Tiller size/density compensation in grazed Tifton 85 bermudagrass swards[1]

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Abstract – The objective of this study was to evaluate the occurrence of the tiller size/density compensation mechanism in Tifton 85 bermudagrass swards grazed by sheep under continuous stocking. Treatments corresponded to four sward steady state conditions (5, 10, 15, and 20 cm of sward surface height), maintained by sheep grazing. The experimental design was a complete randomized block with four replicates. Pasture responses evaluated include: tiller population density, tiller mass, leaf mass and leaf area per tiller, and herbage mass. Tiller volume, leaf area index, tiller leaf/stem ratio, and tiller leaf area/volume ratio were calculated and simple regression analyses between tiller population density and tiller mass were performed. Measurements were made in December, 1998, and January, April, and July, 1999. The swards showed a tiller size/density compensation mechanism in which high tiller population densities were associated with small tillers and vice-versa, except in July, 1999. Regression analyses revealed that linear coefficients were steeper than the theoretical expectation of -3/2. Increments in herbage mass were attributable to increases in tiller mass in December and January. Leaf area/volume ratio values of Tifton 85 tillers were much lower than those commonly found for temperate grass species.

Index terms: *Cynodon*, leaf area index, mass, density, plant morphology.

Compensação tamanho/densidade populacional de perfilhos em pastos de Tifton 85

Resumo – O objetivo deste trabalho foi avaliar a ocorrência do mecanismo de compensação tamanho/densidade populacional de perfilhos em pastagens de Tifton 85 (*Cynodon* spp.). Os tratamentos corresponderam a quatro condições de pasto (5, 10, 15 e 20 cm de altura), mantidas constantes por ovinos em regime de lotação contínua e taxa de lotação variável. O delineamento experimental foi o de blocos completos casualizados com quatro repetições. As variáveis densidade populacional de perfilhos, massa por perfilho, massa de folha por perfilho, área foliar por perfilho, massa de forragem, volume por perfilho, índice de área foliar, relação folha/haste e razão entre área foliar/volume do perfilho (R) foram avaliadas. Além disso, regressões simples foram realizadas entre densidade populacional de perfilhos e massa por perfilho. As medições foram realizadas em dezembro de 1998 e janeiro, abril e julho de 1999. Os resultados mostraram que pastagens de *Cynodon* spp. apresentaram um mecanismo de compensação tamanho/densidade populacional de perfilhos, em que maiores densidades populacionais estiveram associadas a perfilhos pequenos e vice-versa, exceto em julho de 1999. Análises de regressão mostraram coeficientes lineares menores que a expectativa teórica de -3/2. Aumentos em massa de forragem em dezembro e janeiro resultaram de aumentos em massa por perfilho. Os valores de R foram menores que aqueles encontrados para plantas de clima temperado, indicando um maior nível de integração clonal entre plantas de Tifton 85.

Termos para indexação: *Cynodon*, índice de superfície foliar, massa, densidade, morfologia vegetal.

Introduction

Defoliated grass swards exhibit tiller size/density compensation (SDC) with change in defoliation height (Bircham & Hodgson, 1983; Davies, 1988; Matthew et al., 1995; Hernández Garay et al., 1999). As a consequence, short swards are characterized by a large population of small tillers and tall swards by a smaller population of large tillers (Bircham & Hodgson, 1983; Grant at al., 1983). This pattern of self-regulation can be viewed as means by which pastures regulate leaf area index (LAI) in response to change in defoliation height, since tiller population density (TPD) is the component of the sward LAI in which changes in sward structure can be readily expressed (Matthew et al., 2000).

In grazed swards, however, there are limits to phenotypic plasticity represented by the maximum tiller size and the maximum tiller population density sustainable for a given species in a particular environment (Chapman & Lemaire, 1993). Additionally, under very severe grazing, some grasses may lack organic reserves for bud release to increase tiller population density and pastures may collapse (Matthew et al., 1995).

