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Dynamics in lamina size in a bahia grass (*Paspalum notatum*) pasture under cattle grazing

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Abstract

Dynamics in weight, length and weight per unit length of individual laminae (live and dead) on a tiller were investigated for 2 years in a bahia grass (*Paspalum notatum*) pasture under cattle grazing. For the youngest fully expanded lamina, its history, mature length and fate were also estimated to evaluate the degree of removal of lamina length through defoliation by animals and detachment as litter fall. Lamina weight per tiller, ranging from 36–200 mg/tiller DM, was high in May–October (late spring to mid-autumn) and low in the other half of the year. The youngest to sixth youngest laminae (L1–L6; usually live laminae) accounted for 62.5–91.0% of the lamina weight per tiller. Weight, length and weight per unit length of laminae (L1–L12) ranged from 0.0–48.0 mg DM, 0–326 mm and 0.035–0.255 mg/mm DM, respectively, often varying with lamina age and season. Variations in lamina weight were largely explained by variations in lamina length, with no consistent contribution by lamina weight per unit length. Laminae lost 16–64% of their mature length through grazing by animals before and immediately after attaining full expansion. In the 2 months after full expansion, they lost an additional 24–79% of mature length through defoliation by animals and detachment as litter fall, with total removal of 88–99%. The study shows how the history and fate of individual laminae on a tiller can be estimated in terms of their appearance and development. This model, in combination with previously developed models for dynamics in tiller density and tiller weight, is useful for simulation studies on canopy dynamics in bahia grass swards.

Introduction

Analysing a grass sward canopy in terms of morphogenetic and structural components is important for understanding the mechanisms by which the components contribute to pasture production and utilisation (Lemaire 1988; Chapman and Lemaire 1993; Lemaire and Chapman 1996; Hirata 1996, 1999, 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). It is also well adapted to the low-altitude regions of south-western Japan where it is used for both grazing and hay. In previous studies, we analysed a sward canopy of bahia grass under cattle grazing, focusing on tiller appearance and death (Pakiding and Hirata 1999; Hirata and Pakiding 2001), on leaf appearance, death and detachment as litter fall (Pakiding and Hirata 2001), and on tiller weight (Hirata and Pakiding 2002). It was shown that tiller density of bahia grass was stable because of high longevity of tillers (low tiller death rate) despite low tiller appearance rate. Accordingly, variations in herbage mass per unit land area were largely explained by variations in tiller weight, most of which (43–81%) was accounted for by leaf (lamina) weight.

Lamina (leaf) weight per tiller is a sum of the weights of individual laminae on a tiller, which are the products of the length and weight per unit length of individual laminae (Figure 1). In expanding leaves (*i.e.* the youngest live leaves on

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a tiller), lamina length is determined as a balance between extension and defoliation by grazing animals (Figure 1, upper left). Lamina weight per unit length is also determined as a balance between extension and defoliation, because the weight per unit length of a lamina is not constant from its tip to its base (Tallowin *et al.* 1989). In leaves after full expansion (*i.e.* mature, senescent or dead leaves), lamina length is determined as the length at full expansion less any amount removed by defoliation by animals or detachment as litter fall (Figure 1, bottom). Lamina weight per unit length is similarly determined by the weight per unit length at full expansion and the degree of defoliation and detachment. Lamina length at full expansion equals the mature lamina length (*i.e.* potential lamina length) less the length removed by defoliation during extension.

Based on the above mechanics, the present study focused on individual laminae on a tiller, as the fourth step in the analysis of the sward canopy of bahia grass. Weight, length and weight per unit length of individual laminae (live and dead) on a tiller were measured for 2 years in the same pasture as in the previous studies (Pakiding and Hirata 1999, 2001; Hirata and Pakiding 2001, 2002). For the youngest fully expanded lamina, its history, mature length and fate were also estimated to evaluate the residual proportion of lamina length after defoliation by animals and detachment as litter fall. The aims of the study were: (1) to characterise the dynamics in the lamina size variables; (2) to examine contributions by individual laminae to lamina weight per tiller; (3) to compare contributions of length and weight per unit length to weight of individual laminae; and (4) to evaluate the influence of defoliation by animals and detachment as litter fall on lamina length.

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, 2002), *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 1 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 30–34 animals (mean liveweight = 450 kg) for 4–7 days (09.00–16.00 h each day) at 11–38 d intervals. The total duration of grazing was 30–32 d. In addition to grazing, the paddock was mown to a height of about 10 cm above ground level on April 13, 1998 and April 20, 1999, to remove spring weeds.

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.

Measurements

Measurements were made monthly from February 1998–February 2000. On each occasion, 40 vegetative tillers were randomly selected in the paddock and sampled at ground level. Every care was taken to select tillers at random, *i.e.* tillers were selected irrespective of their size and degree of defoliation (grazed or non-grazed). The sample number of 40 was determined taking account of the labour requirements for the measurements, within the range used in past studies on tiller and/or lamina characteristics in a grazed sward (*c.* 25–100 tillers; *e.g.* Wilson and Mannetje 1978; Chapman *et al.* 1983; Barthram and Grant 1984; Tallowin *et al.* 1989).

Each tiller was separated into individual laminae (live and dead: L1, L2, L3 and so on; L1 = the uppermost or the youngest lamina) and stem (inclusive of leaf sheaths). For expanding leaves (usually L1–L3), laminae were cut at their lower (proximal) end, *i.e.* emerging point from the enclosing sheaths. The samples were oven-dried at 85°C for 48 h for determination of dry weight, after recording the length of individual laminae.

