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ROOT DISTRIBUTION OF CREEPING BENTGRASS AND ANNUAL BLUEGRASS ON GOLF COURSE PUTTING GREENS

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ABSTRACT

Creeping bentgrass and annual bluegrass have very different growth habits and survival strategies when found on golf greens. Annual bluegrass invasion into creeping bentgrass golf greens is a prolific problem facing the turfgrass industry today. I compare tiller density and shoot and root growth of Penncross and Penn A-4 cultivars of creeping bentgrass and experimental cultivars of annual bluegrass exposed to various nitrogen management treatments. Finally, response of creeping bentgrass to spatial phosphorus supply in split root experiments and using an alumina bound phosphorus source is also studied.

Three experimental cultivars of annual bluegrass, ‘PSU-97-1’, ‘PSU-97-2’, ‘PSU-97-3’ and two cultivars of creeping bentgrass, ‘Penncross’ and ‘Penn A-4’, were planted on an experimental golf green at Penn State University. Two different nitrogen rates (approximately 130 kg N ha^{-1} year $^{-1}$ and 390 kg N ha^{-1} year $^{-1}$) were applied and tiller densities and root mass at different soil depths were measured for two growing seasons.

The creeping bentgrass cultivars had more root mass, approximately 2.5 times the root mass at the 0-3 cm depth, than the annual bluegrass cultivars throughout the duration of the experiment. In the two deeper soil fractions, 3-12 cm and below 12 cm, creeping bentgrass had greater than 4 times the total root mass than annual bluegrass. In the first year, there was over a 50% decrease in the amount of roots present at all depths for both species from the June to the late summer harvest dates. The root mass did not recover until after the September harvest date. In the second year, the decrease in root mass was

less severe, approximately a 10-15% reduction for creeping bentgrass cultivars and a 25-30% decrease for annual bluegrass and this was only observed in total root mass and in root mass at the 0-3 cm depth. Both Penn A-4 and Penncross had equivalent total root mass and root mass at the more shallow depths of the root zone. Conversely, Penn A-4 had greater root mass than Penncross below 12 cm of depth. Penn A-4 also had greater tiller densities than Penncross throughout the experiment. Generally the annual bluegrass cultivars had greater tiller densities than the creeping bentgrass cultivars, with the exception of the last two harvests dates in 2002, where Penn-A4 had equivalent tiller densities to the annual bluegrass cultivars.

The effects of the nitrogen treatment varied in the two years of the experiment. In 2001, the creeping bentgrass cultivars showed increased root mass below 12 cm at the low nitrogen rate when compared to the high nitrogen rate. The annual bluegrass showed no change in root mass in response to nitrogen rates. In 2002 however, creeping bentgrass showed no response to nitrogen rate while the annual bluegrass showed increased root mass in the top 3 cm of the root zone at the high compared to the low nitrogen rate. Tiller densities increased with high nitrogen rates in both species. Specific root length of creeping bentgrass was similar at the two nitrogen rates while that of annual bluegrass increased in response to the low compared to the high nitrogen rate.

Preliminary experiments showed that alumina bound phosphorus could be used as the sole source of phosphorus for creeping bentgrass and annual bluegrass establishment and growth. In all three spatial phosphorus supply experiments, creeping bentgrass exhibited increased root mass in the areas of the root zone where phosphorus was present compared to the areas where phosphorus was absent. The use of an alumina bound

phosphors buffer (Al-P) was shown to increase root-to-shoot ratios of creeping bentgrass 1.5 to 3 times more than traditional fertilizers and nutrient solutions. It also resulted in higher root masses below 15 cm than the observed in control treatments. When the Al-P was mixed throughout the root zone some increase in deep root (below 15 cm) mass was observed (approximately a 65% increase over the control). However, when the Al-P was mixed only in the bottom 10 cm of the root zone the amount of root mass below 15 cm increased even more (approximately a 100% increase).

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Chapter 1

Creeping bentgrass and annual bluegrass

Generally, turfgrasses are found anywhere humans are found because they are believed to be the evolutionary product of highly grazed systems. Most turfgrasses are native to the eastern hemisphere, although one species (buffalograss, *Buchloe dactyloides* Nutt.) did evolve in North America (Beard, 1973). Human use of turfgrasses can be traced to biblical times when turfgrass was used for lawn gardens. Today, turfgrass is found on home lawns where it is used as an area for play and home recreation. It provides economical, year round soil stabilization along roadsides and airfields without inhibiting the sight line of drivers (Beard and Green, 1994). Turfgrass is found in our parks and around schools where it provides an area to play and gather. Industrial parks, large businesses, and hospitals use turfgrass to create large lawns and natural areas that have been shown to relax and relieve stress, and aid in recovery of patients (Ulrich, 1984; Ulrich, 1986). Churches and cemeteries use turfgrass to allow for movement around the grounds, minimizing the presences of mud and water puddles. It is also used to stabilize soils on nature and fitness trails minimizing the impact of recreational use of our natural areas. Finally, turfgrass is used as athletic playing surfaces in many sports including golf, field hockey, football, soccer, and even horse racing. Thirteenth century literature refers to the use of turf in the sport of lawn bowling and an early form of cricket called club-ball. The use of turfgrass in sports such as lawn bowling, cricket, golf and soccer was important in the development of modern, high quality turfgrass species and cultivars (Beard, 1973).

Although most turfgrass areas are on home lawns and roadsides, golf is a major contributor to the turfgrass industry because turfgrasses occupy most of the playing surface for golf. The industry not only consists of the turf seed sales, but fertilizers, pesticides, and the large industry involved in developing mowers and other turf maintenance equipment. The last comprehensive turfgrass survey conducted in Pennsylvania in 1989 determined that the turfgrass industry was worth more than \$800,000 annually (Evans and Knopf, 1989) and it has expanded rapidly since that time. Another important aspect of the industry is the increase in tourism that golf courses provide. Turfgrasses are economically important for many reasons but primarily because they are used in all aspects of human life such as recreation, soil stabilization to protect the environment, and keeping our roadways safe.

The turfgrass industry is a rapidly growing sector of the urban landscape. The expansion of urban development and the resulting increase in roads has expanded the need for soil stabilization. The turfgrass industry is expanding for many other reasons. The realization that artificial playing surfaces may cause an increase in sports-related injuries has returned turfgrasses to many athletic fields from high school athletics to professional sports. The largest change in the turfgrass industry is probably the large boom in the popularity of golf. As a result, turfgrass is a multi-billion dollar industry. In fact, annual turfgrass seed sales are second only to corn in the United States and rank above soybeans and wheat combined (Kidd, 1993).

Golf is a sport in which clubs are used to hit a small ball into a hole, or cup. A typical golf course consists of 18 holes each with four distinct areas: the tee, the fairway, the rough, and the putting green or green (Beard, 2002). The typical golf cup is located on a green 100-600 yards from the tee, the starting area. The tee is typically elevated and mowed at 7 to 15 mm three times a week, while the fairway, the area between the tee and green, is mowed at 15 to 25 mm (Beard, 2002). Both areas are usually irrigated and fertilized regularly. The rough surrounds the playing areas and typically consists of turf mowed at 50-100 mm, although it can be unmowed turf, shrubs, or wooded areas, and is generally not irrigated or fertilized (Beard, 2002). The green is the most highly cultured area of a golf course. The cup is a hole cut out of the turf that acts as the final receptacle for the ball. The green is mowed between 2 to 5 mm and is kept well watered. Greens on older courses typically consist of native soil pushed up to form a level surface. Newer greens are constructed of sand and gravel and engineered to resist compaction and provide adequate drainage (Beard, 2002). The low mowing heights are maintained because the ball is putted on the golf green (Dernoeden, 2000). Putting is the act of gently striking the ball with a flat edged club to roll the ball along the surface of the grass into the cup. The competitive nature of the sport of golf makes a high quality turf important throughout the course, but essential on the golf green where making a two-meter putt into the cup may be worth over one million dollars.

Turf can be defined as an ecological community of plants, soil, and microbes that form a dense perennial coverage when subjected to grazing or mowing (Turgeon, 1991). Most often, grasses comprise the plant component of a turf system because of their adaptation to close mowing and high traffic. There are approximately 32 grass species that can form turf, but only 16-18 species are commercially available (Beard, 2002). Unlike agronomically grown grain crops, where yield and quality are easily defined, turfgrass quality is not as readily definable. Turfgrass quality is a difficult term to define because it is dependent on the intended use of the turfgrass. It is also dependent on the cultural practices applied to the grass, such as irrigation, fertilization and mowing. Turfgrass quality can be broken down into its component parts: uniformity, density, texture, growth habit, and color. The use of the turfgrass determines relative importance of these components (Beard, 1973). The following definitions of the components of turf quality are currently used in the turf industry.

> *Uniformity* – Uniformity refers to the ability of a turfgrass to provide consistent coverage without the invasion of weeds, disease, or the presence of bare spots. It can also refer to uniformity of the other aspects of turf quality throughout the plot.
>
> *Density* – Turfgrass density is the number of tillers that are found in a given area. It determines the ability of a turfgrass to provide adequate soil stabilization and traction.
>
> *Texture* – Texture refers to the width of the leaf blades. Texture can vary with plant density and affects uniformity of the turf. Wide leaf blades are referred to as having a rough texture and therefore generally lower quality.

Growth habit – The quality of turfgrasses used for athletic fields can be affected by the positioning of the turfgrass leaves, referred to as the growth habit (Beard, 1973). The growth habit can either be upright or prostrate. Prostrate growth habit is the positioning of the leaves horizontally along the ground. While a prostrate growth habit allows for lower mowing heights it also creates a grain, from shoots growing predominately in one direction, which may affect ball roll and may lead to a decrease in wear resistance.

Color – Turfgrass color is greatly affected by the nutrient status of the plants and generally dark green varieties are more desirable. Modern breeding has developed many cultivars that are dark green without requiring added fertilizers.

Using turfgrass as a model system for research

Turfgrass is an ideal system of study because of its importance to everyday human life and it provides opportunities for research that contributes to both applied and basic knowledge. While turfgrass is not considered a “natural system”, turfgrasses have developed around humans and have been altered by humans and therefore are an important component of human ecology. It is also a good model system in which we can study many physiological and ecological mechanisms. Turfgrass systems, unlike many agricultural systems, are perennial in nature yet are less complicated in composition than pastures or native grasslands. The golf green provides us with a definable system in which the plants have been grown under selected conditions for a relatively short evolutionary time (100 years). Golf greens are also ideal for the study of roots because of the high sand content of the root zones and the uniformity of soil and spatial root distribution. Furthermore, the golf green is manipulated easily by fertilization, mowing, or use of pesticides. The relative similarity in golf green construction and maintenance throughout the world increases the applicability of results from research plots to actual golf greens used by the golf industry.

The Golf Green

The typical newly constructed golf green contains a sand-based root zone with approximately 85% sand and 15% sphagnum peat. The root zone is 30 cm deep and is on a 10 cm layer of pea gravel, creating a perched water table between the two layers. This system provides adequate drainage and resists compaction while maintaining sufficient water for plant growth (Turgeon, 1991). The sand particle size distribution is concentrated in the regions of coarse to medium (0.25-0.5mm). Golf greens are typically grown under high fertility (100 kg ha^{-1} to 400 kg ha^{-1}) and are irrigated. Because the turf is mowed at 2-5 mm, the primary stresses in this system are temperature and physical disturbance. Disease pressure is often minimized by the application of pesticides. The controlled environment allows us to monitor the growth habits of different species without the confounding factors of high soil heterogeneity, drought, or variable disease pressures.

The Plants

Agrostis stolonifera L. var. *palustris* (Huds.) Farw. (Creeping Bentgrass)

Creeping bentgrass is a utilitarian and ornamental grass predominantly cultivated in temperate climates throughout the world (Beard, 1973). It is stoloniferous and has a prostrate growth habit allowing it to be maintained at low mowing heights. Creeping bentgrass's ability to tolerate low mowing heights, its uniformity, and its hardiness have made it the standard grass chosen for golf greens in temperate climates. It is a cool-season grass (C_3 photosynthesis) and its range is limited to highly cultured areas in stressful tropical environments. Creeping bentgrass originally was a trace component in South German Bent, a mixture of turfgrass seed sold for golf greens in the early 1900's. South German Bent was highly variable in quality and it was later determined that the quality was based on the presence of creeping bentgrass in the mixture (Huff and Landschoot, 1999). Creeping bentgrass is a cross-pollinating plant species making seed production highly variable and therefore, tillering or sod were initially used for propogation. In the 1920's, commercial seed of a variety called 'Seashore Bent' became available in the Pacific Northwest. In 1954, Penn Cross was released which was a cross-pollination of three different varieties of bentgrass and has become the standard in the industry today (Huff and Landschoot, 1999). Recently, more intensive breeding programs that selected high quality strains from old Penn Cross greens have produced cultivars that appear to have improved heat and drought tolerance. The morphology of the species has also been manipulated, creating varieties that have an increased shoot density, a finer leaf blade width, and a more upright growth habit.

***Poa annua* L. f. *reptans* (Hausskn.) T. Koyama (Annual Bluegrass)**

Annual bluegrass is the dominant weed in creeping bentgrass swards maintained at low heights of cut (<2cm) and is found in temperate climates throughout the world. Annual bluegrass typically has an upright growth habit and is slightly stoloniferous. The shoot densities vary greatly but most are denser than creeping bentgrass when maintained at similar cutting heights. It is a very aggressive self-pollinated species that is able to flower and set seed at heights of less than 4 mm. Annual bluegrass is described as an allotetraploid resulting from the combining of the diploid parents: *Poa supina* Schrad., a grass found in the mountainous regions of Northern Europe, and *Poa infirma* Kunth, a Mediterranean region grass (Tutin, 1957). This diverse evolutionary history may have led to its ability to compete in a wide range of environments. Using RAPD markers it was shown that populations of annual bluegrass taken from golf course greens and fairways showed significant population differences (Sweeney and Danneberger, 1995). For studies on golf greens, the high variability of annual bluegrass makes it necessary to select strains that are adapted to golf greens.

Field Root Dynamics Experimentation

An interesting observation made by Fitts (1925) regarding turfgrass was, "to grow high quality turf, treat the grass at the surface of the soil and ignore the below ground portions all together." This statement was made because the plants with the most extensive root systems had the worst aboveground growth. This observation suggests that having an extensive root system is not always the optimal strategy for carbon allocation in high quality turf. However according to Beard (1973), roots not only provide water, nutrients, and anchorage for plants, but can also be an important factor in determining turfgrass quality. While healthy root systems are important, it is also important to realize that a closely mowed turf system may be limited by its ability to fix a sufficient amount of carbon with limited leaf area (Huang and Gao, 2000). Plant survival and turf quality may be determined by an optimal allocation of carbon between roots and shoots. As stated in the general introduction, the two grass species typically found to be in competition on golf greens are annual bluegrass and creeping bentgrass. Although much has been written about the annual bluegrass vs. creeping bentgrass competition, our understanding of this competition will be enhanced greatly by an extensive study of their rooting habits. Possible rooting factors that affect the outcome of this competition include depth, length, mass and morphology.

Creeping bentgrass and annual bluegrass growing on golf greens provide an excellent system for studying root characteristics correlated to survival strategies, competitive ability, and how these factors are affected by nutrient levels. Grime (1977) defined different strategies for survival and differentiated between competition and the ability to survive stress or disturbance. He used a very narrow definition of competition, “the tendency of neighboring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space” (Grime, 1973). This leads to a classification system to define three major types of plants and the selection pressures that lead to their adaptive traits: competitors (C-selected), stress tolerant (S-selected), and ruderal (r-selected). This classification is similar to the classification of plants as having a reproductive strategy (*r-selected*) or a conservative survival strategy (*K-selected*) (Larcher, 1995), although it separates out the competitive plants from the stress-tolerant plants. Plants within these three categories possess genetic traits that are associated with being selected in a competitive, stressful, or disturbed environment. R-selected plants are typically annual plants that have a large proportion of their productivity being allocated to reproduction and tend to persist in highly disturbed environments. C-selected plants tend to be perennial in nature and allocate more to vegetative growth and acquisition of resources. They typically set seed only after times of prolific vegetative or non-structural carbohydrate production. S-selected plants are typically slow growing and have little resources allocated to reproduction (Grime, 1977). Golf greens are not the ideal system for studying S-selection because classical resource stresses are kept to a minimum through irrigation and fertilization. However, it may be an ideal system for studying r-selected and C-selected plants.

Annual bluegrass can be considered r-selected because it is found in disturbed environments and is a prolific seed producer even when mowed at 2.5mm. Creeping bentgrass can be considered C-selected because of its more perennial nature and its inability to seed under close mowing heights. Thus the golf green allows us to study these two life strategies and root characteristics associated with them under different nutrient regimes in a fairly homogenous environment. One aspect of survival that is considered important is plasticity, the ability of plants to change their growth and physiology in response to the external environment (Larcher, 1995). Plasticity to spatially heterogeneous nutrient supplies is considered to infer a competitive advantage (Casper and Jackson, 1997; Grime et al., 1986; Hodge et al., 1999). Robinson et al. (1999) proposed that in highly cultured, fertile monocultures, plasticity might not lead to increased nutrient uptake. However, golf greens are rarely monocultures. Creeping bentgrass has been shown to be very plastic to heterogeneous nutrient supplies (Crick and Grime, 1987). The plasticity of annual bluegrass occurring on golf greens in unknown and therefore plasticity to spatially heterogeneous nutrient supplies may be an important factor in determining the competition between an r-selected and a C-selected species. Factors other than root proliferation into high nutrient patches may be important aspects of plasticity in ecological systems such as altering uptake kinetics in response to external nutrient levels (Caldwell *et al*., 1992; Fitter, 1994). Plasticity of root growth and distribution to different nutrient-containing soil levels could be an important factor in determining survival and competition on a golf green.

The species composition of turf systems maintained under low mowing heights depends on many factors including the reproductive strategies of the grasses involved. Reproductive strategies can cause differences in carbon allocation that may affect root growth. Annual bluegrass is generally considered an invasive species and has been studied as a competitor in highly grazed pasture systems. McNeilly (1981) confirmed that genetic populations of annual bluegrass differed in their ability to compete with

Lolium perenne L. in systems maintained at 1.5 cm and in systems where plant height was not maintained. Populations of annual bluegrass were collected from open habitats and closed habitats and seeded in pure stands or in mixed stands with *L. perenne*. When in competition or under mowing, the annual bluegrass from the closed habitat performed much better than the annual bluegrass from the open habitat. This is evidence that there is variation among populations of annual bluegrass for the r-selection and c-selection adaptive strategies. Genetic differences in the populations of annual bluegrass collected from the open and closed environments were later confirmed (McNeilly, 1984). These studies show the importance of using a variety of annual bluegrass that is collected from the environment in which it is being tested. Snaydon and Howe (1986) studied the invasion of annual bluegrass and other weed grasses into a sward of *L. perenne* to determine the importance of root and shoot competition. Their study showed that root competition is the major factor determining the ability of the weed seedlings to become established in swards of *L. perenne*. This competition was reduced by increased nitrogen rates in stands of lower densities. There is still limited knowledge regarding root growth of annual bluegrass on golf greens, despite its importance with regard to its invasive properties.

Annual bluegrass's ability to invade golf greens can be affected by many different factors. Most studies comparing creeping bentgrass and annual bluegrass on golf greens have been aimed at eradicating annual bluegrass from the turf system and have used selective herbicides and plant growth regulators as means of annual bluegrass suppression (Callahan and McDonald, 1992 ; Cooper et al., 1987 ; Gaussoin and Branham, 1989). Bensulide was used to control annual bluegrass in creeping bentgrass and it was effective in eliminating an ecotype of annual bluegrass with a more annual life cycle, but it was ineffective in eliminating a more perennial population (Callahan and McDonald, 1992). Mefluidide, an inhibitor of seedhead emergence in annual bluegrass, was shown to increase root mass during the time of seedhead emergence (Cooper et al., 1987). Brede (1991) collected leachate from annual bluegrass plots and applied it to creeping bentgrass plots and found no allelopathic effects in one of the few studies aimed at determining a cause for annual bluegrass's competitive vigor. Finally, an important study of seed competition was conducted and showed that removal of clippings from the litter reduced the amount of annual bluegrass, presumably because of a reduction in seed presence (Gaussoin and Branham, 1989). Therefore, seed production is an important factor in the proliferation of annual bluegrass, although from our observations, some of the most aggressive varieties of annual bluegrass appear to be reproductively sterile (unpublished observations). These studies show that annual bluegrass has multiple strategies that influence competition. These studies also show the ruderal nature of annual bluegrass and prompt us to compare its growth habit including its root distribution to creeping bentgrass, a more C-selected plant.

Historically, annual bluegrass has been categorized as having a shallow root system because it is often found on sites with compacted soils (Beard et al., 1978). In non-compacted soils annual bluegrass was compared to colonial bentgrass and Kentucky bluegrass. No difference was found in the root mass either in the top 7.5 cm or the top 12.5 cm depth (Sprague and Burton, 1937). This result was confirmed in a study that showed no difference when comparing annual bluegrass roots to Kentucky bluegrass and creeping bentgrass roots growing in sandy loam soils at increasing bulk densities

(Wilkinson and Duff, 1972). Despite these two studies, many field observations have reported shallow rooting of annual bluegrass growing in compacted soils and has lead to the idea that annual bluegrass has a less extensive root system than other grasses (Beard, 1973; Sprague and Burton, 1937; Youngner, 1959).

Annual bluegrass also appears to emerge from winter dormancy earlier than creeping bentgrass despite the fact that it requires a higher temperature to initiate growth, 13°C for annual bluegrass and 10°C for creeping bentgrass (Bogart, 1972). The earlier emergence of annual bluegrass than creeping bentgrass from winter dormancy in the field may be due to the temporal component of the increased temperature that was not examined by Bogart and would be evidence of the more ruderal nature of annual bluegrass. Annual bluegrass has also been shown to display much greater growth at soil temperatures of 7°C compared to creeping bentgrass along with more growth allocation towards tillering and spatial expansion (Beard et al., 1978; Hawes, 1965). Creeping bentgrass had greater growth than annual bluegrass in the temperature range of 13-29°C. Evidence for earlier spring growth by annual bluegrass can also be found in results of fertility trials that showed cold weather applications of nitrogen enhanced annual bluegrass growth in creeping bentgrass turf when compared to applications made uniformly over the growing season (Engle, 1974). These studies strengthen the argument for the ruderal nature of annual bluegrass, because of its exploitation of both spatial and temporal gaps to become established in the more c-selected creeping bentgrass. Once annual bluegrass becomes established on creeping bentgrass greens very little is known about its root distribution in comparison to creeping bentgrass.

The maintenance of golf greens at extremely low mowing heights limits much of the above ground competition for light between annual bluegrass and creeping bentgrass. Despite annual bluegrass being classified as a poorly rooted grass, it is a very invasive species on golf greens (Warwick and Briggs, 1978 ; Youngner, 1959). This may be due to the differences in the seasonal growth habits of the two species, leaf orientation, or a difference in spatial distribution of roots. Preliminary findings have shown differences in the seasonal rooting behavior of the two species (Kucharski and Karnok, 1980). Creeping bentgrass showed maximum root depth in the spring with a summer decline in active root length in July and August. Annual bluegrass showed two declines; the first was during seedhead emergence in April and May and the second, during July and August. Kucharski and Karnok (1980) only observed one ecotype of annual bluegrass and their report contained only one year of data, limiting its usefulness in defining seasonal growth habits of the two species.

Creeping bentgrass has been shown to alter its root architecture in response to nutrients. Crick and Grime (1987) showed that creeping bentgrass was able to alter its root growth to increase root allocation to areas of high nitrogen. This strategy was successful in maximizing nitrogen acquisition when the nitrogen was present for extended periods, but less efficient when it was present for shorter, less predictable periods. Golf greens are often fertilized at regular intervals to maintain turf quality. Very little has been reported regarding the ability of creeping bentgrass to respond to traditionally less mobile nutrients such as phosphorus. Phosphorus levels are also implicated in the competition between creeping bentgrass and annual bluegrass and it is suggested that phosphorus may play an important role in annual bluegrass encroachment into bentgrass areas (Waddington, 1978). A study showed that annual bluegrass invasion into creeping bentgrass increased with phosphorus availability (Kuo, 1993). The role of phosphorus in determining the root distribution of grasses on golf greens is not defined. With better knowledge of seasonal root distribution of both creeping bentgrass and annual bluegrass, it may be possible to exploit the ability of creeping bentgrass to respond to spatial phosphorus supply in order to create high quality creeping bentgrass greens with limited invasion of annual bluegrass or other undesirable species.

This dissertation will compare the root distribution, based on the amount of root mass allocated to different depths in the root zone, of two creeping bentgrasses to three annual bluegrasses. This will provide a side-by-side comparison of the two species' growth habits that will guide future research to elucidate some of the mechanisms of annual bluegrass's persistence on golf greens. In addition to comparing the root distribution, this study will examine how two different nitrogen rates affect the root distribution of both creeping bentgrass and annual bluegrass. The low nitrogen rate may be considered low, yet adequate, for a newly established green and the high nitrogen rate may be excessive yet within the normal range for nitrogen fertility found on golf greens. Finally, this dissertation also explores the plasticity of creeping bentgrass root growth to spatial phosphorus supply, possibly resulting in ideas to encourage creeping bentgrass growth while reducing the invasion of annual bluegrass.

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Chapter 2

Root distribution of creeping bentgrass and greens-type annual bluegrass throughout two growing seasons

Introduction

Creeping bentgrass (*Agrostis solonifera* L.) and annual bluegrass (*Poa annua* L.) are the predominant species of grass found on golf course putting greens in the Northern United States. While golf greens are typically planted with creeping bentgrass, annual bluegrass usually invades the stand and is thus considered a weed (Beard, 1973). Most research involving annual bluegrass has been aimed at management practices to eliminate it from the golf green (Callahan and McDonald, 1992; Cooper et al, 1987; Gaussoin and Branham, 1989). The annual bluegrass ecotype that has evolved on golf greens is a high density persistent ecotype that is perennial in nature. Its competitive vigor under low mowing height and persistence on golf greens has led breeding programs to develop commercial cultivars of annual bluegrass for use on golf greens. Perennial ecotypes of annual bluegrass that have been selected for use in breeding programs have been called greens-type annual bluegrass or creeping bluegrass (Beard, 2002). The recent selection of high quality greens-type annual bluegrass has provided opportunities for comparing the growth of annual bluegrass and creeping bentgrass on putting greens in order to gain insights into the reasons for the competitive vigor of annual bluegrass on putting greens.