This tiller size/density compensation issue has been discussed in terms of the -3/2 self-thinning rule originally described by Yoda et al. (1963), according to whom tiller mass and tiller population density would be inversely correlated, following a linear regression line with a -3/2 slope when considered in a logarithm scale. This line has also been called the species boundary line, and would represent the ceiling sward LAI for a given environment and upon which sward LAI would be constant (Chapman & Lemaire, 1993; Matthew et al., 1995; Hernández Garay et al., 1999). However some authors (Matthew et al., 1995; Hernández Garay, 1999) have observed a systematic lack of fit between the field data and the theoretical expectation of -3/2, with the observed slope being steeper than -3/2. Sackville Hamilton et al. (1995) showed that a self-thinning slope of -3/2 is a theoretical expectation where LAI and a measure of plant leaf area/plant size ratio, R, remain constant. Since swards grazed at different heights vary systematically in LAI (Bircham & Hodgson, 1983; Matthew et al., 1995; Fagundes et al., 1999), it ensues

that SDC in defoliated swards should follow slopes different from -3/2. This relationship has been studied recently for some temperate species, but for tropical grasses there are few data available.

The objective of this study was to evaluate the occurrence of the tiller size/density compensation in Tifton 85 bermudagrass swards grazed by sheep under continuous stocking.

Material and Methods

The experiment was carried out at Unidade Experimental de Plantas Forrageiras (UEPF), Departamento de Zootecnia, Escola Superior de Agricultura Luiz de Queiroz, Universidade de São Paulo, Piracicaba, SP, Brazil (22°42' S, 47°38' W, 546 m above sea level). Detailed measurements of sward status and SDC related variables were performed on four occasions during the experimental period: Dec. 15, 1998 - spring; Jan. 25, 1999 - summer; Apr. 7, 1999 - autumn and July 4, 1999 - winter.

The experiment was set up on a Kandiufalfic Eutrudox (United Sates, 1990) with the following chemical characteristics: pH (CaCl$_2$), 5.4; organic matter, 37 g dm^{-3}; P, 99 mg dm^{-3}; K, 4.6 mmol$_c$ dm^{-3}; Ca, 75 mmol$_c$ dm^{-3}; Mg, 26 mmol$_c$ dm^{-3}; H+Al, 30 mmol$_c$ dm^{-3}; sum of bases, 106 mmol$_c$ dm^{-3}; cation exchange capacity, 136 mmol$_c$ dm^{-3}; and base saturation, 78%. No P fertilizer or lime was applied either at establishment or throughout the experimental period.

Pastures were established vegetatively in March 1996. In 1997, 150 kg ha^{-1} of N was applied as ammonium sulphate. In 1998 pastures received 40 kg ha^{-1} of N in January, July and September, 50 kg ha^{-1} in October and 25 kg ha^{-1} in December. For uniformity, all swards were cut to three cm height at the beginning of the experiment in March 1998. Sheep were then introduced to experimental units in May, when the target sward surface heights were reached. In 1999 nitrogen fertilizer was applied twice: 50 kg ha^{-1} of N in February and 75 kg ha^{-1} in March. Nitrogen application rates and timings were planned to generate enough herbage accumulation to maintain at least two animals per experimental unit throughout the experimental period (December 15, 1998 to July 4, 1999). Present and historical (80-years average) climatic conditions for the experimental site are presented in Table 1.

Treatments of sward surface height (SSH) were assigned to 400 m^2 experimental units (plots) in a complete randomized block design with four replications. The Tifton 85 bermudagrass was allowed to grow to the SSH of 5, 10, 15 or 20 cm before grazing sheep were added to

maintain swards at the target SSH through continuous stocking with variable stocking rate. Sward height was monitored twice a week by 20 sward stick readings per plot (Frame, 1981). Animals were either added or removed from experimental units when swards were 20% above or below target SSH, respectively.

For herbage mass evaluation (kg m^{-2}), two 0.25 m^2 quadrats were used per plot. Quadrats were placed on sites representing the target SSH and the herbage was cut to ground level using electric shears. Samples were conditioned in plastic bags and stored in a cold room. Each sample was washed to remove soil and dung contamination and dried in a forced draught oven at 65ºC for 48 hours prior to weighing.

