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Summer Decline
Can Cool-Season Turfgrasses Take the Heat?

By Richard J. Hull, University of Rhode Island

This past summer has not been an easy time for many turf managers. The unrelenting drought and above normal temperatures took their toll on cool-season turfgrasses in lawns, athletic fields and golf courses. If conventional wisdom is to be believed, we have just seen the beginning of bad summers, as global warming sets in and summers generally become drier and hotter. On the other hand, is this really anything unusual? Cool-season turfgrasses always decline during the summer and greater problems should be expected as we try to push these grasses even further south.

In short, there is a fundamental problem inherent in attempting to maintain green, vigorous turf from cool-season grasses during the hottest months of the year. Some years are worse than others, but the problem is chronic. What is behind the summer decline of turfgrasses? Do we know enough about this problem to offer any hope of solving it? In this article, I will take a shot at answering these questions.

High Temperature Stress

What exactly is high temperature stress? This is not a simple question to answer because, in the field, high temperature is often accompanied by high light and insufficient water. Consequently, the resulting decline in turf quality is rarely caused by one stress alone, but by the interaction of several stresses. The principal factor of summer decline of turfgrasses is primarily heat, augmented by other stresses.

OPTIMUM TEMPERATURES FOR SHOOT AND ROOT GROWTH

Table 1. Optimum temperatures for shoot and root growth of cool- and warm-season turfgrasses.

Grass type	Shoot growth	Root growth
	Degrees F	Degrees F
Cool-season	59-75	50-64
Warm-season	81-95	75-84

FROM DIPAOLA AND BEARD (1992)

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This is the opinion of Dr. James B. Beard, who coined the term "summerkill" to describe summer decline of cool-season grasses. He includes opportunistic diseases in the mix of conditions contributing to summer turf decline and death, but heat augmented by drought is the primary cause. Dr. Bob Carrow, with the University of Georgia's Experiment Station at Griffin, lists eight secondary factors that contribute to or result in summer turf decline. He too credits high temperature stress as being the primary culprit.

Turfgrasses vary in their resistance to high temperatures, which is not surprising because the optimum temperature for growth differs markedly among grasses. Warm-season grasses exhibit optimum shoot growth at temperatures some 20 degrees F higher than are optimum for cool-season grasses. Roots of cool-season grasses also grow best at temperatures 20 to 25 degrees F cooler than those best for warm-season grasses. The range in optimum temperatures for both grass types reflects the variation among different species within each type. Optimum temperatures for root growth are also about 10 degrees cooler than for shoot growth.

Given the shape of growth curves, temperatures either below and above the optimum range are by definition stressful. That is, they constitute conditions that in some way are limiting to plant growth. In the context of this discussion, we are concerned with supraoptimal temperatures and how they pose limits to the growth or performance of turfgrasses. There is a clear difference between cool-season and warm season grasses with regard to their tolerance of high temperatures (Table 1). The optimum temperatures for warm-season grasses are well within the supraoptimal range for cool-season grasses for both shoots and roots. This should tell us that a basic difference between these two grass types probably explains their differing high temperature tolerance. This will be addressed in the next section.

When temperatures become very high, plants experience direct thermal injury which leads to rapid death. For most turfgrasses, killing temperatures occur between 131 and 142 degrees F (DiPaola and Beard 1992). Warm-season grasses do require somewhat higher temperatures than cool-season grasses before death occurs, but the differences are not as great as for optimum growth temperatures.

Killing temperatures cause protein denaturation as thermal energy becomes so great that the structural integrity of the proteins can no longer be maintained. This results in a loss of enzyme activity and a collapse of biochemical pathways and their control. Lethal temperatures are not the cause of summer decline in turf quality because they are well above those at which decline is observed. Sublethal temperatures can kill turf, but normally indirectly through the effects of drought or pathogen caused injury. Thus, an explanation of heat injury in cool-season grasses will likely be found in that which distinguishes them from warm-season grasses.

C-3 Photosynthesis and Consequences

The basic difference between cool- and warm-season grasses is in their method of capturing carbon dioxide (CO_2) for photosynthesis. All plants fix CO_2 by means of the same enzyme, ribulose bisphosphate carboxylase/oxygenase (RubisCO). This enzyme catalyzes the following reaction.

$$\mathbf{RuBP + CO_2 > 2\ PGA}$$

Here ribulose bisphosphate (RuBP), a five-carbon sugar, binds with CO_2 to form an unstable 6-carbon molecule that spontaneously decomposes into two three-carbon molecules of 3-phosphoglyceric acid (PGA). This reaction is energetically favored, but only occurs in the presence of the RubisCO enzyme. Because the product of this reaction that contains the carbon of fixed CO_2 is a three-carbon acid (PGA), photosynthesis that fixes CO_2 by this reaction is called C-3 photosynthesis. From PGA, the carbon passes through several

reactions until it is reduced to the level of carbohydrates, sugars and starch, or regenerates the RuBP necessary to keep the photosynthetic carbon fixation cycle going.

