

Is nitrogen stress more apparent in shaded, fruiting almond spurs than in exposed, non-fruiting spurs?

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SUMMARY

Leaf abscission rates and nitrogen concentrations in persistent leaves were tracked on non-fruiting and fruiting almond [*Prunus dulcis* (Mill.) D.A. Webb] spurs located in either well-exposed or shaded canopy positions. Fruiting spurs, especially in shaded positions, had higher mid-season leaf abscission rates than did non-fruiting spurs, and the difference in abscission rates between shaded, fruiting spurs and other spur sub-populations increased with tree nitrogen deficiency. Nitrogen concentrations and contents of persistent leaves were lower on fruiting spurs than on non-fruiting spurs. Nitrogen contents of persistent leaves did not decline substantially over the period of kernel development (a period of high nitrogen demand by the fruit) regardless of spur shading and fruiting status, or tree nitrogen status. This indicates that little net nitrogen remobilisation from persistent leaves occurred during this period, even on fruiting spurs on nitrogen-deficient trees. Nitrogen deficiency accentuated nitrogen stress in shaded and fruiting spurs, as indicated by early leaf abscission. However, such differential stress was not reflected by the nitrogen concentration or content of persistent leaves during kernel development. Thus, sampling of persistent leaves from the shaded, fruiting spur sub-population for nitrogen analyses did not provide a practical, more sensitive diagnostic indicator of tree nitrogen status than did conventional leaf sampling from non-fruiting spurs.

Leaves of well-managed almond [*Prunus dulcis* (Mill.) D.A. Webb] trees typically senesce in the Autumn, but when trees are nitrogen (N)-deficient (i.e., N availability is insufficient to meet tree N demand), leaf senescence can occur mid-season (Brown and Uriu, 1996). Leaf proteins (particularly the Calvin Cycle enzyme Rubisco) are hydrolysed during leaf senescence, and much of the leaf N is translocated out of the leaf prior to leaf abscission (Castagnoli *et al.*, 1990; Millard and Thomson; 1989, Sanchez and Righetti, 1990). Early leaf senescence and N remobilisation in annual plants, especially during the seed-filling period, is part of a well-described process of internal N cycling that allows sustained growth, even when N supply from the soil is low (Sesay and Shibles, 1980; Simpson *et al.*, 1983). Leaf N resorption in response to reproductive N demand has also been reported to occur in fruit-tree species (Sparks, 1977; Uriu and Crane, 1977; Weinbaum *et al.*, 1994).

Symptoms of leaf N stress (i.e., leaf mid-season N remobilisation, senescence and/or abscission) will not necessarily emerge uniformly within an almond canopy, because almond spur shoots seemingly function as semi-independent sub-units of the tree canopy (Heerema, 2005; Heerema *et al.*, 2008). Differences in fruiting status and light exposure between spurs may result in variability among spurs in the balance of N supply and demand, because almond fruit, especially growing kernels, have a high demand for N (Weinbaum and Muraoka, 1986), and N tends to be allocated

preferentially (at least on a per unit leaf area basis) to the well-lit leaves in tree canopies (DeJong *et al.*, 1989; Klein *et al.*, 1991; Weinbaum *et al.*, 1989). Thus, if leaf N stress in an almond canopy is isolated within individual spurs, then leaves on fruiting spurs in shaded canopy positions of N-deficient trees should exhibit more severe symptoms of N stress than leaves on non-fruiting spurs.

To apply N optimally, orchardists need a good diagnostic gauge of tree N status. The aim of this study was to determine whether or not the sensitivity of almond spur leaves to tree N status is related to spur fruiting status and light exposure. Currently, most California almond growers base N management decisions on N concentrations in leaves sampled in July from non-fruiting spurs (Beutel *et al.*, 1983; Brown and Uriu, 1996). If shaded, fruiting spurs are the most sensitive indicators of tree N status, perhaps sampling leaves for N analyses from these spurs would allow detection of N stress before it is evident in conventionally-sampled leaves of non-fruiting spurs.

