Propositions

1. A plant's biological yield potential is not indicative of suitability for turf grass use under intensive management conditions.
   (*this thesis*)

2. Rooting at stolon nodes alleviates the suppression of tillering rate in creeping bentgrass.
   (*this thesis*)

3. Early cessation of growth of creeping bentgrass in the fall reflects retarded spring growth initiation.
   (*this thesis*)

4. Resistance of turf to periods of wear stress and recovery of turf after wear stress are negatively correlated in creeping bentgrass.
   (*this thesis*)

5. Lower seeding rate provides better turf.

6. Genetic improvement of a perennial, obligate out-crossing species utilized for non-reproductive characteristics requires years of field testing.

7. To substantially change the genetic base of a creeping bentgrass turf community, severe stand disturbance is required.

Hunt *et al.* 1987. Growth and root-shoot partitioning in eighteen British grasses. OIKOS 50:53-59.

Kik *et al.* 1990. Life-history variation in ecologically contrasting populations of *Agrostis stolonifera*. J. Ecol. 78:962-973.

Jonsdottir 1991. Tiller demography in seashore populations of *Agrostis stolonifera*, *Festuca rubra* and *Poa irrigata*. J. Veg. Sci. 2:89-94.

Bullock *et al.* 1994. Tiller dynamics of two grasses - responses to grazing, density and weather. J. Ecology 82:331-340.

Sweeney and Danneburger, 1998. Introducing a new creeping bentgrass cultivar through interseeding: Does it work? USGA Greens Section Record, September/October 1998, p. 19-20.

8. Tillering patterns should, theoretically, follow a normal distribution with respect to tiller order; therefore tiller order distribution may be used as a selection criterion for tillering propensity and site usage.

Neuteboom and Lantinga 1989. Tillering potential and relationship between leaf and tiller production in perennial ryegrass. Annals Bot. 63:265-270.

9. In order to be truly objective, you need to forget more than you have learned.

10. Man can never truly grasp the meaning of life without experiencing death.

Propostitions belonging to the thesis of D.J. Cattani, *Vegetative tillering in creeping bentgrass.* Wageningen, 9 February 2000.

Vegetative tillering in creeping bentgrass

Promotoren: dr. ir. P.C. Struik
hoogleraar in de gewasfysiologie

dr. J. Nowak
professor in plant physiology,
Nova Scotia Agricultural College, Truro, Nova Scotia, Canada

Co-promotor: dr. G.N. Atlin
associate professor in plant breeding,
Nova Scotia Agricultural College, Truro, Nova Scotia, Canada

Vegetative tillering in creeping bentgrass

D.J. Cattani

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ABSTRACT

Growth and development of creeping bentgrass (*Agrostis stolonifera* L.) under non-competitive and competitive conditions were studied.

Growth chamber experiments under non-competitive conditions with high and low tiller producing bentgrass populations produced plants with differing tiller appearance rates. However, the plants developed at a similar rate with respect to growth stage (using West's growth stages for stoloniferous plants). The populations produced similar above ground dry weights plant^{-1}. Dry weight partitioning patterns between tillers within the populations were different with the high tiller producing population demonstrating a more even dry matter distribution.

Tiller development patterns were similar under long and short days. Short days led to a reduced growth stage and tillering rate and retarded stolon development. The low tillering population had more coleoptilar tillers than the high tillering population. Coleoptilar tillers accounted for a large portion of the difference in tiller number between the short and long day environments for the low tillering population.

Increased tillering rate in seedlings led to higher turf tiller densities. Stolon internode length was negatively related to turf tiller density. A positive relationship was found between seedling stolon internode length and internode lengths found under turf conditions. Seedling selection may be used to reduce selection cycle duration where tillering characteristics are of interest.

Seeding rate was found to influence the rate of turf development. Lower seeding rates led to an increase in tillers plant^{-1}, larger plant weight and better wear stress resistance potential. Wear stress resistance potential of turf appeared to have equilibrated at 9-12 weeks after seeding.

Tiller density increased with turf age up to three years after seeding. Cultivar differences were consistent over time. Within year fluctuation in tiller density was found. Above ground biomass accumulation increased with time and tiller density.

Cultivars responded differently to ice and snow management in the spring with respect to their survival rate.

Creeping bentgrass growth and development is predictable. Tiller number and growth stage may be utilized to ascertain the relative developmental status of plants under experimental conditions. Controlled environment growth studies are a useful tool in the selection for tiller related traits.

Preface

I would first off like to thank my promotor, dr. Paul C. Struik for the opportunity to pursue this degree. I would also like to thank him for the effort, patience and advice he provided throughout the process. To Dr. Jerzy Nowak, my other promotor, I thank for his encouragement, help and, as importantly, his friendship over these last three years. To Dr. Gary Atlin, co-promotor, I thank you for your help over the last year in the preparation of this document. I am greatly indebted to Wageningen University for the opportunity to qualify for this programme.

The experiments that are reported within took place over a number of years, primarily in Manitoba, Canada. I remember thinking about my lack of common sense as the watering hose was frozen to my glove and my feet soaking wet on many December mornings while conducting the experiment in Chapter 7. My sanity, or at least my ability to discern the difference between dedication and obsession, was definitely questioned. My arthritis will continue to remind me of this time in my life.

There are many people who have been professionally involved in the work reported herein. I wish to thank them all for their assistance. To Dr. S. Ray Smith Jr., Department of Plant Science, University of Manitoba, for allowing me to pursue experimentation related to turf production in creeping bentgrass, I am particularly indebted.

To the summer assistants, Anh Phan, Anthony Mintenko and Alex Avecilla for their hard work in maintaining plots. I am indebted to Mr. Keith Bamford, for his patience. He allowed me to drone on while discussing many of the early experiments described within.

My family has been supportive throughout the time period of the work reported herein. I thank them for allowing me to pursue my desire to understand the processes of what I was observing. (My children still cringe at the sight of a grass plant.)

The final two people that I wish to thank have been very important in my personal and professional development. Dr. Anna K. Storgaard, I owe more than I can repay. I thank you for your instilling in me that I must understand how a perennial grass develops in order for it to be properly managed. Secondly, I thank you for your encouragement over the last 18 years. To Pat, my wife, whose patience, support and love have allowed me to put, and hopefully keep, things in perspective. Your love and encouragement have been invaluable. Thank you dear. Love you all.

ACCOUNT

Parts of this research have been included in the following publications.

Chapter 2	Cattani, D.J. (1999) Early plant development in "Emerald" and "UM67-10" creeping bentgrass. Crop Sci. 39:754-762.
Chapter 3	Cattani, D.J. and P.C. Struik (xx) Tillering, stolon development and dry matter partitioning in creeping bentgrass (*Agrostis stolonifera* L.). (submitted).
Chapter 4	Cattani, D.J., P.R. Miller and S.R. Smith Jr. (1996) Relationship of shoot morphology between seedlings and established turf in creeping bentgrass. Can. J. Plant Sci. 76:283-289.
Chapter 5	Cattani, D.J. and S.R. Smith Jr. (xx) The effect of seeding rate and cultivar on the establishment of creeping bentgrass turf. (submitted).
Chapter 6	Cattani, D.J., M.H. Entz and K.C. Bamford (1991) Tiller production and dry matter accumulation in six creeping bentgrass entries grown in Manitoba. Can. J. Plant Sci. 71:591-595.
Chapter 7	Cattani, D.J., P.R. Miller and S.R. Miller Jr. (2000) The effect of ice encasement and early snow removal on the survival of creeping bentgrass. Can. J. Plant Sci. (in press).

Contents

Vegetative tillering in creeping bentgrass

Chapter 1

Introduction

Creeping bentgrass is a cool season, perennial grass that spreads vegetatively via stolons. Stolons are specialized stems, or tillers, that grow in a prostrate fashion along the soil surface. The ability to root at the nodes (zone of leaf sheath attachment to the stem) allows for the formation of a dense sod. The tolerance to frequent cutting at heights of less than 3 mm has led to its use for golf course putting greens.

Creeping bentgrass has been shown to possess excellent cold temperature tolerance (Gusta *et al.* 1980) and ice-encasement tolerance of up to 60 days (Beard 1964). Creeping bentgrass is an efficient user of nutrients due to the rapid root proliferation in areas of high nutrient concentration (Crick and Grime 1987). In general, however, creeping bentgrass is noted for its preference for high disturbance and low stress habitats (Hunt *et al.* 1987).

Taxonomic Classification

Agrostis stolonifera L. and *A. palustris* Huds. are the two most common species names used for creeping bentgrass. Jones (1953) determined the normal chromosome compliment to be 2n=28. The species is an allotetraploid, therefore behaving as a functional diploid during meiosis (Jones 1953). Funk and Ahmed (1973) cite this work on *A. stolonifera* in describing *A. palustris*. Hitchcock (1935) differentiates between *A. stolonifera* and *A. palustris* by using stolon length, with the latter having longer stolons. Hubbard (1968) suggests that *A. stolonifera* should be broken into two subspecies, namely, *A. s. stolonifera* and *A. s. palustris*, again utilising stolon length as a similar criterion as Hitchcock.

Other cytogenetic studies have found varying chromosome numbers for *A. stolonifera*. Bjorkman (1954) and Kik *et al.* (1992) both reported tetra-, penta- and hexa-ploid *A. stolonifera* plants. Bradshaw (1958) reported naturally occurring hybrids of *A. stolonifera* and *A. tenuis* Sibth. While this is possible, these apparent hybrids could be naturally occurring somaclonal mutants of *A. stolonifera* L.

The above information appears to support that *A. stolonifera* L. should be used to describe creeping bentgrass.

Tillering

Neuteboom and Lantinga (1989) described the potential tiller appearance order for grass plants and the frequency of tiller appearance (site usage). Skinner and Nelson (1992, 1994) with tall fescue and van Loo (1992) working with perennial ryegrass have shown tillering to follow, in general, the predicted sequence. The potential for tillering follows an exponential curve with a high level of synchronisation between tillers on a plant (Nelson and Skinner 1992). Neuteboom and Lantinga (1989) suggested that a single phyllochron separated the appearance of a tiller and its first daughter tiller. Low leaf elongation rate is related to high tillering in tall fescue and is initially due to high coleoptile tiller production (Skinner and Nelson 1994). Many grass species possess specialised plant growth appendages, e.g. rhizomes and stolons, which allow for the vegetative spread of the plant. However, these specialised stems may have an impact on tillering via intra-plant competition for resources.

Robson (1973) described an exponential phase, a linear phase and a static or decreasing phase of tiller appearance in grasses. Jonsdottir (1990) monitored tiller birth and death in a naturally occurring stand of creeping bentgrass and found that they were offsetting.

Tiller development in plants is related to leaf appearance (Davies and Thomas 1983). Leaf length and leaf width (Bos 1999) and leaf density will all impact the level of competition for light (Wilson and Cooper 1969). Red:far red light ratio has been shown to be important in tillering (Casal et al. 1990). Vine (1983) reported that leaf appearance rates are reduced drastically in late-September to late-October in perennial ryegrass, thus reducing tillering potential.

Madison (1960) reported a period of leaf elongation followed by new leaf appearance after mowing in creeping bentgrass. Duff and Beard (1974) reported stolon development to be apparent one week after mowing of leaf blades on a tiller. Tillering in creeping bentgrass is affected by temperature (Duff and Beard 1974; Hawes and Decker 1977), and therefore the performance of cultivars in a cold, dry prairie climate may be different from performance in less severe environments (Hunt *et al.* 1987). At least one new cultivar of creeping bentgrass has been selected for survival under severe Manitoba conditions (Cattani *et al.* 1992). As a creeping bentgrass turf develops, stolons provide surface structure and cushion the surface to help resist tearing.

The development of a turfgrass area will depend upon plant density, the development of individual plants within the turf, and their interaction. The rate and sequence of tiller appearance will influence plant development and may ultimately dictate the rate of turf development. Seeding rate has been shown to influence stand density and number of leaves tiller^{-1} in *Poa pratensis* L. and influenced the developmental rate of individual plants within the turf (Brede and Duich 1982). Germinability, vigour and competition for resources will also greatly influence emergence and establishment of seedlings. Parr (1982) found higher mortality rates at higher seeding rates for *Lolium perenne* and *Poa pratensis*. Above ground biomass was found to be independent of seeding rate after turf establishment with lower seeding rates producing larger plants (Parr 1982).

Once a creeping bentgrass stand is established, very little subsequent growth of new seedlings occurs within a stand (Jonsdottir 1990, Bullock et al. 1994), even where regular overseeding is practised (Sweeney and Danneberger 1998). Therefore, due to this lack of the establishment of new individuals, the genetic make-up of a stand is established in the initial period of growth.

Vegetative growth of creeping bentgrass predominates in areas where growing conditions are favourable (Kik *et al.* 1990) and the environment is undisturbed (Hunt *et al.* 1987). High tiller density provides a dense surface that allows for smooth ball roll and resistance to ingress by other, less desirable plants species.

Ong (1978) found tiller weight to be the important factor in tiller survival under whole plant stress. Dry matter partitioning within the plant will be important for turf plant development and persistence. Stolon development would increase tiller dry weight by increasing tiller length (internode elongation) and the accumulation of cellulose and lignin (Esau 1977). Shearman and Beard (1975) reported that total cell wall content (mg dm^{-2}) accounted for almost all of the variation in wear tolerance differences between turfgrass species.

Dry matter accumulation tiller^{-1} is important for wear stress resistance in *Poa pratensis* L. (Shildrick and Peel 1984). However, it appears that tiller density and dry weight tiller^{-1} are negatively correlated in creeping bentgrass (Cattani 1987). Lush (1990) used tiller density and dry weight per unit area to estimate potential wear stress resistance. Trenholm *et al.* (1999) reported that higher tiller densities resulted in greater wear resistance for seaside paspalum (*Paspalum vaginatum* Swartz).

Tiller density is, therefore, an important morphological characteristic in creeping bentgrass. It is positively related to wear stress recovery (Hawes and Decker 1977) and potential wear stress resistance in turf (Lush 1990). Other research has indicated that tiller density and leaf density were positively associated ($r = 0.97$) and both with visual turf density ratings in creeping bentgrass turf (Cattani and Clark 1991). Lehman and Engelke (1991) found narrow-sense heritabilities for tiller number of 0.31 to 0.41 with creeping bentgrass.

Hunt *et al.* (1987) reported a reduction in the relative growth rate under low light intensity conditions (80% shade) of approximately 50% in creeping bentgrass. High shoot stress was also measured under the low light conditions (Hunt *et al.* 1987). Seeding time may therefore affect the plant development and turf development with a late summer/early fall seeding under shortening days leading to reduced plant development and growth when compared to a late spring seeding.

Wear Stress Resistance

A turfgrass surface is a collection of plants. Inter- and intra-plant competition, both within and between species, dictates the stress performance of the stand. Lush (1990) proposed the use of the power rule (rule of self-thinning (Lonsdale and Watkinson 1982)) to predict potential wear stress resistance of turfgrasses:

$$\log_{10} B = \log_{10} C - 0.5 \log_{10} N.$$

where, B is the population biomass m^{-2}, N is the density (individuals m^{-2}) and $\log_{10} C$ is the estimate of the biomass of a single individual.

Limitations of the power rule are that input and management changes or enhancing performance through genetic advances lead to a shift in the $\log_{10} C$. This will increase or decrease potential wear stress resistance (Lush 1990). At a given $\log_{10} C$, increasing tiller density will be at the expense of tiller size. Implications of this rule are that the potential wear stress resistance within a given turf may be manipulated to enhance tiller size and therefore wear resistance. Within cultivars, the $\log_{10} C$ estimate may therefore provide a measure for determining site-specific management practices to enhance wear stress resistance.

Therefore, an important characteristic among creeping bentgrass cultivars is tiller density (TD). Tiller density is positively related to wear stress recovery in bentgrasses (Hawes and Decker 1977), and wear stress resistance in Kentucky bluegrass (*Poa pratensis* L.)

(Shildrick and Peel 1984), tall fescue (*Festuca arundinacea* Schrib.) (Shildrick and Peel 1983), seaside paspalum (Trenholm *et al.* 1999) and, theoretically all turfgrasses (Lush 1990). However, tiller number and dry weight tiller^{-1} are negatively correlated in creeping bentgrass (Cattani 1987). We previously found visual stand density of turf subjected to wear stress, a measure of wear stress resistance, to be correlated with tiller density (Cattani and Clark 1991).

Greater wear stress resistance among turfgrass is often attributed to higher levels of aboveground biomass (AGB) or thatch (i.e., living and dead material above the soil surface) (Shildrick and Peel 1984). The mathematical relationship between TD and live AGB has been proposed as a method for predicting potential wear stress resistance among bentgrass cultivars (Lush 1990). However, while high levels of AGB may be desirable for turfgrasses (Shildrick and Peel 1983; Lush 1990), higher levels of fertilization and cultural management may be required to maintain the integrity of the green (Shildrick 1985).

Lower mowing heights have been shown to increase tiller populations in creeping bentgrass (Madison 1962). Salaiz *et al.* (1995) reported greater root production and turfgrass quality at 4.8 mm height of cut compared to 3.2 mm.

A greater knowledge of tiller dynamics in turfgrass is also important since TD is becoming an increasingly useful characteristic in turfgrass breeding and management programs (Lush 1990). Information on AGB production among turfgrass cultivars is important, especially for determining the level and type of management required to maintain a good-quality playing surface.

Seeding Rate and Development

Madison (1962, 1966) determined seeding rates and looked at tiller density at different mowing heights. This work is still the basis for seeding rate. Golf course superintendents in Canada are often faced with the demand for a quick establishment of a golf putting green, often within three months. Superintendents have reported using up to 2.5 kg 100 m^{-2}. Recommended seeding rates are between 250-500 g 100 m^{-2} (Beard 1982). Madison (1966) found that a 450 g m^{-2} seeding rate for creeping bentgrass was sufficient to establish a playable turf within a three month period. As creeping bentgrass cultivar availability has increased in recent years, cultivar may affect turf establishment rate.

Lower seedling densities in perennial ryegrass and timothy result in a greater wear stress tolerance due to larger plant and tiller size (Parr 1982). The same author also reported that plant number did not decrease over time under mowing stress. Rossi and Mallett (1996) found self-thinning took place in creeping bentgrass at high seeding rates primarily due to disease. Seedling competitiveness was influenced by early emergence in *Dactylis glomerata* L. (Ross and Harper 1972).

Cultivar Development

Creeping bentgrass has long been cultivated for golf course use, primarily for putting greens (Duich 1985). The practice of vegetative propagation, which was the primary propagation method until the release of "Penncross" in the 1950s, resulted in little interest in plant development and establishment. Penncross has long dominated the industry and is only now in the late 1990s losing its sizable market share. The latest listing from NTEP (National Turfgrass Evaluation Program) lists at least 28 cultivars commercially available in 1997 (NTEP 1999).

Modem cultivars of creeping bentgrass are the result of synthetic development (Brauen *et al.* 1993, Engelke *et al.* 1995a,b). The uniformity of a cultivar is therefore dependent upon the number of parental germplasms making up the synthetic and the genetic uniformity of and between the parentals. Golembiewski *et al.* (1997), using RAPD markers, found repeatable differences between most creeping bentgrass cultivars tested, however, they reported some difficulty in distinguishing between two cultivars, due to seed lot effects. Warnke *et al.* (1997) utilizing isozyme polymorphisms, reported relationships between creeping bentgrass cultivars. "Emerald" and "18th Green" were found to be closest with respect to genetic distance and are therefore thought to be from a similar base population ("Seaside") (Warnke *et al.*, 1997). 18th Green was selected out of UM67-10 (Cattani *et al.* 1992).

Progress in turfgrass breeding has been limited as each cycle of selection requires the establishment and maintenance of turfgrass plots. The ability to relate shoot morphological characteristics of seedlings to established turf would be useful for plant breeders. Important shoot morphological characteristics would include higher tiller densities for improved golf putting green wear-stress tolerance and increased stolon length for quicker colonisation of bare spots in golf greens, fairway and tee-box turfs. Selecting desirable creeping bentgrass plants in the seedling stage would provide an improved methodology for generation advance. This would allow selection of plants with desired shoot morphological attributes at an early stage, enabling earlier transplanting of seedlings to field or greenhouse crossing blocks. If selection for one characteristic can be achieved at an early growth stage and selection for another characteristic at a later stage (e.g., disease tolerance), advancement for both characteristics may be possible without extending the time for generation advancement.

Objectives and Outline of this Thesis

The objectives of this thesis are: 1) to characterize creeping bentgrass growth patterns; 2) to evaluate creeping bentgrass cultivars and germplasms for plant development and turf characteristics; 3) to assess the utility of early plant selection for turf tiller density; 4) to investigate the effect of seeding rate and cultivar on early turf development; 5) to determine the effect of stand age on turf tiller density and; 6) investigate the effect of cultivar selection on ice encasement and snow cover survival.

Chapters 2 and 3 investigate the effect of population and daylength on tillering and stolon development in creeping bentgrass. Chapter 4 contains a study of the relationship between early plant growth and the turf tiller density in creeping bentgrass cultivars. Chapter 5 looks at the effect of seeding rate and cultivar on creeping bentgrass turf establishment. Chapter 6 is a study of turf tiller density over a three year period. Chapter 7 looks at ice encasement and snow management on the survival of creeping bentgrass.

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Part I

Effect of day length on creeping bentgrass plant growth and development

Chapter 2

Early Plant Development in "Emerald" and "UM67-10" Creeping Bentgrass.

Abstract

Creeping bentgrass (*Agrostis stolonifera* L.) is used for fairway and putting green turf. Seeding takes place in late spring or early fall in Atlantic Canada. The objectives of this study were to i) study the effect of daylength on early plant growth and development, and ii) compare plant development in high and low tillering populations. Individual pre-germinated seeds of "Emerald" and "UM67-10" were transplanted into 10 cm pots containing an 80:20 sand:peat medium. Two greenhouse (GH) studies of ≥ 108 pots population^{-1} and two growth cabinet (GC) studies, with 16 h and 8 h photoperiods, and 20/15 °C day/night temperatures with at least 15 pots population^{-1} run^{-1} were conducted. Leaves pl^{-1}, tillers pl^{-1}, senesced leaves pl^{-1}, stolons pl^{-1} and total leaves pl^{-1} were measured at 7, 14, 21, 28 and 35 days after transplanting (DAT). Stolon characters and dry weight pl^{-1} were measured at 35 DAT. Phenological development was monitored daily in the GC. Dry matter and tiller production was greater under LD. Stolon development was delayed under SD. Population influenced tillers pl^{-1} at 35DAT and stolons pl^{-1} under LD. Order of tiller appearance was as expected from studies on other species. Plants producing high tiller numbers generally completed a branching unit (BU) prior to growth in the next BU (the appearance of the next primary tiller). High order tillers (1° and 2°) within a BU appeared prior to lower order tillers. Planting under long day conditions is advantageous for growth of creeping bentgrass with the production of greater stolon mass allowing for a more durable turf.

Key words: creeping bentgrass, tillering, stolon, growth stage, tiller order

INTRODUCTION

Creeping bentgrass (*Agrostis stolonifera* L.) is used in the temperate zone of North America for golf course putting greens and, more recently, for closely mown fairway turf. The stoloniferous growth habit allows creeping bentgrass to withstand close mowing and for a "mat" to form on the soil surface.

In Chapter 4 we report that tiller proliferation by plants within cultivars and populations to 35 d after transplanting was correlated to the field turf tiller density of the cultivars and populations ($r = 0.701$ to 0.826). Positive relationships have been reported for tiller and leaf number in turf of creeping bentgrass (Cattani and Clark 1991, Wright *et al.* 1989). No reports on the plant development process in creeping bentgrass have been published.

Skinner and Nelson (1992, 1994) and van Loo (1992) have shown tillering to be orderly and predictable in tall fescue and perennial ryegrass, respectively. The potential for tillering follows an exponential curve (Nelson and Skinner 1992) with the realisation of this potential being referred to as site usage (van Loo 1992). Specialised plant growth appendages, e.g. rhizomes and stolons, while allowing for the vegetative spread of the plant may have an impact on this process via intra-plant competition for resources.

Turf development potential will depend upon plant density, the development of individual plants within the turf, and their interaction. The sequence of tiller appearance may ultimately dictate the rate of turf development. Seeding rate has been shown to influence stand density and number of leaves tiller^{-1} in *Poa pratensis* L. and influenced the developmental rate of individual plants within the turf (Brede and Duich 1982). Cultivar selection may also influence rate of turf establishment within a given seeding rate (Chapter 6). Germinability, vigour and competition for resources will also greatly influence emergence and establishment of seedlings.

Hunt *et al.* (1987) reported a reduction in the relative growth rate under low light intensity conditions (80% shade) of approximately 50% in creeping bentgrass. High shoot stress was also measured under the low light conditions (Hunt *et al.* 1987). Seeding time may therefore affect the plant development and turf development with a late summer/early fall seeding under shortening days leading to reduced plant development and growth when compared to a late spring seeding. Stolon development would increase tiller dry weight by increasing tiller length (internode elongation) and the accumulation of cellulose and lignin in the stolon tissue (Esau 1977). Shearman and Beard (1975) reported that total cell wall content (mg dm^{-2}) accounted for almost all of the variation in wear tolerance between turfgrass species.

Creeping bentgrass is a cross-pollinated species and modern cultivars are the result of synthetic development. The uniformity of a cultivar is therefore dependent upon the number of parental populations making up the synthetic and the genetic uniformity of and between the parentals. Golembiewski *et al.* (1997), using RAPD markers, found repeatable differences between most creeping bentgrass cultivars tested, however, they reported some difficulty in distinguishing between two cultivars, due to conflicting results when different seed lots were used. Warnke *et al.* (1997) utilising isozyme polymorphisms, reported relationships between creeping bentgrass cultivars. "Emerald" was the closest to "18^{th} Green" with respect to genetic distance and are therefore thought to be from a similar base population ('Seaside') (Warnke *et al.* 1997). These two cultivars have previously been shown to be different in both their plant development rate and in turf tiller density (Chapter 4).

The objectives of this research were to investigate early plant growth, including phenological development, in two related creeping bentgrass populations differing in tillering rates, Emerald and "UM67-10" (parental population of 18^{th} Green (Cattani *et al.* 1992)), under long day and short day conditions.

METHODS AND MATERIALS

Greenhouse Study

Two greenhouse experiments were carried out using Emerald and UM67-10, the parental population for 18th Green (formerly 'Biska') (Cattani *et al.* 1992). Approximately 250 seeds $population^{-1}$ were pre-germinated for 4 d in 90 mm dia. petri dishes containing moistened filter paper at approximately 20 °C. A single seedling was transplanted at the coleoptile stage into a 10 cm dia. pot with a total of 120 pots $population^{-1}$. The growing medium was a 4:1 (vol/vol) sand:peat mixture. Plants were grown in a greenhouse environment (GH) with night temperature not below 15 °C. Light was primarily natural however, supplemental light was present within the greenhouse facility. Fertility regime is found in Table 2.1. The first greenhouse run was from 17 April to 22 May 1997 (LD), and the

Table 2.1. Nutrient application and harvest or measurement schedule for the controlled environment growth room experiment and the greenhouse experiments designed to measure creeping bentgrass growth components.

Day	Treatment
0	transplanting
3	fertilise[z] at 56g N 100 m^{-2}
7	Initial count fertilise at 56g N 100 m^{-2}
10	fertilise at 112g N 100 m^{-2}
14	2nd count fertilise at 112g N 100 m^{-2}
17	fertilise at 225g N 100 m^{-2}
21	3rd count fertilise at 225g N 100 m^{-2}
24	fertilise at 225g N 100 m^{-2}
28	4th count fertilise at 225g N 100 m^{-2}
31	-
35	Final counts and measurements

[z] Fertiliser source was Peter's 20-20-20 water soluble formulation.

second was from 22 Oct to 26 Nov 1997 (SD). Plants showing damage due to transplanting were removed from the study with 118 and 116 and 108 and 118 pots remaining for Emerald and UM67-10 in the LD and SD, respectively. Pots were set up in a completely random design and re-randomised 2 x weekly to remove position effects.

Individual plants were non-destructively sampled at 7, 14, 21, and 28 DAT (days after transplanting). Tiller, leaf, stolon and senesced leaf number pl^{-1} were counted at each sampling date. At 35 DAT, the length of the longest stolon pl^{-1} and the length of the longest internode on the longest stolon were also measured. Dry weight pl^{-1} was measured for 98 and 96 pots (**LD**) and 88 and 98 pots (**SD**) of Emerald and UM67-10, respectively. Dry weight was determined by drying the plant material for 72 hours at 65°C and weighing upon removal. The remaining 20 plants $population^{-1}$ are being utilised in further studies.

Analysis of variance was performed using PROC GLM in SAS (SAS Institute, Gary, NC). Mean comparisons were made using Dunnetts T-test. Regression analysis performed were of tillers pl^{-1} on leaves pl^{-1} and log_n transformation was used on tillers pl^{-1} for regression of log_n tillers pl^{-1} on weeks after transplanting.

Growth Cabinet Study

Twenty-five pots per entry were planted with a single pre-germinated seed and grown under the same fertility regime as the greenhouse study (Table 2.1). The first growth cabinet study (long day (LD)) had a 16 h photoperiod and a 20/15 °C day/night temperature regime. The second study (short day (SD)) had a 8h photoperiod with the temperatures being similar to the day/night values of the LD study. Lighting was at 150 μmol m^{-2} s^{-1} supplied by incandescent and fluorescent bulbs. Plants were set up in a completely random design and re-randomised 2 x weekly to remove position effects.

