Dynamics in tiller weight and its association with herbage mass and tiller density in a bahia grass (*Paspalum notatum*) pasture under cattle grazing

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Abstract

Dynamics in tiller weight and its association with herbage mass and tiller density were investigated for 2 years in a bahia grass (*Paspalum notatum*) pasture under cattle grazing, in an effort to characterise the dynamics in tiller weight and its components (live laminae, dead laminae and stem with leaf sheaths), to compare contributions of tiller density and tiller weight to herbage mass and to examine the existence of the self-thinning rule in bahia grass. Tiller weight (range=67–257 mg DM/tiller) was high from late spring (May) to mid-autumn (October) and low in the other half of the year. The rate of change in tiller weight (range=–4.28 to 4.31 mg DM/tiller/d) reflected high positive rates of change in live lamina weight in April-May and high negative rates of change in stem weight in October-November. The high positive rates in April-May represent a spring flush achieved by consuming reserve substances in stolons and roots as the main energy pools. The high negative rates in October–November may indicate the translocation of reserve substances stored in stems during summer into stolons and roots before the dormant winter season. Variations in herbage mass (range=23–560 g DM/m^2) were largely explained by the variations in tiller weight, with no significant contribution by tiller density (range=3859–4875 tillers/m^2). The tiller weight:density relationship, when combined with previous data having a broader range of tiller density, was in close agreement with the −3/2 self-thinning rule (slope=−1.63).

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Introduction

A grass sward canopy is regarded as a population of tillers and, in more detail, as an integration of many morphogenetic and structural components (Figure 1). Analysing a sward canopy in terms of such morphogenetic and structural components is effective in highlighting quantitative and qualitative characteristics of the canopy and understanding the mechanisms by which they contribute to pasture production and utilisation (Lemaire 1988; Chapman and Lemaire 1993; Lemaire and Chapman 1996; Hirata 1996, 1999, 2000a).

Bahia grass (*Paspalum notatum*), a sod-forming, warm season perennial, is well adapted to the low-altitude regions of south-western Japan and used for both grazing and hay. In previous studies, we monitored tiller density dynamics and leaf dynamics in a bahia grass pasture grazed with cattle (Pakiding and Hirata 1999, 2001; Hirata and Pakiding 2001). Tiller density dynamics were monitored for 4 years in terms of all directly related morphogenetic and structural components (Figure 1, left), and leaf dynamics for 2 years in terms of numbers of live and dead leaves, rates of leaf appearance, death and detachment and leaf longevity (Figure 1, upper right). It was shown that high persistence of bahia grass is achieved by 3 major factors, *i.e.* long life of tillers; long life of autumn-formed leaves; and high leaf detachment in summer and autumn.

Herbage mass, a most important canopy characteristic, is a product of tiller density and tiller weight (Figure 1, bottom), *i.e.* an increase in herbage mass may be attributed to a tiller density increase or a tiller weight increase or both. At the

