

Copper Is Essential Bridge For Many Plant Functions

By Richard J. Hull

Copper (Cu) is present in turfgrasses at low concentrations (5 to 20 parts per million [ppm]) and cycles through its functions quickly. Cu serves a number of essential roles based upon its easy ability to capture and surrender electrons, especially in reactions with free oxygen (O_2).

There is a strong tendency for Cu^{2+} ion to capture an electron and function as an oxidizing agent. The resulting Cu^+ ion, which is unstable, readily gives an electron and acts as a reducing agent, particularly to oxygen. This endows Cu with properties exploited for plant and animal metabolism. The uniqueness of Cu to function as a strong oxidizing and reducing agent enables it to serve in ways that no other element can. What follows is a discussion of how these properties of Cu are utilized in plant metabolism.

Photosynthesis and respiration

Photosynthesis involves the reduction of carbon dioxide (CO_2) to carbohydrates (a gain of 4 electrons per carbon atom), while respiration is the oxidation of carbohydrates back to CO_2 . Consequently both processes depend on the transfer of electrons.

In photosynthesis, electrons are taken from the oxygen of water, while in respiration they are returned to oxygen to make water.

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We have already discussed the central role played by iron (Fe) in this electron transport pathway (Hull, 1999), but Cu also is an essential participant.

In both photosynthesis and respiration, electron transport is a separate process from carbon metabolism. In photosynthesis, electron transport is involved in producing a strong reducing agent (NADPH) needed to

reduce CO_2 to sugars. In respiration, sugars are oxidized to CO_2 with the electrons going to form a similar strong reducing agent (NADH) that channels its electrons down a transport chain that ultimately reduces O_2 to water. In both processes, the electron-transport pathway is coupled to the synthesis of adenosine triphosphate (ATP), which is required to power many biochemical and physiological events. The biosynthesis of cell walls, proteins and lipids all require ATP, as does nutrient ion transport and the opening of water channels across cell membranes.

It's in these electron transport chains that Cu is required. In photosynthetic electron transport, two photosystems use light energy to drive electrons from water to NADPH. They are connected in series by a Cu-containing protein called plastocyanin.

Here, a single Cu atom oscillates between its Cu^{2+} and Cu^+ forms transferring electrons from photosystem II to photosystem I, thereby connecting the two major components of the photosynthetic electron transport chain. More than 50 percent of the Cu in chloroplasts is part of plastocyanin. When Cu becomes deficient, the plastocyanin content of leaves drops sharply, as does the photosynthetic electron transport rate while chlorophyll levels are unchanged.

In respiratory electron transport, electrons flow from NADH (derived from the oxidation of sugars) to O_2 , the final step of which requires the binding of Cu^+ to O_2 and the transfer of four electrons to O_2 , producing two water molecules (H_2O). Here, Cu is part of the enzyme cytochrome oxidase that catalyzes the transfer of electrons to O_2 again through the oscillation of Cu between its Cu^+ and Cu^{2+} forms.

Toxins such as cyanide and azide bind Cu and block its capacity to transport electrons to O_2 . Thus, these chemicals are lethal to both plants and animals. Iron and manganese are also capable of transporting electrons, but they cannot substitute for Cu because their affinity for O_2 is not as great.

Detoxification of oxygen radicals

In a closely related function, Cu is also involved in the detoxification of superoxide radicals in chloroplasts, mitochondria and cytosol of leaf cells (Marschner, 1995). Cu acts as a component of the specific enzyme superoxide dismutase (SOD) that catalyzes the reaction between two superoxide radicals, forming a hydrogen peroxide (H_2O_2) and one free oxygen.

In this SOD, Cu functions in cooperation with a zinc (Zn) atom (CuZnSOD) as we discussed in our article on Zn function in turf (Hull, 2001a). In this case, it's Cu that binds with O_2^- and allows an electron to flow from one O_2^- to another O_2^- , reducing one to H_2O_2 and oxidizing the other to O_2 . When Cu is withheld from plants, the CuZnSOD activity declines dramatically.

The H_2O_2 is also potentially dangerous, but it's detoxified by the enzymes peroxidases or catalase to harmless H_2O and O_2 . In this way, plants are able to protect themselves from toxic O_2 radicals that are inevitable when biochemical oxidation-reduction reactions occur in the presence of free O_2 . There are circumstances when the production of H_2O_2 is useful, and Cu can play an essential role there as we shall see in the next section.

Lignin formation in cell walls

Before plants could successfully invade dry land and achieve any real height, they needed to evolve a means for making their cell walls stiff. Cellulose walls tend to be flexible, like a cotton fiber. The internal accumulation of water causes turgor pressure can generate considerable force within cells that but not much strength.

Also, the water conducting cells (xylem vessels and tracheids) must resist collapsing when subjected to substantial tensions. This need for greater stiffness was achieved through the synthesis of lignin, a cell-wall encrusting substance composed of many six-sided unsaturated rings each containing at least one -OH group (phenols) that become polymerized through the fusion reactions of phenol-free radicals.

