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Such plants fail to grow as well as plants receiving a mixture of NH_4^+ and NO_3^- but they still grow reasonably well, indicating that intact urea must be entering root cells.

In addition, plants have been shown to possess dedicated high affinity urea transporter proteins in their cell membranes that permit urea uptake and distribution throughout the plant. Once inside plant cells, urea is readily hydrolyzed by their abundant urease or loaded into vacuoles by urea transporters that are also present in their tonoplasts (membrane enclosing a vacuole). The induction of these urea transporters appears to be stimulated by external urea and suppressed by the presence of other soluble N sources, e.g. NO_3^- , NH_4^+ and amino acids.

Urea transporters are most abundant in N-starved plants, especially when urea is introduced to their external environment and when plants are provided no N-source except urea.

The urea transporters discussed

above facilitate secondarily active urea uptake. That is, urea crosses a membrane accompanied by a proton (H^+) in a co-transport process. During normal root growth, the surface (epidermal) cells pump H^+ s through their plasma membrane from the cell's interior into the external cell walls via a H^+ -transporting ATPase (H^+ pump).

Put more simply, for each two H^+ s pumped out of a cell, an ATP molecule is expended. ($\text{ATP} + \text{H}_2\text{O} \rightarrow \text{ADP} + \text{H}_2\text{PO}_4^- + 2\text{H}^+$). Since ATP is the chemical energy currency of metabolism, H^+ pumping is an energy expending process that is driven by ATP hydrolysis. As this process continues, the H^+ content within the cell walls increases (becomes more acid) relative to the cell interior that remains the same or actually becomes less acid. This pH gradient across the plasma membrane constitutes an energy gradient equivalent to the energy lost by ATP when it gives up a phosphate and becomes ADP.

How is this H^+ gradient used to pump urea into a plant cell? When urea is introduced as an N-fertilizer, it diffuses into the walls of root or leaf epidermal cells where it activates the synthesis of urea transport proteins in their plasma membranes. These transport proteins have aqueous pores through which H^+ s can move from the cell walls back into the cell's interior. The structure and chemistry of the pores is such that an H^+ can pass through the pore only if accompanied by a urea molecule. Since the H^+ concentration in the cell wall is greater than it is within the cell interior, influx of H^+ is energetically favored. Urea will always be transported inward because the influx of H^+ , its transport partner, is an energetically favored process.

There is recent evidence that urea may also enter plant cells and move across internal cell membranes via aquaporins, the membrane channels by which water enters cells (Witte 2011). Like water, urea is a small, uncharged molecule that probably would not be

excluded from moving passively with water through aquaporin channels. Whether urea can enter cells as an intact molecule by active or passive mechanisms is less important than the emerging idea that urea-N can be absorbed by roots and leaves without first being released as free NH_3 .

MANAGING UREA-N UPTAKE BY TURFGRASSES

To a turf manager, all this may seem pretty academic and of little practical value toward keeping grass green and healthy by maintaining an adequate N supply. Such a judgment may be premature when the vulnerability of NH_3 -N to volatility losses is considered. We know that as much as 30 percent of urea-N applied to turf can be lost to the atmosphere unless it is watered into the thatch/soil by irrigation immediately following application (Hull and Liu 2005). This precaution fails to work very well if the soil is even slightly alkaline or the irrigation water has a pH greater than seven. Even if the soil is acid enough to convert NH_3 to NH_4^+ ion, it will be readily oxidized to NO_3^- that may be subject to leaching loss.

Foliar applied urea initially comes in contact with leaf surfaces that may be populated by enough urease-containing bacteria to cause most of the urea-N to be released as free NH_3 . However, leaf surfaces are generally acidic, so urea-derived NH_3 will likely become NH_4^+ ions in the spray solution retained on leaf surfaces. These NH_4^+ ions can penetrate the leaf cuticle and become absorbed by epidermal cells just as other nutrient ions are during foliar fertilization. If the spray solution dries on the leaf surface, any remaining NH_3 will be lost to the atmosphere.

Does an understanding of urea-N absorption and metabolism suggest ways of making urea use more efficient?

Recent research by our Clemson team (Menchyk et al. 2013) indicates that the efficiency of urea-N use by turf can be optimized by coordinating

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