The Rise of Warm-Season Grasses

By Richard J. Hull

Turf can be maintained in hot climates for landscaping and recreational purposes primarily though the use of warm-season grasses. Unlike their cool-season cousins that fail to grow when temperatures exceed 85 degrees Fahrenheit, warm-season grasses can grow vigorously at temperatures approaching 100 degrees F (Beard 1973). Understanding the fundamental reasons behind this difference in heat tolerance among turfgrasses may enable the turf manager to achieve better turf performance.

In the first part of this series published in November, we traced the origin of the photosynthetic process that operates in cool-season turfgrasses and most plant species that grow in temperate climates. It was noted that photosynthesis evolved about 3.5 billion years ago in a world very different from the one we inhabit today. The biggest difference is the presence of 21 percent oxygen (O_2) in our atmosphere compared to less than 1 percent in that of the ancient world. That oxygen is the by-product of more than three billion years of photosynthesis — initially from bacteria but later mainly produced by algae and plants. The chemical reaction by which most carbon dioxide (CO_2) has been converted into organic matter is catalyzed by the enzyme ribulose bisphosphate carboxylase/oxygenase (aka RubisCO) that functions today pretty much as it did more than 3 billion years ago. In photosynthesis, this enzyme functions as a corboxylase when it assimilates CO_2 into the three-carbon phosphoglyceric acid (PGA).

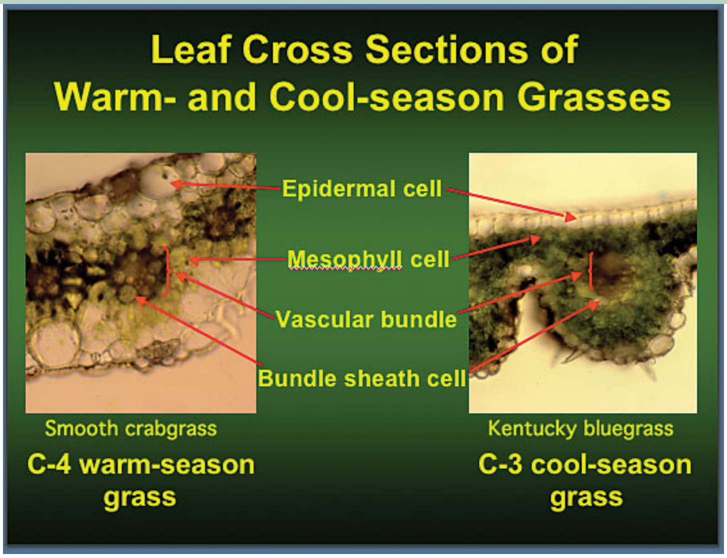
Emergence of warm-season crabgrass in cool-season bluegrass during hot weather.

However, in the presence of O_2, RubisCO functions as an oxygenase binding with O_2 and initiating photorespiration that fixes no CO_2 and actually wastes energy. As atmospheric O_2 levels increased, photorespiration increased and began reducing photosynthetic efficiency until in our present atmosphere of 21 percent O_2 and 0.038 percent CO_2, net photosynthesis is generally inhibited by about 50 percent. At elevated temperatures, photosynthetic efficiency can be decreases by more than 75 percent, a rate insufficient to support plant growth. This is a major reason why cool-season turfgrasses fail to grow well in hot climates during the summer months.

C-4 photosynthesis

This photorespiratory erosion of photosynthesis has been a recurring problem for almost 50 million years. The principal evolutionary response to it has been an increased production of RubisCO. The strategy being: If low CO_2 and high O_2 concentrations make the carboxylase activity of RubisCO inefficient, let's just make more RubisCO. Today, RubisCO is by far the most abundant protein in the world, constituting more than 50 percent of the soluble protein in the leaves of most plants. While high RubisCO concentrations enabled photosynthesis to keep ahead of respiration, they were made and maintained at considerable cost in carbon and nitrogen resources. Growth rates were slowed during hot weather and plants were less able to reproduce and tolerate other environmental stresses.

A significant biochemical response to impaired photosynthesis due to photorespiration evolved about 20 million years ago (mya) in the early Miocene Epoch but really became prominent 10 to 8 mya when atmospheric CO_2 levels fell to below 250 parts per million (ppm). Known as C-4 photosynthesis because the first product of CO_2 fixation is a 4-carbon acid (oxaloacetate or malate), this adaptation was truly ingenious. The strategy is to capture CO_2 from its more abundant HCO_3^- form and use it to increase the CO_2 level within specific cells where RubisCO and the Calvin Cycle are concentrated. To do this, a specialized cel-



Leaf anatomy of C-4 and C-3 grasses showing relationships between mesophyll and bundle sheath cells with a vascular bundle.

PHOTO COURTESY: RICHARD HULL

lular arrangement within leaves is required. The CO_2 capturing cells (mesophyll cells) are grouped in a ring around a layer of CO_2-fixing cells (bundle sheath cells) that surround the vascular bundles (conducting xylem and phloem cells) of the leaf.