Measurements related to individual tiller traits were made in an 8.5x14.7 cm quadrat. Quadrats were placed on sites representing the target SSH and two samples per plot were cut to ground level using scissors and razor blades. A high degree of homogeneity in SSH was achieved, particularly in short swards. Even so, there was some degree of variability in SSH across individual experimental units. To ensure measurements were related to the intended sward state conditions, sampling areas were selected by using a sward stick to place quadrats on sites representing the target SSH. The cut material was placed in plastic bags previously wetted and conditioned in a styrofoam box

with ice to reduce plant dehydration and respiration. All samples were taken to the laboratory and stored in a cold room (2°C).

Twenty tillers were selected at random from the quadrat samples. These were weighed and the average fresh mass per tiller calculated. After weighing, all green leaf laminae were detached from the tiller axis and their total area measured using a LI-3100 leaf area meter. Values were used to calculate the average leaf area per tiller. Leaf laminae were then placed into small paper bags and dried in a forced draught oven at 65ºC for 48 hours. The same procedure was used for the combined stem (stem + leaf sheath) and senescent leaf material. After drying, samples were weighed and the average live lamina dry mass and stem/senescent material per tiller calculated. Total dry mass per tiller was calculated accordingly.

Tiller population density (TPD) was obtained through the following calculation:

TPD = HM (kg m^{-2})/TM (kg tiller^{-1})

where HM is the herbage mass and TM is the individual tiller mass.

Sward Leaf Area Index (LAI) was determined according to the following calculation:

LAI = TPD × LAT

where TPD is the tiller population density (tillers m^{-2}) and LAT is the leaf area per tiller (m^2 tiller^{-1}).

Table 1. Average monthly air temperatures (maximum, minimum and mean), rainfall and sunshine hours from November, 1998 to July, 1999 and the 80-year averages.

Month/year	Maximum	Minimum (^{o}C)	Mean	Rainfall (mm)	Sunshine (h/day)
November					
1998	30.0	16.4	23.2	26.6	7.8
80-year mean	29.6	16.7	23.1	130.0	7.4
December					
1998	30.0	19.2	24.6	292.6	6.1
80-year mean	29.6	18.1	23.9	200.2	6.6
January					
1999	31.4	19.0	25.2	210.8	7.7
80-year mean	30.0	18.2	24.0	142.4	6.8
February					
1999	30.7	20.0	25.4	198.3	5.4
80-year mean	30.2	19.0	24.6	185.9	6.5
March					
1999	31.4	19.0	25.2	210.8	7.7
80-year mean	30.0	18.2	24.0	142.4	6.8
April					
1999	28.5	15.2	21.9	89.0	8.1
80-year mean	28.3	15.4	21.8	64.8	7.5
May					
1999	25.4	11.2	18.3	51.3	7.4
80-year mean	26.1	12.1	19.1	52.7	7.2
June					
1999	23.9	11.0	17.4	68.6	6.0
80-year mean	24.9	10.3	17.6	44.5	7.1
July					
1999	26.8	12.0	19.2	2.7	6.7
80-year mean	25.3	9.5	17.4	26.8	7.8

Source: USP/ESALQ, Departamento de Ciências Exatas Files.

Average tiller volume was estimated by a technique based on the immersion of tillers in liquids with known apparent densities. Water ($1,000$ kg m^{-3} at room temperature) and a lubricant oil (902 kg m^{-3} at 20°C) were used as references. Tillers floated in water but sank in oil, so it was assumed that tiller apparent density was around 950 kg m^{-3}. This degree of precision in measuring tiller apparent density was considered sufficiently robust, because it represented a maximum 5% error in the final tiller volume estimates. Average volume per tiller was calculated as follow:

$$TV (m^3) = TFM/TAD$$

where TFM is the tiller fresh mass (kg) and TAD is the tiller apparent density.

The tiller leaf area/volume ratio (R) proposed by Sackville Hamilton et al. (1995) was calculated as follow:

$$R = LAT^{3/2}/TV$$

where LAT is the leaf area per tiller (m^2) and TV is the tiller volume (m^3). LAT has the exponent 3/2 to make the area/volume ratio dimensionless, so giving a measure of tiller shape (Sackville Hamilton et al., 1995).

