Remobilization and uptake of N by newly planted apple (*Malus domestica*) trees in response to irrigation method and timing of N application

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Summary  Environmentally sound management of N in apple orchards requires that N supply meets demand. In 1997, newly planted apple trees (*Malus domestica* Borkh. var. Golden Delicious on M.9 rootstock) received daily applications of N for six weeks as Ca(NO₃)₂ through a drip irrigation system at a concentration of 112 mg l⁻¹ at 2–8, 5–11 or 8–14 weeks after planting. Irrigation water was applied either to meet estimated evaporative demand or at a fixed rate. In 1997, trees were harvested at 5, 8, 11 and 14 weeks after planting; and in 1998 at 3 weeks after full bloom. The amount of fertilizer N recovered was similar in trees in both irrigation treatments, but efficiency of fertilizer use was greater for trees receiving demand-controlled irrigation than fixed-rate irrigation. This was attributed to lower N inputs, greater retention time in the root zone and less N leaching in the demand-controlled irrigation treatments compared with fixed-rate irrigation treatments. Less fertilizer N was recovered by trees receiving an early application of N than a later application of N and this was related to the timing of N supply with respect to tree demand. Demand for root-supplied N was low until 11 weeks after planting, because early shoot and root growth was supported by N remobilized from woody tissue, which involved 55% of the total tree N content at planting. Rapid development of roots > 1 mm in diameter occurred between 11 and 14 weeks after planting, after remobilization ended, and was greater for trees receiving demand-controlled irrigation treatments compared with fixed-rate irrigation treatments. Less fertilizer N was recovered by trees receiving an early application of N than a later application of N and this was related to the timing of N supply with respect to tree demand. Demand for root-supplied N was low until 11 weeks after planting, because early shoot and root growth was supported by N remobilized from woody tissue, which involved 55% of the total tree N content at planting. Rapid development of roots > 1 mm in diameter occurred between 11 and 14 weeks after planting, after remobilization ended, and was greater for trees receiving a later application of N than for trees receiving a later application of N. Late-season tree N demand was supplied by native soil N, and uptake and background soil solution N concentrations were higher for trees receiving demand-supplied irrigation compared with fixed-rate irrigation. Total annual N uptake by roots was unaffected by treatments and averaged 6–8 g tree⁻¹. Nitrogen applications in 1997 affected growth and N partitioning in 1998. Trees receiving early applications of N had more flowers, spur leaves and bourse shoots than trees receiving later applications of N. Consequently, more N was remobilized into fruits in trees receiving early applications of N compared with fruits in trees receiving later applications of N.

Demand for N in the young apple trees was low. Early season demand was met by remobilization from woody tissues and the timing of demand for root-supplied N probably depends on whether flowering occurs. Method of N delivery affected the efficiency of N use. We conclude that N demand can be met at soil solution N concentrations of around 20 mg l⁻¹.

Keywords: demand-controlled irrigation, fertilization, fertilizer-use efficiency, fixed-rate irrigation, nitrogen, orchard management.

Introduction

Management of N in deciduous fruit orchards to meet plant needs and avoid environmental contamination requires that plant demand is understood and that supply methods are efficient (Tagliavini et al. 1996). Understanding demand for N includes the recognition that N inputs can affect tree growth and development both in the current and subsequent years (Weinbaum et al. 1987). Key processes involved in year to year responses of deciduous trees to N status are storage and remobilization. Nitrogen is considered to be in storage if it can be remobilized from one tissue and subsequently used for the growth of other tissues (Millard 1988). Nitrogen is stored in deciduous trees over winter in roots as amino acids (Tromp 1983) or proteins (Millard and Proe 1991) and in bark as proteins (Titus and Kang 1982). During the summer, N is stored in leaves primarily as Rubisco (Titus and Kang 1982, Millard 1996). Remobilization of N occurs during periods of senescence and growth (Millard 1996). During leaf senescence, N stored in leaves during the summer is withdrawn, stored over winter in woody tissue and subsequently remobilized and used for growth in the spring (Millard 1996). When considering the timing of N inputs it is therefore important to determine when remobilization and root uptake occur. In spring, remobilization in apple (*Malus domestica*
Borkh.) tends to occur before rapid root uptake (Millard 1996) and may provide the majority of N required for spur leaf growth and half of the N used for shoot leaf growth (Neilson et al. 1997). The amount of N remobilized for leaf growth is independent of root supply but may be determined by the previous year’s N supply (Millard 1996). Thus, a poor supply of N from the soil is not likely to limit growth until remobilization is complete. In the fall, uptake of N by roots may occur at the same time as leaf senescence, with N being allocated to storage resulting in more remobilization the following year (Millard and Thomson 1989, Tagliavini et al. 1999). A second factor to be considered in the timing of N inputs is the possible effect on tree development. High-N supply tends to favor vegetative over reproductive growth (Forshey and Elfving 1989).

