

Improving Foliar Fertilization of Turf

Basic research on plant cuticles suggests ways to do it better

By Richard J. Hull
and Haibo Liu

What are the merits of foliar fertilization in turf-management programs? Foliar fertilization, not to be confused with liquid applications or fertigation, has been proposed as an efficient and environmentally safe method of supplying nutrient elements to turf, especially intensively managed turf (Middleton, 2001; Liu et al, 2008; Totten et al., 2008). Foliar fertilization specifically targets turfgrass leaves as the site for nutrient application and absorption, while other liquid methods deliver substantial nutrient to the thatch and soil ultimately available for root absorption.

While there are ample opportunities for nutrient loss from all liquid and granular delivery methods, there seems to be a growing sense that foliar fertilization losses can be minimized if appropriate application methods and materials are used (Middleton, 2001). This may be true, but it depends entirely upon how effectively foliar-applied materials can cross the cuticle of leaf epidermal cells and become assimilated within the living protoplasts of those cells.

Foliar-applied materials are sometimes thought to be at least partially absorbed into leaves through the open stomatal pores (stomata) but there is really little direct evidence to support that notion. True, the underside of leaves, where most stomata normally are present, absorbs more foliar-applied nutrients than the astomatous (lacking stomata) upper surface, but absorption rates are greatest in darkness when stomata are closed. Also, the guard cells bordering stomatal pores and the outer portion of the substomatal chambers are both covered by a waxy cuticle making wetting and penetration of aqueous solutions highly unlikely. Adding surfactants (wetting agents) to a spray solution increases stomatal penetration but only involving a small percentage of stomata. Due to the limitation of space, this review will focus only on the primary barrier to nutrient uptake by leaves: the surface cuticle.

A wax-coated cuticle covers the outer cell walls of upper- and lower-leaf epidermal cells. The primary function of this cuticle is to minimize the evaporative loss of water from the leaf. Leaves are designed for gaseous exchange (carbon dioxide, oxygen and water vapor) between a leaf's interior and the atmosphere to be controlled by the opening and closing of stomata, not by movement across the cuticle. The cuticle's multilayered composition suits it well to function as a hydraulic barrier (Riederer and Muller, 2006).

The outer-most layer consists of epicuticular wax composed of straight-chain alkanes, long-chain (25-35 carbon atoms) fatty acids and alcohols and esters formed by them. Just beneath the surface wax is a lamellate-structured cuticle proper composed of wax and cutin (polymerized hydroxy fatty acids). Still deeper is a thicker cuticular layer composed of wax, cutin, suberin and long cellulose (glucose polymers) microfibrils that are carbohydrate and have a high affinity for water. Finally, the cell wall proper is reached composed almost entirely of highly hydrated carbohydrate polymers (cellulose and hemicelluloses) and glycoproteins. This carbohydrate cell wall is bonded to the cuticular layer by a pectin (polymers of galacturonic acid and sugars) layer. Through calcium linkages and borate esters, pectin binds cell wall carbohydrates with cellulose in the cuticular layer. The protoplasts of epidermal cells abut the cell walls at their plasma membranes, the final barrier that must be crossed before anything applied to a leaf surface can be useful to the plant.

Given the structure and composition of epidermal cell walls exposed to the atmosphere, it's obvious that virtually any leaf-applied substance will have a difficult time crossing the multilayered outer wall to enter the living protoplasts. However, experience indicates that such passage is possible and occurs readily. Lipid-soluble (lipophilic)

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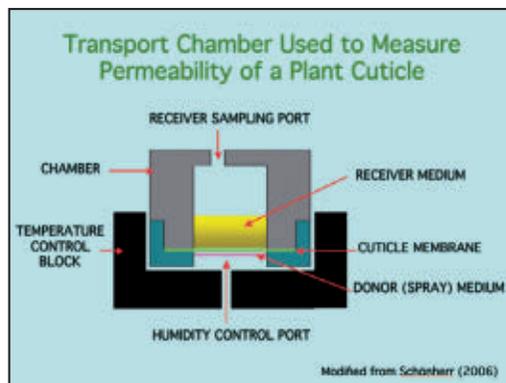
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pesticides and growth regulators have been shown to enter leaves in sufficient amounts to influence plant growth. Plants also utilize water-soluble (hydrophilic) nutrients and agricultural chemicals when they're sprayed on their leaves. Years of experimentation have led to the conclusion that the cuticle of epidermal cell walls provides both a lipophilic pathway as well as aqueous pores by which diverse substances can enter plant leaves.

The structure of a leaf cuticle described above provides no path or mechanism by which a water-soluble nutrient can cross from a leaf surface into living cells. A polar molecule (charged ion or organic dipole) is totally insoluble in the waxes comprising the epicuticular wax surface or the cuticle proper and would have no way to cross such a formidable barrier. Since hydrophilic substances clearly do cross these barriers, it's important to understand how this happens. In a recent review article, Schönherr (2006) summarized the present thinking on mechanisms of foliar absorption based on his extensive research initiated in the late 1960s.

