Regulation of Nitrogen Uptake at the Whole-plant Level: A Study in Almond Trees

Farbod Youssefi,¹ Patrick H. Brown,² and Steve A. Weinbaum³

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SUMMARY. It has been proposed that a pool of amino N, whose size is determined by aboveground N demand, cycles in the plant and regulates soil N uptake by exerting an inhibitory effect at the root level. Several experiments were carried out to study this hypothesis in almond trees [*Prunus dulcis* (Mill.) D.A. Webb]. Based on the evidence found, there is an association, at the whole tree level, between sap N content and soil N uptake. The data are consistent with the possibility that increased phloem sap amino acids result in decreased uptake of soil N.

The use of nitrogenous chemical fertilizers in agriculture, which has benefitted crop production significantly, has also contributed substantially to the nitrate contamination of groundwaters (Davies and Sylvester-Bradley, 1995; Staver and Brinsfield, 1990), not only affecting the ecosystem (Hanley, 1990), but also representing a health hazard for drinking water (Dorsch et al., 1984; Hanley, 1990). This results mainly from nitrogen (N) application in excess of plant nitrogen utilization, and is a function of N rate applied and the timing of application. Fertilizer N applied in excess of that needed to support optimum productivity accumulates in the soil and becomes increasingly vulnerable to a variety of loss mechanisms such as leaching. That is why excessive N application rates are correlated inversely with N-use efficiency, and positively correlated with N leaching (Weinbaum et al., 1992).

The development of improved fertilizer management practices requires an understanding of the dynamics of plant N usage. Plant N demand fluctuates over the annual growth cycle according to variations in the number and strength of the various vegetative and reproductive sinks. The synchronization of N supply with plant N demand is essential to improve N-use efficiency and reduce nitrate losses.

Department of Pomology, University of California, One Shields Ave., Davis, CA 95616.

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¹Research assistant.

²Associate professor.

³Professor.

By understanding the regulation of soil N uptake, and the temporal patterns of tree N demand, the timeliness of fertilizer applications may be improved, and the efficiency of fertilizer N recovery increased.

Whole-plant regulation of soil N uptake

The growth rate of plants determines N uptake rate (Gastal and Saugier, 1989; Lemaire and Salette, 1984; Schenk, 1996; Schubert et al., 1990; Swiader et al., 1991). This suggests a regulatory linkage between plant N uptake and plant N demand. The fact that N deficiency within hours induces the development of an increased capacity of barley roots (*Hordeum vulgare* L.) to absorb N (Siddiqi et al., 1990) suggests that N uptake can be regulated by the N demand, at least when N is deficient. Numerous hypotheses have been proposed to explain this regulatory mechanism of N uptake.

Two major findings have led to the formulation of one of these hypotheses. First, experimentation has clearly established that a pool of amino-N cycles between roots and shoots in the vascular tissues of plants (Keltjens et al., 1986; Simpson et al., 1982; Touraine et al., 1988). Second, certain amino acids supplied to the roots of young plants inhibited nitrate uptake when applied either externally (in a culture medium) or internally (by phloem sap) (Lee et al., 1992; Muller and Touraine, 1992; Padgett and Leonard, 1993, 1996). These two findings together are a basis for the hypothesis that a pool of amino-N cycles in the plant, reflecting the aboveground demand for N and regulating soil N uptake (Cooper and Clarkson, 1989; Larsson et al., 1991; Touraine et al., 1994).

According to this hypothesis, when there is a low demand for N, the cycling pool of amino N would remain large and would inhibit soil N uptake (Fig. 1, tree on left). On the other hand, if a large N-requiring fruit load were present, N would be depleted from the cycling N pool and N uptake inhibition at the root level would not be as strong, allowing greater uptake of soil N (Fig. 1, tree on right).

If this hypothesis is valid, soil N uptake might be inhibited by increasing the size of the cycling amino-N pool, as expressed by amino-N concentration. To test the hypothesis, foliar applications of urea were made to mature almond trees [*Prunus dulcis* (Mill.) D.A. Webb] in the field during nut fill; these appli-

cations significantly increased phloem amino acid concentration and reduced soil N uptake within 14 to 21 d of application (Table 1) (Youssefi, 1998). Foliar-applied urea N moved into the roots of the trees within 14 d after application, and could have played a role in reducing soil N uptake. In a parallel experiment, we observed that low N status almond trees, with lower concentrations of amino acids cycling in the tree sap, demonstrated a higher N uptake capacity than high N status trees when pulsed with abundant N fertilizer (Table 2). These results are consistent with the hypothesis proposed, due to the association between the size of the amino N pool, as expressed by sap amino acid concentration, and soil N uptake.

The relationship between N sinks and the cycling amino-N pool suggested by this hypothesis needs further study. Presumably, the demand imposed by the sum of these sinks would be the prime factor regulating soil N uptake by controlling the size of the cycling amino-N pool. A preliminary study with walnuts (*Juglans regia* L.) showed that the presence of fruit on a branch decreased the movement of N out of that branch, and therefore could lead to a smaller pool of N exported in the tree's vascular system. This suggests that aboveground N demand could shape amino-N levels in the vascular transport stream of a plant.

One could speculate that during periods of higher demand, such as nut fill or fruit development, a larger amount of amino N is removed from the cycling pool, and a lower amino acid concentration would be found in the vascular system. In alternate bearing crops, higher amino-N concentrations would probably be found in low-production years than in high-production ones. By further studying this regulatory mechanism, and relating it to seasonal patterns of crop N demand, greater coordination of fertilization practices and plant N demand cycles might be achieved to help reduce groundwater contamination.

Fig. 1. Cycling pool of amino N in trees with low (left) and high (right) fruit loads according to N uptake regulation hypothesis. The size of the arrows in the tree illustrates the amino N concentration, whereas the size of the arrows in the soil indicates the N uptake level.

Table 1. Effect of foliar applications of urea on the amino acid concentrations in leaf phloem exudate and on soil nitrogen (N) uptake expressed as percentages of tree N content.

Treatment	Amino acid concn of leaf phloem exudate (nmol/50 μ L) ^z	Soil N uptake/tree (%)
Control	1.179	9.70
Foliar-applied	1.988	8.70

^z1 nmol/50 μ L = 1.284×10^{-6} fl oz./inch³.

Table 2. Tree sap amino acid concentrations of almond trees of different nitrogen (N) status, and their estimated uptake from a N fertilizer pulse.

N status	Bark phloem amino acid concn (nmol/50 μ L) ^z	Xylem sap amino acid concn (nmol/50 μ L)	Estimated soil N uptake ^y (g) ^x
Low	12.199	13.263	25.04
High	26.470	50.941	1.59

^z1 nmol/50 μ L = 1.284×10^{-6} fl oz./inch³.

^yIn aboveground tree parts.

^x1 g = 0.035 oz.

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