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Effects of irrigation deprivation during the harvest period on nonstructural carbohydrate and nitrogen contents of dormant, mature almond trees

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Summary Effect of irrigation deprivation during the harvest period on the nonstructural carbohydrate (NC) content of dormant, mature, field-grown almond (*Prunus dulcis* (Mill.) D.A. Webb cv. Nonpareil) trees was studied. Roots, trunk, branches, spurs and stems of 12 trees were subsampled in February 1997, across a gradient of irrigation treatments (FI = fully irrigated, MS = moderately stressed and SS = severely stressed) to relate NC concentration to the degree of water stress experienced by individual trees during the previous (1996) harvest period. To assess the effect of water stress on whole-tree NC content, three dormant FI trees and three dormant SS trees were excavated on December 10, 1997, and dry weights and NC and N concentrations of the tree components were determined. Whole-tree biomass did not differ significantly between FI and SS trees, although SS trees tended to have less total dry weight. Although roots constituted just 13% of tree biomass, they stored 36 and 44% of tree NC and N contents, respectively. There were negative relationships between the seasonal minimum values of both midday (Ψ_{ms}) and predawn (Ψ_{pd}) stem water potentials during the harvest period and root NC content of dormant trees. Severe water stress during the harvest period resulted in a 26% reduction in NC content and a 50% reduction in biomass of current-year stems (> 5 cm in length) per tree. The reduction in NC content is consistent with the previously reported late season reductions in leaf function and persistence. The SS trees exhibited a reduction in NC content but not in N content per tree, indicating that late season accumulation of NC and N were uncoupled in trees subjected to severe harvest-period water stress.

Keywords: Prunus dulcis, reserves, water stress.

Introduction

The relationship between carbohydrate and nitrogen (N) reserves in deciduous trees and growth the following year is well known (Tromp 1983, Oliveira and Priestley 1988, Loescher et al. 1990, Kozlowski 1992). The concentration of nonstructural carbohydrates (NC) is usually expressed as a percentage of dry weight (Tromp 1983, Kozlowski 1992) and has been used to estimate tree reserve status (Worley 1979, Keller and Loescher 1989). Without organ and tree biomass, however, extrapolations to quantify whole-tree reserves based only on carbohydrate concentrations may lead to erroneous interpretations (Tromp 1983, Kozlowski 1992, Rosecrance et al. 1998, Weinbaum and Van Kessel 1998).

There have been few meaningful estimates of carbohydrate reserves in mature, field-grown tree species (Murneek 1942, Goldschmidt and Golomb 1982, Weinbaum et al. 1994*a*, 1994*b*, Rosecrance et al. 1998). In mature almond (*Prunus dulcis* (Mill.) D.A. Webb cv. Nonpareil) trees, neither NC content under favorable conditions nor the impact of water stress on the accumulation of reserves has been documented. As in many deciduous tree fruit species, bud break and the initial phases of reproductive and vegetative growth in almond precede significant leaf expansion and net carbon export from leaves and thus depend on the redistribution of reserves from perennial tree parts (Keller and Loescher 1989). Consequently, any negative impact on reserve accumulation might reduce cropping potential.

Water is withheld intentionally from Californian almond orchards during the harvest period to prevent trunk damage during mechanical shaking (Fridley et al. 1970). The complexity of the orchard planting design (usually three cultivars, with different harvest dates, are interplanted in the same orchard for pollination) and the multiple field operations associated with the highly mechanized harvest frequently delay resumption of post-harvest irrigation. This delay is especially critical in areas with high summer evaporative demand such as the southern San Joaquin Valley, where irrigation cut-off periods of 35 days, or more, commonly result in some premature defoliation.

