Tuft, shoot and leaf dynamics in *Miscanthus sinensis* in a young tree plantation under cattle grazing

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Abstract

This study investigated vegetation structure and dynamics of *Miscanthus sinensis* growing in a young *Chamaecyparis obtusa* (an evergreen conifer) plantation under cattle grazing in southwestern Japan, at 3 hierarchical levels of tuft, shoot and leaf, in an effort to develop a fundamental understanding of the productivity and persistence of this grass in forest grazing. After the initiation of grazing, *M. sinensis* plants were extensively defoliated by animals, leaving 12–26\% of tufts and 10–21\% of shoots undefoliated at the end of the grazing season. The density, mean height and mean basal area of *M. sinensis* tufts were in the range 9.2–16.0 × 10^3 tufts/ha, 26–89 cm and 75–315 cm^2, respectively. Mean shoot number per tuft and shoot density were in the ranges 10–44 shoots/tuft and 111–514 × 10^3 shoots/ha, respectively. There were always considerable tuft-to-tuft variations in height, basal area and shoot number, and distribution was skewed with the majority of tufts being shorter and thinner and having fewer shoots than the mean. All or almost all shoots formed in summer died before the end of the second winter, showing a half-life of 9–10 months. The number of live leaves and rates of leaf appearance (LAR) and leaf death (LDR) were 0.6–8.6 leaves/shoot, 0–0.09 leaves/shoot/day and 0–0.18 leaves/shoot/day, respectively. LAR increased as the mean daily air temperature increased, and LDR as the number of live leaves increased. *M. sinensis* growing in a young tree plantation under cattle grazing has low shoot densities and low LAR, which may limit production and persistence. In addition, *M. sinensis* is intolerant of grazing, with the size and shoot number of tufts, number of live leaves per shoot and LAR declining with time under grazing. Further studies to deepen our knowledge for better use of this grass in forest grazing appear warranted.

Introduction

Productivity and persistence of a grass in a plant community depend on the ability of the grass to maintain a high shoot (tiller) density and the ability of individual shoots to maintain leaves (laminae) as a photosynthetic organ (Hirata and Pakiding 2001; Pakiding and Hirata 2001). For a tufted (caespitose) grass, the ability to maintain a high shoot density depends on the ability to maintain a high tuft density and the ability of individual tufts to maintain shoots.

*Miscanthus sinensis* is a tall (up to 3 m), fully erect, tufted, warm-season (*C_4*), perennial grass, which originated in east Asia. It has been introduced into other parts of the world (*e.g.* Australia, Europe) as an ornamental plant (Lazarides 2002) or a potential crop for biofuel and fibre (Lewandowski et al. 2000; Clifton-Brown et al. 2001; Kern 2002). *M. sinensis* is native to Japan and is widely distributed from northern Hokkaido (sub-arctic climate) to Ryukyu Islands (subtropical climate) (Numata 1969). It commonly occurs as a dominant species in infrequently cut or lightly stocked grasslands developed by clearing of forests and woodlands or as a major undergrowth species in young tree plantations. *M. sinensis* is an important forage resource in native grasslands and forest grazing because of its high palatability to domestic herbivores (Ito 1962; Utsunomiya 1973; Okano and Iwamoto 1989; Nogami et al. 1993).

A number of studies have investigated various aspects of *M. sinensis*, such as physiology
and ecology (e.g. Hayashi and Isawa 1975; Sato et al. 1975; Ito 1990; Clifton-Brown et al. 2001; Kobayashi and Yokoi 2001, 2003a, 2003b), with the emphasis on plants growing in grasslands or croplands. Little information is available on *M. sinensis* in forests and woodlands. No previous studies have simultaneously investigated tufts, shoots and leaves of *M. sinensis* in relation to productivity and persistence.

In this study, we investigated vegetation structure and dynamics of *M. sinensis* growing in a young tree plantation under cattle grazing, at 3 hierarchical levels of tufts, shoots and leaves. The aim of the study was to develop a fundamental understanding of the productivity and persistence of this grass in forest grazing.

