PHYSIOLOGY

Back to Basics How Turfgrasses Grow

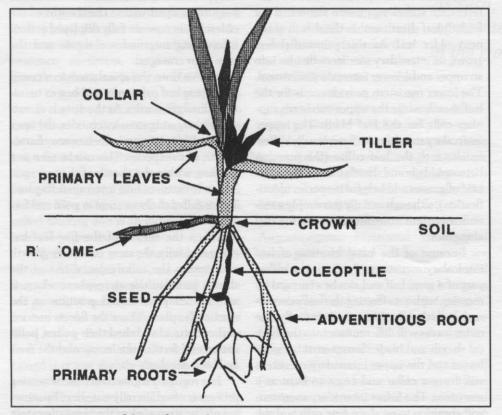
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Turf managers see their grassed areas grow and respond by mowing. They observe some grasses flower in the spring. They note the recovery of divots and other mechanical injuries.

While they would be concerned if these manifestations of turfgrass growth failed to occur (maybe not the flowering), most managers give little thought as to exactly what grass growth entails. This ambivalence toward the growth process can be disastrous because the developmental characteristics of grasses place rather strict limitations on how these plants can be manipulated. This short discussion will try to review the process of turfgrass growth. Leaf initiation and Growth: As in most seed producing plants, all primary leaves originate from a terminal meristem. When a grass caryopsis (dry fruit enclosing a single seed) germinates, the first organ to appear is the primary root called a radicle that, following gravitational cues, grows downward into the soil.

Shortly thereafter, the embryonic shoot emerges and, true to its antigravitational instructions, grows upward to where light should be found. The elongating shoot meristem and first leaf are protected as they pass through the soil by a closed sheath termed a coleoptile.

When the coleoptile breaks the soil surface and perceives light, it soon stops growing and its tip is ruptured by the first leaf



Growth structures of the turfgrass plant.

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which elongates and expands into the light. At the same time, the stem ceases elongating and the shoot apical meri-stem is positioned at, just above or just below the soil surface, depending on the grass species. At a predetermined distance behind the shoot meristem, a node develops in the embryon-

In a regularly mowed turf, the flowering process is cut short by mowing off the stem apex above the mower height, thus preventing all further

growth of that stem.

ic stem from which adventitious roots emerge. These will develop into the permanent root system.

Once the first leaf has emerged into the light, the apical meristem continues to differentiate nodes consisting of a leaf primordium that expands laterally and develops into a cowl-like, sheathing leaf. Just above the center of this sheathing leaf a bud develops. The leaves elongate as a roll enclosed within the first leaf sheath.

Leaf growth occurs from a basal intercalary meristem that produces cells that differentiate and elongate into the rolled (or folded) leaf sheath within the sheath of the next older leaf. As this primordial leaf grows, its intercalary meristem divides into an upper and a lower intercalary meristem. The lower meristem provides cells for the leaf sheath while the upper meristem supplies cells for the leaf blade. The upper intercalary meristem will eventually differentiate into the leaf collar (the junction between blade and sheath that is characteristic of grasses and helpful in species identification), although initially it is simply a second meristem contributing cells for leaf elongation.

Because of the basal location of leaf intercalary meristems, the tip is the oldest part of a grass leaf and can be removed by mowing without affecting the leaf's continued growth (elongation). Eventually the outer leaves will differentiate into the typical sheath and blade characteristic of grass leaves and the upper intercalary meristem will form a collar and cease to exist as a meristem. The lower intercalary meristem will continue to produce new cells and the leaf sheath might continue elongating for a while.

Inner leaves will not form a collar and their intercalary meristems continue producing cells that elongate and allow these leaves to maintain their growth within the sheaths of older leaves. This constitutes the vegetative phase of shoot growth in grasses. It is the growth desired by a turf manager because it produces the most uniformly textured turf.

Flower induction and stem elongation: For many turfgrasses, a cold period or the seasonal changes in day length (photoperiod) trigger the induction of reproductive growth: flowering. This initiates a profound change in the growth of a grass plant. Stem elongation, that had stopped when the seedling coleoptile emerged into the light, now resumes. Intercalary meristems at the base of each node produce cells that elongate and lift the apical meristem above the soil line eventually to assume a position at the apex of the plant. The leaves which had been telescoped within the sheaths of the oldest leaves now are fully displayed as their intervening internodes elongate and the true stem emerges.