Any plant exhibiting damage or a reduction in growth that may have been due to damage during transplanting was removed from the study. There were 15 pl population^{-1} in each of the first runs for the LD and SD conditions and 20 (LD) and 19 (SD) pl population^{-1} for the second run.

Tillering was monitored daily though 35 days after transplanting (DAT). As each new tiller arose, the day and site of appearance were recorded and colour coded wire loops were used to identify the tiller. Stolon appearance and elongation were utilised to assign a growth stage value based upon West (1990). Only stages seedling (4-9) though vegetative (10-19) were utilised due to a vernalisation requirement for reproductive growth and the duration of the study. Monitoring was stopped at 35 DAT as the plants in the LD conditions had stolons outside of the pots and competition for light between plants was becoming a factor. At 35 DAT, the length of the main stem (the longest stolon present), the longest internode on the longest stolon were also measured on each plant. Plants were then paired within populations based on growth stage and tiller number. One plant from each pair was then dissected to get individual tiller weights and measurements and the other is being carried forward for further study.

Analysis of variance was performed using PROC GLM in SAS (SAS Institute, Gary, NC). There were no run x population interactions (Table 2.2), therefore means reported are

Table 2.2. Analysis of variance for greenhouse and growth room studies for day 35.

Source of variance	df	Tillers	Leaves	Dead leaves	Stolons	Stolon Length	Internode	df	Tillers	Leaves	Dead Leaves
		Growth room Studies									
		Long Day							Short Day		
		mean squares							mean squares		
Run	1	16.30	16.02	0.14	2.86	62.27*	5.01*	1	3.63	0.36	12.72***
Population	1	1593.66***	6204.01***	0.01	68.01***	188.93***	27.11***	1	254.65***	895.42***	2.83*
Run x population	1	45.27	258.52	0.74	4.14	3.36	0.01	1	4.55	33.04	0.02
Error	66	20.31	91.08	0.60	2.70	12.26	1.05	64	4.92	15.94	0.45
		Greenhouse Studies									
		Long Day							Short Day		
Population	1	5027.84***	39064.57***	0.57	756.73***	11.50	46.08***	1	406.39***	1443.56***	8.76**
Error	232	17.52	110.10	0.19	3.59	22.40	1.34	224	4.04	17.36	0.86

*,**,*** Significant at $P = \leq 0.05$, 0.01 or 0.001, respectively combined over runs. Mean comparisons were made using Dunnett's T-test. Regression analysis was performed using SAS. Regression analysis performed were of tillers pl^{-1} on leaves pl^{-1} and $\log_n$ transformation was used on tillers pl^{-1} for regression of $\log_n$ tillers pl^{-1} on weeks after transplanting.

RESULTS

Tiller Production and Leaf Growth

Tillering rates of the populations were different in all studies. Both populations followed the exponential pattern as predicted (Skinner and Nelson 1992) (Figures 2.1a and b, Table 2.3). Regression equations for $\log_n$ transformation of tillers pl^{-1} on days after transplanting showed slope estimates that were similar under long day conditions; however the x intercept estimates were different, indicative of the slower initiation of tillering in Emerald (Table 2.3). The regression equations for UM67-10 SD and Emerald LD were nearly identical (Table 2.3). UM67-10 tillered earlier and at a quicker rate than Emerald (Tables 2.4 and 2.5).

Tillering started earlier and was further advanced by day 35 under the LD conditions (Table 2.4). Tiller development began after the appearance of the third leaf on the main stem, however, there was a tendency to delay tiller development until the appearance of the fourth leaf

Table 2.3. Parameter estimates (± standard error in the parenthesis) for the regression equation $\log_n y = a + bx$, for the response of tiller production (y) to weeks after transplanting (x) in creeping bentgrass.

Environment	Population	a	b	R^2
Greenhouse	**UM67-10 LD**	-0.856 (0.039)	0.749 (0.016)	0.915
	Emerald LD	-1.260 (0.042)	0.701 (0.011)	0.889
	UM67-10 SD	-1.233 (0.046)	0.619 (0.013)	0.836
	Emerald SD	-0.966 (0.051)	0.468 (0.014)	0.726
Growth Cabinet	**UM67-10 LD**	-1.443 (0.094)	0.867 (0.025)	0.910
	Emerald LD	-1.369 (0.095)	0.717 (0.025)	0.871
	UM67-10 SD	-1.447 (0.148)	0.728 (0.036)	0.796
	Emerald SD	-1.611 (0.174)	0.645 (0.043)	0.694

under SD conditions. Tiller production of UM67-10 under SD conditions was similar to Emerald under LD conditions (Table 2.4). Total number of leaves pl^{-1} in LD were approximately double that of SD for the individual populations (Table 2.4). UM67-10 produced more leaves pl^{-1} than Emerald (Table 2.4). The number of dead leaves pl^{-1} were similar between studies at 21 DAT; however they increased at a greater rate under the SD conditions and there were more dead leaves pl^{-1} with Emerald than with UM67-10 in all studies except the LD in the GC.

Stolon development also started earlier and was more advanced under LD in the GH (Table 2.5). UM67-10 had more stolons pl^{-1} than Emerald (Table 2.5). UM67-10 showed a greater reduction in stolon production in the SD in the GH as compared to Emerald. Stolon length was similar between populations under long day conditions however, Emerald produced longer stolons in the SD GH (Table 2.5). Emerald produced longer internodes than UM67-10 under all conditions (Table 2.5). Few stolons were produced under the SD conditions in the GC, while UM67-10 produced more stolons under LD conditions in the growth cabinet (Table 2.5). Emerald produced longer stolons with longer internodes under LD conditions (Table 2.5). Dry matter production was similar for the populations with long days producing more dry matter (Table 2.4).

The growth stage curves indicate that UM67-10 reached the tillering stage faster than Emerald under both the LD and SD, however, the stolon elongation was visible at approximately the same time under the LD, (day 25) (Figure 2.2).

Significant differences (P=.05) between slopes for regression equations for tillers pl^{-1} on leaves pl^{-1} were found between populations under short day conditions of the GH, however, the LD growth equations were similar (Table 2.6). The regression equations for tiller production in GC in response to leaf number were similar for the populations in the SD, while the equations were different in the LD conditions (Table 2.6). UM67-10 had a greater slope than Emerald, 0.411 ± 0.0036 and 0.344 ± 0.0056, respectively, under the shorter day conditions in SD in the GH (Table 2.6). UM67-10 had a greater slope in the LD as compared to Emerald (Table 2.6).

Correlation between leaf number and tiller number was high as evidenced by the R^2 values for the regression lines (Table 2.6). The other significant correlation was between longest stolon and longest internode with r values ranging from 0.847 to 0.922 in the LD.

Tiller Appearance and Dry Weight

Tillering was initiated 3 to 4 days earlier in LD than in SD (Table 2.7). The first tiller to arise was usually found in the axil of the first leaf and is designated as 1-1 ° (first primary tiller arising in the axil of the first leaf (T1 in Skinner and Nelson 1992)).

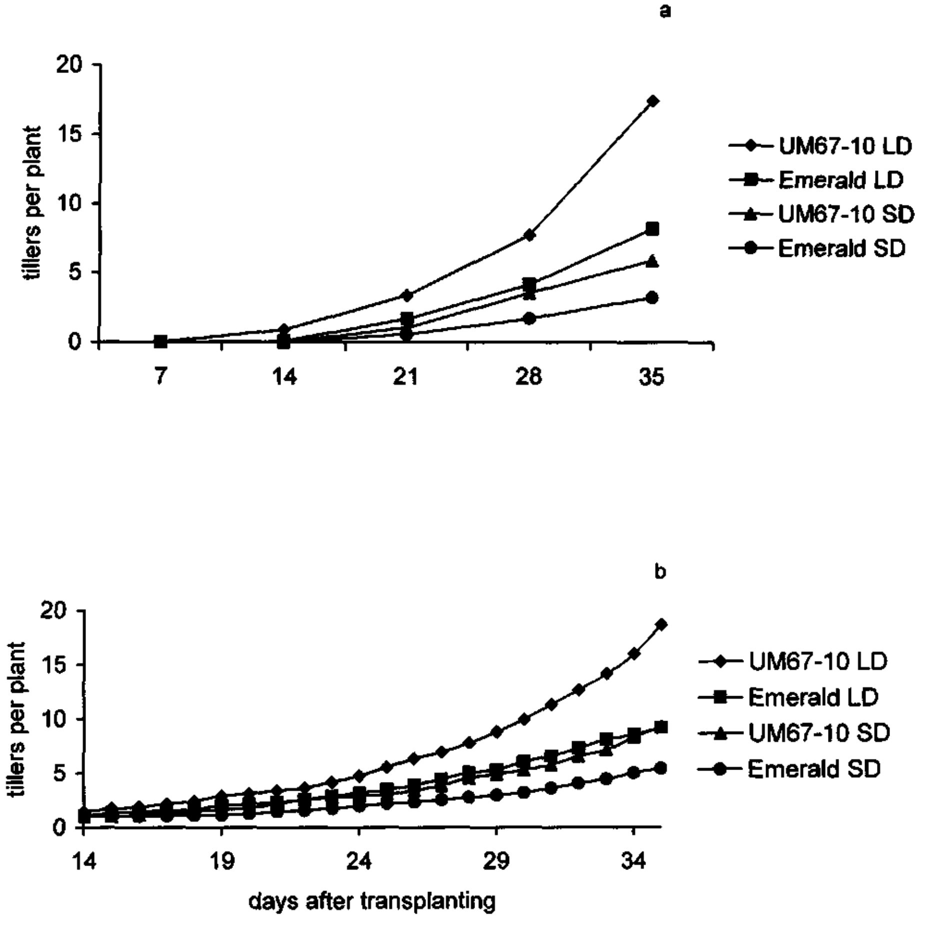

Figure 2.1. Tillers $plant^{-1}$ during initial 35 days of growth after transplanting (DAT) for Emerald and UM67-10 creeping bentgrass grown under long- and short-day conditions. A) greenhouse (measured weekly), B) growth cabinet (measured daily from 14 DAT).

Table 2.4. Tillers plant^{-1}, dead leaves plant^{-1} and total leaves plant^{-1} for the different growing environments for two creeping bentgrass populations at 21, 28 and 35 days after transplanting.

	Tillers plant^{-1}			Dead leaves plant^{-1}			Total leaves plant^{-1}		
Population	**day 21**	**day 28**	**day 35**	**day 21**	**day 28**	**day 35**	**day 21**	**day 28**	**day 35**
Greenhouse - Long day									
Emerald	1.7 b†	4.1 b	8.2 b	0.5 a	0.9 a	1.2a	6.7 b	13.0 b	23.4 b
UM67-10	3.4 a	7.8 a	17.5 a	0.2 a	0.7 a	0.9 a	11.2 a	22.9 a	49.2 a
Greenhouse - Short day									
Emerald	0.6 b	1.7 b	3.2 b	0.4 a	1.3	2.3a	4.6 b	7.6 b	11.1 b
UM67-10	1.1 a	2.5 a	5.9 a	0.2 a	1.0	1.9b	5.3a	9.3 a	17.4 a
Growth Cabinet - Long day									
Emerald	1.3 b	4.1 b	8.2 b	0.3 a	0.5 a	0.6 a	5.8 b	11.6 b	23.8 b
UM67-10	2.5 a	6.8 a	17.7 a	0.3 a	0.5 a	0.6 a	7.9 a	17.3 a	42.6 a
Growth Cabinet - Short day									
Emerald	0.5 b	1.8 b	4.4 b	0.2 a	0.8 a	1.0 a	3.8 b	7.3 b	12.4 b
UM67-10	1.2 a	3.5 a	8.0 a	0.1 a	0.3 b	0.6 a	5.1 a	10.2 a	19.1 a

† Means within environments within columns followed by different letters are significantly different at P=.05 using Dunnett's t-test.

Table 2.5. Stolons plant^{-1} at 28 and 35 days after transplanting, longest stolon plant^{-1}, longest internode and dry matter plant^{-1} at 35 days after transplanting for the different growing environments for two creeping bentgrass populations.

	Stolons plant^{-1}		Longest Stolon (cm)	Longest Internode (cm)	Dry Matter Plant^{-1} (mg)
Population	day 28	day 35	day 35	day 35	day 35
			Greenhouse - Long day		
Emerald	1.3 b†	3.6 b	15.3 a	4.6 a	178.1 a
UM67-10	2.2 a	7.2 a	14.8 a	3.7 b	172.8 a
			Greenhouse - Short day		
Emerald	0.1 a	0.7 a	5.3 a	1.4 a	39.5 a
UM67-10	0.1 a	1.0 a	3.5 b	0.8 b	33.7
			Growth Cabinet - Long day		
Emerald	0.8	3.5 b	12.2 a	3.8 a	161.6 a
UM67-10	1.1	5.5 a	8.9 b	2.6 b	153.3 a
			Growth Cabinet - Short day		
Emerald		0.0 a			25.9 a
UM67-10		0.1 a			28.6 a

† Means within environments within columns followed by different letters are significantly different at P=.05 using Dunnett's t-test.

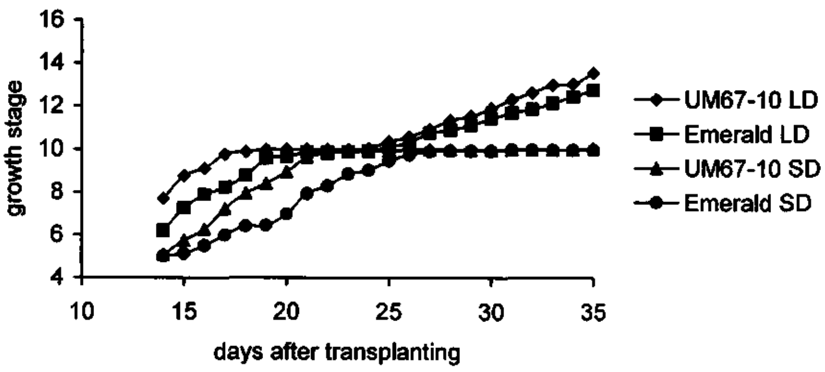

Figure 2.2. Growth stage of Emerald and UM67-10 creeping bentgrass grown under long- and short-day conditions in the growth cabinet.

Table 2.6. Parameter estimates (± standard error in the parenthesis) for the regression equation y = a + bx, for the response of tiller production (y) to leaf production (x) in creeping bentgrass.

Environment	Population	a	b	R^2
Greenhouse				
Long Day	Emerald	-1.138 (0.576)	0.382 (0.005)	0.925
	UM67-10	-0.734 (0.944)	0.370 (0.002)	0.982
Short Day	Emerald	-0.932 (0.493)	0.344 (0.006)	0.898
	UM67-10	-1.162 (0.481)	0.411 (0.004)	0.966
Growth Cabinet				
Long Day	Emerald	-0.293 (1.157)	0.365 (0.011)	0.892
	UM67-10	-1.059 (1.000)	0.443 (0.005)	0.982
Short Day	Emerald	-1.521 (0.465)	0.476 (0.011)	0.952
	UM67-10	-1.446 (0.548)	0.495 (0.008)	0.974

Table 2.7. Mean day of appearance (± standard error of the mean) and the number of observations mean^{-1} (N) for 'UM67-10' and 'Emerald" creeping bentgrass for the short and long day studies in the growth cabinet.

	UM67-10				*Emerald*			
	Short Day		Long Day		Short Day		Long Day	
Tiller	Mean	N	Mean	N	Mean	N	Mean	N
1-1	18.65 ± 0.40	31	15.00 ± 0.28	35	21.93 ± 0.56	28	17.37 ± 0.51	35
2-1	22.69 ± 0.44	35	18.86 ± 0.34	35	26.18 ± 0.45	33	23.36 ± 0.64	33
3-1	27.85 ± 0.30	34	24.63 ± 0.33	35	31.93 ± 0.37	30	27.43 ± 0.43	23
4-1	32.85 ± 0.22	28	29.26 ± 0.38	35	33.25 ± 0.16	4	31.50 ± 0.33	10
5-1			32.80 ± 0.32	25				
6-1			34.25 ± 0.12	8				
7-1			35.00	1				
1-1-1	27.37 ± 0.59	30	23.14 ± 0.50	35	32.05 ± 0.64	21	27.06 ± 0.45	30
1-1-2	31.04 ± 0.34	24	26.35 ± 0.48	34	33.25 ± 0.51	8	29.43 ± 0.59	21
1-1-3	34.00 ± 0.11	7	30.89 ± 0.39	29			32.75 ± 0.31	4
1-1-4			33.18 ± 0.29	11				
1-1-5			34.25 ± 0.08	4				
2-1-1	29.68 ± 0.43	34	26.06 ± 0.39	34	32.16 ± 0.39	19	30.23 ± 0.46	26
2-1-2	33.52 ± 0.15	25	29.69 ± 0.39	32	34.00 ± 0	4	32.13 ± 0.38	15
2-1-3	35.00 ± 0	2	33.55 ± 0.29	22			32.00	1
2-1-4			35.00 ± 0	4				
3-1-1	34.26 ± 0.23	19	30.80 ± 0.33	30	34.67 ± 0.13	3	32.60 ± 0.33	10
3-1-2	34.67 ± 0.13	3	33.58 ± 0.24	19			33.50 ± 0.17	2
3-1-3			35.00 ± 0	3				
4-1-1			34.25 ± 0.26	12			35.00	1
4-1-2			35.00	1				
1-1-1-1	33.75 ± 0.31	8	30.34 ± 0.47	29	33.00	1	32.43 ± 0.54	7
1-1-1-2	35.00	1	33.00 ± 0.35	20			34.50 ± 0.15	2
1-1-1-3			34.67 ± 0.14	6				
1-1-2-1	34.33 ± 0.20	3	32.82 ± 0.22	22			33.40 ± 0.24	5
1-1-2-2			34.14 ± 0.21	7			34.00	1
1-1-2-3			35.00	1				
1-1-3-1			34.75 ± 0.09	4				
2-1-1-1	34.00 ± 0.50	1	32.11 ± 0.35	26				
2-1-1-2			34.09 ± 0.14	11				
2-1-1-3			35.00 ± 0	3				
2-1-2-1			34.00 ± 0.13	12				
2-1-2-2			35.00 ± 0	3				
2-1-3-1			35.00	1				
1-1-1-1-1			33.14 ± 0.49	7				
1-1-1-1-2			34.00	1				
1-1-1-2-1			35.00 ± 0	2				

Occasionally, in the SD, the first tiller arose in the axil of the second leaf on the main stem (2-1°) and this usually was accompanied by a lack of appearance of the1-1° tiller throughout the duration of the study. The first stolon was developed from the main stem, when a stolon was initiated. UM67-10 produced more primary tillers than Emerald regardless of the environment in which they were grown (Table 2.7). The extent of tillering in UM67-10 was also greater with fourth order tillers arising in approximately 20% of plants in LD and third order tillers in approximately 20% of plants in SD (Table 2.7). Emerald in contrast had no fourth order tillers in LD and only one third order tiller in SD (Table 2.7).

Tillers arising below the first leaf were seen in LD but not in the SD. The time of their appearance was not uniform and is not included in the appearance tables. Emerald did have more of these tillers than UM67-10 and it appeared that the increase in tillering in LD for Emerald was due in part to the presence of these tillers.

The dry weight tiller^{-1} for Emerald and UM67-10 can be found in Table 2.8. Emerald had a larger main stem and primary tillers as compared to UM67-10 in LD. Tiller weight of the 1-1-1° tiller of Emerald was higher than for UM67-10, however the remaining dry weights tiller^{-1} were higher for UM67-10 or equal in other secondary and tertiary tillers (Table 2.8). The dry weights tiller^{-1} were less divergent under SD conditions, with the populations having similar total and dry weight tiller^{-1} (Table 2.8). In general, the first tiller within an order or branch of an order is the heaviest followed by the next oldest tiller within the tiller order or branch (Table 2.8). There were two exceptions. One, the last tiller to arise within a branch of an order may have a higher mean than the preceding tiller. This is due in part to the number of tillers that make up the mean and the range of the mean ($\approx \pm 2 \times SE\bar{x}$ at P=0.05) indicates that the mean could actually be smaller. The second exception is found in UM67-10. The dry weight of the 2-1° tiller was equal to the 1-1° tiller as were the dry weights of the 1-1-2° and 1-1-1° tillers equal. This equality between these tillers was also reflected in the relative competitiveness of the arising branches. A high degree of secondary, tertiary and quaternary branching in UM67-10, especially off of the 1-1° and 2-1° tillers, is evident (Table 2.7).

Dry weight pl^{-1} and for individual tillers were greatly reduced under the SD conditions. This reduction was far greater than that experienced by Hunt *et al.* (1987) under shaded conditions.

Table 2.8. Mean dry weight (mg) tiller^{-1} (± standard error of the mean) and the number of observations mean^{-1} (N) for 'UM67-10' and 'Emerald' creeping bentgrass for the short and long day studies in the growth cabinet.

	UM67-10				Emerald			
	Short Day		Long Day		Short Day		Long Day	
Tiller	Mean	N	Mean	N	Mean	N	Mean	N
Whole Plant	28.60 ± 2.02	17	153.30 ± 11.3	17	25.88 ± 2.30	17	161.63 ± 11.5	17
Main Stem	10.18 ± 0.69	17	36.10 ± 2.30	17	12.28 ± 0.79	17	53.05 ± 3.28	17
1-1	4.46 ± 0.32	14	18.64 ± 2.00	17	5.16 ± 0.41	14	33.84 ± 2.49	17
2-1	4.44 ± 0.23	17	19.04 ± 1.42	17	4.41 ± 0.37	17	21.19 ± 2.10	17
3-1	2.91 ± 0.26	17	12.70 ± 1.09	17	2.55 ± 0.35	16	14.48 ± 1.66	13
4-1	1.38 ± 0.20	16	8.43 ± 0.76	16	1.00 ± 0.70	2	9.03 ± 1.59	4
5-1			4.45 ± 0.57	12				
6-1			5.23 ± 0.66	3				
7-1			1.90	1				
1-1-1	2.02 ± 0.22	14	8.14 ± 1.09	17	1.51 ± 0.20	11	12.21 ± 1.42	17
1-1-2	1.72 ± 0.26	13	8.44 ± 0.85	16	1.95 ± 0.24	4	8.38 ± 1.67	11
1-1-3			4.24 ± 0.52	15			5.55 ± 1.41	2
1-1-4			3.48 ± 0.81	5				
1-1-5			1.65 ± 0.16	2				
2-1-1	1.82 ± 0.16	17	7.79 ± 0.74	16	1.29 ± 0.15	9	5.65 ± 0.85	12
2-1-2	0.95 ± 0.11	14	6.05 ± 0.57	16	2.40	1	3.54 ± 0.53	5
2-1-3			3.35 ± 0.63	10			5.00	1
2-1-4			3.80 ± 1.12	2				
3-1-1	0.78 ± 0.12	12	3.62 ± 0.33	15	1.40	1	3.34 ± 0.29	5
3-1-2			2.91 ± 0.34	9			4.65 ± 0.54	2
4-1-1			2.60 ± 0.38	6			0.80	1
4-1-2			2.80	1				
1-1-1-1	0.73 ± 0.11	6	2.23 ± 0.28	15			2.60 ± 0.34	4
1-1-1-2			1.90 ± 0.27	12			2.40	1
1-1-2-1			2.29 ± 0.21	12			1.90	1
1-1-2-2			1.68 ± 0.33	4				
2-1-1-1			2.39 ± 0.23	15				
2-1-1-2			1.96 ± 0.25	5				
2-1-2-1			2.20 ± 0.27	5				
1-1-1-1-1			0.70 ± 0.27	3				
c - 1[z]			8.68 ± 1.43	4			17.50 ± 3.02	9
c - 2			4.60	1			6.78 ± 1.64	4
c - 3			4.00	1				

[z] c – 1, c – 2 and c – 3 refer to coleoptilar tillers in order of appearance.

Site Usage and Dry Matter Partitioning

Site usage is the filling of potential tillering (branching) sites by the plant (van Loo 1992). Plants that fill sites are said to have greater site usage. Tables 2.9 and 2.10 depict site usage charts for the four highest and four lowest tillering plants within UM67-10 and Emerald in the LD environment, respectively. UM67-10 follows the tillering pattern described by Skinner and Nelson (1992). Emerald is not as synchronous, with the BC (coleoptilar tiller branching unit) being the primary reason. Each branching unit (BU) is synonymous with the cycles in Skinner and Nelson (1992). SD plants (data not shown) followed similar patterns. Timing of tillering was based on the appearance of the primary tiller of the next BU. The phyllochron, the duration of time between appearance of leaves on the main stem, although quite similar to this measure in the early stages of growth was affected by the development of stolons (creeping stems) and the use of BU better suits the treatment of the data.

Within UM67-10, the plants that are low tillering (LT) did not fill the sites in the early stages of growth prior to the onset of the next BU whereas high tillering plants filled these sites in a timely fashion (Table 2.9). Tiller counts were made once daily; therefore, tillers with the same date of appearance as the primary tiller of the next BU, were considered to have appeared prior to the onset of the next BU. Leaf size visually decreased as tiller order decreased (primary > secondary > tertiary > quaternary). Higher order tillers had to elongate to a greater extent prior to their visibility due to longer sheaths.

High tillering (HT) plant 2 demonstrates the theory of synchrony, with 4 and 6 new tillers becoming visible over the last two days of observation, respectively (Table 2.9). A general observation within the HT group is that tillers of higher orders within a BU appeared prior to tillers of lower orders within the BU (Table 2.9). In general, BU duration was longer for B2 than B3 for HT plants whereas the opposite was true for the low tillering plants (LT). Appearance of the primary tiller in the B5 of HT plants was before that of the primary tiller of the B4 in the LT group.

Within Emerald, tillering order was disrupted by the appearance of the BC (Table 2.10). The date of appearance was variable, and the order within the branching pattern was not consistent. For example, for HT plant 4 the BC arose between the 2-1 ° and 3-1 ° tillers,

Table 2.9. Presence (1) or absence (0) of tillers (PA), and day of appearance (D) for high and low tillering plants of UM67-10 for the long day growth environment.

Branch Unit	Tiller Designation	Low Tillering Plants								High Tillering Plants							
		Plant 1		Plant 2		Plant 3		Plant 4		Plant 1		Plant 2		Plant 3		Plant 4	
		PA	D	PA	D	PA	D	PA	D	PA	D	PA	D	PA	D	PA	D
BU1	**1-1**	**1**†	**17**	**1**	**17**	**1**	**17**	**1**	**15**	**1**	**14**	**1**	**15**	**1**	**13**	**1**	**13**
BU2	**2-1**	**1**	**18**	**1**	**21**	**1**	**21**	**1**	**22**	**1**	**18**	**1**	**20**	**1**	**16**	**1**	**17**
	1-1-1	*1*‡	*30*	*1*	*27*	*1*	*27*	*1*	*28*	1	19	1	21	1	19	1	18
BU3	**3-1**	**1**	**24**	**1**	**26**	**1**	**25**	**1**	**27**	**1**	**24**	**1**	**25**	**1**	**21**	**1**	**23**
	2-1-1	1	31	1	28	1	29	0		1	23	1	26	1	21	1	23
	1-1-2	1	34	1	28	1	28	0		1	23	1	25	1	21	1	22
	1-1-1-1	0		*1*	*34*	0		0		1	26	1	27	*1*	*27*	1	25
BU4	**4-1**	**1**	**34**	**1**	**31**	**1**	**31**	**1**	**34**	**1**	**28**	**1**	**29**	**1**	**25**	**1**	**27**
	3-1-1									1	29	1	30	1	28	1	30
	2-1-2									1	28	1	28	1	25	1	28
	1-1-3									1	29	1	29	1	26	1	28
	1-1-1-2									1	29	1	31	*1*	*35*	1	28
	1-1-2-1									1	34	1	32	*1*	*30*	0	
	2-1-1-1									1	30	1	31	*1*	*31*	1	29
	1-1-1-1-1									1	31	*1*	*34*	0		1	31
BU5	**5-1**									**1**	**31**	**1**	**33**	**1**	**29**	**1**	**31**
	4-1-1									1	35	1	35	1	32	*1*	*35*
	3-1-2									1	33	1	34	1	31	1	33
	2-1-3									1	32	1	34	1	30	1	32

Table 2.9 con't. Presence (1) or absence (0) of tillers (PA), and day of appearance (D) for high and low tillering plants of UM67-10 for the long day growth environment.

		Low Tillering Plants								High Tillering Plants							
Branch Unit	Tiller Designation	Plant 1		Plant 2		Plant 3		Plant 4		Plant 1		Plant 2		Plant 3		Plant 4	
		PA	D	PA	D	PA	D	PA	D	PA	D	PA	D	PA	D	PA	D
BU5	1-1-4									1	32	1	35	1	30	1	32
	3-1-1-1									0		1	35	0		0	
	2-1-2-1									1	34	1	34	1	34	1	33
	1-1-3-1									1	35	1	35	1	34	*1*	*35*
	2-1-1-2									1	34	1	35	1	34	*1*	*35*
	1-1-2-2									1	35	1	35	1	32	0	
	1-1-1-3									1	35	0		*1*	*35*	1	33
	1-1-1-2-1									1	35	0		0		*1*	*35*
	1-1-1-1-2									0		0		0		1	34
	2-1-1-1-1									0		0		0		0	
	1-1-2-1-1									0		0		0		0	
	1-1-1-1-1-1									0		0		0		0	
BU6	**6-1**									**1**	**35**			**1**	**34**	**1**	**34**
Final Growth Stage		13		13		13		12		13		12		14		15	

[†]Bold type indicates the primary tiller of the branching unit.
[‡]Italicized numbers indicate the appearance of the tiller after the appearance of the primary tiller in the ensuing branching unit.