Understanding successful growth strategies will lead to selection of improved cultivars of both annual bluegrass and creeping bentgrass.

Greens-type annual bluegrass and creeping bentgrass have different above-ground growth habits (Turgeon, 2001). Creeping bentgrass has a stoloniferous growth habit while greens-type annual bluegrass initiates new tillers in a more bunch type fashion from the crown. It has also been observed that greens-type annual bluegrass is more upright in its growth habit than creeping bentgrass (Beard, 2002). The upright growth habit and the smaller stature of greens-type annual bluegrass result in greater tiller densities and an ability to persist under lower mowing heights than creeping bentgrass. More recently released bentgrass cultivars exhibit increased tiller densities, a more upright growth habit and a greater resistance to annual bluegrass invasion than older varieties of creeping bentgrass (Beard *et al*., 2001). Finally, one of the most distinct differences between creeping bentgrass and green-type annual bluegrass is the ability of greens-type annual bluegrass to flower under the 2.5-4 mm mowing heights found on golf greens–thus establishing an avenue for gene-exchange and evolution to proceed.

In recent years, focus on root growth of creeping bentgrass has increased due to increased concern over nutrient leaching and the increased effort to reduce the environmental and economic cost of irrigation and syringing. Two common methods exist for examining the standing root biomass and for tracking root production and mortality: 1) destructive sampling using cores and 2) the use of rhizotrons, including mini-rhizotrons. While root number and length measurements from mini-rhizotrons have been shown to correlate with total root biomass in creeping bentgrass (Murphy *et al*., 1994), the strength of mini-rhizotrons is in the tracking of individual roots for root turnover measurements (McMichael and Taylor, 1987; Ferguson and Smucker, 1989; Cheng *et al.*, 1991; Hendrick and Pregtizer, 1993a,b) and have been used for this purpose on a closely mowed golf green (Huang and Liu, 2003). Using the mini-rhizotron technique in Kansas, a reduction in root number and length was shown at a depth of 5-6 cm from mid-June to mid-September compared to spring and fall (Liu and Huang, 2003). This reduction was due to increased root mortality as well as a decrease in new root production. In the same study, newer varieties of creeping bentgrass showed greater root depth than ‘Penncross’, an older variety. In a rhizotron study, Schlossberg and Karnok (2001) showed that measurements of root length density deeper in the soil is important in finding the difference in rooting between cultivars and nutrient regimes, as opposed to using total root length or root length present within the top few centimeters of the root zone. Creeping bentgrass root growth has also been measured using destructive sampling techniques. These studies usually quantify the entire root biomass or root lengths and do not account for changes in root distribution at different depths (Ralston and Daniel, 1972; Kurtz and Kneebone, 1980; Wang et al, 1998; Yelverton 1999). This may be due to the inability to obtain accurate root weights because of contamination of the sample by soil and sand.

Plant roots have many functions but their primary function is the acquisition of soil-based resources, primarily water and nutrients, and to provide anchorage (Fitter, 1996). Plants that have effective root systems are typically more competitive and have greater agricultural production and growth (Wilson, 1988). High temperatures experienced at times during the growing season are an important factor limiting growth and productivity for cool-season plants (Paulsen, 1994). Roots, typically, are less adapted to extremes and have a small range of optimum temperature for growth (Nielsen, 1974). High root temperatures during summer months may be more important than shoot temperatures in determining the relative health of turfgrass (Xu and Huang 2000). Above-optimum soil temperatures detrimentally affected root growth and enhanced senescence of shoots more than above optimum air temperature (Kuroyanagi and Paulsen, 1988; Ruter and Ingram 1990, 1992). This can be attributed to the fact that root functions are more sensitive to heat stress than shoots, so translocation of hormones and acquisition of soil-based resources is severely limited at high soil temperatures (McMichael and Burke, 1999). The maintenance of a healthy root system throughout the summer months is essential for turfgrass growth (Beard, 1973). Therefore it is reasonable to postulate that creeping bentgrass and annual bluegrass competition may be influenced by their ability maintain a healthy root system throughout the summer growing season.

Historically, annual bluegrass has been categorized as having a shallow root system because it is often found on sites with compacted soils (Beard et al., 1978). In non-compacted soils, however, annual bluegrass root mass was comparable to both colonial bentgrass and Kentucky bluegrass root mass when root mass in the top 7.5 cm or 12.5 cm of soil were measured (Sprague and Burton, 1937). In another study comparing root growth at increasing bulk densities, annual bluegrass, Kentucky bluegrass and creeping bentgrass growing in sandy loam soils at increasing bulk densities showed no difference in root biomass among the species, although all three species showed reductions in root biomass with increasing bulk densities (Wilkinson and Duff, 1972). Despite these two studies, many field observations have reported shallow rooting of annual bluegrass growing in compacted soils, which has led to the idea that annual bluegrass has a less extensive root system than other grasses (Beard, 1973; Sprague and Burton, 1937; Youngner, 1959).

The highly variable nature of annual bluegrass has made it difficult to make comparisons between greens-type annual bluegrass and creeping bentgrass. Annual bluegrass is generally considered undesirable because of its lack of hardiness during times of heat stress presumably because of its susceptibility to desiccation because it is a poorly rooted grass (Beard, 1973). Greens-type annual bluegrass has been shown to be distinct from the invasive species found in lawns, pastures and most areas of the golf course (Sweeney and Dannenberger, 1995). In a study assessing the competitive ability of annual bluegrasses collected from open and closed stands within a pasture, the location of annual bluegrass selection was important in determining its competitive ability against perennial ryegrass (McNielly, 1984). Annual bluegrasses from closed stands were more competitive against perennial ryegrass than those collected from open or disturbed areas of the pasture. This variability in annual bluegrass growth when gathered from open and closed stands and the importance of this variability in its competitive nature indicate that it is essential to choose greens-type annual bluegrass to compare its growth to creeping bentgrass on a putting green. The lack of side-by-side comparisons of root growth between creeping bentgrass and any form of annual bluegrass on putting greens makes it difficult to determine if any below-ground aspects of the competition between the two species are important.

The purpose of this study was to perform side-by-side comparisons of the growth habits, including root distribution and tiller densities, of creeping bentgrass cultivars ‘Penncross’, a cultivar released in the 1950’s, and ‘Penn A-4’, a newer cultivar released in the 1990’s, to three experimental cultivars of greens-type annual bluegrass throughout the summer growing season. This information will also lead to an understanding of successful growth strategies on golf greens resulting in an ability to create better cultivars in the future.

Materials and Methods

Plant materials and growing conditions

Two creeping bentgrass cultivars (Penncross, Penn A-4) and three experimental cultivars of green-type annual bluegrass (‘PSU-97-1’, ‘PSU-97-2’, ‘PSU-97-3’) were seeded in monocultures into 2.75 m wide by 4 m long plots at a rate of 36.5 kg ha^{-1} during late September, 1999, on an experimental putting green. The root-zone consisted of 30.5 cm of an 85% sand and 15% sphagnum peat laid over 10 cm of pea gravel, conforming to the USGA specifications. The seedbed was well watered to maintain a moist surface for 6 weeks following germination. After the first mowing, the plots were covered with a fabric tarp from mid-November 1999 to mid-march 2000 to improve establishment and winter survival. Mowing height was lowered gradually throughout the 2000 growing season and an aggressive topdressing plan was implemented until a mowing height of 3.2 mm was reached in late July. Throughout the experiment, pesticides were applied in both a preventative and curative manner in order to mimic golf green management as closely as possible. Dollar spot and snow mold were the two most prevalent pests present. In 2000, the plots were fertilized identically using granular starter fertilizer (19-25-5) followed by commercially available liquid nitrogen fertilizers supplemented with a micronutrient solution to allow for optimal grow-in and establishment of the turf. In 2001 and 2002, two different nitrogen rates were stripped across the plots. In both years of the experiment, the plots received applications of liquid ammonium nitrate every 10-20 days at a rate of 6.1 kg N ha^{-1} and 18.3 kg N ha^{-1} for the low and high nitrogen treatments respectively. This resulted in approximately 130 kg N ha^{-1} year $^{-1}$ or 390 kg N ha^{-1} year $^{-1}$. Phosphorus and potassium were supplemented with applications of potassium phosphate solution as needed. This chapter concentrates on differences in root distribution among the varieties of creeping bentgrass and greens-type annual bluegrass averaged over the different nitrogen treatments. Fertilizer effects on individual cultivars will be discussed in chapter 3.

Measurements

Soil temperature was measured at 3 cm and 10 cm depth using an outdoor industrial data logger (Onset Technologies, Bourne, MA). Probes were placed under each plot in 2001 and, due to the consistent temperatures from plot to plot, only 3 plot locations were monitored in 2002. Soil temperatures are reported as daily averages of the soil probe at 3 cm of depth; measurements were taken every 30 minutes. Air temperatures were an average of the daily maximum and minimum temperatures from the University Park Campus weather station (approximately 1 kilometer from the field plots) and were obtained from the Penn State Climatologist web site (2003). Tiller density and root mass at three different depths was monitored on 9 dates from mid-June to early-November in 2001, and on 8 dates from late-March to late-September in 2002. Four cores were taken from each plot, with two from each nitrogen treatment. The cores were 3.5 cm in diameter and were taken to a 25 cm depth using a sharpened PVC pipe every 10-20 days throughout the growing season. The cores were frozen within the PVC at –20^{o}C until thawed for washing.

The top 3 mm of the core was removed using a saw to allow for tiller density measurements and to eliminate any stem material from the root samples. The remaining core was then separated into three sections 0-3 cm, 3-12 cm, and below 12 cm. The roots from each section were washed by hand using a 1 mm soil sieve under room temperature running water. Fresh weights were recorded and sub-samples of the roots were weighed and placed in 50% ethanol solution for root length analysis (Described in Chapter 3). The remaining roots were dried for 24-48 hours at 70^{o}C. Dry weights were recorded and the samples were then ashed in a muffle furnace at 605^{o}C until all the organic matter was completely combusted, typically six hours. The samples were weighed and the weight of the ash and any remaining sand in the sample was subtracted from the root dry weight. Tiller densities were obtained by separating the top 3mm into four equal parts and counting the total tillers in one quarter of each core.

Experimental design and statistical analysis

The cultivars were arranged in a randomized strip-split-plot design with three replicates. Two sub-samples were taken from each split-plot and measured, i.e. two from each fertilizer treatment. The measurements were averaged to attain a plot value on each date on which the data was collected (Date of Harvest). Analysis of variance was performed as repeated measures using the PROC MIXED procedure of the Statistical Analysis System (SAS Inc. Carey, NC). The main effects of Date of Harvest (D), and Cultivar (C) were tested with the Date of Harvest × Cultivar (D × C) as the error term. The interaction (D × C) was tested against the residual error. Differences between cultivar means at a given date of harvest or between times for given cultivar were separated by least significance difference test at the 0.05 level. Due to limitations in the repeated measures design the data from 2001 and 2002 were treated separately (Litell *et al*, 1996). Means were separated using LSD at the $P<0.05$ and differences on different days were separated using the “SLICE” command in SAS.

Results

Temperature patterns were similar in both years with the highest temperatures occurring during late July through late August (Figure 2.1). Soil and air temperatures were in close agreement when average daily soil temperature and averages of the high and low air temperatures were calculated for each day. Generally, the daily maximum air temperature was greater than the daily maximum soil temperature. The daily minimum soil temperature was greater than the daily minimum air temperature. The daily fluctuation in soil temperatures was therefore less severe than the fluctuation of the air temperatures. Soil temperatures are not shown after August 10, 2002 due to a malfunction in the three data loggers used to take soil temperature measurements, although air temperatures were still available throughout the remaining 2 months of the experiment.

While some mixing of the species in the plots did occur, we were able to maintain sufficient monocultures for sampling throughout the length of the experimental period. Throughout 2001, the mixing that occurred was predominantly annual bluegrass invasion into the creeping bentgrass plots. Penn A-4 resisted the encroachment better than Penncross, however this was not quantified. In 2002, the opposite mixing occurred with creeping bentgrass invading the annual bluegrass plots. This occurred during a time when phosphorus deficiency symptoms began to appear in both species (symptoms not quantified). Phosphorus was then supplemented to optimize growth of both species.

Tiller Densities

Tiller densities were significantly different among D, C and the D × C interaction ($P < 0.05$) in each year of the experiment (Table 2.1). In 2001, PSU-97-3 (67 tillers cm^{-2}) had greater tiller densities than PSU-97-1 (60 tillers cm^{-2}) and PSU-97-2 (60 tillers cm^{-2}) averaged over the entire growing season (Table 2.2). Penncross had lower tiller densities, approximately 30-40% lower, than the other four varieties of grass while Penn A-4 was intermediate to Penncross and the three varieties of annual bluegrass. In year two of the experiment, Penn A-4 (65 tillers cm^{-2}) was equivalent to PSU-97-1 (64 tillers cm^{-2}) and PSU-97-2 (62 tillers cm^{-2}), while PSU-97-3 (74 tillers cm^{-2}) had the highest tiller density (Table 2.3). An increase in tiller density was observed from June 20 to August 7 and a second increase was observed at the November 1 date of harvest in 2001 (Figure 2.2). During the fall of the second year of the experiment, PSU-97-3 showed a significant reduction in tiller density compared to previous harvests while Penn A-4 showed an increase in tiller density (Figure 2.2).

Root Mass

Total root mass

Day, C and D × C were significant in 2001, but in 2002 the only significance was found in the effects of C and D × C (Table 2.1). The bentgrasses did not differ in their total root mass in 2001 (Penn A-4 = 0.2823 kg m^{-2}, Penncross = 0.2807 kg m^{-2}). While PSU-97-3 (0.1458 kg m^{-2}) had the greatest root mass of the annual bluegrasses, all of which had less root mass than the two bentgrasses (Table 2.2). In 2002, Penn A-4 (0.3444 kg m^{-2}) had approximately 25% more root mass than Penncross (0.2831 kg m^{-2}) and both creeping bentgrass varieties had more than twice the root mass of all three varieties of annual bluegrass (Table 2.3). In 2001, root mass was the greatest on June 20 and October 5 (Figure 2.3). A 50% reduction in root mass was observed throughout the summer compared to spring and a second reduction was observed after the first freeze on November 1, 2001 (Figure 2.3). A decrease in total root mass throughout the summer from June 18 until August 18 was also observed in 2002, approximately 20% for all cultivars pooled, and a recovery was not observed in the second year (Figure 2.3).

Root mass at 0-3 cm of depth

Day and C were significant in both years, while the D × C interaction was not significant in either year (Table 2.1). In 2001, both of the bentgrasses had higher root mass than all three annual bluegrasses. PSU-97-3 (0.1204 kg m^{-2}) had more root mass than PSU-97-2 (0.0922 kg m^{-2}), with PSU-97-1 (0.1006 kg m^{-2}) intermediate (Table 2.2). Root mass was highest on June 20 and October 5 and a reduction in root mass was observed throughout the summer months with the lowest root mass being observed from August 22 until September 21 (Figure 2.4). After the fall recovery, a reduction in root mass was observed on November 1, which was after the first freeze of the fall (Figure 2.4). In 2002, all three annual bluegrass had less root mass than the creeping bentgrasses and Penn A-4 (0.2294 kg m^{-2}) had more root mass than Penncross (0.1792 kg m^{-2}) (Table 2.3). A decrease in total root mass was also observed throughout the summer from June 18 until August 18 in 2002, but a growth recovery was not observed in the fall of the second year (Figure 2.4).

The annual bluegrass cultivars had a higher percentage of their root mass in the top 3 cm than the two creeping bentgrass cultivars. In the first year of the experiment PSU-97-1 had a lower percentage (75%) of root mass in the top 3 cm of the root zone than PSU-97-2 (79%) and PSU-97-3 (82%). In the first year of the experiment, an increase in root-mass percentage was observed in the annual bluegrass cultivars during the summer decline period from August 22 until September 21, but this increase was not observed in the creeping bentgrass cultivars (Figure 2.5). The root mass in the 0-3 cm section of the root zone (Figure 2.5) essentially mimicked that of the total root mass in both years as 75-85% and 60-70% of the root mass was found in the top 3 cm for the annual bluegrass and the creeping bentgrass varieties, respectively.

Root Mass at 3-12 cm of depth

In 2001 D, C and D × C were significant while in the second year of the experiment only C and D × C were significant (Table 2.1). In both years of the experiment the bentgrasses had significantly more root mass at 3-12 cm depth than the annual bluegrass, approximately 3 times as much root mass in this zone in 2001 and 4 times as much root mass in this zone in 2002. There were no significant cultivar differences within the two species (Table 2.1, Table 2.2). Root mass in the 3-12 cm zone was greatest on days June 20, July 7, and October 5, with the reduction in root mass at the deeper depth coming one sampling day later than the decline in the top root mass and the lowest root masses were observed from July 24 until September 21 (Figure 2.6). As with the total root mass, a fall recovery was observed followed by a decline in the late fall (Figure 2.6).

Root mass below 12 cm of depth

In 2001 D, C and D × C were significant while in the second year of the experiment only C and D × C were significant (Table 2.1). Penn A-4 (0.0243 kg m^{-2}, 0.0274 kg m^{-2}) had greater root mass below 12 cm compared to Penncross (0.0159 kg m^{-2}, 0.0192 kg m^{-2}). The difference in root mass below 12 cm of depth was the only consistent difference in root mass between Penn A-4 and Penncross was observed throughout both years of the experiment (Table 2.1, Table 2.2). The annual bluegrass cultivars had very little root mass below 12 cm of depth and in the summer months the root mass in this zone approached zero (Figure 2.7). In 2001, a pattern of root mass decline and recovery was observed in this section of the root zone that was similar to that observed in the zones above it (Figure 2.7). This pattern was not observed in 2002 because Penn A-4 root mass declined from June 18 to the end of sampling while Penncross and the annual bluegrass varieties exhibited no change across the same sampling dates (Figure 2.7)

Discussion

The goal of this study was to provide a side-by-side comparison of creeping bentgrass and greens-type annual bluegrass rooting throughout the growing season. Understanding general growth habits of these grasses may allow us to better speculate on the mechanisms that lead to the highly competitive nature of greens-type annual bluegrass on creeping bentgrass golf greens. Previous studies have shown that annual bluegrass had similar root growth to that of Kentucky bluegrass and colonial bentgrass

(Sprague and Burton, 1937). In these previous studies, only the top 12.5 cm of root mass were measured and the grasses in the experiment were not maintained at the low mowing heights found on golf greens.

Tiller densities are closely related to the competitive vigor of grasses on golf greens. In this study, the greens-type annual bluegrass had the highest tiller densities and Penncross had the lowest (Tables 2.2 and 2.3). It is also important to note that general observations of annual bluegrass invasion into the bentgrass turf appeared greater (data not recorded) in the Penncross plots in comparison to the Penn A-4 plots. Penn A-4 had tiller densities that were similar to the annual bluegrasses, especially in the second year of the study. My observations show that greens-type annual bluegrass had greater tiller densities than the creeping bentgrass cultivars and the newer more competitive creeping bentgrass cultivar, Penn A-4, generally had increased tiller densities compared to Penncross, an older variety. In addition to having increased tiller densities, the newer varieties of creeping bentgrass have been reported to develop a more extensive root system (Beard, 2001) as I observed with Penn A-4 in this study. This indicates that increased tiller densities are not necessarily at the expense of root mass or rooting depth. The increased tiller densities may be associated with the finer leaf texture and stem textures that can be observed in the newer varieties of bentgrass (Beard, 2001) and not necessarily due to a decrease in below-ground carbon allocation. Increased tiller densities may also allow the cultivar to better expand into disturbed areas through increased vegetative propagation. A more dense grass would have a greater number of potential starting points for stolons and daughter tillers to begin to exploit the disturbed area than a grass with lower tiller densities and a coarser texture.

Both creeping bentgrass cultivars and all three annual bluegrass cultivars showed the same basic pattern of summer root biomass decline, with the greatest root mass present in June and then declining until possible recovery in fall. No root mass recovery was observed in the second year of the study, possibly because a harvest was not taken far enough into the fall to allow recovery from the summer stress period yet before the first freeze. The concept of summer root decline has been observed in the past using both rhizotron and traditional coring techniques (Ralston and Daniel, 1972; Kurtz and Kneebone, 1980; Wang et al, 1998; Yelverton 1999). Huang and Liu (2003) showed that the summer root decline in creeping bentgrass was associated with a decrease in the production of new roots and an increase in death of existing roots. The limitation of these studies is that they did not attempt to separate out root distribution at different depths and this can be important in determining differences in growth habit between cultivars (Schlosberg and Karnok, 2001). The primary problem with summer root decline is that it adversely affects shoots by limiting water and nutrient supply to the shoots (Kramer, 1983). Declining root health may also affect cytokinin synthesis in the root (Al-Kahtib and Paulsen, 1984; Kuroyanagi and Paulsen, 1988; Smart *et al*. 1991) and increase ABA transportation to the shoots (Udompraset *et al*., 1995) resulting in closure of stomates and possible leaf senescence that would lead to a decrease in turfgrass growth and quality. While all of the varieties of grass in my study showed significant summer root decline, Penn A-4 was able to maintain the most total root mass and root mass at deeper depths possibly leading to improved stress tolerance during the summer months of the growing season.

The root mortality that occurs during summer root decline may be due to inhibition of carbon supply from shoots to roots at high soil temperatures (Sattelmacher *et al*., 1990; Ruter and Ingram, 1990; Aloni *et al*., 1992). It has been suggested that death in woody roots may be related to carbohydrate reserves being transported by the phloem tissues to maintain root function (Vogt *et al.*, 1985). Root death has been shown to closely follow exhaustion of root tissue starch and sugar reserves in Douglas-fir seedlings (Marshal, 1986). The ability of a plant to maintain roots is regulated by the amount of carbon allocated below ground to support root growth and by the amount of carbon fixed by the shoots of the plants by photosynthesis (Bloomfield *et al*. 1996). In creeping bentgrass, Huang and Liu (2003) found that higher cut turf plants had decreased rate of root mortality when compared to low cut plants, indicating the importance of mowing height in maintaining a healthy root system.

In the present study, patterns of summer root decline were not consistent at across depths. In 2001, all sections of the root zone had similar patterns of summer decline (fig. 2.3-6). This pattern was mimicked only in the 0-3 cm fractions and the total root mass in 2002, showing that roots at different depths may act differently from year to year. The only consistent difference between Penn A-4 and Penncross rooting throughout this study was the greater root mass of Penn A-4 below 12 cm of depth. Compared to the other grasses studied, Penn A-4 may be able to attain water from deeper in the soil profile and therefore tolerate more heat stress throughout the growing season because of an increased ability to support transpirational cooling. This might confer a competitive advantage for the deeper-rooted Penn A-4 on the golf green if water becomes limiting in the late afternoon. If Penn A-4 has a greater ability to survive heat stress and possibly intercept more nutrients throughout the root zone, Penn A-4 would have a competitive advantage over annual bluegrass when water and nutrients are available less frequently and at a deeper depth in the root zone. Under these conditions the annual bluegrass varieties would experience more stress because of their lack of an extensive and deep root system. In most cases root length is the important functional biomass component in determining nitrogen uptake (Tinker and Nye, 1977) not root biomass at deeper depths. In this study the greater root biomass would be indicative of greater root length because the specific root lengths of all the grasses were similar, with the exception of an increase in specific root length in the low nitrogen treatments by annual bluegrass (Figure 3.12).

The greens-type annual bluegrass had less total root mass throughout the growing season than creeping bentgrass. It also had significantly less root mass in each section of the root zone, in particular below 12 cm where root mass approached zero in the summer months. It is important to note that the percentage decline in root mass throughout the summer months was similar for annual bluegrass and creeping bentgrass cultivars. There may be a minimum threshold level of roots needed at different soil depths to provide adequate water and nutrients for healthy turf in the summer months. The percentage of the spring root mass present during summer heat stress may not be as important as the total amount of roots present. While healthy root systems are important, it is also important to realize that a closely mowed turf system with limited leaf area may be constrained by its ability to fix a sufficient amount of carbon to support vigorous growth(Huang and Gao, 2000). Eliminating the stresses to which plants with shallow root systems are susceptible is common management practice. Plant canopy temperature is regulated on golf greens through frequent irrigation and syringing, allowing evapotranspirational cooling. Nutrients are often provided to golf greens on a consistent basis through foliar applications. The shallow root zone found in greens-type annual bluegrass may be an adaptation to the highly cultured system of golf greens. Annual bluegrass's ability to set seed under the low mowing conditions of golf greens may have allowed it to adapt very quickly to the golf green environment which favors aggressive tillering and limits the need for extensive carbon allocation for growth and maintenance of roots.

The measurement of total root biomass may not provide a good estimation of a grass's ability to maintain a healthy root system throughout the growing season or to compare and select varieties of grass that are more stress tolerant. This is because 60-70 % of creeping bentgrass root mass and 75-85 % of annual bluegrass root mass is in the top 3 cm of the root zone. While high root density may explain the quick uptake of nutrients near the surface of mowed turf systems and the low leaching potential of turf systems (Miltner *et al*, 1996; Smith and Bridges, 1996), total root biomass may not be an indicator of a deeper or more extensive root system that will support increased water uptake and high stress tolerance.

As water becomes limiting plants often conserve water by closing their stomates and thus creating a limitation of carbon uptake for phosotynthesis by leaves (Chaves, 1991; Cornic and Massacci, 1996). The signal for stomatal closure is modulated by ABA and begins in the roots in response to soil drying (Gowing *et al*. 1990; Davies and Zang, 1991; Holbreck *et al*., 2002). On golf greens, syringing can provide adequate evaporative cooling and can be used to regulate canopy temperature. This however would not aid in the carbon balance that must be overcome during times of heat stress and temporary drought (Chaves, *et al*. 2002). The deeper root system present in creeping bentgrass compared to annual bluegrass (Figure 2.7) may delay stomatal closure and lead to greater net photosynthesis. Such a response would likely increase summer heat tolerance of creeping bentgrass compared to annual bluegrass. Other factors can affect the ability of the plants to take up water throughout the day. Xylem cavitation can amplify water stress by reducing the amount of water that can be transported to the shoots (Tyree and Sperry 1988; Jones and Sutherland, 1991). Xylem cavitation and its reversal during the times of positive xylem pressure at night have also been shown to be important in the water stress tolerance of rice (Stiller *et al*. 2003).