Previous papers have reported reductions in leaf function (Klein et al. 2001) and crop yield of almond trees (Esparza et al. 2001) in response to water stress during the harvest season. Furthermore, the yield reductions appear to be associated with the cumulative impact of water stress on vegetative growth and fruiting positions over 2 or more years. We hypothesize that

the loss of carbon gain resulting from decreased photosynthesis and premature defoliation in response to severe water stress during the harvest period reduces tree carbohydrate reserves at the end of the year, and negatively impacts cropping. Nonstructural carbohydrate content in dormant trees may link reductions in carbon assimilation during and after water stress periods with reductions in tree growth and yield during subsequent years. The objective of this investigation was to quantify the NC content of dormant, mature almond trees and to assess the effect of water stress imposed during the harvest period on NC content at the end of the season.

Materials and methods

Experimental site and irrigation treatments

The irrigation experiment was initiated in 1995 in an almond orchard (*Prunus dulcis* grafted on *P. persica* (L.) Batsch cv. Nemaguard rootstock) at the Paramount Farming Company, Shafter, CA (35° N, 117° E). The experiment was carried out in a 7-year-old (in 1995), high-yielding orchard, planted at 6.4 × 7.9 m in a quincunx design with rows oriented north–south and irrigated by microjets. The canopy was fully developed when the experiment started, intercepting 73% of daily radiation, measured before harvest in 1995. The orchard comprised rows of cv. Nonpareil (50%) planted alternately with pollinizer rows of cv. Monterey (25%) and cv. Price (25%). Commercially grown almond trees are pruned minimally to maximize flower number per tree. Experimental trees were unpruned during the experiment to avoid masking differences in biomass, NC and N between treatments.

Irrigation treatments

Treatments were applied in a completely randomized block design with four replicates, each replicate representing a 17-tree row. The treatments were applied during the almond harvest period in three consecutive years (1995–1997). Three treatments were evaluated: (1) FI = full irrigation (based on full crop evapotranspiration demand); (b) MS = moderate stress; and (3) SS = severe stress. Because the trees withstood stress better than expected during the first year, a second, more severe stress treatment (SS2) was included in 1996 and 1997. The irrigation treatments were applied during August 1–September 4, August 6–September 22 and July 31–September 23, respectively, for 1995, 1996 and 1997. The irrigation cut-off period (days), number of irrigations withheld, and the respective evapotranspiration (ET_o, mm) during these periods were: 18, 2, 118 (MS, 1995); 35, 5, 219 (SS, 1995); 18, 1, 119 (MS, 1996); 47, 6, 271 (SS, 1996); 20, 1, 123 (MS, 1997); and 53, 5, 283.2 (SS, 1997). Water was applied every 3–7 days in the FI treatment. The irrigation schedule has been described in detail by Klein et al. (2001).

Water stress measurements

To determine the severity and effects of water stress, we measured predawn (Ψ_{pd}) and midday (Ψ_{ms}) stem water potentials, CO_2 assimilation rate, stomatal conductance, and leaf abscission as described by Klein et al. (2001). The lowest values of Ψ_{ms} and Ψ_{pd} achieved by 12 trees across the irrigation treatment gradient during 1996 were considered indicative of the maximum stress experienced and were related to NC concentrations of the various tree organs subsampled from dormant trees.

Nonstructural carbohydrates (NC) and N

Tree excavation Three dormant FI trees and three dormant SS trees were excavated on December 10, 1997, with a backhoe, hand-held equipment, and a crew of 25 people. The dormant mature trees were excavated following natural defoliation of FI trees, when NC and N contents of perennial tree parts are highest (Kang and Titus 1980, Loescher et al. 1990, Kozlowski 1992). Trees were uprooted and divided into: (a) large roots (diameter > 2.5 cm); (b) small roots (diameter < 2.5 cm); (c) trunk (including below- and aboveground stump); (d) main scaffolds (major scaffold branches supporting functional canopy); (e) canopy branches (finer, multiyear canopy branches); and (f) stems (1-year-old stems including small stems and watersprouts).

Because the trees had been fan-jet fertigated, roots were concentrated in a 2 × 2-m^2 area around the trunk. Roots were excavated with a backhoe to a depth of 1.5–2 m in an area of about 4 × 4 m^2 around each tree and recovered with pitchforks. Fresh weights of the various tree portions were recorded. Canopy branches were passed through a large chipper and several, chipped 2–3-kg subsamples were collected. Main trunk and main large scaffold subsamples were obtained by sawing several times through the pieces and collecting 1–2 kg of sawdust. Several 3-kg subsamples of large and small roots and representative 1-kg subsamples of stems and watersprouts were also obtained.