**Materials and methods**

**Study site and grazing trial**

The study was conducted in 1997–1999 at Tano Forest (currently Tano Forest Science Station, Field Science Centre), Faculty of Agriculture, University of Miyazaki, southern Kyushu, Japan (31°51′N, 131°17′E; elevation 100–300 m). The climate of the study site is warm temperate (almost subtropical) with warm, humid summers and cool, dry winters. The medium-term averages (1978–1997) of mean annual air temperature and annual rainfall are 16.7°C and 2764 mm, respectively. The soil is shallow, infertile Brown Forest Soil with chemical properties of: pH (H2O) 5.85–6.50; 30–57 g/kg organic C; 0.5–4 g/kg total N; 0–0.05 g/kg NO3-N; 0–0.25 g/kg NH4-N; 0.6–0.8 mg/kg available P; 0.1–0.8, 1.4–4.9 and 0.4–1.6 cmol/kg K, Ca and Mg, respectively (Nogami 1994; Hasegawa et al. 2001; Hayashi and Isawa 1975; Sato et al. 2001). The Forest has 260 ha of *Cryptomeria japonica* and *Chamaecyparis obtusa* (evergreen conifers) plantations, which have never been used as pastures. The plantations are distributed with some degree by *C. obtusa* trees and some tall undergrowth species, though the level of shading was not measured.

Prior to this study, Paddock 1 had been set-stocked with 3 Japanese Black heifers (initial age 12–14 months, initial live weight 201–240 kg) from early July to late November (mid-summer to late autumn; 149 days) in 1996. In 1997 (commencement of the study), the paddock was set-stocked with the same 3 animals (initial live weight 275–301 kg) from mid-May to mid-November (late spring to late autumn; 191 days). In 1998, grazing started in mid-May with the same 3 animals (live weight 338–361 kg; artificially inseminated at the beginning of the season and referred to as cows hereafter) in Paddock 1 and continued until early September (early autumn), when the fence between Paddocks 1 and 2 (about 30% in length) was opened to make up for decreasing feed resource (mainly *M. sinensis*) in Paddock 1. Grazing of the 2 areas continued until mid-November (total of 191 days). In 1999, Paddocks 1 and 2 were grazed from mid-May to late July (mid-summer) with the same 3 cows (live weight 320–351 kg; artificially inseminated at the beginning of the season) plus 2 calves (age 2 months, live weight 84–96 kg). At that time, Paddock 3 was opened up (about 20% of fence line bordering on Paddock 2) and the animals had access to all 3 paddocks until mid-November (total of 188 days). Thus, the stocking rates during the study were 0.60 head/ha in 1997 [3 heifers in Paddock 1 (5 ha)], 0.60 or 0.38 head/ha in 1998 [3 cows in Paddock 1 (5 ha) or Paddocks 1 + 2 (8 ha)], and 0.63 or 0.45 head/ha in 1999 [3 cows plus 2 calves in Paddocks 1+2 (8 ha) or Paddocks 1 + 2 + 3 (11 ha)]. Throughout the grazing trial, the paddocks were on a south-facing slope between a ridge (240–260 m in elevation) and a valley (150–190 m in elevation). Paddocks 1, 2 and 3 contained stands of *C. obtusa* planted in 1988–1992, 1992–1993 and 1994–1995, respectively (planting density 2600 seedling trees/ha; approximately 2 m × 2 m spacings). Four-, 7- and 11-year-old *C. obtusa* trees were generally 1–1.5, 2–2.5 and 3.5–4 m tall, with breast height stem diameters of <1, 2–3 and 5–6 cm, respectively. *M. sinensis* plants were shaded to some degree by *C. obtusa* trees and some tall undergrowth species, though the level of shading was not measured.

The 3 paddocks were 5, 3 and 3 ha, respectively (planting density 2600 seedling trees/ha; approximately 2 m × 2 m spacings). The paddocks were on a south-facing slope between a ridge (240–260 m in elevation) and a valley (150–190 m in elevation). Paddocks 1, 2 and 3 contained stands of *C. obtusa* planted in 1988–1992, 1992–1993 and 1994–1995, respectively (planting density 2600 seedling trees/ha; approximately 2 m × 2 m spacings). Four-, 7- and 11-year-old *C. obtusa* trees were generally 1–1.5, 2–2.5 and 3.5–4 m tall, with breast height stem diameters of <1, 2–3 and 5–6 cm, respectively. *M. sinensis* plants were shaded to some degree by *C. obtusa* trees and some tall undergrowth species, though the level of shading was not measured.