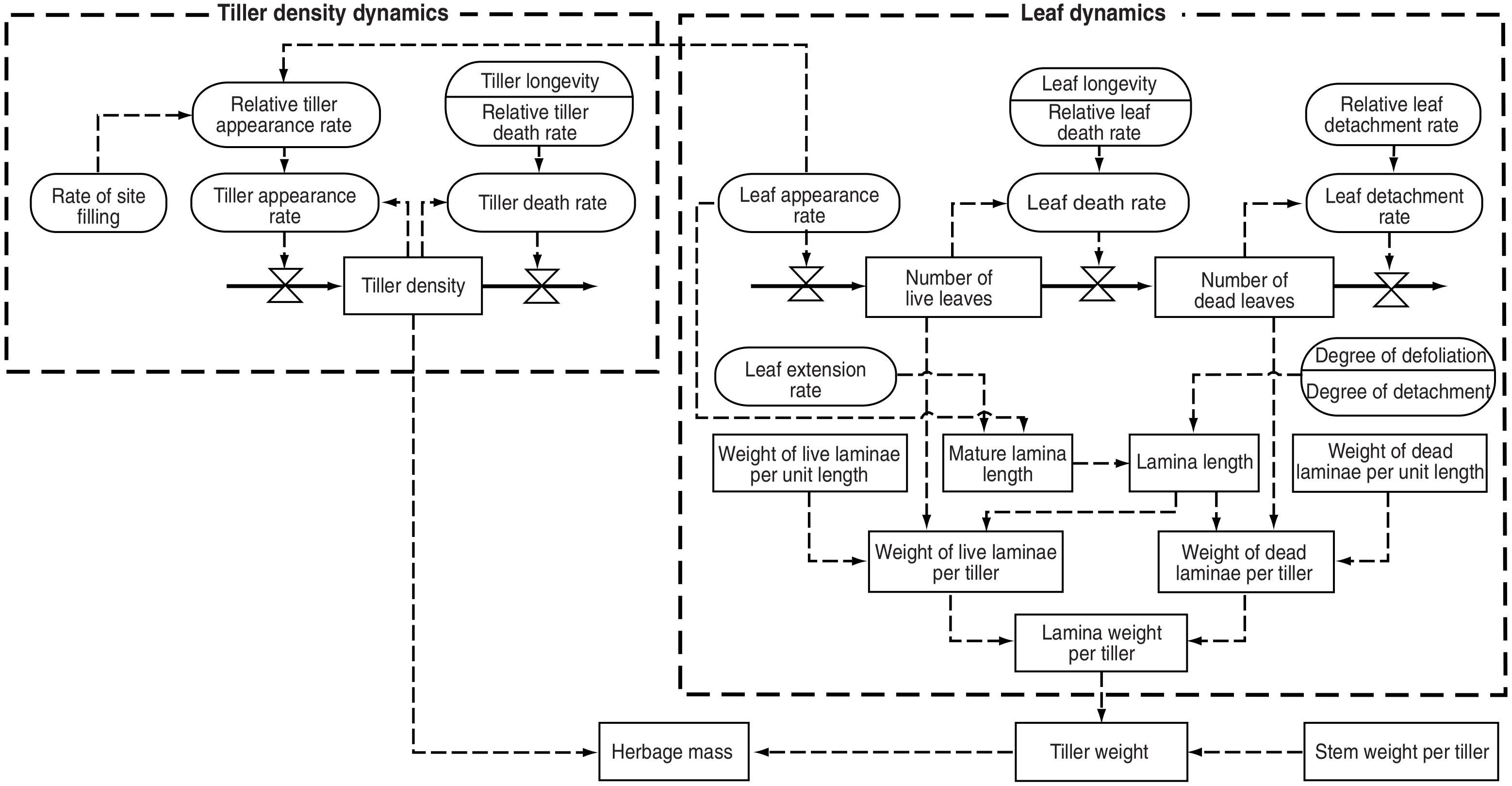

Figure 1. Relationships between morphogenetic ( ) and structural ( ) components of a grass sward canopy. Stem includes leaf sheaths.

same time, tiller weight and tiller density are not independent of each other, *i.e.* a tiller weight increase may be observed with a tiller density decrease (*e.g.* Chapman and Lemaire 1993), which is generally known as the –3/2 self-thinning rule (Yoda *et al.* 1963).

This study, as the third step following tiller density dynamics (Pakiding and Hirata 1999; Hirata and Pakiding 2001) and leaf dynamics (Pakiding and Hirata 2001), deals with dynamics in tiller weight and its association with herbage mass and tiller density. Tiller weight, as a sum of lamina (both live and dead) and stem (inclusive of leaf sheaths) weights per tiller (Figure 1, lower right), was measured for 2 years in the same pasture as in the previous studies (Pakiding and Hirata 1999, 2001; Hirata and Pakiding 2001). Tiller density and herbage mass were also measured (Hirata and Pakiding 2001). The aims of the study were to characterise the dynamics in tiller weight and its components, to compare contributions of tiller density and tiller weight to herbage mass, and to examine the existence of the self-thinning rule in bahia grass.

Materials and methods

The site, pasture and animals

The same paddock as in the previous studies (Pakiding and Hirata 1999, 2001; Hirata and Pakiding 2001), *i.e.* a 1.06-ha paddock of a Pensacola bahia grass pasture at the Sumiyoshi Livestock Farm (31°59'N, 131°28'E), Miyazaki University, Japan, was used. The paddock was one of 5 paddocks (different sizes; total area= 6.3 ha) rotationally grazed by Japanese Black cows from late May to late October-early November.