After recording fresh weights, subsamples were dried to constant weight in forced-air ovens at 65 °C. After drying, subsamples were ground in a Brinkmann industrial grinder to pass a 2-mm mesh sieve and were subsequently ground in a Wiley mill to pass a 20-mesh screen.

Subsampling In addition to the excavated trees, tree organs of 12 non-excavated trees were subsampled across a gradient of tree water stress for NC determination on February 10, 1997 as follows: (a) Roots: several root sections were dug up randomly from around the trunk. After drying the samples in an oven at 65 °C, homogeneous subsamples were selected for NC analysis based on root length and diameter. (b) Trunk: several 5-cm-deep holes were drilled into the trunk with an electric drill; subsamples of the shavings were then pooled and ground for analysis. (c) Branches: similar 1.5-cm-diameter branches were sampled randomly from each tree canopy. (d) Spurs: spurs were picked randomly from branches around the tree. (e) Stems: 1-year-old stems were sampled randomly around the tree.

Analytical procedure Oven-dried and ground subsamples of 0.25 g from the various tree fractions were analyzed for NC at the DANR analytical laboratory at the University of California,

Davis by standard methods (Smith 1969). The analytical procedure consisted of enzymatic hydrolysis of starch followed by high performance liquid chromatography (HPLC) of glucose plus sucrose. Amyloglucosidase was used to hydrolyze starch and a fast carbohydrate column (HPAP, Bio-Rad Laboratories, Hercules, CA) was used for the HPLC determination. Although sorbitol, fructose and other minor sugars were not resolved, our analyses, which were based on the sum of starch-derived glucose plus soluble glucose as well as soluble sucrose, represent a large percentage of the total NC present (W. Loescher, Michigan State University, unpublished data) and should reflect the relative difference in NC content between FI and SS trees. Whole-tree NC contents were obtained by combining NC concentrations with the corresponding dry weights of the various tree fractions. Each tissue subsample was also analyzed for N. Total N concentration was determined conductimetrically according to Carlson (1978, 1986) and calculations of total tree N content were made in the same way as for carbohydrates.

Fruiting positions

Dry weights of all current-year stems longer than 5 cm (including watersprouts) of the three FI and three SS excavated trees were obtained by separating them from the rest of the tree during tree excavation. Stem biomass was also determined for two additional trees that were partially deblossomed in 1996 to compare typical trees with trees subjected to minimum crop competition for carbohydrates. Based on the 1995 reference yields, the trees were similar before the experiment started. At the time of the tree excavations, irrigation treatments had been imposed for three seasons (1995–1997) so the results may reflect multiyear treatment effects on current-year stem growth of whole trees. Whole-tree stem dry weight is associated with the potential number of fruiting positions, because each node on a new stem may give rise to flowers, new spurs or stems in the subsequent year (Kester et al. 1996).

Statistical analysis

The significance of treatment differences in NC and N concentrations of the various tree components and whole-tree NC and N contents was assessed by the Student's *t*-test procedure. The association between NC concentration and water potential was studied by regression analysis. Both analyses were carried out with procedures in the SAS statistical software package (SAS Institute, Inc., Cary, NC).

Results

Severe water stress imposed during the harvest period did not affect the N concentration of tree organs in early December within a month or so of complete leaf abscission; however, the treatment markedly reduced the NC concentration (Figure 1). The NC concentrations in the various organs (except watersprouts) were greater in FI trees than in SS trees (Figure 1a). Differences in NC concentrations between FI and SS trees varied with organ type from 13–14% for trunks, main scaffolds and canopy branches to 18–22% in roots and 23% in stems. Root NC and N concentrations were about 5–6 times higher than those of other organs (Figure 1).