By comparison, leaves of cool-season (C-3) plants have more numerous and randomly organized mesophyll cells loosely arranged around the bundle sheath cells that enclose the vascular bundles, but here they generally lack chloroplasts.

In C-4 plants, atmospheric CO_2 diffuses into the leaves through open stomata, is dissolved on the wet surfaces of mesophyll cells and passes as CO_2 across a cell's plasma membrane into the cell. There it becomes hydrated to carbonic acid (H_2CO_3) and at the prevailing cytoplasmic pH of 7.0, it dissociates to bicarbonate (HCO_3^- & H^+).

The equilibrium between dissolved CO_2 and HCO_3^- favors HCO_3^- over CO_2 by a ratio of 50 to 1. Thus, even when CO_2 levels are very low, the HCO_3^- concentrations within mesophyll cells are 50 times higher. There HCO_3^- reacts directly with phosphoenolpyruvate (PEP), a three-carbon acid, forming the C-4 acid oxaloacetate (OAA). The enzyme PEP Carboxylase (PEPC) catalyzes this reaction. The PEPC enzyme has a high affinity for HCO_3^- but does not react with O_2 so there is no O_2 competition with CO_2 for this enzyme and therefore, no photorespiration.

Oxaloacetate is next reduced to the chemically more stable C-4 acid, malate, that diffuses into adjacent bundle sheath cells via tubular protoplasmic connections (plasmodesmata) that traverse the intervening cell walls. In the bundle sheath cells, malate is decarboxylated to another C-3 acid, pyruvate, releasing CO_2. The pyruvate diffuses back into a mesophyll cell where it's converted to PEP and is ready to bind with another HCO_3^-, completing the C-4 cycle. Within the bundle sheath cells, CO_2 accumulates to levels higher than that in mesophyll cells. This is more than enough CO_2 to inhibit photorespiration and allow RubisCO to introduce CO_2 into the Calvin Cycle at peak efficiency. In warm-season grasses, the Calvin Cycle enzymes are not present in mesophyll cells but are contained exclusively within the chloroplasts of bundle sheath cells. Here, sugars made by the Calvin Cycle are in bundle sheath cells that are adjacent to vascular conducting cells (phloem), and can be efficiently exported from leaves to growing sites where they are needed.

Under hot conditions, when CO_2 levels in leaf cells are low and O_2 is high, C-4 photosynthesis supports a CO_2 fixation rate several times that of C-3 photosynthesis operating alone. However, at cooler temperatures when CO_2 concentrations in leaf cells are higher, C-4 photosynthesis is actually less efficient and supports a lower photosynthetic rate. Thus, C-4 photosynthesis provides a survival advantage only in those climates that routinely experience temperatures 85 degrees F and higher.

C-4 plants are also more efficient in their use of water. Because more CO_2 is photosynthetically reduced to sugars during each hour that stomata of C-4 leaves are open, those leaves will lose less water to transpiration for each gram of CO_2 fixed.

Studies reveal a water efficiency of 700 to 1,300 moles of water lost for each mole of CO_2 fixed in C-3 plants while C-4 plants lose only 400 to 600 moles of water per mole of CO_2 fixed. C-4 grasses also generally have a larger and deeper root system than C-3 grasses.

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C-4 plants are also more efficient in their use of water.

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Having evolved on numerous occasions over many years, it's not surprising there are variations in C-4 photosynthesis and even intermediate plants that exhibit greater photosynthetic efficiency but do not possess all the characteristics of a C-4 plant.

Heat tolerance in turfgrasses is not solely a function of being wended with C-4 photosynthesis. Elevated temperatures can cause other malfunctions in cool-season grasses where root sensitivity to heat can be especially troublesome. The lipid saturation level of cell membranes, the ability to detoxify O_2 free radicals, and the synthesis of heat-stable growth-promoting proteins all appear to play a role in making cool-season turfgrasses more heat tolerant.

However, there is ample evidence that C-4 photosynthesis does contribute to a plant's aggressiveness, especially in warm climates. C-4 plants comprise less than 4 percent of plant species but account for about 18 percent of the Earth's annual plant production.

Of the 18 plants designated as the world's worst weeds, 14 exhibit C-4 photosynthesis. Genetic research has not been successful in transferring C-4 photosynthesis into a C-3 plant. There is a lot involved in the C-4 syndrome and such a genetic feat may not be realistic. However, understanding what really distinguishes a warm-season from a cool-season turfgrass may be helpful in managing each to its fullest potential.

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REFERENCES

Beard, J.B. 1973. Turfgrass: Science and Culture, Prentice-Hall, Englewood Cliffs, NJ, Chapter 17.

Hull, R.J. 2009. The origin of turfgrasses: the rise of warm-season grasses. Golfdom – TurfGrass Trends: November, 2009.

Hull, R.J. and J.T. Bushoven. 2009. Does research offer answers to problems of summer decline? Golfdom – TurfGrass Trends: Jan. 66-70.

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