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animals were supplemented with a mineral-salt lick. The animals drank from streams running in the paddocks. There was no evidence that animals browsed on *C. obtusa* trees at any time during the study.

**Measurements**

Measurements of *M. sinensis* plants comprised quantifying: (a) the relationship between basal area and basal perimeter of tufts; (b) the density, height, basal perimeter, basal area and defoliation of tufts; (c) the relationship between shoot number and basal perimeter of tufts; (d) shoot number per tuft and shoot density; (e) survival of shoots; and (f) number of live leaves, rates of leaf appearance (LAR) and leaf death (LDR) and defoliation of shoots. Seven, 4 and 5 permanent line transects (25 m each) were positioned in Paddocks 1, 2 and 3, respectively, taking account of the locations and ages of *C. obtusa* stands in the paddocks (described earlier), in order that the transect areas should represent the vegetation of the paddock.

**Relationship between basal area and basal perimeter of tufts.** Measurements were conducted 9 times in Paddock 1 at monthly intervals from April to December 1997 (first year of the experiment). On each occasion, 9 or 10 *M. sinensis* tufts were selected (away from the permanent transects), to represent the size range of tufts in the paddock. For each sample tuft, basal perimeter was measured at ground level using a tape measure. Since the base of *M. sinensis* tufts formed an irregular shape (not a simple circle or an ellipse) approximated by a polygon having numerous sides (Kobayashi and Yokoi 2001; 2003a), the tape measure was fitted to follow indentations and irregularities at the base of the tufts as closely as possible. Then, the tuft was cut close to ground level and the basal area was measured by tracing the outline of stubble on a transparent acrylic board, also as accurately as possible (*i.e.*, allowing for indentations and irregularities of the outline). The relationship between basal perimeter and basal area was estimated (Figure 2).

**Density, height, basal perimeter, basal area and defoliation of tufts.** Measurements were conducted in May, July, September and November in 1997 (Paddock 1, Year 1) and 1998 (Paddocks 1 and 2, Year 2), and in May and November 1999 (Paddocks 1–3, Year 3). Height, basal perimeter (as described earlier) and occurrence of defoliation by animals were recorded on all *M. sinensis* tufts in a strip 1 m on each side of the permanent line transects (50 m² area for each 25-m transect). Tuft density was calculated as the number of tufts per unit area. Basal area of individual tufts along the transects was estimated from their basal perimeter, using the area:perimeter relationship described above.

**Relationship between shoot number and basal perimeter of tufts.** Measurements were conducted 15 times in Paddock 1 at monthly intervals during April–November 1998 and May–November 1999, 10 times in Paddock 2 at monthly intervals during September–November 1998 and May–November 1999, and 7 times in Paddock 3 at monthly intervals during May–November 1999. On each occasion, 5–13 *M. sinensis* tufts were chosen (away from the permanent transects), to cover the size range of tufts in the paddock. For each sample tuft, basal perimeter was measured using a tape measure (as described earlier), the tuft was cut close to ground level and the number of live shoots was counted. The relationship between shoot number and basal perimeter of tufts was calculated (Figures 5 and 6).

**Shoot number per tuft and shoot density.** The number of shoots on individual *M. sinensis* tufts along the line transects was estimated from their basal perimeter, using the shoot number:basal perimeter relationship described above. Shoot density was calculated as the number of shoots per unit area.

**Survival of shoots.** Measurements were conducted from August 1997 to February 2000 in Paddock 1 and from July 1998 to February 2000 in Paddock 2. Shoots were tagged immediately after their emergence (<2 months of age) in summer (August 1997 and July 1998 in Paddock 1, and July 1998 in Paddock 2), because *M. sinensis* forms new shoots (current-year shoots) in summer–autumn (Kobayashi and Yokoi 2003b). At each tagging, 50 current-year shoots of *M. sinensis* existing in a strip 1 m on each side of the line transects (50 m²/transect) were randomly selected and tagged with plastic tape bearing an identification number. Current-year shoots of *M. sinensis* are easily distinguished from overwintered shoots by appearance (smaller size, greener colour at the base). Thereafter, the shoots were examined at half-monthly to bi-monthly intervals to record their survival.
Shoots were considered dead when all parts were completely dried.

