Nitrogen Uptake and Assimilation in Woody Crops

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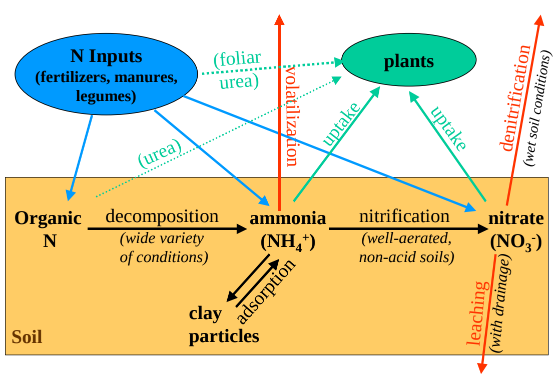
Introduction: Nitrogen (N) compounds are found in all plant tissues, where they play key roles in growth, reproduction, and photosynthesis. Although N is the most commonly supplemented plant nutrient, requirements for orchard crops are not as high as many people think. Estimates are that less than 20% of applied N is used by the trees for growth and crop production; what is not used may become an environmental pollutant. Over-application of N to orchard crops can also result in excessive shoot growth at the expense of fruit or nut set, reduced crop quality, or increased susceptibility to pests. If properly applied, N can improve both crop quality and yield. The challenge is to apply just the right amount at the right time. A little knowledge of the physiology of N uptake and utilization in woody plants may help one understand how better to do this.

Factors affecting N supply (Fig. 1): Plant roots take up primarily ammonium or nitrate from the soil, but they cannot take up significant quantities of organic N. Organic N must first be decomposed. Ammonium is

Soil N Transformations

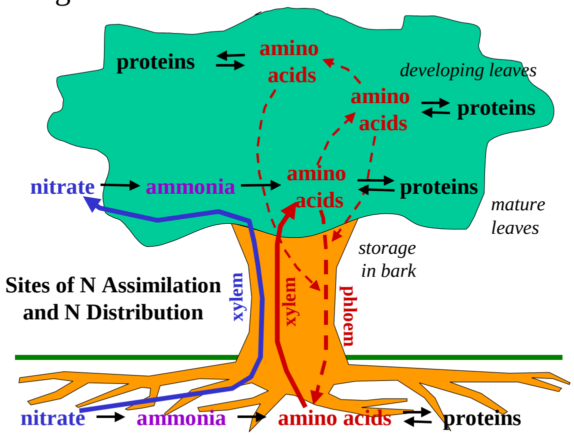


the first product of decomposition, but under ideal conditions very little accumulates in the soil beneath woody crops because conditions which favor the growth of tree crops also favor the nitrification of ammonium to nitrate. Most crops prefer nitrate or a mixture of the two. But a few, such as blueberries, which are native to acidic soils where nitrification is inhibited, lack the ability to take up much nitrate and use ammonium instead.

Both nitrate and ammonia can be lost from the soil as environmental pollutants (italicized in diagram) if present in excess of the crop's ability to take them up, especially nitrate under wet conditions. This is why it is important to apply only as much as the crop is capable of using.

N uptake: Because the concentrations of ammonium and nitrate are higher inside root cells than they are in the soil, plants must actively pump them in, expending energy from photosynthesis to do so. Thus when photosynthesis is limited, such as on cloudy days or during drought, a plant's ability to take up N may also be limited. The "pumps" are special enzymes embedded in the cell membranes that are specific to the kind of N being taken up. These enzymes can be turned on and off to control how much nitrate or ammonia is taken up. If more N is taken up than the plant can assimilate, a feedback mechanism turns the uptake enzymes off.

N assimilation inside plants is basically the reverse of the decomposition of organic matter that occurs in the soil (Fig. 2). Nitrate is first "reduced" to ammonium, which is then added to the skeletons of carbon compounds manufactured during photosynthesis to form amino acids. Amino acids are strung together into long chains to form proteins, which are the working molecules of the plant. Like in N uptake, each of these steps requires energy from photosynthesis, but N assimilation has the additional requirement of carbon skeletons (carbohydrates) from photosynthesis. Thus N assimilation is doubly dependent on conditions that favor photosynthesis: adequate light, heat, moisture, and green leaves.



N distribution and allocation (Fig. 2): N taken up by the roots is transported to the leaves in the xylem sap (solid lines), either as nitrate or as amino acids. After that N is redistributed in the phloem (dashed lines) as amino acids, according to demand, from "source to sink". Because N is a component of chlorophyll and other vital enzymes of photosynthesis, the leaves are very strong "sinks" for N. Nitrogen is also important for growth, so rapidly developing tissues, such as buds, new leaves, and developing fruits and nuts, are also important sinks.