This may be associated with several factors that act to reduce the induction of flowers in vegetative buds of deciduous fruit trees including a rapid rate of initiation of successive leaf primordia, high tree vigor, shading and subsequent low photosynthetic activity (Faust 1989). Conversely, a low N supply may also result in fewer flower buds. Little is known about the effects of the timing of N availability on fruit bud development. Flower bud size is often increased in apple trees receiving spring applications of N (Faust 1989), but increasing the supply of N in the fall may accelerate bud development over winter (Buban and Faust 1982).

Fruit orchards equipped with micro-irrigation systems offer the opportunity to control N and water inputs, by the application of N through the irrigation system at specific times and scheduling irrigation to meet evaporative demand (Neilson et al. 1998). This approach should improve the efficiency of both water and N fertilizer use, thus reducing leaching losses. Previous experiments have indicated that, in a daily irrigation regime, the concentration of N maintained in the soil solution beneath drip emitters is similar to that found in the irrigation solution (Neilson et al. 1997, 1998). In the present experiment, newly planted Golden Delicious/M.9 apple trees were grown in the field with N applied at different times and irrigation supplied at either a constant rate over the growing season or in response to evaporative demand. The N was enriched with \( ^{15} \text{N} \) to allow quantification of fertilizer uptake in a series of destructive harvests to (1) determine the effects of irrigation method on the amount of fertilizer N applied and the efficiency of tree N uptake; (2) quantify the effect of the timing of fertilizer applications on tree N uptake and growth within that year; and (3) determine the impact on N remobilization and fruiting in the following year.

Materials and methods

Experimental design

Golden Delicious on M.9 rootstock apple trees were planted on April 9, 1997 in an Osoyoos loamy sand soil (Wittneben 1986) at the Pacific Agri-Food Research Station, Summerland, BC, (49°33′39″ N, 119°38′39″ W). The trees were irrigated daily with two 4 l h⁻¹ pressure compensating emitters (Hardie Irrigation, El Cajon, CA) per tree, spaced at 25 cm on either side of the trunk. Irrigation was either applied to meet daily requirements, based on demand (I1) estimated by the previous day’s evaporation from an atmometer (ETGage Co., Loveland, CO) linked through a data logger (Campbell Scientific, Logan, UT) to irrigation controls; or applied at a fixed rate of 8 l tree⁻¹ day⁻¹ (I2). Nitrogen was injected into the irrigation system through Mazzei injectors (Model 283; Mazzei Injector Corp., Bakersfield, CA) to give a mean N concentration at the emitter of 112 mg l⁻¹ for both irrigation treatments. Previous greenhouse studies indicated that maximum growth of apple trees on M.9 rootstock occurred when irrigation solutions had N concentrations between 56 and 112 mg l⁻¹ (Neilson et al. 1993). The trees were hand-watered at planting and daily irrigation was supplied from April 23 to October 15.

