Part 2 of 2

See July's TurfGrass Trends for Part 1.

Turfgrass Root Growth: Increasing Nitrate Metabolism

By Richard J. Hull and John T. Bushoven

Last month, we looked at the chemistry of how nitrates work in root systems. Now we want to know why nitrate (NO_3-) absorbed by roots was not metabolized in the roots but rather transported to leaves.

It seemed reasonable that if NO_3- were reduced and assimilated in the roots, the amino acids formed there might stimulate root growth. At the very least, keeping NO_3- from the leaves should eliminate the NO_3- signal from diverting photosynthetic energy toward shoot growth and allow the roots to get their share.

There are two likely reasons for NO_3- metabolism not occurring in roots: 1) Roots might not contain sufficient nitrate reductase (NR) enzyme to accommodate the NO_3- absorbed by roots or, 2) NO_3- simply passes through root cells and is loaded into the xylem, for transport to leaves, so quickly that there is little time for NO_3- reduction to occur.

We tried to decide between these two possibilities by growing perennial ryegrass in solutions containing a range of NO_3- concentrations. We wanted to use NO_3- concentrations that were similar to those encountered by turfgrasses growing on a golf course or lawn. An earlier field study (Liu et al., 1997) showed that soil water under several perennial ryegrass cultivars averaged 1.8 parts per million (ppm) NO_3-N (nitrogen as nitrate) and rarely exceeded 7 ppm.

We grew perennial ryegrass Palmer III cultures in complete nutrient solutions containing 0.14, 1.26, 2.8 & 7.0 ppm NO_3-N for 60 days and determined the concentration of NO_3-N in leaves and roots (Fig. 1).

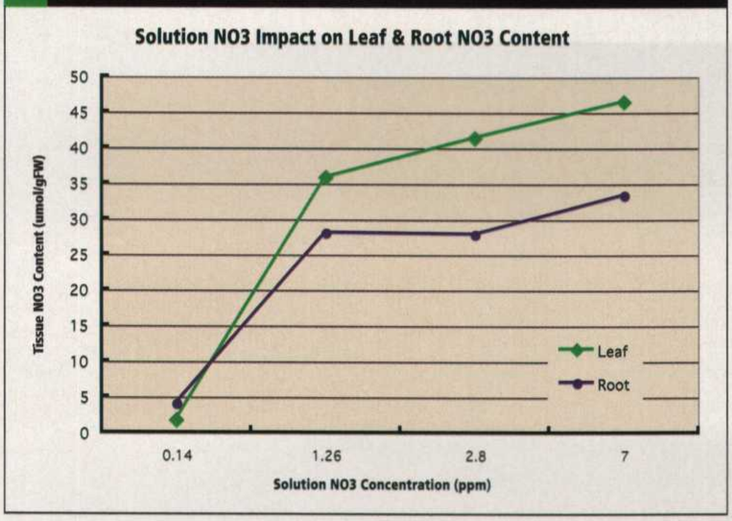
It is evident that the NO_3-N content of both roots and leaves increased as the culture solution NO_3- concentration increased. However, at 0.14 ppm NO_3-N, roots contained more NO_3- than did the leaves but at all higher-solution concentrations, leaf NO_3- was markedly greater than root NO_3-. This indicates that NO_3- metabolism in roots becomes saturated at a soil solution concentration between 0.14 and 1.26 ppm NO_3-N. As solution NO_3- increases, leaf NO_3-N content increases to levels greater than that in roots.

Since soil water beneath perennial ryegrass turf averages less than 2 ppm NO_3-N, it is reasonable to expect that NO_3- uptake by roots will normally saturate the roots' capacity for NO_3- metabolism, and substantial NO_3- will be carried to and accumulate in the leaves.

Is there any way to increase NO_3- metabolism in roots? The good news is that roots can metabolize NO_3-, but they exhibit only 10 percent of the NR activity observed in leaves (Bushoven and Hull, 2005).

We concentrated on NR because it catalyzes the initial step in NO_3- metabolism and is gen-

FIGURE 1



The increase of nitrate content in roots and shoots of perennial ryegrass grown in solutions containing four nitrate levels. Note that at very low nitrate levels, roots contained more nitrate than leaves but as solution nitrate concentrations increased, nitrate levels in leaves increased more rapidly than in roots.

erally considered to be the control point for the entry of NO_3- into its metabolic pathway. This brings us to the matter of speed by which NO_3- passes through root cells on its way to the xylem and transport to leaves. If NO_3- resides in the cytosol of root cells for only a short period of time and at low concentrations, it might not induce the synthesis of enough NR to metabolize more than a trace of the NO_3- passing through. Nitrate Reductase is an inducible enzyme in that it is only made when its substrate, NO_3-, is present. The gene that encodes NR is not expressed unless there is NO_3- in the cytosol. The relatively high concentrations of NO_3- in the roots (Fig. 1) does not mean that NR must be fully induced because most of that NO_3- has likely accumulated in the cell's membrane-bound vacuoles that are separate compartments from the cytosol. If the rate of NO_3- transport through the roots could be slowed, perhaps the cytosolic NO_3- concentration would increase and induce more NR synthesis.