**Number of live leaves, LAR, LDR and defoliation of shoots.** Measurements were conducted from April 1997 to November 1999 in Paddock 1, from May 1998 to November 1999 in Paddock 2, and from June to November 1999 in Paddock 3, using a tagging technique described in Pakiding and Hirata (2001; 2003b). *M. sinensis* shoots were tagged in April 1997 (overwinted shoots), August 1997 (current-year shoots) and July 1998 (current-year shoots) in Paddock 1, in April (overwinted shoots) and July (current-year shoots) 1998 in Paddock 2, and in May 1999 (overwinted shoots) in Paddock 3 (current-year shoots were the same as used for shoot survival measurements). On each occasion, 50 shoots in a strip 1 m on each side of the line transects were randomly selected and tagged with plastic tape bearing an identification number. At the same time, a leaf on each shoot (usually from the third- to the seventh-youngest leaf) was marked with a fibre-tipped permanent marker. Then, the position of the marked leaf [counted from the uppermost (youngest) leaf], the number of live leaves (>2 cm in lamina length and >50% green in lamina area) on the shoot and occurrence of defoliation by animals were recorded. Thereafter, at half-monthly to bi-monthly intervals, all tagged shoots were examined to record the position of the previously marked leaf, the number of live leaves and the occurrence of defoliation by animals were recorded. Then, when necessary, the leaf mark was shifted to a younger leaf and the new position was recorded, to ensure the identification of the leaf at the next measurement. Shoots that died were excluded from the measurements, and their tags were removed. The numbers of leaves appearing and dying between 2 consecutive measurements on each shoot were calculated from the changes in the position of the marked leaf and the number of live leaves. Dividing these numbers by the duration (days) between the measurements yielded LAR and LDR, respectively.

**Results**

**Meteorological conditions**

The mean annual air temperature and annual rainfall were, respectively, 17.1°C and 2775 mm in 1997, 18.2°C and 3701 mm in 1998 and 16.9°C and 3670 mm in 1999 (Figure 1), while the corresponding values during the main growing season of plants (May–October) were 22.9°C and 1981 mm in 1997, 24.3°C and 2304 mm in 1998 and 23.2°C and 2705 mm in 1999. Compared with the medium-term averages, 1998 was a warm, moist year and 1999 was a moist year.

**Defoliation of tufts and shoots by animals**

*M. sinensis* plants in the 3 paddocks were extensively defoliated by animals (Table 1). Proportion of undefoliated tufts decreased throughout the grazing season, leaving 12–26% of tufts undefoliated at the end of grazing (November) in each year. The decrease in Paddock 1 was almost nil.
Table 1. Density, undefoliated proportion, height and basal area of *M. sinensis* tufts.

<table>
<thead>
<tr>
<th>Paddock¹</th>
<th>Time</th>
<th>Sample number²</th>
<th>Tuft density (tufts/ha)</th>
<th>Proportion of undefoliated tufts</th>
<th>Height (cm)</th>
<th>Basal area (cm²)</th>
<th>Correlation coefficient⁴</th>
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¹ Paddocks 2 and 3 were used from early September 1998 and late July 1999, respectively.
² Number of tufts existing in the measurement area along transects (350, 200 and 250 m² in Paddocks 1, 2 and 3, respectively).
³ Zero indicates values between 0.21 and 0.49.
⁴ Spearman's rank correlation coefficient between height and basal area. All coefficients are significant at P<0.001.
during July–November 1998, because Paddock 2 was opened in early September and animals grazed mainly this new paddock thereafter. Proportion of undefoliated shoots also decreased during the grazing season, leaving 10–21% of shoots undefoliated at the end of the grazing season (data not shown). The youngest 3–5 leaves (laminae) on shoots, i.e. expanding leaves and recently fully expanded leaves, were the major tissues defoliated.

