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Effect of plant density and light availability on leaf damage in *Manilkara bidentata* (Sapotaceae)

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ABSTRACT. Variation in herbivory is often associated with plant density and light environment. The effect of these variables was studied on leaf production and herbivory of *Manilkara bidentata* in Puerto Rico. The major herbivore of *M. bidentata* is the leaf miner *Acrocercops* sp. To determine the effect of plant density, twenty-four 20-m × 20-m plots were established and the densities of saplings, juveniles and adults were determined. Leaf production, herbivory and growth were measured on saplings. Plant density was determined in eight 20-m × 20-m plots surrounding the focal plots. The effect of light was determined by comparing leaf phenology, leaf quality and herbivory in vertical and horizontal profiles. Sapling density in 60-m × 60-m plots was associated with herbivory. In the vertical profile, leaf production was continuous only for the canopy: herbivory increased from the canopy (1.3%) towards the understorey (35.6%). In the horizontal profile leaf production was related to light. Saplings in low light environments had narrow peaks in leaf production compared with saplings in high light environments. Differences in leaf phenology did not result in differences in herbivory possibly because of variation in herbivory among leaves. Although many saplings lost more than 80% of new leaf area, there was no detectable effect on growth. High levels of intra-specific variation in herbivory suggest that to better understand plant/herbivore interactions it is necessary to consider all size classes in a population. It is also important to document these pattern across different spatial scales.

KEY WORDS: leaf damage, light availability, *Manilkara bidentata*, plant density, Puerto Rico

INTRODUCTION

Plant density and light environment can affect levels of herbivory, and variation in herbivory can result in differential plant growth and survivorship (Barbosa & Wagner 1989, Clark & Clark 1984, Crawley 1983, Janzen 1970; Marquis 1984, 1992; Mendoza *et al.* 1987, Staton 1983). If herbivores are density responsive (Janzen 1970), they will be attracted to high density patches because of increased visual or chemical cues (Barbosa & Wagner 1989, Bernays & Chapman 1994, Staton 1983), resulting in higher levels of damage. Several studies that have tested this hypothesis were based on seedling or sapling densities (Augspurger 1983; Clark & Clark 1984, 1985; Cromartie 1975, Risch 1980, Staton 1983) and did not consider juvenile and adult densities. Patches with high densities of adult or juvenile trees will produce more leaves and possibly attract more herbivores. If all size classes share the same herbivore, then seedlings in patches with high densities of adults may receive more damage.

Light availability can also influence patterns of herbivory by affecting leaf phenology (Barone 1998) and herbivore preference (Connor *et al.* 1983, Harrison 1987, Niesenbaum 1992, White 1984). In many tropical forests, particularly aseasonal forests, leaf production is associated with light availability (Coley & Aide 1991, van Schaik *et al.* 1993, Wright & van Schaik 1994; but see Reich 1994). Plants in gaps and canopies of adult trees receive more light, and leaf production may be less restricted in comparison with plants in the understorey (Augspurger 1984, Denslow 1987) or lower branches of adult trees. Leaf production in low light environments will be concentrated in periods of high light (Angulo-Sandoval 1998) and leaves produced in community or population peaks could receive less damage than leaves produced in other months (Aide 1993). In addition, variation in herbivory may be due to herbivore preferences for leaves in a particular light environment because of differences in their physical or chemical characteristics (Harrison 1987, Maiorana 1981, Niesenbaum 1992, White 1984). In general, leaves in high light environments are tougher, smaller and have higher concentrations of phenols and lower water content compared with shade leaves; leading to lower levels of herbivory (Harrison 1987, Kimmerer & Potter 1987, Niesenbaum 1992, Scriber & Slansky 1981, Suomela & Ayres 1994, White 1984). Herbivore preferences could also be related to the microclimate. For certain herbivores, the effects of higher temperatures in high light environments on metabolic rates are more important than variation in leaf characteristics (Barbosa & Wagner 1989, Casey 1993, Papaj & Rausher 1983).

This study describes patterns of herbivory in *Manilkara bidentata* (Sapotaceae), a tropical canopy tree in the Luquillo Experimental Forest (LEF) in Puerto Rico. The Sapotaceae are well known for having latex and secondary metabolites (i.e. steroids, terpenoids and tannins) that can act as anti-herbivore defenses (Zomlefer 1994). With the exception of a leaf miner, *Acrocercops* sp. (Gracillariidae), which was responsible for 99% of leaf damage (Angulo-Sandoval 1998), these chemical defenses protect *M. bidentata* from most herbivores present in the LEF. Given that this herbivore has overcome these chemical defenses, this study focuses on the importance of density and light availability as factors influencing this specific plant/herbivore interaction.