Data analysis: weight, length and weight per unit length of laminae

Weight, length and weight per unit length of individual laminae on a tiller were analysed for L1–L12, because sampled tillers seldom had >12 laminae. For each measurement occasion, when a tiller did not have a lamina of a specific age class

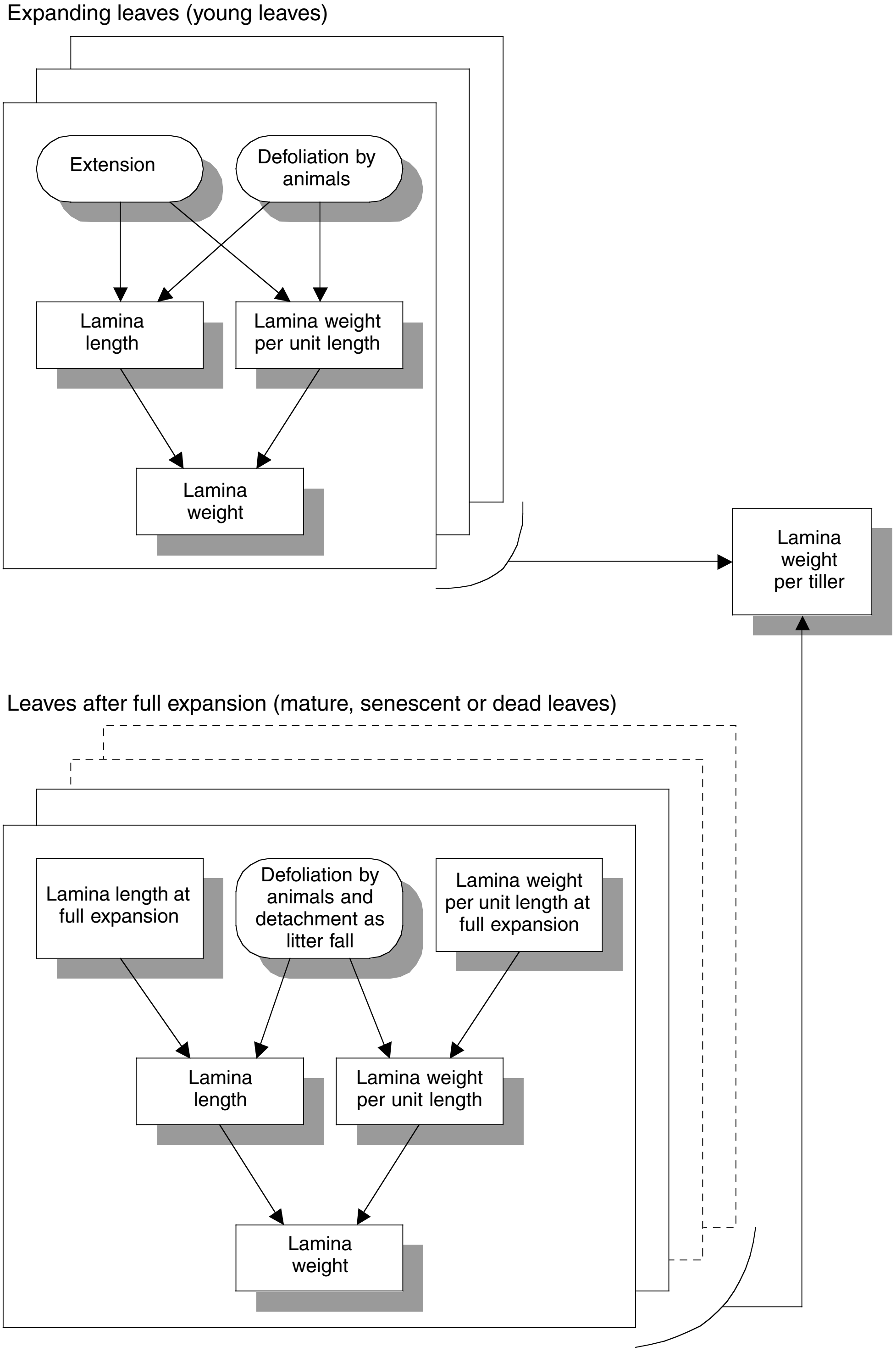


Figure 1. A diagrammatic representation of the relationships between lamina size variables involved in lamina weight per tiller, and the effects of lamina extension, defoliation by grazing animals and detachment as litter fall on the variables. Defoliation and detachment take place as partial or complete removal of a single lamina.

(any of L1–L12), the weight and the length of the lamina were regarded as zero and these zero values were used in producing mean lamina weight and mean lamina length of that class over the 40 tillers. On the other hand, the missing lamina was excluded from the calculation of mean lamina weight per unit length. As a result of this, when all 40 tillers lacked a lamina of a specific age class, the mean lamina weight per unit length for that class was not obtained (see L11 and L12 in Figure 6).

Data analysis: evaluating the effect of defoliation and detachment on lamina length

To evaluate the effect of defoliation and detachment on lamina length, the history, mature length and fate of a lamina that existed as L4 on each measurement occasion in May–October were estimated, using the following model. L4 was selected to evaluate the effect at full expansion of a lamina (see below and Figure 8); *i.e.* L4 was regarded as the youngest fully expanded lamina because laminae of bahia grass elongate when they are the youngest to third-youngest laminae (L1–L3; Hirata 2000).

History of L4. Because of the random sampling of tillers, L4 laminae on a measurement occasion were at different stages of development ranging from an early L4 stage (immediately after becoming L4) to a late L4 stage (immediately before becoming L5); and therefore the developmental stage of each L4 on the observation date ($S_{D,t}$, $t = 0$) was set at 4.5 as a mean. Then, the developmental stage was traced back by progressively subtracting the leaf appearance rate (LAR, leaves/tiller/d) of the previous day until the stage value was nearest to 4, 3, 2 and 1; *i.e.* to estimate the very date when the lamina became L4, L3, L2 and L1, respectively:

$$S_{D,t-1} = S_{D,t} - R_{app,t-1} \qquad (1)$$

where $S_{D,t-1}$ and $S_{D,t}$ are the developmental stages on Day $t - 1$ and Day t, respectively, and $R_{app,t-1}$ is LAR on Day $t - 1$. $R_{app,t-1}$ was estimated using the equation developed in the same paddock as in the present study (Pakiding and Hirata 2001):

$$R_{app,t-1} = 0.117[(T_{t-1} - 7.6)/6.4]^{3.6} / [1 + ((T_{t-1} - 7.6)/6.4)^{3.6}] \qquad (2)$$

where T_{t-1} is the mean daily air temperature (°C) on Day $t - 1$.