The enzyme polyphenol oxidase catalyzes the oxidation of phenol rings, thereby making additional -OH groups (polyphenols). Phenol free radicals are produced when a ring -OH group is oxidized by H_2O_2 that is the

product of cell-wall diamine oxidases. Both polyphenol oxidase and diamine oxidase are Cu-containing enzymes that produce the substrates needed for peroxidative polymerization of phenol-free radicals to form lignin within plant cell walls.

As a consequence, even a mild Cu deficiency causes a sharp decrease in lignin synthesis, resulting in leaf and stem distortions and greater lodging susceptibility of grasses. Because lignin, being composed of many phenol units, is an effective deterrent to the attack of most pathogenic fungi, a lack of lignin due to insufficient Cu can make plants more susceptible to disease. Since lignin synthesis is among the biochemical processes most sensitive to a Cu deficiency, increased disease incidence is an early symptom of low Cu that likely will occur before other Cu deficiency symptoms.

Carbohydrate and lipid metabolism

Since Cu is required for the photosynthetic generation of reducing power necessary for CO_2 fixation, it's not surprising that an inadequate Cu supply will reduce carbohydrate levels and vegetative growth rates. This carbohydrate limitation is most pronounced when plants are well supplied with nitrogen because it stimulates vegetative growth and increases the demand for photosynthetic products.

However, following anthesis (pollen release and fertilization), carbohydrate levels often increase. Because Cu is critical for pollen production, effective pollination and fertilization, few seed are set and a major need for photosynthetic products does not develop. The failure of seed set also delays leaf senescence, so photosynthesis continues but plant demand is low and carbohydrates accumulate. Thus, the impact of insufficient Cu on carbohydrate supply will be a function of a plant's developmental stage. This is unlikely to be noted in turf where frequent mowing maintains plants in a vegetative state.

Another less obvious effect of Cu deficiency in plants is a reduction in the degree of desaturation in membrane lipids (Ayala *et al.*, 1992). When Cu becomes deficient, membrane lipids in chloroplasts (and probably elsewhere) become more saturated (contain fewer double bonds). This is attributed

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to reduced activity of a Cu-containing desaturase enzyme that is responsible for inserting double bonds in the long chain lipid fatty acids.

A loss of lipid double bonds can have profound effects on plant function. In chloroplasts, the ability to tolerate high light levels without damaging the photosynthetic machinery depends on double bonds in carotenoids and other membrane lipids. The capacity for low temperature tolerance is also dependent on a high level of desaturation in membrane lipids. Thus, low Cu levels can drastically restrict the ability of plants to respond favorably to several environmental stresses.

Copper deficiency and toxicity

A Cu deficiency is rarely observed in turfgrass. Most soils provide sufficient Cu to meet turfgrass needs, and Cu may be inadvertently applied to turf in fungicides or soil amendments. However, turf growing on sand-based greens or in high pH organic soils when clippings are removed may experience Cu levels below that needed to supply plant needs. Deficiency symptoms on turf are not well defined and, as is often the case with micronutrient deficiencies, more than a single element might be lacking. Because Cu is essential for chloroplast functions, deficiency normally promotes chlorosis in young growth.

If apical growing points are injured, tillering will be stimulated. This could cause an increase in turf density but a healthy green color will not occur. Nitrogen fertilization can aggravate a Cu deficiency by increasing plant demand and by binding cell Cu with amino acids and proteins. Wilting, even when water is abundant, can be observed if a lack of Cu has prevented lignification of vascular cells and they have collapsed or are less efficient in transporting water to the leaves.

Reduced lignification can also make turf more susceptible to foliage diseases and more attractive to leaf-feeding insects. All of these symptoms will be subtle, and a Cu deficiency is not likely to be the first cause that will come to mind when diagnosing the problem.

Of greater concern to turf managers is the probability of Cu toxicity. The problem of metal toxicity in turf management will be considered in an upcoming issue of this journal and will not be treated in detail here. However, it should be noted that potentially toxic levels of Cu have been reported on golf courses where Cu fungicides have been used over an extended period or Cu-containing sludge-based composts have been used for topdressing.

An excellent study conducted at Iowa State University by Faust and Christians (2000) found that elevated soil Cu is most injurious to roots. In creeping bentgrass, for example, it accumulates to more than 4,000 ppm while Cu concentrations in shoots never exceeded 20 ppm. This means that leaf tissue analysis is not a good indicator of potential

Cu injury to turfgrasses and root growth may be severely impaired before any leaf symptoms are noted.

Even though Cu is not likely to be a problem for the turf manager, it's essential for photosynthesis, respiration, secondary cell wall synthesis and stress tolerance. It is reasonable, therefore, that Cu should be recognized for the important jobs it does in supporting turfgrass growth and health.

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