MATERIALS AND METHODS

Eight-year-old 'Nonpareil' almond trees growing in an orchard in Lost Hills, CA (35° N, 119° W) were used in this experiment. Two extremes of tree N status were established: a row of five trees were subjected to a 'Low N' treatment, and a row of five trees were subjected to a 'High N' treatment. In 2003, the 'Low N' trees received 140 kg ha⁻¹ N (applied as urea ammonium nitrate solution *via* a micro-sprinkler irrigation system) and the 'High N' trees received 280 kg ha⁻¹ N. Both the 'Low N' and 'High N' trees were mildly N-deficient in 2003 (data not shown). In order to ensure differences in tree N

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status between the two treatments, and that the 'High N' trees would not be N-deficient in 2004, the 'Low N' trees received no applications of N during the 2004 season while the 'High N' trees, in addition to receiving 280 kg ha⁻¹ N, had 75% of their fruit removed on 16 April 2004, to reduce tree N demand.

Five spurs in each of four different spur categories, distinguished on the basis of fruiting status and canopy location, were tagged on each of the trees. The four spur categories were: (1) single-fruited spurs in "well-exposed" canopy positions; (2) non-fruited spurs in "well-exposed" canopy positions; (3) single-fruited spurs in "shaded" canopy positions; and (4) non-fruited spurs in "shaded" canopy positions. "Well-exposed" canopy positions were located > 4 m from the ground, in the outer periphery of the canopy on the southern side of the trees. Spurs in these positions received direct sunlight for a substantial part of the day. "Shaded" positions were located in low, interior parts of the canopy, and received very little direct sunlight throughout the day. In 2004, the number of leaves per spur was recorded on 31 May, 29 June, 26 July, and 28 September. Kernel development began shortly after the 31 May sampling date, and harvest occurred shortly after the 26 July sampling date (data not shown). Statistical comparisons of spur leaf persistence were made using logistic regression (SAS Procedure Logistic; SAS Institute, Cary, NC, USA).

Persistent leaves were sampled destructively from two spurs in each of the same four categories as the tagged spurs, on each tree on 1 June and on 26 July 2004. Digital photographs were made of the spur leaves compressed under glass, and spur leaf area was measured using Sigma Scan Pro image analysis software (SYSTAT, Richmond, CA, USA). Leaves were dried in an oven at 60°C for 3 d then ground in a Wiley mill to pass a 40-mesh screen. Nitrogen analyses of leaf tissues were performed at the University of California, Davis Stable Isotope Facility. Samples were combusted to N₂ in a PDZ Europa ANCA sample combustion unit, and total sample N was measured using a PDZ Europa 20-20 continuous flow isotope ratio mass spectrometer (Sercon Ltd., Crewe,

UK). Analyses of variance were performed for spur leaf N concentration and spur leaf N per unit leaf area (SAS Procedure GLM; SAS Institute).

RESULTS

Spur canopy position, spur fruiting status, as well as their interaction, significantly affected spur leaf retention (Table I). Shaded, single-fruited spurs had the lowest average number of leaves, while the exposed non-fruited spurs had the highest number of leaves on the first leaf sampling date (Figure 1). The shaded, single-fruited spurs had much higher rates of premature leaf abscission over the season than any of the other spur categories, therefore the difference in average leaf number per spur between shaded, single-fruited spurs and the other three categories became greater over time (Figure 1). By 28 September, shaded, single-fruited spurs on both 'High N' and 'Low N' trees had lost over 50% of their leaves that had been present on 31 May, while spurs in the other three categories had abscised only 30%, or fewer, of their leaves (Figure 1).

The main effect of tree N treatment on leaf persistence until 28 September was not significant (Table I). Likewise, the interactive effect of tree N

TABLE I
Logistic regression statistics for type III analysis of effects of tree nitrogen treatment^a, spur fruiting status, and spur canopy position^b on whether or not almond spur leaves present on 31 May 2004 were retained through 28 September 2004. Data are shown in Figure 1

| Effect ^c | df | Chi-Square | P > Chi-Square |
|---------------------------|----|------------|----------------|
| Nitrogen Treatment (N) | 1 | 0.00 | 0.9952 |
| Spur Canopy Position (CP) | 1 | 9.22 | 0.0024 |
| Spur Fruiting Status (FS) | 1 | 5.26 | 0.0219 |
| Tree | 8 | 21.45 | 0.0060 |
| N × CP | 1 | 0.34 | 0.5610 |
| N × FS | 1 | 4.26 | 0.0391 |
| CP × FS | 1 | 7.34 | 0.0067 |
| CP × Tree | 8 | 23.37 | 0.0029 |
| FS × Tree | 8 | 23.33 | 0.0030 |
| N × CP × FS | 1 | 0.25 | 0.6189 |

^aNitrogen concentrations in conventionally-sampled leaves were 2.40% (w/w) (within the nitrogen-adequacy range for almond) and 1.62% (w/w) (below the threshold of almond nitrogen-deficiency) for 'High N' and 'Low N' trees, respectively.

