Tiller dynamics in a bahia grass (*Paspalum notatum*) pasture under cattle grazing

M. HIRATA AND W. PAKIDING

*Grassland and Animal Production Division, Faculty of Agriculture, Miyazaki University, Miyazaki, Japan*

**Abstract**

Tiller dynamics were monitored for 4 years in a bahia grass (*Paspalum notatum*) pasture under cattle grazing. Total tiller density ranged from 3819–4875 tillers/m². Tiller appearance rate (TAR) ranged from 0.10–35.42 tillers/m²/d (0.02–12.03 tillers/1000 tillers/d), usually showing distinct peaks in late spring (May) or early summer (June). Tiller death rate (TDR) ranged from 0.52–17.30 tillers/m²/d (0.14–3.79 tillers/1000 tillers/d), with a tendency to peak in summer (June–August). The balance between TAR and TDR was positive in late spring (May) or early summer (June), and usually negative or close to zero in the other seasons. Relative TAR increased as leaf appearance rate (LAR) increased to about 0.09 leaves/tiller/d. Thereafter, the rate continued to increase with increasing LAR in spring (March–May), whereas it remained almost constant in summer and autumn (June–November). The rate of site filling, ranging from 0.0032–0.0461 tillers/leaf, decreased as herbage mass increased to about 77 g DM/m², and remained almost constant thereafter. Relative TDR increased exponentially with increasing mean daily air temperature. Tillers formed in autumn survived longer (half-life = 737 d) than those formed in the other seasons (half-life = 403–559 d). The results confirm that bahia grass tiller density remains stable because tillers are long-lived despite low rates of tiller appearance. The results also indicate that low relative TAR in bahia grass is attributable to low rates of site filling.

**Introduction**

In grassland-based animal production systems, persistence of pasture is a crucial factor in the sustainability of the systems. It is therefore important to understand the mechanisms behind the persistence of a pasture. In a grass pasture, persistence is dependent on the ability of the plant to maintain a high tiller density, and the ability of the individual tillers to maintain live (green) leaves, i.e., a photosynthetic organ and a major feed component for animals.

Bahia grass (*Paspalum notatum*), a sod-forming, warm season perennial, is widespread in the low-altitude regions of south-western Japan and used for both grazing and hay. It is well known that this grass forms a highly persistent sward that maintains tiller density and leaf mass under a wide range of management (Beaty et al. 1970, 1977; Stanley et al. 1977; Hirakawa et al. 1985; Hirata et al. 1986; Hirata 1993a, 1993b; Hirata and Ueno 1993).

Two studies were conducted in a bahia grass pasture grazed with cattle, in an effort to understand the mechanisms behind the persistence of this grass in terms of tiller and leaf dynamics. The first study monitored tiller dynamics for 4 years (May 1996–May 2000) in terms of tiller appearance rate (TAR), tiller death rate (TDR) and survival of individual tillers. The second study monitored leaf dynamics on tillers for 2 years (February 1998–February 2000) in terms of rates of leaf appearance, death and detachment and survival of individual leaves. Results from the first 2 years in the first study (May 1996–May 1998) indicated that bahia grass tiller density remains stable because tillers are long-lived.
despite low rates of tiller appearance (Pakiding and Hirata 1999). Results from the second study showed that high longevity of leaves appearing in mid- and late autumn is a crucial factor in the maintenance of live leaves during winter and that high leaf detachment rate during the growing season (late spring–mid-autumn) is a crucial factor for high live:dead leaf ratio in the season (Pakiding and Hirata 2001).

The second study also showed that rates of leaf appearance, death and detachment can be modelled in relation to meteorological or sward factors. However, such a modelling approach was not made to TAR or TDR in the previous paper (Pakiding and Hirata 1999), because the paper dealt with data only from the first half of the tiller dynamics study (May 1996–May 1998) and data on leaf dynamics during this period were not available. Tiller and leaf dynamics are not independent of each other; e.g. leaf appearance rate (LAR) determines the potential number of sites for tiller appearance, and thus relative TAR is expressed as LAR × rate of site filling (Davies 1974; Thomas 1980; Lemaire and Chapman 1996).