In sand based root zones where nutrients, such as nitrogen, are highly mobile and it has been shown that creeping bentgrass with a deeper, more extensive root zone is associated with less leaching than a creeping bentgrass with a less extensive root system (Bowman *et al*, 1998). In that study, both bentgrasses had similar nitrate uptake rates and the more extensively rooted creeping bentgrass intercepted a greater amount of the applied nitrogen. It is possible that frequent, light fertilization management schemes may help the competitive ability of the less extensively rooted annual bluegrass and reduce the competitive advantage of creeping bentgrass. Even though creeping bentgrass can continue nitrogen uptake from deeper in the root zone where annual bluegrass nitrogen uptake would be minimal, both shallow rooted annual bluegrass and deep rooted creeping bentgrass would be exposed to adequate nitrogen from frequent fertilizer applications.

The less extensive root system present in greens-type annual bluegrass may be due to any number of factors. One factor may be a greater proportion of carbon being allocated to increased tiller production, as opposed to growth and maintenance of roots.

This is different than tiller density in that more carbon is allocated to the production of new tillers to encroach into less dense grasses or disturbed areas. The cost of this allocation may be a less extensive root system. This cost would be overcome by the ability of greens-type annual bluegrass to escape stress and persist as seed under low mowing heights. Under less intensive irrigation regimes the greens-type annual bluegrass would not be able to survive because of its poor root system, but the seed would germinate and reinvade the turf system when conditions become more favorable. This may explain why reducing seed production of annual bluegrass plants on golf greens actually increased the presence of annual bluegrass under a well-irrigated regime (Callahan and McDonald, 1992; Cooper et al., 1987). Energy normally used for seed production could be used to enhance tillering.

The data of the root distribution of creeping bentgrass and greens-type annual bluegrass reported here has many management implications. The increased root mass of Penn A-4 below 12 cm of depth compared to the other grasses allows managers to irrigate Penn A-4 less frequently and delay syringing until later in the day. This will allow for a competitive advantage of the creeping bentgrass over greens-type annual bluegrass. It might be possible to increase the amount of creeping bentgrass by fertilizing at less frequent intervals and at greater application rates, encouraging nutrient movement deeper into the root zone to allow for optimal use of the extensive root system present in creeping bentgrass varieties. The lack of an extensive root system leads to many interesting concerns regarding the management of greens-type annual bluegrass. It is possible that heavy infrequent fertilizations may cause more leaching than found with creeping bentgrass cultivars. As stated earlier, frequent light fertilization will most likely allow greens-type annual bluegrass to thrive despite its reduced root system. The sand-based golf green was designed to allow for adequate drainage while creating a perched water table to provide water for plant growth. In the case of greens-type annual bluegrass this water is still largely unavailable because of its location below the shallow root system of the grass. It is possible that a more shallow root zone, which optimizes water retention where the roots are present, may actually help greens-type annual bluegrass maintain active growth throughout the summer.

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Tables and Figures

Table 2.1: Results of statistical analysis for the effects of harvest date (D) and cultivar (C) on tiller density and root mass at different depths of creeping bentgrass and annual bluegrass cultivars in 2001and 2002 taken from a 3.5 cm diameter core.

		Tiller Density			0-3 cm Depth			3-12 cm Depth			Below 12 cm Depth			Total Root Mass		
	Source of Variation	df	F	P>F	df	F	P>F	df	F	P>F	df	F	P>F	df	F	P>F
2001	D	8	7.45	0.0002	8	79.8	0.0001	8	16.6	0.0001	8	21.3	0.0001	8	84.9	0.0001
	C	4	63.7	0.0001	4	51.3	0.0001	4	9.68	0.0001	4	93.5	0.0001	4	83.6	0.0001
	D × C	32	2.78	0.0003	32	1.53	0.0756	32	63.7	0.0066	32	2.61	0.0003	32	1.79	0.0119
2002	D	7	2.14	0.0499	7	5.98	0.0023	7	2.36	0.0816	7	1.76	0.1750	7	5.23	0.4833
	C	4	35.9	0.0001	4	74.3	0.0001	4	192	0.0001	4	42.7	0.0001	4	153	0.0001
	D × C	28	2.15	0.0052	28	1.13	0.3419	28	2.01	0.0131	28	1.96	0.0159	28	1.41	0.0233

Table 2.2: A comparison of tiller densities and rooting characteristics of creeping bentgrass (Penn A-4 and Penncross) and annual bluegrass (PSU-97-1, PSU-97-2, PSU-97-3) cultivars in 2001 taken from 3.5 cm diameter cores. Means in columns with different letters are significantly different (P<0.05).

Year	Cultivar	Tiller Density (tillers cm-2)	Root Mass 0-3 cm (kg m-2)	Root Mass 3-12 cm (kg m-2)	Root Mass Below 12 cm (kg m-2)	Total Root Mass (kg m-2)	Percent root mass in top 3 cm (%)
2001	Penn A-4	65 b	0.2294 a	0.0891 a	0.0274 a	0.3444 a	65 b
	Penncross	41 c	0.1792 b	0.0868 a	0.0192 b	0.2831 b	61 b
	PSU-97-1	64 b	0.0849 c	0.0191 b	0.0045 c	0.1072 c	79 a
	PSU-97-2	62 b	0.0915 c	0.0172 b	0.0040 c	0.1127 c	81 a
	PSU-97-3	74 a	0.1038 c	0.0141 b	0.0025 c	0.1170 c	83 a
2002	Penn A-4	53 c	0.1903 a	0.0680 a	0.0243 a	0.2823 a	66 c
	Penncross	37 d	0.1959 a	0.0689 a	0.0159 b	0.2807 a	69 c
	PSU-97-1	60 b	0.1006 bc	0.0251 b	0.0059 c	0.1314 bc	75 b
	PSU-97-2	60 b	0.0922 c	0.0206 b	0.0042 c	0.1170 c	79 a
	PSU-97-3	67 a	0.1204 b	0.0212 b	0.0046 c	0.1458 b	82 a

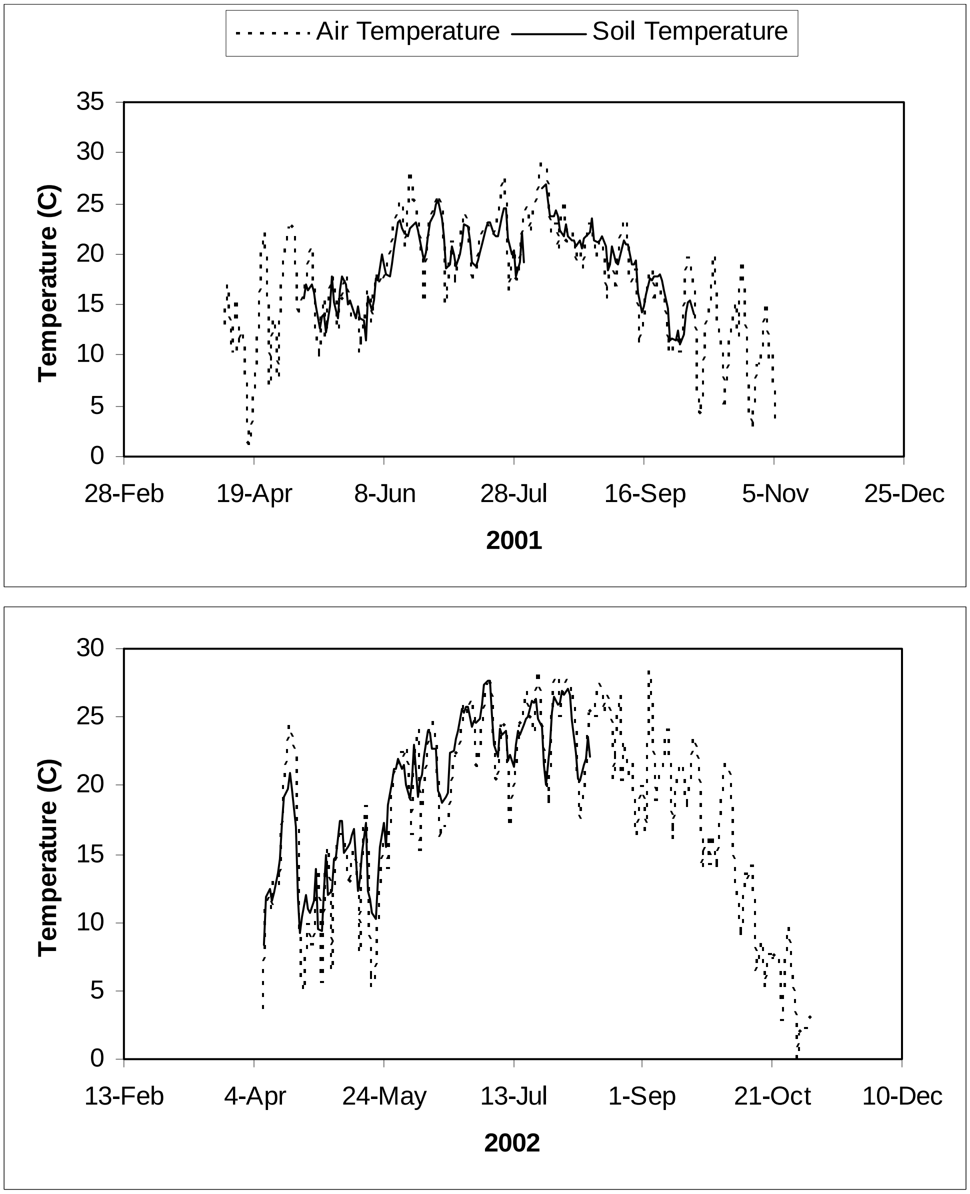


Figure 2.1: The average daily air temperature (from averaging daily high and low temperatures) and average daily soil temperature at 3 cm of depth (from averaging temperatures taken every half hour).

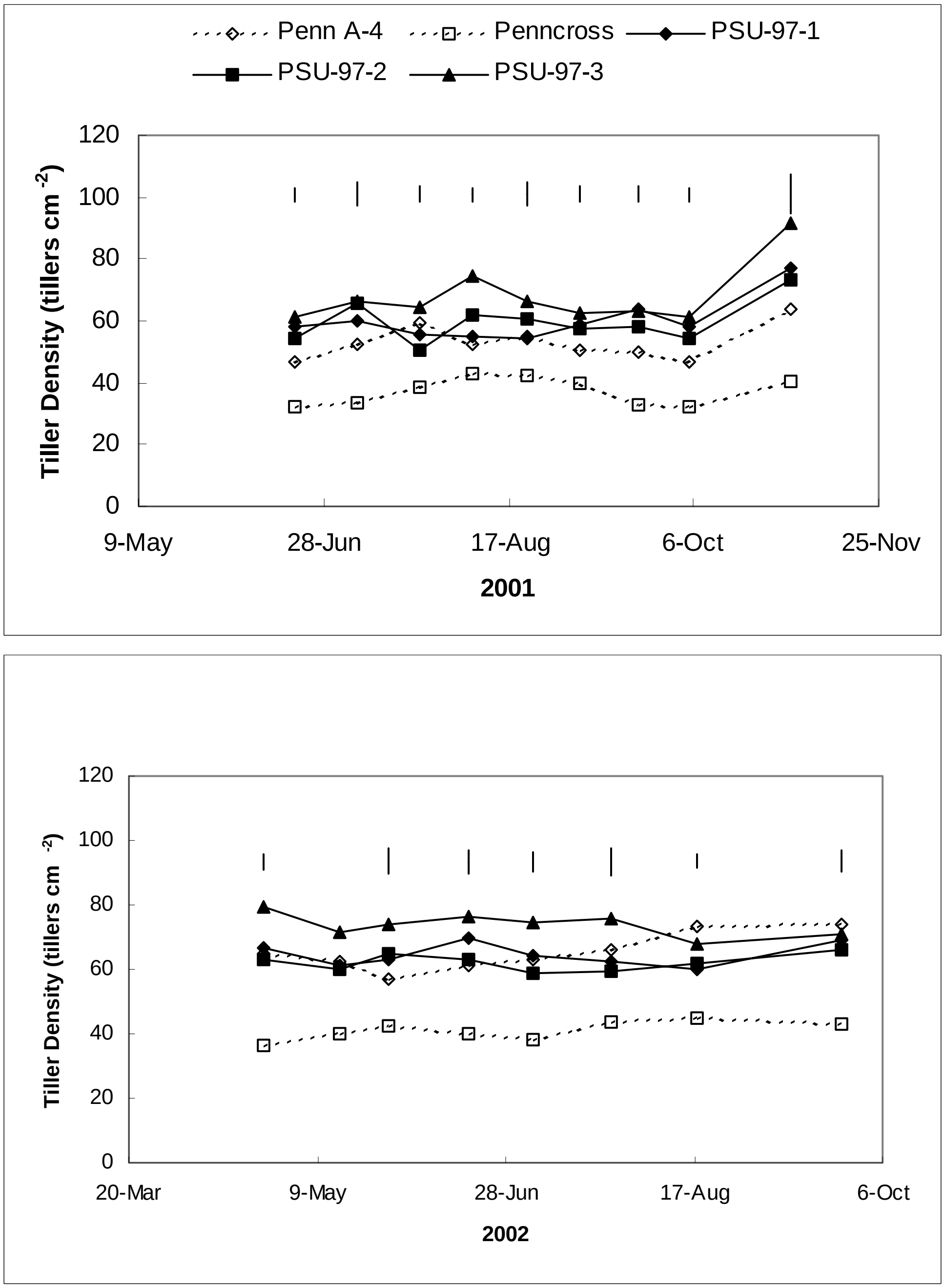
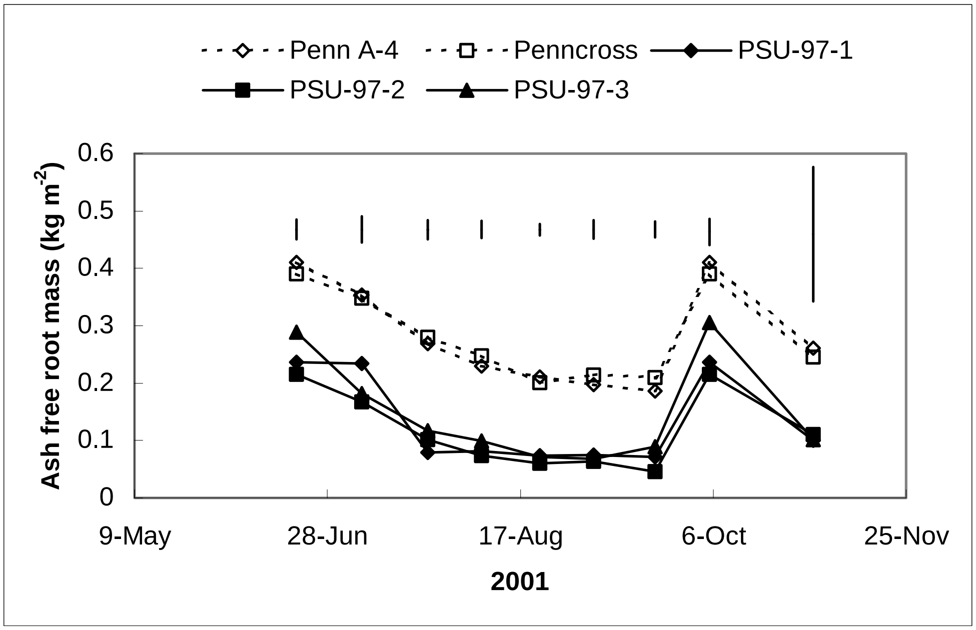


Figure 2.2: Tiller density (tillers cm^{-2}) of two cultivars of creeping bentgrass (Penn A-4 and Penncross) and three cultivars of annual bluegrass (PSU-97-1, PSU-97-2, PSU-97-3) in the 2001 and 2002 growing season. Bars above each day represent standard error values for cultivar difference on each day when Day × Cultivar was significant.



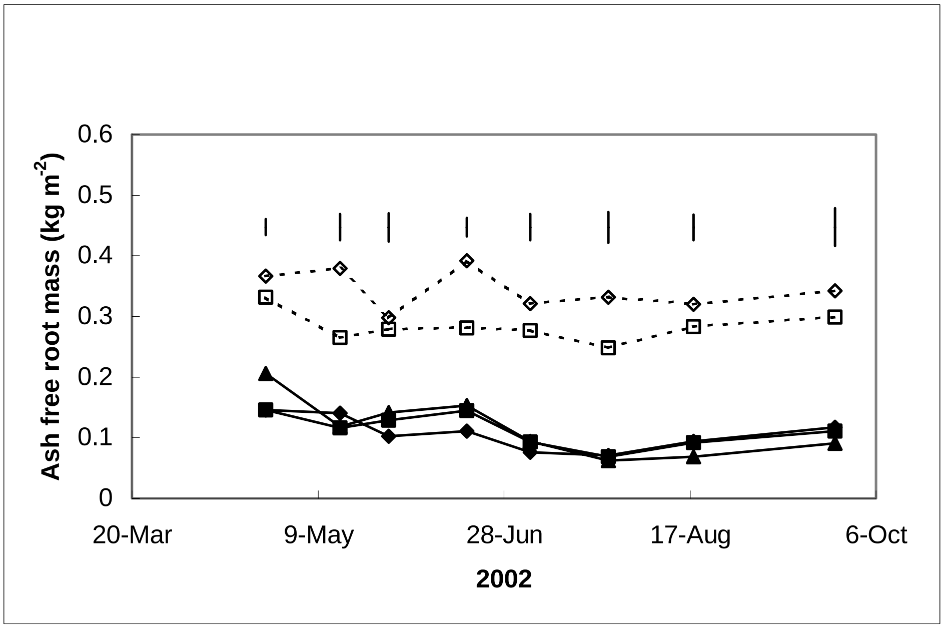


Figure 2.3: Total root mass (ash free) per meter of surface area of ground of two cultivars of creeping bentgrass (Penn A-4 and Penncross) and three cultivars of annual bluegrass (PSU-97-1, PSU-97-2, PSU-97-3) in the 2001 and 2002 growing season. Bars above each day represent standard error values for cultivar difference on each day when Day × Cultivar was significant.

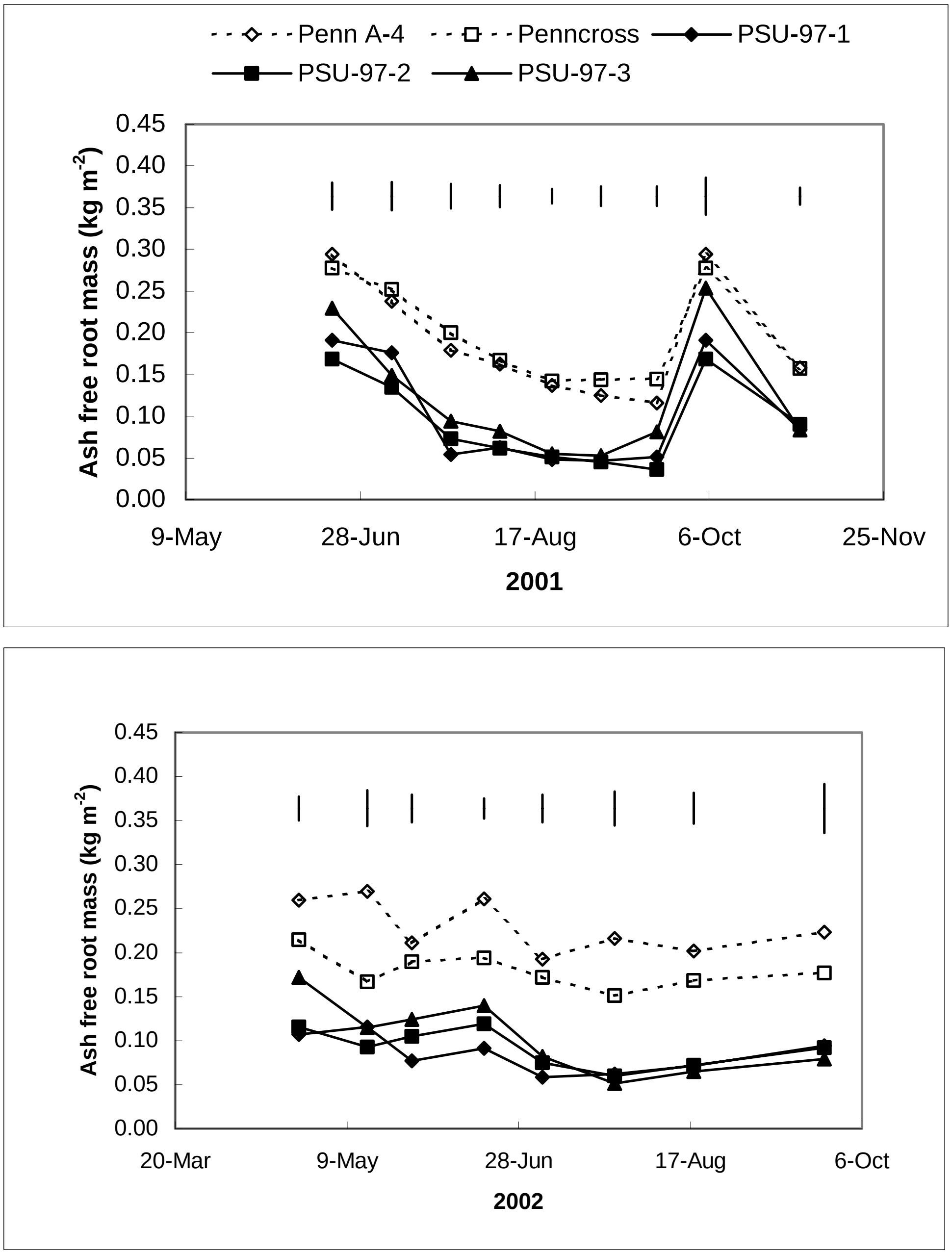
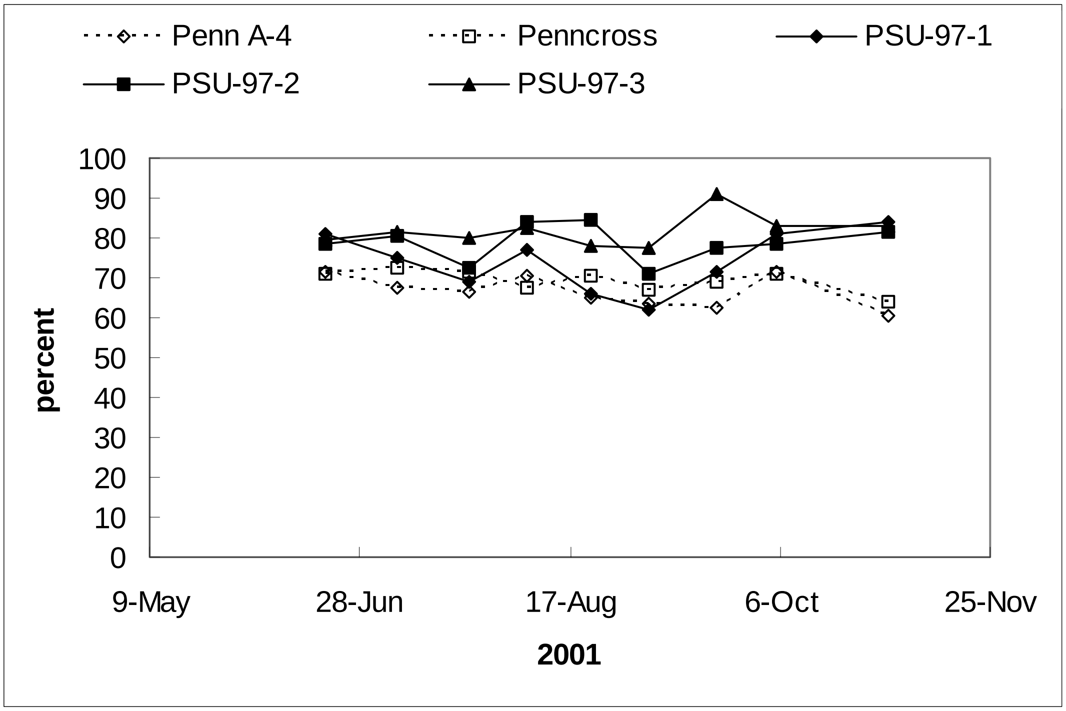


Figure 2.4: Root mass (ash free) in the 0-3 cm fraction per meter of surface area of two cultivars of creeping bentgrass (Penn A-4 and Penncross) and three cultivars of annual bluegrass (PSU-97-1, PSU-97-2, PSU-97-3) in the 2001 and 2002 growing season. Bars above each day represent standard error values for cultivar difference on each day when Day × Cultivar was significant.