Nitrogen was applied daily over a 6-week period at three application timings: (N1) 2–8, (N2) 5–11 and (N3) 8–14 weeks after planting. Thus, as the amount of N delivered varied with the amount of water added, treatments received different amounts of N but at a constant concentration. Nitrogen was supplied as Ca\((^{15}\text{NO}_3)_2\) (1.85 atom% \(^{15} \text{N} \)). The single-tree plots were replicated three times in a randomized complete block design.

Before planting, the trees, which had been removed from the nursery the previous fall and held in cold storage over winter, were pruned to 80 cm above the scion–rootstock union, their roots were trimmed to 2.5 cm and their few side branches removed. The trees were planted at a spacing of 2 × 2 m to allow excavation of individual trees without disturbing adjacent trees. Herbicide was used to keep the area between the trees weed free. The day after planting, all trees received 20 g P as H₂P₂O₅ applied through the irrigation system over a 30-min period followed by 1 h of irrigation.

Soil solution monitoring

Soil suction lysimeters with 2.0-cm diameter porous cups (Irrometer Co. Inc., Riverside, CA) were installed at 30-cm depth below one of the drip emitters for the set of (H5) trees. Installation and sample collection procedures have been described previously (Neilson et al. 1998). Samples were collected daily and NO₃-N was analyzed in the laboratory with a portable ion specific electrode meter (Cardy meter, Horiba Ltd., Kyoto, Japan).

Plant measurement and sampling

Before planting, the trees were weighed and trunk diameter measured at 30 cm above the scion–rootstock union. The trees were harvested on May 14 (H1), June 4 (H2), June 23 (H3) and July 16 (H4) in 1997 and May 26 (H5) in 1998. At harvest, scions were separated from rootstocks in the field and the roots were carefully excavated by hand. For trees harvested at (H4) and (H5), the large root systems required a longer excavation time so that harvest was spread over three days. During this time trees received water but no fertilizer. Trees from the first four harvests (H1)–(H4) were partitioned into leaves, shoots, scion trunk, rootstock, old woody roots, white roots > 1 mm, suberized roots > 1 mm and fine roots < 1 mm. Roots were
washed to remove soil particles. For trees from the last harvest (H5), tissue also included fruitlets and 1-year-old wood. At (H5), leaves and shoots were subdivided into those that were vegetative and those associated with the fruit. The latter included primary spur leaves that develop within the fruit bud and secondary bourse shoots that develop at the base of the floral cluster. Leaf, shoot, fruitlets and fine root samples were dried at 65 °C for 24 h. Woody tissues and coarse roots were dried at 65 °C to constant weight (± 0.1%). Total fresh and dry mass were recorded for all tissues. Trunk diameter, branch length and root length were measured at each harvest. Fine root length was measured with a COMAIR root length scanner (Hawker de Haviland, Ltd., Port Melbourne, Australia). For (H5) trees, branch length was measured on July 9 and then on a weekly basis from July 23 to October 29, 1997.

Analysis of samples
All tissues were milled before analysis. Total N and 15N concentrations in samples were determined with an ANA-SIRA mass spectrometer (VG Isogas, Middlewich, Cheshire, U.K.). The amounts of 15N in the plants were calculated as described by Millard and Neilson (1989). Non-fertilizer (unlabeled) N in the plants at (H1) was considered to be derived from the previous year’s uptake and not from the native soil N pool in the current year, because no 15N (fertilizer), which was supplied for three weeks before (H1), was taken up until after (H1). The difference between unlabeled N content at (H1) and subsequent harvests (H2–H5) was assumed to be derived from current-year uptake from the native soil N pool.

Statistical analysis
Effects of irrigation, N timing and harvest timing were evaluated by analysis of variance with the SAS software package (SAS Institute Inc., Cary, NC, 1985). Effects of irrigation and N timing on branch length over time were evaluated by repeated measures analysis of variance.

