in 2004 (%)[x]
Leaf removal (mid-April)[z]	19	56	25.3 c
Leaf removal (mid-July)[y]	30	58	34.1 b
No leaf removal (control)	59	35	62.8 a

[z]All leaves but the largest spur leaf were removed on 17 April 2003, before the initiation of embryo development.
[y]All leaves but the largest spur leaf were removed on 11–14 July 2003, a few weeks before harvest.
[x]Percentages accompanied by the same lower-case letter are not significantly different ($P < 0.05$) according to least squares means contrasts.

TABLE X
The relationship between leaf area and return bloom of non-fruiting spurs on fruiting and non-fruiting branches

Spur fruiting status[z] (2003)	Spur leaf area in 2002 (cm^{-2})[y]	Number of spurs	Return bloom (%)[x] (2003)
Fruiting branches	0–18	22	4.5
	18–30	41	29.3
	30–42	53	54.7
	≥ 42	16	68.8
Non-fruiting branches	0–18	11	9.1
	18–30	25	72.0
	30–42	47	93.6
	≥ 42	45	97.8

[z]'Fruiting' branches were allowed to set fruit naturally. 'Non-fruiting' branches had all blossoms removed at full bloom on 26 February 2002.
[y]Leaf area was estimated on 21 August 2002, using the regression relationship between spur leaf area and the product of spur leaf number and length of the longest spur leaf ($r^2 = 0.8951$; $P < 0.0001$).
[x]Percentage of spurs with at least one flower bud in Spring 2003.

$$\Pi_S = \frac{e^{-5.06+0.22(LA)}}{1+e^{-5.06+0.22(LA)}}$$

$$\Pi_S = \frac{e^{-3.50+0.10(LA)}}{1+e^{-3.50+0.10(LA)}}$$

FIG. 3
The estimated probability (Π_{RB}) for spurs bearing no fruit in 2002, of having at least one flower bud on 8 February 2003, modelled on the data shown in Table X. 'Non-Fruiting' branches had all blossoms removed on 26 February 2002, while 'Fruiting' branches were allowed to set fruit naturally. Spur leaf area (LA) was estimated non-destructively using a regression relationship between spur leaf area and the product of leaf number per spur and length of the longest spur leaf ($r^2 = 0.8951$; $P < 0.0001$).

fruiting spurs. A large proportion of the bearing units must have synchronised bearing cycles, in order for whole trees to bear alternately. The relationships of whole-tree alternate bearing to the carbon semi-autonomy of individual bearing units, and the synchrony of bearing cycles within tree canopies, are still unclear.

Winter survival of almond spurs was strongly associated with the potential for carbohydrate production by its own leaves, even though the time of spur death may have been during dormancy, when leaves were no longer present on the tree. Non-fruiting spurs, regardless of leaf area or SLW, nearly always survived the Winter (Table II; Table III; Figure 1). But, among single-fruited spurs, high spur leaf area (Table II; Figure 1A), long leaf persistence time (Table IX) and, to a greater extent, high SLW (Table III; Figure 1B) increased the likelihood of subsequent Winter survival. This corresponded to previous studies showing that defoliating (Marquis, 1992; Mitchell *et al.*, 2004; Ruohomäki *et al.*, 1997) or shading (Henriksson, 2001; Klein *et al.*, 1991b; Sprugel, 2002; Stoll and Schmid, 1998; Takenaka, 2000) reduced shoot survival in diverse woody plant species. This phenomenon has been proposed to be a means by which trees prevent weak shoots, that are unable to meet their own carbohydrate demands, from "parasitising" the rest of the tree (Sprugel *et al.*, 1991).

Shaded fruiting spurs had low survival rates (Figure 1). Thus, we expect that very heavily cropping trees, especially those in which a high proportion of the spurs

TABLE XI
Logistic regression statistics[†] for type III analysis of the effects of branch fruiting status[z] and spur leaf area[y] in 2002 on the probability that non-fruiting spurs would have at least one flower bud on 8 February 2003

Effect[x]	Degrees of freedom	Wald Chi-Square	$P >$ Chi-Square
Spur fruiting status (Br)	1	0.50	0.4793
Spur leaf area (LA)	1	85.41	< 0.0001
Tree	2	11.09	0.0039
LA × Br	1	5.08	0.0242
LA × Tree	2	11.51	0.0032