Linear regressions based on Ordinary Least Square between tiller mass (TM) and tiller population density (TPD) were generated using treatment means, which corresponded to four sets of paired data for each evaluation period. Following procedure described by Sackville Hamilton et al. (1995), slopes generated by Ordinary Least Square analysis were divided by the correlation between log(TM) and log(TPD), resulting in the Reduced Major Axis (RMA) slopes, which were used for treatment comparisons.

Estimates of the correction factors for the deviations between the actual regression lines and the -3/2 line for each of the four evaluations were made according to Matthew et al. (1995):

$$C_a = \Delta \log(LAI^{3/2})/\Delta \log(TPD)$$

and

$$C_r = \Delta \log(R)/\Delta \log(TPD)$$

where LAI is the sward leaf area index; TPD is the tiller population density (number m^{-2}) and R is the tiller leaf area/volume ratio.

C_a and C_r were calculated as being the slopes for the regressions between sward LAI and TPD, and R and TPD, respectively. According to Matthew et al. (1995), the perpendicular distance between any given point and the -3/2 line placed below the plotted points can be used as a sward productivity index. In this experiment the perpendicular distance between the plotted points for log(TM) x log(TPD) and the -3/2 line (constant LAI and R) was calculated.

Data were analysed using PROC GLM (General Linear Models) and PROC REG from the statistical package SAS (Statistical Analysis System). Analysis of variance was performed using the Repeated Measures option since all variables were measured sequentially (December, January, April and July) throughout the experimental period, and comparisons between treatment means were performed using LSMEANS.

Results and Discussion

Although ANOVA results revealed no significant time of the year effect, there was an increase in tiller population density (TPD) from December to January (Table 2). The lower population density observed in December was probably a consequence of a dry spell in November (Table 1). In December, when rainfall returned, population increased. Korte (1986) and Davies (1988) related the increase in tiller population in summer to increased light and increased canopy LAI (Fagundes et al., 1999). The data from December, January and April show a pattern for TPD decreasing with the increase of sward surface height (Table 2). In July there was a rosette formation that changed this trend of TPD pattern. These results are consistent with data generated from temperate forages, where higher TPD were associated with more severely defoliated swards, but where TPD can fall under extremely severe defoliation (Bircham & Hodgson, 1983; Matthew et al., 1995; Hernández Garay et al., 1999).

In July, a reverse trend of increasing TPD with increasing sward surface height over the 10 cm to 20 cm height range was observed. This is explained by the formation, at greater cutting heights, of crowns containing numerous small tillers originating from the nodes of decapitated reproductive stems (Carnevalli & Silva, 1999).

Mortality in a self-thinning stand occurs because competition for light (Lonsdale & Watkinson, 1982; Sackville Hamilton et al., 1995). Fagundes et al. (1999) observed that in the 5 cm swards around 62% of the incident light reached the soil surface in September, 1998, and increased to 95% in December, 1998. By contrast, in pastures kept at 20 cm, the corresponding values were around 18% in August, 1998 and, in some situations, approximately 3%. The low amount of incident light reaching the soil surface is a factor associated with reduced tillering in laxly defoliated swards (Langer, 1979); also is the

reduced red/far red ratio of the available light within sward canopy (Casal et al., 1985). In addition, the leaves at the base of tillers growing in an environment with reduced light availability have a major reduction in photosynthetic activity, potentially leading to a negative C balance (Parsons et al., 1983) and accelerated senescence/death of leaves and tillers that support them (Sackville Hamilton et al., 1995).

According to Chapman & Lemaire (1993), grass species are limited in the range over which they exhibit plasticity through increases in tiller population density with reductions in sward surface height (SSH), and these limits arise because of the inability of certain grasses to reduce sheath length to maintain leaf material below a particular cutting height. This plasticity limit was also discussed by Matthew et al. (1995), and was found to be around 2 cm SSH for *Lolium perenne*, but varying with season, in which high defoliation intensity can, under certain circumstances, restrict tillering activity in grass plants. In April, swards maintained at 5 cm had a lower TPD than the ones at 10 cm, indicating that 5 cm SSH was below the plastic limit for Tifton 85. This could be related to the reproductive phase observed on most swards at that time of the year.

