Tiller dynamics in bahia grass (*Paspalum notatum*): an analysis of responses to nitrogen fertiliser rate, defoliation intensity and season

M. HIRATA AND W. PAKIDING
Grassland and Animal Production Division,
Faculty of Agriculture, Miyazaki University,
Miyazaki, Japan

Abstract

Responses of tiller dynamics in bahia grass (*Paspalum notatum*) to nitrogen fertiliser, defoliation and season were analysed using 4-years data from swards under 2 nitrogen rates [50 (LN) and 200 (HN) kg/ha/yr] × 3 cutting heights above ground level [2 (LH), 12 (MH) and 22 (HH) cm].

Total tiller density was ranked LH>MH>HH, and HN>LN in LH treatments. Tiller appearance rate (TAR) was high in June (early summer) or April–May (mid- to late spring), and often characterised by a trend of LH>MH≈HH in the first 2 years and LH<MH<HH thereafter. Tiller death rate (TDR) started to increase in February (late winter) or March–May (spring), peaked in May (late spring) or June–August (summer), and decreased thereafter.

Nitrogen rate and defoliation intensity had an effect on TAR by influencing the rate of site filling in mid-spring to late autumn, which in turn depended on the degree to which actual tiller density deviated from the density expected from the standard relationships where more tillers were carried under higher defoliation intensity (lower tiller weight) and higher nitrogen rate. Season had an effect on TAR by affecting leaf appearance rate (LAR), which increased in the warmer months and by affecting the rate of site filling in mid-spring to late autumn (April–May>June>July–November). Season influenced TDR with higher death rates in the warmer months, and defoliation intensity influenced TDR by varying the magnitude of response of TDR to temperature (LH≈MH<HH).

The study shows how responses of tiller dynamics in bahia grass to management and season can be mechanistically explained and modelled to improve our knowledge. The models developed in the study are useful for future development of an integrated model simulating canopy dynamics of bahia grass swards.

Introduction

Canopy structure of a sward plays an important role in many quantitative and qualitative aspects in pasture production and utilisation. Canopy structure is not static and changes with time and sward management factors such as fertiliser rate and defoliation frequency and intensity. Studying structural (*e.g.* tiller density, number of live and dead leaves per tiller, size of leaves and stem) and morphogenetic (*e.g.* tiller appearance and death, leaf appearance, death and detachment, leaf extension) variables of sward canopy is effective in understanding the mechanisms underlying such dynamics in canopy structure (Lemaire 1988; Chapman and Lemaire 1993; Lemaire and Chapman 1996; Lemaire and Agnusdei 2000).

Bahia grass (*Paspalum notatum*), a sod-forming, warm-season perennial, is widespread in the southern USA and Central and South America (Skerman and Riveros 1989), and is also grown in the low-altitude regions of south-western Japan for grazing and hay. In previous papers, we reported dynamics in structural and morphogenetic variables in bahia grass sward canopies under grazing (Pakiding and Hirata 1999, 2001, 2002b; Hirata and Pakiding 2001, 2002a, 2002b) and under different nitrogen fertiliser rates and cutting intensities (Hirata 2000; Pakiding and Hirata 2003a, 2003b, 2003c). Some of these studies analysed mechanisms underlying

Correspondence: Dr Masahiko Hirata, Division of Grassland Science, Faculty of Agriculture, University of Miyazaki, Miyazaki 889-2192, Japan. E-mail: m.hirata@cc.miyazaki-u.ac.jp

At the time of the study, WP was a student at the United Graduate School of Agricultural Sciences, Kagoshima University, Japan, being on study leave from Faculty of Animal Husbandry, Hasanuddin University, Indonesia.

the variation in canopy structure (tiller density, number of live and dead leaves per tiller, lamina length) with season and management, by modelling morphogenetic variables (tiller appearance and death, leaf appearance, death and detachment, leaf extension) in relation to meteorological, vegetational and managerial variables. However, mechanisms behind the dynamics in tiller density were not analysed fully enough to produce a model which could successfully predict responses to management (Hirata 2001).

In this study, we further analysed the responses of tiller dynamics in bahia grass to nitrogen rate, defoliation intensity and season. The aims of the study were to strengthen the mechanistic basis for explaining variations in tiller appearance rate (TAR) and tiller death rate (TDR) with management and season, and to deepen our understanding of tiller dynamics in bahia grass.

Materials and methods

The study site and experimental treatments

The study was conducted from April 1996–February 2000 in an established sward of Pensacola bahia grass at the Faculty of Agriculture, University of Miyazaki, southern Kyushu, Japan (31°50′N, 131°24′E). For a few years prior to the experiment, the sward had been managed as one unit to maintain uniform vegetation, at annual fertiliser rates of 50 kg/ha N, 15 kg/ha P and 25 kg/ha K (as compound fertiliser) and under monthly cuttings to about 15 cm above ground during May–October. Meteorological conditions during the measurement period (described later), recorded at the Miyazaki Meteorological Station (about 10 km north of the study site), are shown in Figure 1.