RubisCO is an ancient enzyme, almost as old as life itself. It evolved in a world significantly different from what we have today. When photosynthesis first emerged, the atmosphere was enriched in CO_2 and very low in oxygen (O_2). Over the years, atmospheric CO_2 levels have decreased to about 0.035 percent of atmospheric gases, while O_2 has increased to 21 percent of the atmosphere. Under these modern conditions, RubisCO finds itself much less efficient in fixing CO_2. First of all, there is much less CO_2 available, so the enzyme can only operate at about half of its maximum rate. In addition, O_2 competes for the CO_2 binding site on the enzyme where the following oxygenase reaction is catalyzed.

RuBP + O_2 > PGA + P-Glycolate

Here RuBP binds with O_2 but the five-carbon product that is formed degrades to one PGA and one two-carbon phosphoglycolic acid molecule. This oxygenase reaction fixes no CO_2 and the P-Glycolate formed is metabolized via a pathway that releases CO_2 and consumes energy. Because this over-all reaction occurs only in the light, consumes O_2 and releases CO_2, the process is called photorespiration.

When temperatures are high, the solubility of gases in water decreases, which makes both CO_2 and O_2 less available for fixation by RubisCO. However, the ratio of CO_2:O_2 in solution decreases from 0.051 to 0.038 as the temperature increases from 41 degrees to 95 degrees F, which means that as the temperature rises, less CO_2 compared to O_2 remains in solution. Therefore, photorespiration is favored while photosynthesis is hindered (Taiz and Zeiger 1998). As a result, under high temperatures, photosynthetic rates decline as photorespiration increases.

C-4 to the Rescue

The decrease in photosynthetic efficiency caused by low CO_2 and high O_2 has been addressed in some semitropical plants that normally grow under high temperatures. These plants have evolved a separate CO_2 trapping and transport mechanism by which they can concentrate CO_2 in special cells to levels more than ten times that normally available to RubisCO. They do this by initially fixing CO_2 into a four-carbon acid, according to the following reaction catalyzed by the enzyme phosphoenolpyruvate carboxylase (PEPcase):

Under high temperatures, photosynthetic rates decline as photorespiration increases.

PEP + HCO_3- > OAA

Here a three-carbon acid, phosphoenolpyruvic acid (PEP), reacts with a bicarbonate ion and produces a four-carbon acid, oxaloacetic acid (OAA). In water, bicarbonate ion is in equilibrium with atmospheric CO_2 according to the reaction:

$CO_2 + H_2O <> H_2CO_3 <> HCO_3- + H+$

The equilibrium between CO_2 and HCO_3- is such that, in the sap of leaf cells during photosynthesis, HCO_3- is 50 times more concentrated than CO_2. Since PEPcase fixes the more abundant HCO_3- rather than CO_2, its reaction rate is much greater than that of RubisCO which can only react with CO_2, not HCO_3-. In addition, PEPcase does not react with O_2, so there is no photorespiration to decrease carbon fixation.

Once carbon is incorporated into a C-4 organic acid, that acid is transported into bundle sheath cells which surround the vascular bundles of the leaf (Fig. 1). In these bundle sheath cells, the C-4 acid is decarboxylated to form a three-carbon acid and a CO_2. The CO_2 accumulates in these specialized cells to levels 10 times higher than that normally available for photosynthesis. The elevated CO_2 levels in the bundle sheath cells allows RubisCO to fix carbon efficiently; operating at near maximum rates with much less competition from O_2 so little or no photorespiration occurs. The preliminary trap and transport of CO_2 in C-4 plants allows them to maintain high photosynthetic rates at temperatures that

would inhibit photosynthesis in C-3 plants.

You probably are familiar with many C-4 plants. These include the weeds that grow vigorously during the heat of summer when cool-season turfgrasses are barely hanging on. Crabgrass, nutsedge, fall panicum, purslan, and spotted spurge are all C-4 plants. They are highly competitive with turfgrasses during the summer because of the advantage C-4 photosynthesis gives them over C-3 plants. Warm-season turfgrasses are also C-4 plants and they do not experience summer decline because of more efficient photosynthesis.