^bSpur categories included non-fruited and single-fruited spurs located in either well-exposed or shaded canopy positions.

^cAll non-significant three-way and higher interactions, except N × CP × FS, were removed from the model by backwards elimination. The effect of variability in initial (i.e., on 31 May) leaf number among spurs, on spur leaf retention, was significant and was included in the model, but the statistics are not presented.

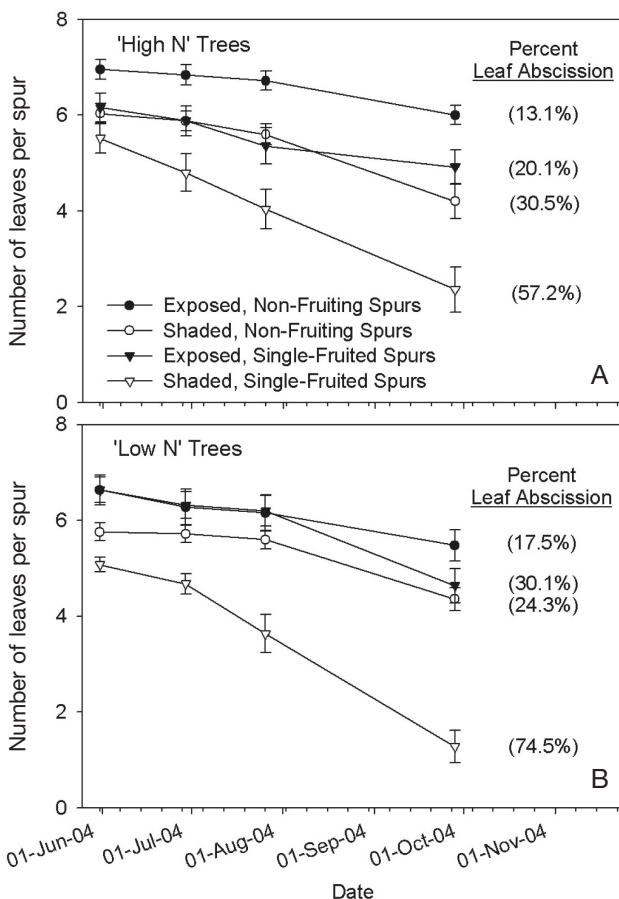


FIG. 1

The temporal pattern of leaf number per spur, from 31 May to 28 September 2004, for four spur sub-populations differing in fruiting status and canopy position. Data are means ± SE and are shown for (Panel A) High N^a [nitrogen adequate; i.e., average conventionally-sampled leaf nitrogen concentration of 2.40% (w/w)] and (Panel B) 'Low N' [nitrogen deficient; i.e., average conventionally-sampled leaf nitrogen concentration of 1.62% (w/w)] almond trees.

TABLE II

The relationship of 'Nonpareil' almond spur leaf nitrogen (N) concentration to spur fruiting status and canopy position on 1 June 2004 and 26 July 2004. Data are shown for trees receiving either a 'High N' or 'Low N' treatment^b

| Spur Category | Leaf N Concentration [% (w/w)] | |
|-------------------------|--------------------------------|--------------|
| | 1 June 2004 | 26 July 2004 |
| Exposed, Non-Fruiting | | |
| 'High N' trees | 3.30 ± 0.04 ^a | 2.40 ± 0.03 |
| 'Low N' trees | 2.40 ± 0.04 | 1.62 ± 0.02 |
| Exposed, Single-Fruited | | |
| 'High N' trees | 3.09 ± 0.08 | 2.30 ± 0.04 |
| 'Low N' trees | 2.01 ± 0.07 | 1.42 ± 0.04 |
| Shaded, Non-Fruiting | | |
| 'High N' trees | 3.07 ± 0.07 | 2.36 ± 0.05 |
| 'Low N' trees | 2.24 ± 0.04 | 1.64 ± 0.04 |
| Shaded, Single-Fruited | | |
| 'High N' trees | 2.63 ± 0.07 | 2.14 ± 0.08 |
| 'Low N' trees | 1.90 ± 0.07 | 1.32 ± 0.05 |

^a'High N' trees received 280 kg ha⁻¹ N in 2003 and 2004 and had 75% of fruits removed in Spring 2004. 'Low N' trees received 140 kg ha⁻¹ N in 2003 and no N applications in 2004.

