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TURFGRASS TRENDS

PLANT SCIENCE

Nutrient Interactions in Turf Management II

A closer look at the cell walls surrounding the protoplasts of plant cells. *By Richard J. Hull & Haibo Liu*

SECOND IN A SERIES

In the first article of this series (Hull & Liu 2010), we introduced nutrient interactions in turf management from a compartmental perspective. The balance among nutrient elements can be considered as it occurs within the soil, especially soil solution, in the root cell wall volume (apoplast) and within interconnected protoplasts of plant cells (symplast). Nutrient composition and pH of the soil solution are most influenced by cations occupying the cation exchange sites on mineral and organic soil colloids. The interaction of the cations K^+, Ca^{2+}, Mg^{2+} and H^+ with exchange sites in determining the solute composition of the soil solution was discussed.

In this article, we will consider 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.

Nutrient interactions in the root apoplast

The cell walls surrounding the protoplasts of all plant cells constitute a nonliving space that extends throughout plant tissues and provides a route by which water-soluble nutrient ions can be transported throughout a plant especially from roots to shoots. This transport route is referred to as the apoplast to distinguish it from the network of interconnected living protoplasts (symplast) through which solutes also can move. In roots, the apoplast of epidermal cells is literally bathed in the soil solution that contains all nutrient ions on which the plant depends to support its growth and well-being. The apoplast is composed of cellulose macrofibrils imbedded in a matrix of gel-like hemicelluloses. Both of these components are long-chain polymers of five- or six-carbon sugars and some sugar acids that are all highly hydrated. Thus, the apoplast constitutes a hydraulic continuum from soil water throughout the cell wall volume of the roots.

This cell wall network contains pores of free water through which solutes can pass. The size of these pores varies with plant species, but the maximum values are in the 5.0 nm (nanometer = 1 billionth of a meter) range. By comparison, a hydrated K^+ has a diameter of 0.66 nm, Ca^{2+} = 0.82 nm and a sucrose molecule

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= 1.0 nm. Consequently apoplastic pores offer little size restriction to the free movement of nutrient ions or small metabolites. On the other hand, larger molecules such as metal chelates, nucleic acids, proteins and viruses would encounter substantial resistance or be restricted completely from moving through cell walls (Marschner, 1995).

The middle region of a cell wall between adjacent cells is known as the middle lamella and consists of pectins (polymers of galacturonic acid). Depending on the pH of the apoplastic aqueous phase, the carboxylic groups (organic acids) will lose a H^+ and become a negatively charged cation exchange site that can ionically bind with any cation.

These exchange sites preferentially bind Ca^{2+} and Mg^{2+} ions in preference to monovalent cations (K^+ & Na^+) much as soil cation exchange sites do. Calcium ions especially can bind with carboxyl anions on adjacent pectin polymers, thereby stabilizing the structure of the first-formed cell walls, the middle lamella.

This is recognized as a major function of Ca in plants (Carrow et al., 2001). Since divalent cations are preferentially bound to exchange sites, monovalent cations (especially K^+) remain comparatively free in the apoplastic solution at a higher concentration than in the soil solution. The presence of cation exchange capacity (CEC) in cell walls causes anionic nutrients (NO_3^-, $H_2PO_4^-$, SO_4^{2-}) to be repelled and become less concentrated than cations in the apoplast water.

The cell wall CEC in grasses is about half that of dicotyledonous plants (Marschner, 1995). Thus, the cation concentration within the apoplast of grass roots is less than it is in other plants, nutrient anions will be slightly more concentrated and the negative binding sites on ion transport proteins on the cell's plasma membranes will have less competition from apoplastic CEC for cationic nutrients.

Nutrient ions move within the soil toward root surfaces and into the apoplasm with the flow of soil water drawn to the roots to replace that lost from plant leaves via transpiration. This mass flow of water to roots, of course, operates mainly during daylight hours when leaf stomata are open and transpiration occurs.

The absorption of some nutrient ions by root cells is sufficiently rapid that a depletion zone occurs at the root surface creating a nutrient concentration gradient between the root surface and the bulk soil solution. Such a gradient provides the energy for the diffusion of nutrient ions toward the root. Diffusion is most likely to be important during times of darkness when mass flow is minimal. Highly mobile readily absorbed ions such as K^+ and NO_3^- are most dependent on diffusion as their delivery mechanism to turfgrass roots.

Carrow et al. (2001) make a strong case for the interaction of NO_3^- and K^+ in turf nutrition. Even though they have opposite charges, both NO_3^- and K^+ are comparatively free within the soil solution and thus are subject to leaching during heavy rain and excessive irrigation. They are also readily absorbed by grass roots, translocated to leaves and are lost when clippings are removed. Thus, they recommend that both nutrients are most efficiently applied during times of greatest demand (rapid growth and recovery from stress) by numerous light fertilizations often known as "spoon feeding," particularly for sand-based turf such as most putting greens and newly built sports fields with a low soil CEC.

However, Woods et al. (2006) tested the effectiveness of this K application method on a calcareous sand green planted to L-93 creeping bentgrass and fertilized every 14 days with N and six rates of K ranging from

0 to 6 g/m^2 over two growing seasons in Ithaca, N.Y. Soil analyses showed a progressive decline in available K at all application rates < 2 g K/m^2 reaching low levels (< 1.25 mmol/K/kg soil). Nevertheless, K applications had no beneficial effects on turfgrass quality or performance. Turf disease incidence was not increased under lower K levels and gray snow mold actually was more prevalent each spring on the higher K turf. The authors concluded satisfactory bentgrass green performance can be achieved over a broad range of soil K levels and tissue concentrations when grown in calcareous sand root-zones. They suggested excessive K applications may be in common practice on greens management (Woods et al., 2006). We will comment on this further in the next section.

In general, the availability of nutrients in the soil water influences the quantity and composition of nutrients within the cell wall space of turfgrass roots. However, moderate nutrient selection occurs within the apoplast with divalent cations becoming concentrated due to their binding with cation exchange sites and anions being partially repelled. Still, the concentration of free (non-bound) ions remains sufficiently low in cell wall water that precipitation of low solubility salts rarely occurs.

Cell walls are a non-living continuum with which water and nutrient ions travel from roots to and throughout shoots.

We mentioned earlier the cell walls constitute a non-living continuum through which water and nutrient ions can travel from the roots into and throughout the shoots. If that were really true, the plant would have no way to discriminate among or control which mineral ions enter and are transported throughout the plant. That clearly is not the case. Ion discrimination is achieved by bands of cells (the endodermis) that encloses the root's vascular cylinder (xylem and phloem) and has a waxy material (suberin) impregnated in its walls. These endodermis cells block the inward flow of water and minerals in their apoplast forcing them to cross a cell's plasma membrane and enter its protoplast (symplasm). To enter the xylem (part of the apoplast) and move into the shoot, water and minerals must again cross the plasma membrane of a cell in the vascular cylinder and reenter the apoplast. Any mineral ion that cannot enter the symplast at the endodermis can go no further and remains within the roots. In this way, a plant's stems and leaves are protected from potentially toxic elements.

Greatest selectivity for and potential interactions in nutrient uptake and distribution within turfgrass plants is centered at plasma membrane transport: loading into the symplast and unloading into the xylem (apoplast). That will be considered in our next article.

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