The following hypotheses were tested: (1) Herbivores of *M. bidentata* are density responsive, and plants in high density patches receive higher levels of herbivory compared with plants in low density patches. (2) Light availability influences patterns of leaf production. Individuals in high light environments (adults and saplings in gaps) produce leaves throughout the year, while leaf production of individuals in low light environments is restricted to periods of high light availability. (3) Differences in leaf phenology result in differences in herbivory. Leaves produced during peaks of leaf production receive less damage in comparison with leaves produced during the rest of the year. (4) Levels of herbivory vary within the vertical (saplings to adults) and horizontal (saplings in different light environments) profiles. Leaves in high light environments (canopy and gaps) receive less damage because of microclimate conditions and leaves with low leaf quality. (5) High levels of herbivory have a negative effect on plant growth.

STUDY SITE AND SPECIES

Study site

The study was conducted in a 16-ha plot, in the Luquillo Experimental Forest (LEF), within the Caribbean National Forest in north-eastern Puerto Rico (18° 20′ N, 65° 49′ W) (Waide & Reagan 1996). The study area is near El Verde Research Station (350 m) on the north-west slope of the LEF. The forest is classified as subtropical wet forest and the dominant tree species are *Dacryodes excelsa*, *Prestoea montana*, *Casearia arborea*, *Inga laurina*, *Manilkara bidentata* and *Sloanea berteriana* (Zimmerman *et al.* 1994). Average height of the forest canopy is 20 m with few emergent trees (Waide & Reagan 1996). Mean annual precipitation is 3460 mm (McDowell & Estrada-Pino 1988), and although January to April is the period of lowest precipitation, monthly means are usually greater than 100 mm mo^{-1} (S. Brown *et al.* 1983) and evapotranspiration is lower than precipitation throughout the year (Waide & Reagan 1996). Mean monthly temperatures range between 21–25 °C (S. Brown *et al.* 1983).

The 16-ha plot was established in 1990. The plot was divided into 20-m × 20-m plots, and all plants with diameter at breast height (dbh) ≥ 1 cm were marked. The plant species composition within the plot varied due to previous land uses. Land-use in the northern part of the plot included a coffee plantation, selective logging, charcoal production and some areas that had been completely cut. The southern part of the plot received much less human impact and was mainly limited to some selective logging and charcoal production. Major human impacts were eliminated in the 1950s when this area was incorporated into the LEF (García-Montiel & Scatena 1994). The different land use patterns have affected the distribution of plant species in the forest. Some species are more common in the southern part of the grid (e.g. *Manilkara bidentata*) whereas others are more common in the northern part (e.g. *Casearia arborea*) (J. K. Zimmerman, *pers. comm.*).

Study species

Manilkara bidentata (A. DC.) A. Chev. (Sapotaceae), is a dominant species in the LEF. It is a shade-tolerant species and can grow to 30 m in height (Crow 1980). *Manilkara bidentata* ranges from near sea level to 600 m and in the LEF it is mainly associated with *Dacryodes excelsa*, *Sloanea berteriana* and *Buchenavia capitata* (You 1991). *Manilkara bidentata* can be found throughout the West Indies, Panamá, Colombia, Venezuela, Guianas, Perú, Ecuador and northern Brazil (Little & Wadsworth 1989).

The principal herbivore of *M. bidentata* is a microlepidopteran, *Acrocercops* sp., (Gracillariidae) (D. Davis, *pers. comm.*). The larval stage is a leaf miner that feeds on young leaves and creates a blotch mine on the upper surface of the leaf. Larvae have two distinct forms and habits. The early sap-feeding stage has a flattened, apodal body and highly specialized mouthparts. Larvae continuously move the mouthparts to increase the size of the mine in the first few layers of subepidermal parenchyma cells without ingesting any solid tissue (Davis 1987). After 3 or 4 d larval morphology and behaviour change. The larvae become cylindrical with a round head, chewing mouthparts and protolegs. During this period the larvae feed on palisade parenchyma cells, deposit frass throughout the mine and do not cross the midrib. Around day 10 larvae stop feeding and emerge from the blotch mine and pupate. After 12–16 d the adult emerges (P. Angulo-Sandoval, *pers. obs.*; Opler 1974). Adults are 1 cm long (P. Angulo-Sandoval, *pers. obs.*) and are diurnal (D. Davis, *pers. comm.*).

METHODS

Leaf phenology and herbivory

All plants were located within the 16-ha plot. In April 1995, 100 saplings of *M. bidentata* (height 20–250 cm) were located haphazardly. Number of leaves, height and diameter at the base were recorded and re-measured in April 1996 and April 1997. In April 1996, 235 saplings were added to the study and the same variables were measured and re-measured in April 1997. These saplings represent all the individuals of *M. bidentata* in twenty-two 20-m × 20-m plots. The plots were chosen based on *M. bidentata* adult density in each 20-m × 20-m plot (low 0–1, medium 2–4, high > 4). In April 1996, five adult trees near a 20-m tower and five adults and 20 juveniles (height 2.6–5 m) in the 16-ha plot were randomly chosen and marked for leaf phenology and herbivory census.

