Nutrient Uptake by Cropping and Defruited Field-grown ‘French’ Prune Trees

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Abstract. Four adjacent heavily cropping 12-year-old ‘Petite d’Agen’ prune (Prunus domestica L.) trees were selected, and two of the trees were defruited in late spring (28 May) after the spring growth flush and full leaf expansion. Trees received K daily through the drip-irrigation system, and 15N-depleted (NH₄)₂SO₄ was applied twice between the dates of defruiting and fruit maturation. Trees were excavated at the time of fruit maturity (28 July) and fractionated into their component parts. The following determinations were made after tree excavation and sample processing: tree dry weight, dry weight distribution among the various tree fractions (fruit, leaves, roots, trunk, and branches), tree nutrient contents, within-tree nutrient distribution, total nonstructural carbohydrates (TNCs), and recovery of labeled N. Trees only recovered ≈3% of the isotonically labeled fertilizer N over the 6-week experimental period. Heavily cropping trees absorbed ≈9 g more K per tree (17% of total tree K content) during the 2-month period of stage III fruit growth than defruited trees. The enhanced K uptake in heavily cropping trees was apparently conditioned by the large fruit K demand and occurred despite greatly reduced levels of starch and TNCs relative to defruited trees. Fruit K accumulation in heavily cropping trees was accompanied by K depletion from leaves and perennial tree parts. Except for K, fruited and defruited trees did not differ in nutrient content.

Fruit fix only a small percentage of their C demands (Bazzaz et al., 1979; Birkhold et al., 1992) and use carbohydrates at the expense of vegetative growth (Glenn and Welker, 1993; Head, 1969, Smith, 1976; Williamson and Coston, 1989). Root growth, sugar transport to roots, and the accumulation of nonstructural carbohydrates in roots are also reduced in cropping trees relative to noncropping or defruited trees (Cannell, 1985; Goldschmidt and Golomb, 1982; Head, 1969; Loescher et al., 1990; Smith, 1976). Stage III of peach fruit development, characterized by rapid cell enlargement and accumulation of soluble solids, is resource limited (Grossman, 1993; Pavel and DeJong, 1993). Although the uptake of many essential nutrients including N and K is energy dependent (Salisbury and Ross, 1985), the potential sensitivity of nutrient uptake by field-grown trees during fruit growth has not been studied. Published results are few, and the results are inconsistent with respect to the occurrence of resource-limited nutrient uptake. In annuals and a few pot-grown trees, ion uptake has been related positively with the nutrient demand (Hansen, 1971; Merhaut and Darnell, 1992; Rodgers and Barneix, 1988). In contrast, ion uptake was reportedly resource limited during episodic shoot growth, but those results may have been conditioned by low light intensity (Hershey and Paul, 1983).

Decreases in leaf K concentration accompany leaf chlorosis, premature defoliation, and shoot dieback during fruit maturation in heavily cropping prune trees in the Sacramento Valley, Calif. (Hansen et al., 1982; Lillegard, 1932; Lillegard and Brown, 1938; Niederholzer et al., 1991; Ryugo et al., 1977). The phenomenon also occurs in pecan (Sparks, 1977).

Despite many determinations of nutrient concentrations in defruited and heavily cropping prune trees (Hansen et al., 1982; Ryugo et al., 1977), our knowledge of whole-tree nutrient contents, annual nutrient usage, and the influence of tree physiology (and particularly cropping) on the periodicity of nutrient uptake is very limited. Heavy crop loads have been associated with reduced root growth, reduced total nonstructural carbohydrates (TNCs), and reduced leaf K concentrations, and these associations led us to hypothesize that the resource demands of a heavy crop might limit nutrient uptake during stage III of fruit development.

Our objectives, therefore, were to assess the effects of cropping on tree capacity for the uptake of selected nutrients—notably N and K—during fruit maturation and on tree nutrient content and distribution.

