What's the Lowdown on Turfgrass Leaves?

By *Richard J. Hull*

To state the obvious, turfgrasses are grown for their leaves. To be sure, new leaf growth is mowed regularly and discarded or left to rot, but still the valued part of a turfgrass plant is its dense, green leaves.

Leaves provide the surface where golfing putts are sunk. Turfgrasses are evaluated for many characteristics but leaf color, texture and density are of primary importance. In this series of *TurfGrass Trends* articles, we have discussed the turfgrass crown (Hull, 2000) and roots (Hull, 2000a & b), so today we will get to the bottom line and consider the biology of turfgrass leaves.

Grass leaf structure

Grass leaves are commonly regarded as consisting of two parts: the blade and the sheath (Figure 1).

The green blade has a roughly horizontal orientation when mature but is more vertical when younger and growing. The blade joins the vertical sheath at an angle in a region known as the collar. The light green sheath encloses the sheaths of younger leaves and may itself be enclosed by sheaths of older leaves. All grass leaves originate from ridge-like horizontally oriented subapical meristems that form just below the apex of the crown. Then an intercalary meristem produces new cells at the base of the emerging leaf. As these cells expand and elongate, the leaf tip is pushed upward inside the sheath of the previously formed leaf.

As the leaf grows, a second intercalary meristem forms below the first just above the crown. This second intercalary meristem generates new cells that will contribute to the elongating sheath. The initial intercalary meristem rises upward along the length of developing leaf and continues to lay down new cells that contribute to further elongation of the blade.

As the leaf grows, the collar region differentiates from the initial intercalary meristem at the junction between blade and sheath. At the collar, structures form that are characteristic of the species. A ligule may grow upward from the sheath at the point where the blade angles toward a horizontal plane. Madison (1971) describes the ligule as "an eruption of the epidermis that is two cells thick."

Ligules are membranous and prominent in bentgrasses, perennial ryegrass and rough bluegrass but are reduced to a fringe of small hairs in bermudagrass, Japanese lawngrass and carpetgrass or are completely absent in barnyardgrass.

In some grasses, an overgrowth of the blade edges at the collar form auricles that clasp claw-like around the upper portion of the sheath. Auricles are not present in most grasses but are prominent in perennial and annual ryegrasses. The collar region can also exhibit hairs at the margins of the sheath or the base of the blade. All these collar features tend to be conservative and are useful in grass identification when flowers and seed are not present.

Essential roles of invisible epidermis

The grass leaf is ideally suited for its primary functions: photosynthesis and the export of sugars (mostly sucrose) to all parts of the plant where growth or storage are occurring.

Leaves consist of three basic tissue types: upper and lower epidermis, mesophyll and vascular bundles (Figure 2). The epidermis is one cell-layer thick and covers both upper and lower leaf surfaces. Its outer cell walls are covered with a waxy cuticle that reduces enormously the evaporative water loss from the leaf. However, since gas exchange between the atmosphere and leaf interior is essential for photosynthesis, the cuticular shield is broken at regular intervals by the presence of guard cell pairs that, when fully turgid, open pores in the epidermis through which gasses can pass. The turgidity of guard cells is regulated such that the stomates are open during daylight hours and closed in darkness.

During drought stress, abscisic acid (ABA) levels increase in the leaves and promote stomatal closure. This was demonstrated in Kentucky bluegrass cultivars by Bingru Huang and her students at Rutgers University. They found that

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greater stomatal sensitivity to ABA concentrations was characteristic of cultivars having greater drought tolerance (DaCosta et al., 2002).

Epidermal cells of turfgrasses leaves appear devoid of pigments but they are able to absorb significant amounts of ultraviolet (UV) radiation that would be harmful to the underlying mesophyll cells where photosynthesis occurs.

The maintenance of photosynthesis requires the repair and synthesis of proteins involved in energy transfer and those processes are sensitive to UV especially UV-B (wavelength = 280-320 nanometers). Yuen et al. (2002) at the University of Nebraska observed that the levels of UV-B radiation declines rapidly as sunlight passes through leaves of turfgrass canopies. Thus the epidermis, while all but invisible, is essential for the proper function of turfgrass leaves.

Leaves designed for controlled gas exchange

The green cells that comprise most of a leaf's volume are the mesophyll. Virtually all of the chloroplasts (subcellular organelles in which photosynthesis occurs) are contained in mesophyll cells. The epidermal guard cells also contain chloroplasts, but their photosynthetic output is devoted entirely to the function of stomates.