Table 2.10. **Presence (1) or absence (0) of tillers (PA), and day of appearance (D) for high and low tillering plants of Emerald for the long day growth environment.**

Branch Unit	Tiller	Low Tillering Plants: Plant 1 PA	Plant 1 D	Plant 2 PA	Plant 2 D	Plant 3 PA	Plant 3 D	Plant 4 PA	Plant 4 D	High Tillering Plants: Plant 1 PA	Plant 1 D	Plant 2 PA	Plant 2 D	Plant 3 PA	Plant 3 D	Plant 4 PA	Plant 4 D
BU1	**1-1**	**1**[†]	**17**	0		**1**	**21**	**1**	**17**	**1**	**14**	**1**	**14**	**1**	**15**	**1**	**15**
BU2	**2-1**	**1**	**26**	**1**	**21**	0		**1**	**28**	**1**	**22**	**1**	**18**	**1**	**22**	**1**	**20**
	1-1-1	*1*	28	0		*1*	29	*1*	28	*1*	21	*1*	23	*1*	26	*1*	26
BU3	**3-1**	**1**	**28**	**1**	**31**					**1**	**28**	**1**	**25**	**1**	**27**	**1**	**27**
	2-1-1	1	35	1	31					1	30	1	25	0		1	25
	1-1-2	1	30							1	25	1	23	*1*[‡]	*35*	1	35
	1-1-1-1									1	34	*1*	*31*	0		1	28
BU4	**4-1**									0		**1**	**29**	**1**	**33**	0	
	3-1-1									1	35	1	32	0		0	
	2-1-2									1	33	1	29	0		0	
	1-1-3									1	33	1	31	0		0	
	1-1-1-2									0		1	34	0		1	34
	1-1-2-1									*1*	30	0		0		0	
	2-1-1-1									0		1	32	0		0	
	1-1-1-1-1									0		0		0		0	
BU5	**5-1**													1	33		
BUC	**c-1**			**1**	**25**	**1**	**23**	**1**	**23**	**1**	**19**			**1**	**24**	**1**	**23**
	c-1-1			1	32	1	32	1	33	1	30			1	30	1	30
	c-1-2													1	34	1	35
Growth Stage		13		12		13		14		13		13		15		13	

[†] Bold type indicates the primary tiller of the branching unit.
[‡] Italicised numbers indicate the appearance of the tiller after the appearance of the primary tiller in the ensuing branching unit.

while for HT plant 1 it arose between the 1-1° and 2-1° tillers. LT plants were much slower to initiate tillering than HT plants within this population (Table 2.10).

Stolon elongation took place at the fourth or fifth node on the main stem for both populations (Table 2.11). Elongation of primary tillers generally took place at one node below this for Emerald, and for UM67-10 the node of tillering was dependent upon its rank within the order (Table 2.11). The secondary order elongated in general at a lower node than the primary tiller that it arose from for both populations.

Non-tillering sites above the last tillering node on the main stem increased as growth progressed (Table 2.12). Emerald had 4 leaves on the main stem above the last appearing tiller while UM67-10 had 2.8 leaves. This decreased with the order of the tiller.

The lack of tiller mortality in these experiments is most likely a factor of the plant age and the lack of interplant competition as Jonsdottir (1991) found an equilibrium between tiller emergence and mortality in creeping bentgrass in a naturally occurring stand.

Table 2.11. Mean number of nodes beneath the internode of elongation on stolons, standard error of the mean and the number of observations mean^{-1} for Emerald and UM67-10 creeping bentgrass grown under long days in the growth cabinet.

	EMERALD			UM67-10		
Tiller	Mean	SE$\bar{x}$	N	Mean	SE$\bar{x}$	N
Main stem	3.29	0.24	17	3.41	0.21	17
1-1	2.12	0.15	17	2.88	0.12	17
2-1	2.14	0.14	14	2.35	0.15	17
3-1	2.00	0.00	8	1.81	0.10	16
4-1	2.00	0.00	2	1.67	0.21	6
1-1-1	1.67	0.17	15	2.25	0.13	12
1-1-2	1.66	0.33	3	2.00	0.00	8
2-1-1	1.50	0.50	2	2.18	0.12	11
2-1-2				1.60	0.24	5

Table 2.12. Mean number of leaves above last visible tiller ± standard error of the mean, and number of observations contributing to the mean (in parenthesis) for main stem or tillers that developed into stolons under long days in the growth cabinet.

Main Stem or Tiller of Development into a Stolon	Emerald	UM67-10
Main Stem	4.00 ± 0.26 (10)	2.80 ± 0.39 (10)
1-1	2.70 ± 0.21 (10)	2.10 ± 0.18 (10)
1-1-1	2.33 ± 0.22 (6)	1.86 ± 0.12 (7)
2-1	2.29 ± 0.15 (7)	2.40 ± 0.16 (10)
2-1-1		1.67 ± 0.16 (6)
3-1	2.50 ± 0.32 (4)	2.11 ± 0.19 (9)

Discussion

Tillering in these studies followed an exponential growth curve as predicted (Skinner and Nelson, 1992). No tiller mortality was experienced throughout the duration of these studies. Differences between the populations were consistent with respect to tillering. Variation within populations was found; however, the difference between populations was greater than within populations for most traits. Emerald has been shown to produce fewer tillers and leaves under growth room conditions and lower tiller densities under turf conditions as compared to a high tillering cultivar such as 18th Green (Chapter 4), which was selected out of UM67-10 (Cattani *et al.* 1992). Dry matter production of the two populations was relatively equal, leading to the appearance of finer leaves and tillers in UM67-10. Skinner and Nelson (1994) reported higher levels of coleoptilar tillering within a low leaf elongation rate in tall fescue, contrary to the results obtained in the present study (Table 2.8). Skinner and Nelson (1992) found that selection for low leaf elongation rate lead to a plant type with more tillers and lower tiller dry weights in *Festuca arundinacea*, similar to results for UM67-10.

The difference in slope for the regression lines of the populations in the LD for the production of tillers in response to leaf number (Table 2.5) implies that there is a greater propensity for tiller production in UM67-10. It is possible that as stolon initiation takes place, more of the resources within the plant are utilised in this production thus reducing the tiller number increase. Stolon initiation took place at approximately the same time, leaving

Emerald with less tillering than UM67-10 prior to the onset of stolon initiation, possibly retarding further tiller number increase. The effect of shorter daylengths in the GH also indicates that photoperiod is important in growth and development. The SD GH had the lowest mean tillers pl^{-1}, however, stolon development was taking place at least seven days earlier than in the SD GC. This is most likely the effect of the longer photoperiod in the GH.

The growth stage curves (Figure 2.2) indicate that tillering was still following the exponential increase (Figure 2.1b) while stolon initiation and elongation were taking place. As stolons developed there was a stronger tendency towards reduced tillering than was seen earlier in the growth. Number of leaves above the last visible tiller on a stolon was greater than two for each of Emerald and UM67-10. Emerald in the LD had a higher percentage of tillers becoming stolons as compared to UM67-10 (Tables 2.3 and 2.4) and this may also explain the lesser slope seen for Emerald.

The delay in stolon production in SD in the GC may be attributed to the daylength, as conditions where daylength is reduced in such a manner in the field are found in late fall in northern areas. At this time of year, plants will have hardened off for overwintering purposes. The greatly reduced dry matter accumulation found in the plants in SD would also reduce the internal resources available for tillering and stolon initiation. In Chapter 6 we indicate that tillering of creeping bentgrass in northern areas had halted and was beginning to decrease in September - early October with an accompanying increase in tiller weight. These results have implications with respect to the establishment of creeping bentgrass. They suggest that planting under LD is advantageous for the growth of creeping bentgrass at northern latitudes. Greater production of stolons would take place in the year of seeding and allow for the establishment of a more durable turf. Another advantage would be the plant size heading into the winter period, with larger plants having greater resources to withstand damage due to the winter stresses.

Differences in the partitioning within the plant (dry matter accumulation) between the populations, may also have implications for growth of the turf. UM67-10 allows earlier arising tillers (1-1° and 2-1°) systems to proliferate, increasing the tiller density within a turf at an earlier stage. This greater amount of tillering may lead to greater interplant competition and reduce plant numbers within the turf. Long term detrimental effects may occur with respect to wear stress tolerance if individual tiller size decreases too far. The proliferation of tillers may also decrease the plants ability to recover from stress or repair damage due to wear stress by reducing tillering sites. Greater stolon elongation may also be important by allowing for a greater area of coverage and reducing open areas for weed infestations.

It is later suggested (Chapter 4) that controlled grow outs of creeping bentgrass may be utilised for selection purposes. The correlation values for leaves and tillers pl^{-1} and for longest stolon and longest internode were similar in range to those in Chapter 4. Low correlation values between tiller number and the stolon characteristics in this present study indicates the possibility of selection for high tillering, long stolon phenotypes from within a population. Results reported in Chapter 4 show a relatively high, negative correlation between tillering and stolon and internode lengths; however, this comparison was between populations, not within populations.

Long day studies in the growth cabinet allow for screening of populations for early developing growth parameters in creeping bentgrass. Controlled studies investigating plant development within a turf in a creeping bentgrass cultivar are also possible.

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Chapter 3

Tillering, stolon development and dry matter partitioning in creeping bentgrass (*Agrostis stolonifera* L.).

Abstract

Early plant development in creeping bentgrass will affect turf characteristics. Stolon development is critical to stand persistence. The objectives of this study were to i) record tiller formation, stolon appearance and stolon development and (ii) determine dry matter partitioning in high and low tillering populations. Individual pre-germinated seeds of cv. "Emerald" and line "UM67-10" were transplanted into 10 cm pots containing an 80:20 (v:v) sand:peat media. One greenhouse experiment (**GH**) (20 pots population^{-1}) and two growth cabinet experiments (**GC**) under 16 h and 8 h photoperiods, and 20/15 °C day/night temperatures (≥15 pots population^{-1} run^{-1}) were completed. Phenological development was monitored throughout the study until 42 d after transplanting (DAT) and 35 DAT in **GH** and **GC** respectively. Tillers plant^{-1}, tiller position and stolon growth were recorded daily. Stolon number, length of main tiller (stolon) and length of longest internode were measured at 35 DAT. Dry weight tiller^{-1} (**DWT**) was determined at 42 and 35 DAT in the **GH** and **GC** studies respectively. **DWT** was positively correlated to tiller age for main stem and 1° (r = 0.98 and r = 0.99) and 2° (r = 0.93 and r = 0.99) tillers for UM67-10 and Emerald, respectively, but not with 3° (r = 0.16) tillers for UM67-10. Population differences for dry weight accumulation day^{-1} were significant (P=0.05) for lower order tillers. Mean stolon appearance was 27 and 33.5 DAT in **GC** long day and **GH** respectively. Stolon development in **GC** short day was not evident at 35 DAT. Stolon weight was related to date of stolon initiation and stolon length. Tillers plant^{-1} and date of first tiller appearance were not correlated to stolon appearance date. Rate of stolon node appearance was similar in **GC** long day and **GH** studies for the growth periods monitored.

Key words: creeping bentgrass, stolon, dry matter partitioning, plant development, tillering

INTRODUCTION

Creeping bentgrass (*Agrostis stolonifera* L.) is an obligate outcrossing species (Bradshaw 1958) which spreads vegetatively via extensive stolon growth (Kik *et al.* 1990). Vegetative growth predominates in areas where growing conditions are favourable (Kik *et al.* 1990) and the environment is disturbed (Hunt *et al.* 1987).

Creeping bentgrass is primarily used for golf green turf in temperate regions. As a creeping bentgrass turf develops, stolons provide surface structure and cushion the surface to help resist tearing. Shorter stolon internode length is related to high tiller density in creeping bentgrass turf (Chapter 4).

High tiller density provides a dense surface that allows for smooth ball roll and resistance to ingress by other, less desirable plants species. Once a creeping bentgrass stand is established, very little subsequent growth of new seedlings occurs within a stand (Jonsdottir 1990, Bullock *et al.* 1994), even where regular overseeding is practised (Sweeney and Danneberger 1998).

Robson (1973) describes an exponential phase, a linear phase and a static or decreasing phase of tiller appearance in grasses. Jonsdottir (1990) monitored tiller birth and death in a naturally occurring stand of creeping bentgrass and found that they were offsetting. Tiller proliferation in young creeping bentgrass plants, under non-competitive conditions was found to be in the exponential growth phase (Chapter 2).

Tiller development in plants is related to leaf appearance (Davies and Thomas 1983). Leaf morphological characteristics such as leaf length and width (Bos 1999), and leaf density will all impact the level of competition for light (Wilson and Cooper 1969). Leaf appearance rates are reduced drastically in late September to late October in perennial ryegrass, thus reducing tillering potential (Vine 1983). Casal *et al.* (1990) demonstrated that the red:far red light ratio was important in tillering.

Dry matter accumulation in tillers is important with respect to survival. Ong (1978) found tiller size (by weight) to be the important factor in tiller survival under whole plant stress. Dry matter partitioning within the plant is therefore important for turf plant development and persistence.

Dry matter accumulation tiller^{-1} is important for wear stress resistance in *Poa pratensis* L. (Shildrick and Peel 1984) and appears to be important in creeping bentgrass (Cattani 1987). Lush (1990) used tiller density and dry weight per unit area to estimate potential wear stress resistance. Trenholm *et al.* (1999) reported higher tiller densities resulted in greater wear resistance for seaside paspalum (*Paspalum vaginatum* Swartz).

Differences in tillering rate were found between two related populations (Chapter 2). Competition between and within plants is an important factor determining rate of formation and long-term persistence of a good quality turf. Individual plant growth will be affected by genetic potential (Chapters 2 and 4) and by population density (Chapter 5).

The objectives of this study were; 1) to investigate the relationship between early stolon development and tillering; and 2) to investigate the dry matter partitioning in tillers and branching systems in developing creeping bentgrass plants.

METHODS AND MATERIALS

Growth Cabinet Study

The design of the study has been described in Chapter 2. In brief, twenty-five pots each of two creeping bentgrass populations, "Emerald" and "UM67-10", were planted with a single pre-germinated seed and grown under the fertility regime as described in Chapter 2. The experiments were conducted in growth cabinets under a long day (GRLD), 16-h photoperiod and a short day (GRSD), 8-h photoperiod, with 20/15 °C day/night temperatures. Lighting was maintained at 150 μmol m^{-2} s^{-1} supplied by a combination of incandescent and fluorescent bulbs. Plants were arranged in a completely randomised design and re-randomised twice weekly to remove position effects.

Any plant exhibiting damage or a reduction in growth that may have been due to damage during transplanting was removed from the study. There were 15 plants per population in each of the first runs in the long day and short day conditions and 20 (long day) and 19 (short day) plants per population for the second run. Tillering was monitored daily until 35 days after transplanting (DAT). As each new tiller arose, the day and site of appearance were recorded. Colour coded wire loops were used to identify the tiller. Stolon appearance and elongation were used to assign growth stage values based on West (1990). The monitoring was terminated at 35 DAT as the plants in GRLD had stolons outside of the pots and interplant competition for light was becoming a factor. At 35 DAT, plants within populations were paired, based on tiller number and growth stage. One plant from each pair was dissected to determine individual tiller dry weight. The remaining plants are being used for field studies related to wear stress resistance.

Values reported in this paper for tiller age are from the plants that were dissected for tiller weights (values for all tillers were reported in Chapter 2). Stolon node appearance was derived from the growth stage measurements. Dry weight tiller order (main stem, 1°, 2°, etc.) and dry weight per tillering system (PS) (1st PS consisted of all tillers arising from and including the1 - 1°; 2nd PS consisted of all tillers arising from and including the 2 - 1° tiller; etc.) were calculated per plant to examine dry matter partitioning within plants. Tiller succession rates were calculated (time (days) between successive primary tillers (i.e. date of appearance for 2 - 1° - date of appearance for 1 - 1°) for each plant.

Analysis of variance was performed with PROC GLM in SAS (SAS Institute, Gary, NC). There were no run x population interactions and therefore means reported are combined over the two successive experiments. Regression analysis was performed with SAS, with mean values for tiller age on dry weight tiller^{-1} for GRLD and GHSD. Tillers were analysed within the following categories, main stem and primary tillers, secondary tillers and in the case of UM67-10 GRLD, tertiary tillers.

Greenhouse Study

A greenhouse study was carried out under natural short day conditions (transplanted on 22 October 1997) as described in Chapter 2. Day length decreased with natural daylight, however some supplemental lighting was present in the greenhouse and temperatures were kept above 15°C. At 14 DAT, 20 plants from each population were selected to monitor tiller and stolon development as described above. Due to the slow plant growth under these conditions, these plants were grown until 42 DAT (3 December). Fertiliser applications (as in Chapter 2) continued through week 6. Dry weight per tiller order and dry weight per tillering system were also determined at harvest (42 DAT) as described above. Tiller succession rates were recorded for primary tillers. All values for the populations reported are for plants utilised in this tiller and stolon development study.

Statistical analysis was performed as above.

RESULTS

Tiller Age

Significant differences were found for tiller age within the two populations in all environments (Tables 3.1 and 3.2). The 1 - 1° tiller appeared before all other tillers, followed by the 2 - 1°. The tillering order, in general, followed the expected pattern (Neuteboom and Lantinga 1989). The 3 - 1° appeared after the 1 - 1 - 1° except for the short day greenhouse study (GH), although the date of appearance was not significantly different (P=0.05).

Comparisons between the populations showed that appearance of tillers in UM67-10 took place at an earlier date, especially for primary tillers (Tables 3.3 and 3.4). For example, tiller age of the 1 - 1° tiller for UM67-10 were 20.6, 17.6 and 23.3 d for the long day growth room study (GRLD), short day growth room study (GRSD) and GH, respectively, compared to 18.8, 13.7 and 17.8 d for Emerald. Exceptions to this trend were with the 4 - 1° and coleoptilar tillers in the (GRLD) and the 1 - 1 - 1° tillers in the GH where there were no significant differences between Emerald and UM67-10 (Tables 3.3 and 3.4).

Dry Weight Tiller^{-1}

Dry weights tiller^{-1} (DWT) for the growth room studies are found in Chapter 2. Dry weight tiller^{-1} (DWT) showed differences within populations in GH (Table 3.2). Within both populations, 1 - 1°, 2 - 1° and 3 - 1° tillers all had dry weights that were statistically similar

(Table 3.2). Emerald had descending values for dry weight of these tillers while the 2 - 1° tiller in UM67-10 was heavier than the 1 - 1° tiller. The trend of declining weight with increasing tiller order was apparent with 1 - 1 - 1° and 1 - 1 - 2°, and 2 - 1 - 1° and 2 - 1 - 2° for UM67-10 (Table 3.2).

Population comparisons did not show significant differences in GH (Table 3.4). A large difference between populations for the main stem was not significant due to the presence of a single Emerald plant that was relatively small. Removal of this plant from the analysis results in a significant difference between populations (t-test, $P = 0.05$).

DWT increases were primarily due to stolon development. In GH stolon development took place at the main stem and 1° tiller level, while in GRLD stolon development was also beginning at the 2° tiller level.

Effect of Tiller Age on Dry Weight Tiller^{-1}

The regression lines of best fit for the individual tiller classes within the two populations are found in Figures 3.1 and 3.2, for UM67-10 and Emerald, respectively. In general, linear regression equations gave the best fit for the data with R^2 values ranging from 0.93 to 0.99. The major exception was for UM67-10 in the GRLD (not shown) where no age and dry weight relationship for tertiary tillers was found. Slopes indicate that main stem and primary tillers are stronger sinks, most likely due to stolon development.

Dry Weight Day^{-1}

Dry weight day^{-1} accumulation (**DWD**) was analysed to evaluate relative dry matter partitioning. Significant differences were found within both populations for **DWD** with the exception of Emerald in the GH (Tables 3.1 and 3.2). UM67-10 had the lowest **DWD** for the first tiller in each branch although it was rarely significantly lower (Tables 3.1 and 3.2).

Between population comparisons indicated that regardless of whether significant differences were found, Emerald had a higher value (Tables 3.3 and 3.4).

The mean dry weight plant^{-1} for Emerald and UM67-10 in the GH study were 99.8 and 93.3 mg respectively at 42 DAT. Population differences for dry weight plant^{-1} were not found in either growth room study (Chapter 2).

Table 3.1. Number of observations per population (n) and mean comparisons for tiller age, dry weight tiller^{-1} and weight gain day^{-1} within populations A (Emerald) and B (UM67-10) grown under short and long day conditions in the growth cabinet.

	Growth Cabinet - Short Day						Growth Cabinet - Long Day					
	n		Tiller Age		Dry Weight Day^{-1}		n		Tiller Age		Dry Weight Day^{-1}	
Pop'n	A	B	A	B	A	B	A	B	A	B	A	B
Tiller			-------- d --------		---------- mg ----------				--------- d ----------		----------- mg -----------	
Main Stem	17	17	35.0	35.0	0.35 c†	0.29 c†	17	17	35.0	35.0	1.51 bc†	1.02 c†
1 - 1°	14	14	13.7 a†	17.6 a†	0.39 c	0.26 c	17	17	18.8 a†	20.6 a†	1.75 a-c	0.88 d
2 - 1°	16	17	9.4 b	13.1 b	0.55 bc	0.36 c	16	17	11.7 b	16.8 b	1.99 ab	1.14 b-d
3 - 1°	16	17	4.2 c	7.9 c	0.71 ab	0.40 bc	13	17	7.6 cd	11.2 cd	1.92 ab	1.16 b-d
4 - 1°		16		3.0 e		0.65 a¶	4	16	5.3 d-f	6.8 f	1.68 a-c	1.27 a-d
5 - 1°								12		3.1 i		1.80 a
C - 1°							9	4	10.0 bc	8.0 ef	1.61 a-c	1.40 a-d
C - 2°							5		4.8 ef		1.85 a-c	
1 - 1 - 1°	11	14	3.8 c	8.7 c	0.51 bc	0.26 c	17	17	8.6 c	12.5 c	1.44 bc	0.63 d
1 - 1 - 2°	4	13	2.4 c	4.8 d	1.04 a	0.38 bc	12	16	6.1 de	9.6 e	1.58 a-c	0.88 d
1 - 1 - 3°								15		4.8 gh		0.94 d
1 - 1 - 4°								5		2.6 i		1.81 a
2 - 1 - 1°	11	17	3.9 c	5.6 d	0.35 c	0.43 bc	12	16	5.4 d-f	9.9 de	1.00 c	0.81 d
2 - 1 - 2°		14		2.3 ef		0.49 a-c	4	16	4.3 ef	6.1 fg	1.28 bc	1.05 cd
2 - 1 - 3°								10		2.7 i		1.45 a-c
3 - 1 - 1°		12		1.5 f		0.58 ab	5	15	3.4 ef	4.7 gh	1.25 bc	1.15 b-d

Table 3.1 con't. Number of observations per population (n) and mean comparisons for tiller age, dry weight tiller^{-1} and weight gain day^{-1} within populations A (Emerald) and B (UM67-10) grown under short and long day conditions in the growth cabinet.

	Growth Cabinet - Short Day						Growth Cabinet - Long Day					
	n		Tiller Age		Dry Weight Day^{-1}		n		Tiller Age		Dry Weight Day^{-1}	
Pop'n	A	B	A	B	A	B	A	B	A	B	A	B
			-------- d --------		--------- mg ----------				-------- d --------		--------- mg ----------	
3 - 1 - 2°								9		2.2 i		1.59 ab
4 - 1 - 1°								6		2.0 i		1.54 a-c
C - 1 - 1°							6		5.5 d-f		2.38 a	
C - 1 - 2°							4		2.3 f		1.73 a-c	
1 - 1 - 1 - 1°		15		2.2 ef		0.39 bc¶	4	15	3.5 ef	5.2 gh	0.90 c	0.50 d
1 - 1 - 1 - 2°								9		2.0 i		1.44 a-d
1 - 1 - 2 - 1°								12		3.3 hi		0.91 d
1 - 1 - 2 - 2°								4		2.0 i		0.98 d
2 - 1 - 1 - 1°								15		3.0 i		1.04 b-d
2 - 1 - 1 - 2°								5		1.8 i		1.34 a-d
2 - 1 - 2 - 1°								5		1.6 i		1.61 ab

† Means followed by the same letter are not significantly different using t-test (P= 0.05).
‡,§,¶ Means followed by these individual symbols are not significantly different using t-test (P= 0.05).

Table 3.2. Number of observations per population (n) and mean comparisons for tiller age, dry weight tiller^{-1} and weight gain day^{-1} within populations A (Emerald) and B (UM67-10) grown under short-day conditions in the greenhouse.

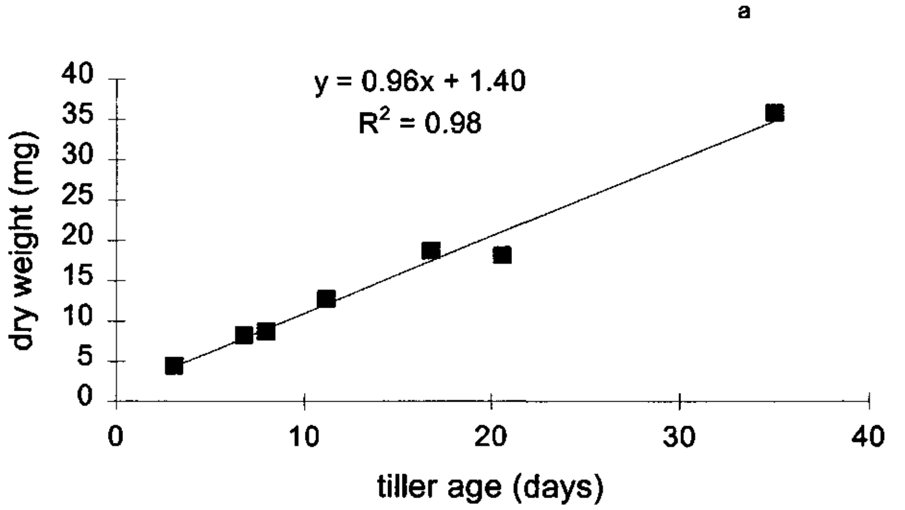
	n		Tiller Age		Dry Weight		Dry Weight Day^{-1}	
Population	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
			---------- d ----------		---------- mg ----------			
Main Stem	10	10	42.0	42.0	41.68 a †	30.01 a †	0.99 a†	0.71 abc†
1-1°	10	10	17.8 a†	23.3 a†	18.09 b	12.36 b	0.94 a	0.56 bc
2-1°	10	10	11.9 b	18.7 b	15.07 bc	13.53 b	1.17 a	0.72 ab
3-1°	8	10	8.3 bc	12.8 c	10.56 bc	10.74 b	1.10 a	0.85 a
4-1°	2	10	2.0 c	7.5 ef	3.80 bcd	6.51 c	1.40 a	0.88 a
5-1°		4		4.0 g		2.40 cd		0.63 abc
1-1-1°	6	10	12.2 ab	11.1 cd	6.53 bcd	3.96 cd	0.59 a	0.33 c
1-1-2°	4	9	3.8 c	7.9 ef	2.67 cd	3.64 cd	0.86 a	0.54 bc
1-1-3°		4		3.5 g		1.88 cd		0.74 ab
2-1-1°	5	10	5.4 bc	9.8 de	2.32 d	4.00 cd	0.65 a	0.37 c
2-1-2°	2	7	3.5 c	7.1 ef	2.15 d	4.90 cd	0.44 a	0.66 abc
2-1-3°		3		2.0 g		1.30 cd		0.69 abc
3-1-1°		6		5.2 fg		1.61 cd		0.35 c
1-1-1-1°		5		3.2 g		0.94 d		0.31 c

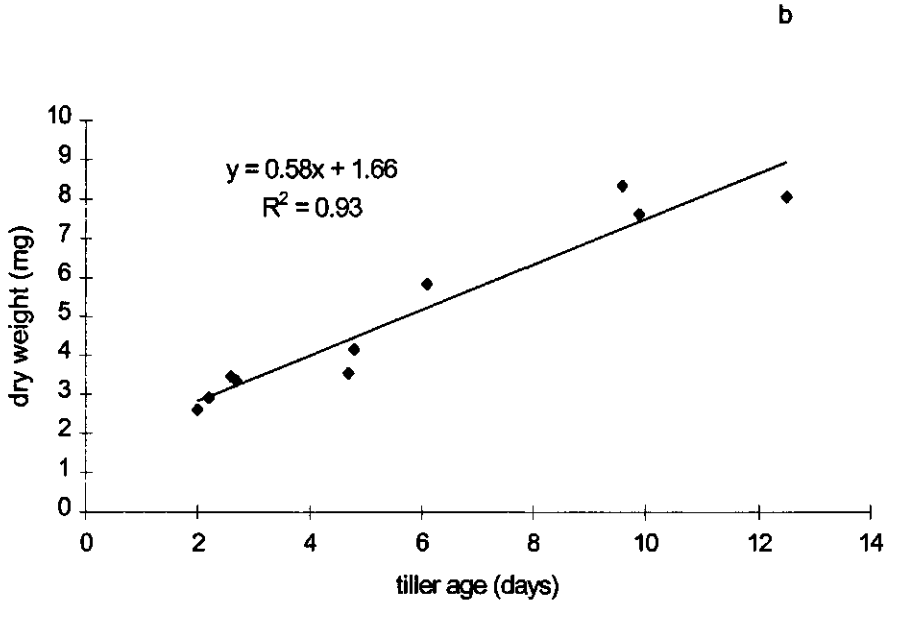
† Means followed by the same letter within columns are not significantly different using t-test (P= 0.05).