Mature length of L4. Mature length (*i.e.* potential length) of L4 (L_M, mm) was estimated as:

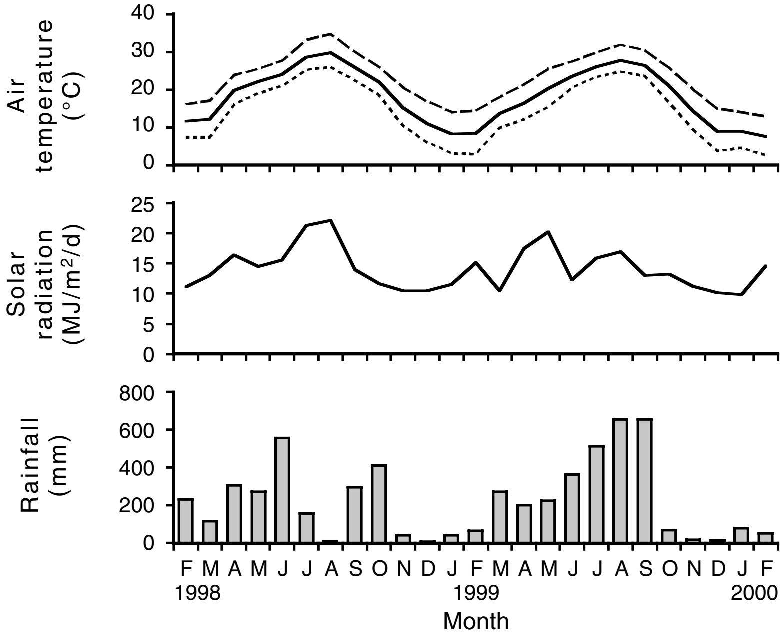


Figure 2. Monthly means of maximum (– – – –), mean (———) and minimum (- - - - -) daily air temperatures, daily total short-wave solar radiation and monthly totals of rainfall during the study.

$$L_M = R_{ext,L1}/R_{app,L1} + R_{ext,L2}/R_{app,L2} + R_{ext,L3}/R_{app,L3} \quad (3)$$

where $R_{ext,L1}$, $R_{ext,L2}$ and $R_{ext,L3}$ are lamina extension rate (LER, mm/d) and $R_{app,L1}$, $R_{app,L2}$ and $R_{app,L3}$ are LAR (leaves/tiller/d) when the lamina remained L1, L2 and L3, respectively. The 3 LARs ($R_{app,Ln}$, n = 1, 2 or 3), as for Equation 2, were estimated from the mean daily air temperature during the corresponding periods estimated as above:

$$R_{app,Ln} = 0.117[(T_{Ln} - 7.6)/6.4]^{3.6}/[1 + ((T_{Ln} - 7.6)/6.4)^{3.6}] \quad (4)$$

where T_{Ln} is the mean daily air temperature (°C) when the lamina remained Ln (n = 1, 2 or 3). The 3 LERs ($R_{ext,Ln}$, n = 1, 2 or 3) were estimated also from the mean daily air temperature during the corresponding periods, using equations developed for bahia grass (W. Pakiding and M. Hirata, unpublished data):

$$R_{ext,L1} = -11.7 + 1.1T_{L1} \quad (5)$$

$$R_{ext,L2} = 0.961(-11.7 + 1.1T_{L2}) \quad (6)$$

$$R_{ext,L3} = 0.627(-11.7 + 1.1T_{L3}) \text{ (for spring)} \quad (7a)$$

$$= 0.374(-11.7 + 1.1T_{L3}) \text{ (for summer–autumn)} \quad (7b)$$

where T_{L1}, T_{L2} and T_{L3} are the mean daily air temperatures (°C) as defined earlier.

Fate of L4. The developmental stage of L4 was calculated not only backward (history) but also forward to estimate the age class of the lamina at the next 2 measurements, by progressively adding LAR of the subsequent day until the next 2 measurement dates:

$$S_{D,t+1} = S_{D,t} + R_{app,t} \quad (8)$$

where $S_{D,t+1}$ is the developmental stage on Day t+1 and $R_{app,t}$ is LAR on Day t. $R_{app,t}$ was estimated from the mean daily air temperature on Day t (T_t, °C), using Equation 2.

Residual proportion of lamina length. The residual proportion of lamina length was defined as [observed lamina length]/[estimated mature lamina length (L_M; Equation 3)], and calculated for the time of full expansion (at the measurement as L4) and 1 and 2 months later (the next 2 measurements). Because laminae before and at full expansion rarely experience detachment as litter fall (Figure 1), a small residual proportion of lamina length at full expansion indicates large relative removal of lamina by defoliation by animals. A small residual proportion at the subsequent observations reflects large relative removal through both defoliation by animals and detachment as litter fall.

Results and discussion

Weight, length and weight per unit length of laminae

Lamina weight per tiller, ranging from 36–200 mg/tiller DM, was high in May–October (late spring to mid-autumn) and low in the other half of the year (Figure 3). L1–L6 (usually live laminae) accounted for 62.5–91.0% (mean = 76.1%) of total lamina weight per tiller.

Lamina weight ranged from 0.0–48.0 mg DM, with an overall trend of: L3 (overall mean = 17.1 mg) ≈ L4 (17.0 mg) > L5 (13.6 mg) > L6 (9.9 mg) ≈ L2 (9.5 mg) > L7 (7.5 mg) > L8 (5.4 mg) > L9 (3.5 mg) > L1 (2.8 mg) > L10 (2.0 mg) > L11 (1.2 mg) > L12 (0.5 mg) (Figure 4). Seasonal variations in lamina weight were relatively large in L2–L6, small in L1 and L7–L9 and almost nil in L10–L12. The seasonal patterns in L3–L6 were similar to that of lamina weight per tiller.