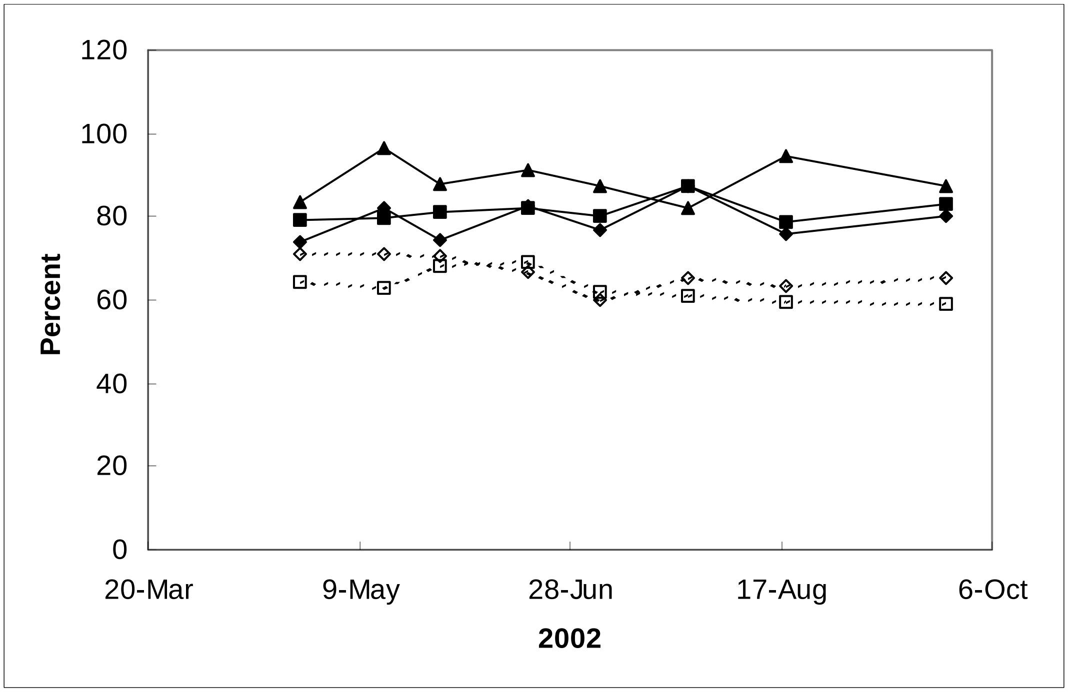
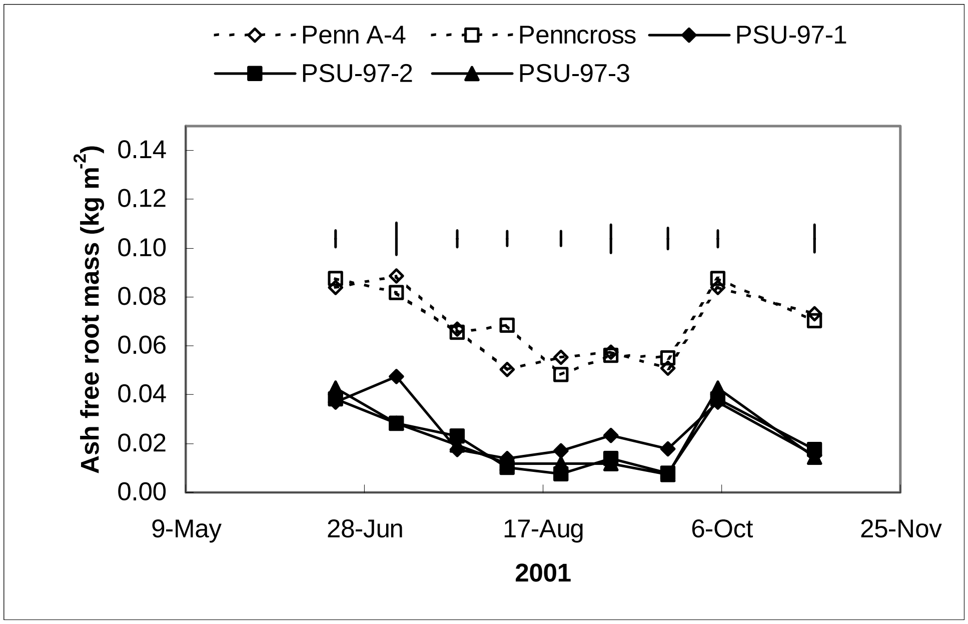


Figure 2.5: Percent root mass in the top 3 cm fraction per meter of surface area of two cultivars of creeping bentgrass (Penn A-4 and Penncross) and three cultivars of annual bluegrass (PSU-97-1, PSU-97-2, PSU-97-3) in the 2001 and 2002 growing season.



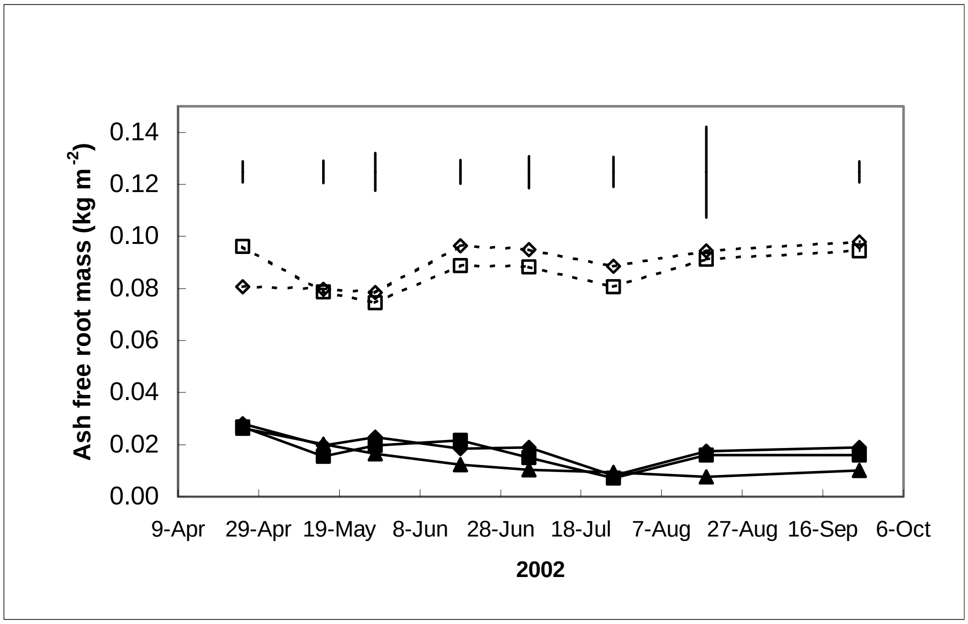
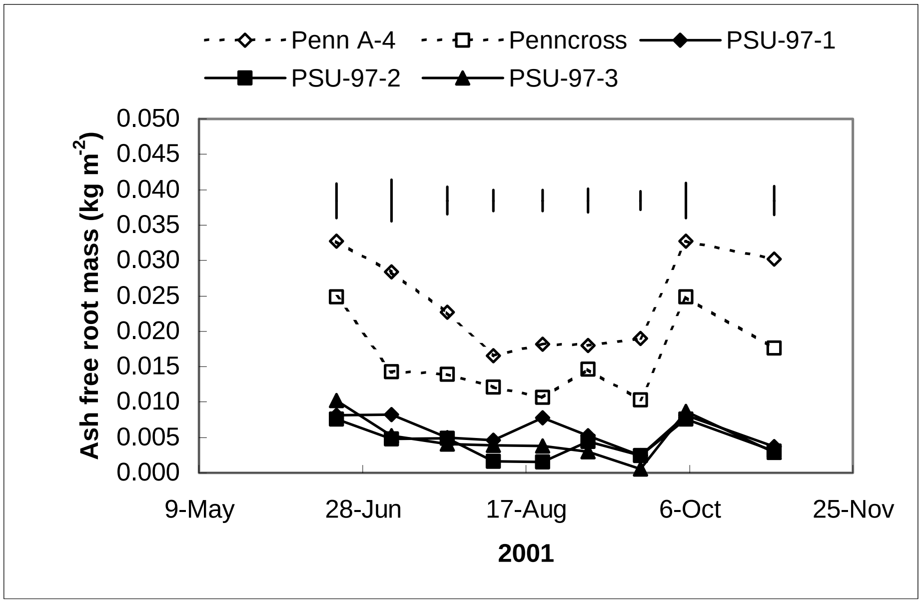


Figure 2.6: Root mass (ash free) in the 3-12 cm fraction per meter of surface area of two cultivars of creeping bentgrass (Penn A-4 and Penncross) and three cultivars of annual bluegrass (PSU-97-1, PSU-97-2, PSU-97-3) in the 2001 and 2002 growing season. Bars above each day represent standard error values for cultivar difference on each day when Day × Cultivar was significant.



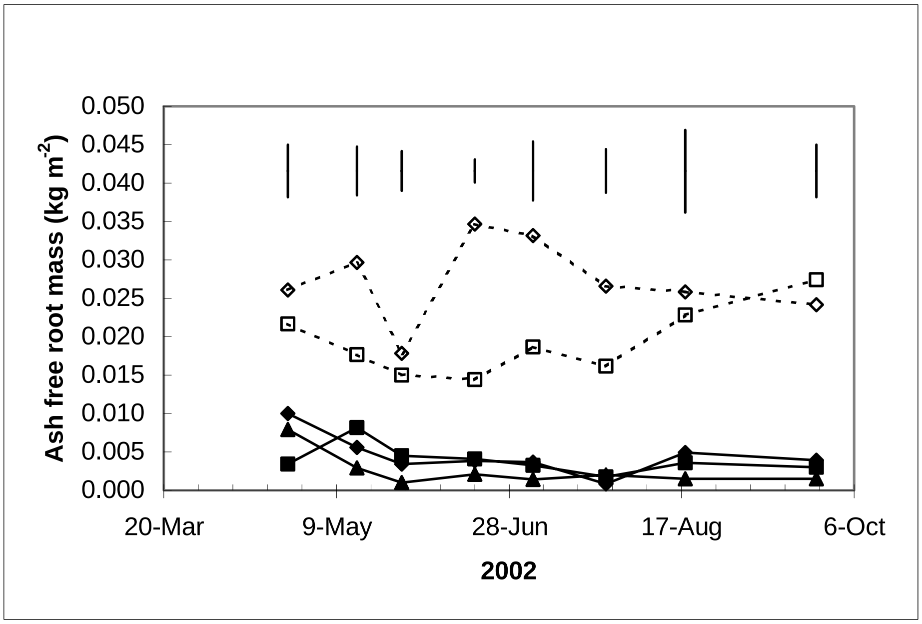


Figure 2.7: Root mass (ash free) in the below 12 fraction per meter of surface area of two cultivars of creeping bentgrass (Penn A-4 and Penncross) and three cultivars of annual bluegrass (PSU-97-1, PSU-97-2, PSU-97-3) in the 2001 and 2002 growing season. Bars above each day represent standard error values for cultivar difference on each day when Day × Cultivar was significant.

Chapter 3

Creeping bentgrass and greens-type annual bluegrass root response to two different nitrogen rates throughout the growing season

Introduction

Nitrogen plays a vital role in the growth and development of plants. Nitrogen has been shown to have a direct relation to creeping bentgrass shoot density, growth rate, and color (Schlossberg and Karnok, 2001; Green and Beard, 1969; Powell *et al*., 1967a; Powell *et al*., 1967b). Generally, as nitrogen increases within reasonable rates turf quality is increased as observed by increased shoot density, darker green color and faster recovery from stress. In one study involoving the influence of temperature, recovery was inhibited at the highest nitrogen rate at 32°C compared to the lower nitrogen rates at that same temperature. Though, at temperatures lower than 32°C the high nitrogen rate had the fastest recovery, showing an interaction between nitrogen rate and temperature (Hawes and Decker, 1977).

Crick and Grime (1987) showed that creeping bentgrass was able to alter its root growth to promote root proliferation into areas of high nitrogen. This strategy was successful for maximizing nitrogen acquisition when the nitrogen was present for extended periods but it was less efficient when it was present for shorter, less predictable periods. This study was conducted in a hydroponic nutrient solution, a different system than a closely mowed golf green with a constructed root zone, so its application to the field is unclear.

While the effects of temperature and other seasonal changes on the rooting of creeping bentgrass on golf greens are becoming better defined, the role of fertility, particularly nitrogen, has been more difficult to ascertain. In contrast, the role of fertility, especially nitrogen, on the shoot growth of creeping bentgrass is well defined (Green and Beard, 1969; Powell *et al*., 1967a; Powell *et al*., 1967b). Some studies have shown reduced root growth in bentgrass species in response to higher nitrogen rates (Schlossberg and Karnok, 2001; Christains *et al*., 1979; Schmidt and Blazer, 1967; Madison, 1962). In contrast, other studies have shown increased root growth in bentgrass species in response to higher nitrogen rates (Kohlmeier and Eggens, 1983; Bell and DeFrance, 1944). It is possible that these discrepancies in results may be caused by differences in the range of nitrogen fertility rates applied in the different studies. The experiments showing reduced rooting in response to higher nitrogen rates may have been applying nitrogen at a rate that ranged from adequate to excessive. When excessive nutrients are present the bentgrass species may allocate more of their resources to above ground tissues to to better compete with other species for aerial resources (Barta, 1975; Caloin *et* al., 1980; Jarvis and Macduff, 1989). Kohlmeier and Eggens (1983) observed increased root growth in turfgrass with high nitrogen treatments, probably because the low nitrogen rate of 1.5 kg 100 m^{-2} per season was low enough to greatly inhibit the overall growth of the plants when coupled with the wear treatments that were applied. Their treatment combinations may have resulted in nitrogen deficient plants with reduced overall soil coverage, resulting in fewer roots per unit land area. Another possible explanation for Kohlmeier and Eggens results is that root growth at different depths in their study may have been affected by their treatments while total root mass reacted in a different manner. Schlossberg and Karnok (2001) showed that it is important to determine the distribution of root length density with soil depth in addition to measuring total root length density to assess differences in rooting between cultivars and nutrient regimes.

Annual bluegrass also is affected by nitrogen rates. Invasion of annual bluegrass into creeping bentgrass swards maintained as golf greens has been observed to increase with increasing nitrogen rates (Kohlmeier and Eggens, 1983). Dest and Guillard (1987) showed that withholding nitrogen fertilization from a golf course fairway for up to three years reduced the amount of annual bluegrass encroachment into the stand. Although phosphorus has been implicated in the importance of annual bluegrass invasion, the specific affects of different nitrogen rates on annual bluegrass growth, beyond color and general turf quality of the stand (Varco and Sartain, 1986; Waddington, 1978), is not well documented. The effect of nitrogen on root growth of annual bluegrass has not been reported.

Increasing biomass allocation to roots will likely increase plant capacity for nutrient capture (Gleeson and Tillman, 1992; Bowman *et al*., 1998), although increased nutrient uptake kinetics can also contribute to increased nutrient capture (Caldwell *et al*., 1992). It is important to note that nutrients such as nitrogen are not the only limiting resources for plant growth. Water and light, often leading to carbon deficiencies, can also be considered limiting resources (Chapin *et al*., 1987; Tillman and Wedin, 1991). Another possible limiting resource is physical space. Annual bluegrass has essentially evolved on golf greens, an environment of steady water and nutrient supply, and may be best suited for competing for space and may not show plasticity of root biomass allocation to areas of high nutrient supply

Understanding how nitrogen affects both creeping bentgrass and annual bluegrass will aid in our understanding of how the growth of these two species interact on a golf course putting green. This chapter concentrates on the comparison of each species to the different nitrogen rates. Comparisons between the root growth between individual cultivars was discussed previously in chapter 2.

Materials and Methods

Plant materials and growing conditions

A description of plant materials and growing conditions for the field plots is described in the chapter Chapter 2. Only differences in analysis described in chapter 2 and methods for the analysis of root length are described below.

Experimental design and statistical analysis

The cultivars were arranged in a randomized strip-split-plot design with three replicates (figure 3.1). Two sub samples were taken from each split-plot (fertilizer treatment). The sub samples were then averaged to attain a value of each split plot on each date on which the data was collected (Date of Harvest). Analysis of variance was performed as repeated measures using the PROC MIXED procedure of the Statistical Analysis System (SAS Inc. Carey, NC). In order to better understand the effects of the nitrogen treatment within a species, the bentgrass and annual bluegrass data were analyzed separately. The main effects of Date of Harvest (D), Nitrogen rate (N) and Cultivar (C) were tested with the Nitrogen rate × Date of Harvest × Cultivar (N × D × C) and the N × D × C interaction was tested against the residual error. Differences between fertilizer means at a given date of harvest or between times for a given cultivar were separated by least significance difference test at the 0.05 level. Due to limitations in the repeated measures design, the 2001 and 2002 seasons were treated separately (Litell *et al*, 1996). For both seasons means were separated using LSD at the 0.05 level and differences on specific days were separated using the “SLICE” command in SAS.

Measurement of Specific Root Length

The ethanol-preserved roots were dyed (neutral red) and root lengths of the samples were attained by scanning them on a flatbed scanner using WinRhizo software (Regent Industries, Canada). Specific root length was determined after calculating the dry weight of the scanned sample from the fresh and dry weights of a sub-sample.

Results

The high nitrogen treatments appeared darker green in color than the low nitrogen treatments throughout the duration of the experiment (Figure 3.1). In the first year of the experiment (2001), both fertility treatments maintained a healthy stand of turf. In 2002, in addition to the color difference, the low nitrogen treatment appeared to be of a lower turf quality than the high nitrogen treatment in both the creeping bentgrass and annual bluegrass plots. Throughout the experiment some mixing of the two species was observed, although it was still possible to sample each plot as a monoculture. The primary mixing that occurred in 2001 was annual bluegrass invasion into the creeping bentgrass plots and in 2002 the creeping bentgrass encroached into the annual bluegrass plots (quantitative data not recorded).

Creeping Bentgrass

A nitrogen rate effect was observed for tiller densities in 2001 between the high nitrogen treatment (47.7 tillers cm^{-2}) and the low nitrogen treatment (42.6 tillers cm^{-2}). In 2002, there was no overall fertilizer effect on tiller density although there was a nitrogen rate by day (N × D) interaction and tiller density increased with the high nitrogen rate on the April 25, August 18, and September 25 harvest dates (Table 3.1, Figure 3.2). Despite finding no nitrogen rate by cultivar (N × C) interaction, the tiller density differences observed in the second year are due to increased tiller densities in the Penn A-4 at the high compared to the low nitrogen rates. In 2001, tiller densities were greater throughout the summer months compared to the spring and fall with an exception of the last harvest date in November where tiller densities equivalent to that of the summer months was observed. Differences in tiller densities were also greatest in the summer months and then diminished on the last two sampling dates, in October and November.

There were no differences between the two nitrogen rates in the total root mass, root mass in the top 3 cm, and root mass in the 3-12 cm section of the root zone (table 3.1). Although in 2001, there was a nitrogen rate by cultivar (N × C) interaction, most likely caused by the reduction in root mass of the Penn A-4 in the low nitrogen treatment in August and September that was not as severe in the high nitrogen treatment (Figures 3.3, 3.4, 3.5). There is also a significant nitrogen rate by day (N × D) interaction in the 3-12 cm section of the root zone ($P = 0.0024$). The low nitrogen rate produced greater root mass than the high nitrogen rate treatment in the 3-12 cm section of the root zone on dates in June and October in 2001.

Below 12 cm in 2001, both cultivars showed significantly more root mass in the low compared to the high nitrogen treatments ($P = 0.006$). Means for Penn A-4 were 0.025 g and 0.022 g for the low and high nitrogen treatments, respectively, and 0.017 and 0.014 g for the Penncross low and high nitrogen treatments, respectively. The nitrogen rate by cultivar by day (N × C × D) interaction was also significant ($P = 0.0068$) because the low nitrogen treatment in the Penn A-4 produced less root mass than the high nitrogen treatment in September (Table 3.1, Figure 3.6). In the second year of the experiment, the root mass below 12 cm was not significant between nitrogen treatments, although the N × C interaction showed a possible trend ($P=0.0672$). This trend is most likely due to a nearly significant treatment difference between cultivars at the low nitrogen treatment ($P = 0.0514$) while there was no difference between cultivars at the high nitrogen treatment ($P = 0.4637$).

Annual Bluegrass

The three annual bluegrass cultivars were pooled together for comparisons of nitrogen treatments because there were no nitrogen rate by cultivar (N × C) interactions (Table 3.2). Increased tiller densities were found throughout both growing seasons in the high nitrogen treatments ($P < 0.0001$). Tiller densities in 2002 were higher than in 2001 although, the general differences between nitrogen treatments remained constant (Figure 3.7).

The fertilizer treatments had no effect on annual bluegrass root growth in the 2001 growing season. In 2002, there were fertilizer effects in the total root mass ($P = 0.0266$) and in the root mass in the top 3 cm of the root zone ($P = 0.0116$). The high nitrogen treatments had more total root mass (0.129 g) than the low nitrogen treatments (0.092) (figure 3.8). A similar pattern was observed with the roots in the top 3 cm, the high nitrogen treatments averaged 0.113 g while the low nitrogen treatments averaged 0.076 g (figures 3.9). These difference were not apparent in the 3-12 cm section of the root zone (figure 3.10). The root mass below 12 cm of depth is not shown because of the very small amount of roots present in that zone.

Specific Root Length

Specific root lengths of the cultivars within the two species were pooled because no differences were observed between cultivars within species. The creeping bentgrass varieties had similar specific root lengths in both the high nitrogen and low nitrogen treatments (figure 3.11). Creeping bentgrass specific root lengths of the high and low nitrogen treatments were the same as the specific root length of the annual bluegrass in the high nitrogen treatment. The specific root length of annual bluegrass in the low nitrogen treatment was higher than that measured in the high nitrogen treatment.

Discussion

The purpose of this study was to explore how tiller densities and root mass, including distribution at different depths, of creeping bentgrass and annual bluegrass cultivars change in response to a high and a low nitrogen rate while being maintained at a mowing height of 3.2 mm. Annual bluegrass invades creeping bentgrass stands and is a highly successful competitor at low mowing heights (Beard *et al.*, 1978). Creeping bentgrass cultivars with high tiller densities resist annual bluegrass invasion better than those with low tiller densities (Beard *et al.*, 2001). While the high nitrogen rate increased tiller densities of both Penncross and Penn A-4 creeping bentgrass in the first year of the experiment, they also increased tiller densities of the annual bluegrass varieties in both years of the experiment. Thus, higher nitrogen rates may not lead to a reduction of annual bluegrass invasion.

Hawes and Decker (1977) showed that increased nitrogen rates hastened turf recovery from stress as long as temperatures were not supraoptimal. In the first year of this experiment, the Penn A-4 roots in the low nitrogen treatment may have been slow to recover from the summer heat stress (Figures 3.3-3.5). This resulted in a decreased root mass in all sections of the root zone in the low compared to the high nitrogen treatment. The absence of this trend in Penncross and the increased tiller densities at the high nitrogen rate of Penn A-4 on 3 dates in 2002 may show an increased sensitivity to nitrogen rate in Penn A-4 compared to Penncross.

The nitrogen in this experiment was applied in liquid form on a regular basis and the plots were watered after fertilizers were applied to maximize root uptake of the fertilizers. The nitrogen may have been available to the plants for only a short time due to the highly mobile nature of nitrogen and the high nitrogen uptake rates of creeping bentgrass (Liu *et al*., 1993). Crick and Grime (1987) showed that temporal availability of nitrogen is important in determining the advantage of changing root growth in response to spatial nitrogen supply. The increase in root mass below 12 cm at the low nitrogen rate that the creeping bentgrass in my experiment experienced in 2001 is evidence that creeping bentgrass is attempting to maximize nitrogen uptake by exploring a greater portion of the root zone. Bowman *et al*. (1998) showed that a cultivar of creeping bentgrass with a deeper, more extensive root zone was able to capture more nitrogen than a shallower rooted cultivar.

The increased creeping bentgrass root mass observed below 12 cm in the low nitrogen treatments in 2001 occurred on harvest dates in June and October but not in July and August. The increased resource allocation to root growth at deeper depths in the low nitrogen treatment may only occur when carbon is not limiting. In the summer months, carbon is limiting in closely mowed turfgrass due to increased respiration rates and limited photosynthesis (Huang and Liu, 2003; Gao and Huang 2000). During these times the plants no longer alter their root growth to increase nitrogen acquisition at the low the nitrogen treatment. Another possible explanation is that as the amount of root mass in the lower portion of the root zone declined in summer, the differences between the high nitrogen and low nitrogen treatments became too small to be detected by my methods.

In a highly cultured system such as a golf green, the plants are rarely presented with a limiting nutrient supply. When water and nutrients are supplied at regular intervals the competitive advantage of plasticity to maximize resource uptake may be limited (Hutchings and de Kroon, 1994; Robinson *et al*., 1999). The annual bluegrass cultivars' lack of increased root mass in response to low nitrogen treatments throughout the experiment may be due to their evolution in highly cultured environments. This evolutionary process is facilitated by annual bluegrass's ability to flower and produce seed at very low mowing heights. Thus, the resulting genetic variation is selected upon resulting in improved adaptation to uniformly available nutrient resources.

Annual bluegrass altered its root growth in response to nitrogen rates. In 2002, the annual bluegrass showed increased root mass at the high compared to the low nitrogen rate, a response similar to what was found with creeping bentgrass in other studies (Kohlmeier and Eggens, 1983; Bell and DeFrance, 1944). One explanation for this response is that high nitrogen treatments stimulated photosynthesis and tillering, leading to enhanced total growth including root mass. Belanger *et al*. (1992) hypothesize that in perennial swards of grass the relative activity of the shoots or roots as a carbon sink may be set, explaining the lack of increased biomass allocation to roots in low nitrogen treatments. The annual bluegrass is instead allocating carbon to the shoots for increased light absorption at all times regardless of its nitrogen status resulting in the observed high tiller densities and competitive ability of annual bluegrass. The greater root mass in the high nitrogen treatment over the low nitrogen treatment was observed only in the top portion of the root zone, providing evidence that it may have been related to the increased tiller densities. Despite this explanation, a similar response was not observed in 2001, when tiller densities also were greater at the high compared to the low nitrogen rate. Increased growth of the roots in response to nitrogen can also be affected by the stage of growth of the grass, weather it is in a vegetative stage or setting seed (Waremburourg and Shakiba, 1987; Waremburg and Paul, 1977). The ability of annual bluegrass to set seed at low mowing heights may limit its ability to respond to the low nitrogen rates. Annual bluegrass may be less plastic in its ability to change its root mass and distribution in response to nutrient availability resulting in a direct relationship among number of plants, photosynthesis rate and root mass. Each individual plant produces a set amount of roots based on resources available for growth. The greater number of plants and resources, the greater the root mass will be in underneath those plants (Charles-Edwards, *et al*., 1986).

Generally, annual bluegrass has less total root growth than creeping bentgrass. Annual bluegrass is most competitive during times when temperatures are moderate, as in the spring and fall (Lush, 1988). The limited root system that annual bluegrass has may be the cause for its lack of competitiveness in the warmer summer months. The plasticity of plants to spatial and temporal nutrient supplies has been determined to be an important factor in determining nutrient uptake by plants and the resulting outcome of plant competition (Crick and Grime, 1987; Hodge *et al*., 1999; Jackson and Caldwell, 1996). Plant growth on golf greens is severely limited by low mowing heights (Hull, 1992). It is possible that annual bluegrass's less extensive root system is a result of evolution under low mowing heights. It also may have lead to different mechanisms than observed in creeping bentgrass to increase nutrient uptake under the low mowing heights of a golf green.