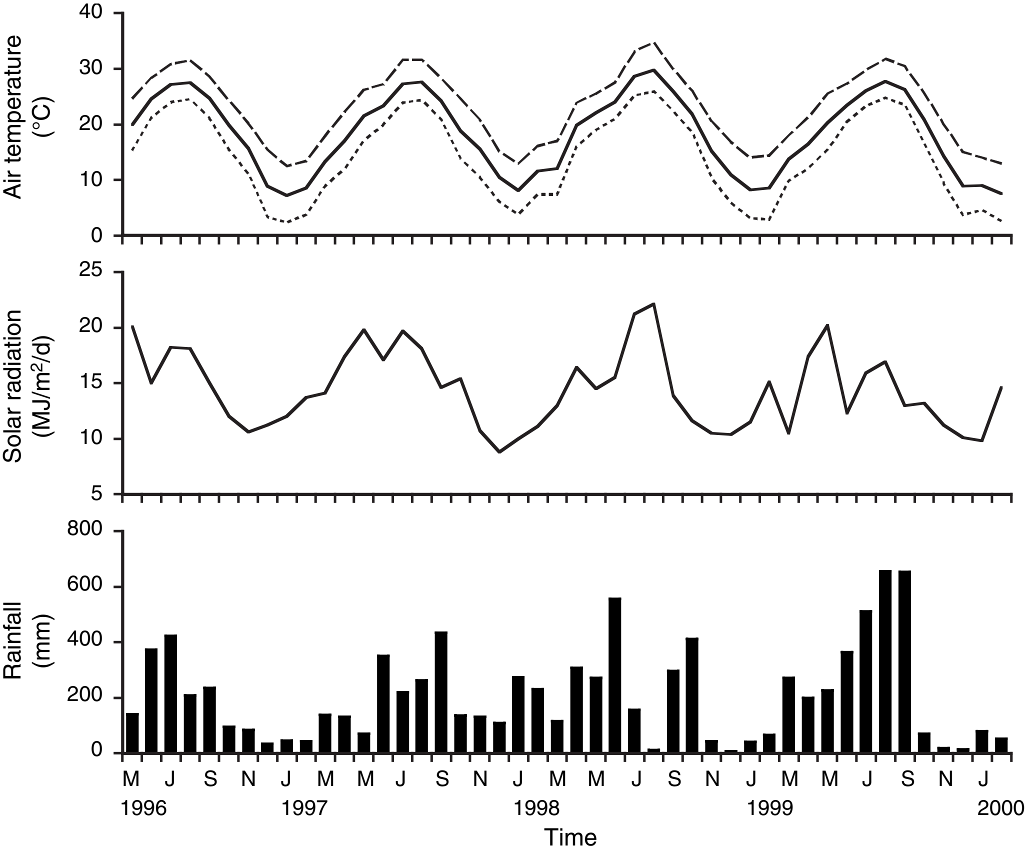

Figure 1. Monthly means of maximum (———), mean (——) and minimum (- - -) daily air temperatures and daily total short-wave solar radiation, and monthly totals of rainfall during the measurements.

In early April 1996, six 1.0 m × 1.2 m plots were laid out on a 10 m × 2 m area of the sward (arranged in a row with spacing of 0.5 m), and 6 treatments consisting of 2 nitrogen fertiliser rates (LN and HN) × 3 defoliation heights (LH, MH and HH) were randomly allotted to the plots. There were thus no replications of the treatments. The nitrogen rates for LN and HN were 50 and 200 kg/ha/yr, respectively. In addition to nitrogen, each plot received 44 kg/ha/yr P and 83 kg/ha/yr K. The sources of N, P and K were ammonium sulphate, superphosphate and potassium sulphate, respectively. The fertilisers were applied as equal dressings in mid-April, early July and early September. The plots were cut during May–October at 15-d intervals in 1996 and at monthly intervals in the following years. The defoliation heights for LH, MH and HH were 2, 12 and 22 cm above ground level, respectively. The inter- and outer-plot areas received nil fertiliser and were defoliated similarly to LH.

Measurements

Three 20 cm × 20 cm permanent quadrats were established in each plot, with 20–40 cm borders around the quadrats. All live tillers within the quadrats were tagged on May 30, 1996 with a wire ring (9 mm in diameter) with a coloured bead at their base and grouped as the original tillers, which were of different, unknown ages. Subsequent taggings were conducted at monthly intervals, when all quadrats were examined, any new tillers were tagged and the rings were removed from dead tillers. The number of new tillers tagged and the number of rings removed from dead tillers were recorded, from which monthly TAR and TDR were calculated as the daily rates relative to the total tiller density at the beginning of the monthly period. Beads of a different colour were used at each tagging. The tillers were classified as dead when all parts were completely dried.

The tillers were classified into the following 16 age categories (cohorts) according to the period of their initiation, with the first category being the original tillers, *i.e.*, formed before May 30, 1996 (pre-measurement). The remaining 15 categories were tillers initiated in the following seasons: summer 1996 (May 31–August 31), autumn 1996 (September 1–November 27), winter 1996–1997 (November 28–February 28), spring 1997 (March 1–May 30), summer 1997 (May 31–August 29), autumn 1997 (August 30–December 1), winter 1997–1998 (December 2–March 2), spring 1998 (March 3–May 31), summer 1998 (June 1–September 3), autumn 1998 (September 4–November 30), winter 1998–1999 (December 1–March 1), spring 1999 (March 2–May 30), summer 1999 (May 31–August 30), autumn 1999 (August 31–November 23), and winter 1999–2000 (November 24–February 28).

Leaf appearance rate (LAR) was measured from April 1997 to December 1999 for 20 tillers in each treatment, using a tagging technique (Pakiding and Hirata 2001; 2003b). LARs before April 1997 and after December 1999 were estimated from air temperature using equations developed by Pakiding and Hirata (2003b).

The rate of site filling (F_S, tillers/leaf), defined as the rate at which axillary buds develop into tillers (visible without dissection) in relation to the rate at which leaf axils are formed (Davies 1974; Thomas 1980), was calculated as:

$$F_S = R'_{\mathrm{tiller,app}} / R_{\mathrm{leaf,app}} \tag{1}$$

where $R'_{\mathrm{tiller,app}}$ is TAR (tillers/tiller/d) and $R_{\mathrm{leaf,app}}$ is LAR (leaves/tiller/d). The rate of site filling was estimated for April–November (mid-spring–late autumn), because LAR in the other months (December–March) was usually less than 0.03 leaves/tiller/d which equals production of <1 leaf per month.