Lamina length ranged from 0–326 mm, with an overall trend of: L3 (overall mean = 150 mm) > L4 (134 mm) > L2 (116 mm) > L5 (103 mm) > L6 (73 mm) > L1 (57 mm) = L7 (57 mm) > L8 (41 mm) > L9 (28 mm) > L10 (17 mm) > L11 (11 mm) > L12 (4 mm) (Figure 5). Seasonal variations in lamina length were relatively large in L1–L6, small in L7–L9 and almost nil in L10–L12. Patterns in L1–L6 were markedly seasonal with relatively high values in May–October and low values in the other half of the year.

Lamina weight per unit length ranged from 0.035–0.255 mg/mm DM, with an overall trend of: L6 (overall mean = 0.138 mg) ≈ L7 (0.135 mg) ≈ L5 (0.134 mg) ≈ L8 (0.131 mg) ≈ L9 (0.127 mg) ≈ L4 (0.126 mg) ≈ L10 (0.122 mg) ≈ L11 (0.118 mg) ≈ L12 (0.116 mg) ≈ L3 (0.110 mg) > L2 (0.079 mg) > L1 (0.048 mg) (Figure 6). In each lamina, the weight per unit length was relatively constant throughout the 2 years.

Hirata *et al.* (1996) reported weight, length and weight per unit length of L4 of Pensacola bahia grass in June and August (summer) as 23–27 mg DM, 191–242 mm and 0.096–0.138 mg/mm DM, respectively. Values from the present study (18–30 mg DM, 131–223 mm and 0.129–0.144 mg/mm DM; Figures 4–6) are of the same order.

However, compared with lengths reported by Hirata (1996) (*i.e.* mean over the grazing season = 47, 115, 147, 126, 93, 90, 68, 54, 29 and 16 mm in L1–L10, respectively), the present study showed 47–92% longer laminae in L1–L5 (91, 174, 217, 189, 145, 99, 73, 51, 36 and 22 mm in L1–L10, respectively; Figure 5). Such differences in the length of younger laminae may be attributed to differences in defoliation intensity, LER (through air temperature and nutrient state of plants) and duration of regrowth after defoliation. Tallowin *et al.* (1989) reported that weight per unit length of the youngest and second youngest fully expanded laminae in *Poa trivialis*, *Agrostis stolonifera*, *Lolium perenne* and *Holcus lanatus* in April and June (mid-spring and early summer) ranged from 0.03–0.05, 0.05–0.07, 0.06–0.11 and 0.06–0.08 mg/mm DM, respectively (mean over 4 quarters). In the present study, values for L4 and L5 in the same months were 0.119–0.156 mg/mm DM (Figure 6), indicating that lamina weight per unit length in bahia grass is higher than that in the temperate grasses.

Lamina weight increased as lamina length increased, with a trend for the weight at the same length to be ranked L1 < L2 < L3 < L4–L12 (Figure 7a). Fitting the data to a power function or an allometry function resulted in:

$$W_{\mathrm{lamina}} = 0.028L_{\mathrm{lamina}}^{1.13} \quad (R^2 = 0.977, P<0.001, n = 25) \text{ (for L1)} \tag{9a}$$

$$= 0.038L_{\mathrm{lamina}}^{1.15} \quad (R^2 = 0.986, P<0.001, n = 25) \text{ (for L2)} \tag{9b}$$

$$= 0.044L_{\mathrm{lamina}}^{1.18} \quad (R^2 = 0.972, P<0.001, n = 25) \text{ (for L3)} \tag{9c}$$

$$= 0.116L_{\mathrm{lamina}}^{1.02} \quad (R^2 = 0.973, P<0.001, n = 216) \text{ (for L4–L12)} \tag{9d}$$

where W_{lamina} and L_{lamina} denote lamina weight (mg DM) and lamina length (mm), respectively. By contrast, there were no such consistent relationships between lamina weight and weight per unit length (Figure 7b). The estimated exponent values in the weight–length relationships for L1, L2 and L3 (Equations 9a, 9b, 9c) were significantly different from 1 at P<0.05 (95% confidence interval = 1.03–1.23, 1.08–1.23 and 1.09–1.28, respectively), and that for L4–L12 (Equation 9d) was not (95% confidence interval = 1.00–1.05). This indicates that lamina weight per unit length in L1–L3 increased as lamina length increased, whereas that in L4–L12 tended to remain stable over the entire range of lamina length.

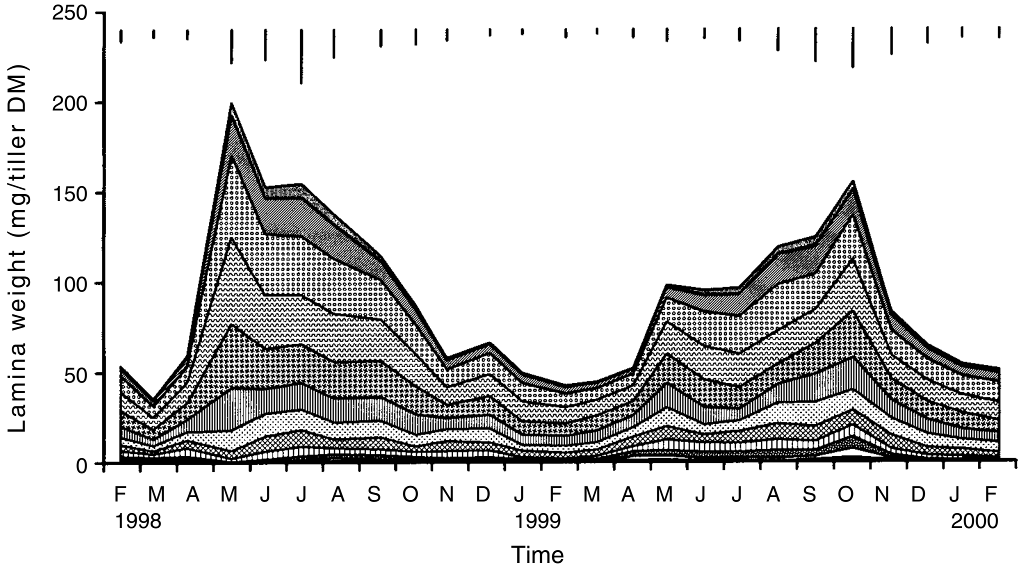


Figure 3. Lamina weight per tiller as a sum of weights of individual laminae; L1 (the youngest lamina) to L12 from top to bottom. Vertical bars show s.e. of mean for total lamina weight per tiller (L1 + L2 + … + L12).

