

# Macronutrient Interactions on Turf Absorption and Distribution

## THIRD IN A SERIES

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In the first article of this series (Hull & Liu, October, 2010), we introduced nutrient interactions in turf management from a compartmental perspective. In the second article (February 2011), we looked at the interaction of mineral nutrient ions within the cell wall phase of plant roots and how it is influenced by the composition of soil water.

This article examines the competition among nutrient ions for carrier sites that deliver nutrients across plasma membranes into living cell protoplasts. Some interactions among these nutrient ions within turfgrass plants also will be considered.

## Macronutrient interactions

In the apoplast of roots, nutrient ions not bound to exchange sites can be attracted to transport proteins that span the cell's plasma membrane. There are four types of transporters (carriers): primary ATP hydrolyzing pumps; cation/ $H^+$  cotransporters; cation/

anion antiporters; and ion channels (Fig. 1).

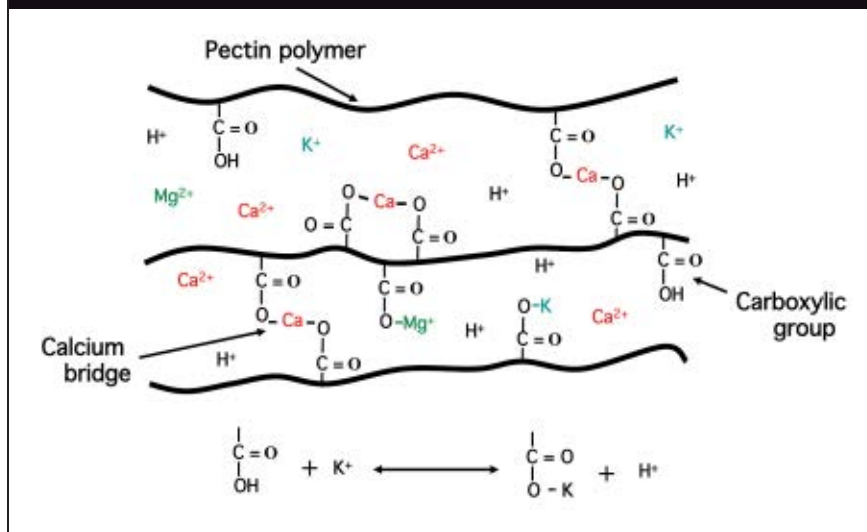
Most nutrient ions are more concentrated in cell sap (cytosol) than they are in the apoplast solution, so nutrient transport across a plasma membrane is normally against a concentration gradient. For such transport to occur, a source of energy must be provided. Nutrient absorption derives its energy from ATP, the universal energy currency generated through respiratory metabolism and photosynthesis. In roots, ATP is generated from respiration centered in mitochondria.

ATP directly powers two primary pumps in a cell's plasma membrane. The most important such pump is the primary  $H^+$  transporting ATPase. At the inner membrane surface, an ATP is hydrolyzed to  $H_2PO_4^-$  and ADP with an  $H^+$  driven through the pump protein into the apoplast. As this pump operates utilizing ATPs,  $H^+$ s accumulate in the apoplast and become less concentrated in the cytosol. This creates an  $H^+$  gradient across the plasma membrane that can be measured as a pH gradient