Leaf phenology and herbivory were measured in two different ways based on accessibility. Every month, new leaves (maximum of 10) were marked with plastic coloured wires on all saplings ($n = 335$) and on 10 branches on each of the five adult trees near the tower. A month later, when the leaves were fully expanded, leaf area and area damaged were measured using a plastic grid. For the remaining five adult trees and 20 juveniles, the number of leaves produced and herbivory was estimated using binoculars. Per cent herbivory was estimated for 50 leaves from juveniles and adults using both binoculars and a plastic grid. The estimates were similar for both techniques. The number of new leaves was counted monthly and per cent herbivory was estimated by dividing each leaf into four sections and estimating the total damage (Nuñez-Farfán & Dirzo 1988).

The annual pattern of leaf production, for all individuals within each size class (saplings, juveniles, adults), was obtained by using the average leaf production of individuals in every month. Leaves produced within 1 mo by a single individual were considered a single event (leaf cohorts). Monthly per cent herbivory was calculated for each leaf cohort. Mean monthly herbivory for the periods April 1995–March 1996 and April 1996–March 1997 were also calculated. Total damaged area on marked leaves was divided by the total potential leaf area. If a leaf was missing, the average size of the remaining leaves was calculated and this area was added to the total damaged area and to the total potential leaf area. Missing leaves could not be detected on the five adults and 20 juveniles that were visually censused, but leaves with high levels of herbivory (>90%) often remained on the plant.

Effect of density

To determine the effect of density on herbivory a distribution map of adult *M. bidentata* (available at El Verde Field Station, LEF) was used to select twelve 20-m × 20-m low-density plots (< three adults) and 12 high-density plots (≥ three adults). A total of 235 saplings were located in the 24 plots. In addition, the density of juveniles (height range = 2.6 – 5.0 m) was determined for each plot. To determine whether plant density at different spatial scales affected levels of herbivory, sapling, juvenile and adult densities were measured in the eight plots that surrounded each of the 24 focal plots (60-m × 60-m plot).

Stepwise regressions (Statistix 1996) were performed to determine the effect of plant density on herbivory. The independent variables were: plant density of saplings (6–250 cm), juveniles (2.6–5.0 m), and adults in the 20-m × 20-m and 60-m × 60-m plots. This analysis was used to determine whether variation in plant density at different spatial scales influenced levels of herbivory (i.e. female search behaviour).

Effect of light

Light environment for all saplings (n = 335) was estimated by determining the number of vegetation layers above each plant (0, 1, 2, ≥ 3). In addition, the light intensity (photosynthetics photon flux density) was measured above 20 plants in each category (randomly chosen) using a Li-cor photometer (quantum sensor) to corroborate the precision of the vegetation layer measurements. Measurements were performed twice during the study and the results were similar. Leaf phenology was compared between saplings, juveniles and adults (vertical profile) and between saplings in different light environments (horizontal profile). The Kolmogorov–Smirnov (KS) test (Ott 1993) was used to compare the patterns of leaf phenology between different size classes and light environments. This test procedure examines whether two samples have the same distribution. Although monthly leaf production within an individual is not independent, the comparison of combined phenologies of many individuals is an appropriate use of the Kolmogorov–Smirnov test (Ott 1993). Repeated-measures analysis of variance was not used, because data are not normally distributed and have unequal variances. It was possible to perform the repeated-measures analysis of variance, where data were grouped into intervals to maintain non-zero variances, but in doing so, information on the cumulative distribution of leaf production was lost.

Within each size class, monthly levels of herbivory were compared. In the vertical profile, herbivory was compared between saplings, juveniles, lower branches of adults and upper branches of adults (adults were divided into two categories due to differences in herbivory). In the horizontal profile, herbivory was compared between individuals in the four light environment categories. The Kruskal–Wallis test (H-statistic) was used for comparisons. In addition, the Mann–Whitney U-test (z) was used for comparing herbivory in saplings between years.

Leaf toughness and water content were measured on 20 young fully expanded leaves from each of the following categories: adult trees-upper canopy, adult trees-lower branches, juveniles, saplings in the four light categories. Leaf toughness was measured using a Chatillon penetrometer (rod diameter = 3.2 mm) (alternative methods are described by Choong 1996). The Kruskal–Wallis (H-statistic) test was used for these comparisons.

Sapling growth

The effect of herbivory and light environment on plant growth was determined using the 100 individuals that were followed for 2 y. The residuals from the regression between the initial and final height and the initial and final diameter of each plant were calculated and used as growth values. A third growth residual was obtained from the regression between the initial number of leaves and the total number of leaves produced. These measures of sapling growth were calculated for the second year and were correlated with levels of herbivory during the first year.