Tiller Order Comparisons

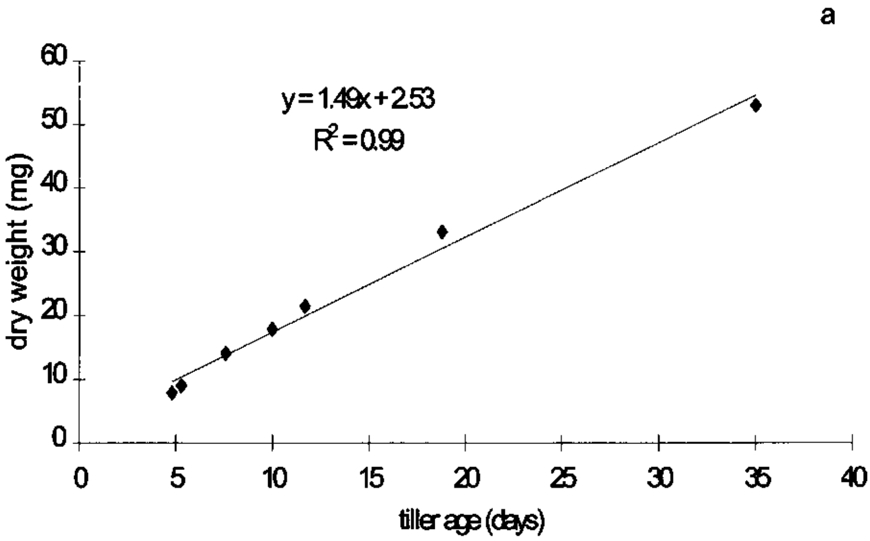
Tiller number order^{-1}, on a plant basis, were found to approximate a normal distribution across the orders (Tables 3.5 and 3.6). A similar distribution pattern was reported by Davies and Thomas (1983) until a major stress was encountered. Dry weight order^{-1} was skewed towards the lower orders with primary tillers making a significantly greater contribution to total above ground dry weight plant^{-1} than the main stem; with the exception of Emerald in the GH (Tables 3.5 and 3.6). Dry weight tiller^{-1} (**DWT**) was in all cases highest for the main stem, followed by primary tillers and then by tiller orders in sequence (Table 3.5).

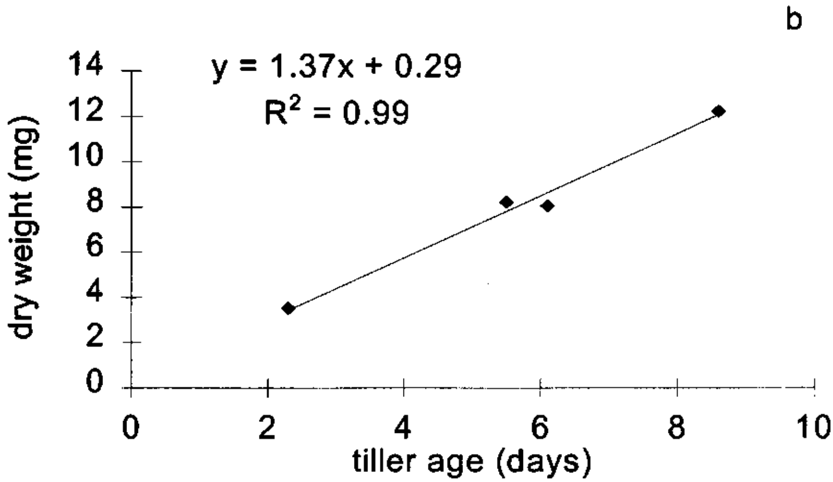
A separate analysis was carried out on GRLD study to determine the contribution of individual main stem branches (primary tillering systems (PS)) to above-ground dry matter accumulation. The 1st PS refers to tillers arising from and including the 1 - 1° tiller, 2nd PS to 2 - 1° tiller and its descendants, and so on. Tiller number distributions between PS branches





Figures 3.1 a,b. Linear regression line, equation and R^2 for UM67-10 for mean tiller dry weight (mg) on mean age of the tiller for; a) main stem and primary tillers; b) secondary tillers.





Figures 3.2 a,b. Linear regression line, equation and R^2 for Emerald under long day conditions for mean tiller dry weight (mg) on mean age of the tiller for; a) main stem and primary tillers; and b) secondary tillers.

Table 3.3. Mean tiller age, dry weight tiller^{-1} and weight gain day^{-1} comparisons between populations A (Emerald) and B (UM67-10) grown under short and long day conditions in the growth cabinet.

	Growth Cabinet - Short Day						Growth Cabinet - Long Day					
	n		Tiller Age		Dry Weight Day^{-1}		n		Tiller Age		Dry Weight Day^{-1}	
Population	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
Tiller			---------- d ----------		--------- mg ---------				---------- d ----------		--------- mg ---------	
Main stem	17	17	35.0	35.0	0.35 a†	0.29 b	17	17	35.0	35.0	1.51 a†	1.02 b
1 - 1°	14	14	13.7 b†	17.6 a	0.39 a	0.26 b	17	17	18.8 b†	20.6 a	1.75 a	0.88 b
2 - 1°	17	17	9.4 b	13.1 a	0.55 a	0.36 b	17	17	11.7 b	16.8 a	1.99 a	1.14 b
3 - 1°	16	17	4.2 b	7.9 a	0.71 a	0.40 b	13	17	7.6 b	11.2 a	1.92 a	1.16 b
4 - 1°							4	16	5.3 a	6.8 a	1.68 a	1.27 a
C - 1°							9	4	10.0 a	8.0 a	1.61 a	1.40 a
1 - 1 - 1°	11	14	3.8 b	8.7 a	0.59 a	0.26 b	17	17	8.6 b	12.5 a	1.44 a	0.63 b
1 - 1 - 2°	5	13	2.4 b	4.8 a	1.04 a	0.38 b	12	16	6.1 b	9.6 a	1.58 a	0.88 b
2 - 1 - 1°	9	17	3.4 a	5.6 a	0.35 a	0.43 a	12	16	5.4 b	9.9 a	1.00 a	0.81 a
2 - 1 - 2°							4	16	4.3 a	6.1 a	1.28 a	1.05 a
3 - 1 - 1°							5	15	3.4 a	4.7 a	1.25 a	1.15 a

† Means followed by the same letter (within row) are not significantly different using t-test (P= 0.05)

Table 3.4. Comparisons for mean tiller age, dry weight tiller^{-1} and dry weight day^{-1} at 42 d after transplanting between populations A (Emerald) and B (UM67-10) grown under short-day conditions in the greenhouse.

	n		Tiller Age		Dry Weight		Dry Weight Day^{-1}	
Population	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
Tiller			---------- d ----------		---------- mg ----------			
Main stem	10	10	42.0	42.0	41.68 a†	30.01 a	0.99 a†	0.71 a
1 - 1°	10	10	17.8 b†	23.3 a	18.09 a	12.36 a	0.94 a	0.54 b
2 - 1°	10	10	11.9 b	18.7 a	15.07 a	13.53 a	1.17 a	0.72 a
3 - 1°	8	10	8.3 b	12.8 a	10.56 a	10.74 a	1.10 a	0.85 a
4 - 1°	2	10	2.0 b	7.5 a	3.80 a	6.51 a	1.40 a	0.88 a
1 - 1 - 1°	6	10	12.2 a	11.1 a	6.53 a	3.96 a	0.59 a	0.33 a
1 - 1 - 2°	4	9	3.8 a	7.8 a	2.67 a	3.64 a	0.86 a	0.54 a
2 - 1 - 1°	5	10	5.4 b	9.8 a	2.32 a	4.00 a	0.65 a	0.37 a
2 - 1 - 2°	2	7	3.5 a	7.1 a	2.15 a	4.90 a	0.44 a	0.66 a

† Means followed by the same letter (within row) are not significantly different using t-test (P= 0.05).

Table 3.5. Mean comparisons within populations (Emerald (A) and UM67-10 (B)) for tiller number, dry weight and dry weight tiller^{-1} at 35 days after transplanting under long day conditions in the growth cabinet.

	n		Tillers		Dry Weight		Dry Weight Tiller^{-1}	
Population	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
Tiller Order			-- number plant^{-1} --		---------- mg ----------			
Main Stem	17	17	1.00 b†	1.00 c†	53.05 b†	36.10 b†	53.05 a†	36.10 a†
Primary	17	17	3.76 a	5.24 b	77.87 a	64.86 a	21.11 b	12.42 b
Secondary	17	17	4.06 a	8.00 a	29.55 c	43.29 b	7.19 c	5.32 c
Tertiary	4	15	1.75 b	4.73 b	4.05 d	10.10 c	2.27 c	2.13 c
Quaternary		3		1.00 c		0.70 c		0.70 c

† Means followed by the same letter (within column) are not significantly different using t-test (P= 0.05).

are similar, where present, for the two populations (Table 3.7). 1st PS had significantly more tillers than 2nd PS and the following tiller orders. Emerald had a higher proportion of coleoptilar tillers (C PS) than UM67-10. Dry weight distributions amongst the main stem and PS's were different between the populations (Table 3.7). For Emerald, main stem and 1st PS had the highest **DWT**, followed by C PS, 2nd PS , 3rd PS and 4th PS (Table 3.7). UM67-10

Table 3.6. Tiller number, dry weight and dry weight tiller^{-1} for the main stem and tillering systems arising off of the main stem (Primary tillering systems) at 42 d after transplanting within Emerald and UM67-10, populations A and B, respectively for short-day conditions in the greenhouse.

	n		Tillers		Dry Weight		Dry Weight Tiller^{-1}	
Population	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
Tiller Order			-- number plant^{-1} --		-------------------- mg	--------------------		
Main stem	10	10	1.0	1.0	41.7 a†	30.0 b†	45.9 a†	29.5 a†
Primary	10	10	2.8 a†	4.3 a†	42.3 a	43.6 a	15.6 b	10.3 b
Secondary	7	10	2.4 a	5.4 a	9.8 b	18.5 c	3.5 c	3.3 c
Tertiary		5		2.0 b		3.4 d		2.0 c

† Means followed by the same letter (within columns) are not significantly different using t-test (P= 0.05).

had the highest **DWT** for 1st PS, followed by 2nd PS, main stem, 3rd PS, C PS, 4th PS and lower orders (Table 3.7). Within a PS, the primary tiller had the highest mean dry weight (Table 3.7). UM67-10 showed a higher mean **DWT** for 2nd , 3rd and 4th PS as compared to 1st PS while in Emerald, 1st PS was significantly higher than 3rd and 4th PS.

Tillering and Stolon Appearance

Tillers appeared first in UM67-10 at 15.0 and 19.0 DAT while for Emerald a first tiller appeared (**TAD**) at 17.3 and 22.1 DAT under GRLD and GH, respectively (Table 3.8). Stolon development under GRSD was not seen at 35 DAT. Therefore, stolon development monitoring in the GH environment required that the plants be grown until 42 DAT.

Mean stolon appearance dates (**STAD**) showed less than a day difference between populations within each environment (Table 3.8). Differences between **TAD** and **STAD**, (**STAD -TAD**), showed that UM67-10 had significantly longer intervals between tiller appearance and stolon appearance than Emerald (Table 3.8).

Stolon development, measured as the appearance rate in days of successive nodes on the main stem was not significantly different between populations nor were the rates in the different environments numerically different for the periods of growth studied (Table 3.8).

Table 3.7. Tiller number, dry weight and dry weight tiller^{-1} for the main stem and tillering systems arising off of the main stem (Primary tillering systems) at 35 d after transplanting within Emerald and UM67-10, populations A and B, respectively under long-day conditions in the growth cabinet.

	n		Tillers		Dry Weight		Dry Weight Tiller^{-1}	
Population	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
Tiller Order			-- number plant^{-1} --		mg			
Main Stem	17	17	1.00 c†	1.00 c†	53.05 a†	36.10 b†	53.05 a†	36.10 a†
First PS	17	17	3.24 a	7.00 a	52.58 a	44.95 a	17.24 b	6.54 bc
Second PS	17	17	2.13 bc	5.12 b	27.11 bc	37.88 ab	13.77 bc	7.97 b
Third PS	13	17	1.54 c	2.53 c	15.91 cd	17.71 c	10.44 c	7.18 bc
Fourth PS	4	17	1.25 c	1.44 c	9.10 d	9.58 d	7.50 c	6.94 bc
Fifth PS		12		1.00 c		4.45 d		4.45 c
Sixth PS		3		1.00 c		5.23 d		5.23 bc
Cotyledonary PS[z]	9	4	2.89 ab	2.75 c	30.17 b	14.70 cd	10.59 bc	4.67 bc

† Means followed by the same letter (within columns) are not significantly different using t-test (P= 0.05).

[z] Cotyledonary PS refers to tillering branches arising at the cotyledonary node.

Mean tiller appearance rate, tillers day^{-1}, was calculated for pre- and post-stolon development. UM67-10 had a significantly higher tiller appearance rate than Emerald (Table 3.8). Emerald in GH showed no change in mean tiller appearance rate after stolon development commenced, whereas tiller appearance rate increased in all other cases (Table 3.8).

No significant differences were found between populations for the internode succession rate with the exception of the time interval between the 2nd and 3rd node in GRLD (Table 3.9). Time interval between the appearance of the 2nd and 3rd nodes was longest in both environments for Emerald (Table 3.9). Once stolon growth was initiated (identifiable nodes), gross tillering rate increased in both populations. Relative tiller appearance rate (new tiller appearance / days between successive stolon node appearances / existing tillers) decreased over time for UM67-10 in GHSD. No clear pattern was seen for Emerald (Table 3.9).

Table 3.8. Mean comparisons for tiller appearance date (TAD), stolon appearance date (STAD), difference between TAD and STAD, stolon growth rate and pre- and post-stolon appearance tiller appearance rate for the long day growth cabinet and short day greenhouse studies.

	TAD		STAD	
Population	GC	GH	GC	GH
	d			
Emerald	17.3 a[†]	22.1 a	27.4 a	33.1 a
UM67-10	15.0 b	19.0 b	26.5 b	33.8 a
	TAD to STAD		Stolon Growth	
	GC	GH	GC	GH
	d		nodes d^{-1}	
Emerald	10.4 b	11.3 b	0.34 a	0.33 a
UM67-10	11.5 a	14.8 a	0.37 a	0.35 a
	Tiller Appearance Rate			
	Pre- Stolon Appearance		Post-Stolon Appearance	
	GC	GH	GC	GH
	tillers d^{-1}			
Emerald	0.35 b	0.23 b	0.65 b	0.21 b
UM67-10	0.48 a	0.39 a	1.37 a	0.72 a

[†] Means followed by the same letter within columns are not significantly different using t-test (P= 0.05).

Correlation coefficients were calculated for **TAD**, **STAD**, nodes stolon^{-1}, stolons plant^{-1}, tillers plant^{-1}, stolon length and dry weight of the first stolon (stolon dry weight) for GRLD (Table 3.10). **TAD** and tillers plant^{-1} did not show any significant correlation with **STAD** with the exception of UM67-10 with r = 0.36. These low values indicate that stolon development and tillering may be independent. Nodes stolon^{-1}, stolons plant^{-1}, stolon length and stolon dry weight all were significantly correlated to **STAD** with the exception of stolon dry weight for Emerald.

Table 3.9. Mean gross tiller appearance rate, relative tiller appearance rate and days between successive stolon node appearances for Emerald and UM67-10 under long day conditions in the growth cabinet and short day conditions in the greenhouse.

					Gross Tiller Appearance Rate					
	---------- tillers day^{-1} ----------									
	Pre Stolon		**Nodes 1 to 2**		**Nodes 2 to 3**		**Nodes 3 to 4**		**Nodes 4 to 5**	
					Growth Cabinet - Long Day					
Population	**n**	**rate**	**n**	**rate**	**n**	**rate**	**n**	**rate**	**n**	**Rate**
Emerald	34	0.346 b†	32	0.559 a†	24	0.620 b†	5	0.640 b†	1	1.330 a†
UM67-10	35	0.480 a	35	0.767 a	34	1.278 a	19	1.974 a	3	2.420 a
					Greenhouse - Short Day					
Emerald	19	0.232 b†	17	0.187 b†	11	0.388 a†	5	0.333 a†	4	0.063
UM67-10	20	0.392 a	18	0.599 a	15	0.699 a	6	0.870 a		
					Relative Tiller Appearance Rate					
	---------- tillers tillers^{-1} day^{-1} ----------									
					Growth Cabinet - Long Day					
			n	**rate**	**n**	**rate**	**n**	**rate**	**n**	**rate**
Emerald			32	0.199 a†	24	0.144 a†	5	0.137 a†	1	0.167 a†
UM67-10			35	0.167 a	34	0.179 a	19	0.166 a	3	0.173 a
					Greenhouse - Short Day					
Emerald			17	0.080 a†	11	0.168 a†	5	0.060 a†	4	0.021
UM67-10			18	0.118 a	15	0.097 a	6	0.097 a		
					Internode Succession Rate (days)					
					Growth Cabinet - Long Day					
			n	**days**	**n**	**days**	**n**	**days**	**n**	**days**
Emerald			34	2.63 a†	24	4.08 a†	5	3.20 a†	1	3.00 a†
UM67-10			35	2.62 a	34	2.79 b	19	2.95 a	3	2.67 a
					Greenhouse - Short Day					
Emerald			17	3.28 a†	11	4.00 a†	5	2.00 a†	4	3.25
UM67-10			18	3.61 a	15	2.87 a	6	3.33 a		

† Means followed by the same letter within columns are not significantly different using t-test (P= 0.05).

Table 3.10. Correlation coefficients and number of observations (in parenthesis) for stolon appearance date (STAD), tiller appearance date (TAD), tillers plant^{-1}, nodes stolon^{-1}, stolon length, stolon weight and stolons plant^{-1} in the growth room long day study for Emerald and UM67-10 creeping bentgrass.

	Pop'n	STAD	TAD	Tillers Plant^{-1}	Nodes Stolon^{-1}	Stolon Length	Stolon Weight
TAD	Emerald	0.214 (33)					
	UM67-10	0.360* (35)					
Tillers Plant^{-1}	Emerald	-0.214 (33)	-0.659*** (34)				
	UM67-10	-0.195 (35)	-0.557*** (35)				
Nodes Stolon^{-1}	Emerald	-0.624*** (33)	-0.325 (33)	0.121 (33)			
	UM67-10	-0.574*** (35)	-0.404* (35)	0.317 (35)			
Stolon Length	Emerald	-0.575*** (33)	-0.401* (33)	0.337 (33)	0.675*** (33)		
	UM67-10	-0.685*** (35)	-0.184 (35)	-0.076 (35)	0.466** (35)		
Stolon Weight	Emerald	-0.347 (16)	-0.299 (16)	0.134 (16)	0.352 (16)	0.919*** (16)	
	UM67-10	-0.614** (17)	-0.203 (17)	-0.117 (17)	0.534* (17)	0.725*** (17)	
Stolons Plant^{-1}	Emerald	-0.652*** (33)	-0.463** (34)	0.498** (34)	0.594*** (33)	0.737*** (33)	0.379 (33)
	UM67-10	-0.448** (35)	-0.596*** (35)	0.750*** (35)	0.355* (35)	0.222 (35)	0.060 (35)

*, **, *** represent significance at the P = 0.05, 0.01 and 0.001levels respectively.

Discussion

The present studies investigated the development of young creeping bentgrass plants in the exponential phase of growth (Robson 1973) under long- and short-day conditions. UM67-10 demonstrated greater dry matter partitioning between tillers than did Emerald, i.e. less variability between tillers of the same order, due in part to the greater number of stolons plant^{-1} (Chapter 2). Provided that the stress survival threshold (Ong 1978) value for tiller dry weight has been surpassed, this should confer greater overall tiller survival to UM67-10.

Tiller size decreased as tiller order increased for both populations studied. The 6th PS was similar in weight to the 5th PS (Table 3.7) for UM67-10. Both consisted of a single tiller, and as the 5th PS was older, this indicates an increasing tiller size with successive tillers to this stage of development. Lower productivity (**DWT** and **DWD**) of the first tiller of each order and branch with UM67-10 is also indicative of the size of the tiller.

Site usage decreases were generally seen in the higher tiller orders (Chapter 2) which are smaller tillers (Figures 3.1 and 3.2). A positive relationship between **DWT** and tiller age was not found for tertiary tillers in UM67-10 but was for primary and secondary tillers. This may indicate that potential tiller size within a plant is important with respect to development. Other possible explanations for this are the consistently lower **DWT** for the first tiller of new branches for UM67-10, the low number of tillers for tertiary tiller means due to their recent development and the possibility that the tillers are still in the elongation phase of growth.

Emerald demonstrated greater **DWD** gains than UM67-10. This is indicative of the larger leaves, tillers and stolons found in Emerald. The effect of mowing on tillering and dry matter partitioning will determine the persistence under use. Emerald has been found to possess low tiller densities and higher **DWT** than high tillering cultivars such as '18th Green', which was selected out of UM67-10 (Cattani *et al.* 1992) when grown under putting green turf conditions (Chapter 4). If higher turf tiller density confers greater wear stress tolerance as is predicted by Lush (1990) and found for seashore paspalum (Trenholm *et al.* 1999) then selection for tiller density via tillers plant^{-1} may provide a simple tool for wear stress resistance selection. However high tillering creeping bentgrasses possess shorter stolons (Chapter 4) which may reduce spread into open areas.

Live leaf number tiller^{-1} under established golf green conditions have been reported as between 2.7 and 3.1 (Cattani and Clark 1991) regardless of tiller density, similar to those reported by Robson (1973) in perennial ryegrass.

Stolon node appearance was not related to the onset of tillering. Emerald initiated tillers later but stolons at a similar date to UM67-10. Therefore, Emerald had a shorter interval between first tiller and first stolon appearance. Population differences were not found with respect to the rate of stolon node appearance. Emerald had longer internodes than UM67-10 (Chapter 2), and given the similar node appearance rate, reinforces the concern regarding reduced plant spread characteristics in high tillering populations.

Population differences were found with respect to the effect of stolon development on tillering. Both populations showed a stolon node appearance rate of approximately one node every three days regardless of the environment in which they were grown. UM67-10 demonstrated a greater gross tiller appearance rate than Emerald, 1.37 versus 0.65 tillers day^{-1} in GRLD day and 0.72 versus 0.21 tillers day^{-1} in GHSD, once stolon development became evident. Fewer and larger stolons in Emerald (Chapter 2) may represent a greater sink capacity than the more numerous, smaller stolons of UM67-10, leading to a reduction in tillering. Short days in the greenhouse appeared to reduce stolon node appearance in UM67-10 while increasing it in Emerald. The major factor appears to be the relatively short succession time between the 3rd and 4th nodes in Emerald in the GH. Manitoba selections have been shown to possess a reduced growth rate in the spring and fall (Chapter 7) and this may be demonstrated by the reduced stolon growth in the GH in the present study. UM67-10 produced stolons significantly earlier than Emerald in GRLD and it produced stolons later, but not significantly so, under GHSD conditions. This is further emphasised by the number of plants within each population reaching the 5th node stage under the two growing conditions.

Photoperiod limited growth under short day conditions. Total dry weight $plant^{-1}$ was similar between populations within growing environments. Total dry weight $plant^{-1}$ for the GRLD was approximately 50% and 500% higher than the GHSD and GRSD respectively. Short days compared to long days restrict tillering and impede stolon initiation in creeping bentgrass (Chapter 2). Casal *et al.* (1990) showed the importance of red/far-red (R/FR) ratio with respect to tillering. Short daylengths and shading will reduce the R/FR ratio and decrease tillering.

Node number below the first internode of elongation may also be indicative of competition for light in the crown area. Node of stolon elongation decreased with each successive tiller, within and between orders (Chapter 2). For example, if stolon internode elongation takes place above the fourth node, there are at least four potential branching systems below. Therefore, as each tiller develops, it is into an increasingly competitive environment for light. Stolon elongation at lower nodes in higher order tillers may be a response to this competition for light (Casal *et al.* 1985) and stolon development places new leaves into more favourable conditions. Further study needs to be carried out to determine the effect of light on continued stolon development.

Stolon development is most likely a response to internal competition for an external resource, light. The decreasing stage of tiller growth at which a stolon development was initiated indicates greater competition for light. Stolon development should therefore be seen as a plant response to place its developing leaves into a more favourable growing environment. The large increase in DWT in plants under long day conditions was primarily due to stolon growth. Due to pot size and duration of the present studies, the impact of rooting at stolon nodes on stolon development was not ascertained.

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Part II

Relationship of plant growth and turfgrass development

Chapter 4

Relationship of Shoot Morphology Between Seedlings and Established Turf in Creeping Bentgrass

Abstract

Shoot morphological characteristics are important determinants of turf quality in creeping bentgrass. The objectives of this research were to determine differences for tiller and stolon characteristics among creeping bentgrass cultivars and lines and compare and relate these characteristics between seedlings and established turf. Two experiments involving 10 and 15 entries were grown in controlled environment chambers and harvested as seedlings at 21, 35 and 49 d and 21, 28 and 35 d after transplanting, respectively. Nine and fifteen creeping bentgrass entries were grown in two separate field experiments on sand-based golf greens and core samples were taken for subsequent measurements at 3 yr and 1 yr, respectively. Tiller and stolon measurements included seedling tillers plant^{-1} in the controlled environment; tillers m^{-2} on established turf; and leaf number, leaf width, plant height/stolon length, internode length, internode number, and stolon diameter in all experiments. The correlation coefficients for seedling tillers plant^{-1} at 35 d between the two controlled environment experiments was $r = 0.835$ and for tiller density between the two field experiments was $r = 0.930$. There were differences among the creeping bentgrass entries for tiller number plant^{-1} (9.7 to 20.2) and internode length (20 to 54 mm) when measured at 35 d and for tiller density (67 to 227 x 10^3 m^{-2}) in established turf. Correlation coefficients between seedling tillers plant $^{-1}$ at 35 d and tiller number m^{-2} in established turf ranged from $r = 0.701$ to $r = 0.826$. There was also a high correlation for stolon internode length between seedling and established turf, with r values ranging from $r = 0.725$ to $r = 0.948$. These results document differences for tiller and stolon characteristics between creeping bentgrass cultivars and lines and indicate the potential for plant improvement of these characteristics in creeping bentgrass using 35 d old seedlings in a controlled environment.

Key words: Creeping bentgrass, tiller number, tiller density, stolons, turf, seedling

Abbreviations: RCBD, randomised complete block design

INTRODUCTION

Creeping bentgrass (*Agrostis stolonifera* L.) is a turfgrass used predominantly in high-maintenance, close-mown situations, such as required for golf putting turf. Tiller density (tiller number per unit area) is an important shoot morphological characteristic in creeping bentgrass and is positively related to wear stress recovery (Hawes and Decker 1977) and potential wear stress resistance in turf (Lush 1990). Shildrick and Peel (1984) found a positive relationship between tiller density and wear stress resistance in Kentucky bluegrass (*Poa pratensis* L.). In Chapter 6 we report differences for tiller density in golf putting green turf among six creeping bentgrass entries. We noted that higher tiller densities were associated with higher aboveground biomass and improved wear stress resistance potential. Previous research indicated that plant tiller and leaf number were positively associated with each other ($r = 0.97$) and with visual turf density ratings (Cattani and Clark 1991). Lehman and Engelke (1991) found narrow-sense heritabilities for plant tiller number of 0.31 to 0.41 with creeping bentgrass.

Currently, progress in turfgrass breeding is limited as each cycle of selection requires the establishment and maintenance of turfgrass plots. The ability to relate shoot morphological characteristics of seedlings to established turf would be useful for plant breeders. Important shoot morphological characteristics include higher tiller densities for improved golf putting green wear-stress tolerance and increased stolon length for quicker colonisation of bare spots in golf fairway and tee-box turfs. Selecting superior creeping bentgrass plants in the seedling stage would provide an improved methodology for generation advance. This methodology would allow selection of plants with desired shoot morphological attributes at an early stage, enabling earlier transplanting of seedlings to field or greenhouse crossing blocks. If selection for one characteristic can be achieved at an early growth stage and selection for another characteristic at a later stage (e.g., disease tolerance), advancement for both characteristics may be possible without extending the time for generation advancement. The objectives of this research were: (1) to demonstrate cultivar differences for shoot morphological traits in creeping bentgrass seedlings, and (2) to compare seedling shoot morphological traits to mature plant shoot morphological traits in established turf.

Table 4.1. Creeping bentgrass cultivars and lines planted in controlled environment growth rooms and under field conditions on golf putting greens in Winnipeg, MB, Canada.