Mesophyll cells are not packed into the leaf tightly. Instead, numerous intercellular spaces are present that make up a gaseous continuum with the atmosphere. Carbon dioxide (CO_2) must enter mesophyll cells while oxygen (O_2) must exit these cells. As CO_2 is consumed in photosynthesis, its concentration in the leaf intercellular spaces becomes depleted, but is replenished from the atmosphere by diffusion through the stomates.

As photosynthetic O_2 is evolved, it accumulates in intercellular spaces and diffuses through the stomates into the atmosphere. At the same time, saturated cell walls of the mesophyll maintain the relative humidity (RH) inside the leaf at about 100 percent. Since the atmospheric RH is normally much lower, a substantial water potential difference exists across the stomatal orifice, driving a rapid diffusion of water vapor out of the leaf.

Much of this water loss is inevitable given the structure of leaves and the easy route for water efflux through open stomates. However, water loss does serve some purpose. The flow of water through the plant from roots to leaves through the xylem constitutes the route and means by which nutrient elements are delivered to the leaves. With little or no transpiration occurring, leaves would soon become depleted of nitrogen, phosphorus, potassium, magnesium and sulfur because these elements are constantly being exported from the leaves through the phloem. Plants growing under near-saturated conditions for extended periods will exhibit nutrient-deficiency symptoms.

When water evaporates and passes from the liquid to the vapor form, it consumes heat energy of vaporization. This constitutes a loss of 580 calories/milliliter of water evaporated at room temperature. This has been calculated to represent .26 calories per square of leaf surface per minute or about half of the radiant energy received by a leaf growing in full sun. The energy consumed in transpiration has a marked cooling effect on turfgrass leaves.

When the water potential of leaves decreases because of reduced availability from a drying soil, the stomates close and transpiration slows dramatically. If such conditions persist, damage to the leaves will occur, but the cause is probably not drought as much as it is excess heat caused by the lack of transpirational cooling.

Photosynthate export is critical leaf function

Extending the entire length of a leaf and embedded among the mesophyll cells are several vascular bundles. In a grass leaf, these vascular strands are oriented parallel to each other so that no mesophyll cell is separated by more than a few cells from a vascular bundle.

FIGURE 1

Grass leaves are commonly regarded as consisting of two parts: the blade and the sheath.

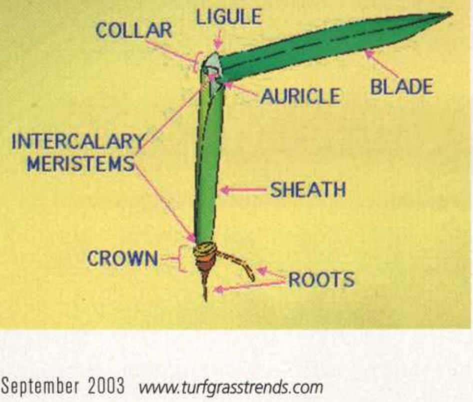
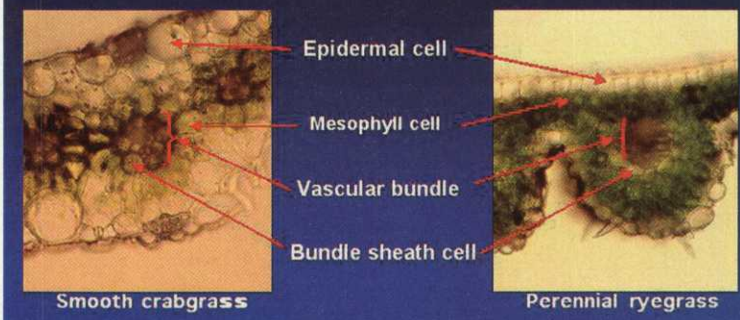


FIGURE 2



There are three basic tissue types within turfgrass leaves: upper and lower epidermis, mesophyll and vascular bundles.

Numerous small bundles connect the larger parallel veins, further increasing mesophyll contact with conducting tissues. Vascular bundles are enclosed in a sheath of cells that in cool-season grasses contain no chloroplasts but in warm-season grasses have abundant, sometimes large, chloroplasts. Within the vascular bundles are several xylem vessels, phloem sieve tubes with their companion cells, and a number of undifferentiated parenchyma cells associated with the xylem and phloem.

Vascular bundles constitute the transport route by which water and mineral nutrients enter the leaf from the roots while photosynthetic products exit the leaf through the phloem for remote meristematic regions where they are needed.