RESULTS

Sapling density at the 60-m × 60-m scale was the only variable that was related toherbivory ($r^2 = 0.34$, df = 23, $P \ll 0.01$). There was a positive relationship between density and herbivory on saplings (Figure 1). The mean herbivory of low density plots (60-m × 60-m with < 60 saplings) was 24.5%, while mean herbivory in the high density plots (≥ 60 saplings) was 38.5% (Figure 1).

In the vertical profile annual peaks in leaf production for saplings and juveniles occurred in June (Figure 2). In contrast, adult trees produced leaves

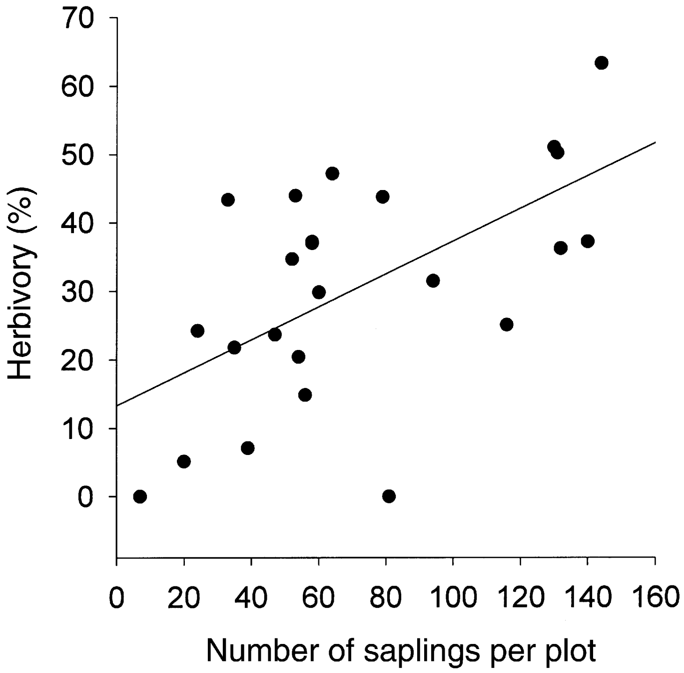

Figure 1. Relationship between sapling density in 60-m × 60-m plots and levels of herbivory in saplings located in focal plots.

throughout the year with no marked peak (Figure 2). Annual patterns of leaf production were similar for saplings and juveniles (Kolmogorov–Smirnov (KS) statistic = 0.04, P = 1.00) and for juveniles and adult trees (KS statistic = 0.16, P = 0.17). Leaf phenology was significantly different when comparing saplings and adult trees (KS statistic = 0.21, P = 0.04).

In the horizontal profile, the number of vegetation layers above each plant corresponded to very different light environments (Table 1). Saplings in high to medium light environments (0–2-layers) produced leaves throughout the year, with peaks in leaf production in June–July 1995 (n = 100) and in June 1996 (n = 335) (Figure 3). Plants in low light environments (≥ 3-layers), did not produce leaves in all months. Most of their leaves (62.5 % in the first year and 40% in the second year) were produced in June (Figure 3). Significant differences were found in leaf phenology in low light environments compared with intermediate and high environments and the difference persisted for the 2 y (Table 2). There were no significant differences in leaf phenology between years, for plants in each of the different light environments (0-layers, KS statistic = 0.08, P = 0.93; 1-layer KS statistic = 0.13, P = 0.43; 2-layers KS statistic = 0.07, P = 0.64; ≥ 3-layers KS statistic = 0.17, P = 0.11).

Differences in leaf phenology in the vertical and horizontal profile (Figures 2 and 3) did not result in significant variation in herbivory among months. In