[z]All flowers were removed from non-fruiting branches on 26 February, 2002. Fruiting branches were allowed to set fruit naturally.
[y]Spur leaf area was estimated on 21 August 2002, using the regression relationship between spur leaf area and the product of spur leaf number and length of the longest spur leaf ($r^2 = 0.8951$; $P < 0.0001$)).
[x]The model was selected by backward elimination of insignificant interactions.
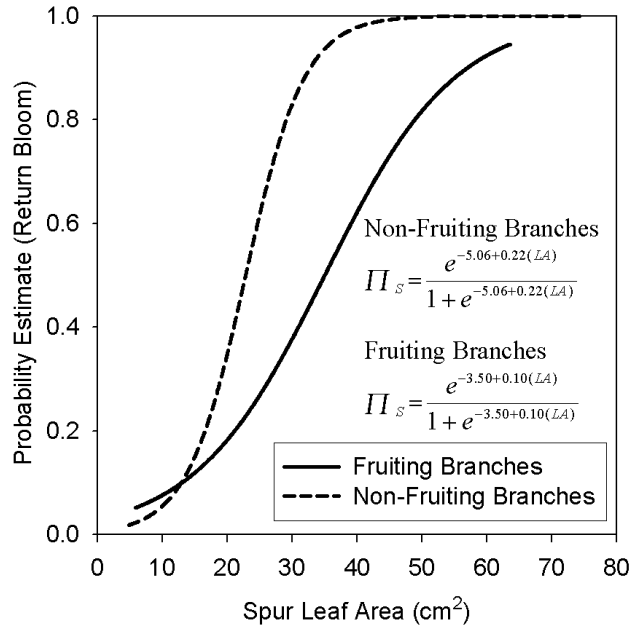[†]Data are shown in Table X.

were in shaded canopy positions, would have decreased overall spur survival rates. The effect of heavy cropping on spur renewal rates has not yet been quantified, but, unless dying spurs are replaced, spur numbers (and presumably yields) on heavily cropping trees with shaded canopies would decline over time.

Floral initiation, in almond, occurs late in the Summer of the year prior to bloom (Lamp *et al.*, 2001). Polito *et al.* (2002) found that the number of flower buds initiated on spurs increased with leaf area. Similarly, we found, for both single-fruited and non-fruiting spurs, that spur leaf area positively affected return bloom (Table V; Figure 2A). Higher leaf areas per spur appeared to compensate for the effect of the additional carbohydrate demands of fruiting spurs on spur floral initiation. Thus, given an additional 12 cm^2 leaf area, single-fruited spurs attained the same levels of return bloom as non-fruiting spurs (Figure 2A). Dramatic reductions in branch-wide carbohydrate demand (i.e., removal of all flowers or fruit), however, decreased the leaf area required for non-fruiting spurs to attain 100% return bloom (Table X; Figure 3), indicating that some movement of carbohydrates between spurs on the same branch probably did occur. Nevertheless, the consistent and strong relationship between spur leaf area and spur return bloom suggests that floral initiation on each spur relied heavily on the active area of its own leaves.

While the localisation of fruiting effects within spurs tended to promote alternate bearing on individual spurs, the localisation of leaf area effects within spurs created spur sub-populations with greater or lesser tendencies toward alternate bearing. Non-fruiting spurs with a low leaf area rarely initiated flower buds, and fruiting spurs

with a high leaf area usually initiated at least one flower bud (Table V; Figure 2A), making these spur sub-populations more likely than other spurs to have two consecutive non-fruiting ('Off') or fruiting ('On') years. The proportion of spurs in the various leaf area sub-populations is probably important in determining return bloom at the whole-tree level after a season when either most spurs in the canopy bore no fruit, or when most spurs had fruit.

In conclusion, it appears that almond spurs have a high degree of carbon-autonomy during the late Summer until the following Spring, with over-Winter survival and return bloom on each individual spur being associated with the potential for carbon fixation by its own leaves. If there was little restriction on carbon movement among spurs in a canopy (i.e., a low degree of spur carbon-autonomy), differences in Winter survival and return bloom between spurs would be expected to be small, because spurs having a high carbohydrate supply relative to their demand could "share" carbohydrates with spurs having a low carbohydrate supply relative to their demand. Our data show that the opposite situation is generally the case in almond. The negative effects of a low spur carbohydrate supply-demand balance on spur floral initiation and Winter survival appeared to be localised, to a large extent, within fruiting, low leaf area, and/or shaded sub-populations of spurs.

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