# **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  $1 - 1^{\circ}$  and  $2 - 1^{\circ}$  tillers; similar dry weight was found in the high tillering UM67-10 population, and not in the low tiller producing Emerald population where the  $2 - 1^{\circ}$  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  $1 - 1^{\circ}$  and  $2 - 1^{\circ}$  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 intraplant competition. Stolons plant<sup>-1</sup> was correlated to tiller number plant<sup>-1</sup> 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)<sup>-1</sup> (existing tillers)<sup>-1</sup>) 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<sup>-1</sup> 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<sup>-1</sup> 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<sup>-1</sup> (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<sup>-1</sup> 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<sup>-1</sup> (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, 18<sup>th</sup> 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<sup>-1</sup> (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<sup>-1</sup> (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 wearstress 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.

#### LITERATURE CITED

- Beard, J.B., P.R. Rieke, A.J. Turgeon and J.M. Vargas Jr. 1978. Annual bluegrass (*Poa annua* L.) description, adaptation, culture and control. Michigan State Univ. Agric. Exp. Sta. Res. Rep. No. 352.
- Bos, B. 1999. Plant morphology, environment, and leaf area growth in wheat and maize. PhD. Thesis, Wageningen University, 149 pp.
- Brégard, A. and G. Allard 1999. Sink to source transition in developing leaf blades of tall fescue. New Phytol. 141:45-50.
- Brede, A.D. and J.M. Duich 1982. Cultivar and seeding rate effects on several physical characteristics of Kentucky bluegrass turf. Agron. J. 74:865-870.
- Bullock, J.M., B. Clear Hill and J. Silvertown 1994. Tiller dynamics of two grasses responses to grazing, density and weather. J. Ecology 82:331-340.
- Cao, W. and D.N. Moss 1989. Daylength effect on leaf emergence and phyllochron in wheat and barley. Crop Sci. 29:1021-1025.
- Casal, J.J., R.A. Sanchez and V.A. Deregibus 1986. The effect of plant density on tillering: The involvement of R/FR ratio and the proportion of radiation intercepted per plant. Envir. Exp. Bot. 26:365-371.
- Casal, J.J., V.A. Deregibus and R.A. Sanchez 1985. Variation in tiller dynamics and morphology in *Lolium multiflorum* Lam. Vegetative and reproductive plants as affected by differences in red/far-red irradiation. Annals Bot. 56:553-559.

Cattani, D.J. 1987. The breeding and turfgrass quality assessment of creeping bentgrass

(Agrostis stolonifera L.). M.Sc. Thesis, University of Manitoba, Winnipeg, MB.

- Christians, N. 1998. <u>Fundamentals of Turfgrass Management</u>, Ann Arbor Press, Inc. Chelsea, MI, USA., p. 12
- Crick, J.C. and J.P. Grime 1987. Morphology plasticity and mineral nutrient capture in two herbaceous species of contrasted ecology. New Phytol. 107:403-414.
- Esau, K. 1977. Anatomy of Seed Plants. 2nd Edition, John Wiley and Sons, Inc., U.S.A., p.43.
- Hunt, R., A.O. Nichols and S.A. Fathy 1987. Growth and root-shoot partitioning in eighteen British grasses. OIKOS 50:53-59.
- Jonsdottir, G.A. 1991. Tiller demography in seashore populations of Agrostis stolonifera, Festuca rubra and Poa irrigata. J. Veg. Sci. 2:89-94.
- Kasperbauer, M.J. and D.L. Karlen 1986. Light-mediated bioregulation of tillering and photosynthate partitioning in wheat. Physiol. Plant. 66:159-163.
- Kik, C., J. Van Andel and W. Joenje 1990. Life-history variation in ecologically contrasting populations of Agrostis stolonifera. J. Ecology 78:962-973.
- Lush, W.M., 1990. Turf growth and performance evaluation based on turf biomass and tiller density. Agron. J. 82:505-511.
- Madison, J.H. 1966. Optimum rates of seeding turfgrasses. Agron. J. 58:441-443.
- Madison, J.H. 1962. Turfgrass ecology. Effects of mowing, irrigation and nitrogen treatments of Agrostis palustris Huds., 'Seaside' and Agrostis tenuis Sibth., 'Highland' on population rooting and cover. Agron J. 54:407-412.
- Neuteboom, J.H. and E.A. Lantinga 1989. Tillering potential and relationship between leaf and tiller production in perennial ryegrass. Annals Bot. 63:265-270.
- Ong, C.K. 1978. The physiology of tiller death in grasses. 1. The influence of tiller age, size and position. J. Brit. Grass. Soc. 33:197-203.
- Ryle, G.J.A. 1974. A comparison of leaf and tiller growth in seven perennial grasses as influenced by nitrogen and temperature. J. Brit. Grass. Soc. 19:281-290.
- Shildrick, J.P. and C.H. Peel 1984. Shoot numbers, biomass and sheer strength in smoothstalked meadowgrass (Poa pratensis L.) J. Sports Turf. Res. Inst. 60:66-72.
- Tallowin, J.R.B., J.H.H. Williams and F.W. Kirkham 1989. Some consequences of imposing different continuous-grazing pressures in the spring on tiller demography and leaf

