

TURFGRASS TRENDS

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BACK TO BASICS

Water How Turfgrasses Obtain and Use Moisture

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Having survived a 1998 summer season that offered some of you the driest weather on record, it might be useful to review some of the basic ideas on how and why turfgrasses use water. Being familiar with these principles of water use may help you decide when water conservation is wise and when it may do more harm than good.

The management of water use on turf has been considered within these pages (Hull 1996a; Richie et al. 1997; Shank, 1998; Qian and Engelke 1999; Richie et al. 1999) and elsewhere (Hull 1996b; Fry et al. 1998; Fry and Jiang 1998). Most of these articles assume that the reader has a basic understanding of how turfgrasses acquire, transport and lose water. This is generally a safe assumption but might not always be true because of advances in our understanding of plant water relations. In this *Back to Basics* piece, I will review some long accepted concepts and add a few new wrinkles to our understanding of water use by turfgrasses.

How water functions in turf

Water is the medium of all biology. Life presumably originated in the primordial seas and to this day operates within an aqueous environment that resembles the probable composition of early oceans. Life is essentially a complex of controlled chemical reactions that function in water. Water is even a substrate for some of these reactions, e.g. photosynthesis and hydrolysis.

As plants invaded and colonized the land about 450 million years ago, they created ways for maintaining the integrity of their aqueous environment while growing and reproducing in a largely dry and often hostile world. Today, turfgrasses are frequently managed under similarly hostile conditions. To survive, plants needed to evolve ways for absorbing water from where it was available (usually the soil), transporting it to above-ground organs (stems and leaves), and controlling its loss so aerial organs would not desiccate and die. Also, this transport of water from roots to shoots soon became the principal route by which plants also transported all essential mineral nutrients from the soil to shoot organs.

As this system evolved, the evaporative loss of water from leaves and other shoot organs could not be entirely prevented and still allow for the necessary exchange of atmospheric gases. This was not all bad because the cooling effect of evaporation proved useful for stabilizing shoot temperatures within a range that was compatible with life chemistry. Thus,

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while plants were able to grow on land, they retained the need for a constant supply of water to support life, transport nutrients and prevent aerial organs from overheating. Even today, plants depend on water for the same functions.

Water uptake from the soil

Water enters a plant root in response to a negative gradient in water potential. In other words, when the activity of water in the soil is greater than it is within the root, water flows into the root. The activity or potential (Y) of water in any situation is governed by its concentration and the pressure imposed on it. This is often expressed by the equation:

$$Y_w = Y_s + Y_p$$

Y_w = the water potential in the soil or within a plant cell and consists of two components: Y_s = solute potential and Y_p = pressure potential. The term Y_s refers to the amount of solute (salts, sugars, acids, etc.) dissolved in water. Such solutes dilute the water and thus compared to pure water it has a negative potential. More stuff dissolved in water makes its solute water potential (Y_s) more negative. The pressure potential (Y_p) indicates the actual pressure exerted on water in the system being considered.

In a soil, the pressure on the soil water is approximately atmospheric pressure, which by convention is set at zero. Within a root cell, the pressure is likely to be positive if the cell is turgid and the root is not wilted. At times when water is under tension, it is under negative pressure and Y_s will have a minus value.

In accordance with the above conditions, water will enter root cells only when the water potential inside the root is less than the water potential of the soil solution. In other words, water will move from a high potential in the soil to a lower potential in the roots, consistent with the general laws of nature and energy. If the soil dries and its water potential decreases (becomes more negative), water will continue to enter plant

roots only if the root's water potential is even lower (more negative). This can occur if root cells increase their solute content or their water comes under negative pressure (tension). Water tension in root cells will cause roots and shoots to wilt and can even cause cells to collapse.