Density and size of tufts

Basal area of _M. sinensis_ tufts increased as basal perimeter increased, with similar degrees of increase across the measurement dates (Figure 2). The relationship was expressed by a power function or an allometry function (\( r = 0.968, P = 0.000 \)). The estimated value of the exponent, 1.849, was not significantly different from 2 (\(<0.05\)), confirming that the area of a plane is a linear function of the square of a measure of the plane size (length of any part).

Density of _M. sinensis_ tufts was relatively stable over time and across Paddocks 1 and 2 (Table 1). At 15 of the 16 observations, tuft density was 11114 to 16029 tufts/ha. Paddock 3 had 9160–9400 tufts/ha. There was always considerable variation in height and basal area of tufts (as shown by minimum, maximum, SD and CV), with a tendency for taller tufts to be thicker (as shown by significant correlations). The tuft-to-tuft variations were always greater for basal area than for height (as shown by CV). The skewed frequency distribution patterns of height and basal area showed that the majority of tufts were shorter and thinner than the mean size (Figures 3 and 4). In contrast to the relative consistency in tuft density, both mean height (range 26–89 cm) and mean basal area (75–315 cm²) of _M. sinensis_ tufts tended to decrease with time in Paddocks 1 (1997 > 1998 > 1999) and 2 (1998 > 1999) (Table 1). Furthermore, mean height and mean basal area of tufts tended to be ranked Paddock 1 < Paddock 2 in 1998 and Paddock 1 < Paddock 2 ≈ Paddock 3 in 1999.

Number per tuft, density and longevity of shoots

Shoot numbers of _M. sinensis_ tufts increased as basal perimeter of the tufts increased, showing variable degrees of increase across paddocks and

![Figure 2. Relationship between basal area and basal perimeter of _M. sinensis_ tufts. Data from Paddock 1 in April (○), May (●), June (△), July (▲), August (▽), September (●), October (□), November (■) and December (○) 1997. The regression equation is \( y = 0.115x^{1.849} \) (n = 88, r = 0.968, P<0.001, RMSE = 444).]
Tuft, shoot and leaf dynamics in Miscanthus sinensis

measurement dates (Figure 5). The relationship on each occasion in each paddock was expressed by a line through the origin ($r = 0.904 – 0.998$, $P = 0.000 – 0.004$). Shoot number per unit basal perimeter, estimated as a regression coefficient, varied from 0.29 to 1.08 shoots/cm, showing no consistent effects of season or paddock (Figure 6). On average, there were 0.64, 0.73 and 0.76 shoots/cm of basal perimeter in Paddocks 1, 2 and 3, respectively.

Shoot number per tuft varied markedly (Table 2). The skewed frequency distribution patterns showed that the majority of tufts had fewer shoots than the mean (Figure 7). Both mean shoot number per tuft (range 10–44 shoots/tuft) and shoot density ($111–514 \times 10^3$ shoots/ha) tended to decrease from 1998 to 1999 in Paddocks 1 and 2 (Table 2). Furthermore, mean shoot number per tuft and shoot density tended to be ranked Paddock 1 < Paddock 2 in 1998 (September and November) and Paddock 1 < Paddock 2 < Paddock 3 in 1999.

Almost all $M. \text{sinensis}$ shoots formed in summer 1997 and 1998 died before the end of the second winter, i.e., February 1999 and 2000, respectively (Figure 8). The survival of shoots was similar across measurement periods (1997–1999 vs 1998–2000) and paddocks (Paddock 1 vs Paddock 2), showing half-life (the time taken for half the shoots to die) values of 9–10 months.

Figure 3. Frequency distribution of height of $M. \text{sinensis}$ tufts in Paddock 1. The statistical parameters are sample number (n), minimum, maximum, mean, standard deviation (SD) and coefficient of variation (CV).
Figure 4. Frequency distribution of basal area of *M. sinensis* tufts in Paddock 1. The statistical parameters are sample number (n), minimum, maximum, mean, standard deviation (SD) and coefficient of variation (CV).

Table 2. Shoot number per tuft and shoot density of *M. sinensis*.