Cultivar	Origin	Year	Growth room Studies		Putting Green Studies	
			1[z]	2	3	4
18th Green	University of Manitoba, MB, Canada	1990[y]	x	x	x	x
Cobra	International Seeds Inc., OR, USA	1987	x	x		x
Emerald	W. Weibull AB, Sweden	1965	x	x	x	x
National	Pickseed West Inc., , OR, USA	1987	x	x	x	x
Penncross	Penn State Univ., PA, USA	1955		x	x	x
Penneagle	Penn State Univ., PA, USA	1978	x	x	x	x
Pennlinks	Penn State Univ., , PA, USA	1986	x	x	x	x
Providence	Seed Research of Oregon, Inc., OR, USA	1988		x		x
Putter	Jacklin Seed Co., ID, USA	1988	x	x		x
Regent	Willamette Valley Breeders, OR, USA	1990		x		x
Seaside	University of Oregon	1923		x	x	x
Southshore	Rutgers University, NJ, USA	1992	x	x		x
SR1020	Seed Research of Oregon, Inc., OR, USA	1987		x		x
UM86-01	University of Manitoba, MB, Canada	exp.	x	x	x	x
UM86-02	University of Manitoba, MB, Canada	1998	x	x	x	x

[z] 1 - Experiment 1, 10 cultivar seedling study in the growth room; 2 - Experiment 2, 15 cultivar seedling study in the growth room; 3 - Experiment 3, 9 cultivar golf putting green turf study seeded in 1986; 4 - Experiment 4, 15 cultivar golf putting green turf study seeded in 1992.
[y] exp. - experimental line developed at the University of Manitoba.

MATERIALS AND METHODS

Controlled Environment Experiments

Experiment 1. The initial growth room experiment was designed to allow measurements of shoot morphological characteristics at the seedling stage for 10 creeping bentgrass cultivars and lines (entries) (Table 4.1). Certified seed was used for all entries except University of Manitoba experimental germplasms (Syn_1) and "18th Green" (breeders seed, Syn_3). All seed was pre-germinated for 4 d in petri dishes containing moistened filter paper at

Table 4.2. Nutrient application and harvest schedule for two controlled environment growth room experiments designed to measure creeping bentgrass morphological characteristics.

Days	Experiment 1[z]	Experiment 2[y]
0	Transplanting	Transplanting
2	Fertilise @[x] 14g N/100 m^2 [w]	-
7	Fertilise @ 75g N/100 m^2	Fertilise @ 56g N/100 m^2
10	Fertilise @ 75g N/100 m^2	Fertilise @ 112g N/100 m^2
14	Fertilise @ 150g N/100 m^2	Fertilise @ 112g N/100 m^2
17	Fertilise @ 300g N/100 m^2	Fertilise @ 225g N/100 m^2
21	1st Harvest	1st Harvest
		Fertilise @ 225g N/100 m^2
24	Fertilise @ 300g N/100 m^2	Fertilise @ 450g N/100 m^2
28	-	2nd Harvest
		Fertilise @ 450g N/100 m^2
31	Fertilise @ 450g N/100 m^2	Fertilise @ 450g N/100 m^2
35	2nd Harvest	3rd Harvest
38	Fertilise @ 450g N/100 m^2	-
45	Fertilise @ 450g N/100 m^2	-
49	3rd Harvest	-

[z] Experiment 1: study of 10 entries.
[y] Experiment 2: study of 15 entries.
[x] @ indicates at the rate of.
[w] Fertiliser source was Peter's 20-20-20 water soluble formulation.

approximately 20 °C and transplanted at the coleoptile stage into 500-mL containers with a 9:1 (vol/vol) sand:peat mixture. The transplanting date will be subsequently referred to as day 0. The soil mixture exhibited soil physical properties within acceptable ranges for all parameters, as recommended for United States Golf Association (USGA) putting greens (USGA Green Section 1993). The plants were grown in a controlled environment at 20/15 °C with a photoperiod of 16/8 h light/dark (approx. 300 $\mu E\ m^{-2}\ s^{-1}$). All containers were watered daily and fertilised with N:P:K (20–20–20 Peter's water soluble formulation, manufactured by W.R. Grace Co., Vogelsville, PA) according to the schedule in Table 4.2. The experimental design was a RCBD with four replicates and four plants per experimental unit, for a total of 16 plants per creeping bentgrass entry mean at each sampling date. Occasionally sample size was reduced to three plants due to plant mortality. Plants were sampled at 21, 35 and 49 d by removing them from the containers and carefully washing soil from the roots.

The number of tillers plant^{-1} was determined at each sampling date. A tiller was counted when a fully emerged leaf was visible. The number of leaves plant^{-1} were determined at 21 d, longest internode on the longest stolon was measured at 35 and 49 d and the number of internodes on the longest stolon was counted at 35 d. A leaf was counted when its length equalled or exceeded the length of the previous leaf on that tiller. All length and width measurements were made to the nearest 0.5 mm.

Experiment 2. The second growth room experiment included 15 creeping bentgrass entries at the seedling stage (Table 4.1). Seed classification, germination conditions, soil mixture, potting containers and transplant procedures were consistent to Exp. 1, but the cultivar Penncross was also included which is a first generation, 3 clone hybrid and therefore marketed seed is from the Syn_1 generation. The plants were grown in a controlled environment at 24/16 °C during 16/8 h light/dark (≈ 300 $\mu E\ m^{-2}\ s^{-1}$) conditions. All containers were watered daily and fertilised with the same formulation as in Exp. 1 according to the schedule recorded in Table 4.2. The experimental design was a RCBD with three replicates and eight plants per experimental unit, for a total of 24 plants per creeping bentgrass entry mean at each sampling date. Occasionally an experimental unit was reduced to seven plants, and once to six plants, due to plant mortality. Plants were destructively sampled at 21, 28, and 35 d after seeding as described in Exp. 1. The 49-d sampling date was not conducted since results from Exp. 1 indicated that tillers had developed on stolon nodes by this date.

The numbers of tillers and leaves plant^{-1} were determined at each sampling date as in Exp. 1. All length and width measurements were made to the nearest 0.5 mm. Plant height was measured at 21 d, and length of the longest stolon was measured at 28 and 35 d. The following measurements were made using the longest stolon at 35 d; (i) the length of the longest internode; (ii) the number of nodes; and (iii) the width of the 4th leaf from the stolon terminus.

Established Turf Studies

Experiments 3 and 4: On 2 September 1986 and 18 August 1992, Exps. 3 and 4 were established on a sand base putting green at the Department of Plant Science Winnipeg Field Research Laboratory. The soil particle size distribution was within the soil particle size guidelines as recommended by the USGA (1993). The 1986 experiment (Exp. 3) included nine creeping bentgrass entries, and the 1992 experiment (Exp. 4) included 15 creeping bentgrass entries (Table 4.1). Seed classes were the same as for Exps. 1 and 2 with the exception of Syn_1 seed for 18th Green in Exp. 3.

Experiment 3. The experimental design for Exp. 3 was a RCBD with four replicates and 1 m^2 plots. The plots were irrigated frequently to prevent wilting and to maintain vigorous turf growth. Mowing was at a 5 mm height with all clippings removed. Aeration and topdressing operations were performed in June of 1988 and 1989 for Exp. 3. The topdressing material was identical in composition to the base media. This experiment received two applications of a 19-25-4 (N:P:K) fertiliser (O.M. Scotts, Marysville, OH) in 1986 with a total application of 1.0 kg N 100 m^{-2}. Fertilisation levels were 2.0 kg N 100 m^{-2} in 1987, 1.95 kg N 100 m^{-2} in 1988 and 1.0 kg N 100 m^{-2} in 1989 prior to sampling (Chapter 6). Phosphorous (P_2O_5) was not applied again until June 1989 at the rate of 250 g 100 m^{-2}. Potassium (K_2O) was included at each fertilisation application at approximately 75% of the nitrogen rate, with the exception of 1989. On 12 July 1989, core samples (6.25 cm in diameter) were taken for tiller density measurements. The perimeter:area ratio for these samples was 0.64:1, well within the 1.1:1 limit for the ratio as established by Lush and Franz (1991). Tiller number was counted for the entire core sample and expressed as functional tillers m^{-2} (Madison 1962).

Experiment 4. The experimental design for Exp. 4 was a RCBD with six replicates and 0.5 m x 1 m plots. In 1993, all plots received irrigation to prevent wilting and produce vigorous turf growth, and mowing height was at 5 mm with all clippings removed. This experiment did not receive aeration or topdressing treatments. The seeding year fertility levels were equivalent to the ones in Exp. 3. Prior to sampling in 1993 fertilisation was 2.5 kg N 100 m^{-2}, 500 g P_2O_5 100 m^{-2} and 1.85 kg K_20 100 m^{-2}. On 29 September 1993, core samples were taken for tiller number m^{-2} and plant morphological measurements.

Tillers m^{-2} were determined as in Exp. 3. Stolon diameter was measured with a dial caliper (Mitutoyo Corporation, Tokyo, Japan) to the nearest 0.05 mm. The length of the 4^{th} internode from the terminus was measured to the nearest 0.05 mm using the ridge of tissue left by the sheath attachment as to determine the internode termini. These detailed measurements were conducted on five stolons per core. Dry weight of live aboveground biomass for each core sample was determined as follows: (1) 100 tillers were randomly selected from each core and dried at 85 °C for 72 h to determine 100-tiller total dry weight; (2) these 100-tiller samples were placed in an ashing oven at 560 °C for 6 h to determine the weight of non-organic matter; (3) ashed weights were subtracted from initial dry weights; and (4) the biomass $tiller^{-1}$ was multiplied by total tiller number $core^{-1}$. To estimate potential wear stress resistance, tiller number m^{-2} and live above ground biomass measurements were used to calculate log *c*:

Solving for log *c*: $$\log10B = \log10c - 0.5 \log10N \qquad (1)$$

where *B* is dry weight of live tillers m^{-2}, *N* is tiller number m^{-2}, and log *c* is an estimate of potential turf wear stress resistance (Lush 1990).

All data were analysed using SAS Institute, Inc. (1988). Cultivar and line means were compared using Duncan's new multiple range test. Spearman's correlation coefficients were calculated between the entry means.

Results and Discussion

Seedling Experiments 1 and 2

There were entry differences for a number of seedling morphological traits in Exps. 1 and 2 including tillers $plant^{-1}$ and leaves $plant^{-1}$ at all dates, stolon internode length at 35 d and 49 d and leaf width at 35 d (Tables 4.3 and 4.4). There was no entry effect for stolon length at 28 d (Table 4.4) and nodes $stolon^{-1}$ at 35 d (Tables 4.3 and 4.4). Leaves $plant^{-1}$ across entries ranged from 4.59 to 37.8 for the 21 to 35 d sampling dates in Exp. 2. 18^{th} Green, UM86-01 and UM86-02 ranked the highest for leaves $plant^{-1}$ for all measurement dates in both experiments. National, Pennlinks, Penneagle and Emerald (except at 35 d in Exp. 2) had the fewest leaves $plant^{-1}$ on all dates in both experiments and Seaside had few

Table 4.3. Seedling morphological attributes in a controlled environment growth room (Experiment 1) for 10 creeping bentgrass entries measured at 21 d, 35 d and 49 d after transplanting.

	Leaves	Tiller			Internode Length		Node Number
Cultivar	**21 d**	**21 d**	**35 d**	**49 d**	**35 d**	**49 d**	**35 d**
Syn1	no. plant^{-1}	----------no. plant^{-1}----------			---------cm--------		Stolon^{-1}
UM86-02	10.1 a[z]	4.7 a	15.6 ab	29.8 abc	3.1 cd	4.8 b	4.8 a
UM86-01	9.1 abc	3.9 bc	15.1 abc	31.8 ab	3.2 cd	4.7 b	4.8 a
Syn2 or Later							
18th Green	9.7 ab	4.5 ab	17.4 a	33.8 a	2.4 d	3.7 b	4.3 a
Cobra	9.1 abc	4.3 ab	12.5 bcd	26.2 bcd	5.4 a	7.0 a	4.9 a
Southshore	8.5 abc	3.9 bc	12.1 cd	24.6 cd	4.8 ab	6.6 a	4.8 a
Pennlinks	7.5 cd	3.6 cd	9.9 d	26.9 bcd	4.1 bc	7.1 a	4.5 a
Penneagle	8.1 bcd	3.5 cd	12.6 bcd	26.3 bcd	4.9 ab	7.1 a	4.8 a
Putter	7.8 cd	3.4 cd	10.2 d	29.5 abc	4.8 ab	7.2 a	3.9 a
National	7.9 cd	3.3 cd	11.0 d	23.3 d	4.3 ab	7.3 a	3.8 a
Emerald	7.0 d	2.9 d	12.1 cd	23.0 d	4.6 ab	7.4 a	3.8 a

[z] Means in each column followed by the same letter within each column are not significantly different ($P \leq 0.05$) using Duncan's New Multiple Range Test.

leaves plant^{-1} in Exp. 2.

UM86-01, UM86-02 and 18th Green consistently expressed the highest tillers plant^{-1} at all three observation dates in both experiments while National and Emerald were in the lowest grouping in Exp. 1 and Seaside and Penneagle in Exp. 2 (Tables 4.3 and 4.4).

Tillers plant^{-1} over all entries ranged from 2.9 to 33.8 from the 21 d to the 49 d sampling date in Exp. 1 (Table 4.3) and 2.0 to 20.2 from the 21 to the 35 d sampling date in Exp. 2 (Table 4.4). Tillers plant^{-1} at 35 d was highly correlated between Exps. 1 and 2 (r = 0.835), indicating a consistent expression for this trait in the controlled environment experiments. The difference in actual tillers plant^{-1} between Exps. 1 and 2 was likely due to the difference in fertility (Madison 1962) and temperature regimes between the two experiments and the fact that *A. stolonifera* L. is an obligate out-crosser (Bradshaw 1958) resulting in plant to plant variation within entries.

Stolon development was not visible at the 21 d measurement date, but by 35 d all entries had initiated stolons. At 49 d stolon development was extensive and tillering was taking place at the nodes. National and Regent had the longest stolons at 35 d in Exp. 2 and 18th Green, UM86-01 and UM86-02 had the shortest. The other entries tested were not significantly different for internode length for any measurement date with the exception of Pennlinks which was shorter than Putter at 35 d in Exp. 1 (Table 4.3). Although the University of Manitoba entries expressed the shortest internode lengths at 35 d, they produced the same number of nodes stolon^{-1} as the other entries, indicating a dwarf-type growth habit. Furthermore, correlation coefficients for internode length and tiller number within Exps. 1 and 2 were $r = -0.772$ and $r = -0.730$, respectively (data not shown). These results indicate that the increase in tiller number may be due to the shortening of internode length and thus stolon length, resulting in a more compact plant.

Stolon elongation occurred between the 21 d and 28 d measurement dates. Therefore, to allow for simultaneous selection for tiller number and stolon elongation plants should be allowed to develop for 28 d or until stolon expression. The appearance of tillers at the stolon nodes by 49 d complicated the measurements and increased the time required for measurements.

Heterotic effects for tillers plant^{-1} may have been present in these experiments since different seed generations were used across entries. The expression of heterosis is usually evidenced by increased biomass through the enlargement of the plant structures (Poehlman 1987). Since 18th Green was of the Syn_3 generation (in all but Exp. 3) and Penncross seed is of the Syn_1 generation, then the expression of tillers plant^{-1} for 18th Green is probably not heterotic in nature. The high tiller number for 18th Green is most likely the result of selection for this trait (Cattani *et al.* 1992).

Experiments 3 and 4

Entry differences for tillers m^{-2} were present in 3-yr-old turf in Exp. 3 and in 1-yr-old turf in Exp. 4 (Table 4.5). There was a high correlation for tillers m^{-2} between entries in Exps. 3 and 4 ($r = 0.930$). This high correlation and the consistent entry performance for tiller number m^{-2} across both experiments, indicated that differences were stable over time and

Table 4.4. Seedling morphological attributes in a controlled environment growth room (Experiment 2) for 15 creeping bentgrass cultivars and lines, measured at 21 d, 28 d and 35 d after transplanting.

	Leaves			Tillers			Plant Height	Stolon Length		Internode Length	Leaf Width	Node Number
Entry	21 d	28 d	35 d	21 d	28 d	35 d	21 d	28 d	35 d	35 d	35 d	35 d
		-----no. plant^{-1}------			-------no. plant^{-1}-------		----------	----------	----mm----	----------	----------	stolon^{-1}
Syn1												
UM86-01	5.85 a-c[z]	14.5 b	32.2 ab	2.67 a-c	8.1 a	15.2 b	51 a	75 a	165 bc	27 cd	3.02 cd	3.4 a
UM86-02	6.25 a	14.4 b	29.8 bc	2.84 a	7.8 a	14.7 b	52 a	88 a	167 bc	27 cd	3.04 b-d	3.3 a
Penncross	4.92 cd	10.3 cd	27.2 b-d	2.37 a-d	6.3 b	13.5 bc	60 a	87 a	230 a	40 a	3.58 a	3.1 a
Syn2 or Later												
18th Green	6.20 ab	16.4 a	37.8 a	2.80 ab	8.7 a	20.2 a	42 a	57 a	139 c	20 d	2.90 d	2.8 a
Emerald	4.70 d	9.4 d	27.2 b-d	2.13 cd	5.4 b	11.6 c-e	61 a	81 a	202 ab	41 a	3.45 a-c	2.7 a
Southshore	4.79 d	10.0 cd	26.1 b-d	2.15 cd	5.9 b	13.0 b-d	52 a	86 a	220 a	38 ab	3.50 ab	3.4 a
Providence	5.06 cd	11.2 cd	25.1 c-e	2.27 b-d	6.4 b	12.6 b-d	56 a	104 a	228 a	40 a	3.58 a	3.2 a
Regent	4.71 d	11.5 cd	24.9 c-e	2.21 cd	5.9 b	12.4 b-d	52 a	102 a	234 a	38 ab	3.69 a	3.3 a
SR1020	5.09 cd	12.0 c	24.5 c-e	2.27 b-d	6.3 b	12.8 b-d	60 a	123 a	216 ab	37 a-c	3.50 ab	3.0 a
Putter	4.99 cd	9.8 d	24.1 c-e	2.38 a-d	5.8 b	11.6 c-e	59 a	101 a	202 ab	38 ab	3.58 a	3.3 a
National	4.59 d	9.4 d	23.1 c-e	2.06 d	5.8 b	11.3 c-e	60 a	81 a	243 a	42 a	3.54 a	3.1 a
Pennlinks	5.51 a-d	9.5 d	22.7 c-e	2.63 a-c	5.7 b	11.3 c-e	62 a	80 a	204 ab	34 a-c	3.56 a	2.7 a
Cobra	5.42 a-d	10.7 cd	22.2 de	2.48 a-d	6.1 b	10.4 de	60 a	83 a	216 ab	37 a-c	3.42 a-c	3.0 a
Penneagle	4.65 d	9.7 d	20.3 de	1.95 d	5.6 b	9.7 e	58 a	76 a	201 ab	35 a-c	3.48 a-c	2.9 a
Seaside	5.27 b-d	9.9 d	18.6 e	2.38 a-d	5.5 b	9.7 e	64 a	81 a	206 ab	34 a-c	3.33 a-c	2.3 a

[z] Means followed by the same letter within columns are not significantly different according to Duncan's New Multiple Range Test ($P \leq 0.05$)

Table 4.5. Morphological attributes for nine creeping bentgrass entries in Experiment 3 and fifteen entries in Experiment 4 in golf putting green turf at Winnipeg, MB, Canada.

	Exp. 3	Experiment 4					
Entry	Tiller Density		Stolon Diameter	Internode Length	Above Ground Biomass	100 Tiller Weight	Log *c*
	---- x 1,000 ----		---------- mm	---------	-- g m^{-2} --	--- mg ---	
Syn 1							
UM86-02	154 ab[z]	227 a	0.29 a	3.5 bcd	277 a	125 bcd	5.11 a
UM86-01	147 b	227 a	0.27 a	3.1 d	254 abc	112 d	5.07 a
Penncross	100 d	155 de	0.31 a	5.3 ab	198 d	128 bcd	4.89 b
18th Green	168 a	-	-	-	-	-	-
Syn 2 or Later							
18th Green	-	221 a	0.29 a	3.3 cd	259 ab	114 d	5.09 a
Southshore	-	188 b	0.33 a	4.9 abcd	218 cd	116 cd	4.97 b
SR1020	-	182 bc	0.39 a	6.0 a	204 d	112 d	4.93 b
Pennlinks	124 c	176 bc	0.35 a	5.1 abc	207 d	118 c	4.94 b
Regent	-	176 bc	0.31 a	5.4 ab	229 bcd	131 abcd	4.97 b
Penneagle	109 cd	171 bcd	0.37 a	6.3 a	200 d	117 cd	4.92 b
Providence	-	170 bcd	0.31 a	4.8 abcd	206 d	121 cd	4.92 b
Putter	-	168 cd	0.38 a	6.4 a	218 cd	129 abcd	4.95 b
Cobra	-	165 cd	0.34 a	5.6 a	228 bcd	137 abc	4.96 b
Emerald	93 d	143 e	0.37 a	5.9 a	204 d	144 ab	4.88 b
National	108 cd	117 f	0.33 a	5.3 ab	159 e	137 abc	4.73 c
Seaside	67 e	82 g	0.29 a	6.3 a	123 f	150 a	4.54 d

[z] Means followed by the same letter within columns are not significantly different according to Duncan's New Multiple Range Test ($P \leq 0.05$)

environment (Table 4.5). In both experiments, 18th Green, UM86-01, and UM86-02 expressed the highest tillers m^{-2} in comparison to all other entries and Seaside, National, Emerald and Penncross consistently expressed the lowest tillers m^{-2}.

Entry differences were also observed for internode length, aboveground biomass, 100-tiller weight and log *c* (estimate of potential wear stress resistance) in Exp. 4 (Table 4.5). 18th Green, UM86-01, and UM86-02 ranked lowest for internode length and there were no differences between the other entries. In general, entries with higher 100 tiller weights expressed lower for tillers m^{-2} as evidenced by the negative correlation (r = -0.79) between these two traits in Exp. 4. Similar results were reported by Cattani (1987).

Entry differences for log *c* in Exp. 4 indicated that the entries differed for potential turf wear stress resistance (Lush 1990). These results were consistent with those reported in Chapter 6. Log *c* estimates were highest for 18th Green and UM86-01 and lowest for Seaside. Creeping bentgrass entries that express high tiller numbers and reduced stolon extension have higher potential wear stress resistance under golf putting green management. Therefore, these characteristics are desirable traits for inclusion in the development of new creeping bentgrass cultivars.

Selection for high tillers plant^{-1} and/or tillers m^{-2} should increase wear stress resistance. Although characteristics that improve wear stress resistance are important for golf putting green conditions, rapid stolon elongation may be a more important characteristic for fairway and tee-box turf conditions allowing the turf to fill in damaged areas. There are a number of plant characteristics which also influence turf quality (e.g. disease resistance) and all should be considered when choosing a creeping bentgrass cultivar.

Seedling vs. Established Turf

Pearson correlation coefficients were calculated to compare seedling tillers plant^{-1} under controlled environmental conditions in Exps. 1 and 2 and tillers m^{-2} from established putting green turf for Exps. 3 and 4 (Table 4.6). Tillers plant^{-1} at 35 d in Exps. 1 and 2 was highly correlated with tillers m^{-2} on established turf in Exp. 3 (r = 0.824 and 0.826) and in Exp. 4 (r = 0.762 and 0.701), respectively.

The consistently high correlations that were observed between seedling tillers plant^{-1} and tillers m^{-2} on established turf suggest that turf density characteristics can be accurately identified and selected using 35-d-old seedlings. The consistently lower correlation coefficients for Exp. 4 were likely influenced by the higher number of entries in this experiment. Also, stand age may have resulted in greater between plant competition in the 1-yr-old turf in Exp. 4 as compared to the 3-yr-old turf in Exp. 3.

The correlation coefficient for stolon internode length was higher (r = 0.919) between Exp. 4 and Exp. 1 at 49 d as compared to the correlation coefficients between Exp. 4 and Exp. 1 at 35 d (r = 0.883) and Exp. 2 at 35 d (0.725) (Table 4.6). The lower correlation value between Exp. 4 and Exp. 2 at 35 d can be partially explained by the greater number of entries (15) thereby encompassing a greater amount of the variation in the population. For

Table 4.6. Pearson correlation coefficients among creeping bentgrass seedlings and established turf for tiller number and internode length.

	Experiment 1[z]			Experiment 2		
	21 d	35 d	49 d	21 d	28 d	35 d
			Tiller Number			
Exp. 3	0.944**[y] n = 7	0.824* n = 7	0.955** n = 7	0.711* n = 9	0.885** n = 9	0.826** n = 9
Exp. 4	0.760* n = 10	0.762* n = 10	0.832** n = 10	0.566* n = 15	0.759** n = 15	0.701* n = 15
			Internode Length			
Exp. 1 - 49d		0.901** n = 10				
Exp. 2 - 35d		0.863** n = 10	0.948** n = 10			
Exp. 4		0.883** n = 10	0.919** n = 10			0.725** n = 15

[z] Experiment 1 - 10 entry growth room experiment; Experiment 2 - 15 entry growth room experiment; Experiment 3 - 9 entry golf putting green experiment seeded in 1986; Experiment 4 – 15 entry golf putting green experiment seeded in 1992.
[y] *,** Significant at the 0.05 and 0.01 probability levels.

example, when only the 10 entries from Exp. 1 were compared the *r* value increased to 0.825.

These results suggest that there may be an upper limit for improvement in turf tiller density through selection for seedling tiller number. Other traits, such as stolon length and internode length, are also affected by selection for tiller number. Internode length is negatively related to increasing tiller number; therefore, both traits must be taken into consideration during creeping bentgrass cultivar development.

The ability to select plants based on shoot morphological characteristics provides an opportunity for creeping bentgrass breeders to improve tiller density for putting greens or to increase stolon length to promote rapid colonisation of damaged areas in fairway or tee-box turf. The potential to select in the seedling stage offers a number of advantages including a reduction in the time required to assess shoot morphology and a reduction in the amount of plant material that requires field testing.

Conclusions

There are measurable cultivar and line differences for shoot morphological traits in creeping bentgrass seedlings. These seedling differences are closely associated with the differences observed in established turf. This research suggests that turf tiller density may be improved by selecting seedlings with high tiller numbers at 35 d under controlled conditions.

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Chapter 5

The Effect of Seeding Rate and Cultivar on the Establishment of Creeping Bentgrass Turf.

ABSTRACT

Wear stress tolerance of newly seeded turfgrass areas may depend on size of individual plants and on cultivar selection. These studies examined effects of four seeding rates, 250, 500, 750 and 1000 g 100 m^{-2}, on growth and turf development of three creeping bentgrass cultivars, 18th Green, Penncross and Putter. One field and one growth room experiment were conducted. Cores were taken at 4, 8, and 12 weeks after seeding (**WAS**) in the field and at 3, 6, and 9 **WAS** in the growth room. Seeding rate and cultivar effects were found for plants m^{-2}, tillers m^{-2}, tillers $plant^{-1}$, plant weight, tiller weight and biomass weight per m^{-2}. Seeding rate x cultivar interactions, including plants m^{-2}, tillers m^{-2}, dry weight $plant^{-1}$ and dry weight $tiller^{-1}$ were found, especially at 9 **WAS** in the growth room. Seeding rate of 250 g m^{-2} gave the largest plants for both tiller number and dry weight. Potential wear stress tolerance (logc) was not significantly different between seeding rates or cultivars by the end of the studies. Seeding rates should not exceed the 250 – 500 g m^{-2} recommended for creeping bentgrass.

Key words: creeping bentgrass, seeding rate, tillers, wear stress resistance, dry weight, cultivars

INTRODUCTION

Golf course superintendents in Canada are often faced with the demand for a quick establishment of a golf putting green, often within three months. Superintendents have reported using up to 2.5 kg 100 m^{-2}. Recommended seeding rates are between 250-500 g 100 m^{-2} (Beard 1983). Madison (1966) found that a 450 g m^{-2} seeding rate for creeping bentgrass was sufficient to establish a playable turf within a three month after sowing.

Lower seedling densities in other grasses, perennial ryegrass and timothy, result in a greater wear stress tolerance due to larger plant and tiller size (Parr 1982). The same author also reported that plant number did not decrease over time under mowing stress. Rossi and Mallett (1996) however, found that self-thinning took place in creeping bentgrass at high seeding rates primarily due to disease. Seedling competitiveness was influenced by early emergence in *Dactylis glomerata* (Ross and Harper 1972).

Creeping bentgrass cultivar availability has increased in recent years and cultivar may affect turf establishment rate. We have already reported that seedlings of creeping bentgrass cultivars tiller at different rates and at different times (Chapter 4), thus the onset of inter- and intra-plant competition may be cultivar specific.

The objective of this study was to investigate the effect of seeding rate on turf establishment in three creeping bentgrass cultivars.