^bData are means ± standard error. All persistent spur leaves on the given date were included in the sample.

treatment and spur canopy position on leaf persistence was not significant, but the interaction between tree N treatment and spur fruiting status was significant (Table I). In shaded canopy positions, leaf abscission rates on single-fruited spurs between 31 May and 28 September were much lower on 'High N' than on 'Low N' trees: 57% and 75% of leaves abscised on 'High N' and on 'Low N' trees, respectively (Figure 1). During the same period, and in the same canopy positions, leaf abscission rates on non-fruited spurs were similar on 'High N' (31% leaf abscission) and 'Low N' (24% leaf abscission) trees (Figure 1).

Nitrogen concentrations were higher for leaves sampled on 1 June than on 26 July (Table II; Table III), but leaf N per unit leaf area changed very little between those two dates (Table IV; Table V). On both sampling dates, shading and fruiting were associated with significantly lower spur leaf N concentrations (Table II; Table III) and leaf N per unit leaf area (Tables IV; Table V). Leaves sampled from 'Low N' trees had significantly lower N concentrations (Table II; Table III) and N per unit area (Table IV; Table V) than leaves sampled from 'High N' trees. No interactive effects of N

TABLE III

Analysis of variance for the nitrogen (N) concentration data shown in Table II

| Sampling date/ Source of Variation | df | SS | MS | F | P > F |
|---------------------------------------|----|-------|-------|--------|----------|
| 1 June 2004 | | | | | |
| N Treatment (N) | 1 | 15.70 | 15.70 | 410.15 | < 0.0001 |
| Spur Fruiting Status (FS) | 1 | 2.41 | 2.41 | 62.91 | < 0.0001 |
| Spur Canopy Position (CP) | 1 | 1.17 | 1.17 | 30.47 | < 0.0001 |
| N × FS | 1 | 0.01 | 0.01 | 0.28 | 0.6007 |
| N × CP | 1 | 0.22 | 0.22 | 5.71 | 0.0195 |
| FS × CP | 1 | 0.04 | 0.04 | 1.03 | 0.3125 |
| N × FS × CP | 1 | 0.10 | 0.10 | 2.60 | 0.1114 |
| 26 July 2004 | | | | | |
| N Treatment (N) | 1 | 12.81 | 12.81 | 554.26 | < 0.0001 |
| Spur Fruiting Status (FS) | 1 | 0.92 | 0.92 | 39.73 | < 0.0001 |
| Spur Canopy Position (CP) | 1 | 0.10 | 0.10 | 4.15 | 0.0453 |
| N × FS | 1 | 0.05 | 0.05 | 2.27 | 0.136 |
| N × CP | 1 | 0.02 | 0.02 | 0.72 | 0.4005 |
| FS × CP | 1 | 0.07 | 0.07 | 3.04 | 0.0856 |
| N × FS × CP | 1 | 0.00 | 0.00 | 0.02 | 0.8893 |

TABLE IV

The relationship of 'Nonpareil' almond spur leaf nitrogen (N) per unit leaf area to spur fruiting status and canopy position on 1 June 2004 and 26 July 2004. Data are shown for trees receiving either a 'High N' or 'Low N' treatment^b

| Spur Category | Leaf N per Unit Leaf Area (mg cm ⁻²) | |
|-------------------------|--|--------------|
| | 1 June 2004 | 26 July 2004 |
| Exposed, Non-Fruiting | | |
| 'High N' trees | 0.26 ± 0.01 ^a | 0.25 ± 0.01 |
| 'Low N' trees | 0.20 ± 0.01 | 0.18 ± 0.01 |
| Exposed, Single-Fruited | | |
| 'High N' trees | 0.23 ± 0.01 | 0.22 ± 0.01 |
| 'Low N' trees | 0.14 ± 0.01 | 0.15 ± 0.01 |
| Shaded, Non-Fruiting | | |
| 'High N' trees | 0.18 ± 0.01 | 0.16 ± 0.01 |
| 'Low N' trees | 0.15 ± 0.01 | 0.13 ± 0.01 |
| Shaded, Single-Fruited | | |
| 'High N' trees | 0.15 ± 0.01 | 0.14 ± 0.01 |
| 'Low N' trees | 0.13 ± 0.01 | 0.11 ± 0.00 |

^a'High N' trees received 280 kg ha⁻¹ N in 2003 and 2004 and had 75% of fruits removed in Spring 2004. 'Low N' trees received 140 kg ha⁻¹ N in 2003 and no N applications in 2004.