Materials and Methods

Plant material and experimental manipulation. Four adjacent, 12-year-old prune trees were selected from a commercial orchard near Orland, Calif., planted in a soil of the Hillgate series (fine, montmorillonitic, thermic Typic Palexeralf). Trees were planted on a 4.88-m square pattern with 408 trees/ha. The orchard was drip-irrigated using 8 × 1.89-liter·h⁻¹ emitters per tree. Nutrients were applied via fertigation. Soil pH (1 soil : 2 water suspension) was 7.8 in the emitter zone (tree row) and 7.0 outside the drip-irrigated zone. Extractable cations were determined by atomic absorption spectrophotometry or flame photometry (Techtron 120; Varian, Sunnyvale, Calif.) after neutral ammonium acetate extraction (Thomas, 1982). Measurements were (in ppm) Ca²⁺ 3299 and 3391, Mg²⁺ 837 and 833, K⁺ 324 and 184, and Na⁺ 63 and 4 inside and outside the drip-irrigated zone, respectively. As a result of miscommunication, the grower applied N as NH₄NO₃/urea solution [32% N (w/w)] in May (0.16 kg/tree) and late July (0.16 kg N/tree). Potassium was applied daily (as K₂SO₄) through the drip-irrigation system, and a total of 0.91 kg K/tree was applied between late March and September. In addition, three foliar applications of dilute KNO₃ solution had been applied by the grower before this experiment began. Multiple foliar applications were made after tree excavation and sample processing: tree dry weight, dry weight distribution among the various tree fractions (fruit, leaves, roots, trunk, and branches), tree nutrient contents, within-tree nutrient distribution, total nonstructural carbohydrates (TNCs), and recovery of labeled N. Trees only recovered ≈3% of the isotonically labeled fertilizer N over the 6-week experimental period. Heavily cropping trees absorbed ≈9 g more K per tree (17% of total tree K content) during the 2-month period of stage III fruit growth than defruited trees. The enhanced K uptake in heavily cropping trees was apparently conditioned by the large fruit K demand and occurred despite greatly reduced levels of starch and TNCs relative to defruited trees. Fruit K accumulation in heavily cropping trees was accompanied by K depletion from leaves and perennial tree parts. Except for K, fruited and defruited trees did not differ in nutrient content.

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of KNO₃, are a common management tool in California to supply prunes with additional K in heavily cropping trees.

Two of the four adjacent trees were selected randomly and defruited manually on 28 May after the spring growth flush and full leaf expansion (Hansen et al., 1982). Trees were defruited during stage II (Niederholzer et al., 1991). Fruit removed from each defruited tree were weighed, 2-kg subsamples were counted to estimate total fruit number per tree, and subsamples were taken to the laboratory for nutrient analysis.

**Application of isotopically labeled N.** Isotopically labeled fertilizer N was supplied to each tree (i.e., two control and two defruited trees) as a 40% solution (w/v) of ¹⁵N-depleted (NH₄)₂SO₄ on 16 June and 7 July. On each date, 1 liter of the labeled N solution was placed in a shallow depression under each of the eight emitters per tree for a total of 16 liters (8 liters/tree per date × 2 dates) of material/tree; 1344 g of N (4.97-g label) were applied per tree. The basins were filled with soil after infiltration of the isotopically labeled N solution, and <2 h elapsed between labeled-N application and soil replacement.

**Tree excavation and nutrient analysis.** Each tree was uprooted at the time of fruit maturity (28 July) and separated into three or four fractions in defruited and heavily cropping trees, respectively: a) roots (i.e., everything below the graft union), b) trunk plus branches, c) leaves, and d) fruit (cropping trees only). Tree stumps and roots were excavated using a backhoe. Soil from a pit with a 3-m radius and 2 m deep was screened using pitchforks, and all visible roots were collected. An unknown but presumably small percentage of fine roots undoubtedly escaped detection and, therefore, was not analyzed.

The cost and effort required for excavating and dissecting mature trees limited the number of replicates per treatment to two (i.e., four trees). However, large physiological differences between fruiting and nonfruiting trees have been reported (Cannell, 1985; Forshey and Elfving, 1989; Head, 1969; Loescher et al., 1990; Maggs, 1963; Smith, 1976; Sparks, 1977) even when only one tree per treatment was studied (Goldschmidt and Golomb, 1982). After recording the fresh weights, 2-kg subsamples of fruit and leaves were collected and placed on ice in coolers. Fresh weights of perennial organs (i.e., trunk plus branches and roots) were obtained using a load-cell scale. The perennial organs were passed through a mechanical chipper, and subsamples of each of the fractions clipped were weighed immediately in the field. Additional subsamples of clipped material were taken for carbohydrate analysis, a fresh weight was obtained, and all samples were placed on ice for transport to the lab.

Leaves were washed in dilute detergent and dried in forced-air ovens at 60°C for 24 h. Fruit samples taken in May (at the time that two trees were defruited) were treated similarly. Mature fruit from the July harvest were washed and split in half, their pits were placed on ice for transport to the lab.

Fruit accumulated N, K, B, and Mn during the 2 month experimental period (Table 2). Except for K, cropping and defruited trees were obtained using a load-cell scale. The perennial organs were passed through a mechanical chipper, and subsamples of each of the fractions clipped were weighed immediately in the field. Additional subsamples of clipped material were taken for carbohydrate analysis, a fresh weight was obtained, and all samples were placed on ice for transport to the lab.