Measurements of herbage mass commenced in August 1996. Immediately before each tagging, herbage mass above ground level within each quadrat was estimated using an electronic capacitance probe (PastureProbe$^{\mathrm{TM}}$, Mosaic Systems Ltd, New Zealand) (Hirata *et al.* 1993). Calibration equations were developed at each measurement time by cutting samples from adjacent swards subjected to cutting heights ranging from 2–30 cm. Herbage mass in June and July 1996 was estimated from meteorological data using mass–meteorology relationships during 1997–1999.

Tiller weight was calculated by dividing herbage mass by total tiller density (sum of densities of all tiller cohorts).

Results and discussion

Herbage mass and tiller density

Herbage mass was higher in summer (June–August) and autumn (September–November) than in winter (December–February) and spring (March–May), with larger seasonal variation under higher defoliation height (Figure 2). The increase in nitrogen rate and defoliation height almost always increased herbage mass (LN<HN and LH<MH<HH).

Tiller density at the first tagging (May 30, 1996) tended to be higher in HN treatments than in LN treatments (Figure 3). This is probably attributable to the facts that the sward was initially deficient in nitrogen and the nitrogen treatment commenced in mid-April, *i.e.*, 1.5 months before the first measurements (tagging); a high nitrogen rate stimulated tillering of the bahia grass until the first measurements. There was no visual difference in the vegetation among the 6 plots when they were established (early April 1996).

In the first 1 or 2 years, total tiller density in LH treatments increased, with a steeper increase in HN than in LN (Figure 3). On the contrary, total tiller density in MH and HH treatments decreased, showing steeper decreases in HH treatments than in MH treatments. Thereafter, in the third and fourth years, total tiller density in all treatments maintained annually constant values, showing seasonal fluctuations consisting of an increase in April–May (mid- to late spring) and a subsequent decrease in June–September (early summer–early autumn). From the second half of the first year onward, total tiller density was ranked LH>MH>HH, and HN>LN in LH treatments. These results reinforce earlier observations that tiller density of bahia grass increased as defoliation height decreased from 22 to 2 cm (Hirata 1993) and when nitrogen fertiliser was applied at the defoliation height of 2 cm (Pakiding and Hirata 2002a). Beaty *et al.* (1977) also reported higher tiller densities of bahia grass at higher nitrogen rates in swards defoliated at 2.5 and 7.5 cm, though the densities were not different between the 2 cutting heights.

The density of original tillers (formed before the first measurements) decreased with time and accounted for 20.5, 18.2, 31.6, 53.8, 24.5 and 34.8% of the final total tiller density in LN/LH, HN/LH, LN/MH, HN/MH, LN/HH and HN/HH, respectively (Figure 3). Among the 15 cohorts formed after the first measurements, tillers appearing in autumn 1996 and spring 1997, 1998 and 1999 showed relatively high densities in LH treatments, and those appearing in the 3 springs showed higher densities in the other treatments.

Standard relationship between tiller density and tiller weight

The relationship between tiller density and tiller weight in summer–autumn of the fourth year (June–November 1999) was defined as the standard density:weight relationship under the management systems imposed. The fourth year was selected because the responses of total tiller density to the treatments appeared to have almost ended by this year (Figure 3), and the

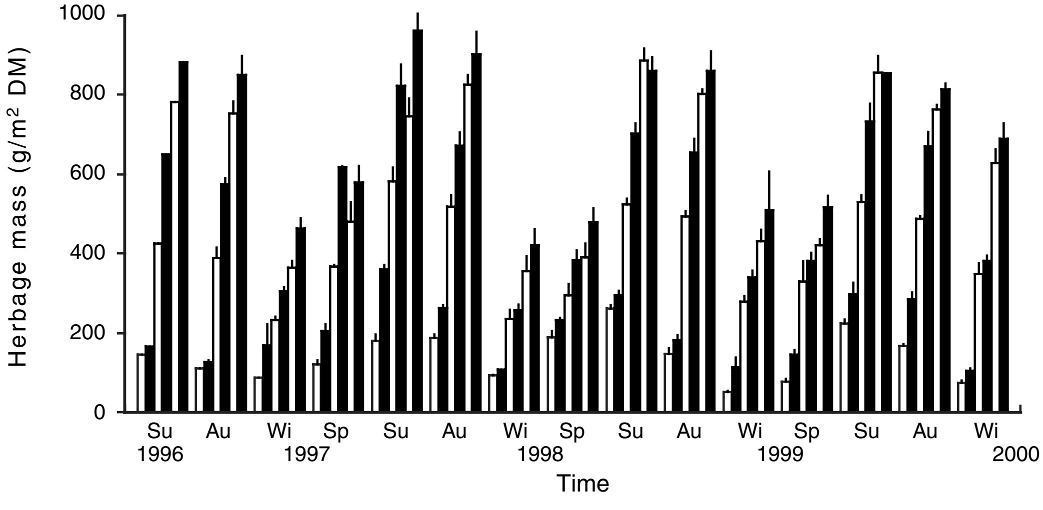

Figure 2. Seasonal means of herbage mass. Six columns in each season indicate LN/LH, HN/LH, LN/MH, HN/MH, LN/HH and HN/HH from left to right (LN=low nitrogen; HN=high nitrogen; LH=low height; MH=medium height; HH=high height of cutting). Vertical bars show standard errors of the means (no s.e. values for summer 1996).