Results
Irrigation and N treatments
The time course of N availability in the root zone, measured as soil solution nitrate-N concentration, reflected the timing of N applications (Figure 1). Soil solution nitrate-N concentration was elevated to near target values (112 mg l⁻¹) during fertilizer application and declined to background values (5–20 mg l⁻¹) when applications ended. There was some evidence of increases in soil solution nitrate-N concentrations in late August in the demand-controlled irrigation plots receiving N at the two earlier timings that was probably the result of N mineralization. This increase was not observed in the fixed-rate irrigation plots, possibly because of leaching as a result of excess application of water (1280 l tree⁻¹ year⁻¹ for (I2) compared with 377 l tree⁻¹ year⁻¹ for (I1)).

Irrigation method resulted in large differences in the amount of N applied (Table 1). Less N was applied to the demand-controlled irrigation plots (I1) than to the fixed-rate irrigation plots (I2) because of the smaller amount of water applied. However, similar N concentrations were maintained in the root zone in both irrigation regimes (Figure 1) and both N and water were replenished on a daily basis, indicating that excess N applied in the fixed-rate irrigation treatment was leached in the drainage water and unavailable to the tree. Thus, in both irrigation treatments, the amount of available fertilizer N was probably similar. Uptake of fertilizer N was unaffected by irrigation treatment, indicating that N availability was probably not a limiting factor in either irrigation regime. Although timing of N applications had less effect on the amount of fertilizer applied than the irrigation method, N uptake was lower when applied at 2–8 weeks after planting (N1) than at later application times (N2, N3). With the exception of the (I1N1) treatment, there was little uptake of labeled N between early July (H4) and early spring of the following year (H5). The efficiency of fertilizer use was calculated from the ratio of fertilizer N content of trees at (H5) plus that removed during leaf abscission, to the amount of fertilizer added (Table 1). Fertilizer recovery was much lower for trees grown with fixed-rate irrigation than with demand-controlled irrigation. There was significantly higher uptake of native soil N by early July (H4) in (N1) and (N2) trees than in (N3) trees. These differences
were still evident the following spring (H5), but were no longer significant. After early July (H4), N uptake from the soil was greater than N uptake from fertilizer applications for all trees. Because there was no effect of irrigation method on N uptake and because N-uptake efficiency of trees in the fixed-rate irrigation treatment was low, further effects of N timing on tree N use will be considered only for trees in the demand-controlled irrigation treatments.

Tree growth

Increases in trunk cross-sectional area between planting and the following spring (H5) were unaffected by N timing treatments and ranged from 253 to 285 ± 43 mm$^2$. In the first year, tree growth rate was low between mid-May (H1) and early June (H2) but increased with each successive harvest (Figure 2a). Tree growth rate was unaffected by N treatments until mid-June (H3), but growth rate increased by mid-June (H3), recovery of unlabeled N from new roots $<1$ mm in diameter at (H5) (Table 2) exceeded the amount that was remobilized into leaves before mid-June (H3). Consequently, we used the redistribution of N supply affected N uptake (Table 1), there was little effect on early season vegetative growth in Year 2. There was, however, an effect on fruiting in Year 2 (Table 2). Total mass of fruitlets on trees receiving the early application of N (N1) in Year 1 was greater than that on trees receiving later applications of N (N2, N3). This reflected the numbers of fruiting spurs, which were 195, 151 and 132 fruiting spurs tree$^{-1}$ ($P = 0.031; SE = 10.6$) for (N1), (N2) and (N3) trees, respectively. The amount of growth that occurred by the third week in May (H5) in Year 2, was much greater than the amount of growth over a similar period in Year 1. In particular, the mass of roots $<1$ mm in diameter at (H5) (Table 2) exceeded the amount that had developed by early July (H4), in the year of planting (Figure 2c). Shoot growth was measured for (H1)–(H4) trees at each harvest and for (H5) trees from Days 194 to 300 in Year 1. Shoot growth ended around Day 250 for trees in all treatments. By the end of the growing season, (N1) trees had greater shoot length than (N2) and (N3) trees (821 cm versus 673 and 611 cm, respectively; $P < 0.01$, SE = 38).