Another explanation for the competitive nature of annual bluegrass on creeping bentgrass golf putting greens is its ability to alter its specific root length in response to nutrient availability. Specific root length often increases in response to low nutrient availability (Fitter, 1985). The increase in specific root length could also have implications in the carbon balance of the plant. While thicker roots are more costly to produce they have a greater transport capacity (Fitter, 1987), possibly aiding in water acquisition. Since the nitrogen in my study was applied uniformly to the soil surface the increase in specific root length of the annual bluegrass may have been more apparent because most of the roots are to the surface of the soil and the greater percentage of root mass in the surface soil layers in the annual bluegrass cultivars (Figure 2.5). Plants with higher specific root lengths, or finer roots, tend to have more rapid proliferation of roots than plants with thicker roots such as in tussock grasses (Caldwell and Eissentstat, 1988). Increased proliferation of roots into high nutrient patches within the soil can significantly increase the accumulation of photosynthates for transport into the root systems and alter root construction cost and uptake kinetics (Eissenstat and Caldwell, 1988; Drew and Saker, 1975, Jackson *et al*. 1990; Jackson and Caldwell, 1991). High specific root length is associated with roots growing into nutrient rich patches (Huang, 1999; Lariguaderie and Richards, 1994; Huante *et* al. 1998) and construction costs based on root length are lower for plant root with a higher specific root length (Eissenstat, 1992; Huang and Eissenstat, 2000). Low mowing heights severely limit the energy available for root growth and have been shown to limit the total root mass in creeping bentgrass (Hull, 1992). The ability of annual bluegrass to increase its specific root length in response to the low nitrogen rate observed in the present study may allow it to increase its total root length without increasing its root mass and thereby increase nutrient acquisition with lower root construction costs than other grasses (Huang and Eissenstat, 2000). This would allow the annual bluegrass to acquire nutrients more efficiently than creeping bentgrass in a carbon limited environment.

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Tables and Figures

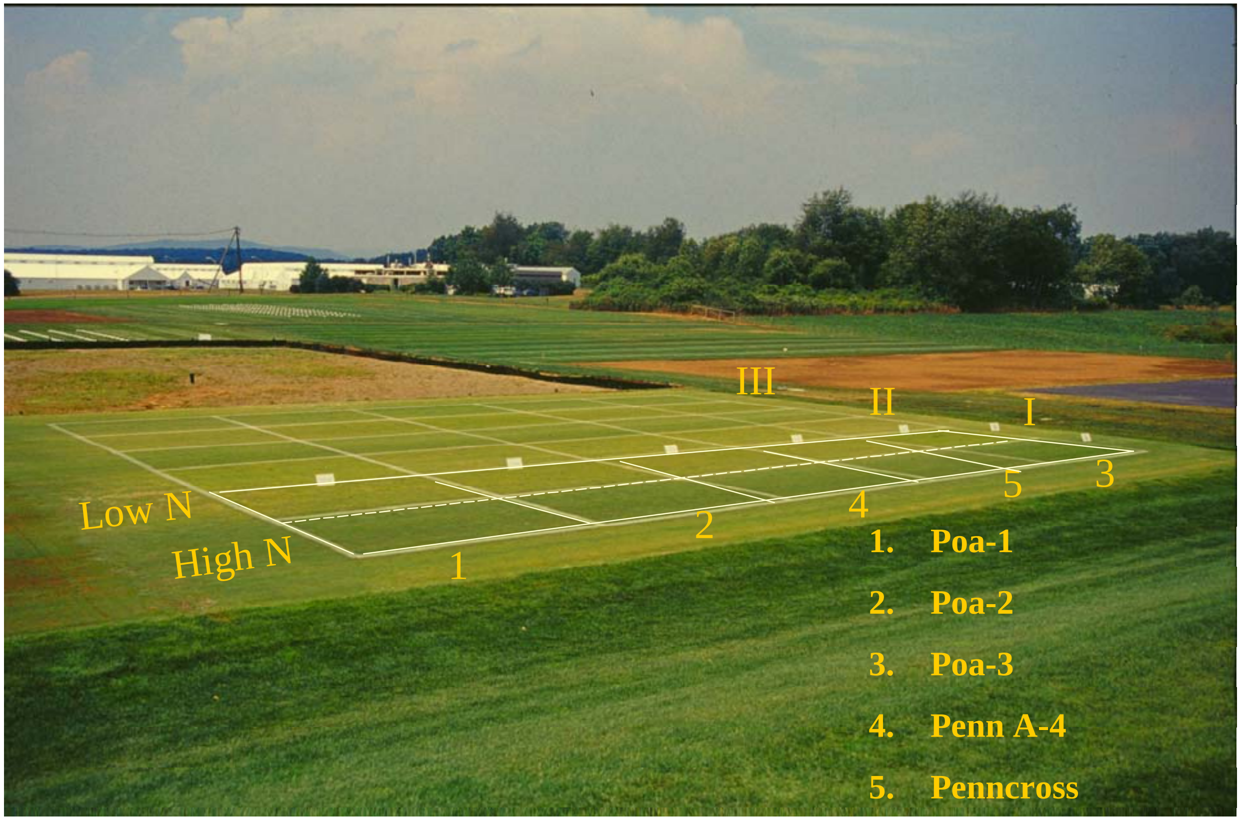
Table 3.1 Results of statistical analysis for the effects of nitrogen rate (N), harvest date (D) and cultivar (C) on tiller density and root mass at different depths of creeping bentgrass cultivars in 2001and 2002 taken from a 3.5 cm diameter core.

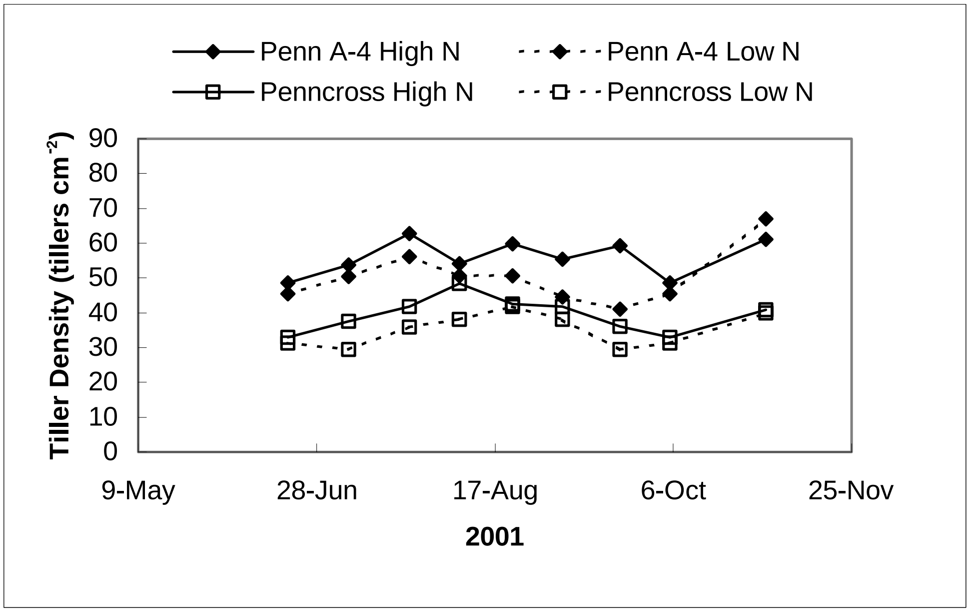
	Source of Variance	Tiller Density			Total Root Mass			0-3 cm Depth			3-12 cm Depth			Below 12 cm Depth		
		df	F	P>F	df	F	P>F	df	F	P>F	df	F	P>F	df	F	P>F
Year 1	N	1	17.2	0.0001	1	1.21	0.3335	1	0.28	0.6498	1	2.00	0.2647	1	8	0.006
	D	8	3.96	0.0092	8	56.9	<.0001	8	42.2	<.0001	8	18.3	<.0001	8	14	<.0001
	N × D	8	1.27	0.2805	8	1.38	0.2219	8	0.76	0.6367	8	3.56	0.0024	8	3.6	0.0017
	C	1	167	<.0001	1	0.03	0.8714	1	0.86	0.3570	1	0.20	0.6888	1	29	0.0058
	N × C	1	0.34	0.5620	1	9.50	0.0030	1	8.21	0.0060	1	6.60	0.0132	1	0.2	0.6437
	D × C	8	1.71	0.1161	8	0.60	0.7768	8	0.68	0.7081	8	1.86	0.0883	8	1.1	0.3475
	N × C × D	8	0.84	0.5740	8	1.39	0.2184	8	1.09	0.3846	8	1.03	0.4256	8	2.95	0.0068
Year 2	N	1	1.50	0.2974	1	3.67	0.1278	1	3.58	0.1313	1	10.5	0.0837	1	0.1	0.7869
	D	7	4.17	0.0009	7	1.21	0.3596	7	1.53	0.1762	7	2.77	0.0146	7	1.2	0.3427
	N × D	7	2.52	0.0251	7	0.95	0.4754	7	0.83	0.5632	7	1.58	0.1575	7	1.6	0.1604
	C	1	106	0.0009	1	19.8	<.0001	1	18.3	<.0001	1	0.47	0.4944	1	3.5	0.1525
	N × C	1	2.02	0.1604	1	0.11	0.7437	1	0.66	0.4188	1	1.90	0.1737	1	3.5	0.0672
	D × C	7	1.68	0.1317	7	0.75	0.6313	7	0.65	0.7115	7	0.57	0.7777	7	1.2	0.3458
	N × C × D	7	2.23	0.0447	7	1.13	0.3594	7	1.23	0.3025	7	0.67	0.6973	7	0.5	0.835

Table 3.2 Results of statistical analysis for the effects of nitrogen rate (N), harvest date (D) and cultivar (C) on tiller density and root mass at different depths of annual bluegrass cultivars in 2001and 2002 taken from a 3.5 cm diameter core.

	Source of Variance	Tiller Density			Total Root Mass			0-3 cm Depth			3-12 cm Depth			Below 12 cm Depth		
		df	F	P>F	df	F	P>F	df	F	P>F	df	F	P>F	df	F	P>F
Year 1	N	1	21.1	<.0001	1	0.31	0.6247	1	1.21	0.3478	1	0.34	0.6019	1	1.6	0.3372
	D	8	8.81	<.0001	8	51.4	<.0001	8	55.8	<.0001	8	27.9	<.0001	8	8.2	<.0001
	N × D	8	0.12	0.9982	8	0.82	0.5848	8	0.91	0.5099	8	0.51	0.8479	8	0.5	0.8472
	C	2	6.94	0.0298	2	1.93	0.2328	2	3.02	0.1295	2	0.76	0.5170	2	1.5	0.3229
	N × C	2	0.06	0.9460	2	2.79	0.0673	2	1.84	0.1657	2	2.49	0.0891	2	0.8	0.4488
	D × C	16	1.95	0.0265	16	2.70	0.0018	16	2.34	0.0065	16	1.93	0.0279	16	0.9	0.5912
	N × C × D	16	0.81	0.6836	16	0.61	0.8694	16	0.91	0.5583	16	0.58	0.8920	16	0.93	0.5430
Year 2	N	1	18.0	<.0001	1	15.5	0.0226	1	25.7	0.0116	1	1.42	0.3209	1	0.2	0.6978
	D	7	1.35	0.2437	7	12.6	<.0001	7	8.95	0.0002	7	7.65	0.0006	7	2.2	0.0490
	N × D	7	0.74	0.6368	7	1.70	0.1358	7	2.64	0.0232	7	0.88	0.5334	7	0.6	0.7863
	C	1	7.97	0.0477	1	0.22	0.6706	1	4.71	0.1240	1	0.79	0.4375	1	0.9	0.4139
	N × C	1	0.82	0.3680	1	0.10	0.7555	1	2.12	0.1522	1	0.44	0.5083	1	0.3	0.5647
	D × C	7	1.68	0.1311	7	2.07	0.0637	7	2.14	0.0596	7	1.97	0.0817	7	2	0.0759
	N × C × D	7	0.29	0.9510	7	1.19	0.3272	7	1.21	0.3189	7	0.78	0.6114	7	0.7	0.7095

Figure 3.1: A photograph of the field plots; the low N and high N strips represent 6.1 kg ha^{-1} or 18.3 kg ha^{-1} applied every 10 to 20 days, respectively.





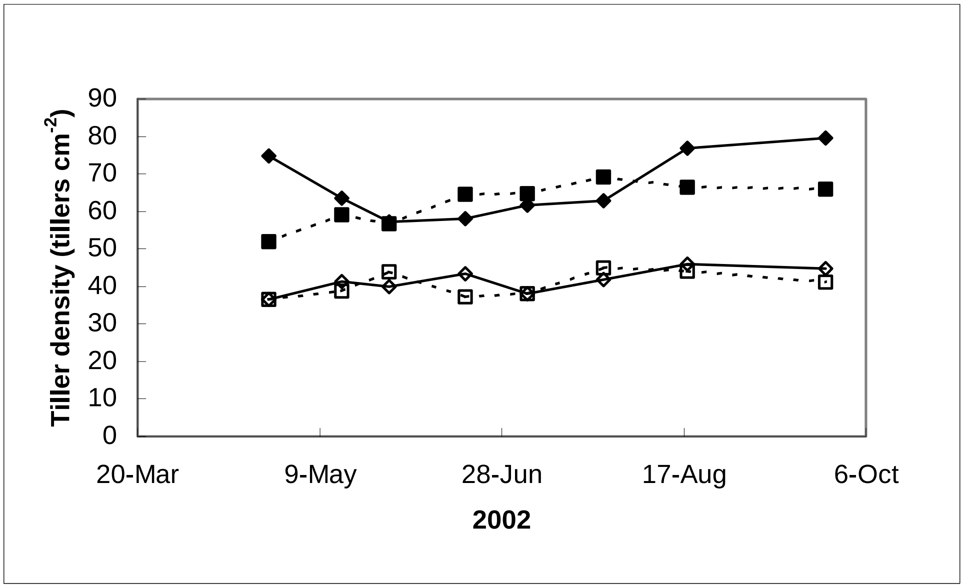


Figure 3.2: Tiller density (tillers cm^{-2}) of two cultivars of creeping bentgrass (Penn A-4 and Penncross) at two nitrogen rates in the 2001 and 2002 growing season.

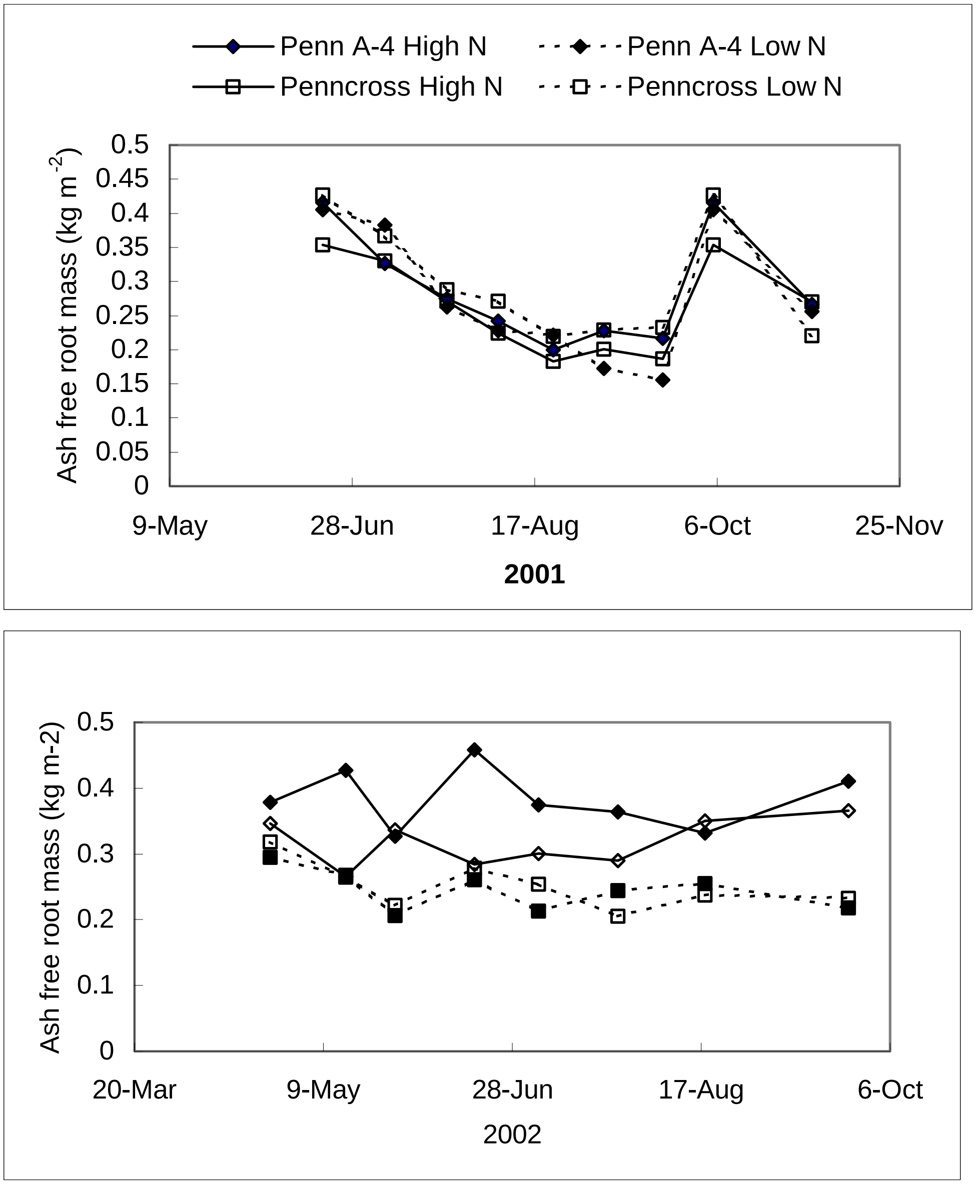


Figure 3.3: Total root mass (ash free) per meter of surface area of two cultivars of creeping bentgrass (Penn A-4 and Penncross) at two nitrogen rates in the 2001 and 2002 growing season.

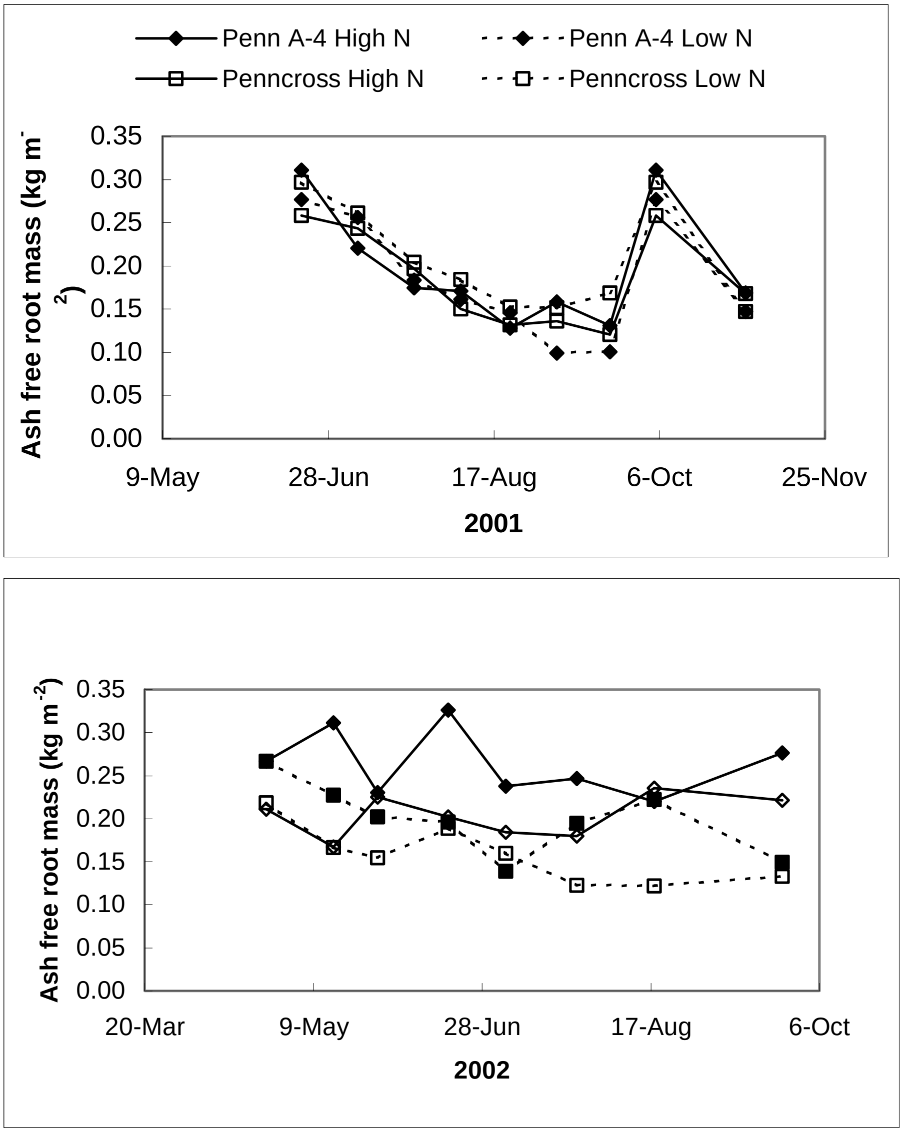
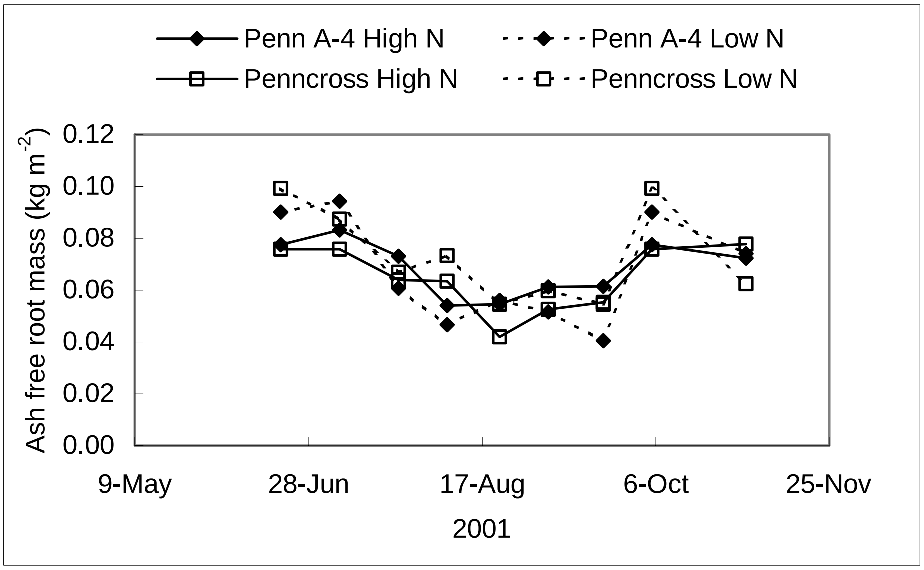


Figure 3.4: Root mass (ash free) in the 0-3 cm fraction per meter of surface area of two cultivars of creeping bentgrass (Penn A-4 and Penncross) at two nitrogen rates in the 2001 and 2002 growing season.



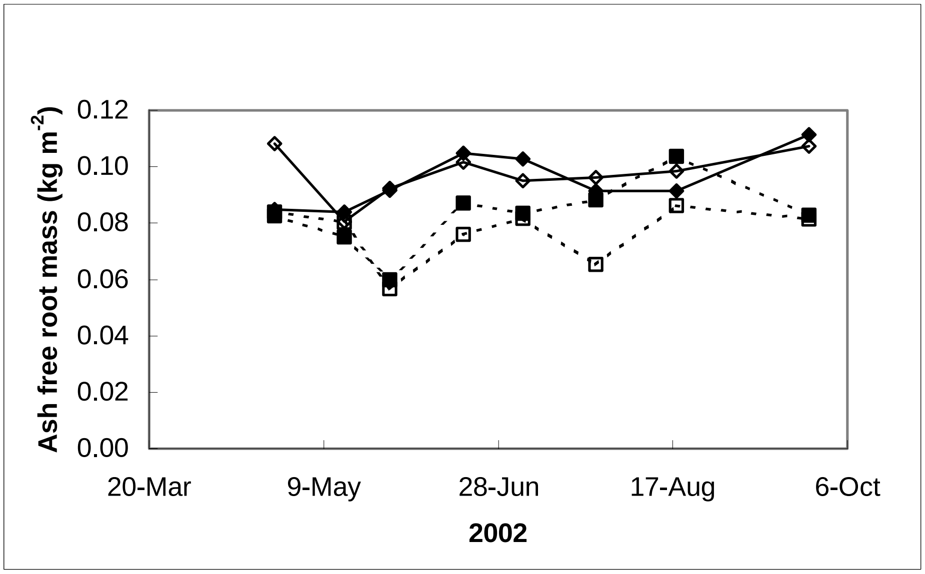


Figure 3.5: Root mass (ash free) in the 3-12 cm fraction per meter of surface area of two cultivars of creeping bentgrass (Penn A-4 and Penncross) at two nitrogen rates in the 2001 and 2002 growing season.

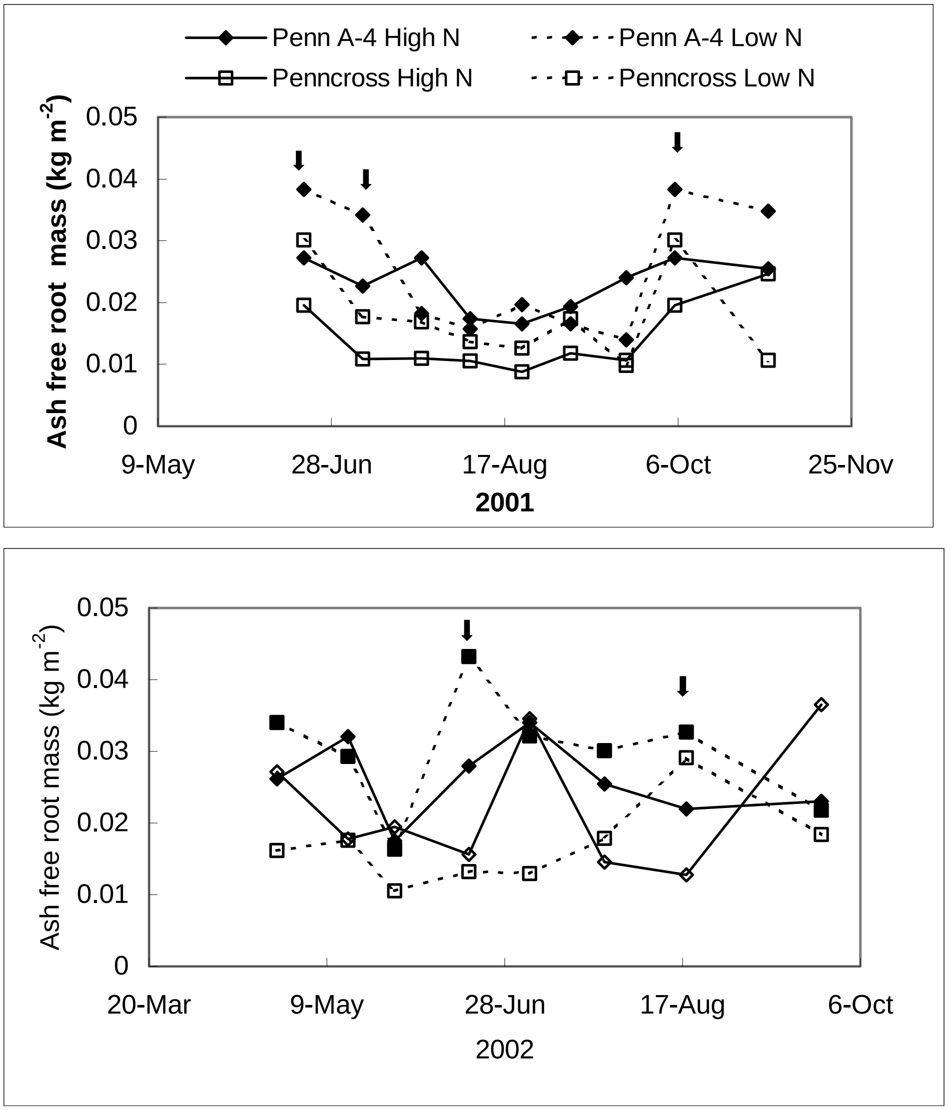


Figure 3.6: Root mass (ash free) in the below 12 cm fraction per meter of surface area of of two cultivars of creeping bentgrass (Penn A-4 and Penncross at two nitrogen rates in the 2001 and 2002 growing season. Arrows represent dates on which there was greater root mass in the Low N plots.