<table>
<thead>
<tr>
<th>Paddock</th>
<th>Time</th>
<th>Shoot number per tuft (shoots/tuft)</th>
<th>Shoot density (10^3 shoots/ha)^1</th>
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<td>213</td>
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^1Tuft density × mean shoot number per tuft.
Figure 5. Relationship between shoot number and basal perimeter of *M. sinensis* tufts. Data from April (○), May (●), June (△), July (▲), August (▼), September (▲), October (■), November (●) 1998, May (○), June (●), July (▲), August (★), September (□), October (○) and November (★★) 1999.
Leaf dynamics

The number of live leaves on *M. sinensis* shoots (range 0.6–8.6 leaves/shoot) was high from May to November (late spring–late autumn) and low in other months (Figure 9). LAR (range 0–0.09 leaves/shoot/day) increased in spring (April–May), maintained high values until early autumn (September), and decreased thereafter. LDR ranged from 0 to 0.18 leaves/shoot/day, with sharp peaks between July (mid-summer) and September (early autumn). The number of live leaves tended to decrease with the progression of years in Paddocks 1 (1997>1998>1999) and 2 (1998>1999), and tended to be ranked Paddock 1<Paddock 2 in 1998 and Paddock 1<Paddock 2≤Paddock 3 in 1999. LAR in Paddock 1 tended to decrease with time (1997>1998>1999).

LAR on *M. sinensis* shoots increased as the mean daily air temperature increased (Figure 10). The relationship was expressed by a threshold response function \( r = 0.627, \ P = 0.000 \). The regression equation indicated that LAR attained its half-maximal response when temperature was 16.2°C, and approached the maximum (asymptote) of 0.052 leaves/shoot/day at higher temperatures. Regression analysis using subsets of data for individual years (1997, 1998, 1999) or paddocks (Paddocks 1, 2, 3) was usually unsuccessful.

LDR tended to increase as the number of live leaves, i.e., the amount of substrate, increased (Figure 11). The relationship was expressed by a linear function \( r = 0.360, \ P = 0.002 \). The estimated value of the intercept, 0.0046, was not significantly different from zero (\( P > 0.05 \)), showing no leaf death occurs when no substrate exists. The slope indicated that leaves died at a relative rate of 0.0079 leaves per live leaf per day, when the intercept was regarded as zero. Regression analysis using subsets of data for individual years (1997, 1998, 1999) or paddocks (Paddocks 1, 2, 3) was also usually unsuccessful.

Discussion

Shoot density

A major finding from the present study was the very low shoot density of *M. sinensis* in forest grazing (Table 2). Even in open grasslands, the shoot densities of *M. sinensis* pasture (74–205/m²; Hayashi and Isawa 1975; Ito 1990) are much lower than those in swards of other perennial herbage.
Figure 7. Frequency distribution of shoot number for *M. sinensis* tufts in Paddock 1. The statistical parameters are sample number (n), minimum, maximum, mean, standard deviation (SD) and coefficient of variation (CV).
grasses [e.g. 5 000–16 000/m² in Lolium perenne (Korte 1986), 2 000–6 000/m² in Phleum pratense (Matthew et al. 2000), 4 000–6 000/m² in Festuca pratensis (Matthew et al. 2000), 2 000–8 000/m² in Raspalum notatum (Hirata and Pakiding 2001; Pakiding and Hirata 2003a)]. In the present study, very much lower densities of 11.1–51.4 shoots/m² were obtained for M. sinensis grown within a young tree plantation (Table 2).

The 2 structural components determining shoot density, i.e., tuft density and mean shoot number per tuft, ranged from 0.9 to 1.6 tufts/m² (Table 1) and from 10 to 44 shoots/tuft (Table 2), respectively. Data from M. sinensis in open grassland (tuft density = 1.5/m², mean shoot number per tuft = 100; Kobayashi and Yokoi 2001) indicate that the low shoot densities of M. sinensis in this tree plantation were attributable mainly to low shoot numbers per tuft, i.e., tillering. In fact, the great majority of M. sinensis tufts in the paddocks had small basal areas (Figure 4) and low shoot numbers (Figure 7). Mean shoot number per tuft was low even prior to (27 shoots/tuft in May 1999 in Paddock 3) and at the beginning (38 shoots/tuft in September 1998 in Paddock 2) of the grazing trial, so defoliation by animals is not considered a cause for the low shoot number per tuft (cf. the decrease in shoot number/tuft with time; see later discussion). It is likely that youthfulness of tufts in Paddock 3 (≤ 5 years old; M. sinensis emerges after timber clearing) and limited availability of light, nutrients and/or moisture under competition with abundant undergrowth (Nogami et al. 1993) and C. obtusa tree seedlings in Paddocks 1 and 2 restricted the shoot numbers in individual M. sinensis tufts. Tillering in grasses is depressed under increased competition among shoots for nitrogen and light (Simon and Lemaire 1987; Lemaire and Chapman 1996).