In 1998 and 1999, the paddock was grazed 6 times by 29–34 animals (mean liveweight= 450 kg) for 4–7 days (0900–1600 h each day) at 12–39 d intervals. The total duration of grazing was 30–32 d.

The paddock was fertilised with compound fertiliser and urea. The fertilisation rates in 1998 were 97 kg N (60 kg in April and 37 kg in September), 26 kg P (April) and 40 kg K (April) per ha. The rates in 1999 were 70 kg N (30 kg in April and 40 kg in August), 17 kg P (April) and 20 kg K (April) per ha. The meteorological conditions are shown in Figure 2.

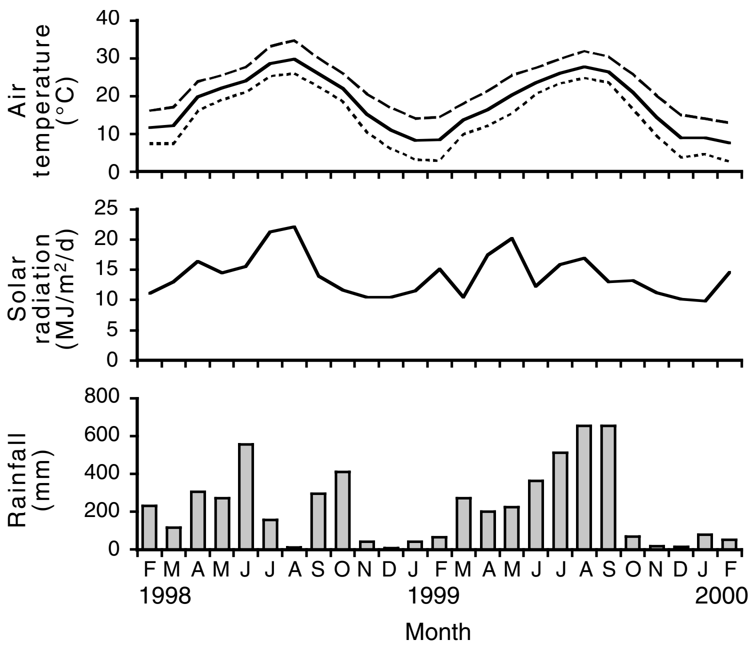

Figure 2. Monthly means of maximum (– – –), mean (——) and minimum (-----) daily air temperatures, daily total short-wave solar radiation and monthly totals of rainfall during the study.

Measurements and data analyses

Tiller weight of bahia grass was measured at monthly intervals from February 1998–February 2000. On each occasion, 40 vegetative tillers were randomly selected in the paddock and sampled at the soil level. Then, each tiller was separated into live laminae, dead laminae and stem (inclusive of leaf sheaths). For expanding or emerging leaves, laminae were cut at their lower (proximal) end, *i.e.* emerging point from the enclosing sheaths. Laminae were classified as dead when <10% of their area remained green. The samples were oven-dried at 85°C for 48 h for determination of dry weight. The relatively small number of tillers sampled, *i.e.* 40 in a 1.06-ha paddock, may have resulted in some bias in the estimation of tiller weight, though care was taken not to discriminate tillers (*e.g.* grazed or non-grazed).

Herbage mass and tiller density were measured on the same occasions as above, for 8 randomly selected 20 cm × 20 cm permanent quadrats in the paddock. An electronic capacitance probe (PastureProbe™, Mosaic Systems Ltd, New Zealand) was used to non-destructively estimate herbage mass in the quadrats. For each quadrat, corrected meter reading (CMR) of electronic capacitance probe was measured at 5 points (4 at individual corners and 1 in the centre), and the mean value was recorded as the CMR of the quadrat. Then, the CMR was converted into herbage mass (g DM/m^2 above a height of 3 cm) using a calibration equation. Calibration equations were developed every 1–2 months by cutting samples from the paddock. Tiller density in each quadrat was estimated using a tagging technique where the number of initial tillers and the numbers of tillers appearing and dying subsequently were recorded (Hirata and Pakiding 2001).