Root Starvation

The initial impact of high temperatures on cool-season turfgrasses is less photosynthesis due to increased rates of photorespiration. With less photosynthetic product, there are fewer sugars available for translocation to the roots. The relationship between photosynthetic efficiency and root activity was described in an earlier *TurfGrass Trends* article (Hull 1996) on managing turf for optimum growth of roots. When roots are deprived of sugars, their growth rate slows and this limits their ability to seek water and nutrients. This, however, is just the beginning of root decline.

Unlike drought stress, which occurs progressively as the soil column dries, heat stress can come on suddenly and create a lethal condition before the grass can respond to it.

Turfgrass shoots do not experience high temperatures without the soil also becoming warm. Elevated soil temperatures cause root respiration to increase and this speeds the rate of sugar consumption in roots. This respiratory increase is not photorespiration, but normal oxidative respiration that burns sugars to produce the energy needed by roots to support their growth and function.

However, by the time root respiration is stimulated by soil heating, high shoot temperatures have already stimulated photorespiration in leaves and reduced the flow of sugars to the roots. Thus, roots find themselves consuming sugars more rapidly, while their supply is curtailed. If this condition persists for more than a day or two, root starvation will occur and death soon follows.

Even in humid climates, the death of shallow roots causes a release of organic mucilage into the soil that binds with water and fills pore spaces retarding water percolation through the soil (Carrow 1996). The retention of water in the soil reduces the O_2 levels on which roots depend for their respiration and metabolism. Anaerobic soil conditions further stress roots. Soon, the entire root system is sick or dying, and water transport to shoots is seriously impeded.

During hot weather, reduced transpiration caused by a failing root system allows leaves to overheat and direct thermal injury can occur. If all this happens rapidly, grasses will not have the time or energy necessary to go into summer dormancy, and turf death will result.

Unlike drought stress, which occurs progressively as the soil column dries, heat stress can come on suddenly and create a lethal condition before the grass can respond to it. A gradual heating of cool-season turfgrasses gives the grass time to acclimate to the stress and become slightly more tolerant of high temperatures (DiPaola and Beard 1992). Thus, rapid summer decline is most likely to occur during hot spells of late spring and early summer. If grass is already under stress from disease, wear, salinity, etc. when high temperatures occur, death may result even more rapidly.

High temperature is no stranger to grasses growing in full sun. Most of our turfgrasses evolved under just such conditions. Under normal circumstances, however, grasses progress from a vegetative into a reproductive phase during early summer. With this progression heat tolerance increases (Larcher 1995).

In turf management, grasses are generally not permitted to enter a reproductive phase since elongating culms are normally mowed before flowering can occur. Retention of grasses in a vegetative state keeps