In the current paper, we present the whole 4-year (May 1996–May 2000) results of tiller dynamics of bahia grass under cattle grazing. Using these data, tiller dynamics of bahia grass were characterised again to confirm the previous findings about the mechanisms behind the persistence of this grass (Pakiding and Hirata 1999). At the same time, TAR and TDR were modelled in relation to meteorological or sward factors, taking account of the linkage of tiller appearance to leaf appearance.

**Materials and methods**

**The site, pasture and animals**

A 1.06 ha paddock of a Pensacola bahia grass pasture at Sumiyoshi Livestock Farm (31°59′N, 131°28′E), Miyazaki University, Japan, was used. The paddock was one of 5 paddocks (total area = 6.3 ha) rotationally grazed by Japanese Black cows.

During the grazing season (May to October–November) in 1996–1999, the paddock was grazed 6 times by 28–34 animals (mean live-weight of 450 kg) for 2–7 days (09.00–16.00 h each day) at 11–39 d intervals. The total duration of grazing was 22–32 d.

The paddock was fertilised with compound fertiliser and urea in 1996, 1998 and 1999, and with compound fertiliser in 1997. The fertilisation rates per ha were 77 kg N (March and August), 20 kg P (March) and 30 kg K (March) in 1996, 45 kg N (April), 20 kg P (April) and 30 kg K (April) in 1997, 97 kg N (April and September), 26 kg P (April) and 40 kg K (April) in 1998, and 70 kg N (April and August), 17 kg P (April) and 20 kg K (April) in 1999. The meteorological conditions are shown in Figure 1.

**Measurements**

Tiller dynamics of bahia grass were monitored from May 1996–May 2000 in 8 randomly selected 20 cm × 20 cm permanent quadrats in the paddock. All live tillers within the quadrats were tagged on May 18, 1996 with a wire ring (9 mm in diameter) with a coloured bead at their base and grouped as the original tillers. This group consisted of tillers with 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 on both a per unit ground area basis and a relative basis. Beads with 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 17 age categories according to the period of their initiation, with category A being the original tillers, i.e., formed before May 18, 1996 (pre-measurement); category B, summer 1996 (May 19–August 19); category C, autumn 1996 (August 20–November 13); category D, winter 1996–1997 (November 14–February 14); category E, spring 1997 (February 15–May 13); category F, summer 1997 (May 14–August 15); category G, autumn 1997 (August 16–November 14); category H, winter 1997–1998 (November 15–February 15); category I, spring 1998 (February 16–May 18); category J, summer 1998 (May 19–August 11); category K, autumn 1998 (August 12–November 14); category L, winter 1998–1999 (November 15–February 20); category M, spring 1999 (February 21–May 14); category N, summer 1999 (May 15–August 15); category O, autumn 1999 (August 16–November 14).
Tiller dynamics in bahia grass under grazing

category P, winter 1999–2000 (November 18–February 15); and category Q, spring 2000 (February 16–May 18).

Herbage mass (above a 3 cm height) in the quadrats was estimated immediately before each tagging using an electronic capacitance probe (PastureProbe™, Mosaic Systems Ltd, New Zealand) (Hirata et al. 1993). Calibration equations were developed every 1–2 months by cutting samples from the paddock.

The rate of site filling (F_S, tillers/leaf) was calculated using data for tiller appearance (present study) and leaf appearance (Pakiding and Hirata 2001) in the overlapped 2-year period (February 1998–February 2000):

\[ F_S = \frac{R'_{\text{tiller,app}}}{R_{\text{leaf,app}}} \]  \hspace{1cm} (1)

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

The proportion of tillers surviving (S) with time (t, days) was fitted by an exponential equation as:

\[ S = \exp(-b \, t) \]  \hspace{1cm} (2)

where \( b \) is the decay constant (proportion/d). Then the half-life of tillers (t_{1/2}) (the time in days taken for half the tillers to die) was calculated as:

\[ t_{1/2} = \ln 2 / b \]  \hspace{1cm} (3)

Results

Herbage mass

Herbage mass was lowest in late winter to mid-spring (February–April) and highest in summer (July–August) or autumn (September–October) (Figure 2). The peak herbage mass was higher in 1997 and 1999 than in 1996 and 1998.
Figure 2. Changes in herbage mass. Vertical bars indicate s.e. of mean.