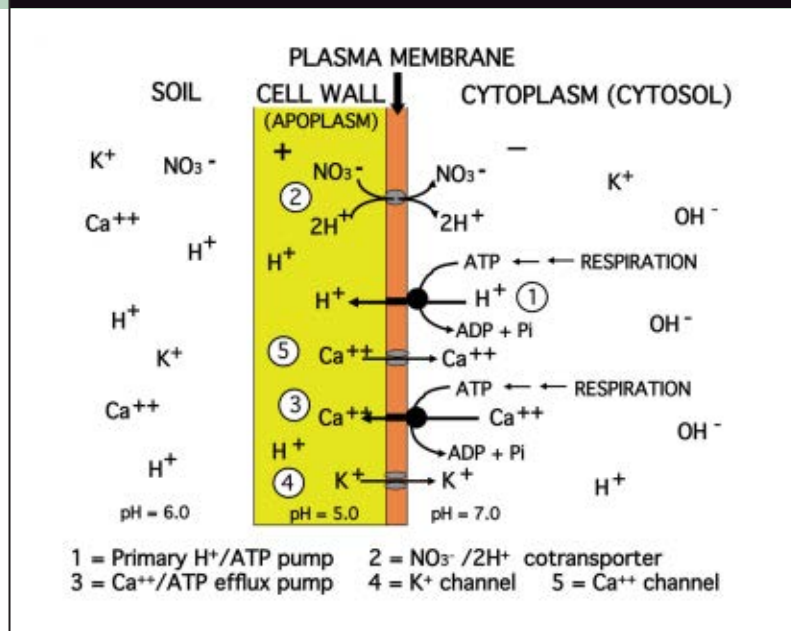
( $\Delta pH$ ). Because each  $H^+$  carries a positive charge, the  $\Delta pH$  also generates an electrical potential across the membrane with the apoplast becoming positive and the cytoplasm negative. This pH gradient is the energy source that transports nutrient ions into root cells.

Apoplastic  $K^+$  being a cation is attracted to the negative protoplast compartment and can cross the plasma membrane passively via  $K^+$  channels. The same holds for  $Ca^{2+}$  except its  $Ca^{2+}$  channels are normally blocked and open only in response to stress signals. Nitrate being an anion, would be repelled by the negative protoplast compart-

FIGURE 1: CATION EXCHANGE



Cation Exchange within Pectin Region of Apoplast

**FIGURE 2: TRANSPORTERS**

### Nitrate, Potassium & Calcium Transporters in Roots

ment but can enter via a  $NO_3^-/2H^+$  co-transporter. Nitrate enters with two  $H^+$ s that are strongly attracted to the negative cytoplasm. Calcium ions normally are excluded from the cytosol and most  $Ca^{2+}$ s that do get inside are pumped back into the apoplast by a primary  $Ca^{2+}$ /ATP efflux pump. Here the energy of ATP hydrolysis is expended in driving a  $Ca^{2+}$  through a transport protein into the cell wall apoplast or across a tonoplast membrane into cytoplasmic vacuoles. It is important to keep the  $Ca^{2+}$  concentration in the cytosol very low ( $\sim 0.1$ - $0.2 \mu M = 0.006$  ppm) to prevent it from precipitating phosphate ions that are critical for essential metabolic reactions. Most of the Ca in plant tissues is bound onto cell wall exchange sites or sequestered in vacuoles or other cytoplasmic organelles.

Competition for transport proteins is a major source of nutrient interaction in turf. The competition between  $K^+$  and  $NH_4^+$  for a common trans-membrane channel has often been cited as an example of nutrient competition (Marschner 1995). However, this has rarely been regarded as having much practical significance given the low concentration of  $NH_4^+$  in most soil solutions. If  $NH_4^+$  is in fact accountable for as much as fifty percent of the N absorbed by turf, as we have suggested (Hull and Liu 2005), competition between these two ions could cause an availability interaction especially when one is in short supply. That condition may be unlikely since both ions have equal affinity for both soil and apoplastic cation exchange sites.

When  $NO_3^-$  is the major source of available N, a steady supply of  $K^+$  is essential because within turf roots,  $K^+$  is needed as a companion ion for  $NO_3^-$  transport from roots to leaves within the xylem. This nutrient interaction would appear to justify applying K with N when fertilizing greens or other turf growing on a medium of low CEC. In calcareous sand greens, the abundant  $Ca^{2+}$  would so dominate the apoplastic CEC that both K and N would be free to bind with their respective transport proteins and be absorbed readily. Potassium is absorbed efficiently by

roots and generally requires low soil solution concentrations to satisfy plant needs.