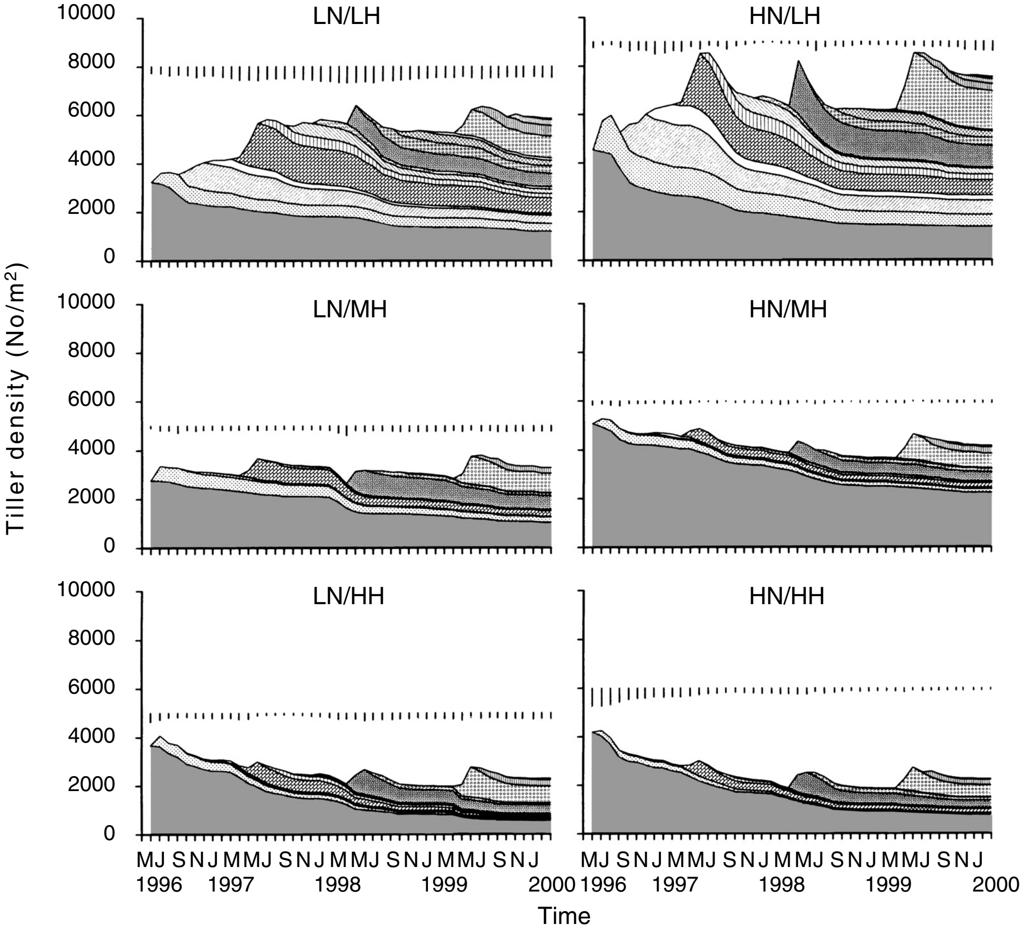

Figure 3. Density of tillers in different age cohorts (different seasons of initiation). Tiller cohorts are stacked in order of their age (the oldest at the bottom and the youngest at the top); pre-measurement (▒), summer 1996 (░), autumn 1996 (▨), winter 1996–1997 (□), spring 1997 (▩), summer 1997 (▥), autumn 1997 (▧), winter 1997–1998 (▦), spring 1998 (▓), summer 1998 (▓), autumn 1998 (▩), winter 1998–1999 (░), spring 1999 (▤), summer 1999 (▥), autumn 1999 (▧), winter 1999–2000 (■). LN=low nitrogen; HN=high nitrogen; LH=low height; MH=medium height; HH=high height of cutting. Vertical bars show standard errors of the means of total tiller density.

summer–autumn period was selected because bahia grass tillers are fully green during this period (Hirata and Pakiding 2002a). There were negative linear relationships between log (tiller density) and log (tiller weight) (Figure 4). HN treatments showed a significantly greater intercept and a significantly steeper slope (both $P<0.001$) than LN treatments. The equations thus indicate that the number of tillers carried on a unit area of land increased as tiller weight decreased, with higher numbers on HN treatments than LN treatments in a tiller weight range below 493 mg/tiller DM [log (tiller weight)<2.69].

These standard relationships between tiller density and tiller weight are the reverse (in terms of x- and y-axes) of the well-known self-thinning rule (Yoda *et al.* 1963), and enable us to calculate expected tiller density from an arbitrary tiller weight value of 27–355 mg/tiller DM [$1.43 < \log$ (tiller weight) < 2.55]:

$$N = 10^{(4.355 - 0.376 \log W)}$$

(for LN treatments) (2a)

$$N = 10^{(4.726 - 0.514 \log W)}$$

(for HN treatments) (2b)

where N and W are tiller density (tillers/m^2) and tiller weight (mg/tiller DM), respectively.

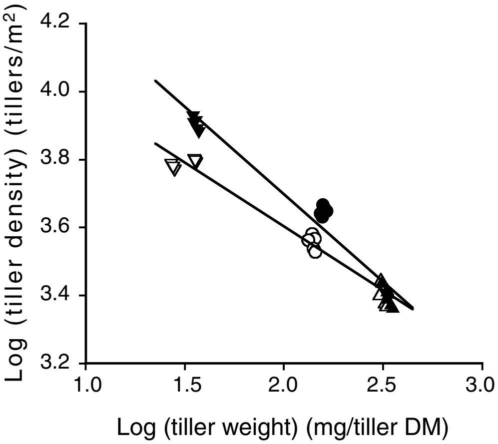

Figure 4. Relationship between log (tiller density) and log (tiller weight) during summer and autumn in the fourth year (June–November 1999). Regression lines are: log N=4.355–0.376 log W (r=–0.986, P<0.001) for LN treatments [LN/LH (▽), LN/MH (○) and LN/HH (△)]; log N=4.726–0.514 log W (r=–0.983, P<0.001) for HN treatments [HN/LH (▼), HN/MH (●) and HN/HH (▲)]; where N and W are tiller density and tiller weight, respectively. LN=low nitrogen; HN=high nitrogen; LH=low height; MH=medium height; HH=high height of cutting.

