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 "18th 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 18th 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.

		Growth room Studies									
		Long Day						Short Day			
Source of variance	df	Tillers	Leaves	Dead leaves	Stolons	Stolon Length	Internode	df	Tillers	Leaves	Dead Leaves
		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).

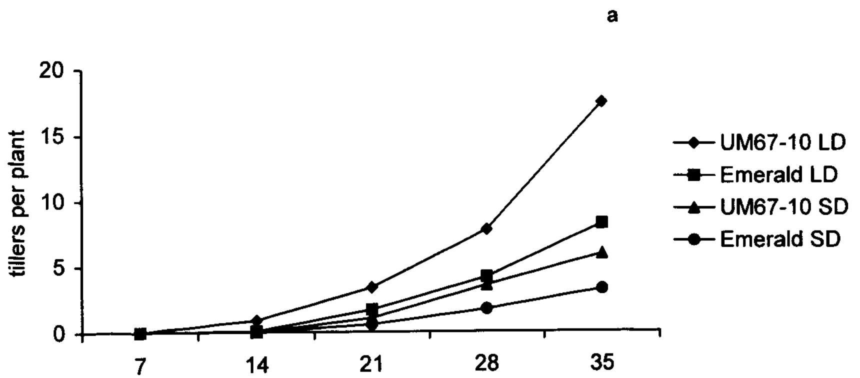
The growth stage curves indicate that UM67-10 reached the tillering stage faster than Emerald under both the LD and SD, however, the stolon elongation was visible at approximately the same time under the LD, (day 25) (Figure 2.2).

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)).



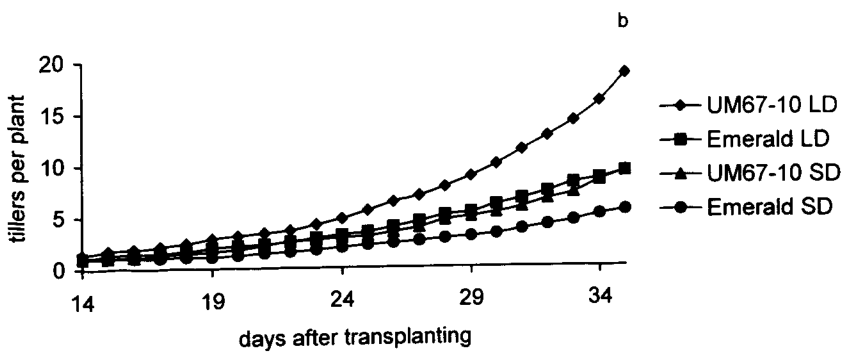


Figure 2.1. Tillers plant^{-1} during initial 35 days of growth after transplanting (DAT) for Emerald and UM67-10 creeping bentgrass grown under long- and short-day conditions. A) greenhouse (measured weekly), B) growth cabinet (measured daily from 14 DAT).

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.

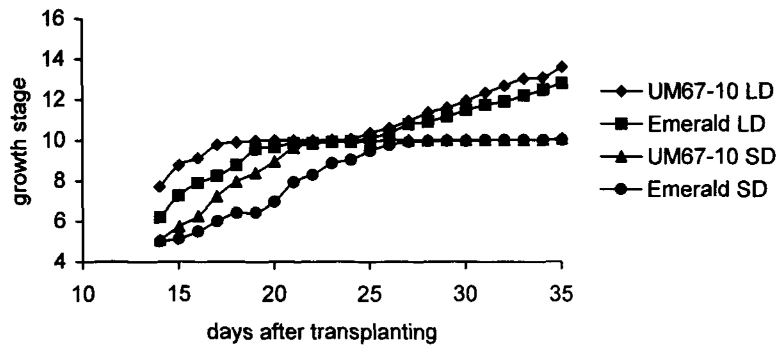


Figure 2.2. Growth stage of Emerald and UM67-10 creeping bentgrass grown under long- and short-day conditions in the growth cabinet.

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.

		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
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.

		Low Tillering Plants								High Tillering Plants							
Branch Unit	**Tiller**	**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**	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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