Tiller density

Total tiller density (range = 3819–4875 tillers/m²) remained almost constant for 4 years, except for an increase in mid-spring to early summer (April–June) and a subsequent decrease until early autumn (September) in 1996 and 1999 (Figure 3). Density of original tillers (category A) decreased with time and accounted for 18.2% of the final total tiller density. On the other hand, proportion of tillers appearing in the following seasons increased. Tillers formed in spring (categories E, I, M and Q), summer (categories B, F, J and N) and autumn (categories C, G, K and O) showed relatively high densities.

Tiller appearance and death

Seasonal patterns of TAR, TDR and their balance were similar on a per unit ground area basis (Figure 4) and on a relative basis (Figure 5). TAR ranged from 0.10–35.42 tillers/m²/d (0.02–12.03 tillers/1000 tillers/d), usually showing distinct peaks in late spring (May 1998–2000) or early summer (June 1996). Seasonal means of TAR in summer, autumn, winter and spring were 8.99, 5.46, 1.73 and 8.63 tillers/m²/d (2.46, 1.40, 0.43 and 2.18 tillers/1000 tillers/d), respectively.

TDR ranged from 0.52–17.30 tillers/m²/d (0.14–3.79 tillers/1000 tillers/d) (Figures 4 and 5). It tended to show peaks in summer (June–August). Seasonal means of TDR in summer, autumn, winter and spring were 8.33, 6.87, 1.91 and 4.27 tillers/m²/d (1.92, 1.62, 0.47 and 1.06 tillers/1000 tillers/d), respectively.

The balance between TAR and TDR (TAR minus TDR) was positive in late spring (May 1997–2000) or early summer (June 1996), and usually negative or close to zero in other seasons (Figures 4 and 5).

Figure 4. Tiller appearance rate, tiller death rate and their balance on a per unit ground area basis. Vertical bars indicate s.e. of mean.
Figure 5. Tiller appearance rate, tiller death rate and their balance on a relative basis. Vertical bars indicate s.e. of mean.

Figure 6. Relationship between relative tiller appearance rate and leaf appearance rate in spring (○), summer (△) and autumn (▽).
Relative TAR (Figure 5) increased as LAR increased to about 0.09 leaves/tiller/d (Figure 6). Thereafter, the rate continued to increase with increasing LAR in spring (March–May), whereas it remained almost constant in summer (June–August) and autumn (September–November). The rate of site filling ($F_s$, tillers/leaf), ranging from 0.0032–0.0461 tillers/leaf, decreased as herbage mass ($M$, g DM/m$^2$) increased to about 77 g DM/m$^2$, and remained almost constant thereafter, as shown by the broken-line function (Figure 7):

$$F_s = \max[0.0134, 0.0476 - 0.00044M]$$

($r = 0.732, P<0.001$) (4)

![Figure 7. Relationship between rate of site filling ($F_s$) and herbage mass ($M$) in spring (○), summer (△) and autumn (▽). $F_s = \max[0.0134, 0.0476-0.00044M], r = 0.732, P<0.001.$](image)

![Figure 8. Relationship between relative tiller death rate ($R_{tillerdeath}$) and mean daily air temperature ($T$) for 3 ranges in herbage mass ($M$): $M<150$ g DM/m$^2$ (○), 150≤$M<300$ g DM/m$^2$ (△) and $M\geq300$ g DM/m$^2$ (▽). $R_{tillerdeath} = 0.00021\exp(0.084T), r = 0.710, P<0.001.$](image)
Relative TDR (R'_{tiller,death, tillers/tiller/d}; Figure 5) increased exponentially with increasing mean daily air temperature (T, °C) (Figure 8):

\[ R'_{tiller,death} = 0.00021 \exp(0.084 T) \]

\( r = 0.710, P<0.001 \) (5)

There was no clear effect of herbage mass on this relationship.