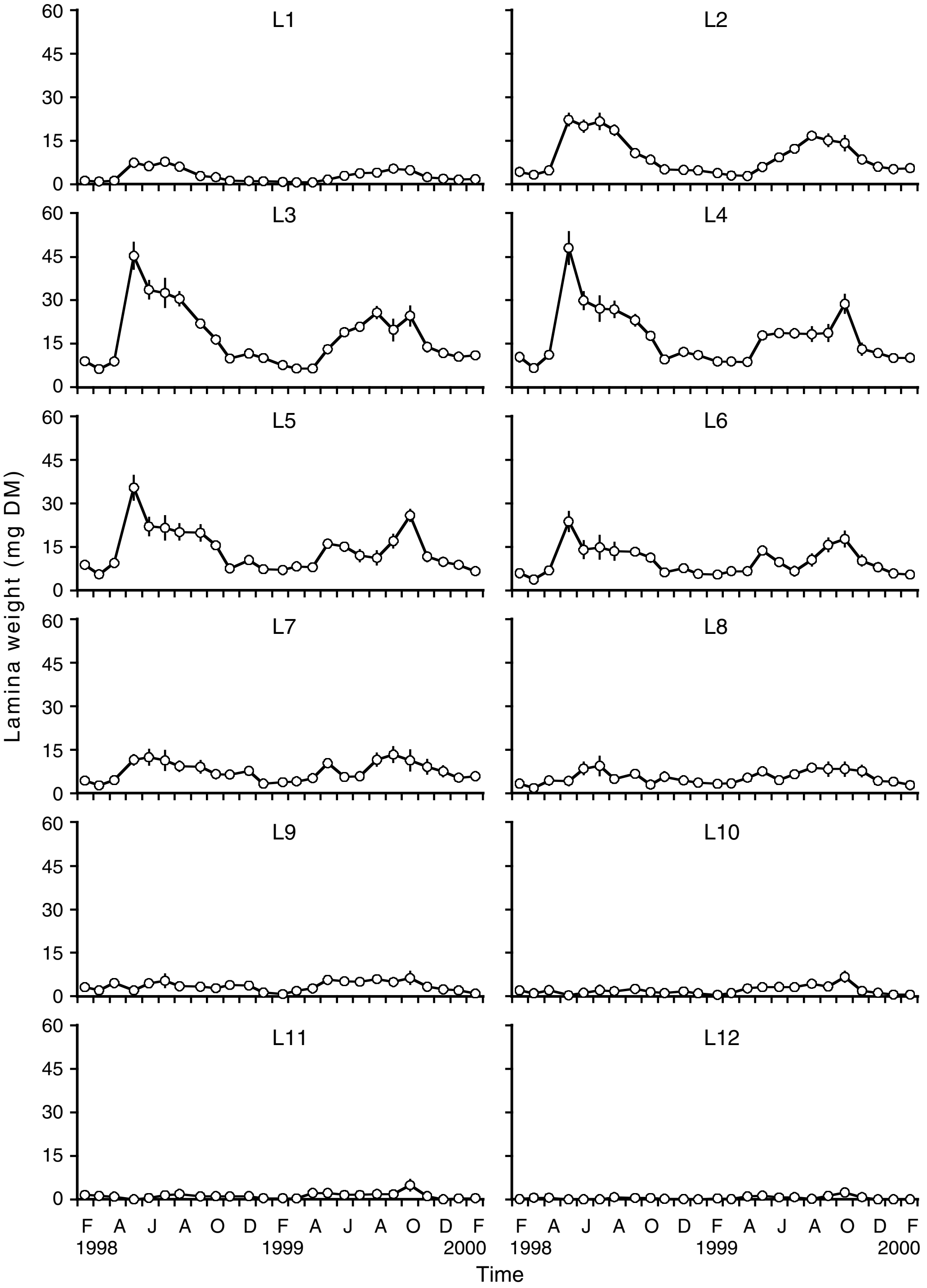


Figure 4. Weight of individual laminae (L1 = the youngest lamina). Vertical bars show s.e. of mean.