There was an increase in individual tiller mass, leaf mass, and volume as SSH increased from 5 to 20 cm (Table 2). These results corroborate those

reported for temperate forage plants in which taller swards had higher values for tiller mass, leaf mass per tiller (Matthew et al., 1995; Hernández Garay et al., 1999) and tiller volume (Matthew et al., 1995) than shorter ones. The highest values for tiller mass, leaf mass per tiller and tiller volume were observed in December (Table 2), a likely consequence of the low rainfall in November (Table 1), since other growth factors such as light availability, mineral nutrients and temperature were not limiting, and plants probably continued to accumulate carbon via photosynthesis but did not generate growth to commensurate with that accumulation.

Herbage mass measured in December and July was higher than that in January and April (Table 3). Values of herbage mass can be viewed as a result of the sum of the mass of all individual tillers per square meter. Thus, a reduced tiller population density observed in taller swards in December and January was compensated by a proportionately higher tiller mass, which ultimately determined the higher values of herbage mass (Table 2). Volenec & Nelson (1983) recognized that tiller mass can be more important than tiller population density in determining sward productivity, or vice-versa, depending on the circumstances. Tiller population density was more important than tiller mass as a determinant of herbage mass particularly for the 10 cm SSH in April, where

Table 2. Tiller population density, tiller mass, leaf mass per tiller and tiller volume in Tifton 85 pastures continuously stocked by sheep.

Month	Sward surface height (cm)				Significance level	Mean±SEM[1]
	5	10	15	20		
	Tiller population density (tillers m^{-2})					
Dec.	16,320	13,350	8,910	7,170	*	11,440±1,360
Jan.	17,730	14,850	14,230	13,550	ns	15,090±2,380
Apr.	10,930	17,415	16,260	13,760	*	14,590±2,520
July	18,820	9,300	13,360	21,330	ns	15,700±4,940
	Tiller mass (mg $tiller^{-1}$)					
Dec.	22.8	40.8	84.9	123.9	**	68.1±13.23
Jan.	12.3	26.6	36.2	54.9	**	2.5±7.88
Apr.	20.1	26.2	34.8	59.5	*	35.1±6.62
July	20.8	51.5	52.7	67.8	ns	48.2±19.36
	Leaf mass per tiller (mg $tiller^{-1}$)					
Dec.	9.1	15.3	27.6	35.2	***	21.8±1.61
Jan.	5.9	12.3	15.1	21.0	**	3.6±2.21
Apr.	8.4	9.6	13.7	20.5	**	13.1±1.74
July	9.8	21.3	24.5	21.7	*	19.3±4.62
	Tiller volume (cm^3 $tiller^{-1}$)					
Dec.	0.133	0.238	0.497	0.725	***	0.398±0.077
Jan.	0.072	0.155	0.211	0.321	*	0.189±0.046
Apr.	0.124	0.191	0.319	0.815	*	0.362±0.239
July	0.121	0.301	0.308	0.396	ns	0.281±0.113

[1]SEM: standard error of the mean. nsNo-significant. *, ** and ***Significant at 0.05, 0.01 and 0.001 probability levels, respectively.

swards were below their plastic limit when kept at 5 cm SSH.

The highest values of leaf area per tiller were observed in December but there was no statistically significant time of the year effect on sward leaf area index (LAI) (Table 3). Among all the structural characteristics that determine LAI, TPD allows for a greater flexibility of plants for adjusting to different defoliation regimes, and this is why LAI is optimized in intensively grazed swards through a high population of small tillers. Conversely, in laxly-grazed swards, optimization of LAI is achieved through a low population of bigger tillers (Matthew et al., 2000). Despite the highest values of leaf area per tiller reached in December, LAI did not follow the same pattern because TPD tended to increase during the season as leaf area per tiller decreased, resulting in a fairly constant sward LAI throughout the experiment.