Tiller longevity

Survival of tillers decreased exponentially with time after appearance (Figure 9). Tillers formed in autumn (categories C, G, K and O) survived longer (half-life = 737 d) than those formed in the other seasons (half-life = 403–559 d) (Figure 9 and Table 1).

Table 1. Decay constant (b, proportion/d) and half-life \( t_{1/2}, \text{d} \) for survival of tillers initiated in different seasons (Equations 2 and 3), with correlation coefficients \( r \) and level of significance \( P \).

<table>
<thead>
<tr>
<th>Season of initiation</th>
<th>b</th>
<th>( t_{1/2} )</th>
<th>r</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer</td>
<td>0.00124( ^a )</td>
<td>559</td>
<td>-0.963</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Autumn</td>
<td>0.00094( ^b )</td>
<td>737</td>
<td>-0.882</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Winter</td>
<td>0.00172( ^c )</td>
<td>403</td>
<td>-0.829</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Spring</td>
<td>0.00141( ^a )</td>
<td>492</td>
<td>-0.900</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

\( ^a \) Values followed by the same letter are not significantly different at 5% level.

Discussion

Tillering characteristics of bahia grass

The 4-year results of tiller dynamics of bahia grass presented in this paper confirm the main findings from the first 2 years (Pakiding and Hirata 1999), i.e., the grass maintains a very stable tiller density because tillers are long-lived with low rates of tiller death, despite low rates of tiller appearance.

The range in TAR of 0.10–35.42 tillers/m\(^2\)/d (0.02–12.03 tillers/1000 tillers/d) is in the lower end of TAR ranges in grasses reported so far. It has been reported that TAR ranged from 23–239 tillers/m\(^2\)/d and from 2.9–9.2 tillers/1000 tillers/d in cut perennial ryegrass swards (Lolium perenne) (Korte 1986), and from 6–308 tillers/m\(^2\)/d and from 2.1–48.9 tillers/1000 tillers/d in grazed swards (Chapman et al. 1983; Korte et al. 1984; Bullock et al. 1994; Hernández Garay et al. 1997). In 2 grazed Agrostis species (Chapman et al. 1983; Jónsdóttir 1991; Bullock et al. 1994), Festuca rubra (Jónsdóttir 1991) and Poa irrigata (Jónsdóttir 1991), TAR was in the range of 1.3–44.6, 0.8–8.8 and 0.0–9.3 tillers/1000 tillers/d, respectively.

The range in TDR of 0.52–17.30 tillers/m\(^2\)/d (0.14–3.79 tillers/1000 tillers/d) contrasts with the 13–234 tillers/m\(^2\)/d (0.9–14.9 tillers/1000 tillers/d).
tillers/d) in cut perennial ryegrass swards (Korte 1986), and 7–79 tillers/m²/d (1.4–15.2 tillers/1000 tillers/d) in grazed swards (Korte et al. 1984; Bullock et al. 1994; Hernández Garay et al. 1997). In grazed Agrostis stolonifera (Jónsdóttir 1991; Bullock et al. 1994), Festuca rubra (Jónsdóttir 1991) and Poa irrigata (Jónsdóttir 1991), TDR was in the ranges of 1.5–12.5, 0.7–5.2 and 0.0–7.0 tillers/1000 tillers/d, respectively. Thus, bahia grass is characterised by low rates of tiller death.

Such low rates of tiller death are reflected in the high longevity of tillers. The half-life of bahia grass tillers (403–737 d) greatly exceeds the half-life of tillers of 36–143 d in cut perennial ryegrass (Korte 1986), and of 60–230 d in grazed perennial ryegrass (McKenzie 1997) (calculation by the present authors) and is similar to the 437–746 d in northern wheatgrass (Agropyron dasystachyum) (Zhang and Romo 1995) (calculation by the present authors).

Our current results also confirm that survival of tillers formed in autumn is superior to that of tillers formed in summer, winter and spring. As discussed previously (Pakiding and Hirata 1999), this may be attributable to the fact that autumn tillers had less competition with parent tillers for nutrients and light, because autumn tillers emanated from reproductive tillers and replaced the space of reproductive tillers soon after they died.