The tip of a grass leaf is its most mature part, and it's the first to carry on sufficient photosynthesis to load sugars into the phloem and begin exporting energy to less mature parts of the leaf and to the rest of the plant. As the leaf matures, its contribution to the energy needs of the plant increases until it becomes a full source leaf and a major supplier of the plant's energy needs. Such a leaf displays its blade in a horizontal plane at right angles to the sheath enabling it to capture maximum solar radiation.

Of course, a turfgrass leaf gets clipped as it grows, losing its most mature and most productive part. However, as growth slows and the remaining blade assumes its horizontal orientation, it will be below the cutter blade and no longer subject to mutilation.

As a leaf becomes overtopped by newer leaves that shade it from the light, its photosynthetic productivity declines. Eventually its photosynthesis barely meets its own energy needs but rather than becoming an energy parasite on the plant, senescence is induced and the leaf mobilizes its remaining resources and transports them to the crown or stem. When this is complete, the leaf dies.

Leaf structure and photosynthetic efficiency

The difference in photosynthetic efficiency between cool-season and warm-season grasses is reflected in its leaf anatomy. The cool-season perennial ryegrass shown in Figure 2 has all of its chloroplasts and photosynthetic activity concentrated in mesophyll cells. Here, CO_2 is fixed by the Calvin Cycle where the first product is the 3-carbon (C-3) compound phosphoglyceric acid. This is soon reduced to glyceraldehyde phosphate, the first true sugar produced in photosynthesis. Two of these C-3 sugars are then combined to form the C-6 sugar glucose that in turn is further combined to form the C-12 sugar sucrose.

Sucrose moves from the mesophyll cells through the symplasm to the bundle sheath cells and in turn is loaded into the sieve tubes and exported from the leaf. In cool-season grasses, oxygen (O_2) competes with CO_2 for its fixation site causing wasteful photorespiration. This can reduce the efficiency of photosynthesis by 50 percent or more, especially under high light and elevated temperatures when CO_2 levels in chloroplasts are particularly low.

Warm-season grasses have evolved a means of avoiding this inefficiency in photosynthesis. They separate the CO_2 fixation and reduction steps in two different cell types, mesophyll and bundle sheath cells, respectively.

In the mesophyll cells, the carbon fixed is not CO_2 but bicarbonate (HCO_3^-) that is 10 times more abundant in the chloroplast sap than is CO_2. The HCO_3^- combines with a 3-C acid phosphoenolpyruvate (PEP) to produce a 4-C acid, oxaloacetate (OAA). This reaction is favored because of the relatively high concentrations of HCO_3^- and because it is not inhibited by O_2. The OAA is next reduced to the 4-C acid malate and shuttled into the bundle sheath cells. There, malate is decarboxylated to CO_2 and the 3-C acid pyruvate.

Within the bundle sheath chloroplasts, CO_2 accumulates where it favors the Calvin Cycle that then can fix and reduce CO_2 much more efficiently. The remaining pyruvate diffuses back

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to the mesophyll cells where it is phosphorylated to PEP and can start the cycle all over again.

This process in warm-season grasses is called C-4 photosynthesis after the number of carbon atoms in its first product.

Conversely, CO_2 fixation in cool-season grasses relies exclusively on the Calvin Cycle and is known as C-3 photosynthesis. The large bundle sheath cells, well-endowed with chloroplasts, are characteristic of plants having C-4 photosynthesis as illustrated by crabgrass in Figure 2. Because C-4 photosynthesis is favored by high temperatures, warm-season grasses do not exhibit the summer decline so evident in cool-season turf.

On the other hand, C-3 photosynthesis is favored by cool temperatures and that makes cool-season grasses better suited for growth early in the spring and during mid to late fall. The advantages of C-4 photosynthesis during high temperatures gives C-4 weeds (crabgrass, fall panicum, yellow nutsedge, prostrate spurge and goosegrass) a competitive edge over cool-season turf during mid summer.

It is evident that turfgrass leaves are not only the source of all energy available to turfgrasses but also are capable of receiving environmental cues and transmitting chemical messages to other parts of the plant where growth patterns may be influenced dramatically. Perhaps those leaves that are mowed with much abandon by the turf manager should be treated with a little more respect.

Hull, a professor of plant sciences at the University of Rhode Island in Kingston, R.I., who specializes in plant nutrition, also offered his insights into turf leaves as antennae for environmental signals in the Aug. 27 issue of The Golfdom Insider. It can be found at www.golfdom.com.

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