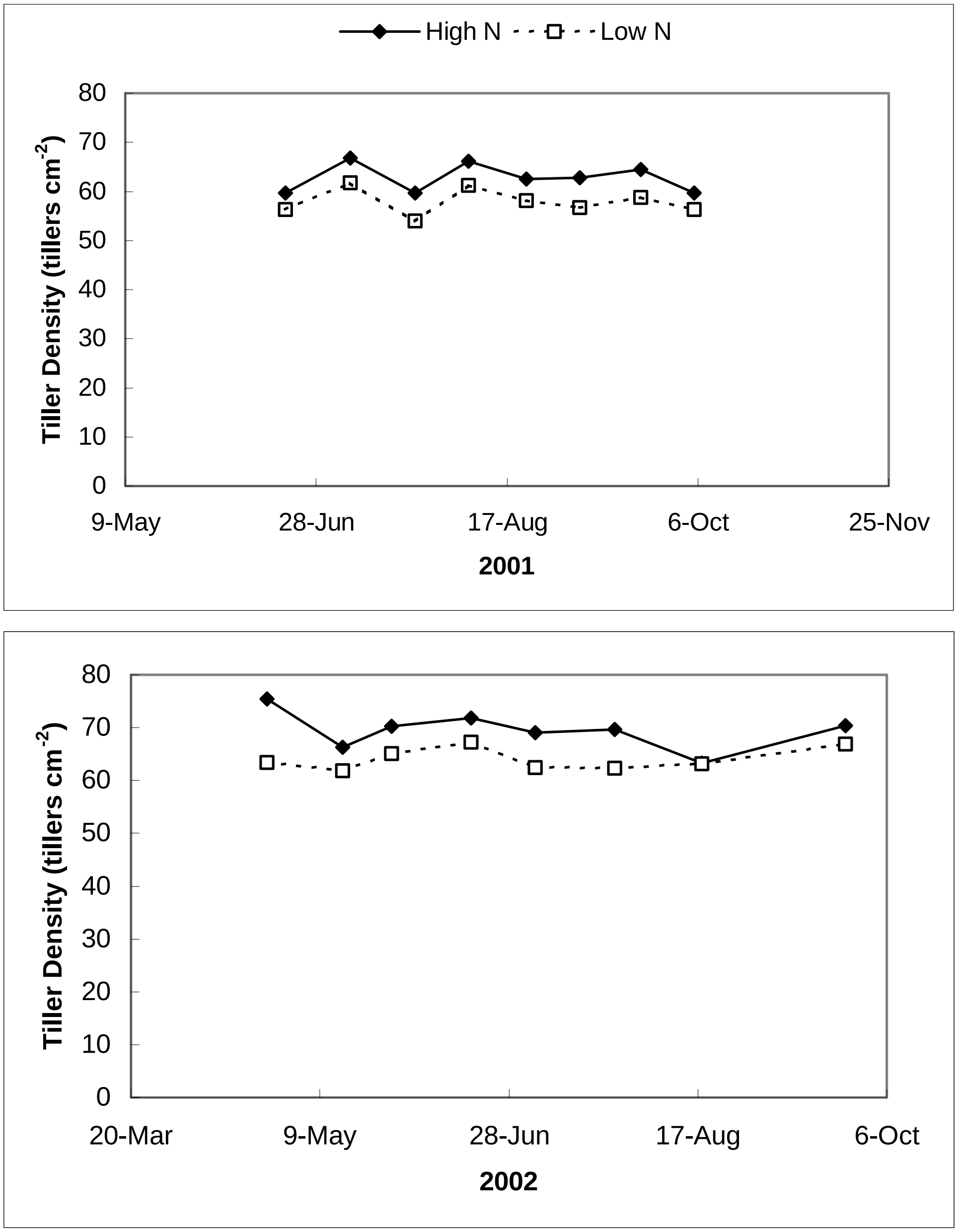


Figure 3.7: Tiller density (tillers cm^{-2}) of three annual bluegrass cultivars pooled together at two nitrogen rates in the 2001 and 2002 growing season.

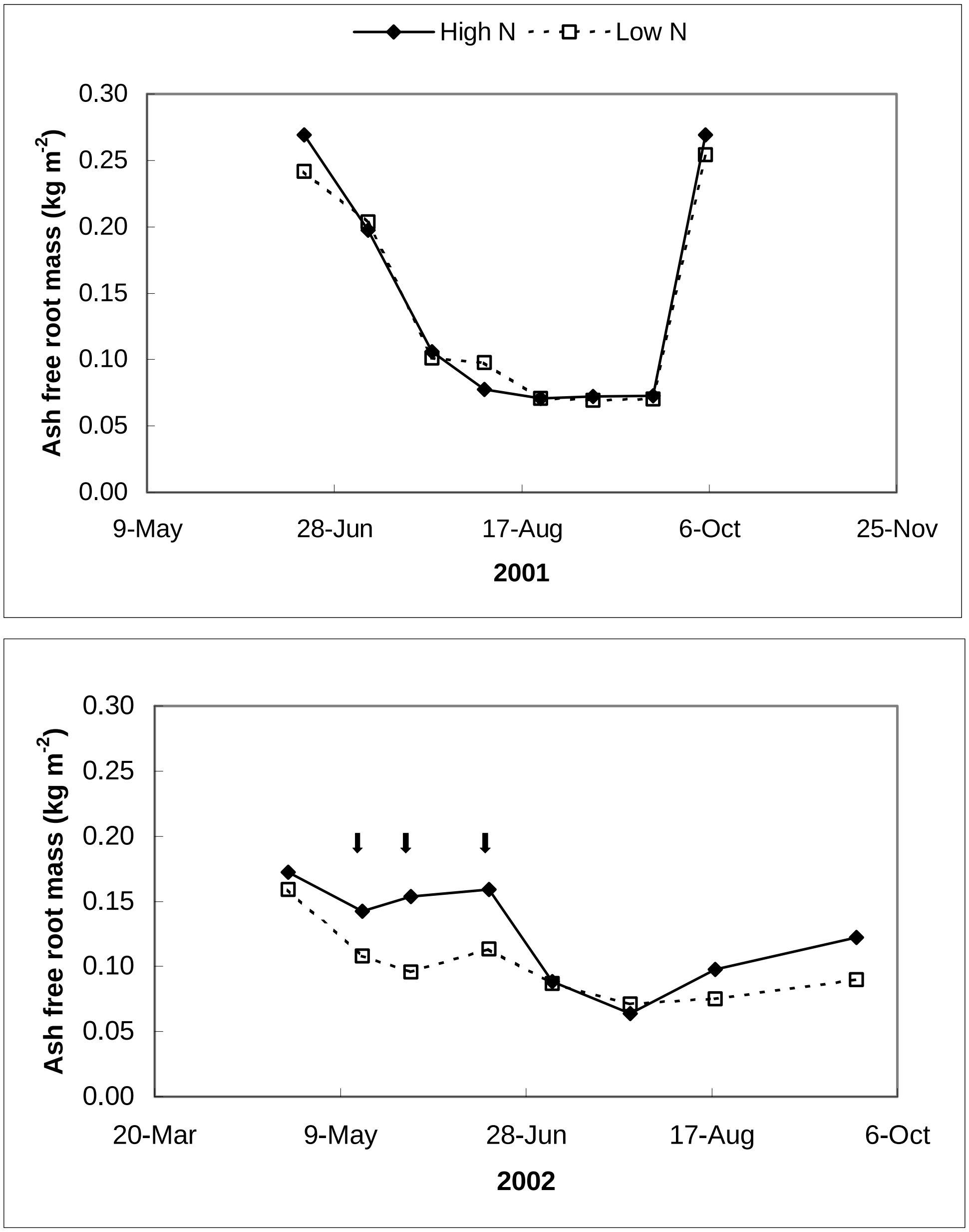


Figure 3.8: Total root mass (ash free) per meter of surface area of three annual bluegrass cultivars pooled together at two nitrogen rates in the 2001 and 2002 growing season. Arrows represent dates on which there was greater root mass in the High N plots.

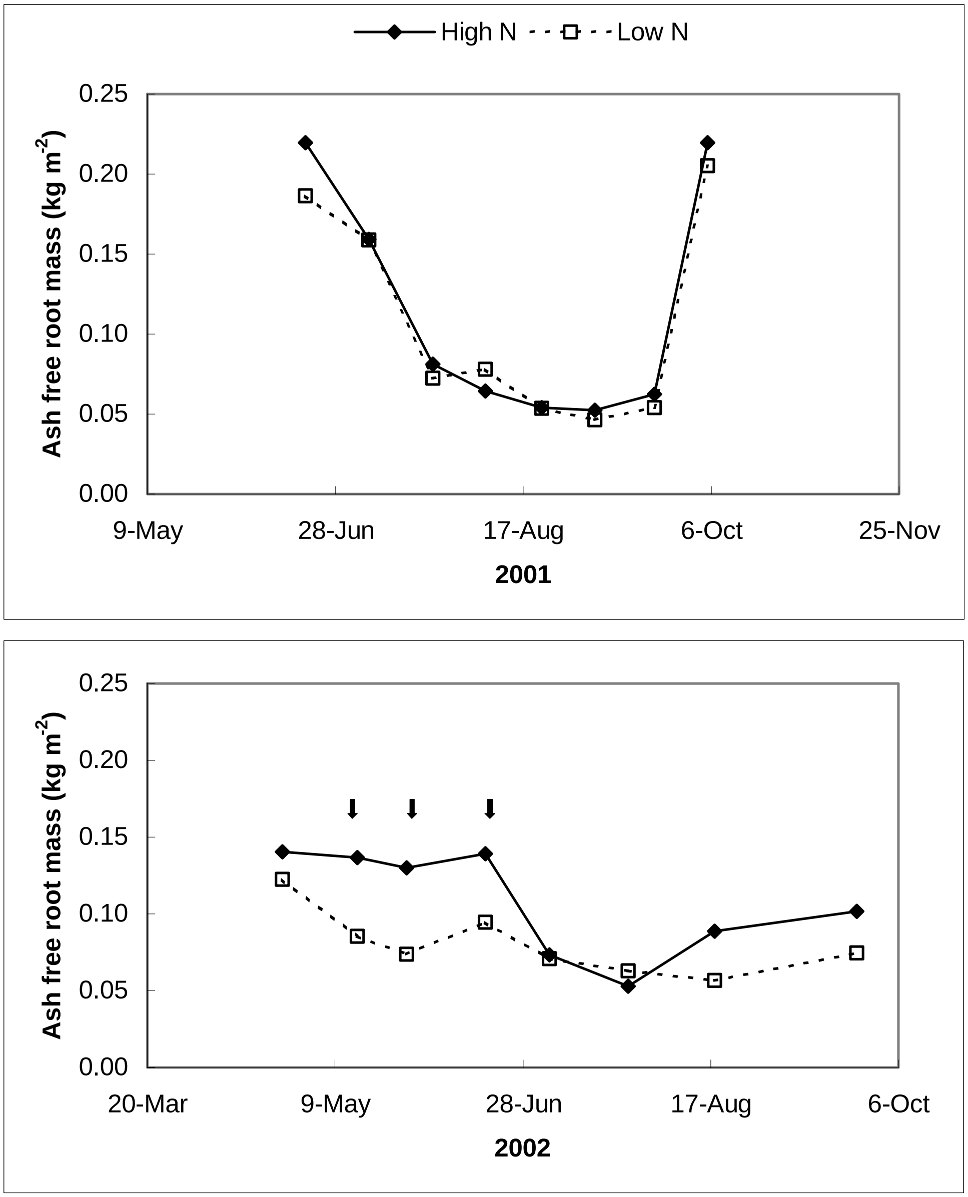


Figure 3.9: Root mass (ash free) per meter of surface area in the 0-3 cm fraction of three annual bluegrass cultivars pooled together at two nitrogen rates in the 2001 and 2002 growing season Arrows represent dates on which there was greater root mass in the High N plots.

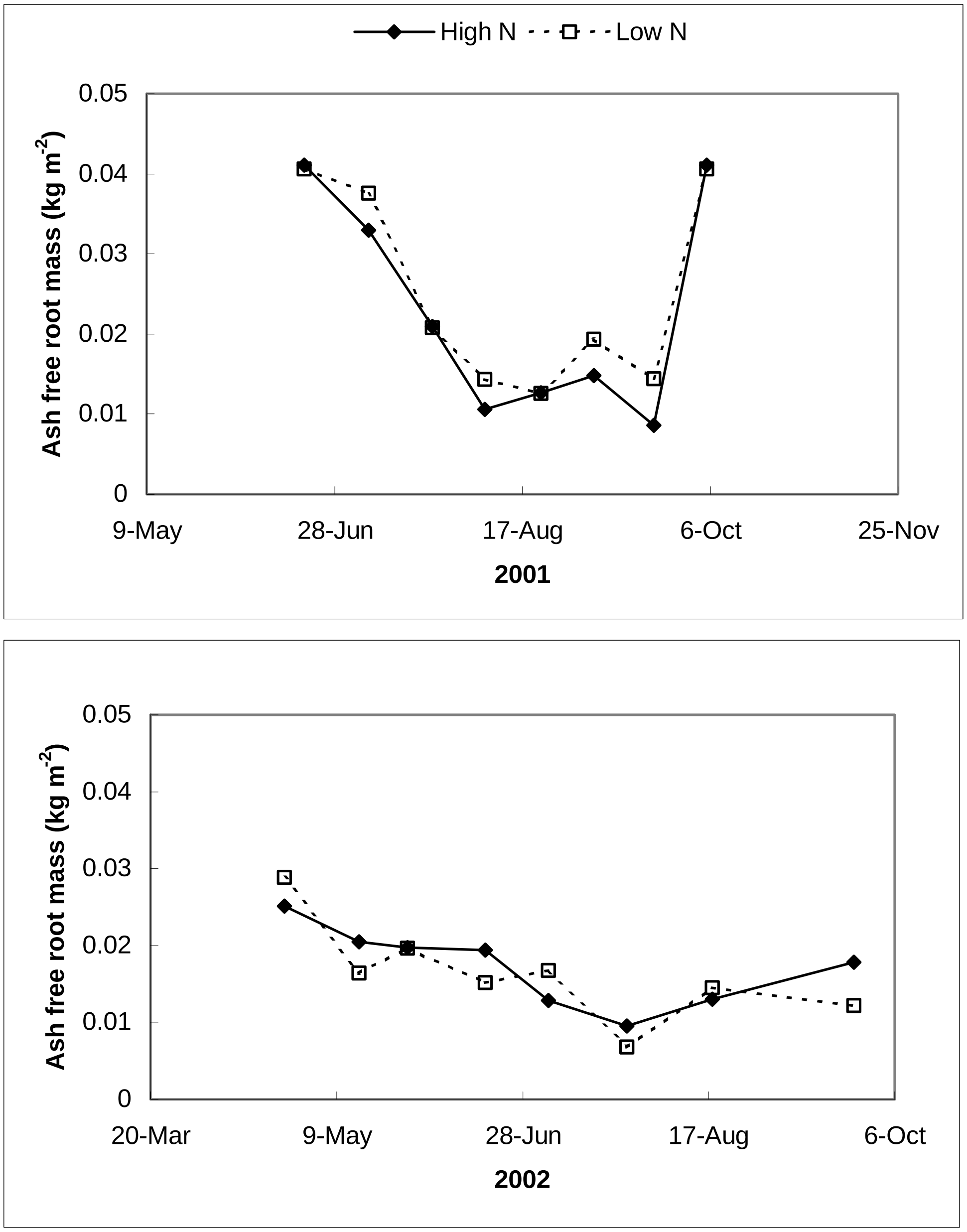


Figure 3.10: Root mass (ash free) in the 3-12 cm fraction per meter of surface area of three annual bluegrass cultivars pooled together at two nitrogen rates in the 2001 and 2002 growing season

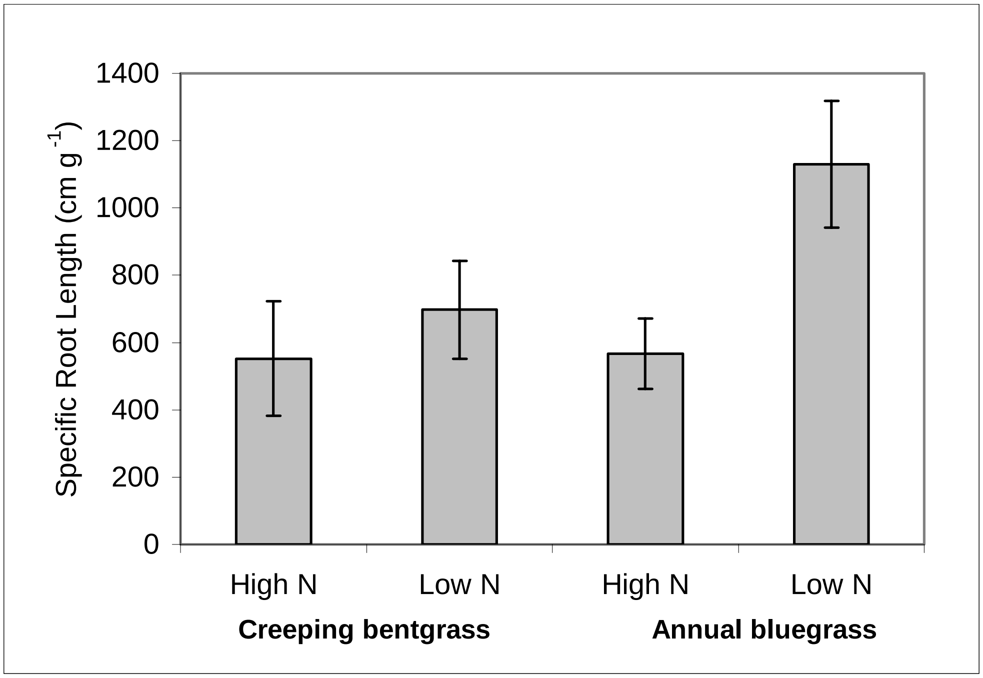


Figure 3.11: Specific root length of creeping bentgrass and annual bluegrass at high and low nitrogen rates from a field experiment conducted in the 2001 and 2002 growing season.

Chapter 4

Response of creeping bentgrass (*Agrostis stolonifera* L.) to spatial phosphorus supplies

Introduction

One of the most important functions of plant roots is to acquire nutrients needed for growth. The general role of phosphorus in plant nutrition is well defined. Plants growing in low phosphorus soils often are shorter in stature and typically have darker green shoots (Marschner, 1995). Phosphorus availability has also been shown to alter many aspects of root architecture and plants grown in low phosphorus soils have increased root-to-shoot ratios (Lynch and Beebe, 1995). Creeping bentgrass has been shown to alter its root architecture in response to nutrients. Crick and Grime (1987) showed that creeping bentgrass altered its root growth to increase root mass allocation to support proliferation into areas of high nitrogen. They demonstrated that this strategy was successful in maximizing nitrogen acquisition when the nitrogen was present for extended periods but less efficient when it was present for shorter, less predictable periods. It is probable that creeping bentgrass will also respond to spatial phosphorus supply.

Many mechanisms have evolved in plants to acquire phosphorus, including the release of root exudates that acidify the surrounding soil, releasing phosphorus into solution making it available for uptake by the plant (Bar-Yosef, 1996). Plants growing in soils with low, yet adequate, phosphorus levels tend to be more drought tolerant than plants growing in high phosphorus soils (Brown *et al*., 1998). These characteristics of plants growing in low phosphorus soils appear to be desireable for grasses on golf greens. If creeping bentgrass responds to spatial phosphorus supply, there is potential to encourage deeper rooting by strategically providing phosphorus deeper in the root zone.

Phosphorus is rarely applied as a single nutrient and most studies with phosphorus deal with a complex interaction of applied nutrients and nutrients already present in the soil. However, the few studies that have been conducted provide preliminary evidence that regulating root zone phosphorus levels may be important in manipulating turf quality. A decrease in bentgrass root weights was observed when a complete fertilizer was applied as opposed to a fertilizer without phosphorus (Holt and Davis, 1948). Creeping bentgrass receiving phosphorus applications was often lighter in color than creeping bentgrass not receiving phosphorus (Waddington *et al*., 1978). Phosphorus fertilizers have been incorporated into turfgrass seedbeds to improve seedling establishment. However, Turner, 1980 reported that surface applications of phosphorus appeared more effective than incorporation into the entire seedbed. Pellet and Roberts (1963) noted rates of high phosphorus caused the deterioration of Kentucky bluegrass during drought and adequate phosphorus levels are needed for rapid recovery after drought. Phosphorus levels are also implicated in the competition between creeping bentgrass and annual bluegrass and it is suggested that phosphorus may play an important role on annual bluegrass encroachment into bentgrass turf (Waddington *et al.,* 1978). Another study on acidic soils showed that adding phosphorus or making phosphorus more available increased the presence of annual bluegrass (Kuo, 1993). Despite these studies, there is still little understanding of how phosphorus affects turfgrass root distribution or the role of phosphorus in turf systems.

Phosphorus is a powerful regulator of plant growth and may be an important tool in improving the quality of close-cut turf such as golf greens. Conventional phosphorus fertilizers deliver high doses of phosphorus for limited times. The ideal situation in turf would be to hold the available phosphorus levels at a constant low level as would be found in natural soils. Conventional fertilizers do not allow for the delivery of phosphorus to a specific place in the root zone. This means that in order to study how turfgrass roots respond to spatial phosphorus supply the root zone must be split into different compartments. A novel fertilizer, originally developed for growing horticultural crops in soilless growth media (Coltman *et al*. 1982), could provide a method for studying optimal phosphorus placement in the root zone and eventually controlling phosphorus levels to manipulate plant growth by adsorbing PO_4 to alumina (Al_2O_3 X H_2O). The fertilizer is a solid-phase-buffered alumina bound phosphorus fertilizer (Al-P) and can be mixed into sand culture to maintain phosphorus levels at realistic low phosphorus concentrations (Elliott *et al*., 1983; Elliott, 1989).

Al-P is new technology that allows controlled release of phosphorus into the soil medium throughout multiple growing seasons, in amounts determined by actual plant need, without the need for grower monitoring and without nutrient leaching (Brown *et al*., 1999; Lin *et al*., 1996). Solid-phase buffering of phosphorus is provided by a solid aluminum oxide compound, formulated in granules the size and shape of sand grains. The alumina is treated with phosphorus and added to the growing media in very low concentrations. The phosphorus bound to the solid alumina releases a very low concentration of phosphorus into the root-zone in the range of concentrations found in natural soils (Elliot, 1989). Typically root distribution is correlated with nutrient distribution in the soil and both decrease exponentially with depth (Pregitzer *et al*., 1993). The Al-P could be mixed into the root zone at a specific depth, creating an environment where root depth and branching would be maximized, aiding in increased drought tolerance and in reducing both phosphorus and nitrogen leaching. If we define an optimum level and placement of phosphorus for creeping bentgrass and maintain these levels and placement, turf would be healthier and invasion of weed species would be reduced.

Research with soilless root mixes indicates that addition of phosphorus-charged alumina at 1% of the volume of the dry medium is sufficient for optimal plant performance of floriculture crops (Lin *et al.*, 1996). Preliminary work in turf species demonstrated that creeping bentgrass will grow satisfactorily in 80% sand: 20% peat with 1% Al-P as the sole source of phosphorus (Lyons *et al*., 2000). Because soluble phosphorus concentrations remain very low, negligible amounts of phosphorus are lost even if large quantities of water are flushed through the medium. In the systems that have been tested, leaching has been reduced to less than 1% of that in conventionally fertilized systems (Borch *et al*., 1998; Lin *et al*., 1996). Although the solid alumina releases very low concentrations of phosphorus, it acts as a buffer and is able to maintain that concentration under any condition. Thus, the alumina can be used to provide optimal phosphorus nutrition over time. This is in contrast to slow-release fertilizers, which can maintain adequate phosphorus concentrations in the root zone over extended periods of time, but release phosphorus as a function of pellet dissolution rather than plant requirements and do not prevent phosphorus leaching (Havis and Baker, 1985). Deep roots are usually associated with increased drought avoidance and healthy actively growing turf (Beard, 1973) and it has been shown that bentgrass genotypes with deeper more highly branched roots have less nitrogen leaching than shallower rooted genotypes (Bowman *et al*., 1998).

This chapter consists of 3 experiments. The first two experiments were to determine if creeping bentgrass would respond to spatial phosphorus supply and utilized a traditional split root apparatus and phosphorus in the form of nutrient solution. The third experiment was conducted to see if placement of phosphorus at deeper depths in the root zone, using Al-P, would result in an increased number of roots deeper in the root zone.