With the exception of July, when the normal pattern of size/density compensation with increasing sward height was reversed by the formation of rosettes, leaf area per tiller increased with increase in SSH, and was the principal contributor to a strong positive correlation between LAI and SSH (Table 3).

Tiller leaf/stem ratio was generally higher at low SSH than at high SSH, and was significant (P<0.01) in December and January. Conversely, the measure of tiller geometry, R, tended to be highest at higher SSH, although this trend was not statistically significant. The reason for the contrasting values of the two measures of tiller geometry was explained by Hernández Garay et al. (1999) in their work with

miniature swards of perennial ryegrass. They also found an increase in R and decrease in tiller leaf/pseudostem ratio at high SSH. Leaf/pseudostem ratio approximately reflects simple area/volume ratio, which decreases as size increases for any given geometrical shape. The conversion to a dimensionless ratio, R, by raising leaf area to the 3/2 power removes the size effect, and reveals that larger tillers in fact tend to have proportionally longer leaves and shorter stems than smaller tillers simply scaled up in size. Additionally, increments in SSH can lead to decreased tiller leaf/stem ratios simply because in order to support the mass of leaves, stem diameter is altered proportionally to the strength required to support them, and not isometrically to the organ mass (McMahon, 1973; McMahon & Kronauer, 1976; Niklas, 1994). However, if this was the dominant mechanism controlling tiller geometry, then R would decrease rather than increase with increasing tiller size, indicating that this effect can be assumed to be minor.

The overall mean value for R was around 15 (Table 4). Hernández Garay et al. (1999) reported R values around 50 for perennial ryegrass and those values became higher as SSH increased, indicating that perennial ryegrass grew by developing proportionally more leaf length than stem length per tiller, as discussed above. In order to visualize what this difference in R means, the R value for a sphere (9.45) can be considered. In calculating R, the surface area of pseudostem is not taken into account and only one side of the leaf is considered, but a tiller of

Table 3. Herbage mass, leaf area per tiller and sward leaf area index in Tifton 85 pastures continuously stocked by sheep.

Month	Sward surface height (cm)				Significance level	Mean±SEM[1]
	5	10	15	20		
Herbage mass (kg dm m^{-2})						
Dec.	0.37	0.51	0.68	0.84	***	0.60±0.05
Jan.	0.20	0.37	0.48	0.66	***	0.43±0.03
Apr.	0.21	0.42	0.53	0.75	***	0.48±0.02
July.	0.37	0.46	0.62	0.79	**	0.56±0.05
Leaf area per tiller (cm^2 tiller^{-1})						
Dec.	1.19	1.96	3.82	5.01	***	2.81±0.47
Jan.	1.08	1.76	2.02	3.38	**	2.06±0.37
Apr.	1.36	1.47	2.31	3.24	**	2.10±0.28
July.	1.39	3.17	3.46	2.64	*	2.66±0.53
Leaf area index						
Dec.	1.94	2.54	3.52	3.63	ns	2.90±0.77
Jan.	1.90	2.48	2.74	4.16	***	2.82±0.28
Apr.	1.46	2.47	3.46	4.26	***	2.91±0.37
July	2.50	2.89	4.48	3.83	*	3.42±0.60

[1]SEM: standard error of the mean. nsNo-significant. *, ** and ***Significant at 0.05, 0.01 and 0.001 probability levels, respectively.

Cynodon spp. has only about 2 to 5 times the leaf area as the surface of a sphere of the same volume, whereas a tiller of *Lolium* has several times that leaf area. A low R value implies a high carbon cost for producing new leaf area, and such a plant might be expected to be uncompetitive. However, a plant with lower R value could maintain competitiveness having a higher level of clonal integration, since the R value of an object which is a cluster of similar modules is much greater than the R value of a module in isolation (Matthew et al., 1995). Those authors showed that the R value in alfalfa (which has a high degree of integration among shoots since they are all generated from common crowns) is higher when calculations are based on the whole plant rather than on single shoots by a factor of $n^{1/2}$, where n is the number of shoots per crown. Table 4 also presents R values assuming an hypothetical clonal integration among four tillers for Tifton 85. Under this assumption, R values increased two-fold in all situations and became closer to values reported by Hernández Garay et al. (1999) for perennial ryegrass. Thus, the contrasting R values for *Cynodon* spp. measured in this experiment and for *Lolium* measured by Matthew et al. (1995) and Hernández Garay et al. (1999) lead to the hypothesis that a higher R value or a higher degree of clonal integration are alternative strategies available to a plant to increase competitiveness.