Rates of tiller appearance and death

TAR was high in June (early summer) 1996, and in April and May (mid- and late spring) in the following years (Figure 5). TAR was often characterised by a trend of LH>MH≈HH in the first 2 years (1996 and 1997) and by a trend of LH<MH<HH thereafter. The effect of nitrogen rate on TAR was smaller and less consistent. TDR started to increase in February (late winter) or March–May (spring), peaked in May (late spring) or June–August (summer), and decreased thereafter. There appeared to be no consistent effects of treatments on TDR. The balance between TAR and TDR was positive and high in June 1996, and in April and May in the following years, except for May 1998. The balance tended to be ranked LH>MH>HH in the first 2 years (June 1996 and April–May 1997) and LH<MH<HH in the following years (April–May 1998 and 1999). In the other months, the balance was usually close to zero or negative, except for LH treatments in the first year.

Modelling tiller appearance rate

Since TAR is determined as LAR × rate of site filling (Davies 1974; Thomas 1980), variation in TAR with season and treatments (Figure 5) can be attributed to variation in LAR or variation in the rate of site filling or both. TAR in relation to LAR showed 2 major seasonally different patterns (Figure 6).

In December–March (early winter to early spring), TAR was always close to zero with low rates of leaf appearance (usually <0.03 leaves/tiller/d, *i.e.*, <1 leaf per month), indicating that low LAR was a major factor limiting tiller appearance in this period. By contrast, in April–November (mid-spring to late autumn), TAR varied in relatively wide ranges (particularly April–June) with varying values in both LAR and rate of site filling (shown as a ratio of TAR:LAR). TAR varied even at similar rates of leaf appearance. Thus, TAR in this period was regulated by both LAR and the rate of site filling.

Variation in LAR throughout the year (Figure 6) is attributable to variation in air temperature. In our previous studies, LAR in bahia grass showed a close, positive association with air temperature (Pakiding and Hirata 2001; 2003b), being stable across nitrogen rates and defoliation intensities (Pakiding and Hirata 2003b).

Variation in the rate of site filling in April–November was explained by the degree to which actual tiller density deviated from the density expected from the standard relationships (Figure 4, Equations 2a and 2b); *i.e.*, there were negative linear relationships between the rate of site filling and the actual:expected ratio in tiller density (Figure 7). These equations show that the rate of site filling was high when actual tiller density was lower than the density expected from the standard relationships and decreased to zero as the actual:expected ratio increased to 1.05–1.50 (mean=1.19). Values of the rate of site filling at low actual:expected ratios (*e.g.* $N_{A:E}$=0.6) or the steepness of the regression lines tended to be ranked April–May>June>July–November, indicating that the rate of site filling was regulated by season as well.

Thus, nitrogen rate and defoliation intensity had an effect on TAR in April–November, initially by affecting tiller weight, then by varying actual:expected ratio in tiller density, and finally by influencing the rate of site filling. Nitrogen rate