Because  $Ca^{2+}$  binds strongly to apoplastic CEC sites and plays a critical role in stabilizing the structural integrity of plasma membranes, it is unlikely that there is much direct competition between  $Ca^{2+}$  and  $K^+$  for binding sites on their respective transport proteins. However, the low binding energy of  $Mg^{2+}$  with exchange sites makes it likely that both  $Ca^{2+}$  and  $K^+$  would be effective inhibitors of its absorption by roots. When Mg, Ca and K were present at equivalent concentrations in a nutrient solution, Mg absorption by barley roots was reduced by 90% [Schimansky (1981) in Marschner (1995)]. Magnesium deficiency is likely in the presence of Ca and K making foliar applications of Mg more effective than soil treatments. Manganese ions ( $Mn^{2+}$ ) also are especially strong competitors for  $Mg^{2+}$  transport proteins. Fortunately free  $Mn^{2+}$  is rarely present at significant levels in the solution phase of most soils.

### Micronutrient interactions on absorption and distribution in turf

Interactions among micronutrients during absorption, distribution and metabolism are numerous and few are generally appreciated in turf management. One curious observation reported from Japan (Kobayashi et al.

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2003) is that tobacco plants deficient in iron (Fe) exhibit classic deficiency symptoms, mainly highly chlorotic young leaves and reduced growth. However, if zinc (Zn) and manganese (Mn) are deficient as well as Fe, leaf chlorosis is much less evident and growth is near normal. This masking of deficiency symptoms occurs with no increase in tissue Fe concentrations. Clearly the nutrient imbalance of Fe being deficient while Zn and Mn are not is what triggers the expression of deficiency symptoms.

Later research from Iran (Ghasemi-Fasaei & Ronaghi 2008) explored the frequent failure of Fe applications to deficient wheat plants to restore normal growth and sometimes even to exacerbate Fe deficiency. Here wheat was grown in calcareous soils that tend to reduce the availability of cationic micronutrients and promote deficiency symptoms. They grew wheat on such a soil and applied an Fe-chelate to the soil or FeSO<sub>4</sub> to the foliage. Neither Fe application increased growth. While tissue levels of Fe increased in response to treatment, tissue levels of Zn, Mn and Cu decreased increasing the ratio of Fe to other cationic micronutrients individually and combined. This imbalance was attributed to an antagonistic effect of Fe on the absorption of other nutrients and the practice of applying Fe to correct its deficiency in grasses growing on calcareous soils was questioned.

While the relevance these studies to turfgrass nutrient management on non-calcareous soils or sand is not immediately obvious, it is evident that a proper balance of nutrients is critical for optimum grass performance. This balance can be disturbed by imbalanced nutrient supply or by nutrient antagonisms during absorption by roots or partitioning within the plant.

A more obvious lesson can be drawn from a very recent report from Italy (Astolfi et al. 2010) that described an interaction of sulfur (S) availability with Fe nutrition in barley. They noted that improvements in air quality and the use of fertilizers of greater purity seemed to be related to increased incidences of Fe deficiency in grain crops. When S was withheld from barley plants, Fe deficiency

symptoms increased sharply. This was shown to be related to a failure by plant roots to release a chelate into the soil when confronted with an Fe shortage. These chelates called phytosiderophores (PS), bind Fe<sup>3+</sup> very efficiently and allow it to be captured and absorbed by roots. PS synthesis is induced by low Fe availability and depends upon a ready supply of S since they are made from the S-containing amino acid methionine. In this case, a micronutrient (Fe) becomes seriously deficient because a macronutrient (S) was insufficient to permit a normal plant response to the deficiency stress.

Only a few of the many nutrient interactions known to be critical for normal turf growth and performance have been discussed in these two articles. There are undoubtedly many other such interactions that are not recognized and may be responsible for some most perplexing management problems, such as interactions with pesticides and surfactants in the soil or on the turf leaf surface. It is evident that maintaining basic nutrient balances and beneficial interactions can be added to the long list of grass requirements with which the turf manager must be familiar. However, such knowledge must be based on sound research of nutrient interactions conducted on turfgrass species. Those funding turf research should be encouraged to devote greater attention to this critical aspect of turfgrass nutrition.

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