Leaf dynamics

Another major finding from the present study was the relatively low values of LAR in M. sinensis (Figure 9). The range of LAR in this study (0–0.09 leaves/shoot/day) was lower than the 0–0.16 found for P. notatum (Pakiding and Hirata 2001; 2003b), 0.05–0.16 for Cenchrus ciliaris and Panicum maximum var. trichoglume (combined data for the 2 species), 0.02–0.13 for L. perenne, 0.05–0.11 for Dactylis glomerata and 0.05–0.10 for Agrostis spp., and only higher than 0.03–0.06 for Festuca arundinacea (see discussion in Pakiding and Hirata 2001). In the threshold response regression against air temperature (Figure 10), the maximal LAR (0.052 leaves/shoot/day) is less than half the 0.10–0.16 found for P. notatum (Pakiding and Hirata 2001, 2003b), 0.05–0.16 for C. ciliaris and P. maximum var. trichoglume (combined data for the 2 species), 0.02–0.13 for L. perenne, 0.05–0.11 for D. glomerata and 0.05–0.10 for A. spp., and only higher than 0.03–0.06 for F. arundinacea (see discussion in Pakiding and Hirata 2001). Temperature for the half-maximal response of LAR (16.2°C) is higher than the 13–15°C for P. notatum (Pakiding and Hirata 2001, 2003b; Islam and Hirata 2005) and about half the 0.09–0.10 for Eremochloa ophiuroides (Islam and Hirata 2005). Temperature for the half-maximal response of LAR (16.2°C) is higher than the 13–15°C for P. notatum (Pakiding and Hirata 2001, 2003b; Islam and Hirata 2005) and 14°C for E. ophiuroides (Islam and Hirata 2005).
It is unlikely that the low LAR in *M. sinensis* in the present study is attributable to the forest environment (e.g. limited availability of light, nutrients and/or moisture under competition with abundant undergrowth). Although no information is available on LAR of *M. sinensis* in other environments (e.g. open grasslands), the LAR values from the present study are considered typical for the grass, because *M. sinensis* is a tall grass, producing laminae of 50–85 cm (low LAR contributes to long laminae). Low LAR and long laminae in grasses may be a disadvantage in
Figure 10. Relationship between leaf appearance rate (LAR) on *M. sinensis* shoots and mean daily air temperature. Data from Paddock 1 in 1997 (○), 1998 (●) and 1999 (■), Paddock 2 in 1998 (△) and 1999 (▲), and Paddock 3 in 1999 (□). The regression equation is \( y = 0.052(x/16.2)^{8.5}/(1+(x/16.2)^{8.5}) \) (\( n = 74, r = 0.627, P<0.001, \text{RMSE} = 0.019 \)).

Figure 11. Relationship between leaf death rate (LDR) and number of live leaves on *M. sinensis* shoots. Data from Paddock 1 in 1997 (○), 1998 (●) and 1999 (■), Paddock 2 in 1998 (△) and 1999 (▲), and Paddock 3 in 1999 (□). The regression equation is \( y = 0.0046 + 0.0079x \) (\( n = 73, r = 0.360, P<0.01, \text{RMSE} = 0.030 \)).
terms of persistence under defoliation, because long laminae are more easily and intensely defoliated, and low LAR extends the time to replace lost laminae with new laminae (Hirata 2004).