MATERIALS AND METHODS

Experiment 1

On 16 June 1993, a field trial was established on a USGA specification sand based putting green at the University of Manitoba, Winnipeg, MB. Three cultivars, "Penncross" (standard entry), "Putter" and "18th Green" were seeded at four seeding rates, 250, 500, 750 and 1000 g 100 m^{-2}. Seeding rates for each cultivar were adjusted to equal Penncross, based on the 1000 seed weight and a 90% germination rate. A randomized complete block design with four replicates was used with all cultivar and seeding rate combinations. Plots were 1 m^2 in size and were raked before and after manual seeding. A 1 m x 1 m x 0.4 m seeding frame was used to keep seed within plots during broadcast seeding. Plots were immediately covered with a fiberglass filter material (Famcomat, American Air Filter, Kansas City, Mo.) and rolled prior to first irrigation to prevent seed movement between treatments. The covering was removed once emergence was clearly visible at 6 d after sowing. Plots were maintained as golf green turf with mowing 5 x weekly and a final mowing height of 4.5 mm. Plots received a total of 1350 g N 100 m^{-2} during the experiment. An application of 450 g N 100 m^{-2} was incorporated prior to seeding and the remainder applied in equal increments 20 d apart. Pre-establishment fertiliser carrier was a 19-26-5 product (O.M. Scotts, Marysville, OH). Initial mowing height was 12 mm at 4 weeks after seeding (WAS). Final mowing height was reached at 6 WAS. Wear stress was applied using a spiked roller (Cattani 1987), starting at 9 WAS, with three wear stress applications weekly until 12 WAS. Each wear stress treatment consisted of 6 passes across each plot.

Core samples (6.25 cm dia.) were taken at 4, 8 and 12 WAS. Tillers $core^{-1}$ were counted and above ground live dry matter (**AGLB**) determined by drying at 65 °C for 72 h. Plants $core^{-1}$ were counted at 4 WAS only.

Tillers m^{-2} and dry weight m^{-2} were used to calculate potential wear stress resistance (logc) as per Lush (1990):

$$\log c = \log 10\ b + \log 10\ (n*0.5),$$

where: b = dry weight m^{-2}, n = tillers m^{-2}.

One replicate was lost between 5 and 6 WAS due to a management error, therefore, the 8 and 12 WAS measurements were reduced to 3 replicates.

Experiment 2

A controlled environment study was carried out using 12.5 cm dia. pots. USGA specification sand, similar to the field study, was used. Seeding rates and cultivars were similar to Experiment 1. Harvest dates were 3, 6 and 9 WAS, to coincide with the period of growth prior to wear stress treatment in the field. A randomized complete block design with four replicates was used. Harvest dates were blocked and pots rotated to lessen position effects. Seeds were broadcast on the surface then covered with 5 mm of media, then packed. Pots were clipped at 6 mm 3 times weekly, starting at 3 WAS. Destructive sampling was practised with 6.25 cm dia. cores being removed from the center of each pot. Plant number $core^{-1}$ and tillers $core^{-1}$ were counted and **AGLB** determined as noted above for all harvests.

Analysis of variance was performed using SAS (SAS Institute, Gary, NC).

Results of the statistical analysis for tiller density and Dry weight in Exp. 1 and for plants, tiller density and dry weight in Exp. 2 are found in Table 5.1.

Table 5.1. Source of variation, degrees of freedom, mean square, F value and probability of F for tillers m^{-2}, dry weight m^{-2} and plant number for the field and growth room studies.

		Field Study								
		Tillers								
		4 Weeks			**8 Weeks**[z]			**12 Weeks**[z]		
Source	**df**	**ms**	**F**	**P>F**	**ms**	**F**	**P>F**	**ms**	**F**	**P>F**
Seeding Rate	3	160923	17.1	.001	25841	10.5	.001	30540	13.0	.001
Cultivar	2	23343	2.49	.099	2650	1.08	.357	32752	13.9	.001
SR x Cv	6	11127	1.19	.338	2610	1.06	.413	3335	1.42	.252
		Dry Weight Tiller^{-1}								
Seeding Rate	3	.910	7.45	.001	1.256	18.2	.001	741	6.25	.003
Cultivar	2	.042	0.34	.712	.385	5.57	.011	349	2.95	.074
SR x Cv	6	.043	0.35	.902	.493	7.13	.001	117	0.99	.456
		Growth Room Study								
		Tillers								
		3 Weeks			**6 Weeks**			**9 Weeks**		
Seeding Rate	3	48684	58.8	.001	56436	20.7	.001	148049	24.4	.001
Cultivar	2	1424	1.72	.195	5658	5.74	.007	95289	15.7	.001
SR x Cv	6	939	1.13	.365	2649	0.97	.460	18664	3.08	.017
		Plant Number								
Seeding Rate	3	52421	65.0	.001	32177	31.5	.001	32554	51.3	.001
Cultivar	2	5478	6.79	.003	5954	8.75	.001	7403	11.7	.001
SR x Cv	6	1016	1.26	.303	2011	1.97	.099	3656	5.62	.001
		Dry Weight Tiller^{-1}								
Seeding Rate	3	0.498	15.2	.001	.104	17.5	.001	0.175	14.8	.001
Cultivar	2	0.073	2.22	.124	.011	1.81	.179	0.001	0.04	.957
SR x Cv	6	0.088	2.71	.030	.009	1.52	.203	0.028	2.32	.056

[z] Error term df for 8 and 12 weeks is reduced by 12 due to the loss of one replicate.

Table 5.2. Plants m^{-2}, tillers m^{-2}, and tillers plant^{-1} for the field experiment at 4, 8 and 12 weeks after seeding (WAS).

	Plants m^{-2}	Tillers m^{-2}			Tillers plant^{-1}
	(x 1000)				
Cultivar	**4 WAS**	**4 WAS**	**8 WAS**	**12 WAS**	**4 WAS**
Penncross	82.6 a^z	91.5 a	89.3 a	106.6 b	1.25 c
18th Green	61.3 a	76.4 a	97.5 a	140.1 a	1.54 a
Putter	55.2 a	66.8 a	88.9 a	118.2 b	1.39 b
lsd (.05)	*23.9*	*22.7*	*13.7*	*13.4*	*0.12*
Seeding Rate (100 m^{-2})					
1000 g	110.3 a^z	120.2 a	113.1 a	136.4 a	1.13 c
750 g	89.2 a	96.3 a	96.1 b	131.1 a	1.19 c
500 g	46.5 b	62.1 b	87.2 b	125.0 a	1.42 b
250 g	19.5 b	34.4 c	71.2 c	94.0 b	1.83 a
lsd (.05)	*27.6*	*26.2*	*15.8*	*15.4*	*0.14*

^{z} Means followed by the same letter within columns are not significantly different using Fishers Protected LSD (P=.05).

Experiment 1

No significant cultivar differences were found (Table 5.2) for plant m^{-2} at 4 WAS. The 1000 and 750 g 100 m^{-2} seeding rates (**SR4X** and **SR3X**, respectively) were highest for plants m^{-2} at 4 WAS.

18th Green was highest for tillers m^{-2} at 12 WAS, while no significant differences were found at the earlier dates. **SR4X** was highest for tillers m^{-2} on all dates, significantly higher at 8 WAS (Table 5.2). The 250 g 100 m^{-2} (**SR1X**) seeding rate was significantly lower than the other seeding rates on all dates (Table 5.2).

Significant differences were found between all cultivars for 250 g 100 m^{-2} tillers plant^{-1} at 4 WAS, with 18th Green having the highest values followed by Putter, then Penncross (Table 5.2). **SR1X** was significantly higher for tillers plant^{-1} at 4 WAS (Table 5.2). The 500 g 100 m^{-2} seeding rate (**SR2X**) was next highest followed by the two highest seeding rates.

Dry weight plant^{-1} (**DWP**) was highest for 18th Green at 4 WAS. Increasing seeding rates led to a decrease in **DWP** at 4 WAS (Table 5.3).

Dry weight tiller^{-1} (**DWT**) was higher for **SR1X** followed by the other seeding rates in order (Table 5.3) for 4 and 12 WAS respectively. A seeding rate x cultivar interaction was found at 8 WAS for **DWT** (Figure 5.1). Penncross and Putter both demonstrated a decrease in **DWT** as seeding rate increased, while 18th Green had a uniform **DWT** across all seeding rates (Figure 5.1).

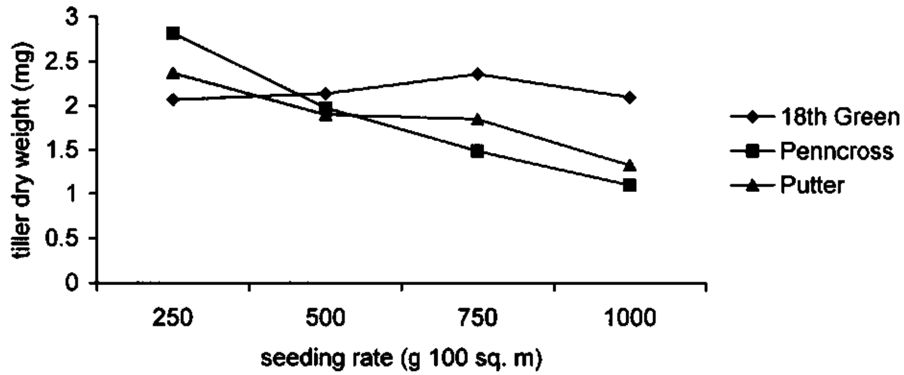

Figure 5.1. Dry weight tiller^{-1} interaction between cultivar and seeding rate at 8 weeks after seeding for the field study.

Higher seeding rates produced greater above ground live biomass (**AGLB**) at 4 WAS, which were taken prior to first clipping (Table 5.3). Mowing tended to equalize **AGLB** production under the canopy (Table 5.3). At 12 WAS, the two lowest seeding rates were maintaining or increasing for **AGLB** while the higher seeding rates were decreasing (Table 5.3).

Visual plot coverage and density ratings showed that 18th Green had the highest rating on all dates, and significantly was higher than Putter at 8 WAS and Penncross as well at 12 WAS (Table 5.4). Penncross showed the greatest decrease in plot density after wear stress was applied at 9 WAS.

Estimates of wear stress resistance (log *c*) were similar at all dates with the exception

Table 5.3. Dry weight plant^{-1} (DWP), dry weight tiller^{-1}, and dry weight of above ground live biomass accumulation for the 1993 field study at 4, 8 and 12 weeks after seeding (WAS).

	DWP	Dry Weight Tiller^{-1}		Above Ground Live Biomass (Dry Weight)		
	mg			g m^{-2}		
Cultivar	**4 WAS**	**4 WAS**	**12 WAS**	**4 WAS**	**8 WAS**	**12 WAS**
18th Green	1.77 a[z]	1.09 a	1.33 b	216 a	216 a	173 a
Putter	1.59 ab	1.09 a	1.46 ab	201 a	186 a	166 a
Penncross	1.30 b	1.00 a	1.73 a	230 a	200 a	185 a
lsd (.05)	*0.45*	*0.25*	*0.33*	*36*	*37*	*37*
Seeding Rate (g 100 m^{-2})						
250	2.59 a	1.42 a	1.83 a	147 c	169 a	173 a
500	1.64 b	1.11 b	1.52 ab	194 b	171 a	190 a
750	1.10 c	0.93 bc	1.24 b	255 a	183 a	160 a
1000	0.89 c	0.78 c	1.43 c	268 a	192 a	175 a
lsd (.05)	*0.51*	*0.29*	*0.38*	*42*	*44*	*44*

[z] Means followed by the same letter are not significantly different using Fishers Protected LSD (P=.05).

Table 5.4. Plot coverage and visual density ratings and estimates of wear stress resistance (log c) for cultivars and seeding rates of creeping bentgrass at 4, 8, and 12 weeks after seeding (WAS) for the field study.

	Field Study, 1993			Growth room Study, 1994		
	Plot Coverage[z] (%)	Visual Density Ratings (9 - best, 1 - no turf)		Log *c*		
Cultivar	**4 WAS**	**8 WAS**	**12 WAS**	**4 WAS**	**8 WAS**	**12 WAS**
18th Green	98 a[Y]	7.75 a	7.42 b	4.28 a[z]	5.64 b	5.74 a
Putter	98 a	7.06 b	6.67 b	4.24 a	5.80 a	5.77 a
Penncross	97 a	7.88 a	6.50 a	4.18 a	5.66 b	5.73 a
lsd (.05)	*1.5*	*0.5*	*0.54*	*0.12*	*0.08*	*0.1*
Seeding Rate g 100m^{-2}						
1000	99 a	8.42 a	7.44 a	4.46 a	5.73 ab	5.74 a
750	99 a	7.92 ab	7.11 ab	4.38 a	5.74 a	5.74 a
500	97 b	7.50 b	6.78 b	4.16 b	5.69 ab	5.81 a
250	95 c	6.42 c	6.11 c	3.92 c	5.64 b	5.70 a
lsd (.05)	*1.7*	*0.57*	*0.63*	*0.14*	*0.09*	*0.12*

[Z] Percentage of plot covered by turf (visually estimated).
[Y] Means followed by the same letter are not significantly different using Fishers Protected LSD (P=.05)

Table 5.5. Plants m^{-2}, tillers m^{-2}, and tillers $plant^{-1}$ for the growth room experiment at 3, 6 and 9 weeks after seeding (WAS).

	Plants m^{-2}		Tillers m^{-2}		Tillers $plant^{-1}$		
	3 WAS	6 WAS	3 WAS	6 WAS	3 WAS	6 WAS	9 WAS
Cultivar	------------(x 1000)------------						
Putter	50.3 a[z]	47.5 b	53.1 a	117.1 b	1.07 b	2.67 a	5.71 b
Penncross	48.6 a	55.2 a	50.5 a	128.2 ab	1.06 b	2.58 b	5.62 b
18[th] Green	39.1 b	39.7 c	46.9 a	137.5 a	1.28 a	3.56 a	8.23 a
lsd (.05)	*6.6*	*7.5*	*6.7*	*14.1*	*0.07*	*0.27*	*0.86*
Seeding Rate (100 m^{-2})							
1000 g	67.6 a[z]	64.8 a	71.1 a	146.8 a	1.06 b	2.39 c	4.89 c
750 g	59.7 b	52.0 b	62.9 b	136.0 ab	1.07 b	2.73 b	5.47 c
500 g	35.9 c	48.5 b	46.9 c	132.3 b	1.18 a	2.88 b	6.57 b
250 g	20.8 d	24.4 c	25.4 d	94.5 c	1.25 a	4.73 a	9.15 a
lsd (.05)	*7.7*	*8.7*	*7.8*	*14.1*	*0.08*	*0.31*	*0.99*

[z] Means followed by the same letter are not significantly different using Fishers Protected LSD (P=.05).

of 18[th] Green and Penncross having a higher value at 8 WAS (Table 5.4).

Experiment 2

Significant differences were found among cultivars and seeding rates at 3 and 6 WAS for plants m^{-2} (Table 5.5). 18[th] Green had significantly fewer plants m^{-2} at both dates. **SR1X** was lowest at both dates and 500 g 100 m^{-2} (**SR2X**) and 750 g 100 m^{-2} (**SR3X**) were similar at 6 WAS (Table 5.5). A seeding rate x cultivar interaction was found at 9 WAS for plants m^{-2}. 18[th] Green had similar levels of plants m^{-2} at **SR3X** and **SR4X** while plants m^{-2} increased with increasing seeding rate for Penncross and Putter (Figure 5.2).

Significant differences were found at 6 WAS between cultivars for tillers m^{-2} with 18[th] Green being higher than Putter. Significant differences between seeding rates for tillers m^{-2} were found at 3 and 6 WAS (Table 5.5). Tillers m^{-2} increased with increasing seeding rate. A significant seeding rate x cultivar interaction was found at 9 WAS for tiller m^{-2} (Table 5.1). Putter and 18[th] Green showed a leveling off or a decrease at **SR4X** as compared to **SR3X** while Penncross increased with seeding rate (Figure 5.3).

18[th] Green was significantly higher than Penncross at 3, 6 and 9 WAS and Putter at 6 and 9 WAS for tillers $plant^{-1}$ (Table 5.5). **SR1X** was in the highest grouping on all dates and

SR4X was in the lowest grouping on all dates (Table 5.5).

18th Green had a higher dry weight plant^{-1} (**DWP**) at 6 WAS (Table 5.6). Lower **DWP** was found as seeding rate increased for 3 and 6 WAS (Table 5.6). A significant seeding rate x cultivar interaction was found at 9 WAS for **DWP**. **DWP** increased at **SR4X** as compared to

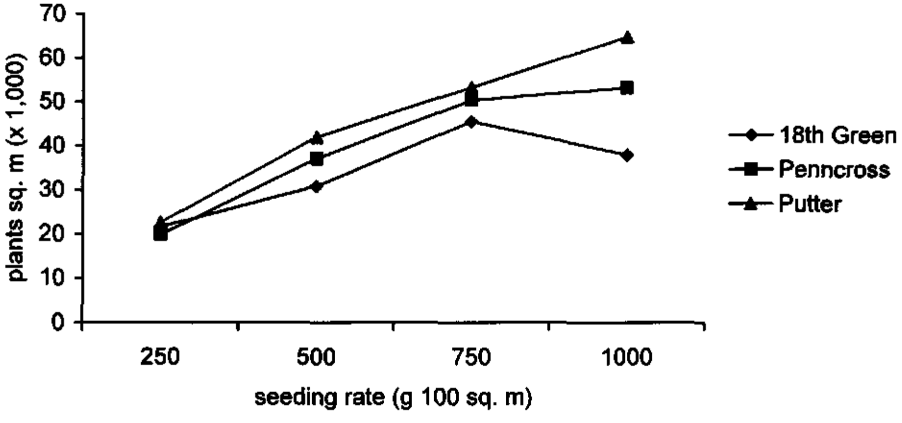

Figure 5.2. Plant m^{-2} interaction between cultivar and seeding rate at 9 weeks after seeding for the growth room study.

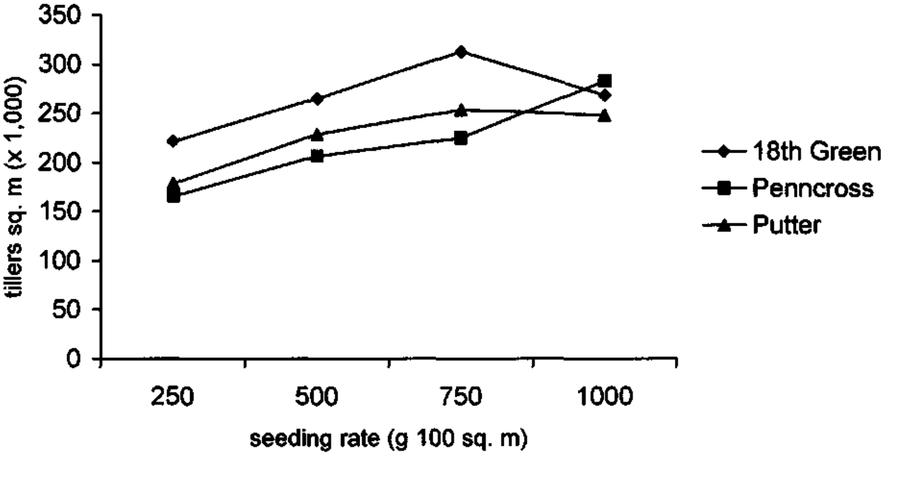

Figure 5.3. Tillers m^{-2} interaction between cultivar and seeding rate at 9 weeks after seeding for the growth room study.

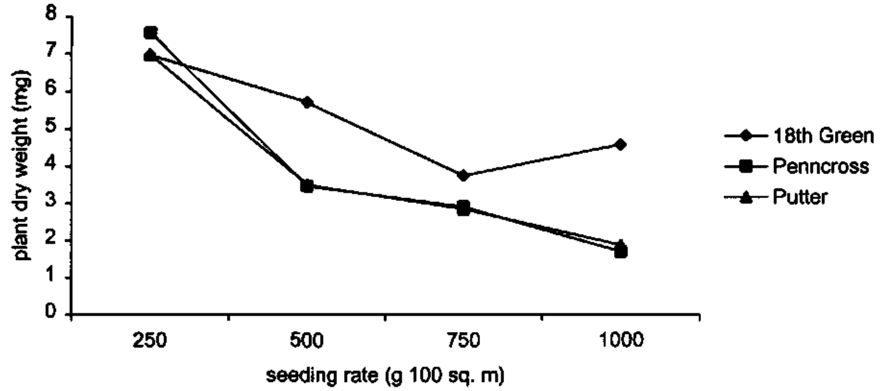

Figure 5.4. Dry weight plant^{-1} interaction between cultivar and seeding rate at 9 weeks after seeding for the growth room study .

Table 5.6. Plant height (cm), plant weight (g), tiller weight (g), above ground live biomass (g m^{-2}) and visual density ratings for the growth room study.

	Plant Height	Dry Weight Plant^{-1}		Dry Weight Tiller^{-1}		Above Ground Live Biomass (Dry Weight)		
	3 WAS	3 WAS	6 WAS	6 WAS	9 WAS	3 WAS	6 WAS	9 WAS
Cultivar		---------- *mg* ----------				---------- *g m^{-2}* ----------		
Penncross	7.0 a[z]	0.96 a	1.65 b	0.62 a	0.64 a	126 a	233 b	413 b
Putter	6.5 b	0.93 a	1.68 b	0.62 a	0.63 a	122 ab	252 ab	425 b
18th Green	4.6 c	0.98 a	2.48 a	0.62 a	0.63 a	106 b	273 a	510 a
lsd (.05)	*0.4*	*0.17*	*0.24*	*0.06*	*0.08*	*18*	*22*	*53*
Seeding Rate (g 100 m^{-2})								
250	6.2 a[z]	1.37 a	3.00 a	0.76 a	0.80 a	86 c	226 b	459 a
500	6.2 a	1.00 b	1.82 b	0.63 b	0.64 b	109 b	252 a	452 a
750	6.0 ab	0.75 c	1.62 b	0.61 bc	0.57 bc	136 a	251 a	453 a
1000	5.8 b	0.71 c	1.30 c	0.54 c	0.53 c	142 a	240 ab	432 a
lsd (.05)	*0.4*	*0.19*	*0.28*	*0.07*	*0.09*	*21*	*25*	*62*

[z] Means followed by the same letter are not significantly different using Fishers Protected LSD (P=.05).

SR3X for 18th Green while the other cultivars continued to decrease as seeding rate increased (Figure 5.4). This mirrors tillers m^{-2} (Figure 5.3).

DWT showed no cultivar differences once clipping was implemented (Table 5.6). A significant seeding rate x cultivar interaction was found at 3 WAS (Table 5.1). 18th Green exhibited little difference for **DWT** across seeding rates while Penncross and Putter showed a decrease in **DWT** (Figure 5.5) as seeding rate increased similar to 8 WAS in the field (Figure 5.1). **AGLB** increased throughout the study (Table 5.6). Cultivar differences changed as clipping was implemented (Table 5.6). Prior to clipping at 3 WAS, Penncross was significantly higher than 18th Green. However at 9 WAS 18th Green was significantly higher than Penncross and Putter (Table 5.6). Seeding rate differences were not seen by 9 WAS.

Cultivar differences for visual density ratings changed as clipping began with 18th Green being higher at 6 and 9 WAS (Table 5.7). Visual density ratings were higher for higher seeding rates throughout the study (Table 5.7).

Cultivar differences for log *c* values were variable at 6 and 9 WAS (Table 5.7). Log *c* values increased throughout the study with initial seeding rate differences disappearing by 9 WAS (Table 5.7).

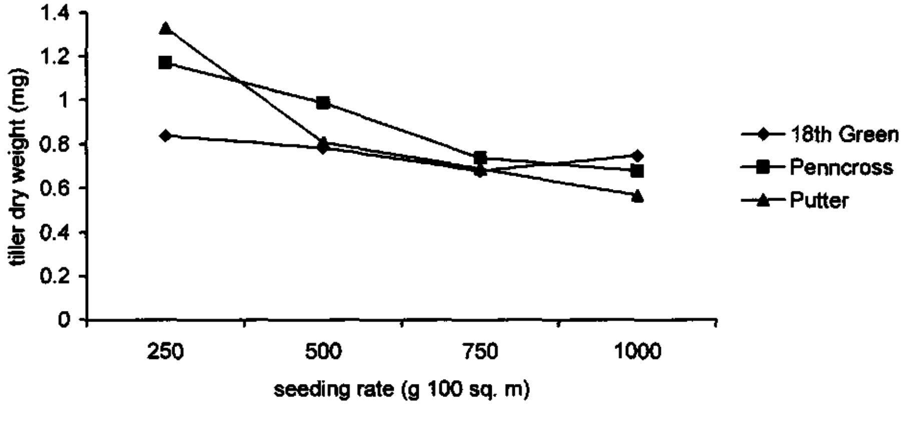

Figure 5.5. Dry weight tiller^{-1} interaction between cultivar and seeding rate at 3 weeks after seeding for the growth room study (prior to first clipping).

Table 5.7. Turfgrass visual density ratings and estimates of wear stress resistance (log c) for cultivars and seeding rates of creeping bentgrass at 3, 6, and 9 WAS in the growth room.

	Visual Density Ratings (9 - best, 1 - no turf)			Log c		
Cultivar	**3 WAS**	**6 WAS**	**9 WAS**	**3 WAS**	**6 WAS**	**9 WAS**
Penncross	5.04 a[z]	5.50 b	6.25 b	6.93 a	7.42 b	7.79 b
Putter	4.88 a	5.13 b	6.13 b	6.92 a	7.38 b	7.93 a
18th Green	3.50 b	6.06 a	6.75 a	6.83 a	7.50 a	7.81 b
lsd (.05)	*0.4*	*0.27*	*0.37*	*0.09*	*0.05*	*0.06*
Seeding Rate (g 100 m^{-2})						
1000	6.47 a[z]	7.08 a	7.42 a	7.08 a	7.46 a	7.85 a
750	5.56 b	6.13 b	7.33 a	7.03 a	7.47 a	7.87 a
500	4.06 c	5.21 c	5.83 b	6.84 b	7.47 a	7.84 a
250	1.81 d	3.83 d	4.92 c	6.63 c	7.34 b	7.81 a
lsd (.05)	*0.47*	*0.31*	*0.42*	*0.1*	*0.06*	*0.07*

[z] Means followed by the same letter are not significantly different using Fishers Protected LSD (P=.05).

DISCUSSION

SR1X produced fewer, heavier plants, a lower tiller density and heavier tillers. Larger plant and tiller size for **SR1X** account for the comparable log*c* values obtained by the end of the studies. Larger plants withstand wear stress better than smaller plants (dry weight and tiller number) (Parr 1982). Tallowin *et al.* (1989) reported that tiller order was influenced by severe grazing stress, promoting only primary tiller production in *Lolium perenne*. This could account for the relatively equal tiller weights found for 18th Green at 8 WAS (Figure 5.1) and 3 WAS (Figure 5.5). A similar trend was found for primary tillers in UM67-10 (Chapter 2), the parental population of 18th Green (Cattani *et al.* 1992). Results of Kays and Harper (1974) would suggest that as the turf develops, **DWT** would eventually converge between seeding rates. Lower **DWT** values found in the growth room are most likely the result of lower light intensity (Kays and Harper 1974).

Our results suggest that **SR1X** and **SR2X** are better for establishment of creeping bentgrass, regardless of cultivar used, as found by Madison (1966). Cultivar did affect **DWP** in the growth room study and **DWT** at 8 WAS in the field and 9 WAS in the growth room. Wear stress was applied at 9 WAS in the field and lower seeding rates appeared to perform better as evidenced by increasing log *c*'s. Higher seeding rates remained relatively stable for log *c*, however there was a decrease in **AGLB** between 8 and 12 WAS.

Higher plant densities for the seeding rates were found in the field study than in the growth room study. Covering to prevent seed movement during establishment appeared to have provided a more favorable environment for germination and emergence. Seed was raked into the soil surface while in the growth room, seed was placed at a 5 mm depth. Madison (1966) reported that creeping bentgrass had higher plant populations when seeded at the soil surfaces compared to seeding into the soil.

Putter and 18^{th} Green showed evidence of interplant competition at 9 WAS. 18^{th} Green had fewer plants at **SR4X** than **SR3X** while Putter had similar tiller densities at these rates. Inter-plant competition could be a negative factor with respect to early upright growth of turfgrass. Increased disease incidence has been noted for higher seeding rates in creeping bentgrass possibly due to smaller plant size (Rossi and Mallett 1996). Cultivars that possess longer leaves may be subject to greater tissue removal during mowing. As distal portions of blades are more physiologically mature (Bregard and Allard 1999), greater removal may mean a greater reduction in photosynthetic capacity.

Plant growth rate will also impact occupation of biological space within a population. Earlier emergence of a seedling confers a competitive advantage to that seedling within the developing plant community (Ross and Harper 1972). 18^{th} Green produced more tillers plant^{-1} in the present studies. 18^{th} Green has been shown to have a high tillering rate relative to other creeping bentgrass cultivars (Chapter 4). This higher tillering rate may be exerting greater inter-plant stress, thus reducing plant numbers, especially at higher seeding rates (Figure 5.2). Higher plant densities have been reported to lead to stand thinning in creeping bentgrass turf (Rossi and Mallett (1996), however the seeding rated in the present studies are in the low to mid range of their study.

AGLB had equilibrated between seeding rates by 8 and 9 WAS for the field and growth room studies respectively. This would appear to indicate that the respective mowing heights had restricted AGLB accumulation. Kays and Harper (1974) found a similar trend with *L. perenne* between seeding rates.