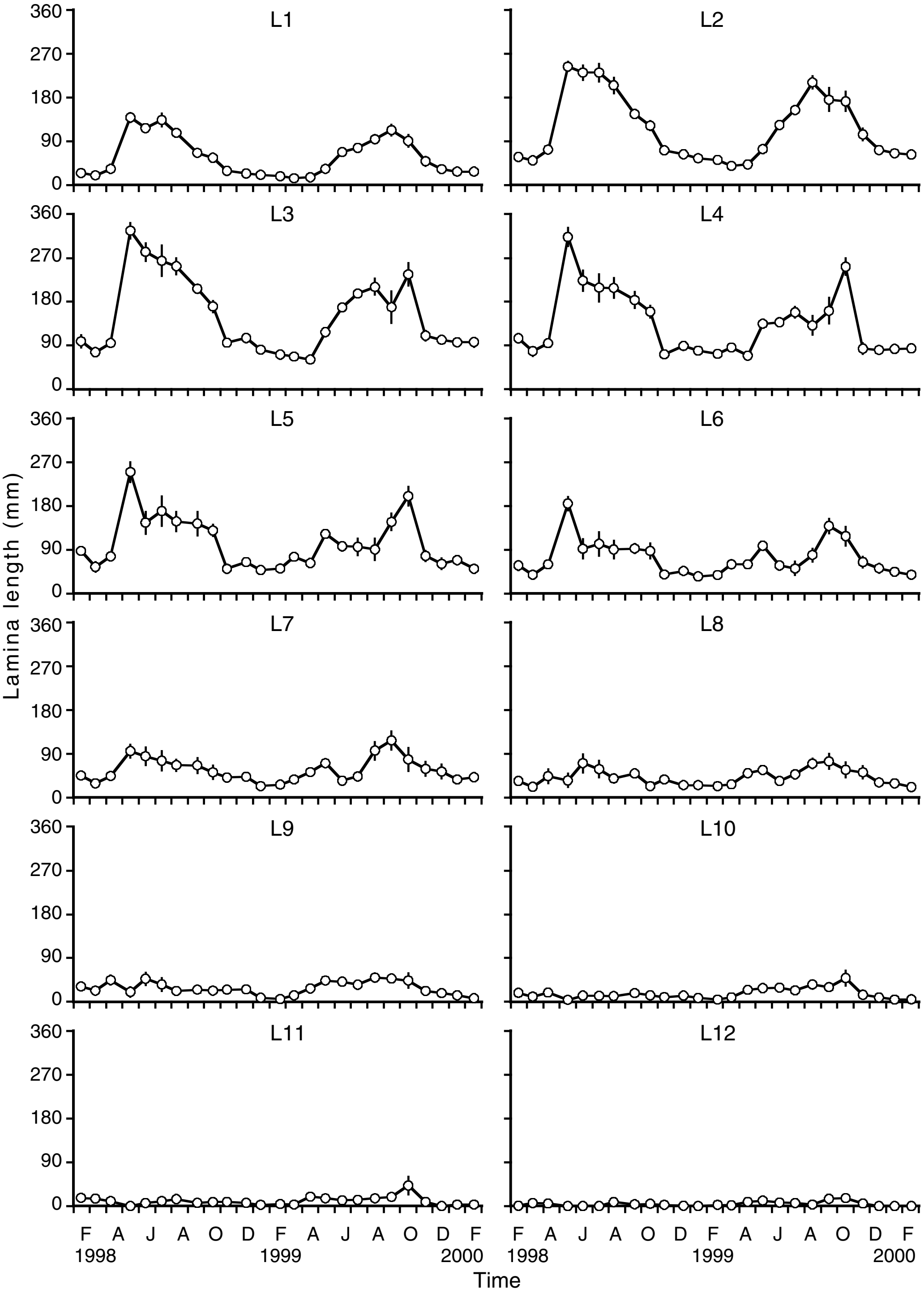


Figure 5. Length of individual laminae (L1 = the youngest lamina). Vertical bars show s.e. of mean.

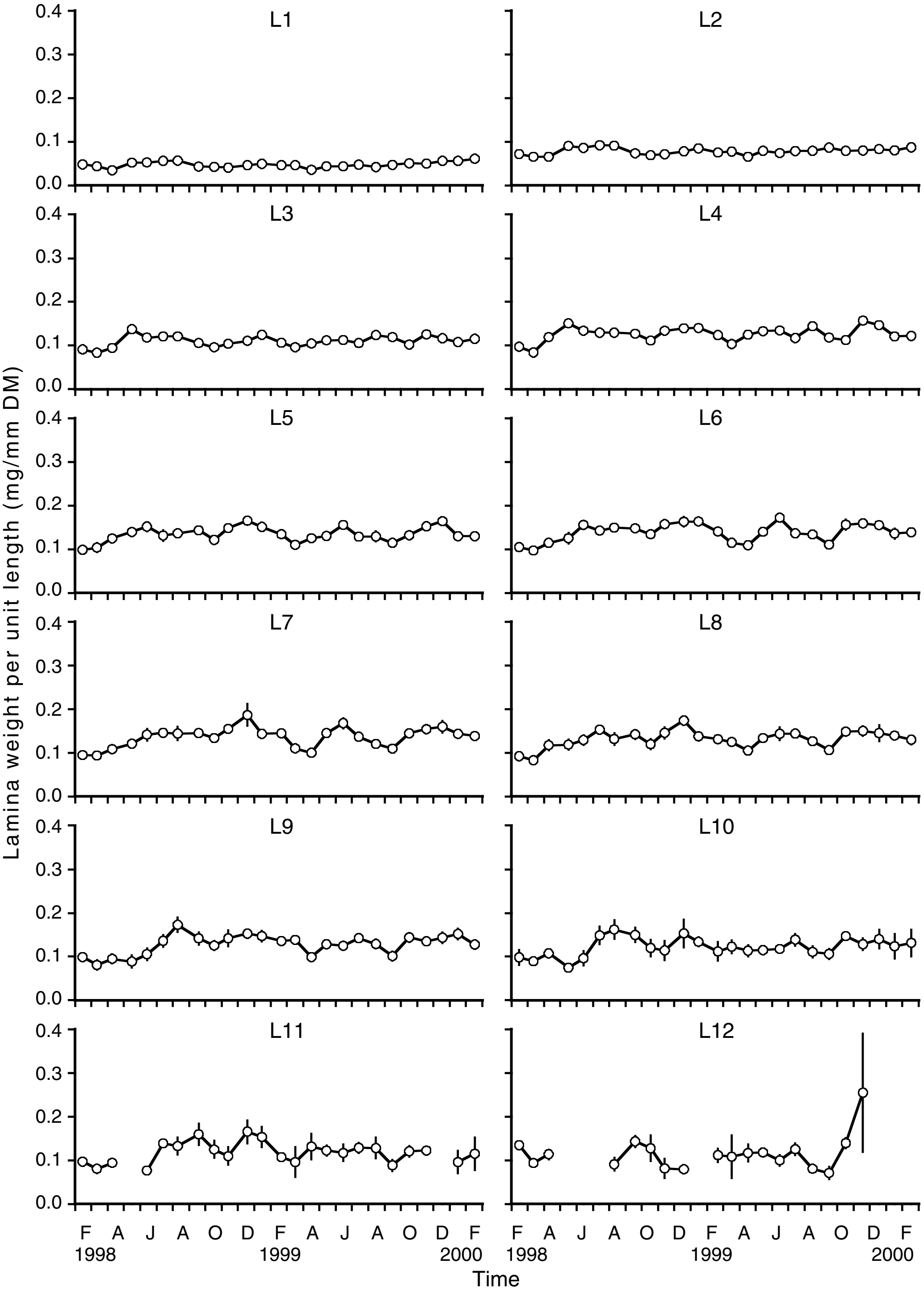
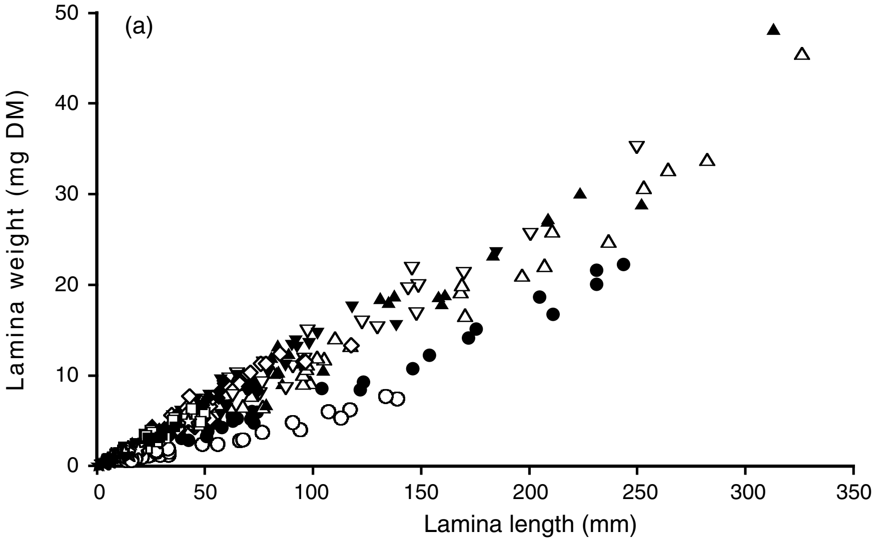