The tiller weight:density relationship was examined on a logarithmic (log) basis to check the −3/2 self-thinning rule (Yoda *et al.* 1963). Since tiller density remained almost constant throughout the measurements (Hirata and Pakiding 2001; Figure 5b), the tiller weight:density relationship was analysed by combining the current data with previous data which displayed a broader range of tiller density, in order to ensure enough range for detecting the rule. Combined data were derived from Hirata and Ueno (1993) and Hirata (1993) in which above-ground herbage mass and tiller density were measured for 3 years in bahia grass swards subjected to 5 cutting heights ranging from 2–22 cm (60 data sets from late January, late May, early August and early November) were used.

Results

Tiller weight (weights of live laminae + dead laminae + stem per tiller; stem includes leaf sheaths), ranging from 67–257 mg DM/tiller, was high from late spring (May) to mid-autumn (October) and low in the other half of the year (Figure 3). Live laminae, dead laminae and stem accounted for 19-62%, 7–42% and 19–57% of tiller weight, respectively. The seasonal variations in tiller weight reflected variations in weights of live laminae and stem, *i.e.* tiller weight was positively correlated with weights of live laminae and stem per tiller (r=0.952 and r=0.870, respectively; both P<0.001).

The rate of change in weight of live laminae per tiller (range=–2.15 to 3.32 mg DM/tiller/d) was highly positive in April-May and usually around zero in the other months except for a highly negative value in October–November 1999 (Figure 4a). The rate of change in weight of dead laminae per tiller (range=–0.77 to 0.65 mg DM/tiller/d) always remained around zero, showing smallest seasonal variations (Figure 4b). The rate of change in stem weight per tiller (range=–3.06 to 1.21 mg DM/tiller/d) was highly negative in October–November and usually positive in March–September (Figure 4c). The rate of change in tiller weight (range=–4.28 to 4.31 mg DM/tiller/d) was highly positive in April–May and highly negative in October–November (Figure 4d), which reflected variations in the rates for live laminae and stem, *i.e.* the rate of change in tiller weight was positively correlated with the rates of change in weights of live laminae and stem per tiller (r=0.892 and r=0.727, respectively; both P<0.001).

Herbage mass (range=23–560 g DM/m^2) was lowest in spring (March–April) and highest in summer (July–August) or autumn (October) (Figure 5a). Tiller density (range=3859–4875 tillers/m^2) remained almost constant for 2 years (Figure 5b).

Herbage mass was more closely associated with tiller weight than with tiller density, showing

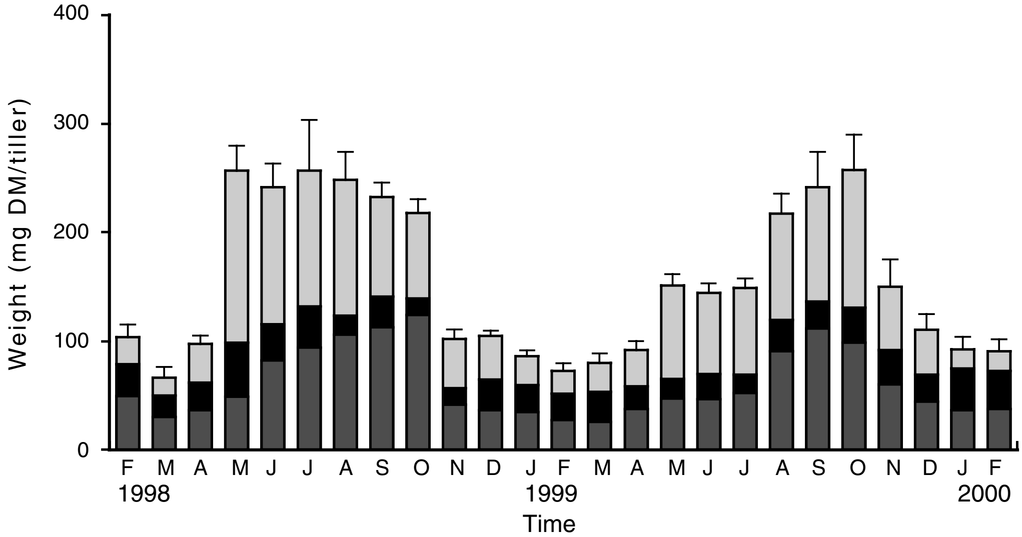

Figure 3. Tiller weight and its components: weights of live laminae ( ), dead laminae ( ) and stem (; inclusive of leaf sheaths) per tiller. Vertical bars show s.e. of mean for tiller weight.