An additional advantage of clonal integration that has been pointed by Chapman et al. (1992) is that species that display strong physiological integration, a highly tillered or highly branched plant structure, should have an advantage because there are more intermodule linkages and, therefore, more intermodule resource fluxes would operate to buffer whole-plant growth against localized environmental variation (e.g., partial defoliation) affecting only part of a clone. This is in agreement with field observations of this experiment where a new cluster of tillers was formed along a stolon at regular intervals of three phytomers (node with roots and a daughter tiller followed by two successive leaves). Description of this pattern of growth and development of *Cynodon* grasses has not been found previously in the literature. Another consequence of this strategy is that Tifton 85 pastures may acquire competitive advantage through clonal integration of tillers. The pattern of growth observed in field conditions would suggest that a first leaf would support root development, a second, the tiller development and a third, the stolon internode elongation (Sbrissia et al., 2001), revealing another potential fundamental difference in growth strategy between Tifton 85 and perennial ryegrass. Further studies under controlled conditions are necessary, however, to elucidate the degree and nature of this integration in order to allow a better understanding of plant persistence, competitive ability and productivity.

Simple regression analyses between tiller mass and population density from December, January and April revealed significant functional linear relationships (Table 5). The fitted slopes (β_1) were steeper than the theoretical expectation of -3/2. According to Sackville Hamilton et al. (1995), a -3/2

Table 4. Tiller leaf/stem ratio, tiller leaf area/volume ratio (R), and tiller leaf area/volume ratio assuming a clonal integration of four tillers (R1) in Tifton 85 pastures continuously stocked by sheep.

Month	Sward surface height (cm)				Significance level	Mean±SEM[1]
	5	10	15	20		
	Tiller leaf/stem ratio:					
Dec.	0.73	0.81	0.55	0.46	**	0.64±0.13
Jan.	0.97	1.07	0.76	0.68	**	0.87±0.13
Apr.	0.85	0.69	0.68	0.63	ns	0.71±0.11
July	0.91	0.81	1.27	0.83	ns	0.96±032
	Single tiller leaf area/volume ratio (R)					
Dec.	9.94	12.50	16.58	18.19	ns	14.30±4.60
Jan.	18.79	17.24	13.88	19.74	ns	17.41±4.09
Apr.	13.14	9.95	14.66	14.68	ns	13.11±2.27
Juy	13.70	19.54	22.88	12.46	*	17.15±3.05
	Cloned tiller leaf area/volume ratio (R1)					
Dec.	19.88	25.00	33.16	36.38	ns	28.60±9.20
Jan.	37.58	34.48	27.76	39.48	ns	34.82±8.18
Apr.	26.28	19.90	29.32	29.36	ns	26.22±4.54
July	27.40	39.04	45.76	24.92	*	34.30±6.10

[1]SEM: standard error of the mean. nsNo-significant. *, ** and ***Significant at 0.05, 0.01 and 0.001 probability levels, respectively.

line would be a theoretical expectation when LAI and R remained constant. Since LAI varied with SSH (Table 4), it was expected that the slopes would be different from -3/2. Hernández Garay et al. (1999) also found slopes steeper than -3/2 (close to -5/2) for perennial ryegrass swards.

The slope corrections for change in leaf area with increasing SSH (C_a) and change in tiller leaf area:volume ratio (R) (C_r) proved to be effective in accounting for the deviations between the calculated slope lines and the -3/2 theoretical expectation in December and January. One of the main factors that could have influenced the discrepancy between the observed slope and the value predicted by C_a and C_r in April, could be the effect of canopy size on reproductive growth presented by Tifton 85, where swards at different SSH flowered at different times. This could have modified sward structure and affected key variables used for predicting the slopes: tiller population density, leaf area per tiller and tiller volume (Tables 2 and 3). This seems to confirm, however, that the equations proposed by Matthew et al. (1995) are robust enough to account for and explain the deviation from the -3/2 SDC line for Tifton 85 swards within the range of SSH studied. In January and April the calculated slopes were much higher than those observed for ryegrass (Matthew et al., 1995; Hernández Garay et al., 1999), suggesting that a less drastic reduction in tiller population density followed the increases in SSH for the range of sward heights studied.