Balancing the low LAR, the LDR in *M. sinensis* seems relatively low, except for the peaks between mid-summer and early autumn (0–0.10 leaves/shoot/day; Figure 9), when compared with 0–0.19 for *P. notatum* (Pakiding and Hirata 2001, 2003b; Islam and Hirata 2005), 0–0.15 for *E. ophiuroides* (Islam and Hirata 2005), 0.02–0.13 for *L. perenne* and 0.05–0.11 for *Agrostis* spp. (see discussion in Pakiding and Hirata 2001). In the linear regression against the number of live leaves (including peak values; Figure 11), the relative LDR (0.0079 leaves/live leaf/day) is lower than 0.016–0.034 for *P. notatum* (Pakiding and Hirata 2001; 2003b). However, the regression equation showed lower predictability ($r = 0.360$, RMSE = 0.030; Figure 11) than previously developed equations for *P. notatum* ($r = 0.692 – 0.869$, RMSE = 0.020 – 0.031; Pakiding and Hirata 2001; 2003b). Further analysis is therefore needed to develop a model with enhanced predictive ability.

**Effects of grazing on vegetation**

The mean height and basal area of *M. sinensis* tufts tended to decrease as the paddocks aged with increased grazing experience (e.g. 1997 >1998 >1999 in Paddock 1; Paddock 3 = Paddock 2 > Paddock 1 in 1999) (Table 1). Similar trends were also observed for the mean shoot number per tuft, shoot density (Table 2); number of live leaves per shoot and partly for LAR (Figure 9).

The extent to which ageing of trees and defoliation by animals contributed to these decreases is open to question. There was a confounding between age of the tree stands and time when grazing commenced. Grazing commenced earlier in paddocks with older tree plantations, *i.e.*, grazing commenced in 1996, 1998 and 1999 for Paddocks 1 (planted in 1988–1992), 2 (planted in 1992–1993) and 3 (planted in 1994–1995), respectively. In the absence of ungrazed control plots, we are unable to partition the response to the 2 factors. One might suspect that *M. sinensis* would decline in the absence of animals as the *C. obtusa* trees grew taller and the forest canopy became closed. However, *M. sinensis* continues to grow well in ungrazed tree plantations near the study site (Tano Forest) at least until 9–10 years after tree planting (Nogami et al. 1993), and plantations in Paddocks 1 and 2 in 1999 were 7–11 and 6–7 years old, respectively. This suggests that grazing contributed significantly to the decline of *M. sinensis* in the current study. Previous reports indicate that *M. sinensis* is susceptible to intense or frequent defoliation (Hayashi and Isawa 1975; Sato et al. 1975) and that it declines rapidly in forest grazing, being preferentially grazed by the animals (Nogami et al. 1993).

The decrease in shoot density of *M. sinensis* with increased grazing experience is primarily attributable to a decrease in shoot number per tuft, because tuft density remained relatively constant throughout. Since survival of shoots was not affected by grazing history, the decreasing shoot number per tuft must be attributable to a decrease in shoot generation in tufts, though this variable was not measured in the present study.

The decreased ability of *M. sinensis* to generate new shoots in tufts and new leaves on shoots under grazing may be related to carbohydrate and nitrogen status of the plant. Low carbohydrate supply (reduced photosynthesis) and nitrogen deficit restrict the generation and/or development of new shoots and leaves in grasses (Vine 1983; Coughenour et al. 1984; Lemaire and Chapman 1996; Bélanger 1998; Hirata 2004), though the response of leaf generation to N may vary with species (Lemaire and Chapman 1996; Hirata 2004). During the grazing season, 79–90% of shoots completely or partially lost the youngest 3–5 leaves, which have high nitrogen concentrations and high photosynthetic rates.

**Conclusions**

*M. sinensis* growing in a young tree plantation under cattle grazing is characterised by low shoot densities per unit area (11.1–51.4 shoots/m$^2$) and low LAR on shoots (0.052 leaves/shoot/day as a maximum in the LAR:temperature relationship), which may limit production and persistence of the grass. In addition, *M. sinensis* is not tolerant of grazing, with a decline in size (height and basal area) and shoot number of tufts, number of live leaves per shoot and LAR over time under grazing. Further studies are necessary to deepen our knowledge for better use of this grass in forest grazing, e.g. optimum stocking rate, and timing and duration of a rest (spelling).
Acknowledgements


References


(Received for publication July 13, 2006; accepted November 27, 2006)