a linear increase with increased tiller weight (Figure 6):

M = -37.0 + 1.45 W

(n=25, r=0.814, P<0.001) (1)

where M and W are herbage mass (g DM/m^2) and tiller weight (mg DM/tiller), respectively. The intercept was not significantly different from zero (P=0.319).

There was a negative linear relationship between log [tiller weight] and log [tiller density] across data from the current and previous (Hirata 1993; Hirata and Ueno 1993) studies (Figure 7):

log W = 8.02 − 1.63 log N

(n=85, r=−0.882, P<0.001) (2)

where N is tiller density (tillers/m^2). The slope was not significantly different from −3/2 at P=0.05, with a standard error of 0.096.

Discussion

Characteristics of tiller weight dynamics

Tiller weight ranged from 67–257 mg DM/tiller, being high from late spring (May) to mid-autumn (October) and low in the other half of the year (Figure 3). Such a range and a seasonal pattern in tiller weight are in close agreement with previous results from bahia grass pastures under cattle grazing (Hirata *et al.* 1986; Hirata 1996).

The rate of change in tiller weight (Figure 4d) reflected the April–May peaks in the rate of change in live lamina weight (Figure 4a) and the October–November troughs in the rate of change in stem weight (Figure 4c). We consider that the high rates of increase in live lamina weight in April–May (3.32 and 1.95 mg DM/tiller/d) are a spring flush that is achieved by consuming reserve substances in stolons and roots as the main energy pools (Hirata *et al.* 1990). A previous study in the same pasture (Pakiding and Hirata 2001) showed that the leaf appearance rate in bahia grass increased most sharply with increasing air temperature around this time of the year. In other months, the rates of change in live lamina weight were usually around zero (Figure 4a), indicating that leaf production was almost balanced with leaf death and consumption by animals during the grazing season, and with leaf death during the non-grazing season.

The high rates of decrease in stem weight in October–November (−3.06 and −1.20 mg DM/tiller/d; Figure 4c) suggest that reserve substances stored in stems during summer (shown by the positive rates of change in stem weight) were translocated into stolons and roots before the dormant winter season (Hirata *et al.* 1990). Although the 2 months partly overlap the grazing season, consumption by animals cannot explain such