N remobilization and uptake

There was a small, nonsignificant change in total unlabeled N per tree during Year 1 until after mid-June (H3), probably indicating that there was little soil N uptake before that time (Figure 3a). Consequently, we used the redistribution of unlabeled N before mid-June (H3) to assess remobilization. By mid-June (H3), recovery of unlabeled N in leaves and shoots was 750 ± 42 mg of which 110 mg was already remobilized into leaves before mid-May (H1) (Figure 3b). Thus, around 640 mg of N was remobilized into leaves and shoots between mid-May (H1) and mid-June (H3). By mid-June (H3), recovery of unlabeled N from new roots $>1$ mm was $26 ± 8.3$ mg and from new roots $<1$ mm was $42 ± 4$ mg of which 14 and 3 mg, respectively, had accumulated before mid-May (H1) (Figure 3c). Thus, around 51 mg of un-

| Treatment | Fertilizer N applied | N1 = 2–8 weeks after planting | N2 = 5–11 weeks after planting | N3 = 8–14 weeks after planting | Fertilizer recovery (%) | Native soil N uptake$^1$
|---|---|---|---|---|---|---|
| I | N | (H4) | (H5)$^2$ | (H4) | (H5)$^2$
| I | 1 | 1 | 8.8 | 0.9 | 1.45 | 16 | 2.24 | 6.47
| 1 | 2 | 9.4 | 2.12 | 1.52 | 16 | 1.98 | 5.53
| 1 | 3 | 11.9 | 2.06 | 2.3 | 19 | 1.52 | 3.96
| 2 | 1 | 37 | 0.86 | 0.86 | 2 | 1.68 | 4.76
| 2 | 2 | 37 | 2.42 | 2.06 | 6 | 2.01 | 6.3
| 2 | 3 | 37 | 2.87 | 3 | 8 | 1.58 | 4.94

$^1$ Calculated from the difference between unlabeled N content at Harvest 1 and later harvests.

$^2$ Includes the amount of N lost in senescent leaves.

$^3$ P-Values are indicated by asterisks: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, and NS = not significant.
labeled N was remobilized into new roots between mid-May (H1) and mid-June (H3). During the same period, the unlabeled N content of woody tissue decreased from 1088 ± 22 mg at (H1) to 505 ± 22 mg at (H3), a difference of 583 mg (Figure 3d). Thus, there was a difference of 108 mg between the amount of N removed from woody tissues and the amount remobilized into new growth. The difference may be explained by sampling error because each sample represented a different set of trees, or it may reflect a small amount of soil N uptake. About half of the N remobilized from woody tissue came from the rootstock/old root system and the remainder from the trunk. The timing of current-year (labeled) N supply had no effect on the amount of N remobilized (Figure 3).

After mid-June (H3), there was an increase in native soil N taken up by the roots (Figure 3a). More native soil N was taken up by (N1) trees than by (N2) and (N3) trees (Table 1), but for individual plant organs, this only translated into a significant difference for new roots < 1 mm if (N1) trees had a higher unlabeled N content than (N2) and (N3) trees by early July (H4) (Figure 3c). The timing of N applications affected the uptake of labeled N (Figure 4). By early July (H4), there was significantly less N taken up by (N1) trees than by (N2) and (N3) trees. Uptake of labeled N by (N1) trees continued after irrigation with N solution had ended, i.e., between early June (H2) and early July (H4), despite a reduction in soil solution N concentration over that period to 15–20 mg l⁻¹ (Figure 1).

Nitrogen contained in new growth in the year after planting was derived from both fertilizer and soil sources (Table 3). We assumed that remobilization was complete by the time of sampling (three weeks after full bloom), because Neilsen et al. (1997) had found that, in similar young, fruiting apple trees, remobilization ended by five days after full bloom. Only data for N content in aboveground growth are shown, because it

**Table 2. Impact of the timing of N applications on the biomass of trees measured three weeks after full-bloom (day of the year 145) the following year. The asterisk indicates P < 0.05.**