Figure 6. Weight per unit length of individual laminae (L1 = the youngest lamina). Vertical bars show s.e. of mean.

Effect of defoliation and detachment on lamina length

The history, mature length and fate of the youngest fully expanded lamina (L4) observed in May–October were estimated as shown in Table 1. For instance, L4 observed on May 18, 1998 (mean length = 313 mm; Figure 5) was estimated to have become L1, L2, L3 and L4 on April 16, April 25, May 4 and May 13, respectively. The mature length of the lamina was estimated at 276 mm. Furthermore, the lamina was estimated to be L7 (mean length = 85 mm; Figure 5) and L11 (mean length = 10 mm; Figure 5) at the next and the subsequent measurement (June 15 and July 15), respectively. Thus, the residual proportions of lamina length at full expansion and 1 and 2 months later were



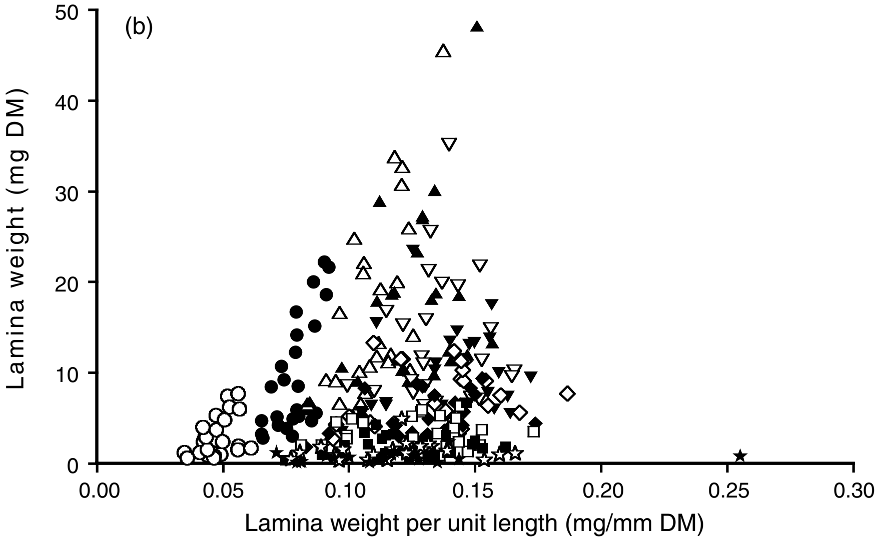


Figure 7. Relationships of lamina weight to: (a) lamina length; and (b) lamina weight per unit length. Symbols indicate lamina age classes: L1 (○; the youngest lamina), L2 (●), L3 (△), L4 (▲), L5 (▽), L6 (▼), L7 (◇), L8 (◆), L9 (□), L10 (■), L11 (☆) and L12 (★).

calculated as 1.13, 0.31 and 0.04, respectively (○ for May in Figure 8). Here, the residual proportion at full expansion was not significantly different from 1 at $P<0.05$ (95% confidence interval = 0.99–1.27). This reflects the fact that the lamina was not defoliated between its appearance (April 16) and the observation date (May 18) because the sward was mown on April 13 and the grazing season commenced in late May. It indicates the accuracy of the method for estimating the history, mature length and fate of laminae (Equations 1–8). By contrast, the residual proportion of L4 observed on May 15, 1999 was 0.65 at full expansion (● for May in Figure 8), indicating that 35% of the mature length was already defoliated. This is understandable as the lamina was defoliated by mowing on April 20 when it was at a late L1 stage (Table 1).

After the commencement of the grazing season, the residual proportion of lamina length at full expansion was 0.36–0.84, showing that 16–64% of the mature length of laminae was removed by grazing animals before and immediately after they attained full expansion. After a further 2 months, the proportion had decreased to 0.01–0.12 or by 0.24–0.79, indicating that 24–79% of mature length was further removed through defoliation by animals and detachment as litter fall, with total removal of 88–99%.

The relatively high utilisation of laminae by animals before and immediately after full expansion is attributable to the fact that L2–L4 were longest (Figure 5) and distributed in the top layer of the sward canopy (Hirata 1996). Barthram and Grant (1984) reported that the grazing frequencies by sheep of laminae on *Lolium perenne* tillers reflected the frequency of occurrence of the laminae at the top of the sward, *i.e.* accessibility to the laminae by animals in terms of their length and tip height. Further studies are needed to model the degree of removal of individual laminae in relation to grazing intensity in bahia grass swards.