In order to make the best use of their N supply, plants recycle it from tissues where it is no longer needed to ones where it is needed. For example, after growth is complete in a new leaf, some of the proteins in it may be broken down into amino acids and transported to younger leaves, or to a developing fruit or seed. Likewise, if a leaf becomes shaded, so that it no longer photosynthesizes efficiently, its N may be translocated to another leaf that is in the full sun.

In the fall, trees withdraw most of the N from their leaves before leaf-fall and transport it in the phloem to winter storage sites either just beneath the bark or in the roots. In the spring this stored N can be remobilized for bud break much more efficiently than N from the soil because it is already present as either amino acids or simple proteins, sparing the energy expenditure for uptake or assimilation. This is fortunate because until the new leaves are functional they cannot supply the energy that would otherwise be needed. Moreover, bud break often occurs at a time when root uptake and soil N availability are poor due to cold soils.

Early-season tree growth depends almost entirely on stored N, with N contributions from spring-applied fertilizer becoming important only later in the season. Because flowering and fruit set occur early, spring-applied N fertilizer might not affect yield until a whole season after application. Thus the objective of fertilization should be to build reserves for flowering and early shoot growth in future years. Nitrogen applied after harvest may be taken up efficiently as long as leaves have not yet senesced. It goes directly into storage for the next season's growth.

Two key concepts and implications:

1) Trees are very efficient at recycling N. The older they get, the more N they are able to store from one season to the next and the less important new uptake becomes. Thus fertilization of mature trees needs only to replace the N removed by harvest and pruning. Young trees, which are still building their reserves, need more N relative to their size, but, with fewer roots, are more limited in their capacity to take it up and use it.

2) N uptake and assimilation require energy from photosynthesis. The development of photosynthetic capacity by young trees must be balanced with N uptake, or excess N may be lost to the environment. Thus young

trees should be fertilized in proportion to their size or age. Nitrogen fertilizer applied at times of year when photosynthesis is low, such as winter or during mid-summer drought, may not be taken up and may also be lost.

Recommended References:

Sanchez, E.E., H. Khemira, D. Sugar, and T.L. Righetti. 1995. Nitrogen management in orchards. p. 327 – 380. *In* P.E. Bacon (ed.) Nitrogen fertilization in the environment. Marcel Decker, New York.

Titus, J.S. and S.M. Kang. 1982. Nitrogen metabolism, translocation, and recycling in apple trees. Hort. Reviews 4:204-246.

Important concepts not covered:

1. Urea: Urea is a very simple organic compound that can be taken up in small quantities by some roots and also by leaves. Foliar urea sprays may be very efficient because there are no N leaching losses and because urea assimilation can bypass nitrate reduction, thereby saving the plant energy.

2. Competition between ions for uptake: N uptake is influenced by other nutrients in the soil. Ammonium, which is positively charged, may inhibit the uptake of other positively charged nutrients, such as calcium or magnesium. Nitrate, which is negatively charged, may compete with other negatively charged nutrients, such as phosphate or sulfur. This is not common in nature, but it can be a significant problem if large quantities of unbalanced fertilizers are applied, especially in containerized plants.

3. The effects of NH_4^+ vs NO_3^- on soil pH
Plants roots exude either H^+ or OH^- to balance the charges of the N ion taken up, which can have profound effects on soil pH.

4. Sites of assimilation
Conversion of nitrate to amino acids occurs in the roots in most fruit trees, but nitrate may be translocated to leaves if nitrate supply is high, such as in the case of very high N fertilization.

5. Root:shoot ratios
N may also be sent to grow more roots. This is especially likely if the N supply in the soil is low, because additional roots can explore the soil for previously unexploited N. This is why plants in N-deficient soils tend to grow proportionately larger root systems whereas plants well fertilized with N grow larger tops. This is another example of how N allocation is determined by demand. Although we may think that trees with larger tops would be more productive, they may have other problems, such as susceptibility to drought and weak anchorage. Balanced root to shoot growth is important.

6. Effect of excess N on fruit or nut quality: Fruit set is enhanced by high N. With excessive N more fruit may be set than the plant is able to support to photosynthetically: the number of developing fruit supported by each spur may be too high for the number of leaves supplying them. This results in smaller fruit. In nuts this results in poorly filled out kernels. In fruit there may be additional metabolic problems caused by imbalances between N and other nutrients, especially Ca^{2+}, leading to poor firmness and susceptibility to diseases.

7. Interpretation of Leaf N Concentrations for Figuring N application rates.
Growers wishing to fertilize responsibly are often advised to base their N rates on leaf N concentrations, but leaf N is not easy to interpret: high N supply may stimulate growth, which may lower leaf N concentration by dilution, and vice versa. Leaf analysis is, however, still useful if considered together with plant vigor. If shoot growth or yield are high and leaf N is also high, that is a sign of past over-fertilization, whereas if both are low fertilization should be in-

creased. If shoot growth or yield are low but leaf N is high, then there is probably a deficiency of some other nutrient or growth requirement. If shoot growth or yield are high but leaf N is low, then fertilization is probably optimal.