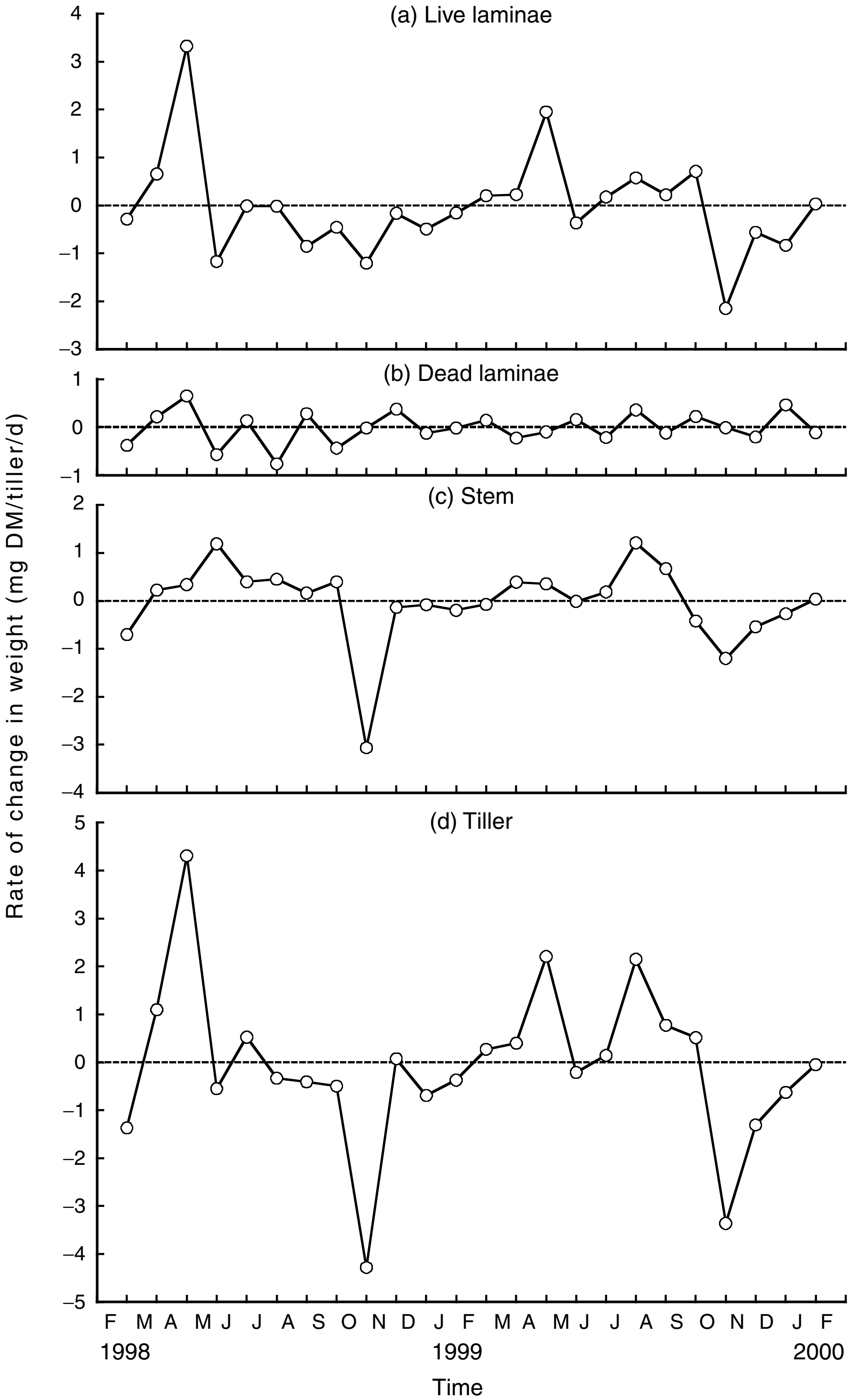

Figure 4. Rates of change in weights of (a) live laminae per tiller, (b) dead laminae per tiller, (c) stem (inclusive of leaf sheaths) per tiller and (d) tiller (live laminae + dead laminae + stem).