Conclusions

The present study, investigating dynamics in lamina size variables in a bahia grass pasture under cattle grazing, revealed the following:

- The youngest to sixth youngest laminae (L1–L6; usually live laminae) contributed 62.5–91.0% of lamina weight per tiller that ranged from 36–200 mg/tiller DM.

Table 1. Estimated history, mature length and fate of the youngest fully expanded lamina (L4)[1] observed in May–October.

Date of observation	Estimated date when the lamina became: L1[1]	L2[1]	L3[1]	L4[1]	Estimated mature lamina length	Estimated lamina age class[1] at the next observation[2]	Estimated lamina age class[1] at the subsequent observation[3]
1998					(mm)		
May 18	Apr 16	Apr 25	May 4	May 13	276	L7	L11
Jun 15	May 14	May 24	Jun 2	Jun 11	265	L7	L11
Jul 15	Jun 14	Jun 23	Jul 2	Jul 11	351	L7	L12
Aug 11	Jul 12	Jul 20	Jul 29	Aug 7	382	L8	L12
Sep 19	Aug 19	Aug 28	Sep 6	Sep 15	376	L7	L10
Oct 18	Sep 17	Sep 26	Oct 5	Oct 14	327	L7	L8
1999							
May 15	Apr 8	Apr 21	May 1	May 10	207	L7	L11
Jun 15	May 14	May 23	Jun 1	Jun 10	245	L7	L11
Jul 14	Jun 13	Jun 22	Jul 1	Jul 10	315	L8	L11
Aug 15	Jul 16	Jul 24	Aug 2	Aug 11	365	L8	L11
Sep 15	Aug 16	Aug 24	Sep 2	Sep 11	376	L8	L11
Oct 16	Sep 15	Sep 24	Oct 3	Oct 12	331	L7	L8

[1] L1 = the youngest lamina.
[2] Approximately 1 month later.
[3] Approximately 2 months later.

- Variations in lamina weight (range = 0.0–48.0 mg DM) were largely explained by the variations in lamina length (range = 0–326 mm), with no consistent contribution by lamina weight per unit length (range = 0.035–0.255 mg/mm DM).
- Laminae lost 16–64% of their mature length through grazing by animals before and immediately after attaining full expansion. In the 2 months after full expansion, they lost an additional 24–79% of mature length through defoliation by animals and detachment as litter fall, with total removal of 88–99%.

The study also showed how the history and fate of individual laminae on a tiller can be estimated in terms of their appearance and development. This model is useful for simulation studies aiming at better management and a deeper understanding of canopy dynamics in bahia grass swards, in combination with previously developed models for dynamics in tiller density (Pakiding and Hirata 1999; Hirata and Pakiding 2001) and tiller weight (Hirata and Pakiding 2002).

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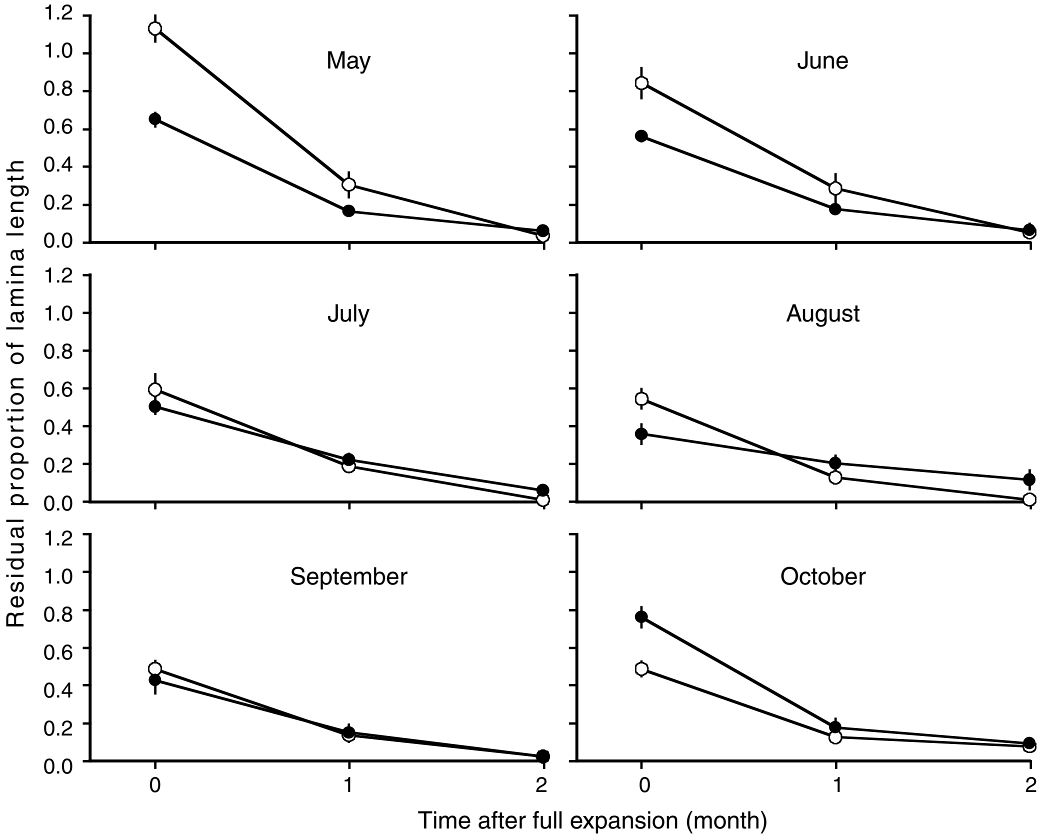

Figure 8. Residual proportion of lamina length with time after full expansion, in the youngest fully expanded lamina (L4) observed in May to October in 1998 (○) and 1999 (●). Residual proportion = [observed lamina length]/[estimated mature lamina length (Table 1)]. Vertical bars show s.e. of mean.

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