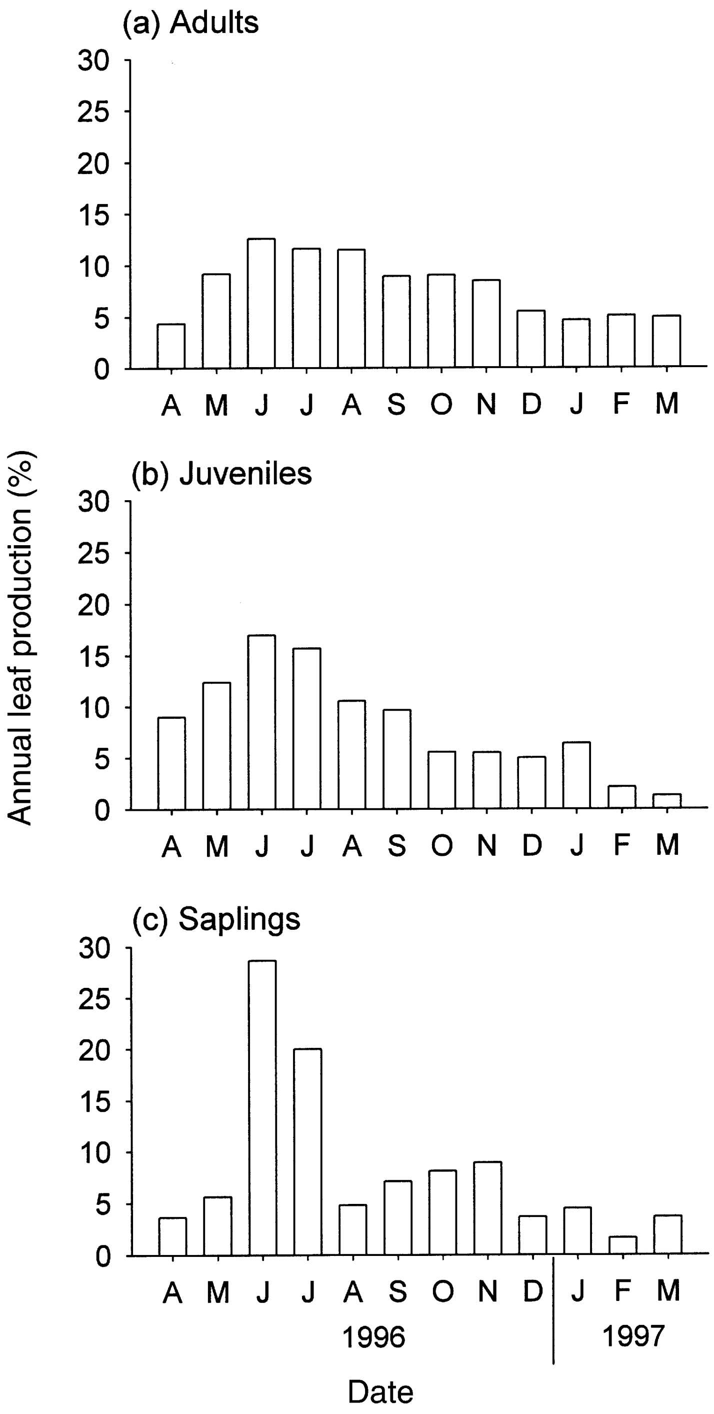

Figure 2. Patterns of leaf phenology of saplings, juveniles and adults of *M. bidentata* in the vertical profile. Data from April 1996 to March 1997.

Table 1. Photosynthetic photon flux density (PPFD µmol m^{-2} s^{-1}) for each vegetation layer category. Light intensity was measured for 20 individuals in each category.

Number of vegetation layers	Mean	SE
0	1948.2	12.6
1	737.1	21.0
2	232.9	9.0
≥ 3	81.4	8.7

the vertical profile there were significant differences in herbivory among size classes (Kruskal–Wallis H = 273.03, P < 0.001) (Figure 4). Adults produced leaves throughout the year (Figure 2), and mean monthly herbivory was low in the upper branches (median = 0.33%) and constant throughout the year (H = 15.7, P = 0.10). Herbivory in the lower branches of the adult trees was higher (median = 3.5%) compared with upper branches (Figure 4) and although there was greater variation in herbivory there was no difference among months (H = 7.02, P = 0.79). Juveniles and saplings had peaks in leaf production in June (Figures 2 and 3) and, for both categories, levels of herbivory where higher than levels of herbivory for adults (juveniles median = 10%, saplings median = 18%) (Figure 4). In addition levels of herbivory during the peak in leaf production and the rest of the year were not significantly different (juveniles, H = 5.5, P = 0.85; saplings H = 12.9, P = 0.22). Even in high light environments (canopy branches and saplings in gaps) there was a significant effect of the vertical profile on herbivory. Levels of herbivory in the canopy (<1%) were significantly lower in comparison with saplings in gaps (54%) (Mann–Whitney U-test, z = 8.1, P < 0.001).

In the horizontal profile, levels of herbivory were not significantly different among the four light environments (Figure 5) (H = 2.6, P = 0.4, in the first year; H = 5.3, P = 0.1, in the second year). Herbivory of saplings was similar in year one (40.6 ± 13.7%) and two (42.4 ± 24.2%) (z = 1.3, P = 0.21). The lack of difference between light environments could have been due to the bimodal distribution of herbivory. Leaves either received little damage (0–10%) or were almost completely eaten (90–100%) (Figure 6). Leaves that had more than 90% herbivory remained attached to the plants.

Toughness and water content of leaves varied depending on the microhabitat. Leaf toughness decreased in the vertical profile from adults to saplings in low-light habitats (H = 77.78, P < 0.01) (Table 3). In the horizontal profile, leaves were tougher in gaps in comparison with low-light environments. Leaf water content was lowest in leaves of adult trees and highest in saplings (H = 17.02, P < 0.01).