<table>
<thead>
<tr>
<th>Component</th>
<th>Dry mass (g tree⁻¹)</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(N1)</td>
<td>(N2)</td>
</tr>
<tr>
<td>Leaves</td>
<td>107</td>
<td>93</td>
</tr>
<tr>
<td>Shoots</td>
<td>11</td>
<td>11</td>
</tr>
<tr>
<td>Frame</td>
<td>528</td>
<td>480</td>
</tr>
<tr>
<td>Roots &gt; 1 mm</td>
<td>60</td>
<td>65</td>
</tr>
<tr>
<td>Roots &lt; 1 mm</td>
<td>21</td>
<td>16</td>
</tr>
<tr>
<td>Fruitlet</td>
<td>33</td>
<td>23</td>
</tr>
<tr>
<td>Total</td>
<td>760</td>
<td>687</td>
</tr>
</tbody>
</table>

Figure 2. Dry mass partitioning of newly planted Golden Delicious/M.9 apple trees at four harvest times (H1–H4) in response to timing of N fertilizer applications, (weeks after planting: 2–8 (N1, ▲); 5–11 (N2, ◦); and 8–14 (N3, ▼)); (a) total, (b) shoots and leaves, (c) new roots, and (d) trunk, rootstock and old roots. Vertical bars represent the mean of three replicates ± 1 SE for the interaction between harvest time and N application timing. Horizontal dashed lines denote the length of time of fertilizer application for (N1), (N2) and (N3).
was not possible to separate new and old root growth. Leaves, which included those from fruiting spurs, non-fruiting, spur bourse shoots and shoots, were the dominant sink for N and contained between 79 and 83% of the total N content of new growth followed by fruitlets, which contained between 11 and 17% (Table 3). On average, spur leaves contained around 55%, bourse shoot leaves around 22% and shoot leaves around 23% of the total N content in leaves (data not shown). The amount of 15N that was remobilized into leaves was higher for (N3) trees than for (N1) and (N2) trees. The total amount of N contained in annual tissues was related mainly to dry matter accumulation (Table 2). Thus the amount of N contained in fruitlets was higher for (N1) trees than for (N2) and (N3) trees (Table 3), because (N1) trees had more fruitlet dry mass (Table 2). The proportion of total N in annual tissues that was derived from fertilizer was greater for (N3) trees than for (N1) and (N2) trees (Table 3), reflecting the relatively larger proportion of fertilizer N in (N3) trees compared with (N1) and (N2) trees (Table 1).

Discussion

N demand and supply

In our experiment, tree growth was high for intensively managed apple trees planted on dwarfing rootstocks when compared with the optimal trunk growth rate of 80 mm² in the first
Table 3. Effects of timing of N supply on the remobilization of fertilizer-derived N and the total N content of aboveground tissues the following year. Application times in weeks after planting: (N1) = 2–8; (N2) = 5–11; and (N3) = 8–14.

<table>
<thead>
<tr>
<th>N source</th>
<th>Tissue</th>
<th>N content (mg tree−1)</th>
<th>P-value1</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(N1)</td>
<td>(N2)</td>
<td>(N3)</td>
</tr>
<tr>
<td>Fertilizer</td>
<td>Leaves</td>
<td>363</td>
<td>346</td>
</tr>
<tr>
<td></td>
<td>Shoot wood</td>
<td>19</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>Fruitlets</td>
<td>89</td>
<td>66</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>471</td>
<td>431</td>
</tr>
<tr>
<td>Fertilizer + soil</td>
<td>Leaves</td>
<td>3002</td>
<td>2524</td>
</tr>
<tr>
<td></td>
<td>Shoot wood</td>
<td>146</td>
<td>147</td>
</tr>
<tr>
<td></td>
<td>Fruitlets</td>
<td>655</td>
<td>444</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>3803</td>
<td>3115</td>
</tr>
<tr>
<td>Proportion of N from fertilizer</td>
<td>Total</td>
<td>12.5%</td>
<td>14.1%</td>
</tr>
</tbody>
</table>

1 - P-Values are indicated by asterisks: * = P < 0.05, ** = P < 0.01 and NS = not significant.