^bData are means ± standard error. All persistent spur leaves on the given date were included in the sample.

treatment, spur fruiting status, and spur canopy location, on spur leaf N concentration were statistically significant, except that of N treatment and spur canopy location on 1 June (Table III). The interactive effect of N treatment and spur canopy location on spur leaf N per unit leaf area was significant on both leaf sampling dates (Table V). None of the other interactive effects of N treatment, spur fruiting status, and spur canopy location, on spur leaf N per unit leaf area were significant on either leaf sampling date (Table V).

DISCUSSION

Other studies in almond have shown that the reductions in shoot survival, return bloom, leaf growth, and fruit set associated with fruiting are observed principally at the spur level (Heerema, 2005; Heerema *et al.*, 2008). The data in the present study are also consistent with the idea that spurs function as semi-independent sub-units in almond canopies and, consequently, stresses are expressed locally within individual spurs.

The N supply-demand balance in an almond spur

TABLE V

Analysis of variance for the nitrogen (N) per unit leaf area data shown in Table IV

| Sampling date/ Source of Variation | df | SS | MS | F | P > F |
|---------------------------------------|----|------|------|--------|----------|
| 1 June 2004 | | | | | |
| N Treatment (N) | 1 | 0.05 | 0.05 | 51.91 | < 0.0001 |
| Spur Fruiting Status (FS) | 1 | 0.02 | 0.02 | 26.37 | < 0.0001 |
| Spur Canopy Position (CP) | 1 | 0.06 | 0.06 | 66.67 | < 0.0001 |
| N × FS | 1 | 0.00 | 0.00 | 1.31 | 0.2559 |
| N × CP | 1 | 0.01 | 0.01 | 14.48 | 0.0003 |
| FS × CP | 1 | 0.00 | 0.00 | 1.00 | 0.3218 |
| N × FS × CP | 1 | 0.00 | 0.00 | 1.31 | 0.2559 |
| 26 July 2004 | | | | | |
| N Treatment (N) | 1 | 0.05 | 0.05 | 92.45 | < 0.0001 |
| Spur Fruiting Status (FS) | 1 | 0.02 | 0.02 | 34.18 | < 0.0001 |
| Spur Canopy Position (CP) | 1 | 0.08 | 0.08 | 156.61 | < 0.0001 |
| N × FS | 1 | 0.00 | 0.00 | 0.11 | 0.7362 |
| N × CP | 1 | 0.01 | 0.01 | 10.48 | 0.0018 |
| FS × CP | 1 | 0.00 | 0.00 | 0.39 | 0.5319 |
| N × FS × CP | 1 | 0.00 | 0.00 | 0.00 | 0.9616 |

apparently affects its sensitivity, in terms of mid-season leaf abscission rate, to differences in tree N status. Almond trees are considered N-deficient when the N concentration of conventionally-sampled leaves (i.e., from non-fruiting spurs in July) is at, or below 2.0% (w/w) (Weinbaum *et al.*, 1996). In our experiment, 'Low N' trees had an average leaf (conventionally-sampled) N concentration of 1.6% (w/w) (Table II). Early leaf senescence and abscission are associated with a number of different plant stresses, including N stress (Thomas and Stoddard, 1980). N-deficiency in 'Low N' trees clearly accentuated early leaf abscission on spurs with a high N-demand (i.e., fruiting spurs), but had little effect on leaf abscission of non-fruiting spurs (Figure 1; Table I). Reidel *et al.* (2004) found that, in almond, potassium (K) deficiency also accentuated stress in fruiting spurs. They showed that fruiting spur mortality rates over Winter were higher in K-deficient almond trees than in high-K trees, but that mortality rates of non-fruiting spurs were not affected by tree K status.