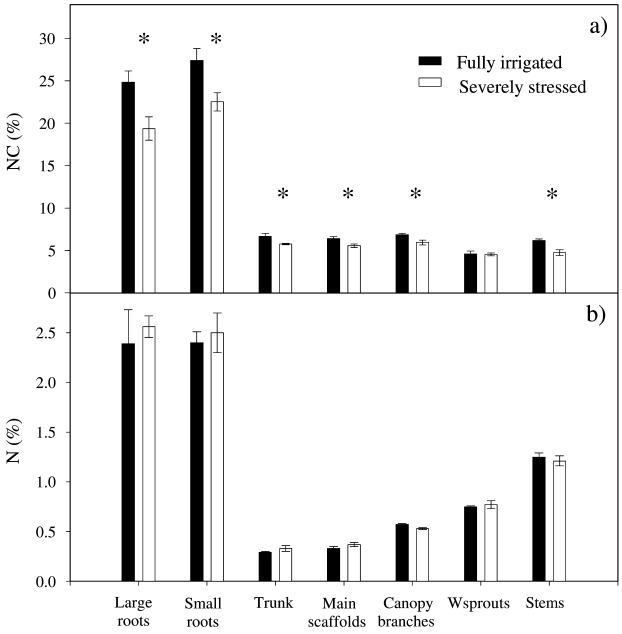

Figure 1. Effects of two contrasting irrigation treatments during the 1995–1997 harvest periods on concentrations of (a) nonstructural carbohydrates (NC) and (b) N measured in the various tree fractions of dormant Nonpareil almond trees on December 10, 1997. Bars represent the standard errors of the mean of three excavated trees per treatment. Asterisks represent statistical difference between treatments according to Student's *t*-test ($P < 0.05$). Abbreviation: Wsprouts = watersprouts.

Tree biomass did not differ significantly between FI and SS trees (Figure 2a). However, whole-tree stem biomass was greater in FI trees than in SS trees (Figure 3), indicating the importance of water stress on annual stem growth. Early flower thinning in 1997 increased stem dry weight per tree, but the increase was not statistically significant (Figure 3).

Calculated mean NC contents were significantly less for SS trees (23.1 kg tree^{-1}) than for FI trees (31.2 kg tree^{-1}), a difference of 26.1% (Figure 2b). Differences in NC contents between FI and SS trees were proportionally greater in roots (34.9%) than in aerial tree parts (21.1%). Water stress did not affect tree N contents, which, on a dry weight basis, averaged 2.52 kg for a 336-kg FI tree.

Although roots represented only 13.4% of whole-tree biomass, they accounted for 36.4 and 44.2% of tree NC and N contents, respectively. In contrast, the aerial parts, which constituted 86.5% of the tree biomass, accounted for only 63.6 and 55.8% of tree NC and N contents, respectively, during the dormant season (Figure 2). Although NC and N concentrations were lower in aerial organs than in roots, the aerial organs represented a larger storage pool because of their greater biomass.

There was a negative association between root NC concentrations and the water stress that individual trees experienced