Additionally, the estimated values of C_a were higher than those of C_r, indicating that, as in the perennial ryegrass (Matthew et al., 1995; Hernández Garay et al., 1999), the variation in sward LAI is the main factor causing the tiller size/density compensation in Tifton 85 pastures. The variation in R is a comparatively minor element of plant growth strategy in the vegetative phase, but R falls in the reproductive phase, allowing the sward to accommodate greater tiller population density than would otherwise have been the case. This is similar to perennial ryegrass (Matthew et al., 1995), but not necessarily true for all grasses.

Matthew et al. (1995) suggested that the distance between any given point defined by its coordinates tiller mass and population density (both in a log scale) and an arbitrarily positioned theoretical -3/2 size/density compensation line can be viewed as a sward productivity index. As demonstrated by Sackville Hamilton et al. (1995), the -3/2 line defines a situation where LAI is constant. It follows that the greater the distance between the observed points and a -3/2 line placed below those points, the higher the sward LAI and, consequently, the bigger the sward capacity to accumulate herbage dry matter. This hypothesis was confirmed for temperate species in micro swards (Hernández Garay et al., 1999) and in field conditions (Bahmani et al., 1997; Hernández Garay et al., 1997).

Simple correlation coefficients between the perpendicular distance of the observed points from the -3/2 line and the actual sward LAI (Table 6) indicated

Table 5. Linear coefficients (β_0), intercepts (β_1), determination coefficients (R^2) and levels of significance (LS) for the Log_{10} x Log_{10} regressions between TPD and TW and C_a and C_r values in Tifton 85 pastures continuously stocked by sheep[1].

Month	β_0	β_1	R^2	LS	C_a	C_r	Predicted slope (β)[2]
Dec.	3.85	-2.02	0.989	**	1.19 (0.06)	-0.74 (0.02)	-1.95
Jan.	17.60	-5.37	0.973	**	4.16 (0.12)	-0.07 (0.08)	-5.59
Apr.	10.00	-3.45	0.996	*	3.42 (0.09)	-1.86 (0.09)	-3.06

[1]Numbers in parenthesis are standard errors of the estimate. [2]Calculated according to Matthew et al. (1995) where slope = -(C_a + C_r + 3/2). * and **Significant at 0.05 and 0.01 probability levels, respectively.

Table 6. Correlation coefficients (r) between the distance of points with coordinates x/y (in a log scale) and the -3/2 line and the sward leaf area index (LAI) in Tifton 85 pastures continuously stocked by sheep.

Sward surface height (cm)	December		January		April	
	Distance	LAI	Distance	LAI	Distance	LAI
5	0.207	1.94	0.146	1.90	0.145	1.46
10	0.276	2.54	0.276	2.48	0.376	2.47
15	0.307	3.52	0.326	2.75	0.420	3.47
20	0.319	3.64	0.409	4.16	0.489	4.25
r	0.957*		0.933*		0.943*	

*Significant at 0.05 probability level.

that the distance measured can be used to predict LAI in Tifton 85 swards. LAI is a key sward structure variable for the proper understanding of the herbage accumulation processes in pastures (Lemaire & Agnusdei, 2000). Tiller mass and population density are more easily measured than LAI, justifying further studies in order to allow a better understanding of the relationship with sward LAI and intraspecific competition processes that could generate conditions for using them as predictors of sward LAI and herbage dry matter production.

Conclusions

1. A tiller size/density compensation mechanism also operates in Tifton 85 pastures.

2. There is an indicative that Tifton 85 bermudagrass tillers operate in groups (clusters) in order to ensure competitive ability and optimize LAI.

Acknowledgements

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