The number of flowering and fruiting spurs is one of the major determinants of yield in mature almond trees (Kester and Asay, 1975; Weinbaum and Spiegel-Roy, 1985). Artificial defoliation of fruiting almond spurs decreased subsequent spur survival. Furthermore, both spur survival and return-bloom rates were positively related to previous season spur leaf area (Heerema *et al.*, 2008). Thus, it seems probable that, for N-deficient almond trees, increased early leaf abscission on fruiting spurs, especially in shaded parts of the canopy, leads to reduced overall survival and return bloom rates of spurs, and thus may be a significant factor in causing declining yields over time.

Leaf N levels were related to spur canopy position (Tables II – V). On 26 July, specific leaf weight (i.e., leaf dry weight per unit leaf area) was approx. 30% lower for spurs in "shaded" than in "well-exposed" canopy positions (data not shown). Specific leaf weight on a given date is a reliable indicator of the relative exposure of leaves to light (Klein *et al.*, 1991; Marini and Marini, 1983; Weinbaum *et al.*, 1989), so it appears that there was a large difference in light exposure between the two canopy positions. In diverse tree species, shade leaves have been characterised by having lower leaf N contents per unit leaf area than sun leaves (Huett *et al.*, 2001; Klein *et al.*, 1991; Niinemets *et al.*, 2004; Walcroft *et al.*, 2002), and our data confirm this relationship for almond (Table IV; Table V). The relationship between leaf N concentration and leaf light exposure, however, varies between species. In walnut (*Juglans regia* L.) canopies, leaf N concentration was constant across a range of leaf photon flux densities (Klein *et al.*, 1991). In other tree species, both positive (Huett *et al.*, 2001; Kull and Niinemets, 1993; Warren and Adams, 2001) and negative (Kull and Niinemets, 1993; Syvertsen *et al.*, 2003) relationships between leaf light exposure and leaf N concentration have been reported. Our data suggest that there may be a positive relationship between light exposure and leaf N concentration for almond, especially on fruiting spurs, because leaves in "well-exposed" canopy locations had higher leaf N concentrations than those sampled from "shaded" canopy locations (Table II).

Intra-spur competition for N between developing fruit and leaves was apparent by 1 June, before kernel growth

had begun, when fruiting spurs had lower spur leaf N concentrations (Table II; Table III) and leaf N per unit leaf area (Table IV; Table V) than non-fruiting spurs. However, despite higher levels of leaf abscission on fruiting spurs than on non-fruiting spurs (Figure 1), there was no evidence that any net remobilisation of N from persistent leaves was occurring on fruiting spurs during kernel development (1 June to 26 July). During leaf senescence, usually about half of leaf N is remobilised and translocated from leaves (Aerts, 1996; Castagnoli *et al.*, 1990), but leaf N contents per unit leaf area in the current study were similar before kernel growth had begun, and when the kernel was almost mature (Table IV). Thus, the difference in N content between leaves of fruiting and non-fruiting spurs was, for the most part, already established before kernel growth had begun. Single-fruited and non-fruiting spur leaf N concentrations declined considerably during the period of kernel development (Table II), but this was not apparently due to net N remobilisation from leaves. Instead, this decline appeared to be related to increases in specific leaf weight over this period (data not shown).

Data from the present research agree with an isotopically-labelled-N study by Weinbaum and Muraoka (1986). They showed that N was exported from the leaves of fruiting almond spurs during the period of kernel development, but that N-efflux from the leaves was balanced by N-influx (probably from uptake from the soil) during the same period, so that leaf N content per unit leaf area remained stable. Contrasting results have been reported in walnut, where both non-fruiting and fruiting spurs exhibited a considerable reduction in N content during the period of kernel growth, but the level of N demand by developing kernels on a spur affected the balance of N-influx and N-efflux into spur leaves, so that fruiting spurs had two-to-four-times greater net leaf N remobilisation during kernel growth than non-fruiting spurs (Weinbaum *et al.*, 1994). Our work showed that, even under N-deficient conditions, local N demand by a growing kernel apparently did not affect the N influx-efflux balance of persistent almond spur leaves and, as a result, no net N remobilisation from these leaves could be detected during kernel growth. We did not measure N contents in abscised leaves; but, since there were increased leaf abscission rates on N-deficient trees, it is likely that there were increases in N remobilisation from the abscising leaves of fruiting spurs on N-deficient trees. This probably accounted for a relatively small percentage of total spur leaf N, however, because the small basal leaves are usually the first to senesce and abscise (personal observation).