We tested this idea by withholding potassium (K) from or adding sodium chloride (NaCl) to the nutrient solution. Potassium ions (K+) serve as a counter-ion for the loading of NO_3- into the xylem and during its transport to the leaves. If K+ is deficient in the roots, NO_3- transport in the xylem is slowed (Rufty et al., 1981). Adding NaCl to the nutrient solution increases the concentration of chloride ions (Cl-) that compete with NO_3- for entry into the xylem. It has been observed that plants subjected to salinity stress will increase NO_3- metabolism in their roots while decreasing it in their leaves (Cramer et al., 1995). We observed that both of these treatments did increase root NR activity as well as the percentage of NO_3- metabolized in perennial ryegrass roots, but the increases were small and not practically significant (Bushoven and Hull, 2005). However, these experiments did support the hypothesis that slowing the passage of NO_3- through roots could increase NO_3- retained and metabolized in roots.

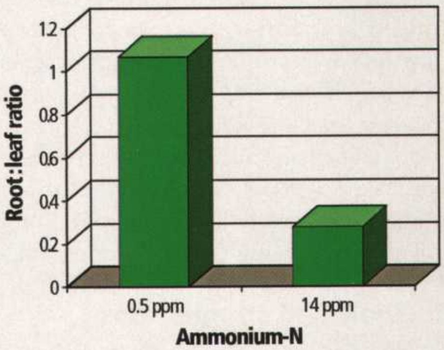
Turf grown without nitrate

In order to remove any possible NO_3- influence on root and shoot growth, perennial ryegrass was cultured in solutions containing ammonium (NH_4+) as the only nitrogen source. We supplied NH_4+ at a low and high concentration (0.5 & 14 ppm NH_4-N) to observe the effect of nitrogen concentration on relative root and shoot growth without the complication of NO_3- signaling.

FIGURE 2

Root Growth and Site of Nitrate Metabolism

Confining nitrogen assimilation to roots increases root:leaf ratios significantly.



Confining nitrogen assimilation to roots by growing perennial ryegrass in solutions containing low or high concentrations of ammonium resulted in less inhibition of root growth but markedly greater shoot growth at high nitrogen levels.

In solution culture, NH_4+ is rarely oxidized to NO_3- (nitrification) as it is in the soil. No NO_3- was detected in our solutions when NH_4+ was the nitrogen source. We found that, similar to NO_3-, high concentrations of NH_4+ markedly reduced the root:shoot ratio (Fig. 3). However, unlike NO_3-, the high NH_4+ concentration increased shoot growth 170 percent while NO_3, at the same concentration, actually reduced shoot growth 4 percent. Thus, the lower root:shoot ratio caused by high NH_4+ was caused mostly by increased shoot growth and not by dramatic reductions in root production.

Still, high NH_4+ concentrations did reduce root growth 30 percent but not as severely as high NO_3- (35 percent). This can be explained by the fact that NH_4+ is more readily absorbed by root than is NO_3-. Also, once absorbed, NH_4+ is rapidly assimilated because it can easily become toxic if accumulated in root cells. Thus, as Bowman and Paul (1988) earlier showed, rapid NH_4+ uptake by roots will likely divert much available energy (sugars) in the roots to support NH_4+ assimilation into amino acids and not to growth. These excess amino

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Recent evidence might cast the nitrate problem in a somewhat different light and can offer a few solutions.

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acids will be transported to the leaves where leaf growth will be stimulated as was demonstrated in the above experiment.

Thus, while NH_4+ can avoid the negative signaling problem of NO_3-, it presents some problems of its own that can reduce root growth. It is clear that root growth is fundamentally driven by photosynthetic energy obtained from the leaves, and anything that diverts this energy from the roots (high NO_3- in leaves) will depress root growth and compromise turf quality. This limitation to root growth will be considered in a future article.

Outlook and suggestions

The preceding discussion clearly suggests some strategies by which turfgrasses might be made more efficient in their use of nitrogen while increasing their utility as turf. All reactions involved in NO_3- metabolism and transport within plants are regulated by enzymes (proteins), which are ultimately under genetic control.

The application of molecular genetics to problems of NO_3- partitioning within turfgrasses, identified above, clearly have the potential to produce grasses that will be better adapted to the turf environment and more efficient in their use of nitrogen resources. Until this happens, however, there may be some turf management suggestions that emerge from our studies.

1) Do not apply NO_3- directly to turf. All nitrogen sources will ultimately be converted to NO_3- in the soil, but the process can at least be slowed by applying NH_3 forms, especially if they have slow-release properties.

2) Perhaps the use of nitrification inhibitors (slow the oxidation of NH_4+ to NO_3- in the soil) should be reconsidered. We and others have concluded that surface applications of these compounds are largely ineffective for increasing nitrogen use efficiency and minimizing NO_3- leaching in established turf. However, when incorporated into the soil prior to seeding or sod laying, some modest improvements in nitrogen use and retention were observed. Perhaps applying nitrification inhibitors using the high-pressure injectors employed for pesticide applications might prove effective in making more NH_4+ and less NO_3- available to turfgrass roots.

3) Nitrification occurs most readily in soil of near neutral pH. There might be some benefit in maintaining a more acid soil pH to slow the production of NO_3-. This might be most practical on sand-based greens where aluminum (Al) toxicity is less likely to be a problem. With the identification of more Al-tolerant turfgrass cultivars, lowering the soil pH may be realistic even on fairways and lawns. Of course, potential side effects (moss growth, disease, etc.) may complicate this approach.

4) Foliar applications of NH_4+ based soluble fertilizers should be investigated for their potential to increase root growth while maintaining high quality turf. In situations where soil NO_3- can be maintained at low levels, applications of NH_4+ sources designed for foliar absorption might have the same potential benefits as NO_3- metabolism concentrated in the roots.

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