Herbivory during the first year of the study did not have a significant effect on sapling growth during the second year (height, diameter and leaf production: all $r^2 < 0.03$, $P > 0.05$) in the second year. Light environment also did not have a significant effect on sapling growth (height, diameter and leaf production: all $r^2 < 0.04$, $P > 0.05$).

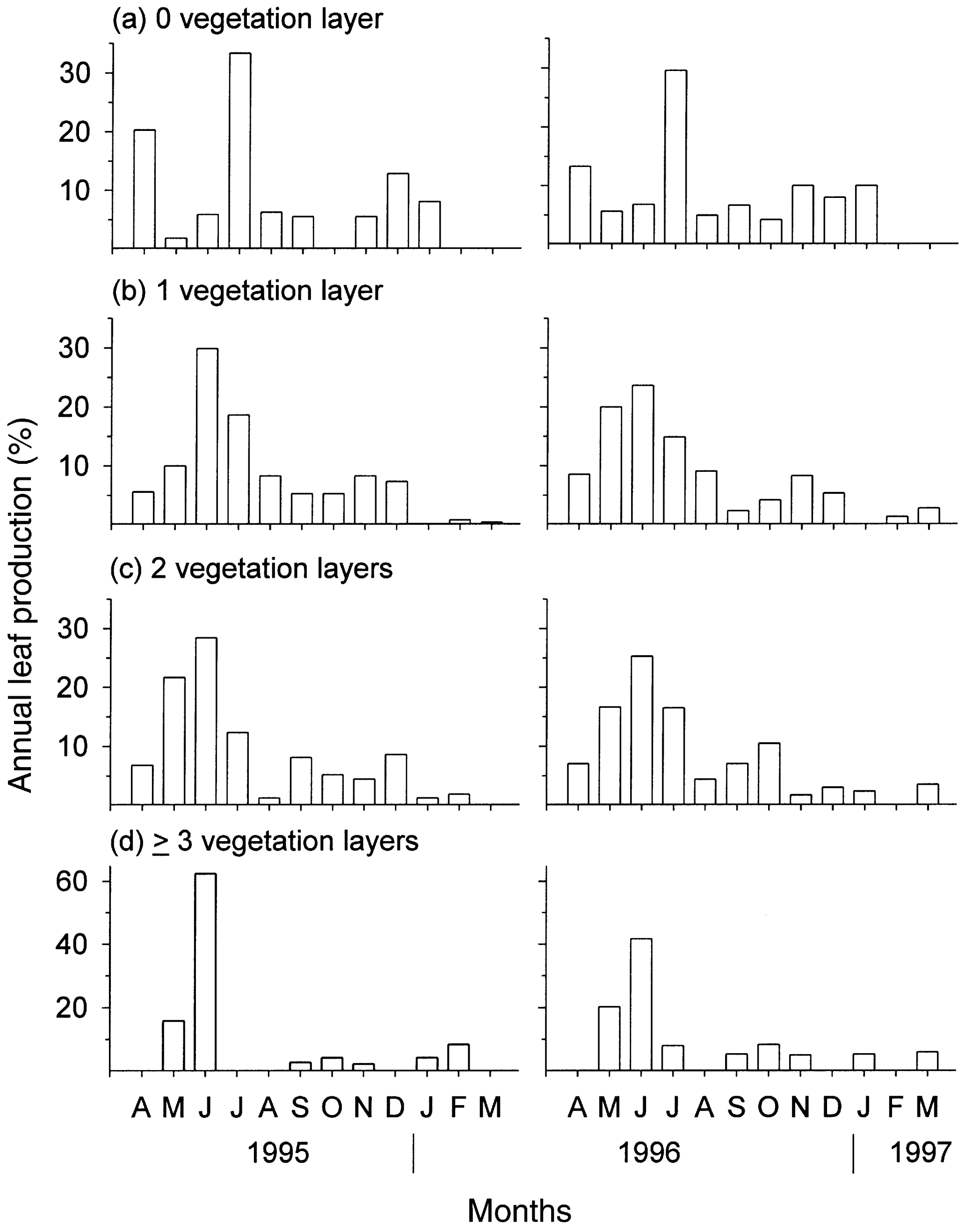

Figure 3. Patterns of leaf phenology in different light environments. (Vegetation layers 0 = gap, to vegetation layer 3 = 2% full sun). Data from the first year correspond to 100 plants; data from the second year correspond to 335 plants. Note that the *y*-axis for the (≥ 3 layers) is different from the others.

Table 2. Comparison of the distribution of leaf production for year 1 and year 2, for saplings in different light environments (number of vegetation layers). Kolmogorov–Smirnov statistic and corresponding P-values.