At this time, the apical meristem ceases producing leaf primordia and begins to initiate floral primordia. As the apex is elevated by elongating stem internodes, the apex differentiates into an inflorescence characteristic of the species. This can be seen as a swelling within the sheath of the youngest leaf as it matures into a terminal flag leaf. This is called the boot stage in grain and forage grasses.

When the sheath of the flag leaf has elongated fully, the stem continues growth and pushes the inflorescence out of the sheath and into the atmosphere where it assumes its preordained position at the apex of the plant. There the florets mature, anthers extend and shed their pollen, pollination and fertilization occur and the fruit and seed develop.

In a regularly mowed turf, the flowering process is often literally cut short by mowing off the stem apex as the elongating stem lifts it above the mower height. Removing the apical meristem, and the developing leaves enclosed within the sheaths of older leaves, prevents all further growth of that stem.

Annual bluegrass, and some cultivars of Kentucky bluegrass, when maintained as a mowed turf, do not experience much stem internode elongation so the apical meristem and developing inflorescence are not removed by mowing until the inflorescence has fully emerged. This is why unsightly inflorescences (erroneously called seed heads) are often observed in turf containing these grasses during the flowering season.

Some weedy grasses, which assume a prostrate growth habit in turf, are able to develop inflorescences and produce mature seed because these organs remain below the mowing height. Crabgrass and goosegrass are notorious for this and are serious weeds, in part, because they have an extended flowering season which produces objectionable inflorescences throughout much of the summer.

Flowering triggers the death of a grass stem: A second undesirable feature of grass flowering is that it ends the life of a grass stem (culm). Because the apical vegetative meristem has become a reproductive inflorescence meristem, further vegetative growth of the stem is impossible even if it were not decapitated by mowing. This means that the grass stem will produce no new leaves and is destined to die. Such a developmental sequence would be disastrous for turf maintenance were it not for the plant's capacity to generate new stems from buds present at the base of young shoots. This initiation of basal shoots is called tillering and is an indispensable feature of turfgrasses.

When a young grass plant (seedling) initiates its fifth leaf, it has stored enough photosynthetic energy (carbohydrates) to initiate growth of axillary buds. These buds are located at the nodes inside the sheaths of basal leaves. Because the stem internodes have not elongated, these nodes are maintained at or just slightly above the soil level, protected from mowing injury.

Basal bud growth initially occurs within the enclosing sheath of the subtending leaf

and does not break free until its elongating leaves rise above the level of the collar (intravaginal tillering). Because each primary leaf contains an axillary bud at the base of its sheath and these buds are all concentrated at the base of the stem, several tillers can emerge before the parent stem is induced to flower. When flower induction does occur, the internodes between nodes, from which tillers have emerged, are not stimulated to elongate so the tillers are not lifted from the soil during elongation of the parent culm. In fact the tillers become pretty much autonomous of their parent culm producing their own adventitious roots. They fail to senesce when the parent culm flowers and undergoes senescence.

Tillers can remain vegetative and not flower until the following growing season.

As such, they serve as overwintering portions of the grass crown. In this way, an extensive crown re-gion composed of numerous tillers and culm bases constitutes the truly perennial portion of a turfgrass plant.

Rhizomes and stolons: Early in the life of some turfgrass plants, buds enclosed by the sheaths of the oldest leaves will resume growth. However, instead of growing

upright to form tillers, they assume a horizontal growth habit. In Kentucky bluegrass, creeping red fescue and bahiagrass, these horizontal shoots break through the sheath of the subtending leaf (extravaginal growth) and produce underground stems called rhizomes. In creeping bentgrass, velvet bentgrass, rough bluegrass, buffalograss and St. Augustinegrass, horizontal extravaginal stems grow along the soil surface and are called stolons. Some grasses, such as colonial bentgrass, bermudagrass, Japanese lawngrass (zoysiagrass) and seashore paspalum, produce both rhizomes and stolons. All of these turfgrasses form a dense sod and are referred to as spreading or creeping.