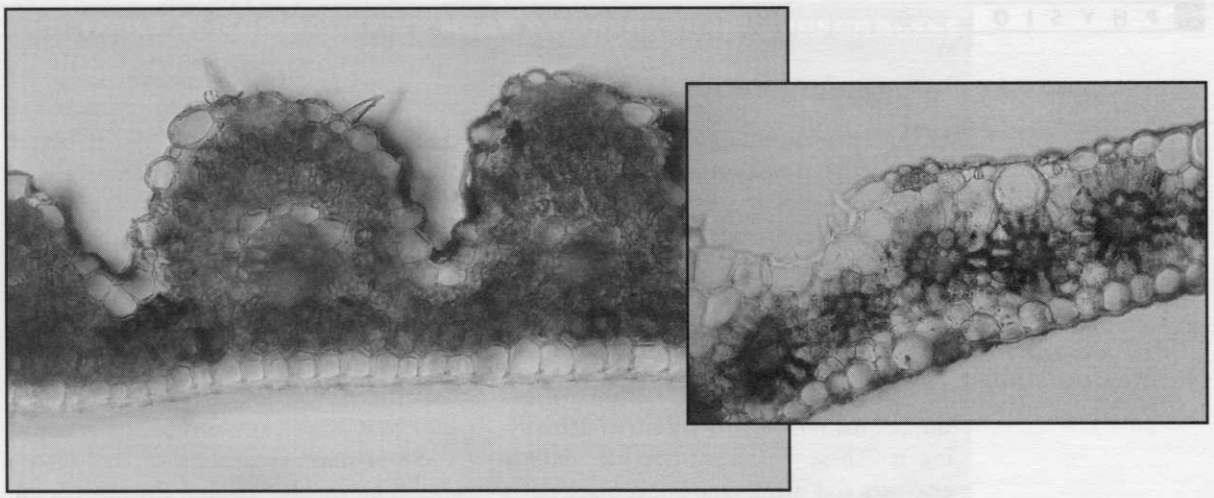

Figure. 1. Leaf structure of a C-3 plant, Kentucky bluegrass (top), and a C-4 plant, smooth crabgrass (right). In Kentucky bluegrass, note the large number of poorly organized green mesophyll cells adjacent to the large bundle of sheath cells surrounding the vascular bundles. In smooth crabgrass, note the dark bundle sheath cells and the small number of light green mesophyll cells. In C-4 plants, CO_2 is initially fixed in the outer mesophyll cells and transported as a four-carbon acid into bundle sheath cells where CO_2 is released and concentrated for fixation by RubisCO.

them more vulnerable to heat injury during the hottest times of the year, which would not be the case under natural conditions.

Oxygen Radicals and Membrane Peroxidation

The actual destruction of turfgrass shoots by high temperatures is complex, but, except in rare circumstances, is probably not due to thermal denaturation of proteins that occurs when temperatures exceed 120 degrees F. Such temperatures can occur when transpirational cooling is inhibited and kill exposed leaves. But they are not likely to affect entire shoots in a turf sod. Toxic O_2 radicals are a more likely cause of high temperature induced death.

During photosynthesis, light energy causes the formation of numerous short-lived electron transport intermediates.

When CO_2 is being reduced to carbohydrates, it constitutes a natural sink for these electrons, and their carriers cycle back to pick up additional electrons to keep photosynthesis going. However, if high temperatures cause a shortage of CO_2 or promote stomates to close and prevent gas exchange between leaf and atmosphere, these electron carriers will accumulate and reduce other substances such as O_2.

$$O_2 + e\text{—}\ Carrier > O_2\bullet^- + Carrier$$

The first O_2 radical formed is superoxide ($O_2\bullet^-$), which can readily reduce metal ions present in the cell such as ferric iron (Fe^{3+}) or cupric copper (Cu^{2+}).

$$O_2\bullet^- + Fe^{3+} > O_2 + Fe^{2+}$$

These reduced metal ions along with superoxide can damage sensitive enzymes and membranes, so most plants make an enzyme specifically designed to destroy superoxide: superoxide dismutase (SOD). Here, two superoxide ions interact and redistribute electrons:

$$2O_2\bullet^- + 2H+ > O_2 + H_2O_2$$

One is oxidized back to O_2 while the other is reduced to a peroxide ion (O_2^{2-}) which combines with two H+s to form a hydrogen peroxide (H_2O_2) molecule. Normally, the H_2O_2 is degraded to two water molecules by a peroxidase enzyme that is closely associated with the photosynthetic machinery. However, if the normal flow of reducing power (electrons) to CO_2 is impaired,

H_2O_2 is produced in greater amounts and will react with reduced metal ions to form hydroxide radicals (•OH). These are among the most destructive substances known to biology.

$$H_2O_2 + Fe^{2+} > OH^- + {\bullet}OH + Fe^{3+}$$

Not only is •OH highly destructive, but the cell has no effective means of detoxifying it. These •OH radicals can oxidize enzymes and membrane lipids, inactivating them and, in the case of membranes, making them leaky.

These reactions occur most readily in the chloroplasts of green leaf cells because that is where photosynthetic reactions are concentrated and where light energy is converted to chemical energy. However, the sites of respiratory oxidation (mitochondria) are also places where O_2 radicals will form and can be destructive, especially under conditions promoted by high temperatures. The plasma membrane, which encloses the protoplast of every cell, contains many lipids and these can be oxidized by O_2 radicals changing their properties, disrupting uptake processes and even the integrity of the membranes.

The significance of these reactions to heat injury in turfgrasses has been supported by recent research from Kansas State University (Liu and Huang 1998). Dr. Jun Huang's group has demonstrated a nice correlation between heat injury to creeping bentgrass and a decline in the $O_2{\bullet}^-$ degrading enzyme (SOD) and an increase in lipid peroxidation accompanied by greater cellular leakage.

What Can a Turf Manager Do?

