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.

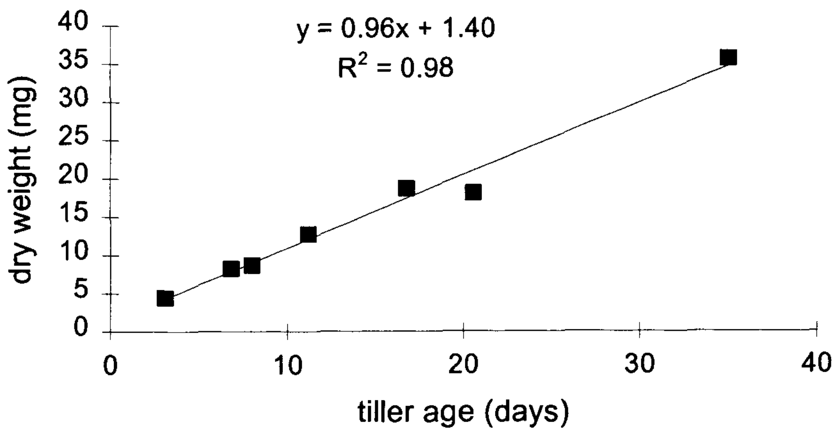
	n		Tiller Age		Dry Weight		Dry Weight Day^{-1}	
Population	A	B	A	B	A	B	A	B
			d		mg			
Main Stem	10	10	42.0	42.0	41.68 a †	30.01 a †	0.99 a†	0.71 abc†
1-1°	10	10	17.8 a†	23.3 a†	18.09 b	12.36 b	0.94 a	0.56 bc
2-1°	10	10	11.9 b	18.7 b	15.07 bc	13.53 b	1.17 a	0.72 ab
3-1°	8	10	8.3 bc	12.8 c	10.56 bc	10.74 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).

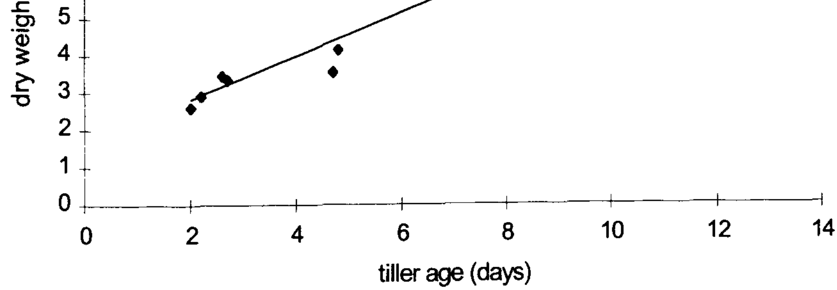
Tiller Order Comparisons

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).

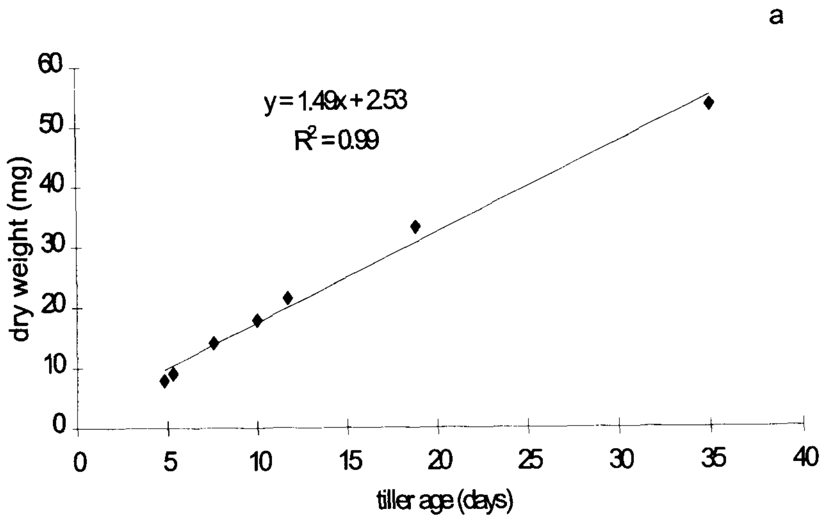
A separate analysis was carried out on GRLD study to determine the contribution of individual main stem branches (primary tillering systems (PS)) to above-ground dry matter accumulation. The 1st PS refers to tillers arising from and including the 1 - 1° tiller, 2nd PS to 2 - 1° tiller and its descendants,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

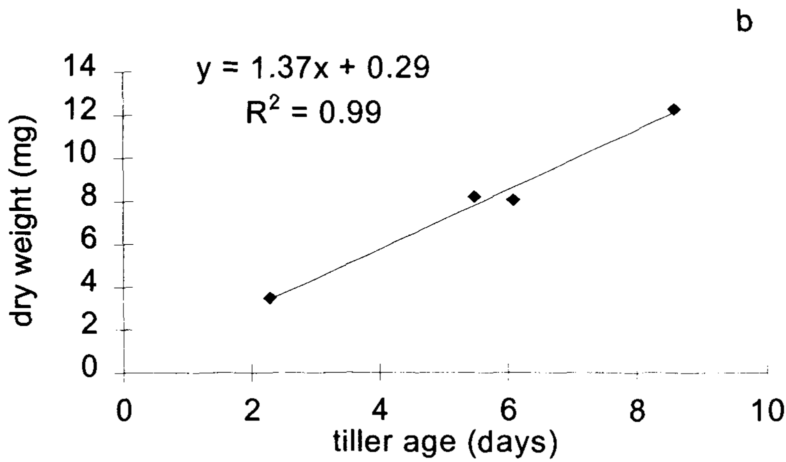


b



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.

	Pre Stolon		Nodes 1 to 2		Nodes 2 to 3		Nodes 3 to 4		Nodes 4 to 5	
Gross Tiller Appearance Rate (tillers day^{-1})										
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 6^{th} PS was similar in weight to the 5^{th} PS (Table 3.7) for UM67-10. Both consisted of a single tiller, and as the 5^{th} 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 '18^{th} 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