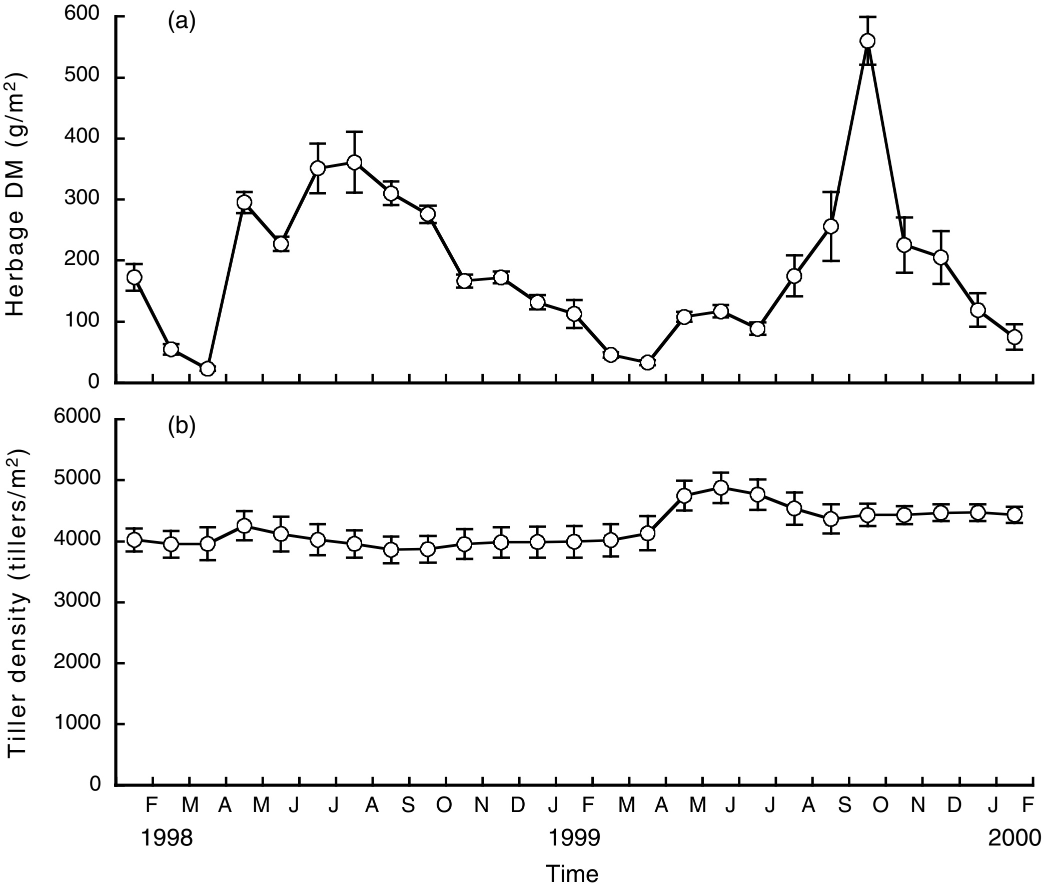

Figure 5. Changes in (a) herbage mass and (b) tiller density with time. Vertical bars show s.e. of mean.

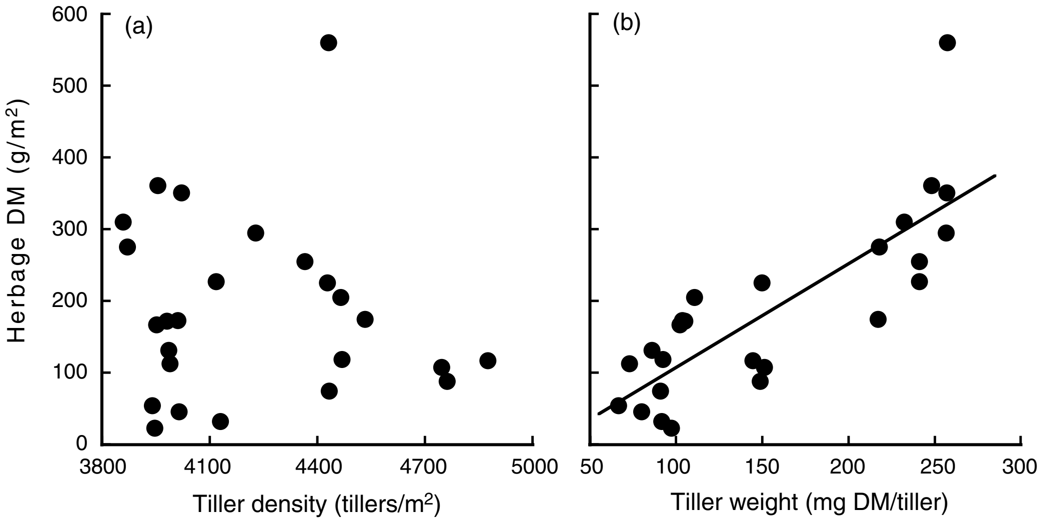

Figure 6. Relationships of herbage mass to (a) tiller density and (b) tiller weight. Regression line in (b) is M=−37.0+1.45W (r=0.814, P<0.001); where M and W are herbage mass and tiller weight, respectively.

great decreases in stem weight per tiller, because animals consume mainly live laminae.

When tiller weights of 67-257 mg DM/tiller (Figure 3) and their rates of change of −4.28 to 4.31 mg DM/tiller/d (Figure 4d) are compared with those in perennial ryegrass (*Lolium perenne*), *i.e.* a most common temperate grass, bahia grass is characterised by a greater tiller weight and a broader range in the rate of tiller weight change. The literature reports tiller weights of 1–90 mg DM/tiller and rates of 0.22–1.10 mg DM/tiller/d (summer-autumn) in perennial ryegrass (Chapman and Lemaire 1993; Hernández Garay *et al.* 1997).

