Small Amounts of Molybdenum Streamlines Nitrogen Uptake

By Dick Hull

Of all the mineral nutrients known to be essential for plants, molybdenum (Mo) is required in the least amount. To put this in perspective, for every Mo atom required by most plants, 1 million nitrogen (N) atoms are needed. Even with respect to those micronutrients generally recognized as being required in small amounts, such as copper (Cu) or zinc (Zn), a plant needs 100 Cu and 300 Zn atoms for every one of Mo present. Only nickel (Ni) comes close to being needed in amounts as low as Mo.

Little research has been conducted on the needs of turfgrasses for Mo. In their analyses of nutrient levels present in several turfgrasses, Butler and Hodges (1967) found a range of Mo concentrations from 1.77 to 8.45 parts per million (ppm) in common Kentucky bluegrass and perennial ryegrass, respectively (Table 1.). These values are the lowest among all mineral nutrients analyzed by these investigators.

However, no critical Mo concentrations have been published for turfgrasses so it's impossible to say if these values even approach the amounts actually required by turf.

Critical concentrations for Mo could be less than one-tenth the levels reported by Butler and Hodges. For several agricultural crops, critical Mo concentrations ranged from .1 to 1 ppm dry-leaf weight (Gupta and Lipsett, 1981).

Molybdenum in soils

The form of Mo most available to plants is the divalent molybdate anion (MoO_4^{-2}) where it exists in its most oxidized form (Mo^{+6}).

In some chemical properties, MoO_4^{-2} resembles other divalent oxyanions, especially sulfate (SO_4^{-2}) and phosphate (HPO_4^{-2}), that are the most available forms of sulfur and phosphorus, respectively. Because the sulfate content of the soil solution is vastly greater than that of molybdate, the two ions can compete for uptake sites on plant roots with molybdate invariably being the loser.

Plants are more likely to experience a Mo deficiency when fertilized with single superphosphate that contains substantial amounts of gypsum ($CaSO_4$), than with triple superphosphate that contains much less sulfate. Thus, the availability of molybdate to plant roots is heavily influenced by the concentration of other anions in the soil solution (Marshner, 1995).

Soil pH also exerts a strong influence over the availability of molybdate to plant roots. Unlike most metal micronutrients that increase in availability as the soil pH becomes more acid, molybdate acquires hydrogens and becomes less ionic as soil acidity increases.

The more acid forms of molybdate are not only less readily absorbed by plant roots but they can also form molybdate polyanions, (up to six molybdates per ion) rendering them completely unavailable to plants.

In addition, several metallic elements (iron, manganese and copper) become more ionized in acid soils and can form insoluble salts with molybdate rendering it unavailable to plant roots. Thus, liming a soil from pH of 4.5 to 6.5 will markedly increase the availability of Mo. This has been shown to preclude the need for applying Mo to some soils where plants had exhibited deficiency symptoms.

TABLE 2

Molybdenum concentration in common turfgrass varieties

Grass	Concentration (ppm)
Kentucky bluegrass	1.77
Kentucky bluegrass (Merion)	3.35
Perennial ryegrass	8.45
Creeping red fescue	2.72
Tall fescue	4.05
Colonial bentgrass	2.25
Meyer zoysiagrass	1.77
Bermudagrass	8.20

SOURCE: BUTLER & HODGES (1967)

Mo functions in turfgrasses

Being required in such small amounts, Mo can't perform numerous essential functions in plants. It may be surprising then to realize that Mo is required for the efficient use of a plant's most abundant mineral nutrient, nitrogen.

Nitrogen can be assimilated into a plant's metabolism only in its reduced ammonium (NH_4^+) form (Hull, 1996a).

However, since nitrogen is generally available to plants in its oxidized nitrate (NO_3^-) form, it must first be reduced to NH_4^+ before a plant can use it. This process involves a gain of eight electrons and occurs in two steps. After a NO_3^- ion enters a root and while it is in the cell's cytoplasm, it is acted upon by the enzyme nitrate reductase (NR) that transfers two electrons from the electron donor NADH to form nitrite (NO_2^-).

Within the cell, the nitrate then enters a plastid and is reduced to NH_4^+ by the addition of six additional electrons through the action of the enzyme nitrite reductase (NiR). Thus, the whole process of NO_3^- assimilation begins with the enzyme nitrate reductase, an essential component of which is a Mo atom. This Mo is the business end of the enzyme because it transfers the two electrons to NO_3^- forming NO_2^-.

To accomplish this, the Mo must first be reduced to its Mo^{+4} redox form before it can transfer two electrons to NO_3^- with the Mo then being oxidized back to its original Mo^{+6} form. No element except Mo can function within the NR enzyme. Without Mo, plants could not use nitrate, causing extreme nitrogen deficiency. In very acid soils, where nitrogen is present in its NH_4^+ form, plants can absorb NH_4^+ and assimilate it directly without a need for NR and its Mo.

Mo has a unique ability to reduce nitrogen because it is also the functional component of the nitrogenase enzyme that transfers six electrons to a diatomic nitrogen molecule (N_2) reducing it to two NH_4^+ ions. Nitrogenase is present only in bacteria that have the ability to fix atmospheric N_2 to the biologically useful NH_4^+ form. This occurs in nodulated roots of legumes and some woody shrubs, in cyanobacteria of rice fields and in various free-living soil bacteria.