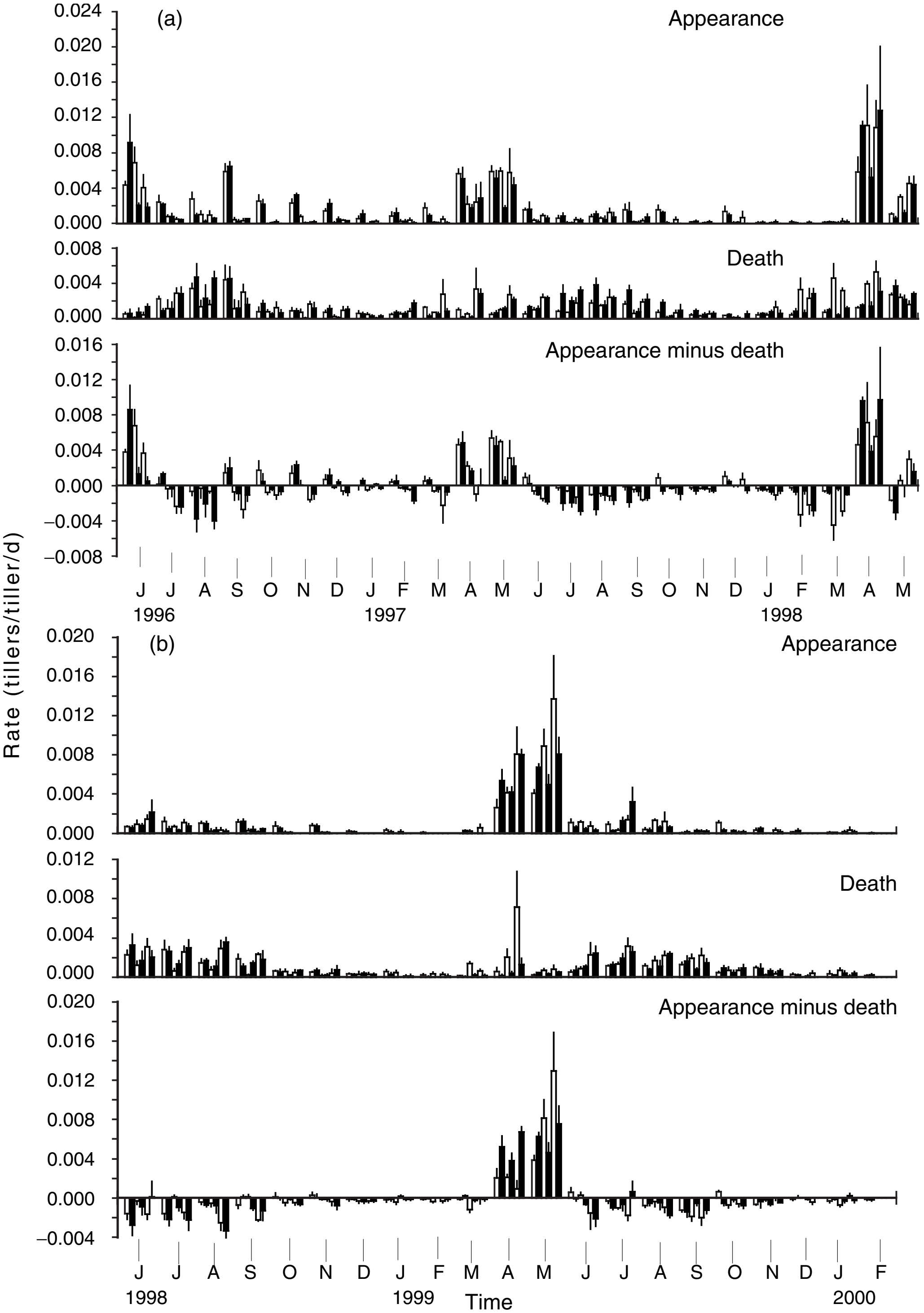

Figure 5. Tiller appearance rate, tiller death rate and their balance (appearance rate minus death rate) in the first (a) and second (b) 2 years of the experiment. Six columns in each month indicate LN/LH, HN/LH, LN/MH, HN/MH, LN/HH and HN/HH from left to right (LN=low nitrogen; HN=high nitrogen; LH=low height; MH=medium height; HH=high height of cutting). Vertical bars show standard errors of the means.

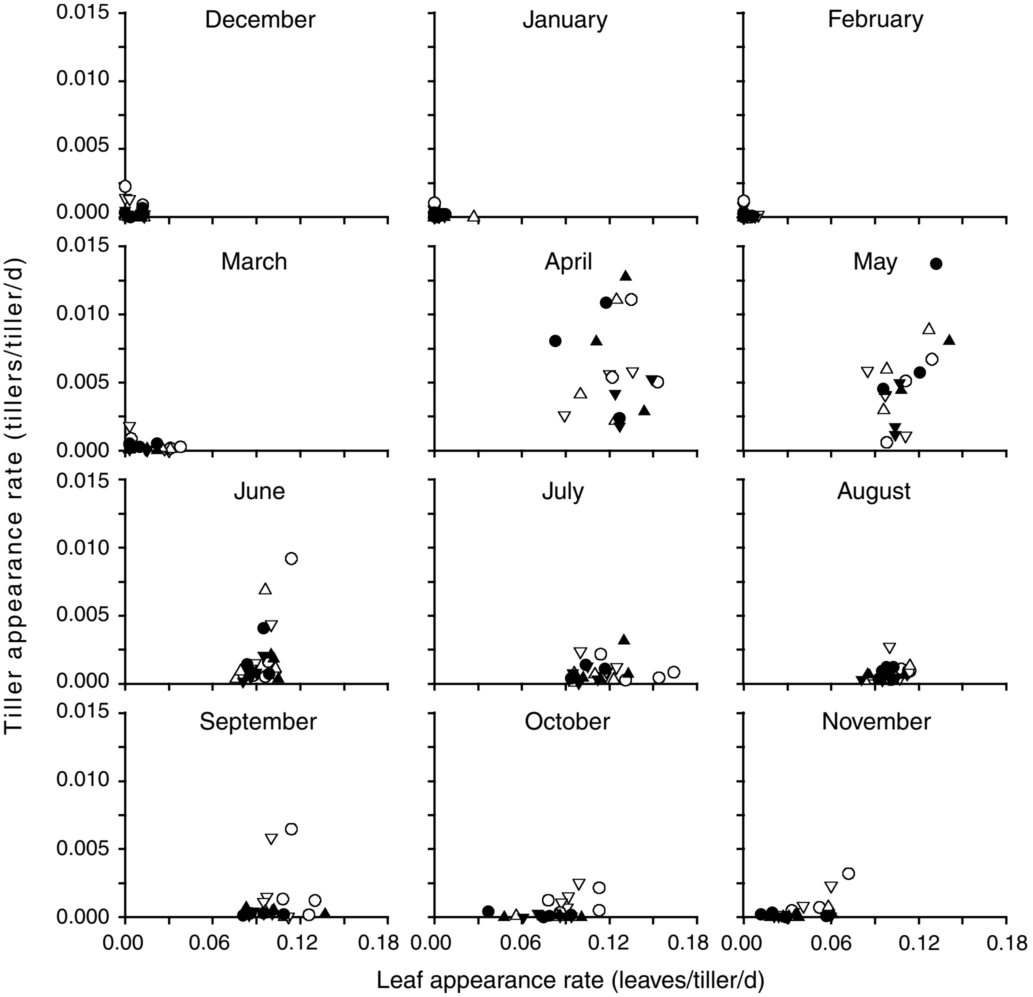

Figure 6. Relationships between tiller appearance rate and leaf appearance rate in different months. Treatments are LN/LH (▽), HN/LH (○), LN/MH (△), HN/MH (▼), LN/HH (●) and HN/HH (▲) (LN=low nitrogen; HN=high nitrogen; LH=low height; MH=medium height; HH=high height of cutting).

also affected the standard density:weight relationship where more tillers were carried under higher defoliation intensity (lower tiller weight) and higher nitrogen rate (Figure 4). Season had an effect on TAR by affecting LAR throughout the year through variation in air temperature, and by affecting the rate of site filling in April–November (April–May>June>July–November). These mechanics are more logical and robust than those in our previous study (Pakiding and Hirata 2003a), and more appropriate for predicting responses of tiller appearance to management and season (Hirata 2001).

TAR in bahia grass during the spring–autumn period was density-dependent (not shown as a figure) because of the density-dependence of the rate of site filling (Figure 7). Bullock *et al.* (1994) also reported the density-dependence of TAR in *Agrostis stolonifera* and *Lolium perenne* but smaller effects of management.