Light environments	Year 1		Year 2	
	Statistic	P	Statistic	P
High light (0) – intermediate (1)	0.19	0.06	0.18	0.07
High light (0) – intermediate (2)	0.14	0.38	0.13	0.44
High light (0) – low light (3)	0.52	<0.05	0.28	<0.05
Intermediate (1) – intermediate (2)	0.13	0.43	0.07	1.0
Intermediate (1) – low light (3)	0.33	<0.05	0.21	<0.05
Intermediate (2) – low light (3)	0.21	<0.05	0.31	<0.05

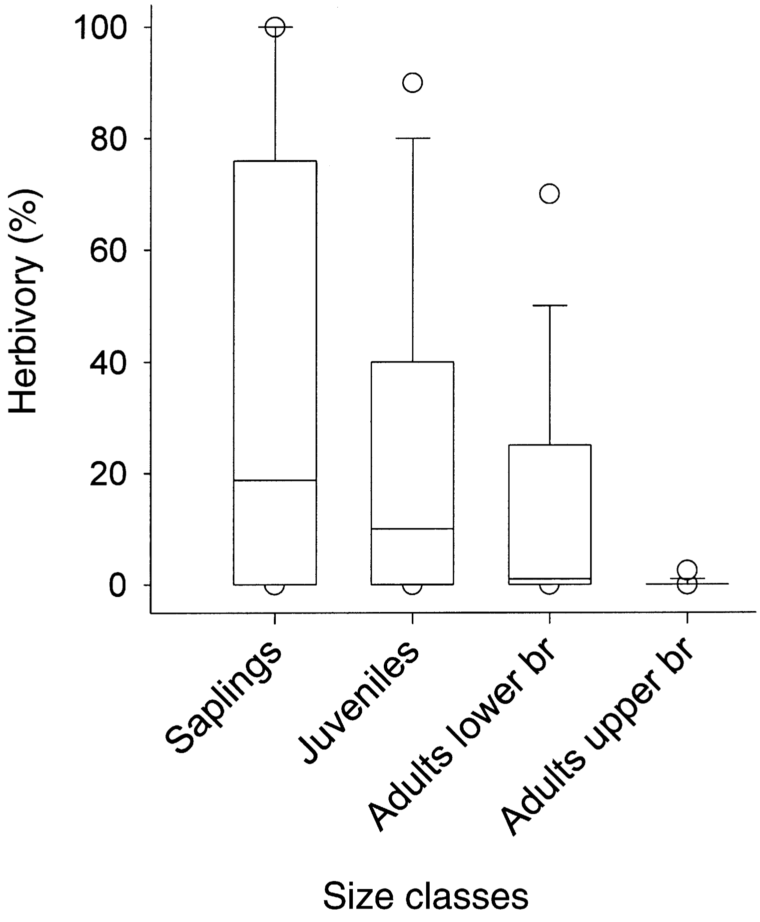

Figure 4. Herbivory in different size class of *M. bidentata*. Box plots illustrate the median (horizontal line within the box), 25–75th percentiles (the box), 10–90th percentiles (T-bar) and the values greater than the 10–90th percentiles (o). Data correspond to 1996 and 1997.

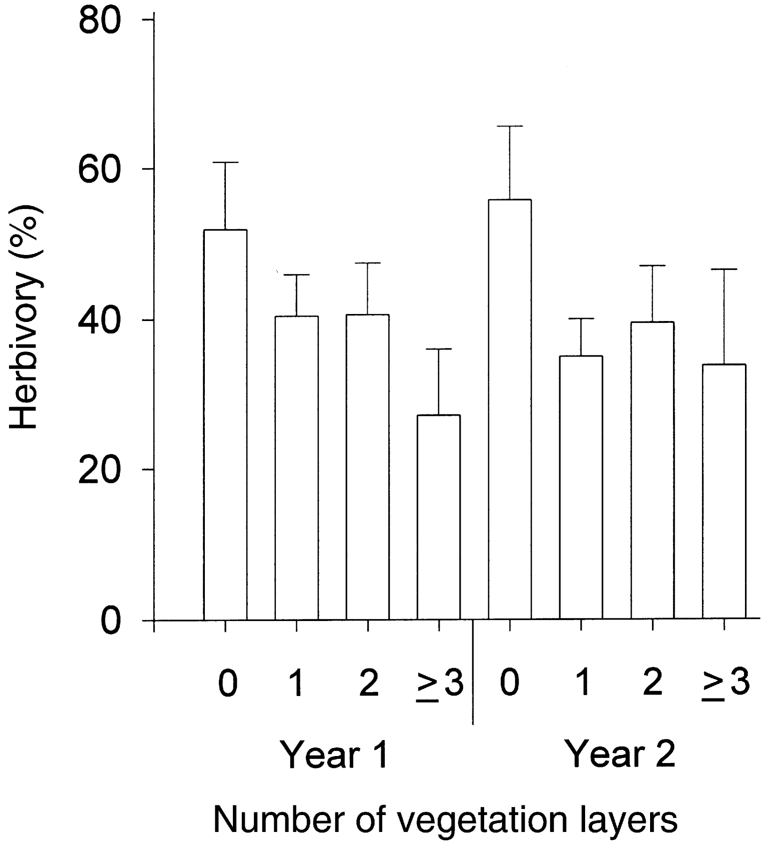

Figure 5. Mean herbivory (± SE) on saplings of *M. bidentata* in the different light environments. Data from two years are presented (year 1 = April 1995 – March 1996; year 2 = April 1996 – March 1997).