The process is not directly important as a nitrogen source for turfgrasses, so we will consider it no further here. It is worth considering, however, that most nitrogen that enters the biosphere through natural means does so through the nitrogenase enzyme and thus depends on Mo.

Another role for Mo generally recognized in plants is its function in the enzyme xanthine dehydrogenase or xanthine oxidase. Here it also acts as a carrier of electrons during the oxidation of purines that are components of nucleic acids.

Mo draws electrons away from a nitrogen-containing organic ring structure and donates them to oxygen (oxidase) or NAD^+ (dehydrogenase). These enzymes are important in recycling nitrogen from degraded nucleic acids and in the synthesis of ureids that are important nitrogen transport molecules in some plants, especially legumes. The oxidative properties of these enzymes also make them important players in the antioxidative defense reactions of many plants.

On sand-based greens and light soils, applications every two to three years constitute good insurance against micronutrient limitations.

Closely related to the purine oxidizing enzymes is another that oxidizes aldehydes to acids. This Mo-containing aldehyde oxidase is responsible for the oxidation of several plant aldehydes, but most significantly it catalyzes the final step in the synthesis of abscisic acid (ABA) and the auxin indole-acetic acid (IAA). In both cases, an aldehyde surrenders two electrons to the Mo^{+6} of aldehyde oxidase and in the process being oxidized to an acid.

These two acids are primary plant hormones that are essential for orderly growth and the plant's ability to react to environmental stresses.

Mo and plant stress

A new concept is emerging that places Mo at the center of a plant's ability to respond to stress conditions by signaling information between roots and shoots (Lips et al., 2000).

In an earlier article (Hull, 1996b), we discussed the ability of turf to sense the drying of shallow roots by producing abscisic acid that, when translocated to shoots, slowed leaf growth and closed stomates, thereby conserving water use. This enabled the grass to sense the onset of drought before the plants actually were experiencing any moisture stress. Now we have a bet-

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ter idea of how Mo-enzymes coordinate several processes to allow plants a more comprehensive response to the imposition of stress conditions.

Drought, salinity and even elevated ammonium levels, when perceived by roots, increase the activity of the aldehyde oxidize enzyme that promotes the synthesis of ABA from abscisicaldehyde. The ABA moves in the transpiration stream to leaves where it promotes stomates to close and reduce the rate of water loss.

At the same time, nitrate loading into the xylem of roots is reduced and this induces the activation of nitrate reductase, and more nitrate is then assimilated in the roots.

With less nitrate moving to the leaves, more photosynthetic product (sugars) are directed to roots because nitrate in leaves serves as a signal directing photosynthate toward amino acid synthesis and that promotes shoot growth. Also, higher ABA concentrations in the leaves will inhibit shoot growth.

The greater nitrate assimilation in roots and additional photosynthate being delivered through the phloem from the shoots stimulates deeper root growth and makes additional water available. The greater nitrate assimilation in roots also induces xanthine dehydrogenase that promotes ureide biosynthesis. Ureides are transported to leaves where they provide nitrogen for shoot function and growth without diverting sugars from transport to roots.

Xanthine oxidase/dehydrogenase in leaves may also contribute some antioxidative protection from drought and high-temperature stress experienced by the shoots. Many details of this stress response sequence are still poorly understood, but the general process has been observed in several plants including perennial ryegrass (Lips et al., 2000).

You will note that many of the key enzymes involved in this complex plant response contain Mo, which places the micronutrient at the center of plant tolerance responses to stress conditions.

Mo in turfgrass management

In turfgrass culture, where soils are normally limed to a pH of more than 6, any Mo present will likely be available to the turf. However, on a sand-based green or turf growing on a light soil, additions of micronutrients such as iron or manganese could form insoluble salts with molybdate making it less available.

In general, grasses have a lesser requirement for Mo than legumes or other plants that depend on N_2 fixation so deficiencies are rarely if ever observed. However, turf managers are not normally looking for Mo deficiencies and likely would not observe the subtle reduction in growth or chlorosis that could result from inadequate Mo.

The best approach to insuring adequate Mo for turf is similar to that for most other micronutrients: periodic applications of a commercial mixture of such elements. On sand-based greens and light soils, applications every two to three years constitute good insurance against micronutrient limitations.

Molybdate is an oxyanion and like phosphate and sulfate is mobile in both the xylem and phloem of turfgrasses. This makes a foliar application of ammonium molybdate especially effective because it can be translocated to all plant organs once absorbed by leaves. If soils are acid or high in sulfate and likely to immobilize Mo, foliar treatments can be the most practical means of insuring adequate levels in turfgrasses.

Normally the turf manager need not be concerned about Mo adequacy. However, if clippings are regularly removed and organic topdressings are not applied, Mo along with other micronutrients should not be ignored. Mo offers a large safety margin in plants so toxicity problems are not likely. Even if reclaimed water is used for irrigation, problems with Cu, Mn or B toxicity are more likely than injury from excess Mo.

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