Modelling tiller death rate

Unlike TAR, variation in TDR (Figure 5) was not associated with actual:expected ratio of tiller

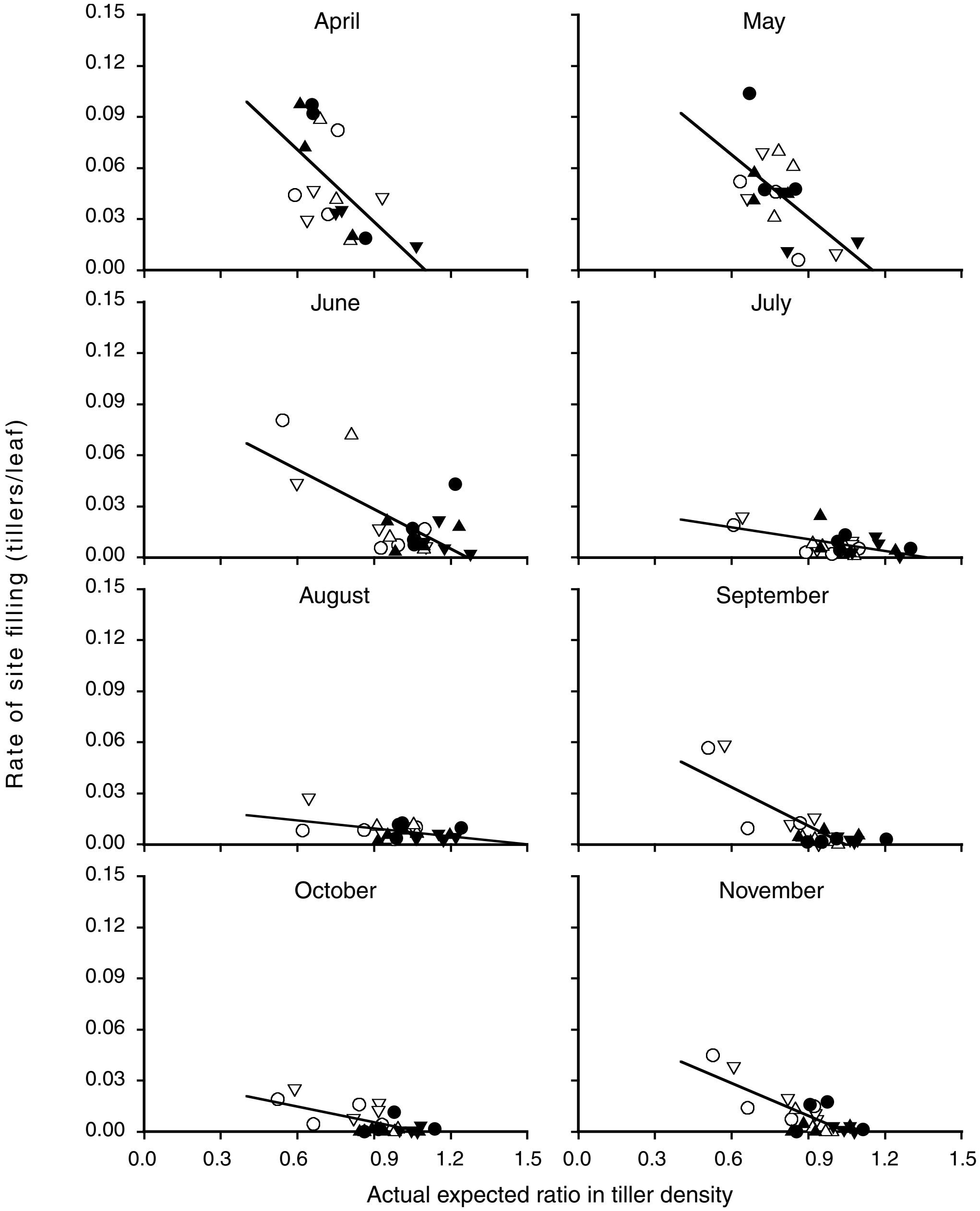

Figure 7. Relationships between rate of site filling and actual:expected ratio in tiller density in different months. Treatments are LN/LH (▽), HN/LH (○), LN/MH (△), HN/MH (▼), LN/HH (●) and HN/HH (▲) (LN=low nitrogen; HN=high nitrogen; LH=low height; MH=medium height; HH=high height of cutting). Regression lines are: F_S=0.155–0.141$N_{A:E}$ (r=–0.583, P<0.05) for April; F_S=0.141–0.123$N_{A:E}$ (r=–0.598, P<0.01) for May; F_S=0.098–0.078$N_{A:E}$ (r=–0.661, P<0.001) for June; F_S=0.032–0.023$N_{A:E}$ (r=–0.576, P<0.01) for July; F_S=0.023–0.016$N_{A:E}$ (r=–0.449, P<0.05) for August; F_S=0.079–0.076$N_{A:E}$ (r=–0.787, P<0.001) for September; F_S=0.033–0.031$N_{A:E}$ (r=–0.624, P<0.01) for October; F_S=0.067–0.064$N_{A:E}$ (r=–0.779, P<0.001) for November; where F_S and $N_{A:E}$ are rate of site filling and actual:expected ratio of tiller density, respectively. Expected tiller densities were calculated from tiller weight using the standard relationships between tiller density and tiller weight (Figure 4, Equations 2a and 2b).