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Fruit dry weight increased 2-fold between 28 May and fruit maturity (Table 1). Also, the dry weight in trunk and branches, roots, and leaves did not differ statistically between the cropping and defruited trees. Although vegetative growth is reduced on heavily cropping trees relative to nonfruiting and thinned trees (Forshey and Elfving, 1989; Heim et al., 1979; Maggs, 1963), our experimental protocol minimized crop load effects on shoot extension and leaf biomass because trees were defruited after the spring growth flush and full leaf expansion.

**Results**

The uniformity of experimental trees before defruiting was corroborated by the similarity in fruit number determined on 28 May (defruited trees) and 8 July (cropping trees) (Table 1). Also, the dry weight in trunk and branches, roots, and leaves did not differ statistically between the cropping and defruited trees. Although vegetative growth is reduced on heavily cropping trees relative to nonfruiting and thinned trees (Forshey and Elfving, 1989; Heim et al., 1979; Maggs, 1963), our experimental protocol minimized crop load effects on shoot extension and leaf biomass because trees were defruited after the spring growth flush and full leaf expansion.

Fruit dry weight increased 2-fold between 28 May and fruit maturity (Table 1). Furthermore, fruit dry weight per tree was substantially greater than the combined dry weight of roots and leaves. These data suggest that fruit were the major physiological sink during the experiment. Projected yields of 17 tons of dried prunes per ha [calculated as the product of individual tree yields (Table 1) and tree density (408 trees/ha)] indicated that the yield of cropping trees was 3 times the average prune yields in California (S. Southwick, personal communication).

The developing crop apparently competed with the lateral meristems for resources, as the increment in tree girth between 28 May and 28 July was statistically greater in defruited trees than in heavily cropping trees (Table 1).

Fruit accumulated N, K, B, and Mn during the 2 month experimental period (Table 2). Except for K, cropping and defruited trees
Potassium and Ca represent the extremes of total tree nutrient percentages in fruit. Mature fruit contained nearly 70% of the total tree K content in heavily cropping trees. The entire perennial structure (i.e., trunk, branches, and roots) of cropping trees accounted for only ≈10% of the total tree K content. In contrast, the fruit accounted for <7% of the total Ca content of the tree, whereas 65% of total tree Ca was found in the perennial tree parts.

Leaf concentrations of N, Ca, Mg, Mn, and Zn were higher in cropping trees than in defruited trees at the time of fruit maturity (Table 4). Fruit demand for K would seem to explain the sharp decline in leaf K concentrations in cropping trees during fruit maturation relative to defruited trees during the same interval. Leaf concentrations of B and Cu did not vary with crop load.

Trees recovered only ≈3% of the labeled N applied during the study period.
Table 3. Nutrient distribution and removal in fruit of heavily cropping prune trees at the time of fruit maturity (28 July).

| Nutrient | Trunk and branches (% of tree nutrient content) | Roots | Leaves | Fruit (kg·ha⁻¹) | Fruit nutrient removal (kg·ha⁻¹) |
|----------|-----------------------------------------------|-------|--------|----------------|---------------------------------|
| N        | 31.0                                          | 9.2   | 23.8   | 35.9           | 102                             |
| K        | 8.3                                           | 2.3   | 19.4   | 69.3           | 147                             |
| Ca       | 54.8                                          | 9.7   | 28.6   | 6.9            | 14                              |
| Mg       | 24.3                                          | 1.8   | 47.7   | 19.6           | 9                               |
| Zn       | 41.6                                          | 14.2  | 15.5   | 28.7           | 0.4                             |
| B        | 28.9                                          | 15.1  | 16.2   | 39.8           | 0.5                             |
| Mn       | 37.1                                          | 21.4  | 25.0   | 16.6           | 0.2                             |
| Cu       | 37.7                                          | 11.0  | 11.0   | 40.5           | 0.1                             |

Data are means of two heavily cropping trees.

Calculation based on nutrient content of fruit per tree (Table 2) multiplied by 408 trees per ha.

Table 4. Leaf nutrient concentrations in heavily cropping and defruited prune trees at the time of fruit maturity (28 July).

| Treatment | % dry wt | ppm | Treatment | % dry wt | ppm |
|-----------|----------|-----|-----------|----------|-----|
| Cropping  | 2.40     | 1.47 | 0.72      | 33       | 6.69 |
| Defruited | 2.23     | 2.15 | 1.59      | 0.59     | 28  |
|           | *        | *    | **        | **       | **  |
|           | NS       | NS   | NS        | NS       | NS  |

Non-significant or significant at P < 0.10 or 0.05, respectively.