By comparison, perennial ryegrass, tall fescue, chewings fescue and some colonial bentgrass cultivars produce no horizontal basal shoots and are known as bunch-type

Tillers can remain vegetative and not flower until the following growing season. As such, they serve as overwintering portions of the grass crown. grasses. These grasses depend on seeding rate to produce a thick turf and do not recover from mechanical injury as rapidly as the rhizomatous or stoloniferous grasses.

Rhizomes and stolons differ from tillers, not only in their direction of growth, but in the fact that they grow entirely as a result of stem elongation. Their apical meristem is covered by several layers of scale leaves and

Rhizomes and stolons differ from tillers, not only in their direction of growth, but in the fact that they grow entirely as a result of stem elongation. is thereby protected as it pushes through the soil or along the soil surface. The meristem produces nodes, each with a leaf primordium, bud and internodes, which elongate.

As a result, the horizontal stem differentiates into reasonably distinct nodes and internodes. At each node, the axillary bud is covered by a scale leaf. Nodes also produce adventitious roots and these

extend the plant's root system to encompass a larger volume of soil.

Depending on the grass species and on environmental conditions, the tip of horizontal stems will turn upward and produce a new terminal shoot at some distance from the parent plant. When the tip turns upward, internodal elongation stops and the shoot that develops is like any other young grass plant; consisting mostly of telescoped leaf sheaths that overtop the shoot apex. The length of rhizomes and stolons varies with the species and environmental conditions.

The intervening axillary buds will probably not form shoots unless the apical meristem of the rhizome or stolon is injured, or the soil in which the horizontal stem is growing is largely free of other plants. Under such conditions, several shoots or branches can emerge from axillary buds along the horizontal stem.

In a dense sod, rhizome and stolon growth is limited. But, where bare soil is available, the growth of these horizontal stems is stimulated. In this way, turfgrasses that produce stolons or rhizomes can quickly invade disturbed sites and repair turf injury.

I have not been able to determine exactly what environmental or internal stimulus promotes horizontal stem initiation, but I suspect it has something to do with the plant's energy status. In cool-season grasses, rhizome and stolon growth occurs mostly in the spring and fall. Those are the times when such grasses experience their most favorable energy status. Even during the summer, grasses at the margins of turf areas will receive more solar radiation and are more likely to produce rhizomes or stolons.

Warm-season grasses experience their most favorable energy status during the summer. Their lack of photorespiration makes these grasses more photosynthetically efficient during the high light and elevated temperatures of summer. It is then that maximum rhizome or stolon growth occurs. Photoperiod and day/night temperature range might influence horizontal stem initiation, but I would bet on plant energy status being the primary trigger. Rhizomes are normally shorter and their apical bud turns upward to produce a new shoot closer to the parent plant in the fall than in the spring. This may be environmentally controlled.

Growth responses to adverse climates: Cold, heat and drought are climatic variables that will influence turfgrass growth. Cool-season grasses are generally stimulated to grow more vigorously when temperatures are cool and moisture is abundant. By contrast, warm-season grasses normally grow best under hot temperatures and adequate but not excessive water supplies.

As mentioned above, favorable growth conditions often stimulate tillering and horizontal stem growth in species that have the capacity for such growth. When the temperature drops to near freezing or below, warm-season grasses cease shoot growth and root growth is largely curtailed. These grasses essentially go dormant and will not resume growth until an extended period of warm weather is encountered.

Cool-season grasses do not go dormant under cold temperatures. Photosynthetic

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activity continues and nutrient absorption by roots persists at respectable rates. Aerial shoot growth (leaf elongation) pretty much stops, but rhizomes might continue to grow, if slowly. Root growth and cell divisions in root meristems have been observed in the heart of winter. In short, cool-season grasses continue growing under cold temperatures at a reduced rate. They do not become dormant and will resume growth quickly when temperatures warm.

Drought affects all turfgrasses in a similar way. The first response is a slowing of growth, although shoots are more affected than are roots. This reduces transpiration rates and helps conserve soil moisture. If dry conditions continue, growth stops altogether. Under high-light conditions, most grasses will suffer leaf damage and turn yellow or brown. An induced growth cessation occurs, which cannot be regarded as a true dormancy. When moisture is restored, most turfgrasses quickly resume growth and recovery can be rapid and complete.