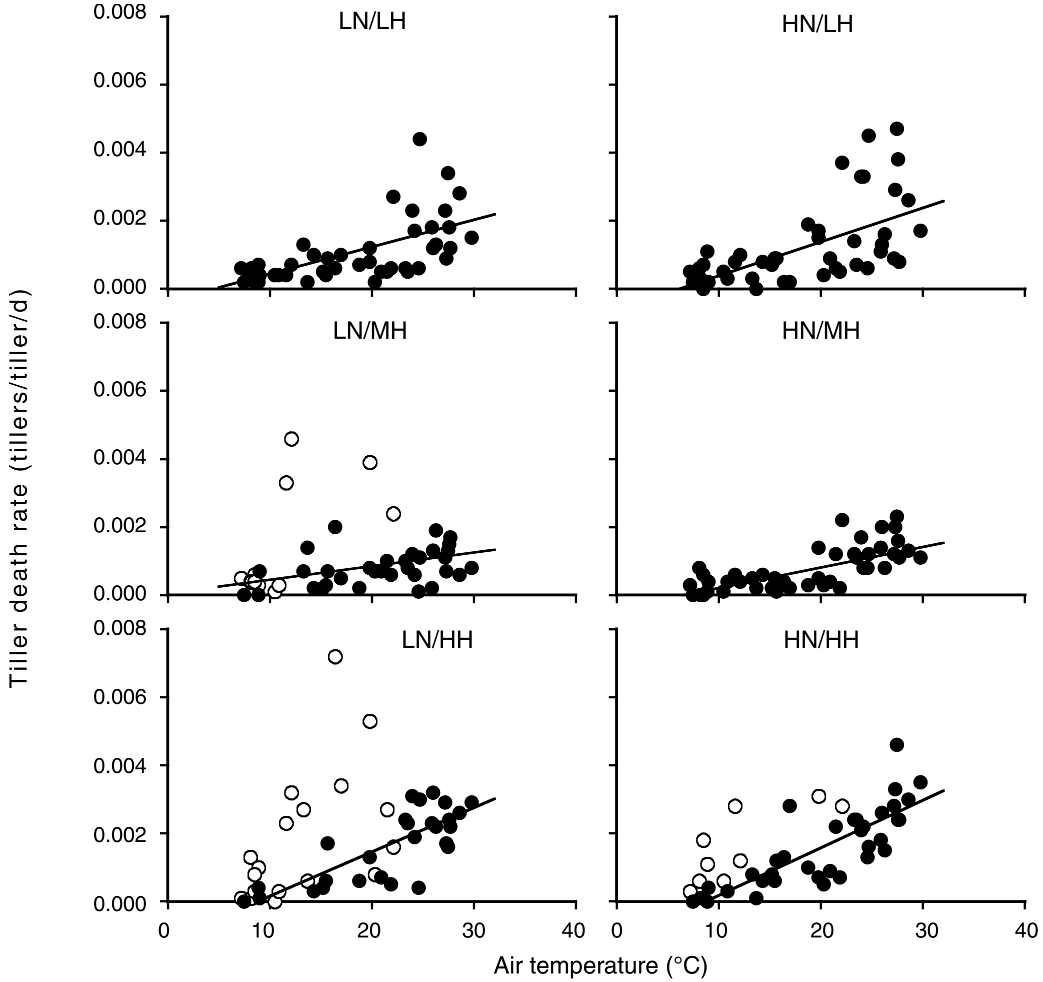

Figure 8. Relationships between tiller death rate and mean air temperature in different treatments (LN/LH, HN/LH, LN/MH, HN/MH, LN/HH and HN/HH) (LN=low nitrogen; HN=high nitrogen; LH=low height; MH=medium height; HH=high height of cutting). Regression lines are:
$R'_{tiller,death}=-0.00037+0.00008T$ ($r=0.603$, $P<0.001$) for LN/LH; $R'_{tiller,death}=-0.00062+0.00010T$ ($r=0.608$, $P<0.001$) for HN/LH; $R'_{tiller,death}=0.00005+0.00004T$ ($r=0.425$, $P<0.05$) for LN/MH; $R'_{tiller,death}=-0.00039+0.00006T$ ($r=0.731$, $P<0.001$) for HN/MH; $R'_{tiller,death}=-0.00115+0.00013T$ ($r=0.779$, $P<0.001$) for LN/HH; $R'_{tiller,death}=-0.00123+0.00014T$ ($r=0.817$, $P<0.001$) for HN/HH; where $R'_{tiller,death}$ and T are tiller death rate and mean air temperature, respectively. Regressions for LN/MH, LN/HH and HN/HH exclude data when herbage mass is <300, <500 and <500 g/m^2 DM, respectively (open circles).

density (not shown as a figure), indicating density-independence of TDR. Such unimportance of tiller density in the regulation of TDR in bahia grass contrasts with the results from *Agrostis stolonifera* and *Lolium perenne* (Bullock *et al.* 1994).

Instead, TDR in each treatment increased as mean daily air temperature increased (Figure 8). The slope of the regression lines was higher in HH than in LH and MH ($P<0.10$) within each nitrogen rate, although consistent effects of treatments on TDR were difficult to discern in Figure 5.

Thus, season had an effect on TDR mainly through variation in air temperature. Among the treatments, only defoliation intensity had an effect on TDR by affecting the magnitude of response of TDR to temperature (LH≈MH<HH). Such a result on the effects of treatments on TDR

partly agrees with our previous results that longevity of bahia grass tillers decreased with increasing nitrogen rate and defoliation height (Pakiding and Hirata 2003a).

In LN/MH, LN/HH and HN/HH, however, dependence of TDR on temperature was detected only when data with low herbage masses (<300, <500 and <500 g/m^2 DM, respectively) were excluded (Figure 8). Further analysis is needed to clarify the reason for this relationship.

Conclusions

Tiller dynamics in bahia grass were influenced by nitrogen fertiliser rate, defoliation intensity and season. Nitrogen rate and defoliation intensity had an effect on TAR by influencing the rate of site filling in mid-spring to late autumn, which in turn depended on the degree to which actual tiller density deviated from the density expected from the standard relationships, where more tillers were carried under higher defoliation intensity (lower tiller weight) and higher nitrogen rate. Season had an effect on TAR by affecting LAR throughout the year (through air temperature; Pakiding and Hirata 2001; 2003b) and by affecting the rate of site filling in mid-spring to late autumn (April–May>June>July–November). Season had an effect on TDR through variation in air temperature, and defoliation intensity affected TDR by varying the magnitude of response of TDR to temperature (LH≈MH<HH). The current study shows how responses of tiller dynamics in bahia grass to management and season can be mechanistically explained and modelled to improve our knowledge. The models developed in this study are useful for future development of an integrated model simulating canopy dynamics of bahia grass swards.

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