In addition, the current paper has provided new information about tillering characteristics in bahia grass. Relative TAR is expressed as LAR × rate of site filling (Davies 1974; Thomas 1980; Lemaire and Chapman 1996), and the previous study showed that bahia grass has similar LAR to many other grasses (Pakiding and Hirata 2001). Therefore, the low relative TAR in bahia grass discussed above can be attributable to low rates of site filling. In fact, the range in the rate of site filling of 0.0032–0.0461 tillers/leaf is much lower than 0.1–0.5 tillers/leaf in tall fescue (Simon and Lemaire 1987), 0.2–0.5 in perennial ryegrass and 0.1–0.5 in Agrostis species (Chapman et al. 1983) (calculation by the present authors), though limited information is available about the rate of site filling in grasses growing as a sward and the rate would vary to some extent with factors such as leaf area index (see later discussion) and nitrogen availability (Simon and Lemaire 1987; Lemaire and Chapman 1996).

As mentioned earlier, the paddock where measurements were made was grazed by animals with almost constant numbers (28–34 head) and mean liveweights (about 450 kg) throughout the grazing season of the 4-year period. Consequently, as the growth rate of bahia grass increased from spring to summer, herbage mass increased sharply (Figure 2), reducing grazing pressure. In addition, the paddock was not utilised in winter–early spring because bahia grass is dormant in these seasons. Therefore, one may question whether the high tiller longevity of bahia grass presented in our current study is true under wider management conditions, particularly under intensive defoliation. However, our data from a 4-year experiment on bahia grass swards under different nitrogen rates and cutting heights (W. Pakiding and M. Hirata, unpublished) show that this grass maintains high tiller longevity (half-life = 408–537 d) with a trend for longevity to increase as management becomes more severe (low nitrogen rate or low cutting height).

Modelling tiller appearance and death

Relative TAR is expressed as LAR × rate of site filling (Davies 1974; Thomas 1980; Lemaire and Chapman 1996). The previous study successfully modelled LAR in relation to mean daily air temperature (Pakiding and Hirata 2001). In the current study, the rate of site filling was modelled in relation to herbage mass, using a broken-line function. The rate decreased as herbage mass increased to about 77 g DM/m², and remained almost constant thereafter. This trend basically agrees with our knowledge that actual tillering is lower than potential tillering and decreases as the sward canopy becomes dense and closed because of increased competition of tillers and decreased light at tiller bases (Simon and Lemaire 1987; Lemaire and Chapman 1996). However, the broken-line function we obtained was due to 3 spring data sets, and excluding these, the rate of site filling was almost independent of herbage mass. At the same time, the model explained only 54% of the variation in the rate of site filling. Further data collection is therefore needed for evaluating the effects of season and herbage mass separately and developing a better model.

Relative TDR was modelled in relation to mean daily air temperature. Lemaire and Chapman (1996) listed the removal of apices by grazing animals as a major cause of tiller death. They also listed carbon starvation resulting from competition for light as another important cause. The
positive relationship between relative TDR and air temperature may partly reflect the positive effect of grazing on tiller death, because the pasture was grazed during late spring–autumn (May to October–November) with higher temperatures. On the other hand, there was no apparent effect of herbage mass on the relationship between relative TDR and temperature, suggesting that competition for light is not a crucial factor for tiller death in bahia grass. Since the model accounted for only 50% of the variation in relative TDR, further studies are warranted to enhance the predictive ability of the model.

Conclusions

Bahiagrass commonly forms a highly persistent sward. This was confirmed by the constant total tiller density of 3819–4875 tillers/m² during our 4-year study. The study also confirmed that tiller density in bahia grass is so stable because of high longevity of tillers (low TDR) despite low TAR. In addition, the present study showed that low relative TAR in bahia grass is attributable to low rates of site filling. Further studies are necessary to develop better models of tiller appearance and death, because current models showed relatively poor predictive ability.

Acknowledgements

We thank Mr K. Fukuyama and the staff of the Sumiyoshi Livestock Farm for the management of pasture and cattle. WP also thanks the Japanese Ministry of Education, Science, Sports and Culture for financial support in his postgraduate study.

References


(Received for publication October 9, 2000; accepted January 10, 2001)