Materials and Methods

Plant Material

All three experiments used ‘Penn Lu’ a vegetative cultivar of creeping bentgrass. The source material was a stand of Penn Lu maintained in a greenhouse. In experiment 1 and 2, tillers were transplanted, one each, into root growth tubes. Experiment 1 was performed when each tube still had a single tiller. The remaining tubes were then allowed to grow with a nutrient solution and mowed at 2.5 cm until experiment 2 was to take place. Tillers from the original maintained stand were then used in experiment 3.

Experiments 1 and 2 (horizontal split root experiments)

These experiments were conducted in a climate controlled green house in the summer of 2000 and in the winter and spring of 2001. The experiments utilized an apparatus that allowed the roots to be separated horizontally into two different 2.5 cm diameter root growth tubes. In experiment 1, Penn Lu creeping bentgrass was transferred from 2.5 cm diameter root tubes, with one tiller per tube, and were maintained under optimal growing conditions in the greenhouse within the split root apparatus. In experiment 2, Penn Lu from root growth tubes containing multiple tillers, essentially a plug or core, was transferred into the split root apparatus. The tillers were removed from the growth tubes, the sand was washed from the roots and the existing root mass was separated so that equal amounts of roots were on both sides of the apparatus. The separation was accomplished by using 1.25 cm PVC plumbing junctions. The tillers were placed through a T junction and an elbow joint on each side directs the roots down into a root growth tube. After transplanting the plants, the PVC-T junction was filled with sand to hold moisture and to protect the top portion of the roots from desiccation.

Immediately after transferring the plants to the split-root system, the variable nutrient treatments were applied to the root growth tubes on each side of the apparatus. Three treatments were applied: plants received nutrient solution containing phosphorus (i) in both sides of the root zone (HH); (ii) with no phosphorus on both sides of the root zone (LL), (iii) with phosphorus on one side and nutrient solution without phosphorus on the other (HL). Nutrient solutions were added twice weekly and the plants were watered daily or as needed with tap water. The nutrient solutions were ½ strength Hoagland's solution with and without phosphorus (Hoagland and Arnon, 1950).

In experiment 1, the plants were transferred on June 15th and data collected August 15th is presented. In experiment 2, the plants were transferred on February 7th and the plants were harvested on April 27th. The plants were harvested by clipping the roots at the end of the PVC elbows where they entered the 2.5 cm diameter root growth tube. The shoots were clipped at the top of the PVC T Joint . The root mass contained within the PVC elbows and T joint was not measured because it was difficult to remove completely. The roots from each growth tube were washed by hand using a sieve and both these roots and plant shoots were dried at 70ºC for 48 hours and mass was recorded. The last harvest of experiment 1 included phosphorus analysis of the root and shoot materials using Murphy Riley colorimetric analysis (Lynch and Beebe, 1995). In experiment 2, the roots were then ashed at 605ºC and the resulting ash was subtracted from the dry weight resulting in an ash free dry weight. This eliminated any sand from the initial dry mass and resulted in more consistent root biomass measurements.

Both experiments used a completely random design; experiment 1 had five replicates per treatment per harvest date and experiment 2 had 10 replicates per harvest date. Differences in root mass and phosphorus content between the two sides of the split root system were analyzed using a paired student's T test. Differences in shoot mass and shoot phosphorus content were evaluated using LSD ($P<0.05$) tests.

Experiment 3 (Vertical phosphorus distribution)

Experiment 3 was a ten-week growth study in which plants were grown in 38 cm deep, 10 cm diameter, schedule 40 PVC pots in an attempt to simulate a golf green root zone. The pots were filled with 7.5 cm of pea gravel and then topped with 30 cm of sand conforming to USGA specifications for golf greens. This chapter will report the results from three treatments in order to show the effects of spatial phosphorus supply on root distribution. The control contained a non-amended sand throughout the root zone. The other treatments included the sand mixed with alumina-P fertilizer (Al-P) buffering the soil solution at 30 uM phosphorus with two different application techniques; a homogenous mix, and a 10 cm deep band starting 20 cm below the surface. The Al-P was mixed into the sand at a rate of 1% weight by volume (i.e. 10 grams per liter of soil mix). The only phosphorus supplied to the alumina-amended plants after transplanting came directly from the alumina-P mixed into the sand. The three treatments reported in this experiment are the control, 1% Al-P mixed and 1% Al-P Band. Two other treatments included in the study were a 2% Al-P Band and 4% Al-P band but the results were similar to the 1% Al-P band and therefore are not reported.

The plants were transplanted from a maintained stand of Penn Lu creeping bentgrass from a greenhouse. Three to four tillers were planted in each pot on December 16th and 17th, 2002, and the pots were placed in a completely random design in a climate controlled greenhouse. The plants were hand watered for one week and then irrigated daily with nutrient solution. The control received a complete nutrient solution and the AL-P amended treatments received a nutrient solution without phosphorus. The complete nutrient solution provided 4.4 mM nitrogen, 1.5 mM potassium, 0.5 mM phosphorus, 0.94 mM calcium, 0.25 mM magnesium and 0.25mM sulfur. The phosphorus free solution was identical without the phosphorus. Both solutions were supplemented with a complete micro-nutrient solution and were brought to a pH of 6.5 using 0.5 N NaOH and HCl.

The plants were mowed at 5 cm height on January 13th and the first of ten weekly harvests was performed on January 15th, 2003. Four replicates per treatment were harvested on each date. The plants were clipped just below the surface of sand to assure that the crown and stem tissue was included in the shoot mass. The tillers were separated and counted and the shoots were dried at 60ºC and weighed. The shoots were then ashed in a 500ºC muffle furnace and analyzed for phosphorus content. After the seventh week the tillers were no longer counted due to the large number present in each pot. The roots were washed by hand using a sieve. The entire root zone was harvested in mass for the first 7 weeks. In weeks 8-10 the root zone was split into the top 15 cm and the bottom 15 cm. The two portions of the root zone were then washed separately. The roots were dried at 60ºC and dry weights were taken. The sample was ashed in a muffle furnace at 605°C until the organic matter was burned off, typically 6-10 hrs. The ash weight was then subtracted from the dry weight to adjust for sand in the sample resulting in an ash free dry weight for the root samples.

Results

Experiments 1 and 2 (horizontal split root experiments)

In both experiments, the plants receiving no phosphorus in either side of the root zone had a greater than 50% reduction in shoot growth compared to treatments receiving phosphorus (figure 4.1). The treatments receiving phosphorus on only one side of the root zone had shoot growth that was similar to the growth of the plants receiving phosphorus on both sides of the root zone (figure 4.1). The plants in experiment 2 had two to four fold greater shoot mass and approximately half of the root mass of the plants in the first experiment (figure 4.1, 4.2). In both experiments, root growth was reduced in the no phosphorus treatment providing evidence of phosphorus deficiency resulting in reduced mass of the entire plant (figure 4.2). Root mass in the side of the root zone receiving phosphorus (0.309g for experiment 1; 0.1661g for experiment 2) was greater than the side receiving no phosphorus (0.0188 for experiment 1; 0.1351 for experiment 2).

Phosphorus content response of the shoots and roots from treatments in experiment 1 paralleled the root and shoot dry weight responses (figure 4.3). The shoots from the no phosphorus treatment had 30% of the phosphorus content of the treatments containing phosphorus and those treatments, whether spatially supplied or not, had equivalent phosphorus content. The phosphorus content of roots in the high phosphorus side of the HL treatment had 17% more phosphorus than roots in the no phosphorus side. Moreover, the phosphorus content of roots in the no phosphorus side of the HL treatment was greater than the phosphorus content of roots in the treatment (LL) receiving no phosphorus in either side of the root zone.

Experiment 3 (Vertical phosphorus distribution)

The objectives of experiment 3 were to examine whether creeping bentgrass roots would respond to a vertical distribution of phosphorus and to determine if deeper root growth could be induced by placing a spatial phosphorus supply deeper in the root zone. Differences in shoot and root characteristics in all treatments did not begin to appear until after week 6 of the experiment ($P<0.05$). Shoot growth of the control treatment was 3-5 fold greater than that of the two treatments using Al-P as the sole source of phosphorus (figure 4.4). This same pattern was observed in the tiller densities measured throughout the first 7 weeks of the experiment (data not shown). The reduced shoot growth may be due to a reduction in the phosphorus content of the shoots in the Al-P treated plants (1.5-2 mg P g^{-1}) compared to 3.5-11.5 mg P g^{-1} in the control treatment (figure 4.5). Shoot tissue phosphorus content of the control treatment declined during the latter weeks of the experiment as the plants grew larger those in the Al-P treatments. The smaller Al-P treated plants maintained consistent shoot phosphorus content throughout the experiment and never showed phosphorus deficiency symptoms (figure 4.5). Despite the differences in shoot growth, root growth for the first 9 weeks of the experiment appeared to be identical among treatments with the exception that the 1% Band treatment in week 7 had less than half of the root mass of the control treatment and the 1% Al-P Mixed treatment. The root-to-shoot ratios of the Al-P treated plants were approximately 100% higher than that of plants in the control treatment because these plants produced lower shoot mass while maintaining similar root growth to plants in the control treatment (figure 4.6).

For the last three weeks of the experiment the root zone was divided into the top 15 cm and bottom 15 cm. The control treated plants had more root mass in the top half of the root zone than the Al-P treated plants at week 10 of the experiment (figure 4.7). Both Al-P treated plants had the same root mass in the top half of the root zone. The control treated plants had significantly ($P < 0.05$) less root mass below 15 cm of depth, despite having equal or greater total root mass, than both of the Al-P treated plants. The root zones with the Al-P banded in the lower portion of the root zone had a greater root mass in the lower half of the root zones than both the control and the Al-P mixed treatment.

Discussion

Preliminary work had shown that Al-P could provide adequate phosphorus for creeping bentgrass growth (Figure 4.8adapted from Lyons *et al*., 2000). The present work demonstrated that banded Al-P also provided phosphorus to a specific place in the root zone (experiment 3) and these results were similar to that of the split root experiment (experiment 1 and 2) where nutrient solutions were used in separate compartments to determine the plasticity of creeping bentgrass roots to phosphorus availability. This study showed that creeping bentgrass responds like other plants when encountered with non-uniform nutrient supply (Robinson, 1994) despite being selected for growth in the uniform environment of a golf green (Huff and Landschoot, 1999).

Turfgrass species have been found to have a wide range of tissue phosphorus levels. Waddington and Zimmerman (1972) found that creeping bentgrass had average tissue phosphorus levels of 7.6 mg g^{-1}. In a later study, creeping bentgrass was found to have tissue phosphorus levels of 5 mg P g^{-1} when growing on a soil with an average phosphorus level of 27 kg ha^{-1} (Waddington *et al*., 1978). No change in growth occurred when tissue phosphorus levels were found as high as 8.4 mg g^{-1}. Jones (1980) concluded that the sufficiency range for most turfgrass species falls into the range of 3.0–5.5 mg g^{-1}. It is important to note that seasonal conditions and developmental state are also important for reduction of growth correlated with lower tissue phosphorus levels in Kentucky bluegrass (Hall and Miller, 1974). The tissue phosphorus levels of the control treatment plants in experiment 3 could be considered very high based on these numbers reported in the literature and may be evidence supporting the concept that most turfgrass species are “luxury consumers” of nutrients when nutrients are available in large amounts (Hull, 1992). The Al-P treated plants may have become phosphorus deficient with tissue phosphorus levels falling below 1.8 mg g^{-1} in week 8 and 9 of experiment 3. In experiment 1, shoot tissue phosphorus levels seemed excessively high and deficiency systems were observed in the LL treated plants that had tissue phosphorus contents of approximately 5 mg g^{-1}.

Experiments 1 and 2 demonstrated creeping bentgrass roots preferentially grew into the high phosphorus side of the root zone. The mechanism for this preferential root allocation is believed to be a function of increased lateral branching of fine roots off of a parent root in zones of enriched nutrient availability (Huang and Eissenstat, 2000). Determining the relative ability of annual bluegrass to respond to spatial phosphorus supply was also an initial goal of these first two experiments. Unfortunately, the experimental cultivars of annual bluegrass chosen for the experiment did not have extensive enough root systems to be effectively analyzed using this split root technique. The reduced rooting depth of annual bluegrass (figure 2.5) may lead to interesting applications for the technology and the results found in experiment 3.

In experiment 3, the delay in treatment effects on root or shoot characteristics until the sixth week may have been due to the fact that the plants were transplanted from an environment adequate in phosphorus. The delay may also have been due to the small plant size and an inability to get accurate measurements from small tissue samples. Although the Al-P treated plants showed reduced shoot growth compared to plants in the control treatments, they did not display typical phosphorus deficiency symptoms, a purplish leaf color that is darkest at the crown (Turner and Hummel, 1992), which was observed in the low phosphorus treatments of experiments 1 and 2. The increase in plant root-to-shoot ratios found in the Al-P treated pots compared to the control treated pots (figure 4.6)could be the result of the reduced overall size of the plants in the Al-P treated pots. Within a cultivar (Larcher, 1995) and across broad taxonomic ranges (Enquist and Niklas, 2002) found smaller, less mature plants have a tendency to have higher root-to-shoot ratios (Wilson, 1988). The Al-P treated plants exhibited reduced shoot growth, but the similarities in the root mass among all treatments in weeks 8 and 9 (figure 4.4) show that the carbon allocation between roots and shoots in the Al-P treated plants was being shifted from shoots to roots, in contrast to being a function of reduced plant growth as was observed in experiments 1 and 2 (figure 4.1, 4.2). In experiment one and two shoot growth was inhibited and in experiment three there was not a decline in shoot growth, rather an increase in root growth that accounted for the increased root to shoot ratios in the Al-P treated plants.

The Al-P treatment increased root-to-shoot ratios over the control treatment throughout the duration of the experiment and appears to be an effort by the plants to attain greater amounts of phosphorus by exploiting more of the Al-P throughout the root zone, or in the bottom 10 cm of the root zone. In natural soils nutrient availability, particularly phosphorus, is greatest at the surface of the soil (Chu and Chang, 1966; Pothuluri *et al*. 1986; Pegitzer *et al*., 1993). Bean plants with shallower basal root angles are more competitive for surface phosphorus (Rubio *et al*., 2003) presumably because of increased root length density near the soil surface where phosphorus is present. The control treated plants were given phosphorus in a nutrient solution applied to the surface of the pots and would mimic typical turfgrass growth situations. The addition of the Al-P to soil in the bottom half of the pot reversed the phosphorus availability regime that is typically found in soils. It was shown that mixing Al-P throughout the root zone could increase root mass below 15 cm of depth but that banding the Al-P deeper in the root zone would result in an even greater root mass below 15 cm depth compared to that observed in the other treatments. The increased root mass at deeper depth has many potential benefits. Deep root systems are important for healthy turf in that they allow the plant to attain water from deeper in the soil profile (Huang and Gao, 2000). This allows leaf stomates to remain open, supporting continued transpirational cooling and carbon fixation during times of periodic heat stress and drought. Future research may explore the affects of Al-P as the sole source of phosphorus on the ability of creeping bentgrass to survive temporary drought conditions experienced during the late afternoon on golf greens where the majority of the irrigation is applied overnight.

Other than encouraging deeper root growth, another potential benefit of providing phosphorus deeper in the root zone using Al-P is the inhibition of annual bluegrass invasion into creeping bentgrass. Increasing phosphorus availability has been shown to increase annual bluegrass growth in creeping bentgrass turf (Kuo, 1993). High phosphorus has also been noted as being potentially important in encouraging annual bluegrass invasion on golf greens (Waddington *et al*., 1978). If phosphorus were only available below 20 cm of depth, annual bluegrass would not be able to attain phosphorus necessary for growth because annual bluegrass found on golf greens has very little root mass below 12 cm of depth (figure 2.5). It is also possible that placing phosphorus deeper in the root zone may select for more deeply rooted eco-types of annual bluegrass. While this may increase the ability of annual bluegrass to invade creeping bentgrass, it may also eliminate some of the undesirable plant characteristics related to the shallow root system typically found with annual bluegrass.

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Figures

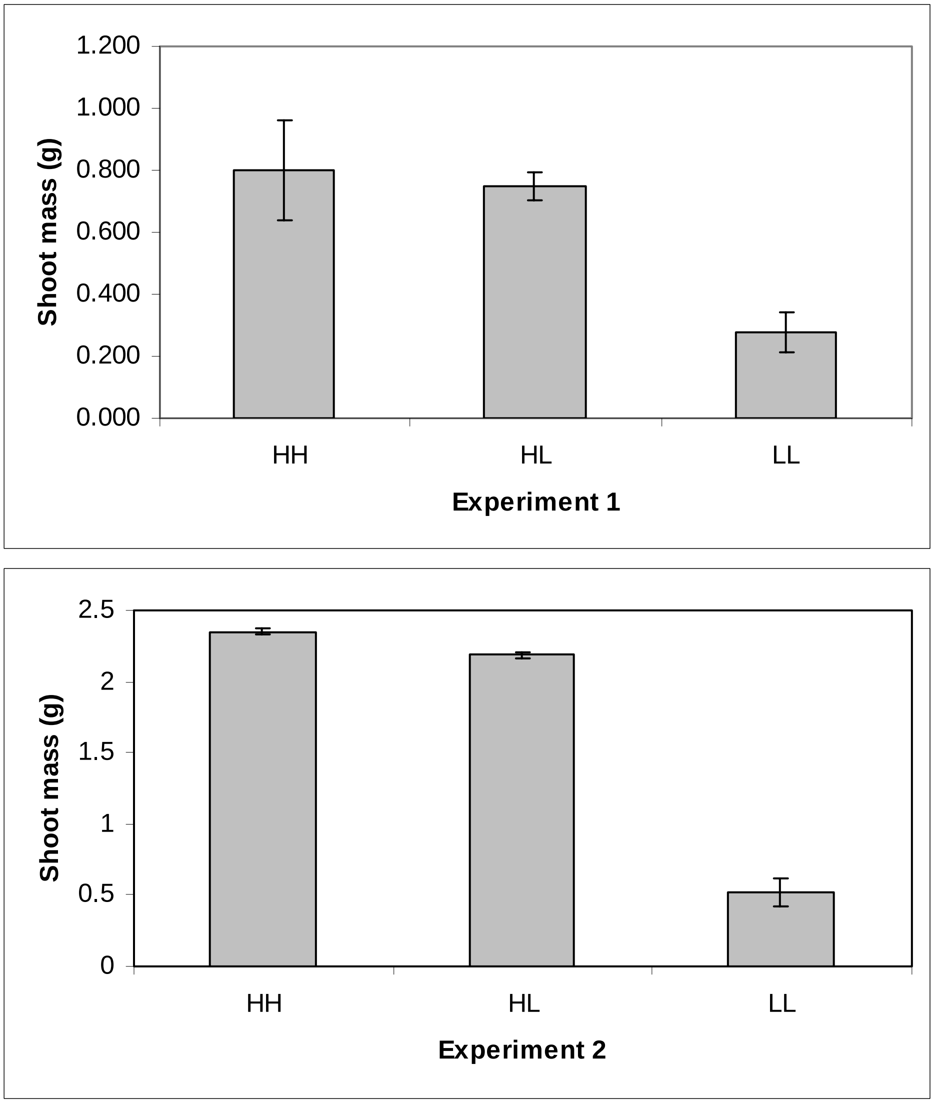
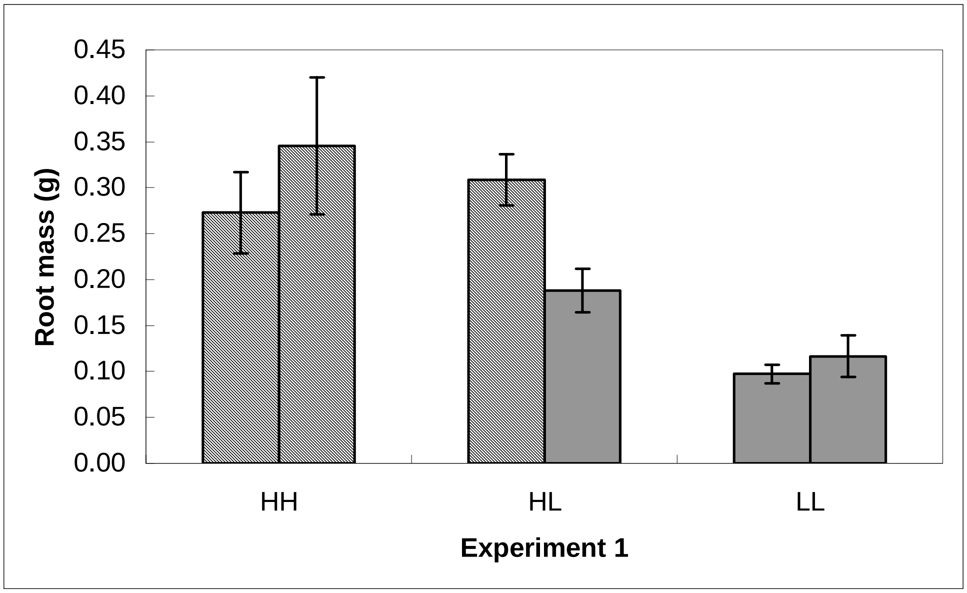


Figure 4.1: Shoot mass from split root experiments. HH received phosphorus on both sides of the root zones. HL received phosphorus on only one side of the root zone. LL received no phosphorus on either side of the root zone. Error bars represent the standard error.



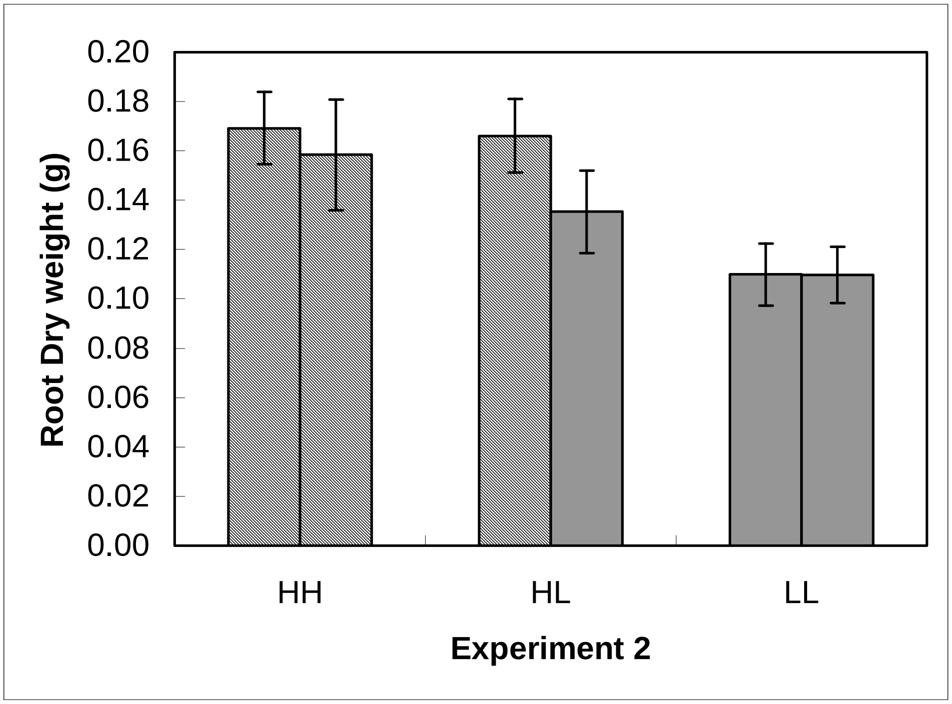


Figure 4.2: Root mass from split root experiments. HH received phosphorus on both sides of the root zones. HL received phosphorus on only one side of the root zone. LL received no phosphorus on either side of the root zone. Solid bars represent root mass from the no phosphorus portion of the root zone and hashed bars represent root mass from the side with phosphorus added. Error bars represent standard error.

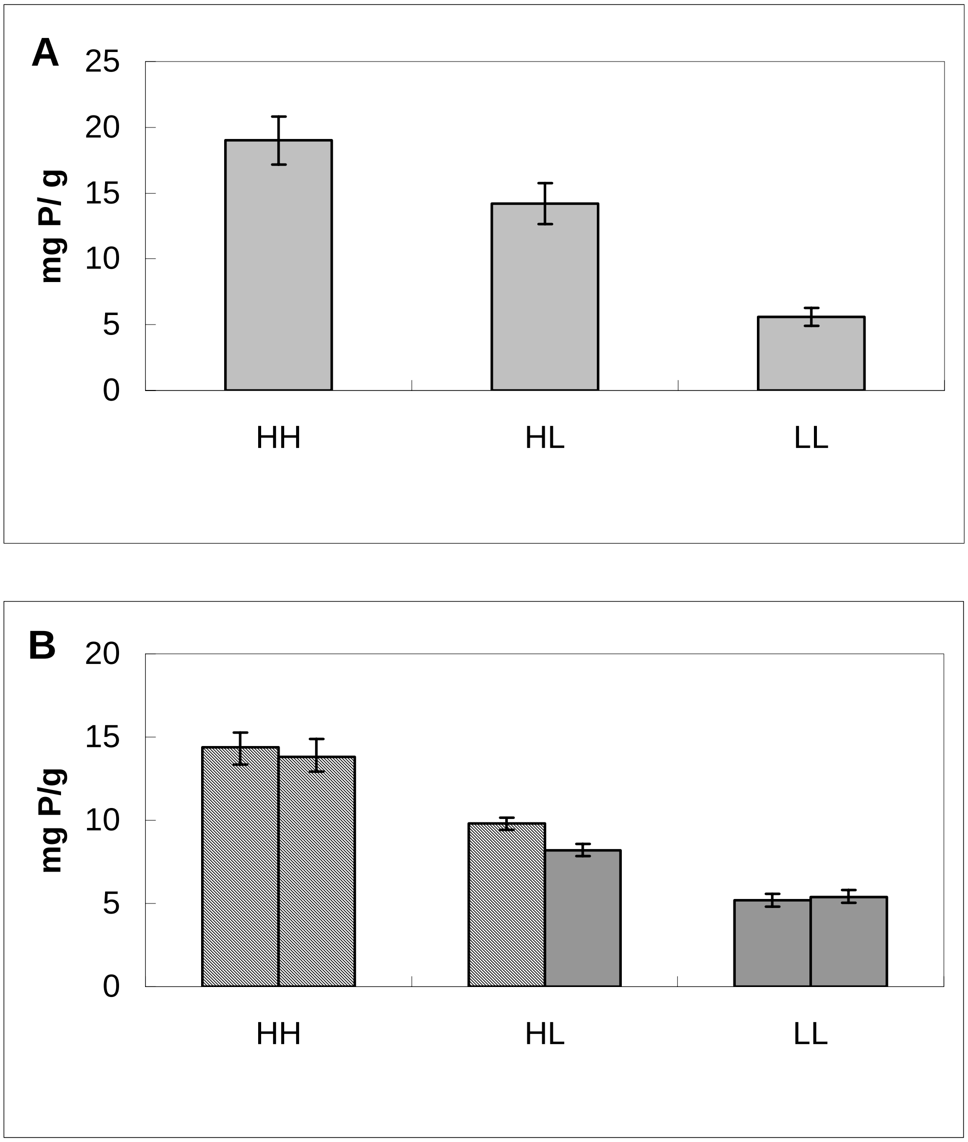


Figure 4.3: Phosphorus content of different tissues in experiment 1. HH received phosphorus on both sides of the root zones. HL received phosphorus on only one side of the root zone. LL received no phosphorus on either side of the root zone. A: shoots. B: roots. Solid bars represent root mass from the no phosphorus portion of the root zone and hashed bars represent root mass from the side with phosphorus added. Error bars represent standard error.