Lower seeding rates may be more desirable as they should allow for greater horizontal growth via stolons due to less crowding. Duff and Beard (1974) reported that tillers began stolon growth one week after experiencing mowing. Once mowing is initiated, stolonization should quickly follow. Leaf blade orientation may be more horizontal at lower plant densities allowing for less removal during mowing events. Stolon internode elongation may be controlled by light competition (Casal *et al.* 1990). Higher tiller densities with upright growth of tillers may encourage stolon development through greater shading of tiller bases (Casal *et al.* 1985). Without adequate space for horizontal expansion, growth may continue in a vertical direction leading to removal during mowing. Lower seeding rates should allow for horizontal stolon growth and thus higher tiller weights (Chapter 3), increasing wear stress tolerance (Lush 1990). Lower seeding rates should also provide greater turf strength, if root formation at stolon nodes takes place.

Stolon production did not take place until at least 3 weeks after transplanting in non-competitive environments (Chapter 3). This may be a factor of light competition. Stolon length differs between cultivars (Chapter 4) and this may have ramifications on potential wear stress resistance as the turf matures. In the present studies, tiller initiation was somewhat delayed as compared to non-competitive plants (Chapter 2). Stolon growth was only seen in a single creeping bentgrass plant prior to tillering, and only under a short daylength (Chapter 3).

Rossi and Mallett (1996) found that self-thinning took place at high seeding rates, similar to SR4X and higher. This was only seen for 18th Green at the highest seeding rate (Table 5.2, Figure 5.1). Increasing tiller densities as the study progressed also suggest that tiller density had not reached its maximum. We found that tiller density increased over a three year period in creeping bentgrass grown as golf green turf seeded at a single rate (SR2X) (Chapter 6). Brede and Duich (1982) found that a five-year period was required in *Poa pratensis* L. for tiller densities of turf seeded at four rates to converge. Therefore turfgrass development takes place over an extended period.

Expectations are that a turf will persist for a number of years. Turf health (Rossi and Mallett 1996) and stress resistance will impact the longevity of the stand. Seeding rates used in these studies are well within rates used by the turf industry. Higher seeding rates will lead to turf comprised of more immature plants. Ability of a turfgrass to withstand and recover from stress, especially wear and diseases, will also be important with respect to weed competition, especially *Poa annua* L., which readily invades creeping bentgrass turf.

CONCLUSIONS

Turfgrass areas established with increased seeding rates appeared better suited for early initiation of play. However, turfgrass areas seeded at high rates were comprised of less developed plants than those seeded at lower rates. Mature plant development appears to enhance wear stress resistance. Cultivar selection did not appear to affect turf development at the end of the studies. Seeding rate differences were found with respect to turf wear stress resistance (log *c*) development. Newer cultivars were often different from the standard cultivar.

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Chapter 6

Tiller production and dry matter accumulation in six creeping bentgrass entries grown in Manitoba.

ABSTRACT

Tiller production and dry matter accumulation were monitored in six creeping bentgrass (*Agrostis stolonifera* L.) entries maintained as a putting green. Core samples for tiller density and aboveground biomass determinations were collected at intervals between October 1987 and October 1989. Two experimental lines, UM84-01 and UM86-01, produced more ($P<0.05$) tillers and higher ($P<0.05$) aboveground biomass than commercial cultivars Penneagle, National, Emerald and Seaside. Both tiller density and aboveground biomass among entries were consistent over the study period. Although lower tillering entries had a significantly higher aboveground biomass tiller^{-1}, total aboveground biomass was influenced more by tiller density than by biomass tiller^{-1}. The relationship between density and tiller dry weight was expressed as, $\log c = \log_{10}$ tiller dry weight m^{-2} - $0.5 \log_{10}$ tiller density m^{-2}, to determine potential wear stress resistance among entries.

Key words: creeping bentgrass, tillering, biomass accumulation

INTRODUCTION

Creeping bentgrass is used in Canada predominantly in putting green turfs and very rarely in lawns. An important characteristic among creeping bentgrass cultivars is tiller density (TD). Tiller density is positively related to wear stress recovery in bentgrasses (Hawes and Decker 1977), and wear stress resistance in Kentucky bluegrass (*Poa pratensis* L.) (Shildrick and Pell 1984), tall fescue (*Festuca arundinacea* Schrib.) (Shildrick and Peel 1983), and all bentgrasses (Lush 1990).

Greater wear stress resistance among turfgrass is often attributed to higher levels of aboveground biomass (AGB) or thatch (i.e., living and dead material above the soil surface) (Shildrick and Peel 1984). The mathematical relationship between TD and AGB has been proposed as a method for predicting potential wear stress resistance among bentgrass cultivars (Lush 1990). However, while high levels of AGB may be desirable for turfgrasses (Shildrick and Peel 1983; Lush 1990), higher levels of fertilisation may be required to maintain the integrity of the green (Shildrick 1985).

There is little information on tillering characteristics of creeping bentgrass cultivars grown on the Canadian prairies. Tillering in this species is affected by environmental factors such as temperature (Duff and Beard 1974; Hawes and Decker 1977). The performance of cultivars in the cold, dry prairie climate may be different from the performance in less severe environments. A greater knowledge of tiller dynamics in turfgrasses is also important since TD is becoming an increasingly useful characteristic in turfgrass breeding and management programs (Lush 1990). Information on AGB production among turfgrass cultivars is important, especially for determining the level of management required to maintain a good-quality playing surface. The objectives of this study were to monitor (1) tiller production and (2) AGB accumulation in a number of creeping bentgrass cultivars or lines grown on the Canadian prairies.

METHODS AND MATERIALS

A creeping bentgrass (*Agrostis stolonifera* L.) putting green was established on a sand base (Beard 1983) at the Department of Plant Science Winnipeg Field Research Laboratory in the first week of September 1986. This study included four cultivars: "Penneagle", "Emerald", "Seaside" and "National", and two lines, "UM84-01" and "UM86-01". UM84-01 is a five clone synthetic (Registered as "Biska" and renamed "18th Green" (Cattani *et al.* 1992). UM86-

01 is a three clone synthetic. UM84-01 and UM86-01 were selected at the University of Manitoba. The experimental design was a randomized complete block with four replicates. Each plot was 1 m^2 in size.

Immediately prior to seeding, fertiliser (19-25-4) (N - P_2O_5 - K_2O) was broadcast applied at a rate of 21 g product m^{-2}, and incorporated to a depth of 5 cm. Seed was sown by means of broadcasting at a density of 15000 seeds m^{-2}. Immediately after seeding, the plot area was packed and then covered with fibreglass furnace filter material in order to reduce evaporative soil moisture loss and to prevent seeds from being splashed or blown into adjacent plots. This covering was removed 14 d after seeding. A second fertiliser application (rate similar to pre-plant application) was made on 16 October 1986.

The turfgrass plots were maintained similar to golf course putting greens. Beginning on 27 May 1987, the turf height in each plot was measured and grasses immediately cut to a 5 mm height. Cuttings during this and subsequent summers were conducted five times a week, except when the frequency was reduced to two times $week^{-1}$ in September and to once $week^{-1}$ in October. The plot area was irrigated regularly to prevent wilting and to promote vigorous turf growth. Turf plots were fertilised, aerated and topdressed as shown in Table 6.1. Plots were aerated with a hollow-core aerator with 1 cm dia. tines. Topdressing consisted of spreading a sand mixture onto the plot area and sweeping it into the turf (Beard 1982).

Core samples (6.25 cm diameter x 7.5 cm depth) for TD and AGB determinations were taken at intervals between October 1987 and October 1989. Sample number consisted of one core $plot^{-1}$ and sampling procedures followed those described by Madhi and Stoutemeyer (1953). TD and AGB were measured on the entire core sample and were expressed as functional tiller number and AGB m^{-2}, respectively (Madison 1962). AGB was determined as follows: The core was cut off at the original soil level and dried at 85 °C for 48 hours to determine total above ground dry weight. Samples were then placed in an ashing oven (Sybron Thermolyne Model 10500 Furnace) at 560 °C for 5 h to determine weight of non-organic aboveground matter. AGB was then calculated as: total aboveground dry weight minus non-organic aboveground dry weight. AGB $tiller^{-1}$ was calculated from AGB and TD values. Dry weight live $tiller^{-1}$ was measured on 100 tillers $plot^{-1}$ from samples taken on 12 July 1989. The tiller density and live AGB measurements of July 12 were used to calculate log C (an estimate of wear stress resistance) using Equation 1 (Lush 1990).

$$\log_{10} B = \log_{10} C - 0.5 \log_{10} N \quad (1)$$

where B is dry weight of live tillers m^{-2}, N is tiller density m^{-2}, and log C is an estimate of turf wear stress resistance.

Results and Discussion

Plant height before first cut (27 May 1987) was 7.9 cm for Seaside, 3.5 cm for each of National and Emerald, 2.8 cm for Penneagle, 1.8 cm for UM86-01 and 1.4 cm for UM84-01 (LSD 0.05 = 1.4). After the initial cut, all entries exhibited a more horizontal growth habit, similar to the trend observed by Duff and Beard (1974).

TD measurements were consistently highest for the two experimental lines, UM84-01 and UM86-01, and consistently lowest for Seaside (Table 6.2). Within entries, TD

Table 6.1. Fertilisation and aeration schedule for creeping bentgrass trial; 1987 to 1989.

Date	Fertiliser formulation	Rate (g product m^{-2})	Aeration and Topdressing
1987			
05 May	22 - 0 - 16	20.5	
12 June	22 - 0 - 16	20.5	
13 August	22 - 0 - 16	20.5	
17 September	22 - 0 - 16	20.5	
1988			
16 May	22 - 0 - 16	20.5	
20 June	22 - 0 - 16	20.5	Yes
18 August	22 - 0 - 16	20.5	
14 September	30 - 0 - 14	15.0	
1989			
08 May	15 - 0 - 0	30.0	
02 June	27-14 - 0	16.7	Yes
03 August	22 - 0 -16	20.5	
07 September	22 - 0 -16	20.5	

measurements were relatively stable over time. For example, mean TD across all sampling dates varied by less than 30% while late-season TD levels (October samples) varied by less than 20%. Slight increases in TD levels between May and July 1989 (Table 6.2) may be attributed to increasing day length and average daily air temperature (Hawes and Decker 1977). Penneagle had a similar TD ($P>0.05$) to the UM lines on two sampling dates. Tiller density levels in this study are similar to those reported for bentgrasses by Madison (1962) and Cattani and Clark (1991).

Levels of AGB closely reflected TD for all six entries. For example, UM84-01 and UM86-01 always had the highest ($P<0.05$) AGB, followed by Penneagle, Emerald, National and Seaside (Table 6.3). Similar to results for TD, AGB for Seaside was consistently lower than all other entries. Ranking among entries was also similar over sampling dates suggesting that phenotypic variation in TD and AGB expressed early in the stand life was maintained throughout the three-year test period.

Similar to observations for other turfgrasses (Lush 1990), total biomass per tiller was consistently highest for the low tillering entries (Table 6.4). Interestingly, entries with the highest AGB tiller^{-1} also achieved the greatest height prior to initial cutting. However, while entries with the lowest TD had the highest AGB tiller^{-1}, they still had the lowest total AGB (Table 6.3). This observation is similar to Shildrick and Peel (1984) and suggests that TD was more important than AGB tiller^{-1} in determining total AGB. Correlation coefficients for AGB and TD across genotypes ranged from 0.93 to 0.98 ($P<0.01$: $n=6$).

By the end of the study period (October 1989), the highest AGB producing entry, UM86-01, had accumulated 113, 131, 124 and 154% more AGB than Penneagle, Emerald, National and Seaside, respectively (Table 6.3). These data suggest that UM86-01 should provide the most wear stress resistance. Potential wear stress resistance was calculated using 12 July 1989 TD and live AGB measurements (Eq. 1). Results showed that the UM lines had significantly higher log c values than the other entries (Table 6.2), further supporting the conclusions that these lines should provide the greatest wear stress resistance of any of the entries tested in this study. However, because these lines yielded the highest levels of AGB, they may require additional management to ensure turf quality.

Results from the 12 July 1989 sampling date also show that the dry weight live tiller^{-1} was approximately 25% as high as the total AGB tiller^{-1} (Tables 6.2 and 6.4, respectively).

Table 6.2. Tiller density m^{-2} (x 1,000) (TD) for six creeping bentgrass entries, 1987-1989; plus dry weight live $tiller^{-1}$ (DWT) and log *c* (Equation 1) for 12 July, 1989 sampling date.

	Date											
	15 Oct. 1987	27 July 1988	14 Oct. 1988	31 May 1989	21 June 1989	12 July 1989			02 Aug. 1989	23 Aug. 1989	13 Sep. 1989	04 Oct. 1989
	TD						DWT	log *c*	TD			
Cultivar							(mg)					
UM84-01	138 a[z]	142 a	156 a	125 b	170 a	181 a	1.23 b	4.97 a	168 a	189 a	186 a	171 a
UM86-01	125 ab	138 a	143 b	145 a	148 b	165 b	1.19 b	4.89 a	147 b	189 a	189 a	172 a
Penneagle	114 bc	117 b	138 b	100 c	107 c	118 c	1.38 b	4.47 b	109 c	148 b	134 b	128 b
Emerald	94 cd	90 d	99 c	87 d	97 c	95 d	1.68 a	4.69 bc	93 c	125 c	113 b	100 c
National	88 d	105 c	102 c	77 d	94 c	100 d	1.42 b	4.63 c	108 c	121 c	118 b	98 c
Seaside	63 e	68 e	66 d	59 e	71 d	63 e	1.83 a	4.44 d	67 d	76 d	76 c	77 d
Mean	104	110	117	99	115	120	1.46	4.73	115	141	136	124
LSD (0.05)	23	11	13	11	18	14	0.25	0.09	20	18	22	12
CV (%)	15.0	6.4	7.6	7.6	10.2	7.5	11.4	1.4	11.6	8.3	10.5	6.6

[z] Values within column followed by the same letter are not significantly different using Fisher's Protected Least Significant Difference (P=0.05).

Table 6.3. Aboveground biomass (g m^{-2}) for six creeping bentgrass entries, 1988 and 1989.

	Date								
Entry	**27 July 1988**	**14 Oct. 1988**	**31 May 1989**	**21 June 1989**	**12 July 1989**	**02 Aug. 1989**	**23 Aug. 1989**	**12 Sept. 1989**	**04 Oct. 1989**
UM84-01	613 a[z]	722 a	822 a	827 a	890 a	809 a	984 a	1043 a	1064 ab
UM86-01	577 a	658 b	805 a	766 ab	890 a	764 a	961 a	1064 a	1139 a
Penneagle	487 b	588 c	740 b	703 bc	725 b	670 b	918 ab	942 bc	1047 b
Emerald	402 bc	531 d	668 bc	656 cd	703 b	612 b	775 c	856 cd	871 c
National	426 bc	531 d	663 c	621 d	692 b	600 b	810 bc	812 d	861 c
Seaside	366 c	410 e	541 d	509 e	555 c	489 c	598 d	689 e	695 d
CV (%)	10.0	4.9	7.1	6.5	8.8	7.8	8.7	7.8	5.8

[z] Values within columns followed by the same letter are not significantly different using Fisher's Protected Least Significant Difference (P=0.05).

Table 6.4. Aboveground biomass $tiller^{-1}$ (mg) for six creeping bentgrass entries, 1988 and 1989.

	Date								
Entry	**27 July 1988**	**14 Oct. 1988**	**31 May 1989**	**21 June 1989**	**12 July 1989**	**02 Aug. 1989**	**23 Aug. 1989**	**12 Sept. 1989**	**04 Oct. 1989**
UM84-01	4.0 b[z]	4.5 cd	6.4 cd	4.7 b	4.8 d	4.7 c	5.2 c	5.6 c	5.6 c
UM86-01	4.1 b	4.5 cd	5.4 d	5.1 b	5.3 cd	5.1 bc	5.1 c	5.6 c	6.5 b
Penneagle	4.1 b	4.1 d	7.2 c	6.4 a	6.0 bcd	6.0 ab	6.3 b	7.2 bc	8.0 a
Emerald	4.5 ab	5.3 b	7.5 bc	6.6 a	7.2 b	6.1 ab	6.3 b	7.7 ab	8.6 a
National	3.9 b	5.0 bc	8.4 a	6.5 a	6.8 bc	5.6 bc	6.8 b	6.9 bc	8.5 a
Seaside	5.3 a	6.1 a	8.9 a	7.1 a	7.2 a	7.2 a	7.9 a	9.5 a	8.7 a
CV (%)	13.4	9.5	9.7	11.6	16.6	14.7	10.5	19.2	7.5

[z] Values within column followed by the same letter are not significantly different using Fisher's Protected Least Significant Difference (P=0.05).

This relationship between live tiller and other organic material suggests that for all six entries, approximately three-quarters of the AGB on that sampling date consisted of plant material other than functional tillers. Part of this would have consisted of stolon internodes which were between functional tillers (a functional tiller is subtended by a root system) and would account for a large portion of the AGB.

In the present study, all entries received similar amounts of nitrogen fertiliser. While low tillering entries such as Seaside performed poorly in terms of TD and AGB production, results may have been different if different nitrogen levels had been tested. Madison (1962) observed dramatic increases in TD in Seaside due to high rates of nitrogen fertiliser (approximately twice the rate used in this study). However, given the negative effects of high nitrogen rates in turfgrasses, such as the invasion by annual bluegrass (*Poa annua* L.) (Kohlmeier and Eggens 1983) and increased incidence of disease (Beard 1983), plus the additional cost and environmental hazards associated with high nitrogen rates, achieving a superior and more wear resistant playing surface by genetic means appears to be a more practical approach.

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Chapter 7

The effect of ice encasement and early snow removal on the survival of creeping bentgrass.

Abstract

Field studies conducted in 1992-1995 evaluated turf injury to creeping bentgrass following winter ice encasement. During the 1995 winter, ice encasement accompanied by early snow removal caused high stand mortality for two of five cultivars/lines, but ice encasement with snow cover had no effect. Our results suggest that dormancy of the cultivars affect bentgrass survival under ice encasement.

Key words: creeping bentgrass, ice encasement, snow removal, survival

INTRODUCTION

Creeping bentgrass (*Agrostis stolonifera* L.) is primarily used for golf putting green and fairway turfs in the temperate regions of North America. It has been shown to possess excellent cold temperature tolerance (Gusta *et al.* 1980) and ice-encasement tolerance of up to 60 days (Beard 1964). Newer cultivars of creeping bentgrass have been selected for survival under severe Manitoba conditions (Cattani 1987). The objective of this study was to compare bentgrass cultivar survival under winter-long ice encasement.

METHODS AND MATERIALS

In August 1992 four cultivars "18th Green", "Cobra", "Penncross" and "Southshore" and one line "UM86-02" were seeded at 5 g m^{-2} over a base material of fine sand at Winnipeg, Manitoba. 18th Green and UM86-02 were derived from selections for survival in Manitoba (Cattani 1987) and exhibit an early onset of fall dormancy (Cattani and Smith 1996).

The experimental area was maintained as golf course putting green turf with a mowing height of 4.5 mm. Three separate areas were established to allow for natural snow (**NAT**), where undisturbed snow accumulated all winter, or ice encasement with snow (**ICE**), where snow accumulated after ice treatment, or ice encasement plus snow removal (**ICE-SR**) where snow was removed continuously after March 1. Within each of these treatments, three replications of the five cultivars/lines were established in a randomised complete block design. Plot size was 0.5 m^2. This arrangement of treatments did not allow for comparison of **NAT**, **ICE** and **ICE-SR**, however it facilitated the application of the ice treatments.

The **ICE** and **ICE-SR** areas were cleared of snow in early December and boards (5 cm x 15 cm) were placed 0.5 m outside the perimeter of the area resulting in an ice treated area of 36 m^{-2}. These areas were flooded several times during the following two weeks (5 times in 1992, 7 times in each of 1993 and 1994). Snow was removed until 21 December to facilitate flooding. Snow was allowed to accumulate on both areas from December 22 to March 1. All snow was removed manually with a snow scoop. The ice melted earlier on the **ICE-SR** area than the other areas. It melted on 16 March 1993, 3 March 1994, and 18 March 1995 on the **ICE-SR** area compared to 26 March 1993, 17 March 1994 and 2 April 1995 on **ICE** and **NAT** areas.

Two methods were used to determine winter survival. In1993 and 1995, visual recovery ratings were made 28 April and 5 May as growth began. In1994, turf plugs (6.25 cm diameter x 5 cm deep) were removed from each plot on 23 March and 07 April, held at 2 °C for three days and transplanted indoors into a greenhouse set at 20/15 °C temperatures and a 16/8 hr photoperiod. After 11 days in the greenhouse, visual ratings for growth (1= dead, 5= full regrowth) on a 5 point scale were assigned to each. There was little or no green growth visible in the field when the plugs were sampled.

Data analysis was carried out with SAS (SAS Institute, 1988). Since no valid comparisons of **NAT, ICE** and **ICE-SR** could be made, ANOVA was calculated for each area separately and Fisher's protected LSD (P = 0.05) was used for cultivar/line comparisons.

Results and Discussion

In 1993, there were no differences among cultivars/line in any of the three treatment areas (data not shown).

In 1994, 18th Green and UM86-02 had significantly higher regrowth ratings than Cobra or Penncross (Table 7.1) for plugs removed from the **ICE** area on 7 April. There was no difference among cultivars/line for regrowth on plugs removed from the **NAT** or **ICE-SR** areas on either sampling date or from **ICE** area on 24 March (Table 7.1).

In 1995, 18th Green and UM86-02 had significantly higher regrowth ratings than

Table 7.1. Two week greenhouse regrowth ratings (measure of turf damage) for the natural snow cover, ice and snow cover and the ice and snow removed trials (1 - dead, 5 complete regrowth) for samples taken on March 24 and April 07, 1994.

	Natural Snow Cover (NAT)		Ice and Snow (ICE)		Ice and Snow Removal (ICE-SR)	
Cultivar	March 24	April 07	March 24	April 07	March 24	April 07
18th Green	4.0 a[z]	3.3 a	3.7 a	4.3 a	3.7 a	3.3 a
UM86-02	4.0 a	4.0 a	4.3 a	4.7 a	3.3 a	4.7 a
Southshore	3.7 a	3.3 a	2.7 a	4.0 ab	3.3 a	3.3 a
Cobra	3.7 a	2.3 a	2.7 a	2.0 c	2.7 a	3.0 a
Penncross	3.0 a	2.3 a	3.0 a	2.7 bc	2.7 a	3.0 a

[z] Means followed by the same letter within each column are not significantly different using Fisher's Protected LSD (P=0.05)

Table 7.2. 1995 percentage of plot showing active regrowth of creeping bentgrass cultivars for 28 April and 05 May, 1995.

	Natural Snow Cover (NAT)		Ice and Snow (ICE)		Ice and Snow Removal (ICE-SR)	
Cultivar	**April 28**	**May 05**	**April 28**	**May 05**	**April 28**	**May 05**
18th Green	73.3 a[z]	83.3 a	68.3 a	100.0 a	66.7 a	86.7 a
UM86-02	38.3 a	61.7 a	66.3 a	100.0 a	56.7 ab	81.7 a
Southshore	48.3 a	68.3 a	51.7 a	98.3 a	33.3 abc	50.0 ab
Cobra	78.3 a	83.3 a	41.7 a	96.7 a	18.3 bc	35.0 b
Penncross	51.7 a	71.7 a	36.7 a	96.7 a	10.0 c	25.0 b

[z] Means followed by the same letter within each column are not significantly different using Fisher's Protected LSD (P=0.05)

Penncross (Table 7.2) in the **ICE-SR** area. 18[th] Green also showed superior recovery to Southshore. Similar results were observed on 5 May for the **ICE-SR** area but no differences among the cultivars/line were observed on the **NAT** or **ICE** areas at either rating date in 1995 (Table 7.2). The differences observed in 1995 may be related to the 18 days of daytime temperatures above 0 °C which were followed by two consecutive night time temperatures of –15 °C on 2-4 April. Since the **ICE-SR** area was free of ice and snow on 18 March, it is possible that regrowth had begun prior to the frost. If low temperatures follow adequate growth conditions in the spring, then crown hydration injury may occur (Tompkins *et al.* 1996). This injury is caused by ice crystal formation and cell rupture producing tissue death. If snow removal is practised to enhance spring regrowth and earlier initiation of play on golf putting greens, then there will probably be a greater risk of crown hydration injury. The use of cultivars such as 18[th] Green will reduce this risk, however, play may be delayed to a later date.

While the Cobra and Penncross plots fully recovered in the **ICE** area in 1994, they did not recover to adequate levels from the damage in the **ICE-SR** area in 1995. Some snow mold injury (*Typhula* sp.) was observed on plots in the **NAT** area in 1995 but its occurrence was random and not related to cultivars/line.

These cultivars/line differ in fall dormancy ratings which is reflected in a decrease in relative turfgrass colour and quality ratings (Table 7.3). The expression of fall dormancy is dependent upon the environmental conditions being experienced, and therefore is not

Table 7.3. Cultivar or line, country of origin and fall visual colour ratings in 1985 and fall visual quality ratings in 1996 for selected cultivars and lines tested at the University of Manitoba Field Research Station.

		Visual Colour Ratings (9 - green, 1 – dormant)					
		1982 Creeping Bentgrass Trial[z]		1985 Creeping Bentgrass Trial[y]		1993 Creeping Bentgrass Trial[x]	
Cultivar	Origin	Sept. 23, 1985	Oct. 22, 1985	Sept. 23, 1985	Oct. 22, 1985	Sept. 30, 1996	Oct. 30, 1996
S4979	Canada	9.00	5.33				
Sobel	Sweden	8.33	5.00				
Manitoba	Canada	8.67	5.33				
Penncross	USA	8.33	8.67	7.00	6.88	5.67	4.67
UM67-10	Canada			9.00	7.00		
18th Green	Canada			8.63	6.63	8.33	3.00
UM85-01	Canada			8.13	7.13		
UM85-02	Canada			7.63	7.00		
Emerald	Sweden			6.13	5.25		
Southshore	USA					6.67	5.67

[z] 1985 University of Manitoba Turfgrass Research Report p. 5.
[y] 1985 University of Manitoba Turfgrass Research Report p. 6.
[x] 1996 University of Manitoba Turfgrass Research Report p. 5.

necessarily seen each year. However, this does not preclude the expression of later spring growth initiation.

Further research is presently underway to examine the relationship between fall dormancy and the different responses in this research. Early fall dormancy may be related to greater resistance to frost injury in the spring, such as that observed for 18th Green and UM86-02. However, if these physiological traits reduce end of season play, or delay the initiation of play in the spring, then golf superintendents must make a management decision based on these conflicting needs. Sampling and grow-out of turf plugs in early spring would be a useful management tool for superintendents to determining the status of their putting green turf.

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Chapter 8

General Discussion

In this thesis, plant development under non-competitive and competitive conditions were studied in creeping bentgrass. Time and site of tiller appearance, stolon development and dry matter partitioning under non-competitive conditions were used as indicators of plant development in both high and low tiller producing populations. Turf tiller density was studied with different cultivars, under various seeding rates, growing seasons and under ice encasement and snow removal management. Tillering propensity under non-competitive conditions was easily measured and was related to turf tiller density. Cultivar differences were consistent between studies. The techniques utilised and the findings can be adapted to plant improvement programs.

Plant Development

The phenological development of young creeping bentgrass plants were as described for other grass species (Neuteboom and Lantinga 1989) (Chapter 2). Differences between the two studied populations were primarily due to differences in tillering rates. Tillering rate is dependent upon leaf size (Bos 1999). A significant difference between populations was in 1 - 1° and 2 - 1° tillers; similar dry weight was found in the high tillering UM67-10 population, and not in the low tiller producing Emerald population where the 2 - 1° tillers had a lower dry weight (Chapter 2). This population difference was seen under both long and short day conditions (Chapter 2).

The appearance of coleoptilar tillers was only seen under the most favourable growth conditions (long days) (Chapter 2), and more predominantly in Emerald, the low tiller producing population. Coleoptilar tillers generally appeared after or between the 1 - 1° and 2 - 1° tillers (Chapter 2). The presence of prophylls (Neuteboom and Lantinga 1989) was not noticed except in rare cases. This may be due to the small size of both the prophylls and the plants at the early stage of growth studied. The base of the tillers that arise below the node of stolon elongation is hidden. If studied for a longer growth period, prophylls may have been more evident, especially on tillers arising above the node of stolon elongation.

UM67-10 produced more stolons than Emerald (Chapter 2). There were no significant differences between populations found for growth stage (Chapter 2) or the number of visible nodes on longest stolon between the cultivars and lines evaluated in Chapter 4. This indicates that stolon growth was not dependent upon tiller number but most likely a response to intra-plant competition. Stolons plant^{-1} was correlated to tiller number plant^{-1} in both populations studied in Chapter 3, with $r = 0.75$ for UM67-10 and more weakly, $r = 0.50$, for Emerald.

High tiller producing cultivars/lines had shorter stolons and stolon internodes (Chapter 4). However, within the populations studied in Chapter 2, this tiller and stolon relationship was not seen. This latter result indicates that selection within a given population may result in material that is high for both tiller number and stolon length.

Many processes are taking place simultaneously during early plant growth. During early plant growth the development of tillers and stolon takes place in a stage of vegetative expansion associated with increasing competition for assimilates, light and nutrients. Stolon development represents a high investment by the plant due to the structural components involved (Esau 1977). Unlike the development of seed culms, which is generally followed by death, the development of a stolon does not have a predetermined terminus (Jonsdottir 1991).