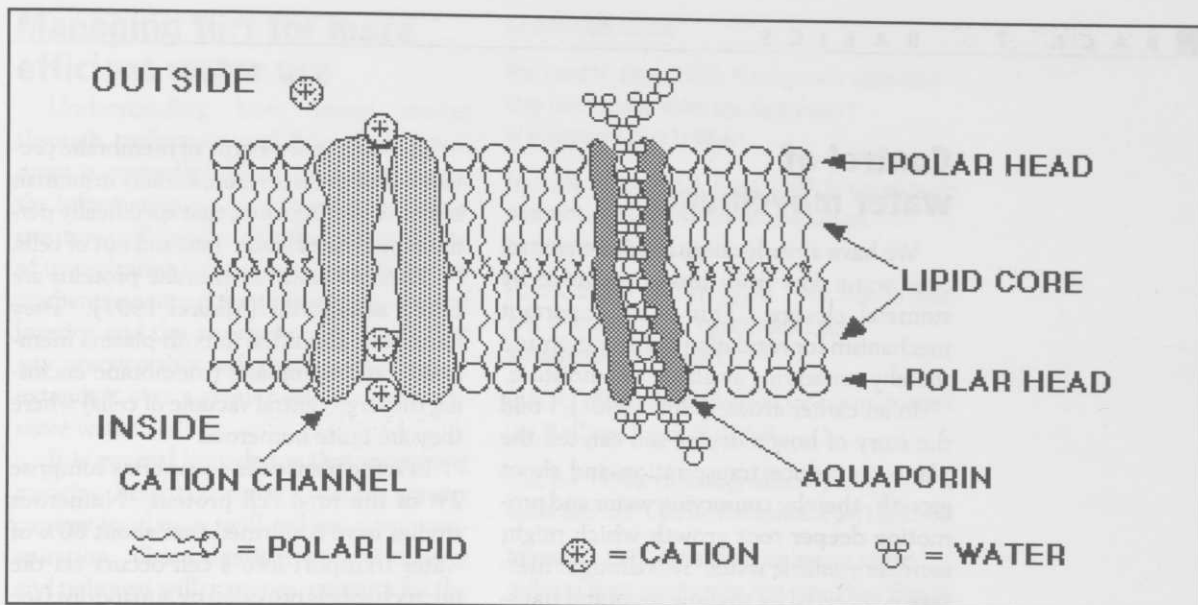
Transpiration — the force that keeps water flowing

The force that drives the flow of water from roots to shoots is generated by the evaporation of water from leaf surfaces (transpiration). Actually, it is not the leaf surface that loses water but the wet cell surfaces bordering the substomatal chambers within the leaves. These chambers are in contact with the atmosphere via small pores called stomata. Normally concentrated on the under surface of leaves, stomata provide openings to the leaf interior through which carbon dioxide can enter and oxygen can exit the leaf.

Stomata are open during the daylight hours while photosynthesis is occurring. They close during the night, virtually sealing off the leaf interior from the atmosphere and preventing most transpiration.

The force generated by water evaporating from leaves can be substantial. The magnitude of this force depends on the difference between water potential (Y_w) within the substomatal chambers in the leaves and that of the atmosphere. Even under dry conditions, the substomatal chambers have a high relative humidity (~99 percent). This translates into an atmospheric water potential of -1.35 megapascals (MPa). A pascal is a very small unit of pressure but a million pascals (MPa) is equivalent to 145 pounds per square inch (psi).

If the atmospheric relative humidity is 50 percent, which is not unreasonable for a summer day, the atmospheric water potential would be -93.6 MPa (see figure). Under these conditions, the water potential gradient between the inside and outside of a leaf would be $-93.6 - (-1.35) = -92.2$ MPa, which is equivalent to a pressure of 13,376 psi. That constitutes the force driving water



Portion of a cell membrane showing polar lipids and two membrane spanning intrinsic proteins, an aquaporin and a cation channel.

vapor out of a leaf through the stomata into the atmosphere. It also represents the force that lifts water from the soil to the tops of tall trees or into the leaves of turfgrasses. With forces of this magnitude, is it any wonder that turfgrasses lose water rapidly and will dry out the soil within a few days?

Water transport to leaves

The roots, where water is available, and the leaves, where water is lost, are connected by specialized cells called vessel elements. When mature, these cells are dead, lose their end walls and are lined up end-to-end forming long tubes. These tubes, called vessels, are ideal for transporting large amounts of water with relatively little resistance.

Vessels resemble corrugated pipes that are imbedded within the vascular bundles of leaf blades, leaf sheaths and stems and are continuous with similar vessel elements in the core of roots.

The negative water potential (suction) generated by transpiration from the leaves is transmitted through the vessels to the roots, where it causes water to flow toward the leaves replacing that lost through transpiration. This lowers the water potential of the roots and water flows into the roots from the soil.

As a result of the efficient transport of water through vessels from roots to leaves, the actual water potential gradient within the grass plant between roots and leaves is rarely more than one megapascal. As long as water is available in the soil, grass plants should experience little moisture stress even in the face of enormous forces driving water out of the leaves. When the soil begins to dry or roots are damaged by insects or disease, the influx of water will be limited and water loss from the leaves may easily exceed water absorption by roots.

When this occurs, the water potential in the leaves drops below that of the leaf cell solute potential (Ψ_s), eliminating cell turgor pressure and the leaves will wilt. The guard cells that border the stomata also wilt (lose turgor) causing the stomatal apertures to narrow or close thereby reducing further water loss. If this reduced rate of transpirational water loss becomes less than the rate of water uptake by roots, plants will recover from wilting often with little damage having been done.