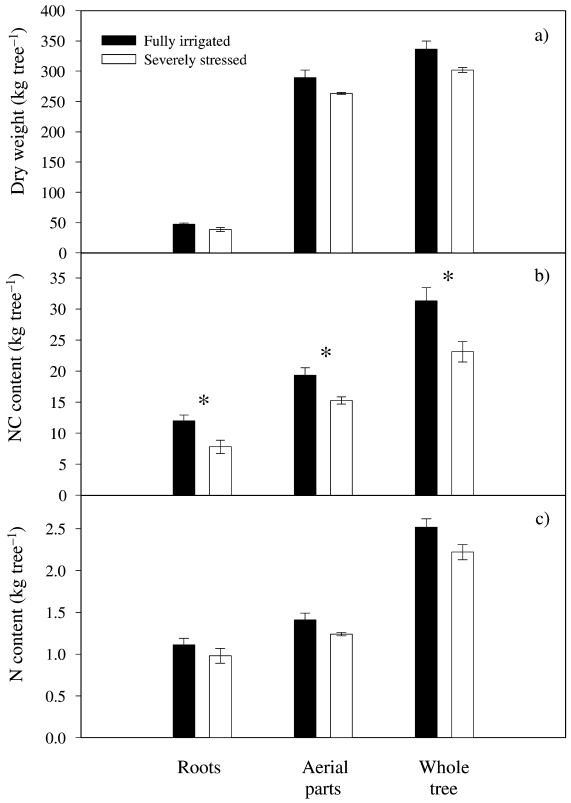

Figure 2. Effects of two contrasting irrigation treatments during the 1995–1997 harvest periods on biomass (dry weight), whole-tree nonstructural carbohydrate (NC) content and N content measured in dormant Nonpareil almond trees on December 10, 1997. Bars represent the standard errors of the mean of three excavated trees per treatment. Asterisks represent statistical differences between treatments according to Student's *t*-test ($P < 0.05$).

during the 1996 harvest period (represented by the most negative values of water potential during the summer stress; Figure 4). Minimum values of both predawn (Ψ_{pd}) and midday (Ψ_{ms}) stem water potential were linearly associated with root NC concentrations. No association was found between stem water potential and NC concentrations of the other organs or N concentrations in any organ (data not shown).

Discussion

Severe water stress during the harvest period resulted in a significant 26% reduction (8.1 kg of NC per tree) in NC content and a 50% reduction in biomass of current-year stems of mature almond trees. Loescher et al. (1990) concluded that "accumulation of these [carbohydrate] reserves in deciduous fruit trees is very sensitive to late season stresses and management practices, and decreased accumulation can profoundly affect a tree's performance the following year." The reduction in NC in SS trees is also consistent with the late season reduction in leaf function and persistence reported previously (Klein et al. 2001). Based on a preliminary carbon budget model for almond growth, which considers growth and maintenance respiration of whole trees on a daily basis (Esparza et al. 1999), we estimated that up to 31.2 kg of total NC may be consumed between anthesis and shortly after completion of fruit set (about 400 degree days after bloom). This simulation assumes, however, that all the NC content represents reserves and that all the reserves are available for the next spring flush. This preliminary model also indicates that nearly all the NC content of almond trees would be consumed around the time the new foliage starts supporting current growth (end of March).

Because these calculations are based on total-tree NC, and may, therefore, overestimate the actual availability of reserves for new growth (Lacointe et al. 1993), early season carbohy-

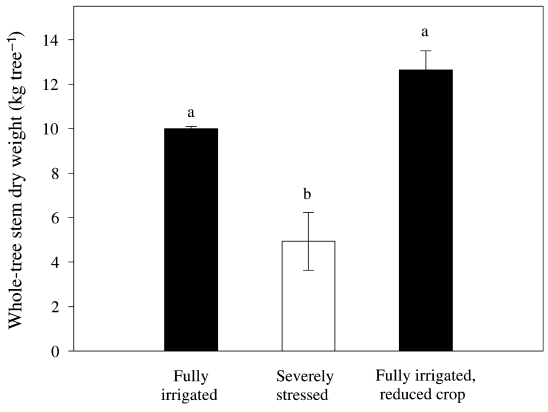

Figure 3. Effects of water stress during the harvest period and reduced crop load (flower thinning) during 1997 on stem dry weight per tree at the end of the year (December 10, 1997) in Nonpareil almond trees. Bars represent the standard errors of the mean of three trees per treatment in the case of fully irrigated and severely water-stressed trees and two trees in the case of reduced crop-load (flower-thinned) trees. Different letters indicate statistical differences according to the Duncan's procedure ($P < 0.05$).