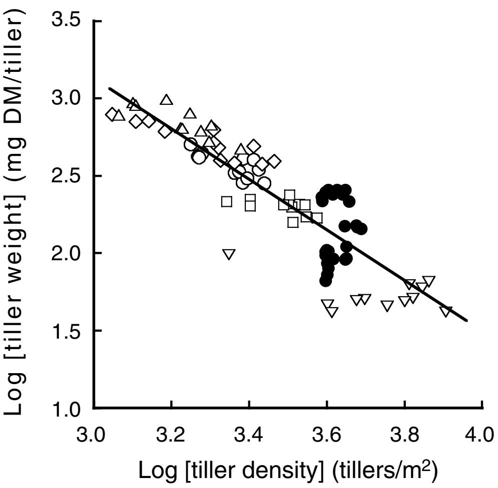

Figure 7. Relationship between log [tiller weight] and log [tiller density] across data from the current study (●) and previous studies (Hirata 1993; Hirata and Ueno 1993: cutting heights = 2 (▽), 7 (□), 12 (○), 17 (◇) and 22 (△) cm). Regression line is log W=8.02−1.63 log N (r=−0.882, P<0.001); where W and N are tiller weight and tiller density, respectively.

Relationships between herbage mass, tiller weight and tiller density

In contrast with the considerable seasonal variations in tiller weight (Figure 3) and herbage mass (Figure 5a), tiller density remained almost constant throughout 2 years (Figure 5b). Accordingly, the variations in herbage mass were largely explained by the variations in tiller weight, with no significant contribution by tiller density (Figure 6 and Equation 1). Matthew *et al.* (2000) point out that the seasonal stability of tiller density in bahia grass is a clear contrast to seasonally variable densities in many temperate grasses.

A decrease in tiller density was compensated for by an increase in tiller weight with a slope of −1.63, which was not significantly different from −3/2 at P=0.05 (Figure 7 and Equation 2). Such a negative linear relationship was not detected when only data from the current measurements (● in Figure 7) were used, due to the constancy of tiller density (Figure 5b), *i.e.* the narrow range covered by tiller density (3859–4875 tillers/m^2). In fact, previous examinations of the self-thinning rule have generally used data from swards with widely varying tiller densities under different management in terms of seeding, fertiliser application, defoliation and so forth (*e.g.* Terai and Kanda 1979; Chapman and Lemaire 1993; Hernández Garay *et al.* 1999). It has been shown that tiller density in bahia grass swards varies in a range of about 900–8500 tillers/m^2 (scale of about 10^3–10^4) in response to management strategies (Hirata 1993; Pakiding and Hirata 2000). The current analyses thus show that the tiller weight:density relationship in bahia grass as a clonal plant follows the −3/2 self-thinning rule (Yoda *et al.* 1963) in an almost entire range of tiller density of the grass.

Practical implications

In the low-altitude regions of south-western Japan, utilisation of bahia grass commences in mid- to late May (late spring) to ensure herbage availability. However, because of increasing pasture production with increasing temperature, this management tends to result in an oversupply of herbage in summer-autumn (*e.g.* Higashiyama and Hirata 1995; Hirata 2000b; Hirata and Pakiding 2001), which also leads to a reduction in herbage quality (*e.g.* Higashiyama and Hirata 1995; Hirata 1996). In fact, herbage mass showed considerable seasonal variations with peaks in summer-autumn (Figure 5a). These peaks originated from an increase in tiller weight in April–May (Figures 3 and 4d), which in turn was attributed to an increase in live lamina weight per tiller (Figure 4a). The results of the present study thus suggest a possibility of depressing the summer-autumn peak in herbage mass in a bahia grass pasture by starting its utilisation earlier than the conventional time by 2–4 weeks.

In addition, the present study showed high rates of decrease in stem weight in October–November, and these were considered to reflect the translocation of reserve substances stored in stems during summer into stolons and roots before the dormant winter season. There is thus a possibility that heavy defoliation of bahia grass in mid- to late autumn has some adverse effects on the persistence of this grass by decreasing energy pools in stolons and roots. Wilson (1998) reported that harvesting green panic in late autumn weakened the plants, allowing other species to invade in the following spring–summer.

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