Table 5. Amounts, distribution, and percentage recovery of isotopically labeled N by heavily cropping and defruited prune trees.

| Treatment | Trunk and branches (g/tree) | Roots (g/tree) | Leaves (g/tree) | Fruit (g/tree) | Fertilizer N recovered (g/tree) | (%) |
|-----------|-----------------------------|----------------|----------------|---------------|---------------------------------|-----|
| Cropping  | 14.6                        | 3.7            | 12.3           | 11.5          | 42.0                           | 3.1 |
| Defruited | 15.1                        | 10.5           | 9.9            | ---           | 34.9                           | 2.6 |
|           | NS                          | *              | NS             | NS            | NS                             | NS  |

15N-depleted (NH₄)₂SO₄ was applied on 16 June and 7 July.

Data represent means of two trees.

Non-significant or significant at P < 0.10, respectively.

Table 6. Contents (kg/tree) and concentrations (% dry weight) of total nonstructural carbohydrates (TNCs) in cropping and defruited prune trees.

| Tree part | Treatment | Starch (kg/tree) | Soluble sugars (kg/tree) | TNCs (kg/tree) | Starch (kg/tree) | Soluble sugars (kg/tree) | TNCs (kg/tree) |
|-----------|-----------|------------------|--------------------------|---------------|------------------|--------------------------|---------------|
| Fruit     | Cropping  | 0.23             | 17.54                    | 17.77         | 0.62             | 48.5                     | 49.1          |
|           | Defruited | ---              | ---                      | ---           | ---              | ---                      | ---           |
| Leaves    | Cropping  | 0.02             | 0.73                     | 0.75          | 0.28             | 10.4                     | 10.7          |
|           | Defruited | 0.20             | 1.05                     | 1.25          | 2.60             | 13.7                     | 16.3          |
|           | ***       | NS               | *                        | **           | ***              | NS                       | *             |
| Trunk and branches | Cropping | 0.50             | 0.95                     | 1.45          | 0.82             | 1.6                      | 2.4           |
|           | Defruited | 2.53             | 1.61                     | 4.14          | 4.1              | 2.6                      | 6.7           |
|           | **        | *                | **                       | **           | **               | **                       | **            |
| Root      | Cropping  | 0.14             | 0.10                     | 0.24          | 1.00             | 0.7                      | 1.7           |
|           | Defruited | 0.63             | 0.12                     | 0.75          | 4.40             | 1.6                      | 6.0           |
|           | **        | NS               | *                        | **           | **               | NS                       | **            |
| Total     | Cropping  | 0.89             | 19.32                    | 20.21         | ---              | ---                      | ---           |
|           | Defruited | 3.36             | 2.78                     | 6.14          | ---              | ---                      | ---           |
| Total (excluding fruit) | Cropping | 0.66             | 1.78                     | 2.42          | ---              | ---                      | ---           |
|           | Defruited | 3.36             | 2.78                     | 6.14          | ---              | ---                      | ---           |

Non-significant or significant at P < 0.10, 0.05, or 0.01, respectively, according to F test.
experimental period (Table 5), and labeled N recovery by cropping trees and defruited trees did not differ statistically. The likelihood of high levels of available soil N and high tree N status (see Materials and Methods) may have greatly diluted the labeled N in the root zone and limited tree N uptake (Weinbaum et al., 1992) during the experimental period. The within-tree distribution of labeled N in cropping and defruited trees also did not differ statistically at the time of fruit maturity. The fruit contained 25% of the labeled N absorbed by cropping trees. In contrast, roots in defruited trees contained three times as much labeled N as roots in heavily cropping trees, and this difference was significant at $P < 0.10$ (Table 5).

A heavy crop of developing fruit limited TNC accumulation within vegetative tree parts between 28 May and 28 July and altered TNC distribution among the various tree parts (Table 6). Cropping trees contained $>3$ times the TNCs than the defruited trees, and the mature fruit contained $≈88\%$ of the TNCs in the tree. Thus, the vegetative tree parts, (leaves, trunk, branches, and roots) of defruited trees contained 2.5 times as much TNC as the comparable parts of cropping trees. Soluble sugars constituted 95% of the TNCs in cropping trees as opposed to 45% in the defruited trees. Starch was stored throughout the perennial structure of the tree. Although the starch concentration was higher in the roots than the trunk and branches, more starch was stored in the above-ground perennial tree parts than in the roots because the above-ground biomass was $>4$ times that of the recovered root biomass (Table 1). Starch and TNC contents and concentrations were significantly greater in the roots of defruited trees than in the roots of heavily cropping trees.