Efficient use of fertilizer N requires that the supply of N matches plant demand. When water and N are applied through irrigation systems, there is the potential to achieve this match (Haynes 1985) by controlling: (1) the amount of water flowing through the soil; (2) the residence time of N in the root zone; (3) the concentration of N in the soil solution; and (4) the timing of N availability (Neilsen et al. 1998), provided that plant demand for N is known. We found that fertilizer N use by trees in demand-controlled irrigation treatments was more efficient than in fixed-rate treatments, mainly because, as less water was used, less total N was needed to meet the target soil solution concentration of 112 mg l−1 NO3-N. With fixed-rate irrigation, excess water results in drainage below the root zone and N leaching (Neilsen et al. 1998) and thus added N is retained for a shorter time in the root zone than with demand-controlled irrigation. However, even in plots receiving demand-controlled irrigation, fertilizer N-use efficiency was low, ranging from 16 to 19% for the three N timing treatments. This is lower than fertilizer N recovery found for 2-year-old, non-bearing prune trees receiving a supply of N in spring (Weinbaum et al. 1978).

The trees took up more N from the pool of native soil N than from fertilizer N, particularly after the final harvest in the year of planting (end of July). At this time, soil solution NO3-N concentrations averaged between 5 and 40 mg l−1 and were much lower than during the time of fertilizer applications, but were apparently sufficient to maintain plant growth, because there were no differences in growth by the spring of the following year. Higher soil solution NO3-N concentrations after fertilizer additions ended were related to higher uptake of non-fertilizer N. This relationship may result from the incorporation of fertilizer N in soil pools (Huett and Stewart 1999) and the “priming” effect in which mineralization processes are enhanced by the addition of N fertilizer (Jenkinson et al. 1985). Thus, the amount of N applied in the demand-controlled (N1) and (N2) treatments, 8.8 and 9.4 g tree−1 respectively, closely matched the total N taken up to support new growth, 7.9 and 7.1 g tree−1 respectively, calculated from soil and fertilizer uptake. Nevertheless, because the amount of N taken up by the trees in the two irrigation treatment was similar, it is likely that much of the inefficiency was caused by a mismatch of supply to demand.

Two factors contributed to this mismatch. The first was that the target concentration of N in the soil solution was probably too high, even though it was lower than, or similar to, concentrations in previous studies where growth responses have been reported (Robinson et al. 1991). Bhat (1983) measured maximum uptake rates of NO3-N by field-grown apple roots from nutrient solutions with N concentrations as low as 0.28 mg l−1, and concluded that, within the soil, uptake occurs either at near maximum rates or not at all. Thus, the benefits of high soil solution concentrations may be associated with avoiding difficulties in maintaining adequate nutrient flux to roots or where a root system is only partially functional (Robinson et al. 1991). In irrigated soils, severe reductions in mass flow to roots would likely occur only if the water supply was less than plant demand, which was not the case in the present study.

The second factor affecting N uptake was timing of N supply. Demand for root-supplied N was not evident until between 35 and 55 days after planting because earlier growth, in particular that of shoot leaves, was supported mainly from remobilization of N from woody tissue. Thus, N supplied prior to 35 days after planting was not used by the tree. Because rapid uptake of N did not begin until after the first N timing treatment ended, total N fertilizer uptake by trees in that treatment was lower than for trees receiving the later applications of N. When N remobilization ended, the increase in N demand was accompanied by a rapid increase in the rate of development of the fibrous root system in all treatments. This effect was most evident for trees receiving early N where the high demand for N coincided with low-N supply and resulted in the development of a large fine root system. Consequently, al-
though fertilizer N uptake was lower for trees receiving the earliest N supply (N1) than for those receiving later N supply, (N1) trees were able to compensate by taking up more native soil N, presumably because a larger soil volume was explored by the larger root system.