In recent years, a type of membrane protein has been discovered that specifically permits the flow of water into and out of cells. These intrinsic membrane proteins are called aquaporins.

Control of water movement

We have already considered the control over water loss from leaves provided by stomatal closure. This is an important mechanism for regulating transpiration and thereby conserving available soil moisture.

In an earlier article (Hull 1996a), I told the story of how a drying soil can tell the plants to reduce transpiration and shoot growth, thereby conserving water and promoting deeper root growth which might increase available water. This drought message is received by shallow roots and translated into production of the hormone

abscisic acid (ABA).

This hormone is carried via the transpiration stream to the leaves, where it promotes stomatal closure and inhibits leaf growth.

Inhibited shoot growth makes more photosynthetic product available for transport to the roots,

where those deeper roots that still have adequate water are enabled to increase their growth and explore additional water supplies. In this way, the plant is warned well before drought stress occurs that water shortage is imminent and conservation measures need to be taken.

For many years, physiologists assumed that water movement was passive, responding to gradients in water potential, and was largely uncontrolled except by stomatal closure. Water crossed the outer cell membranes (plasma membrane) by moving through integral proteins that spanned the largely lipid (fat) membrane (see figure). It was believed that water could move only slowly across the lipid core of biological membranes, so most water had to cross via intrinsic membrane spanning proteins that exerted little or no control over water passage. Thus, water movement into root cells was pretty much uncontrolled.

In recent years, a type of membrane protein has been discovered, initially in animals but now also in plants, that specifically permits the flow of water into and out of cells.

These intrinsic membrane proteins are called aquaporins (Maurel 1997). They have been identified in both plasma membranes and tonoplasts (membrane enclosing the large central vacuole of cells) where they are quite numerous.

In some plant cells, aquaporins comprise 2% of the total cell protein. Numerous studies have confirmed that about 80% of water transport into a cell occurs via the microchannels provided by aquaporins (see figure).

This is not universally true in that some cells permit only about 20% of their water influx through aquaporins; the remainder moving through other intrinsic membrane proteins or diffusion through the lipid core. However, such cells have a much greater resistance to water uptake than cells better endowed with aquaporins.

The discovery of aquaporins not only explained how water can enter cells rapidly, it also indicated that the process of water uptake is regulated to a greater extent than had generally been recognized. Because aquaporins are proteins, their synthesis is directly under genetic control, which in turn is influenced by environmental, developmental and positional factors.

Plants can alter their rate of water uptake by synthesizing more or fewer aquaporin molecules. It also appears that the activity of aquaporins can be controlled by environmental signals such as drought, temperature and oxygen availability.

Binding a phosphate ion to an aquaporin molecule has been shown to increase its capacity to transport water. This process of phosphorylation is known to regulate biochemical reactions and this finding suggests that water transport may be under similar levels of control.

In short, water entry into cells and transport throughout a plant is much more tightly regulated than was ever thought possible only a few years ago.

Increasing mowing height creates greater canopy insulation and reduces evapotranspiration. Similarly, grass stands of greater density and tightness will conserve moisture.

Managing turf for more efficient water use

Understanding how water moves through turfgrasses and how this movement is controlled gives the turf manager the information necessary to manage water use more efficiently. Knowing that the rate of transpiration is influenced mostly by the gradient in water potential between the leaf interior and the atmosphere suggests that any practice that reduces this gradient or extends it over a greater distance will conserve water.

It is general knowledge that increasing mowing height, thereby creating greater canopy insulation, will reduce evapotranspiration. Grass stands of greater density and tightness will conserve moisture for the same reason.

Allowing turf to sustain mild drought stress before irrigating will induce physiological water conservation by the grass plants and promote deeper rooting. This both reduces water usage and makes the turf better able to exploit soil water resources. Less frequent but deeper irrigation is generally acknowledged to be more water efficient and promotes a tougher turf.

The recognition of aquaporin mediated water transport is too recent to have influenced water management strategies. However, it is reasonable to expect that turfgrass breeders will be able to use this information to create grass cultivars that are better able to absorb water and respond favorably to changes in water availability.

Understanding what environmental signals will enhance water movement also can be exploited by turf managers to increase water use efficiency or increase drought tolerance. Within a short time, this knowledge will likely be translated into improved turf management practices for greater water economy.

Dr. Richard J. Hull is professor of plant science and chairman of the Plant Sciences Department at the University of Rhode Island. His research has concentrated on nutrient use efficiency and photosynthate partitioning in turfgrasses and woody ornamental plants.

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