Because warm-season grasses are more efficient users of water, under drought conditions they are able to divert carbohydrates to roots and stimulate deeper root penetration into the soil, thereby tapping a larger water supply. In this way, they can forestall serious drought injury. However, once subjected to drought, warm-season grasses are likely to sustain more injury than cool-season grasses.

Cool-season grasses have fewer energy reserves during periods of summer drought, which limits their capacity to avoid moisture stress through the stimulation of deeper root growth.Consequently, they may exhibit drought stress more quickly than warm-season grasses. However, cool-season grasses appear to be better able to recover from periods of prolonged drought than warm-season grasses. Soil conditions (depth, moisture holding capacity and aeration) will, of course, influence the timing and extent of grass responses to drought.

Root growth has been discussed above in the context of development and environmental conditions. In an earlier Back-To-Basics article, I concentrated on seasonal root growth as it influences nutrient absorption. It would be approriate to point out that seedling grasses develop two root systems, primary (seminal) roots that emerge from the seed (embryo) and adventitious roots that emerge from the coleoptile node which develops when the coleoptile breaks through the soil and experiences light.

The primary roots develop largely from seed reserves and also from current photosynthesis of the seedling. However, their growth is limited and their function is primarily to establish water contact between seedling and soil. Nutrient uptake will also occur but this function is soon taken over by the more rapidly developing adventitious root system. The primary roots may survive and make modest contribu-

tions to the plant during the first year but not thereafter. In some species, primary roots disintegrate within a month or two.

Adventitious roots emerge from the coleoptilar node and establish the base of the crown. This is set at the same depth within the soil regardless of how deeply the seed was planted. Because several adventitious roots normally emerge from the coleoptile node, and these branch freely, the grass root system always

has a fibrous structure. Tiller bases produce additional adventitious roots, as do the nodes of horizontal stems, and these benefit the grass by extending its reach into unexplored soil.

This capacity for rapid root generation also allows grasses to reestablish a root system following stress induced root death or feeding by soil insects. Because such events are not uncommon during most growing seasons, cool-season turfgrasses often must regrow much of their root system during late summer and early fall. Warm-season grasses are able to support more rapid root growth during the summer and, therefore, enter the fall season with a more-or-less intact root system.

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Cool-season grasses appear to be most resilient to periods of prolonged drought. Warm-season grasses can sustain more injury than cool-season but normally will also recover.

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nutrient use efficiency and photosynthate partitioning in turfgrasses and woody ornamentals.

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Refining Turf Management Practices

Understanding the patterns and timing of turfgrass growth can help refine turf management practices. Some ideas that emerge from the above discussion are listed below.

1. Because of their capacity to expand by horizontal stem growth, rhizometous and stoloniferous grasses need not be seeded as heavily as bunch-type grasses.

2. The ability to repair mechanical damage to turf makes the inclusion of sodforming grasses in any turf seed mix a sound practice.

3. Because flowering and inflorescence production detract from turf uniformity and the flowering culms will die and introduce dead stems into the turf, selecting cultivars that are less likely to flower under turf management conditions would be desirable. Careful use of plant growth regulators can minimize this problem.

4. Close mowing or drastic changes in mowing height should be avoided because the apical meristem of grass shoots is near the soil surface and will tend to be elevated and damaged by mowing when grasses are allowed to grow too much between mowings.

5. Tillering of turfgrasses contributes to stand density and is encouraged by mowing but not by removing so much leaf tissue that insufficient energy is available to support tiller initiation and development.

6. Because root loss during the summer is to be expected in cool-season grasses, it is wise to raise the mowing height during summer to provide the photosynthetic products needed for adventitious root regeneration.

7. Turfgrasses respond to drought conditions by allocating more energy for root system expansion. Therefore, it is best to reduce mowing frequency during midsummer and allow more leaf surface to capture additional energy.

8. Because cool-season turfgrasses continue photosynthetic activity during the winter and root growth depends upon energy captured at that time, it is important to remove tree leaves promptly and avoid any unnecessary winter shading of the turf.

9. Turf growing in shaded locations will have less photosynthetic energy to support tillering and horizontal stem growth, so close mowing should be avoided.

10. Turf recovery from mechanical injury depends on tiller, rhizome and stolon growth which relies on photosynthetic energy. Such turf should be mowed as high as is compatible with its use and should be protected from shading even for short periods of time.