All this chemistry and recent research does not paint a very encouraging picture for the turf manager. The basic vulnerability of cool-season grasses to heat stress is inherent to their photosynthetic physiology. High temperatures will cause a decline in photosynthesis and the follow-up destructive events will occur with very little the turf manager can do to prevent them. The prospects for improvement on the genetic front are not much better. While cultivars of several turfgrasses have been identified that exhibit greater resistance to heat stress, the differences are not great and the mechanisms behind their heat resistance have not been well defined, although they are being studied. In short, there is little likelihood that any cool-season turfgrass will be developed that can tolerate heat as well as warm-season grasses.

So is summer decline of cool-season grasses inevitable? Yes, but the process can be avoided or at least delayed by proper turf management. Some suggestions proposed over the years follows:

Prevent Heating — Since the primary stress involves leaf heating and the resulting decline in photosynthetic output, managing turf to prevent heating would be the most direct strategy. Transpiration is the natural way plants prevent overheating, so managing grass to encourage transpiration would seem reasonable.

Maintaining adequate, but not excessive, moisture levels would be a good start. Managing for maximum root growth will also help turf to obtain water and tolerate some root injury near the soil surface. Encourage good air flow over the turf. That will reduce humidity and increase transpirational cooling.

Thinning thick vegetation and installing fans may be necessary. Syringing just before the hottest time of the day will help reduce leaf temperatures in dry climates, but may have little benefit when humidity is high. Increasing the mowing height will give the turf more leaf surface and increase photosynthetic production. It will also provide more shading and insulation of the soil surface and delay root zone heating.

Reduce Nitrogen Fertilization — Fertilization can be adjusted to maximize heat tolerance. Reduce nitrogen to maintenance levels so shoot growth will not be stimulated at the expense of root growth. This needs to be initiated before hot weather arrives and will probably require the use of slow-release materials. This nitrogen effect has been clearly demonstrated under controlled environments

TABLE 2. COMPARATIVE HEAT RESISTANCE OF TURFGRASSES

Heat Resistance Rating	Turfgrasses
Excellent	Bermudagrass, buffalograss Seashore paspalum, Zoysiagrass
Good	St. Augustine grass, centipedegrass Medium Tall fescue, hard fescue, Kentucky bluegrass
Fair	Chewings fescue, red fescue, sheep fescue, perennial ryegrass
Poor	Creeping bentgrass, colonial bentgrass, redtop, Canada bluegrass
Very poor	Annual bluegrass, annual ryegrass, rough bluegrass

FROM BEARD 1997

(greenhouses and growth chambers), but frankly, field results have been less consistent. However, the depressing effect of high nitrogen on root growth is likely and should be avoided when any summer stress is anticipated.

Beard (1997) favors higher potassium availability during the hot season. This makes sense because potassium controls stomate function and helps stabilize plant water status. Essentially, turf should enter the hottest time of the year under balanced nutrition that does not stimulate excess shoot growth.

Plant Right Species and Cultivars — Species and cultivar selection for heat resistance should be considered when new construction or renovation is planned. Beard (1997) has ranked turfgrasses according to their heat resistance (Table 2). Naturally, the warm-season grasses are best, but among the cool-season options, tall fescue, hard fescue and Kentucky bluegrass are generally most heat resistant. Annual ryegrass, annual bluegrass and rough bluegrass are among the least heat tolerant turfgrasses. Unfortunately, all the bentgrasses exhibit little heat resistance which gives you few options for greens and tees. However, cultivar differences in heat resistance have been identified so even here, some choices are available.

Delay Aerification — Cultivation can be scheduled to minimize summer decline. On sand greens, Carrow (1996) emphasizes the importance of maintaining proper infiltration of water and air. The plugging of soil pores during the death of shallow roots can seriously aggravate a heat stress problem. Aerification with light top-dressing prior to the onset of summer heat will likely be helpful. Continued cultivation during the summer is also encouraged (Carrow 1996), but reduce top-dressing and minimize abrasion, since leaves are more subject to mechanical injury during heat stress.

The new technology for forcing air through putting greens by utilizing drainage tiles will probably have value for reducing heat associated stresses (Dodd et al. 1999). Although this approach to managing heat stress on greens has not yet been critically tested, it offers promise for alleviating several adverse conditions that are known to contribute toward heat injury.

While the prospects for dramatic advances in managing summer decline in cool-season turf are not encouraging, the situation is anything but hopeless. Thoughtful and conscientious turf management clearly is the answer. I hope this overview of the physiological causes of summer heat injury will contribute to your understanding of the problem and will be useful in helping you refine and improve your summer turf management strategy.

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