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Copper as a Beneficial Nutrient in Agriculture

Since the 1930's copper has been recognised as essential to both higher and lower plant life. Whereas copper is required by lower plant forms in minute amounts, it is particularly toxic in higher concentrations; these concentrations can be tolerated by higher plant roots and leaves. It is this differential in sensitivity that is exploited in practical agriculture for protection of crop foliage, and by higher plants to protect their roots. When soil copper is adequate, roots accumulate copper in high concentrations, mostly in the apoplast, while transport to the shoot is under tight control. Typically, the adequate level of copper in soil is in the range of 4-15 mg/kg.

Conversely, in copper deficient soil, root copper concentrations are low, and there is much evidence to indicate that such roots are vulnerable to fungal and bacterial attack. From the foregoing, we may generally expect that applied copper will increase production when soil-available copper is low by stimulation of growth through overcoming the host-plant deficiency, by direct toxicity to the pathogen and by stimulation of host defenses.

1. Direct Effects on the Pathogen

Copper has been used extensively as a fungicide, but at concentrations 10 to 100 times greater than those normally needed as a foliar spray (0.1 – 0.2 kg/ha^{-1} copper) to cure copper deficiency. Most of its fungicidal properties have been used against foliar pathogens, since copper added to soil is quickly adsorbed and only a low concentration remains in the soil solution. The exception to this may be the accumulation in the root cell walls. Copper fungicide sprays are frequently neutralized, that is, precipitated with lime, to reduce their phytotoxicity to permit the high dose rates and to make the product more rain-fast.

2. Effects on Resistance of the Host

Perhaps the best evidence of an effect of copper on host-plant resistance to disease is when copper is applied to the soil and the disease control is observed in the leaves. Invariably, these cases involve copper deficient soils, and the concentrations in the leaves which effectively reduce disease severity are only 1 – 10 mg/kg^{-1} copper (free Cu^{2+} is probably $<1 \mu g/kg^{-1}$), concentrations too low to directly affect the pathogen.

Fertilization with copper has decreased the severity of a wide range of fungal and bacterial diseases. Many reports describe control of foliar disease with soil applications; for example, mildew on wheat, *Alteranaria* on sunflower (*Helianthus annuus* L.), *Pseudomonas cichorii* on ginseng (*Panax pseudoginseng* Wallich), *Puccinia triticina* on wheat and ergot on rye (*Secale cereale*) and barley. Other reports include *Pyricularia oryzae* on rice and *Septoria* on wheat. Many soil-borne diseases are also suppressed by copper supplementation. These include *Heterodera* on sugarbeet (*Beta vulgaris* L.) and *Verticillium albo-atrum* on tomato *[Lycopersicon esculentum (L.)], Verticillium dahliae* on cotton*, Streptomyces scabies* on potato*, Phytophthora cinnamomi* on eucalyptus and *Gaeumannomyces graminis* var. *tritici (Ggt)* on wheat.

3. Mechanisms of Control with Copper

a) ***Direct Toxicity.*** Copper is a transition metal with great affinity for nitrogenous organic ligands, including proteins. Its ability to denature proteins may well be fundamental to its direct toxicity to micro-organisms. Microbes have a low requirement for copper compared with higher plants, and a low tolerance of excess copper. Copper remains an effective fungicide and evolution of resistance to it has been slow, perhaps because tolerant mutants are unable to transmit this character through asexual spores. Copper accumulation in the apoplast of normal roots in copper-adequate soil may be a defense mechanism that takes advantage of the copper sensitivity of fungal exoenzymes involved in the infection court.

b) ***Lignification.*** The indirect effects of copper on host-plant resistance are almost certainly much more important than direct toxicity, especially in its vital role in the synthesis of lignin. Lignin is recognized as a partial barrier to the penetration of many pathogens including powdery mildews and *Ggt*, two fungal groups for which there have been repeated records of the inhibitory effects of lignin. Lignin synthesis may well be the basis of the effect of copper on adult plant resistance to powdery mildew of wheat.

c) ***Polyphenol Oxidase.*** As a component of the suite of enzymes known as polyphenol oxidase (PPO) or phenolase, copper also is involved in the synthesis of soluble phenols and in their oxidation to the more toxic quinones. A rise in level and activity of PPO is a frequently measured plant response to invasion of pathogens. A concomitant rise in toxic oxidized phenolics in the infected tissues results from enzymatic oxidation of reduced phenols stored in the cell vacuole. Toxic quinones may kill not only the invading micro-organism, but also the surrounding cells of the host and give rise to a local lesion, an important auto-immune response which constrains infections by obligate parasites such as powdery mildews and rusts. With copper deficiency, these soluble phenols remain in the reduced states owing to inactivation of PPO.

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