If the difference in N concentration between trees of high and low N status was greatest for leaves sampled from shaded, fruiting spurs, growers could detect variations in tree N status by sampling leaves from these spurs more easily than from non-fruiting spurs. This would be true if, under tree N-deficiency, net N remobilisation were to occur from shaded, fruiting spur leaves to a greater extent than from non-fruiting spur leaves. However, it appears that such differential leaf N remobilisation may have occurred for only a portion of the spur leaves (i.e., the leaves which had already abscised); but the difference in N concentration in

persistent leaves between 'High N' and 'Low N' trees was similar for all four sub-populations of spurs. Apparently, leaves undergoing senescence on shaded, fruiting spurs abscise too quickly to be captured consistently in a leaf sample. Thus, contrary to our original hypothesis, using leaves sampled from shaded, fruiting spurs for diagnostic N analyses would not provide a practical, more sensitive indicator of tree N

status than leaves sampled according to the conventional protocol.

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REFERENCES

- AERTS, R. (1996). Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology*, **84**, 597–608.
- BEUTEL, J., URIU, K. and LILLELAND, O. (1983). Leaf analysis for California deciduous fruits. In: *Soil and Plant Tissue Testing in California*. University of California Division of Agriculture and Natural Resources, Oakland, CA, USA. 15–17.
- BROWN, P. H. and URIU, K. (1996). Nutrition deficiencies and toxicities: diagnosing and correcting imbalances. In: *Almond Production Manual* (Micke, W. C., Ed.). University of California Division of Agriculture and Natural Resources, Oakland, CA, USA. 179–188.
- CASTAGNOLI, S. P., DEJONG, T. M., WEINBAUM, S. A. and JOHNSON, R. S. (1990). Autumn foliage applications of ZnSO₄ reduced leaf nitrogen remobilization in peach and nectarine. *Journal of the American Society for Horticultural Science*, **115**, 79–83.
- DEJONG, T. M., DAY, K. R. and JOHNSON, R. S. (1989). Partitioning of leaf nitrogen with respect to within canopy light exposure and nitrogen availability in peach (*Prunus persica*). *Trees*, **3**, 89–95.
- HEEREMA, R. J. (2005). *Compartmentalization of Carbon and Nitrogen Stresses within Almond [Prunus dulcis (Mill.) D. A. Webb] Spurs*. Ph.D. Thesis. University of California-Davis, Davis, CA, USA. 103 pp.
- HEEREMA, R. J., WEINBAUM, S. A., PERNICE, F. and DEJONG, T. M. (2008). Spur survival and return bloom in almond [*Prunus dulcis* (Mill.) D. A. Webb] varied with spur fruit load, specific leaf weight, and leaf area. *Journal of Horticultural Science & Biotechnology*, **83**, 274–281.
- HUETT, D. O., GOGEL, B. J., MEYERS, N. M., MCCONCHIE, C. A., MCFADYEN, L. M. and MORRIS, S. C. (2001). Leaf nitrogen and phosphorus levels in macadamias in response to canopy position and light exposure, their potential as leaf-based shading indicators, and implications for diagnostic leaf sampling protocols. *Australian Journal of Agricultural Research*, **52**, 513–522.
- KESTER, D. E. and ASAY, R. (1975). Almonds. In: *Advances in Fruit Breeding*. (Janick, J. and Moore, J. N., Eds.). Purdue University Press, West Lafayette, IN, USA. 387–419.
- KLEIN, I., DEJONG, T. M., WEINBAUM, S. A. and MURAOKA, T. T. (1991). Specific leaf weight and nitrogen allocation responses to light exposure within walnut trees. *HortScience*, **26**, 183–185.
- KULL, O. and NIINEMETS, Ü. (1993). Variations in leaf morphometry and nitrogen concentration in *Betula pendula* Roth., *Corylus avellana* L. and *Lonicera xylosteum* L. *Tree Physiology*, **12**, 311–318.