growth. J. Agric. Sci., Camb. 112:115-122.

- Tompkins, D.K., C.J. Bubar and J.B. Ross 1996. Physiology of low temperature injury with an emphasis on crown hydration in *Poa annua* L. and *Agrostis palustris*. 1996 Annual Report of the Prairie Turf. Res. Centre, p. 40-49.
- Trenholm, L.E., R.R. Duncan and N. Carrow 1999. Wear tolerance, shoot performance, and spectral reflectance of seashore paspalum and bermudagrass. Crop Sci. 39:1147-1152.
- Vine, D.A. 1983. Sward structure changes within a perennial ryegrass sward: Leaf appearance and death. Grass and Forage Sci. 38:231-242.
- van Loo, E.N. 1992. Tillering, leaf expansion and growth of plants of two cultivars of perennial ryegrass grown using hydroponics at two water potentials. Annals Bot. 70:511-518.
- Wilson, R.E. and A.S. Laidlaw 1985. The role of the sheath tube in the development of expanding leaves in perennial ryegrass. Annals App. Biol. 106:385-391.

# 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;
- study tillering, stolon development and dry matter partitioning in a high and a low tillering population;
- 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;
- 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<sup>-1</sup>.

Studies were carried out under 16 h and 8 h days in growth cabinets at temperatures of  $20/15^{\circ}$ C with light at 150 µmol m<sup>-2</sup> sec<sup>-1</sup>. 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.

turf tiller density as affected by six cultivars or lines and growing season.

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<sup>-1</sup> were obtained with the lowest seeding rate. Cultivar x seeding rate interactions were found including for plants m<sup>-2</sup> and dry weight tiller<sup>-1</sup>. 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<sup>-1</sup> 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 binnenplant 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;
- de uitstoeling, stoloonontwikkeling en drogestofverdeling in een sterk uitstoelende en een weinig uitstoelende populatie;
- de relatie tussen de zijspruitvorming van een zaailing en de spruitdichtheid van de grasveldzode voor een aantal rassen en selecties van wit struisgras;

- het effect van zaaizaadhoeveelheid en ras op de ontwikkeling van de grasveldzode;
- 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:

- het verschijnen en de positie van zijspruiten, alsmede de snelheid van zijspruitvorming;
- het verschijnen van stolonen, de lengte van de internodia en de totale lengte van de hoofdas;
- 3. individuele spruitdrooggewichten;
- 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  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>. 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 126 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:

- de verbanden tussen spruitvermeerdering van de zaailing enerzijds en de spruitdichtheid van de gevestigde grasveldzode anderzijds bij 15 rassen of selecties;
- de effecten van zaaidichtheid en raskeuze op de vestiging van een zode van wit struisgras bij drie rassen;
- de effecten van ras en groeiseizoen op de spruitdichtheid van de zode bij zes rassen of selecties;
- 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 stolooninternodia 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.