**Nitrogen remobilization**

Nutrient withdrawal from senescing leaves makes an important contribution to whole-tree nutrient budgets (e.g., Taylor and May 1967, Chapin and Kedrowski 1983). In turn, such nutrient withdrawal contributes to both vegetative and reproductive growth of trees in subsequent years (May and Killingbeck 1992). Deciduous trees, however, can also take up N by their roots in late summer and autumn, even while their leaves are senescing (e.g., Millard and Thomson 1989, Millard and Proe 1991, Wendler and Millard 1996). Several studies have shown that autumn uptake of N alters partitioning within the tree. Weinbaum et al. (1984) showed that, in *Prunus dulcis* (Mill.) D.A. Webb, N absorbed by the tree in late summer was retained in the roots and more proximal aboveground tissues, and suggested that late-season uptake of N may be important for internal cycling. Several other studies have subsequently shown that fertilizer applied in the autumn increases partitioning of N to roots (e.g., Sanchez et al. 1992, Munoz et al. 1993). Soil N uptake has been shown to contribute as much, or more, to N allocated to storage and subsequently remobilized as that withdrawn from leaves during senescence (Rosecrance et al. 1998, Tagliavini et al. 1998). Thus, the timing of N uptake during the growing season might be expected to influence the amount of N remobilized the following year.

We assessed N remobilization over two years. In the first year, 55% of N in the tree at planting was subsequently remobilized. This included some N remobilized into the root system. Because of the difficulties associated with recovery and separation of new and established root systems, most studies report only N remobilized for growth above ground. Our newly planted trees had pre-existing root systems that consisted of only a few woody roots, making identification of new roots feasible; consequently we were able to demonstrate that remobilization for root growth accounted for about 10% of the total N remobilized by the trees. The timing or amount of N supply did not affect remobilization in the first year, as it has been found for a range of other species (Millard 1996). The finding that the amount of N remobilized depends only on the amount of N in store suggests that the process is source rather than sink driven.

The timing of N supply affected N remobilization in the second year of our study. Late application of N in the first year resulted in more fertilizer N being remobilized for leaf growth the following year. This could have occurred because the (N3) trees took up more fertilizer N than the (N1) trees. However, it could also have been caused by differences in the balance between reproductive and vegetative growth, because early N applications were associated with increased bloom and fruiting. This, in turn, resulted in less remobilization of N for leaf growth as is evident from the leaf:fruit ratio of fertilizer N content, which was 4:1 and 7:1 for trees receiving early and late applications of N, respectively.

Increased bloom in trees receiving early N was related to the timing of N availability, because there were no treatment differences in total N uptake. Flowering in apple trees occurs on short spurs that are at least 2 years old and on terminal and lateral buds of 1-year-old shoots (Westwood 1978). We found that, with the exception of a few spurs on the trunk, all fruit was borne on 1-year-old shoots. Forshey and Elving (1989), in summarizing the literature, concluded that flower bud initiation, particularly of lateral buds, often begins after extension growth ceases, and that factors that stimulate or prolong vegetative growth, such as high-N supply, may reduce flowering. In our study, increased bloom and fruiting occurred in trees receiving early N, and these trees had longer shoots than, and a similar growing period to, trees receiving later N applications. Increased flower bud development in trees receiving early N was thus more probably related to factors other than the effects of N supply on shoot growth. Low-N supply during the period of high-N demand immediately following the end of remobilization increased fine root growth in (N1) trees. Perhaps a larger fine root system in (N1) trees allowed for greater uptake of soil N later in the growing season that was then available for flower bud differentiation, because low-N supply can inhibit flower bud development (Faust 1989). Tromp (1968) reported that differentiation of flower buds in late summer can occur in non-bearing apple trees, and Luckwill and Silva (1979) found that flower bud differentiation in “Golden Delicious” was much shorter and more sudden than in many other apple varieties. Thus, in our study, there was apparently sufficient time for both histological differentiation of flower buds in late summer and subsequent morphological differentiation over the winter (Buban and Faust 1982) despite the vigorous shoot growth that is often associated with the suppression of flower bud development.

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