- MARINI, R. P. and MARINI, C. M. (1983). Seasonal changes in specific leaf weight, net photosynthesis, and chlorophyll content of peach leaves as affected by light penetration and canopy position. *Journal of the American Society for Horticultural Science*, **108**, 600–605.
- MILLARD, P. and THOMSON, C. M. (1989). The effect of autumn senescence of leaves on the internal cycling of nitrogen for the spring growth of apple trees. *Journal of Experimental Botany*, **40**, 1285–1289.
- NIINEMETS, Ü., KULL, O. and TENHUNEN, J. D. (2004). Within-canopy variation in the rate of development of photosynthetic capacity is proportional to integrated quantum flux density in temperate deciduous trees. *Plant, Cell and Environment*, **27**, 293–313.
- REIDEL, E. J., BROWN, P. H., DUNCAN, R. A., HEEREMA, R. J. and WEINBAUM, S. A. (2004). Sensitivity of yield determinants to potassium deficiency in 'Nonpareil' almond (*Prunus dulcis* (Mill.) D.A. Webb). *Journal of Horticultural Science & Biotechnology*, **79**, 906–910.
- SANCHEZ, E. E. and RIGHETTI, T. L. (1990). Tree nitrogen status and leaf canopy position influence postharvest nitrogen accumulation and efflux from pear leaves. *Journal of the American Society for Horticultural Science*, **115**, 934–937.
- SESAY, A. and SHIBLES, R. (1980). Mineral depletion and leaf senescence in soya bean as influenced by foliar nutrient application during seed filling. *Annals of Botany*, **45**, 47–55.
- SIMPSON, R. J., LAMBERS, H. and DALLING, M. J. (1983). Nitrogen redistribution during grain growth in wheat (*Triticum aestivum* L.). *Plant Physiology*, **71**, 7–14.
- SPARKS, D. (1977). Effects of fruiting on scorch, premature defoliation, and nutrient status of 'Chickasaw' pecan leaves. *Journal of the American Society for Horticultural Science*, **102**, 669–673.
- SYVERTSEN, J. P., GOŃI, C. and OTERO, A. (2003). Fruit load and canopy shading affect leaf characteristics and net gas exchange of 'Spring' navel orange trees. *Tree Physiology*, **23**, 899–906.
- THOMAS, H. and STODDARD, J. L. (1980). Leaf senescence. *Annual Review of Plant Physiology*, **31**, 83–111.
- URIU, K. and CRANE, J. C. (1977). Mineral element changes in pistachio leaves. *Journal of the American Society for Horticultural Science*, **102**, 155–158.
- WALCROFT, A. S., LE ROUX, X., DIAZ-ESPEJO, A., DONÈS, N. and SINOQUET, H. (2002). Effects of crown development on leaf irradiance, leaf morphology and photosynthetic capacity in a peach tree. *Tree Physiology*, **22**, 929–938.
- WARREN, C. R. and ADAMS, M. A. (2001). Distribution of N, Rubisco and photosynthesis in *Pinus pinaster* and acclimation to light. *Plant, Cell and Environment*, **24**, 597–609.
- WEINBAUM, S. A. and SPIEGEL-ROY, P. (1985). *Prunus dulcis*. In: *Handbook of Flowering. Volume IV*. (Halevy, A. H., Ed.). CRC Press Inc., Boca Raton, FL, USA. 139–145.
- WEINBAUM, S. A. and MURAOKA, T. T. (1986). Nitrogen redistribution from almond foliage and pericarp to the almond embryo. *Journal of the American Society for Horticultural Science*, **111**, 224–228.
- WEINBAUM, S. A., SOUTHWICK, S. M., SHACKEL, K. A., MURAOKA, T. T., KRUEGER, W. and YEAGER, J. T. (1989). Photosynthetic photon flux influences macroelement weight and leaf dry weight per unit of leaf area in prune tree canopies. *Journal of the American Society for Horticultural Science*, **114**, 720–723.
- WEINBAUM, S. A., MURAOKA, T. T. and PLANT, R. E. (1994). Intracanalopy variation in nitrogen cycling through leaves is influenced by irradiance and proximity to developing fruit in mature walnut trees. *Trees*, **9**, 6–11.
- WEINBAUM, S. A., MICKE, W. C. and PRICHARD, T. L. (1996). Nitrogen usage. In: *Almond Production Manual*. (Micke, W. C., Ed.). University of California Division of Agriculture and Natural Resources, Oakland, CA, USA. 189–195.