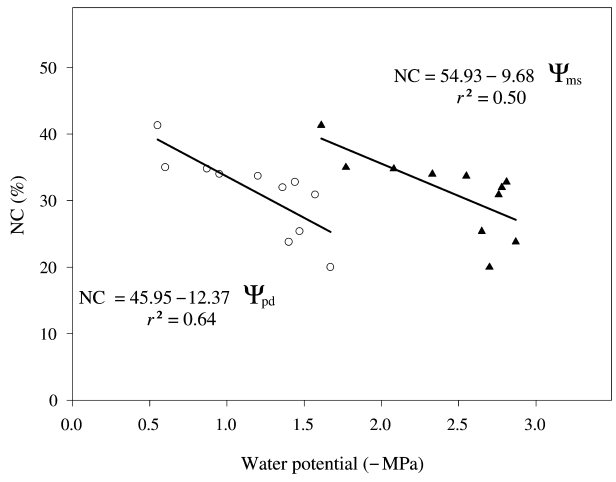

Figure 4. Relationships between the lowest midday (Ψ_{ms}; ▲) and predawn (Ψ_{pd}; ○) stem water potentials during the 1996 harvest period and nonstructural carbohydrate (NC) concentrations of roots on February 10, 1997, in dormant Nonpareil almond trees across the irrigation treatment gradient imposed during 1996.

drate demand is likely to be higher than carbohydrate supply, resulting in competition among the various carbohydrate-demanding growing organs. Under these circumstances, growth would be source-limited (Grossman and DeJong 1995). Such source limitation should occur earlier and be more severe when reserves are more limited, as is likely following water stress. Under these conditions, fruit growth is anticipated at the expense of vegetative growth (Heim et al. 1979).

Weinbaum et al. (1978) reported that young, nonbearing potted prune (*Prunus domestica* L.) trees absorbed soil N during the fall as long as leaf function was maintained. However, more recent work with mature pistachio (*Pistacia vera* L.) trees (Rosecrance et al. 1996) and almond trees (P. Brown, Pomology Dept., University of California, Davis, personal communication) indicates that soil N uptake ceases following harvest, despite the persistence of functional leaves. The prolonged seasonal growth of young trees (Borchert 1976) may prolong seasonal tree demand for N. Although water stress during harvest compromised leaf function and persistence (Klein et al. 2001) and reduced NC content per tree, tree N content and probably functional N reserves were unaffected. This suggests that soil N uptake during and subsequent to almond harvest was relatively insignificant in both FI and SS trees, and that post-harvest N accumulation in perennial tree parts was primarily a result of leaf N resorption rather than soil N uptake (see Rosecrance et al. 1998). Leaf N resorption was unaffected by severe water stress during the harvest period. Thus, late season NC and N accumulation appear to be uncoupled in mature almond trees.

Stem biomass per tree was reduced by 50% in SS trees compared with FI trees by the end of 1997 (Figure 3). In almond trees, vegetative growth, including the production of potential fruiting positions, occurs mostly during March, the first month after bud break (Kester et al. 1996, Esparza et al. 1999). Stem growth coincides with a period of suggested carbohydrate limitation, because early season growth of almond stems was greater in trees in which competition for storage carbohydrates was mitigated by deblossoming than in trees carrying a normal fruit load (Esparza et al. 2001). Grossman and DeJong (1995) also reported a source-limited period for vegetative growth of peaches early in the growing season. Rachitic growth and yellowing leaves have been reported early in the season in association with low amounts of reserves in cherries (*Prunus avium* L.) (Loescher et al. 1990).

Water stress during the harvest period resulted in a physiologically significant decrease in NC in dormant almond trees. Water stress reduced almond yields in subsequent years and appears to be associated with reductions in the renewal of fruiting positions (Esparza et al. 2001). We suggest that carbohydrate reserves (as reflected by NCs) at the end of the year are the link between the physiological effects caused by water stress during the harvest period (decreased photosynthesis and premature defoliation (Klein et al. 2001)) and the bearing capacity of almonds in subsequent years, particularly the renewal of fruiting positions.

Other studies have reported that water stress and defoliation reduce yield in the following year by affecting bud development (Brown 1953, Worley 1979). Under our experimental conditions, floral differentiation in almond was temporarily delayed by water stress (data not presented). However, we conclude that the marked reduction in NC content per tree in response to water stress during the harvest period limited vegetative growth in the following year, and impacted subsequent fruit-bearing capacity (Kester et al. 1996) rather than directly affecting flowering, fruit set or fruit growth (Esparza et al. 2001).

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