**Discussion**

Higher whole-tree K contents have been reported in fruiting than defruited citrus trees (Golomb and Goldschmidt, 1987) and young pot-grown apple trees (Hansen, 1971). Our data (Tables 2 and 6), however, provide novel evidence that K uptake by heavily cropping prune trees is increased, not reduced, during stage III of fruit growth. This period of enhanced K uptake coincided with the period of fruit K demand (150% increase in fruit K content) (Table 1), despite reduced TNC levels. Also, published literature (Glenn and Welker, 1993; Head, 1969) and our own unpublished field observations suggest that fine root growth was reduced in the cropping trees relative to the defruited trees. Declining leaf K concentrations in heavily cropping trees (Table 4) (Hansen et al., 1982; Sparks, 1977) indicate only that leaf K resorption exceeded the concurrent influx of K to leaves. The implication (Hansen et al., 1982) that declining leaf K concentrations reflect a reduction in tree uptake of K is not necessarily valid. Sparks (1977), working with pecan, suggested that leaves may serve as a K reservoir for fruit when K uptake by the tree is limited. Our data (Tables 2 and 4) are consistent with this assessment. K uptake by heavily cropping trees may have been insufficient to fully meet K demand, as evidenced by the K depletion of the perennial tree parts and leaves during fruit maturation. The relative uptake of other nutrients did not increase similarly in cropping trees (Table 2). The implication of these data is that the uptake of each element is regulated individually; i.e., the uptake of a nutrient is regulated by the specific demand for that nutrient within the tree (Mauk and Wooden, 1992).

Previous studies also reported that cropping reduced TNC concentrations in the roots and other tree parts (Goldschmidt and Golomb, 1982; Loescher et al., 1990; Ponchner, 1992). Although C allocation to root systems is necessary for nutrient acquisition, we did not observe a positive correlation between TNC and nutrient uptake. We have no standards for assessing the functional relationships between TNC level in roots and nutrient uptake.

Our data are consistent with those of Crapo and Ketellaper (1981), who reported that insufficient photosynthesis severely reduced root growth in seedlings of several annual plant species, whereas the same conditions did not affect the active root uptake of K. These authors concluded that maintaining existing tissue and processes had a higher energy priority than producing new tissue (i.e., root growth). These data were obtained from plants grown in solution culture; i.e., K availability was not limiting. Simulated annual C cost of mature kiwifruit root growth amounts to 40% of all C transported below ground—35% to growth and 5% to growth respiration (Buwalda, 1993). Maintenance respiration and ion uptake-associated respiration accounted for 56% and 4% of all C translocated below ground during the same year (Buwalda, 1993). If these relative values can be extrapolated to other fruit crops, then the C cost of root growth in mature prune trees may greatly exceed the C cost of nutrient uptake. Since woody root portions (Atkinson and Wilson, 1980; Van Rees and Comerford, 1990) are capable of nutrient uptake rates similar to those of young, growing roots and mature trees maintain substantial perennial root surface area through a growing season, reductions in root growth may be rather inconsequential to tree ion uptake capacity during periods of low carbohydrate flux below ground.

In most agricultural and natural ecosystems, plant nutrient uptake may be limited by a) the delivery rate of soil solution K to the root surface and/or b) the tree’s capacity to uptake K at the root surface.

Under natural conditions, K moves to the root surface primarily via diffusion (Barber, 1985). When root uptake exceeds soil K delivery, a K depletion zone develops in the rhizosphere (Barber, 1985). We suggest that daily K fertilization, as occurred in this study, may have maintained soil solution K concentrations at the root surfaces even as root growth declined during fruit maturation in June and July.

Potassium fertigation increases the potential soil-to-root K delivery rate in several ways. Drip irrigation maintains high soil water content, which increases K diffusion rates relative to drier soils (Uriu et al., 1980). K fertigation and subsequent saturation of soil K adsorption and fixation sites under and nearby the drippers may also result in more rapid movement of K to root surfaces by mass flow (Rolston et al., 1979) than occurs by diffusion (Hillel, 1980). We suggest that, in this study, K fertigation significantly improved cropping prune tree K uptake by increasing rhizosphere soil solution K concentrations during a period of high tree K demand and significant root K uptake capacity but of reduced root growth and subsequent diminished tree capacity to actively access soil K reserves. It is conceivable that the difference in K uptake of cropping trees vs. defruited trees (Table 2) would have been smaller had the irrigation and fertilizer management in the study orchard followed common practices of sprinkler or flood irrigation and massive, local K fertilization (usually in the fall or winter).

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