Much of Schönherr's research used isolated cuticles, referred to as cuticular membranes (CM), through which the passage of various substances and the impact of altering environmental conditions on the process were measured. Removing the cuticle from a leaf is tricky. However, by incubating an epidermal peel or leaf piece in a solution of pectinase enzyme, the pectin layer between cellulose cell wall and cuticular layer can be dissolved and the cuticle removed easily. The enzyme causes no physical or chemical damage to the CM and transport across it in either direction is thought to occur by natural means and can be observed by positioning donor and receiver media (filter paper or gelatin sheets) on either surface of a CM. In this way, much critical information on the permeability of cuticles from many plant species to both lipophilic and hydrophilic substances has been obtained. Combining such observations with knowledge of the chemistry and physics of CMs has provided a convergence of ideas that should be very helpful in understanding how foliar fertilization works in the field.



The device used by Schönherr (2006) to measure foliar transport of chemicals applied to the surface of a cuticular membrane.

It's generally agreed that hydrated metal cations and less-hydrated but bulky oxy-radical anions require an aqueous pathway to cross a leaf cuticle. They are simply too insoluble in the cuticular wax layers (surface wax and cuticle proper) to dissolve sufficiently for measurable diffusion across these barriers. However, there are no microscopically observable aqueous pores traversing a cuticle through which charge bearing ions or hydrated organic molecules could pass. When ionic fluorescent dyes are applied to a leaf surface, they can be observed crossing the cuticle in aqueous pores having a diameter ranging from 0.9 to 2.36 nm (nanometer = 1 billionth of a meter = 3.9×10^{-8} inches). These values were obtained by measuring CM permeability to molecules of known diameter. Dyes exceeding a diameter of 2 nm generally failed to penetrate a leaf cuticle. Since most nutrient ions fall within this size range, they should be able to traverse a leaf cuticle via these aqueous pores.

The nature of these aqueous pores is somewhat conjectural but the current thinking seems to view them as forming around clusters or groupings of permanent dipoles (polar uncharged groups) and ionic units (+ or - charge) of cutin, carbohydrates, sugar acids and polypeptides (protein). All these groups have an affinity for water and within the waxy cuticular layers they would be hydrated and could form an aqueous path along which hydrated ions or polar molecules

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 could migrate single file from the leaf surface to the highly hydrated cellulosic walls of epidermal cells. These pores would be unstable, forming and breaking with the kinetic movement of the large cuticular polymers. Their existence depends on a near-saturated external atmosphere or free water on the leaf surface to insure hydration of polar and potentially ionic groups within the cuticle layers.

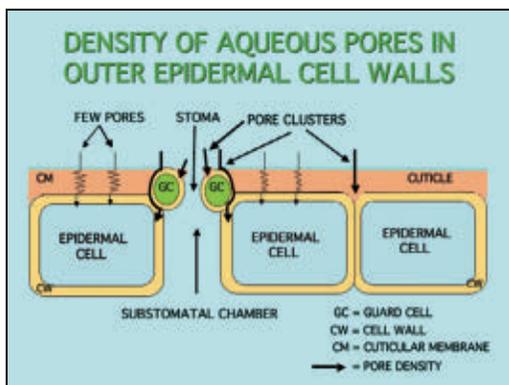


Diagram of a leaf epidermal segment showing the sites of greatest concentration and activity of aqueous cuticular pores.

That is consistent with field observations that show greatest nutrient penetration while spray is in the liquid form on leaf surfaces and when humidity is near 100 percent. Organic ions within the cuticle originate mostly from carboxyl groups (organic acids) that ionize in the presence of water to form fixed negative charges along the aqueous pores and on the leaf surfaces. These negative charges attract cationic nutrients and tend to repel anions while small nonionic (no charge) but hydrated molecules move along readily with the flux of water.

This is pretty much what has been observed in field experience with foliar fertilization (Totten, 2006; Totten et al., 2008). Cations are absorbed through leaves more rapidly than anions and urea is absorbed most rapidly of all. The absorption rate of foliar-applied nutrients also is dependent on their concentration gradient between the leaf surface and the cellulosic cell walls. However, the cell wall concentration is normally low because nutrient uptake across the plasma membrane of living cell protoplasts is rapid. Only calcium and some micronutrients are likely to accumulate within the cell wall of healthy leaves following a foliar application.

Therefore, high concentration spray solutions penetrate turfgrass leaves more rapidly than more dilute solutions and this can easily

cancel out any repulsion of anions by negative charges in the aqueous pores. Bowman and Paul (1992) observed that increasing spray concentrations eliminated differences in uptake rates of ammonia, nitrite and urea.

The distribution of cuticular aqueous pores across a leaf surface is not at all uniform. Studies involving fluorescent dyes, heavy-metal precipitation within pores and radio-labeled nutrient distribution have shown aqueous pores to be much more densely concentrated in cuticular ledges of guard cells facing the open pore of stomata, at the base of surface glandular trichomes (multicellular surface hairs) and in cuticle over anticlinal cell walls. Also, pores in guard cell ledges and those associated with trichomes are substantially greater in diameter and could readily accommodate large metal chelates and other hydrophilic organic solutes of molecular weights up to 800 grams per moles. This would explain the more rapid uptake of nutrients applied to stomata-rich lower leaf surfaces than astomatous upper surfaces even in darkness when stomata are closed.

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