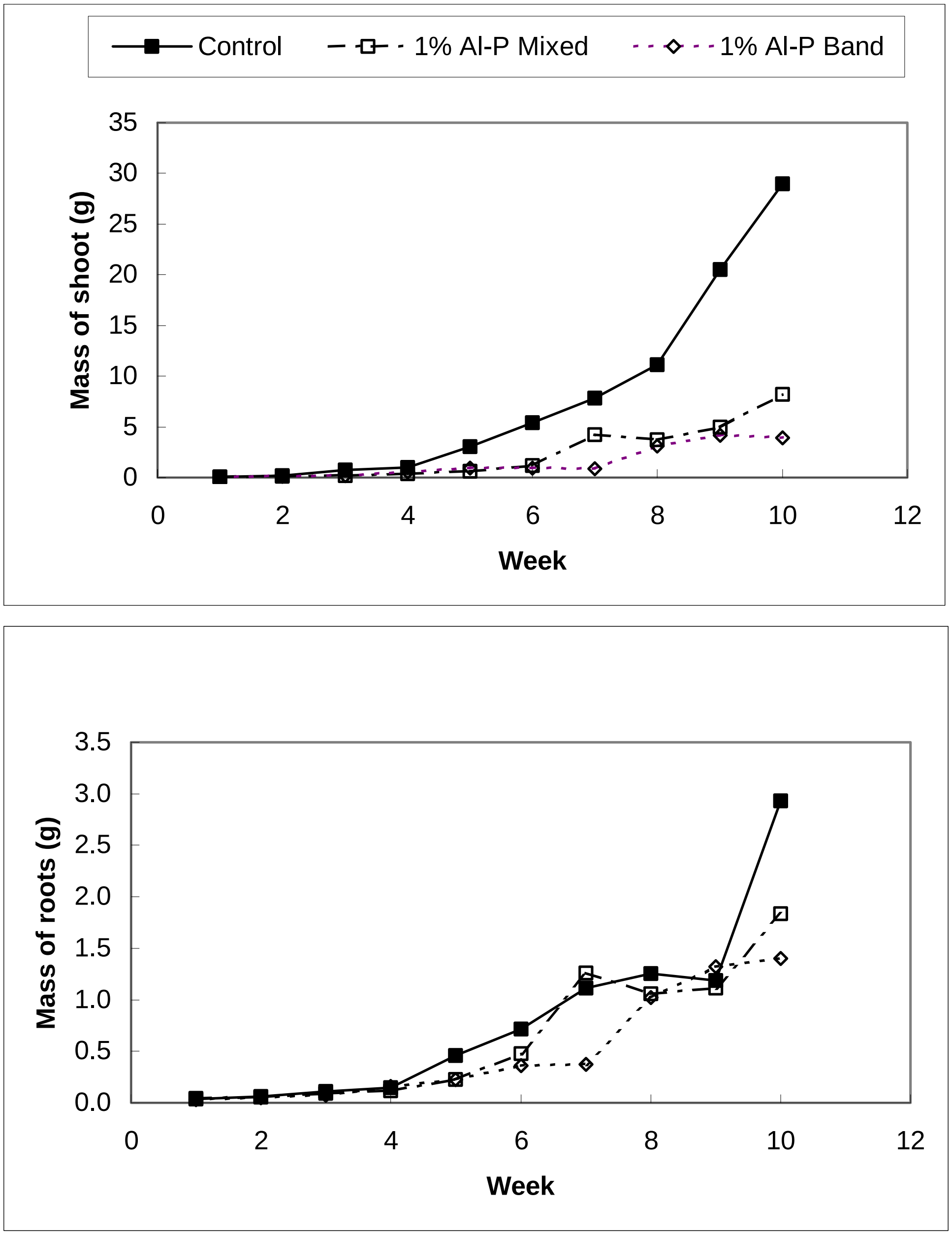


Figure 4.4: Shoot and root mass of creeping bentgrass during a 10-week growth experiment in response to a complete nutrient solution (control) and phosphorus free nutrient solutions with alumina bound phosphorus fertilizer mixed throughout the root zone (1% Al-P Mixed) and banded in the lower 10 cm (1% Al-P Band) of a 30 cm root zone.

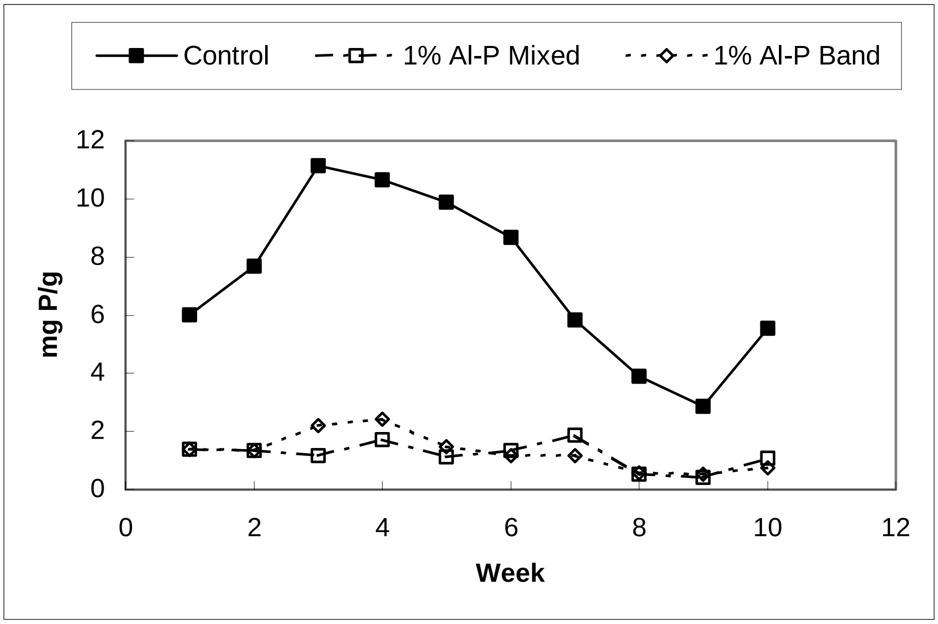


Figure 4.5: Phosphorus content of creeping bentgrass shoots during a 10-week growth experiment in response to a complete nutrient solution (control) and phosphorus free nutrient solutions with alumina bound phosphorus fertilizer mixed throughout the root zone (1% Al-P Mixed) and banded in the lower 10 cm (1% Al-P Band) of a 30 cm root zone.

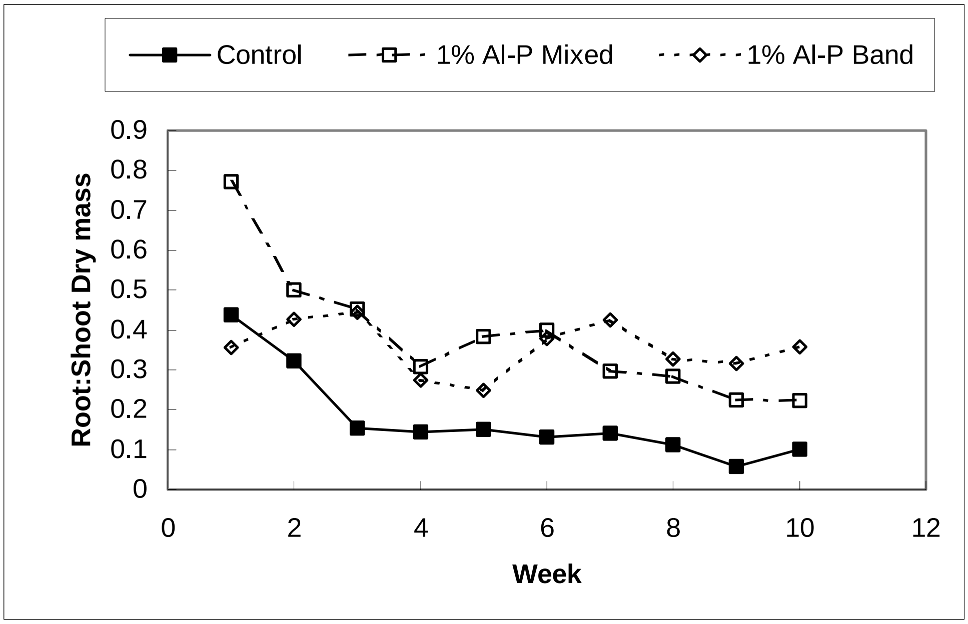


Figure 4.6: Root to shoot ratio of creeping bentgrass during a 10-week growth experiment in response to a complete nutrient solution (control) and phosphorus free nutrient solutions with alumina bound phosphorus fertilizer mixed throughout the root zone (1% Al-P Mixed) and banded in the lower 10 cm (1% Al-P Band)of a 30 cm root zone

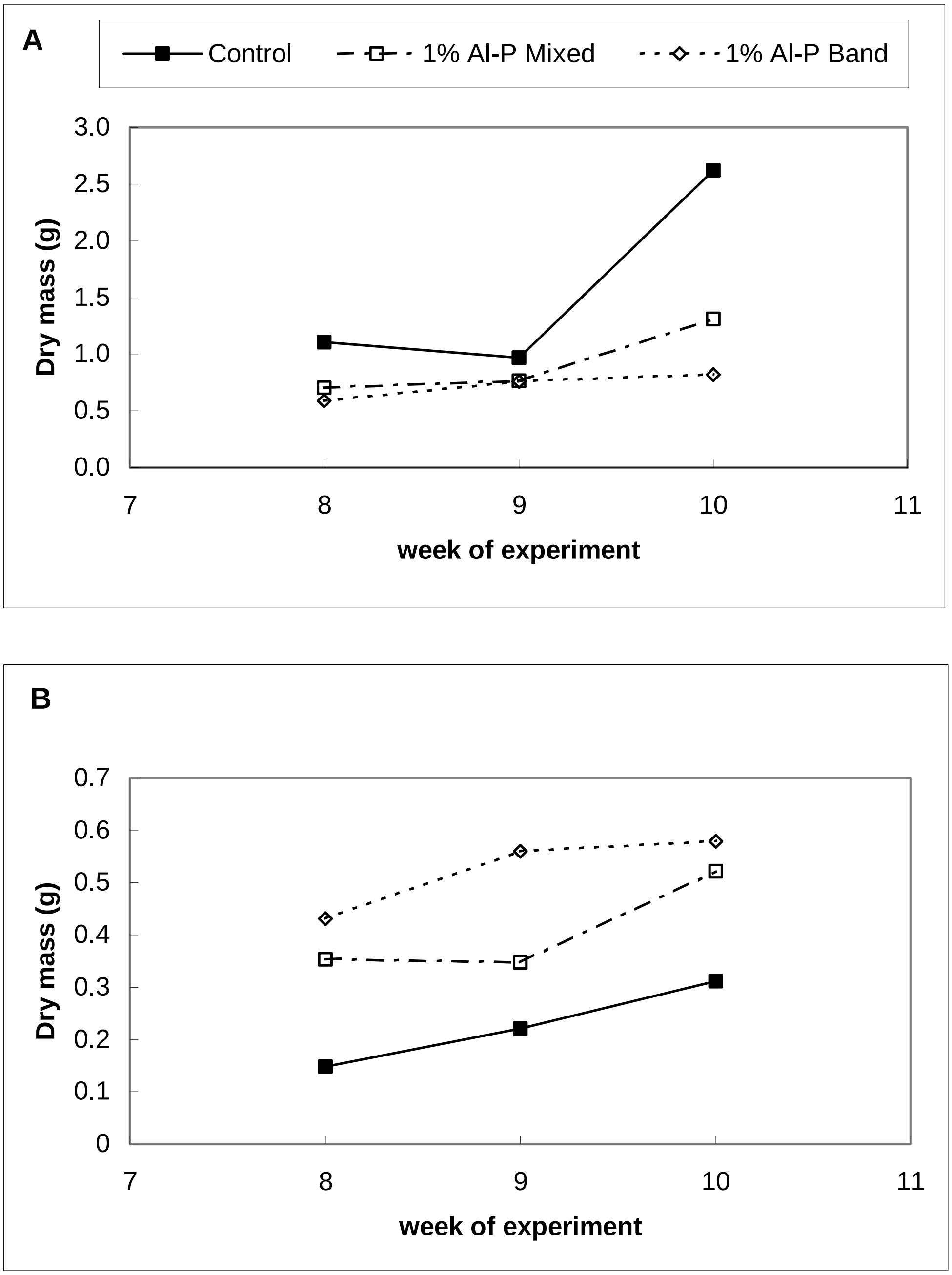


Figure 4.7: Root mass in the top 15 cm (A) and bottom 15 cm (b) of the root zone of creeping bentgrass during the last three weeks of a 10-week growth experiment in response to a complete nutrient solution (control) and phosphorus free nutrient solutions with alumina bound phosphorus fertilizer mixed throughout the root zone (1% Al-P Mixed) and banded in the lower 10 cm (1% Al-P Band)of a 30 cm root zone.

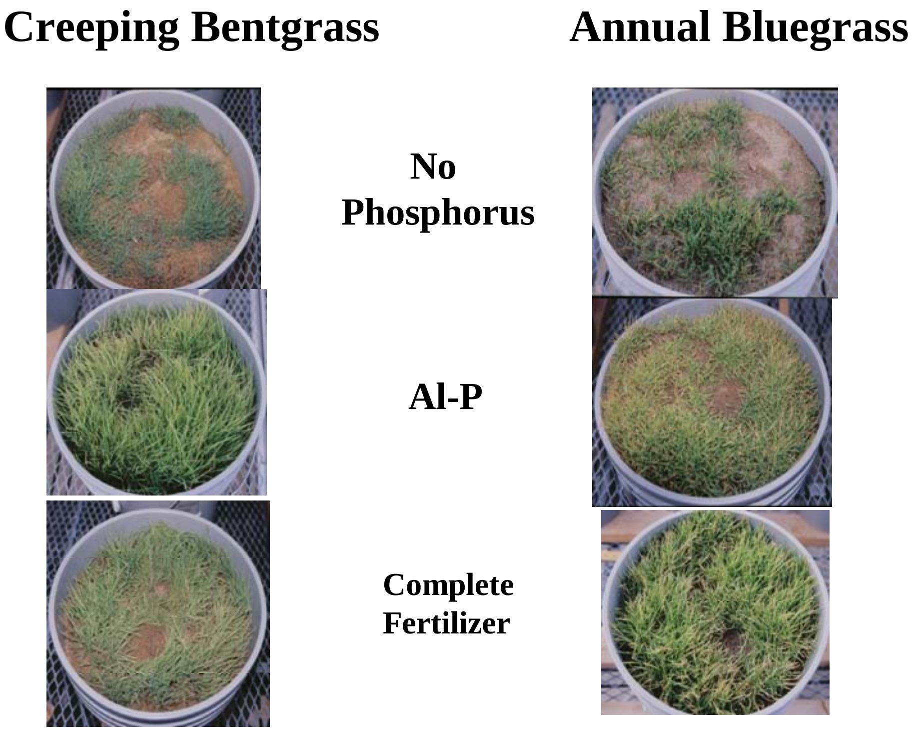


Figure 4.8: Establishment of creeping bentgrass and annual bluegrass in response to a fertilizer with no phosphorus, phosphorus provided from alumina bound phosphorus source (AL-P) and a fertilizer with phosphorus.

Chapter 5

Implications for Competition

Plant roots have two primary functions. The first is to acquire soil-based resources and the second is to provide anchorage or stability (Fitter, 1996). The structure and distribution of the roots in the soil will affect the plant's ability to acquire soil-based resources (Huang and Eissenstat, 2000) and to provide anchorage (Couts, 1983). Root systems vary greatly and there have been many different systems that attempt to classify roots based on root system development (Cannon, 1949). Root systems can develop primarily from the seed, or from adventitious rooting at the stem base (Cannon, 1949). Annual bluegrass and creeping bentgrass have similar root systems in that they are primarily adventitious root systems (Turgeon, 1991). Despite their developmental similarities, this thesis demonstrates that the root systems of annual bluegrass and creeping bentgrass can vary greatly in total biomass and biomass distribution at different depths.

In the past annual bluegrass has been reported as a poorly rooted grass (Beard *et al.*, 1978) making it more susceptible to summer decline (Dernoeden, 2000), a decline in turf quality associated with the climatic and disease pressures of the summer growing season in the Northern Untied States (Beard, 2002). Previous studies that have attempted to explain the reports of annual bluegrass as a poorly rooted grass have determined that the species is often associated with highly compacted soils. On comparable soils annual bluegrass had equivalent root masses to that of the desired species (Sprague and Burton, 1937; Wilkinson and Duff, 1972). These studies, however, were not performed under conditions characteristic of golf greens and may explain why I observed much greater differences in rooting depth between creeping bentgrass and annual bluegrass in my studies and compared to those studies. Despite the limited root system of annual bluegrass, it is well adapted to the low mowing heights of golf greens and often invades and persists in creeping bentgrass golf greens, eventually becoming the dominate grass species present on greens of older golf courses (Beard, 2002). Most studies reported in the literature involving the competition between annual bluegrass and creeping bentgrass are aimed at eliminating annual bluegrass from the golf green (Callahan and McDonald, 1992; Cooper et al, 1987; Gaussoin and Branham, 1989). This thesis provides solid evidence that annual bluegrass has a more limited root system than creeping bentgrass. Annual bluegrass has 40% of the root mass of creeping bentgrass in the top 3 cm of the root zone and 25% of the root mass of creeping bentgrass at 3-12 cm of depth and almost no roots below 12 cm of depth throughout the growing season.

Another component of this thesis was to determine how nitrogen rates would affect the rooting of creeping bentgrass and annual bluegrass. Deeper more extensive root systems have been shown to increase nitrogen capture in golf green root zones (Bowman *et al*., 1998). In both years the 2-year field study creeping bentgrass had increased root mass below 12 cm of depth on some sampling dates with the low nitrogen rate compared to the high nitrogen rate (figure 3.6). Annual bluegrass did not show a similar response. In fact, the annual bluegrass had increased root mass at 0-3 cm of depth with the high nitrogen rate compared to the low nitrogen rate in the second year of the experiment, most likely associated with the increased tiller densities present in the high nitrogen treatment. Annual bluegrass, the smaller, shallower rooted species, also has been able to sexually reproduce under the low mowing heights on golf greens (Beard *et al.*, 1978). Sexual reproduction actually may have provided a mechanism for the adaptation of annual bluegrass to the golf green environment. Golf greens are intensively managed and in most cases adequate water and nutrients are provided (Beard, 2002). The availability of water and nutrients on golf greens limit the need for an extensive root system because one of the primary functions of the root system is being provided by irrigation and fertilization. This explains why annual bluegrass has fewer roots throughout the growing season and does not demonstrate an ability to exhibit a plastic response to high and low nitrogen rates. Instead, annual bluegrass utilizes the limited carbon resources found under low mow heights to vegetatively and sexually reproduce. There is a cost involved in responding to varying nutrients or a heterogeneous nutrient supply (Eissenstat, 1992; Huang and Eissenstat, 2000). In a competitive environment, this cost is related to the duration that the fertility differences are present and subsequently to the increased acquisition of nutrients achieved by response to the differences in nutrient supply (Crick and Grime, 1987).

An alternative view of competition than the life history model presented by Grime, which is discussed in the introduction of this thesis, is the mechanistic approach to competition that is presented by Dave Tilman and his colleagues (Grace, 1991). Tilman (1982) proposed that the competitively dominant species would be the species that could reduce the availability of a resource to a level that would inhibit the growth of competing species. The reports that low nutrient levels, particularly phosphorus, inhibit annual bluegrass invasion on golf greens demonstrate how creeping bentgrass may be more competitive in a natural environment where ionic nutrients limit growth. Another possible mechanism of competition is presented by Grace (1990), where the most competitive species actually acquires the limiting resources at a faster rate than the less competitive species. In this model the competitive species essentially preemptively inhibits the less competitive species by consuming the nutrients, leaving none available for the less competitive species to utilize. This concept of competition may be particularly applicable to turfgrass species, which are considered to be luxury consumers of nutrients. Luxury consumers acquire nutrients at higher concentrations than needed for growth and store the nutrients, presumably to aid in growth when disturbance occurs and the resource that normally limits growth is no longer limiting (Hull, 1992). This thesis has demonstrated that creeping bentgrass appears to have retained its mechanisms for increasing nutrient capture in the case of nitrogen despite its selective breeding for highly cultivated environments. Creeping bentgrass also responds to spatial phosphorus supply in order to maximize acquisition of phosphorus in natural soils (figure 4.2, 4.7). In natural environments, where nutrients are not supplied at regular intervals, creeping bentgrass may be a much more competitive species than annual bluegrass. Despite this, annual bluegrass appears to be highly competitive with creeping bentgrass on golf greens (Beard *et al*. 1978).

Under the low mowing heights of the golf green annual bluegrass may have a more effective strategy than creeping bentgrass for increasing nitrogen capture. This thesis demonstrated that annual bluegrass had a higher specific root length under the low nitrogen regime than under the high nitrogen regime (figure 3.11). While the annual bluegrass may have had less total root mass (table 2.2) and did not increase its root mass in response to low nitrogen availability, it may have increased its nitrogen acquisition under the low nitrogen regime by increasing its total root length (Lariguaderie and Richards, 1994). This strategy is more effective under low mowing heights because finer roots with a higher specific root length actually are more carbon efficient than roots with lower specific root length, based on calculations of carbon cost to root length (Eissenstat, 1992). This more efficient adaptation for nutrient acquisition under closely mowed environments such as the golf green may be helpful in explaining the competitive nature of annual bluegrass on golf greens, but I believe that there is probably a larger factor involved in the competition between these two species on golf greens.

Resource limitation appears to be an important factor in plant growth and in plant competition (Rubio, 2003; Wedin and Tilman, 1993). Discussions of the essential resources needed for plant growth included mineral nutrients, essential gases (including: O_2, CO_2), water and light (Larcher, 1995). One resource essential for plant growth that may be overlooked and may be especially important on golf greens is physical space. A deficiency in physical space has been shown to limit the growth of plants in the case of potted plants where root growth is inhibited and subsequently total plant growth is limited, even if all nutrients are provided in excess including CO_2 (Thomas and Strain, 1991). The root zones on golf greens have been constructed in order to provide ideal conditions for root growth (Beard, 2002) and therefore the space limitation on a golf green would not be below ground. The space limitation that occurs on golf greens would instead occur above ground. This would be different than most ecological systems in that the above ground limiting resource and factor in competition is typically light (Larcher, 1995). The constant mowing of golf greens limits competition for light. Space, or more precisely surface area on the ground for growth, becomes the limiting resource and light becomes secondary. In other words the plant gaining the greatest amount of ground area space, would then preemptively out compete its neighbor for light and any immobile nutrients available in the soil below.

While an ability to colonize disturbed areas has long been considered an important trait in species composition (Grime, 1977), the competition for space that is being discussed here is independent of the need for disturbance. In the crowded environment of the golf green the species that can continue to proliferate under ever increasing space restraints would be the most competitive. The classic resources for which plants compete are provided at sufficient levels to inhibit any competition for these resources and mowing restricts the vertical competition for light. The annual bluegrasses used in my study were smaller plants that grew with higher tiller densities than the creeping bentgrass varieties (figure 2.2). Under the resource limitation model of competition discussed by Tilman the ability of the annual bluegrass to survive under severe space limitation would explain its ability to out compete creeping bentgrass when other resources are not limiting. As tiller densities increase under the low mowing heights, the annual bluegrass varieties may be able to vegetatively produce new tillers that can survive in the space between existing creeping bentgrass tillers. The annual bluegrass would effectively crowd out the creeping bentgrass by limiting the space available for growth and being able to survive in that lower available space. The unique aspect of competition of these two species growing on golf greens is that they are typically not limited by water or nutrients.

How annual bluegrass successfully invades and out competes creeping bentgrass on golf greens is still not known. My research has shown that annual bluegrass, while having higher tiller densities than creeping bentgrass, has less root mass than creeping bentgrass. I have also shown that annual bluegrass did not increase its root mass in response to a low nitrogen rate as did creeping bentgrass but rather, it increased its specific root length. The increased specific root length would be a more efficient mechanism for maintaining mineral nutrient acquisition under the carbon-limited environment of a golf green. Creeping bentgrass showed plasticity to different nitrogen rates and to heterogeneity of available phosphorus in the root zone. These traits are often associated with competitive species in more natural environments (Grime *et al*., 1986). These traits may also allow us manipulate the root zone of creeping bentgrass golf greens to increase the rooting depth of creeping bentgrass.

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Majors: Biology, Philosophy. Minors: Chemistry, Ethics
University of Northern Iowa, Cedar Falls, Iowa, Magna Cum Laude

Academic Positions

Graduate Student: Penn State University. Served as a graduate assistant and as a Root Biology Fellow. Developed and taught courses and lectures while attaining my PhD.
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Assistant Offensive Line Coach: University of Northern Iowa. Taught techniques and game plans, supervised athletic study halls and tutored students.
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Research Assistant: Iowa Waste Reduction Center. Worked with the Mobile Outreach for Pollution Prevention, researched the Farm*A*Syst program explored the possibility of implementing the program in Iowa.
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Research Assistant: University of Northern Iowa. Conducted an independent research project on the effects of abscisic acid on light avoiding leaf movements (paraheliotropism) in *Phaseolus*
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