Stolon internode development allows the plant to increase its competitiveness in several ways. Expansion of the area of soil covered, and new tiller and leaf production away from the established portions of the plant are two important competitive advantages of stolon growth. The development of tillers and leaves on the periphery of the plant allows for greater light interception and therefore greater growth potential. The rooting at stolon nodes also allows for an expanded nutrient base for the plant near the developing apices of the stolon. Crick and Grime (1987) demonstrated the ability of *Agrostis stolonifera* L. to exploit its environment with respect to nutrient uptake through rapid root initiation in areas of high nutrient status. Stolon development is, therefore, critical to the persistence and perennial nature of creeping bentgrass.

Tiller Appearance Rate

The reduction in relative tillering rate (new tillers (internode appearance)$^{-1}$ (existing tillers)$^{-1}$) with the onset of stolon internode elongation signifies a shift in plant growth from plant establishment to vegetative colonisation of its environment. This decrease in tillering rate, has also been reported for perennial ryegrass (van Loo 1992). As the plant grows, the investment of resources in higher order tillers decreases (Chapter 2). These tillers are also smaller, with shorter leaves. When lower order and earlier arising tillers have a size advantage, and thus a competitive advantage, the potential for new tiller initiation is reduced. The probable suppressing environmental factor is the high far-red:red (fr:r) light ratio (Vine 1983).

Several factors are involved in the reduction in relative tiller appearance rate. Firstly, the plant has established a base site, i.e. its roots are sufficiently mining the soil for nutrients. Secondly, the foliage has reached its optimum leaf area index and has maximised its photosynthetic capacity for the area of occupation, as signalled by an increase in fr:r light reaching the plant organ (Casal *et al.* 1985). Therefore, the plant increases resource allocation to areas where new growth will provide the greatest net return; stolon elongation. Node of elongation decreased as tiller order increased and the age of the tillers decreased (Chapter 2). The plant is responding to the growth environment (light reduction) and moving new growth either up through the canopy or to the periphery where there is less competition. Competition becomes greater in the crown area of the plant (below the node of elongation) as all preceding orders of tillers are present.

Loss of Tillers

Lack of tiller and stolon development in the short day environment (Chapters 2 and 3) was most likely also due to light quantity and duration (Cao and Moss 1989). This reduction in plant growth has implications with respect to turfgrass use in seasons restricted by daylength and/or temperature. Hunt *et al.* (1987) reported that 80% shade resulted in high shoot stress in creeping bentgrass. Vine (1983) found a drastic reduction in leaf appearance rate in perennial ryegrass from late October to mid-February. Reduction in tillering is implied and therefore stress recovery is not realistic at this time. Stress damage avoidance may be via senescence of the smallest tillers. Circumstantial evidence of this in creeping bentgrass turf is presented in Chapter 6, where tiller density decreased in late September-early October, and above ground biomass tiller^{-1} increased or remained constant for the six creeping bentgrass cultivars/lines grown as golf green turf in Manitoba. Overwinter loss of tillers was also apparent (Chapter 6) although this loss may have been due to early spring growth followed by environmental stress (Chapter 7) or through reproductive tiller competition (see ***Reproductive Tillering*** section).

The present study investigated tillering and stolon development in early growth stages of *A. stolonifera* and further studies are required to ascertain the response of the plant to environmental stress at later growth stages.

Turf Tiller Density

Turf tiller density increased up to three years after seeding for some cultivars/lines (Chapter 6). Population differences were apparent within 12 weeks of seeding (Chapter 5). Populations with a higher number of tillers plant^{-1} produced a turf with greater tiller densities (Chapter 4). Although tiller density in turf fluctuated throughout the growing season, the relative cultivar ranking for turf tiller density remained consistent (Chapter 6).

Dry matter accumulation throughout the growing season (Chapter 6) followed, in general, turf tiller density (Chapter 6) and the shoot growth pattern for cool-season grasses as shown in Christians (1998). Peaks of growth in the late spring/early summer and again in the fall, with a growth reduction throughout most of the summer were seen.

High tiller density is also associated with lower dry weight tiller^{-1} (DWT) (Chapters 4 and 6). In order to increase DWT in a turf, space for growth is required. Cultivation is difficult due to the playing surface considerations. Core aeration is the primary method of cultivation practised, however environmental disturbance has negative effects on creeping bentgrass (Hunt *et al.* 1987).

Evidence of genetic diversity has been found with respect to tiller densities and stolon internode length both at the early plant and established turf levels (Chapter 4). These should be measured on the main stem of the plant. Genetic differences may be masked if vegetatively produced plants of a selection are used. Kik *et al.* (1990) warn against generalisations about genets (plant level) behaviour through the performance of ramets (tiller level), i.e., individual ramets are not necessarily representative of the genet from which they were taken. Given the variation in tiller sizes found (Chapter 2), the origin of the ramet may strongly influence the growth of the resultant plant. Previously, I found that seed production characteristics were highly variable between plants started from stolons of the same plant (Cattani 1987).

Correlation between sheath length and blade length has been reported for tall fescue (Brégard and Allard 1999) and perennial ryegrass (Wilson and Laidlaw 1985). In summary, the potential for tiller growth and plant development may be influenced by tiller position (Ryle 1974) and order of the tiller (Chapter 3) utilised for new plant culture.

Selection for a high turf tiller density creeping bentgrass with a high tiller dry weight is possible as evidenced by the results obtained for UM86-02 (Chapter 4). This line was selected for high tiller density under wear-stress (Cattani 1987).

Selection for tiller and stolon characteristics may therefore be made at an early growth stage in controlled environments (Chapter 4). This selection procedure can substantially reducing cultivar development time as turf plot establishment will not be required in the early selection cycles.

Plant and Community Relationships

A strong relationship was found between tillers plant^{-1} under non-competitive conditions and tiller density in turf (Chapter 4). The seeding rate studies allowed us to determine the effect of plant density on tillering in a turfgrass community (Chapter 5).

Seeding rate increase led to a turf comprised of smaller plants with fewer tillers (Chapter 5), similar to results found by Madison (1966). Cultivar differences were found for tillers plant^{-1} (Chapters 2 and 4). Biomass accumulation under the mowing height used had equilibrated by 12 weeks after seeding across seeding rates, leading to higher tiller dry weights at the lower seeding rates (Chapter 5). Recommendations made by Madison (1966) are still valid for the cultivars studied despite the difference in their growth and development characteristics (Chapters 4 and 5).

Self thinning was only seen at the highest seeding rate (Chapter 5) and only for the highest tiller producing cultivar, 18th Green (Chapter 5). The high tillering propensity in this cultivar may have resulted in an earlier onset of inter-plant competition, thus reducing plant number. Mowing may reduce the competitive advantage of more aggressive individuals within the turf due to proportionally greater removal of above ground growth. Penncross is grown from Syn 1 seed and was the tallest of the cultivars tested (Chapter 5). Therefore, the increased height and population uniformity may reduce inter-plant competition under mowing.

Seeding rate affected early turf and plant development (Chapter 5). Casal *et al.* (1985) found an increased fr:r light ratio to lead to a greater interval between leaf blade expansion and tiller appearance in the leaf axil. Closely spaced plants in wheat received a higher fr:r light ratio and produced fewer tillers plant^{-1} (Kasperbauer and Karlen 1986). Increasing daylength leads to an increased leaf extension rate (LER) (Cao and Moss 1989). DWT increased with decreasing seeding rate (Chapter 5) with an increase in above ground biomass (AGB) being primarily through tiller increase. DWT tiller remained fairly constant once clipping was initiated (Chapter 5). High tiller density leads to increased AGB and smaller plant size (Chapters 5 and 6). This has also been reported with *Poa pratensis* (Brede and Duich (1982) and for *Paspalum dilatatum* and *Lolium multiflorum* (Casal *et al.* 1986).

Mowing will affect the dynamics of turfgrass communities. A reduction in mowing height or canopy height, within the limits of the species, can lead to higher tiller densities (Madison 1962, Tallowin *et al.* 1989) through the increased appearance of daughter tillers (Tallowin *et al.* 1989). Studies have shown that some cultivars increase in tiller density under decreasing mowing heights (Madison 1962, D. Cattani, unpublished data). The prolonged effect of lower mowing heights was not followed (D.Cattani, unpublished data), however the cultivars that did not initially show an increase in tiller density had, in general, higher tiller densities at the beginning of the study. These cultivars have also been shown to be somewhat shorter in stature (Chapter 5).

Once a canopy height is established, a stable leaf area index (LAI) is also achieved by inference. Providing the canopy height (or mowing height) is within the tolerances of the cultivar, LAI should remain relatively constant. In Chapter 5, we found that three years after establishment tiller densities were still increasing for some of the cultivars. This tiller increase will be at the expense of tiller weight, i.e. increased tiller density = decreased TDW, and possibly a reduced wear-stress resistance.

As previously mentioned, the apparent times of stress for creeping bentgrass turf in Manitoba, Canada are early spring (Chapters 6 and 7) and in the summer (Chapter 6). Kik *et al.* (1990) found seasonal transition to be the major time of stress for *A. stolonifera* L., which is consistent with our findings. Creeping bentgrass turf is intensively managed and rarely suffers from drought stress for longer than a single day. Turf loss within creeping bentgrass golf greens during the summer is most likely the result of high temperature stress in the root zone due to a high sand content. Early spring damage was most likely due to crown hydration damage (Tompkins *et al.*1996) and appeared to be greater in alien populations (Chapter 7, Kik *et al.* 1990).

Wear-stress Resistance Potential

Turf tiller density and TDW are both important with respect to potential wear stress resistance in turfgrasses (Lush 1990). The Power Rule equation (Lush 1990) has been utilised in Chapters 4 and 5 to characterize turfgrass communities. Further evidence as to the utility of the Power Rule equation can be seen when applied to the data in Cattani (1987) where higher tiller densities, combined with relatively higher individual TDW, gave increased wear-stress tolerance. High tiller density has been shown to confer wear-stress resistance in seaside paspalum turf (Trenholm *et al.* 1999). In our study UM67-10 demonstrated greater dry matter partitioning between tillers of the same order than did Emerald. This is due in part to a greater stolon number plant^{-1} (Chapter 2). The dry matter partitioning within tillering systems on the main stem in UM67-10 (Chapter 3) may indicate a more durable turf by producing tillers of a more uniform size. Providing that DWT remained at or above the stress-survival threshold (Ong 1978), resistance to wear stress should be higher. A follow-up (in progress) will determine a wear-stress threshold level.

The Power Rule equation (Lush 1990) is most likely only useful for estimating wear-stress resistance, and is not predictive of wear-stress recovery. Preliminary data indicate that high tiller density may slow down turf healing and allow for the ingress of weeds such as *Poa annua* L. when core aeration is practised (D. Cattani, not published). This points to a possible negative relationship between potential wear stress resistance and turf wear stress recovery.

The point at which turf wear-stress resistance potential is compromised by decreasing tiller dry weight has not been identified, although Shildrick and Peel (1984) found that individual tiller dry weight was positively related to wear stress resistance in *Poa pratensis* L. Therefore, selection for increased turf tiller density as an aim in a plant improvement program has an upper limit.

The relationship between tiller density and stolon length, as found in Chapters 2 and 4, should be examined in relation to the ability of the turf to recover from injury sustained during usage or as a result of management practices such as core aeration. Management practices must therefore be adapted to increase turf healing in high tiller density cultivars.

Reproductive Tillering

The primary importance of sexual reproduction in creeping bentgrass is the establishment of new stands. In nature, this may be in new areas or areas where gross disturbance has taken place or extinction of the stand has occurred. Establishment and renovation of golf course turf is the major use of improved cultivars of creeping bentgrass. Seed production is important with respect to the development of high quality, non-vegetatively propagated cultivars. Broadening of the genetic base through the production of synthetic cultivars should allow for increased stress tolerances, e.g. disease resistance. Vegetatively produced cultivars are comprised of single genotypes and unforeseen stress events, especially diseases, may be devastating.

The perennial nature of creeping bentgrass turf, as with most perennial grasses, must also include a discussion as to fertile tiller development in years following establishment. Fertile tiller initiation is often seen in turf communities where mowing height and frequency allow for their notice. In golf putting greens, fertile tillers of creeping bentgrass are rarely noticeable and do not pose a problem with respect to surface irregularities such as found with *Poa annua* L. (Beard *et al.* 1978). Fertile tillers of creeping bentgrass generally emerge at the end of May in Manitoba, Canada (Cattani 1987). However, the production of fertile tillers may influence vegetative tiller production during this time. In Chapters 4 and 6, I report that turf tiller density was affected by the environment in which the plant growth took place. Most of the cultivars and lines followed a similar pattern of tiller density dynamics throughout the growing season (Chapter 6). Tiller density increased between 31 May and 21 June. Fertile tiller removal through mowing would mostly take place in this period, and therefore, the 21 June increase in tiller density may be due to increased vegetative tillering as a result of reduced fertile tiller competition within the turf.

Recommendation Regarding Cultivar Selection For Turfgrass Professionals

There has been a lack of knowledge pertaining to the developmental aspects of culture in creeping bentgrass. This thesis provides some fundamental information which can be utilised in development of new creeping bentgrass cultivars and cultivar specific management recommendations.

Turfgrass professionals require local data to make informed choices with respect to cultivar selection. The response of a cultivar to the environment will be affected by at least three important factors, the genetic make-up of the cultivar which will dictate plant growth and development patterns (Chapters 2-6), the environment in which the parental material was selected (Chapter 7), and the type and level of cultural management practices implemented, such as fertility levels, core aeration and mowing height. Cultivar choice may also be influenced by the time of year in which the turfgrass is used. Cultivar selection should, thus, be site/user specific.

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Summary

Tiller development processes are important for understanding the establishment of a durable perennial turf by grass species. In this thesis, tiller and stolon appearance and development in creeping bentgrass (*Agrostis stolonifera* L.) are examined in non-competitive and competitive environments. Creeping bentgrass is the primary species utilized in temperate areas for golf putting greens.

Turf development is a function of the potential growth rate of individual plants, and competition between plants within the turf. Tiller development patterns have been reported for several perennial grass species. There is a lack of knowledge with respect to plant development in creeping bentgrass. Stolon production in creeping bentgrass allows for plant spread, however, the effect on tillering is not known. Plant density will dictate the onset of inter- and intra-plant competition. A great increase in the number of available cultivars requires the understanding of plant growth and how individual cultivars develop. Factors under genetic control will be influenced by cultivar selection. This knowledge will aid in development of cultivar specific management programs needed to maintain the integrity of the turf over time.

The objective of this research was to examine the growth and morphological development of creeping bentgrass plants and turf areas. The approach was to conduct experiments as follows.

1. determine the tillering patterns for a high and a low tillering population of creeping bentgrass;
2. study tillering, stolon development and dry matter partitioning in a high and a low tillering population;
3. examine the relationship between seedling tiller proliferation and turf tiller density among creeping bentgrass cultivars and lines;
4. examine the effect of seeding rate and cultivar on turf development;
5. monitor turf tiller density over time under field conditions;
6. examine the effects of ice encasement and snow management on survival of creeping bentgrass cultivars and lines.

In Part I, the following aspects of plant development were investigated in two populations of creeping bentgrass:

1. tiller appearance and position, and tillering rate;
2. stolon appearance, internode length and total length of the main stem;
3. individual tiller dry weights;
4. growth stage of the plant using West's scale for stoloniferous plants.

Tiller age and dry weight were used to determine dry matter accumulation day^{-1}.

Studies were carried out under 16 h and 8 h days in growth cabinets at temperatures of 20/15°C with light at 150 µmol m^{-2} sec^{-1}. Plant measurements were taken until 35 days after transplanting (DAT). Long and short day studies were also carried out in the greenhouse under natural light conditions. A high ("UM67-10") and a low ("Emerald") tillering population were used. Tillering rate, stolon length, internode length and plant dry weight were measured through 35 DAT. A sub-set of plants from the greenhouse short day study were allowed to grow until 42 DAT to investigate stolon growth.

Tillering rate was higher for UM67-10 under all conditions. Growth stage was similar between populations in all studies with the exception of UM67-10 reaching the first tiller stage earlier than Emerald. Stolon initiation and growth were similar for both populations. Emerald produced longer stolon internodes and stolons. Stolon development of a tiller led to a higher tiller dry weight. Stolon growth was retarded under short day conditions as evidenced by a later date of stolon initiation. Populations produced similar plant dry weights within growth environments, although allocation amongst tillers was different.

Plants within populations that produced more tillers generally filled a branching unit prior to the appearance of the next primary tiller. Branching unit refers to all tillers predicted to arise between successive primary tillers.

In Part II, plant and turf development in creeping bentgrass were studied under controlled environment and field conditions by assessing:

1. relationships between seedling tiller proliferation and established turf density of fifteen cultivars or lines.
2. effects of four seeding rate and three cultivars on creeping bentgrass turf establishment.
3. turf tiller density as affected by six cultivars or lines and growing season.

4. ice encasement and snow management on turf survival of five cultivars or lines.

Growth room studies were carried out to investigate seedling tiller proliferation in creeping bentgrass cultivars under non-competitive conditions. Field studies were conducted to investigate cultivar effects on turf tiller density. Seeding rate studies were carried out under growth room and field conditions. Field turf plots were monitored over a three-year period to investigate tiller density as affected by season and turf age. Ice encasement and snow removal experiments were conducted to ascertain their effect on turf survival.

Seedling tiller proliferation at 35 d after transplanting and established turf tiller density were found to be correlated (r values ranging from 0.701 to 0.826). Stolon internode length was also found to be correlated between seedlings and established turf (r values ranging from 0.725 to 0.883). Selection for turf tiller density may be made using 35 d old seedlings under controlled growth conditions.

Larger plants (dry weight) and more tillers plant^{-1} were obtained with the lowest seeding rate. Cultivar x seeding rate interactions were found including for plants m^{-2} and dry weight tiller^{-1}. Although lower seeding rates appeared to give less turf coverage, the estimates of wear stress risk (foot traffic stress) were similar to the higher seeding rates by the end of the studies. Therefore, the present seeding rate recommendations are suitable for the cultivars tested.

Turf tiller density increased over the first three years of growth. Seasonal fluctuations in tiller density were similar for all cultivars and lines tested. Turf tiller density decreases were seen in the spring and summer. Fall tiller densities were higher than mid-July tiller densities. Cultivar differences were consistent throughout the period of the study.

Early snow removal was found to decrease turf survival of some cultivars in one of the three years of the test. Consecutive overnight lows of −15 °C following 18 consecutive days of above 0 °C temperatures was most likely the primary factor. Early snow removal increases the risk of damage.

The general discussion looked at the results from Parts I and II and put them in the context of turfgrass plant and community development. The phenological development of the creeping bentgrass plant is discussed with specific reference to tillering and stolon growth. The relationship between turf tiller density and tiller dry weight is put into the context of potential wear stress resistance. Dry matter partitioning, dry weight tiller^{-1} and wear stress resistance are then discussed with respect to tiller proliferation under turf conditions and cultivar influences. The potential impact of reproductive tillering on turf growth is considered.

Vegetative tillering in creeping bentgrass can be used to differentiate between cultivars, estimate turfgrass quality parameters and can be utilized for selection in a plant improvement program.

SAMENVATTING

Voor een goed inzicht in de factoren die de vestiging van een duurzaam, overblijvend grasveld (bijvoorbeeld een 'green' van een golfbaan) bepalen, is het belangrijk om meer te weten over de processen die een rol spelen bij de ontwikkeling van zijspruiten. In dit proefschrift wordt onderzoek beschreven naar het verschijnen en ontwikkelen van zijspruiten en stolonen van wit struisgras (*Agrostis stolonifera* L.), zowel in milieus zonder als met concurrentie. Wit struisgras is de belangrijkste grassoort in de gematigde gebieden voor de 'greens' van golfbanen.

De ontwikkeling van een zode in een grasveld is een functie van de potentiële groeisnelheid van individuele planten en van de concurrentie tussen planten in de zode. Voor verschillende grassoorten zijn ontwikkelingspatronen van spruiten reeds beschreven. Er is echter weinig bekend over dergelijke patronen bij wit struisgras. Wit struisgras vormt stolonen die de soort de mogelijkheid bieden zich te verspreiden, maar het effect van stoloonvorming op de uitstoeling is onbekend. Plantdichtheid is daarbij bepalend voor het moment waarop de tussen-plant concurrentie en de binnen-plant concurrentie beginnen.

Een sterke toename van het aantal beschikbare rassen maakt het nodig meer te weten over de groei en ontwikkeling van specifieke rassen. Immers, de keuze voor een ras brengt met zich mee dat voor specifieke eigenschappen en daarmee specifiek gedrag wordt gekozen. Kennis over het gedrag van specifieke rassen kan benut worden voor het ontwerpen van rasspecifieke beheerssystemen, gericht op het behoud van een gesloten zode in het grasveld.

Het onderzoek beoogde de groei en morfologische ontwikkeling van individuele, vrijstaande planten en van planten in grasvelden van wit struisgras te bestuderen. In verschillende experimenten werden daarom de volgende aspecten nader onderzocht:

1. de uitstoelings*patronen* voor een sterk en een weinig uitstoelende populatie van wit struisgras;
2. de uitstoeling, stoloonontwikkeling en drogestofverdeling in een sterk uitstoelende en een weinig uitstoelende populatie;
3. de relatie tussen de zijspruitvorming van een zaailing en de spruitdichtheid van de grasveldzode voor een aantal rassen en selecties van wit struisgras;

4. het effect van zaaizaadhoeveelheid en ras op de ontwikkeling van de grasveldzode;
5. het verloop van de spruitdichtheid in de zode in de tijd onder veldomstandigheden;
6. de effecten van (het verwijderen van) een ijs- of sneeuwdek op het grasveld op de overleving van verschillende rassen en selecties.

In Deel I worden de resultaten beschreven van onderzoek in twee populaties van wit struisgras naar de volgende aspecten:

1. het verschijnen en de positie van zijspruiten, alsmede de snelheid van zijspruitvorming;
2. het verschijnen van stolonen, de lengte van de internodia en de totale lengte van de hoofdas;
3. individuele spruitdrooggewichten;
4. de groeistadia volgens de Schaal van West, die gebruikt wordt voor stoloonvormende planten.

Spruitleeftijd en drooggewicht werden gebruikt om de drogestoftoename per dag te bepalen.

De proeven werden uitgevoerd in klimaatkamers bij daglengtes van 16 of 8 uur en dag/nachttemperaturen van 20/15 °C en bij een stralingsintensiteit van 150 μmol m^{-2} s^{-1}. De planten werden gemeten tot 35 dagen na overplanten (DNO). In kassen werden experimenten uitgevoerd onder natuurlijke lichtintensiteiten bij lange en korte dag. De proeven bevatten een sterk ("UM67-10") en een zwak ("Emerald") uitstoelende populatie. Uitstoeling, stoloonlengte, internodiumlengte en drooggewicht werden bepaald tot aan 35 DNO. Een deel van de planten in het kasexperiment onder korte dag werd tot 42 DNO gehandhaafd om de stoloongroei nader te bestuderen.

De uitstoeling was onder alle proefomstandigheden sterker voor UM67-10. De verschillende groeistadia werden in alle proeven door beide populaties ongeveer gelijktijdig bereikt, maar UM67-10 bereikte eerder het stadium waarop de eerste zijspruit zichtbaar was dan Emerald. Stoloonaanleg en -groei waren voor beide populaties gelijkwaardig, maar Emerald produceerde langere stolooninternodia en stolonen. Bij korte dag waren de plantdrooggewichten lager, vooral vanwege een lager aantal zijspruiten en minder stoloongroei. De totale plantdrooggewichten waren voor beide populaties vergelijkbaar, maar de verdeling van de droge stof over de zijspruiten was verschillend.

Binnen een populatie vulden planten met meerdere zijspruiten een vertakkingseenheid meestal op voor het verschijnen van de volgende primaire zijspruit. Daarbij verwijst de vertakkingseenheid naar alle spruiten waarvan wordt voorspeld dat ze ontstaan tussen opeenvolgende primaire zijspruiten.

Stoloonontwikkeling aan een zijspruit resulteert in een hoger drooggewicht van de zijspruit. Stoloongroei was bij een daglengte van 8 uur vertraagd. Echter, er trad wel degelijk stoloongroei op onder omstandigheden van afnemende lichtintensiteiten in het kasexperiment bij korte dag, ook al vond de stolooninitiatie later plaats dan bij 16 uur daglengte.

In Deel II wordt onderzoek beschreven waarin onder gecontroleerde omstandigheden en in het veld, de plant- en zodeontwikkeling van wit struisgras werden bestudeerd door de volgende aspecten nader vast te stellen:

1. de verbanden tussen spruitvermeerdering van de zaailing enerzijds en de spruitdichtheid van de gevestigde grasveldzode anderzijds bij 15 rassen of selecties;
2. de effecten van zaaidichtheid en raskeuze op de vestiging van een zode van wit struisgras bij drie rassen;
3. de effecten van ras en groeiseizoen op de spruitdichtheid van de zode bij zes rassen of selecties;
4. de effecten van (de verwijdering van) een ijs- of sneeuwdek op de overwintering van de zode bij vijf rassen of selecties.

Er werden proeven uitgevoerd in klimaatkamers om de spruitvermeerdering van zaailingen van rassen van wit struisgras te onderzoeken onder omstandigheden zonder concurrentie. In veldproeven werden de effecten van ras op de spruitdichtheid onderzocht. Proeven met verschillende zaaizaadhoeveelheden werden zowel in de klimaatkamer als in het veld uitgevoerd. Grasveldzodes in de volle grond werden gedurende een periode van 3 jaar waargenomen om te bezien in hoeverre de spruitdichtheid werd beïnvloed door seizoen en ouderdom van de zode. Tenslotte werden proeven uitgevoerd om de effecten vast te stellen van een ijs- of sneeuwdek, of van de verwijdering ervan, op de overwintering van de zode.

De spruitvermeerdering van een zaailing op 35 DNO bleek goed gecorreleerd met de spruitdichtheid van een gevestigde zode, met r-waarden van 0.701 tot 0.826. Ook voor de lengte van stoloninternodia werd een goed verband aangetoond tussen de waarden bij de zaailing en die in een gevestigde zode (r-waarden van 0.725 tot 0.883). Derhalve is het mogelijk reeds bij zaailingen op spruitdichtheid van de grasveldzode te selecteren, als daarvoor zijspruiten worden gebruikt van 35 dagen oud, opgekweekt onder gecontroleerde groei-omstandigheden.

Bij de laagste zaaidichtheid bleken de planten groter te zijn (een hoger drooggewicht te hebben) en meer spruiten te bezitten. Er werden ras x zaaidichtheid interacties aangetoond, onder andere voor het aantal planten per m^2 en voor het drooggewicht per zijspruit. Lagere zaaidichtheden bleken te resulteren in een minder goede zodedichtheid. Desondanks waren de schattingen voor het risico van slijtage als gevolg van stress door het betreden door spelers voor de lagere zaaidichtheden vergelijkbaar met die voor de hogere zaaidichtheden. Derhalve zijn de huidige adviezen met betrekking tot de zaaidichtheden ook geschikt voor de getoetste rassen.

De spruitdichtheid van de zode nam gedurende de eerste drie jaren toe. De rassen en selecties die werden getoetst, bleken nauwelijks te verschillen ten aanzien van hun fluctuaties in spruitdichtheid over de seizoenen. In het voorjaar en de zomer namen de spruitdichtheden af. De spruitdichtheden in een zode waren in de herfst hoger dan half juli. De verschillen tussen de rassen waren gedurende de gehele onderzoeksperiode consistent.

Het vroeg verwijderen van een sneeuwdek bleek de overleving van de grasveldzode van sommige rassen in één van de drie proefjaren negatief te beïnvloeden. Opeenvolgende nacht minima van -15 °C volgend op 18 opeenvolgende dagen met temperaturen boven het vriespunt waren waarschijnlijk de belangrijkste oorzaak van dit effect. Het vroeg verwijderen van een sneeuwdek verhoogt het risico van schade.

De algemene discussie plaatst de gevonden resultaten in de context van de ontwikkeling van de plant of van de zode van grasveldgrassen. De fenologische ontwikkeling van wit struisgras wordt bediscussieerd, vooral in relatie tot de uitstoeling en de stoloongroei. De relatie tussen spruitdichtheid van de zode en het drooggewicht van de spruit wordt in verband gebracht met de potentiële resistentie tegen slijtage. De verdeling van de drogestof, het drooggewicht per zijspruit en de resistentie tegen slijtage worden vervolgens besproken in het licht van spruitvermeerdering onder veldomstandigheden en rasverschillen.

Vegetatieve uitstoeling in wit struisgras kan worden benut om onderscheid te maken tussen rassen, om kwaliteitsparameters van grasveldgrassen te schatten en als selectiecriterium in veredelingsprogramma's.

Curriculum Vitae

Douglas John Cattani was born on 28 September 1956 in Port Arthur, Ontario, Canada. He completed a Bachelors of Science in Agriculture in 1983 at the University of Manitoba, Winnipeg, Manitoba, Canada. He completed a Masters of Science at the University of Manitoba in 1987. He worked as a Genetic Resource Technician from January 1987 to February 1988 for dr. P.R. Dyck at Agriculture Canada in Winnipeg. In February 1988, he took up a position as Research Technician, Forages and Turfgrass at the University of Manitoba. In 1994, he became a Research Associate at the University of Manitoba working on turfgrass management, breeding and seed production. Since April 1997, he has been Research Chair, Turfgrass, at Nova Scotia Agricultural College, Truro, Nova Scotia, Canada.