DISCUSSION

Effect of density

In the LEF, *Acrocercops* sp. feeds on all size classes of *M. bidentata*, but only sapling density in 60-m × 60-m plots was positively correlated with levels of herbivory. In addition, saplings had the highest levels of herbivory, suggesting that *Acrocercops* sp. is mainly attracted to this size class. *Acrocercops* sp. is density responsive (hypothesis 1) and high densities of saplings could attract more herbivores because visual or chemical cues are concentrated in these patches (Barbosa & Wagner 1989, Bernays & Chapman 1994, Staton 1983). Although a focal plot may have a low density, if it was surrounded by plots with higher densities, there was a greater probability of being attacked. Similar patterns have been observed in pollination studies, where individuals with few flowers receive higher visitation rates if surrounded by other flowering individuals (Feinsinger 1978, Feinsinger *et al.* 1991, Kunin 1992, Silander 1978, Waser 1978). If the oviposition strategy of *Acrocercops* sp. females is to lay a few eggs on many leaves, it will be advantageous for them to find and remain in high

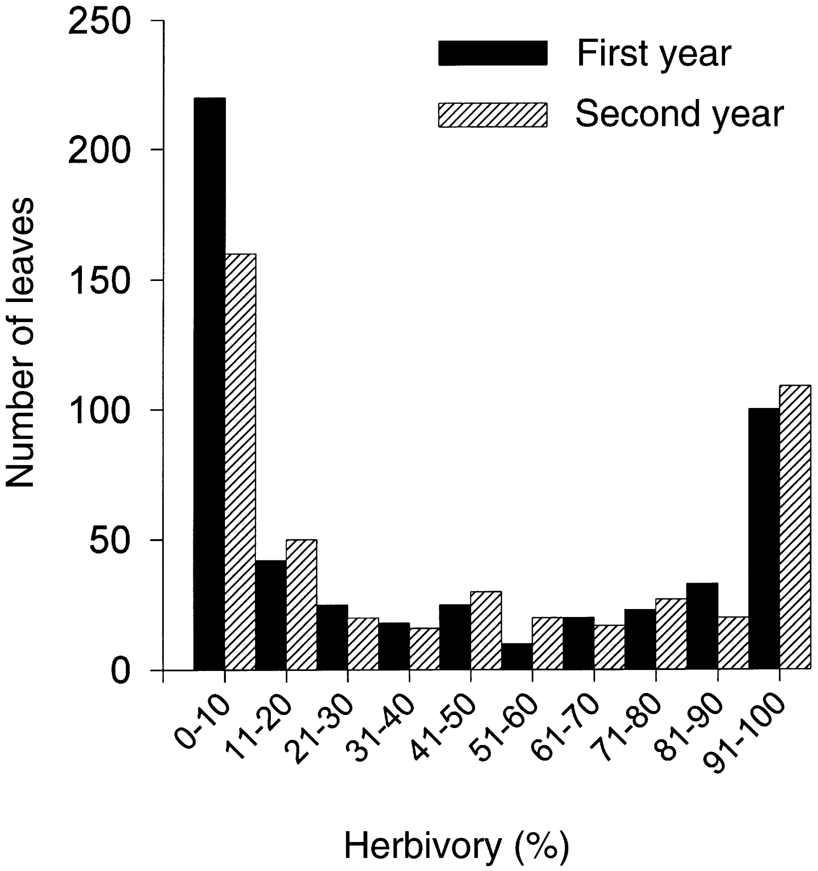

Figure 6. Distribution of herbivory in *M. bidentata*. Data from the first year (■) correspond to 100 plants; data from the second year (▨) correspond to 335 plants.

Table 3. Leaf toughness and water content of young leaves of *M. bidentata* (mean ± SE; n = 20 for each group).

	Leaf toughness (g)	Water content (%)
Adults – upper branches	162.5 ± 16.3	62.7 ± 2.3
– lower branches	148.5 ± 39.7	62.1 ± 2.1
Juveniles	108.5 ± 16.6	64.1 ± 3.8
Saplings – sun	75.5 ± 11.9	65.8 ± 3.6
– shade	63.0 ± 18.6	64.7 ± 2.6

density patches. After completing the larval and pupal stage, it is possible that new adults remain within the same area, maintaining high levels of herbivory in high density patches. Although juvenile and adult densities are lower, these plants produce more young leaves per area in comparison with saplings, but they receive lower levels of damage possibly due to differences in leaf phenology or leaf quality.

Light and phenology

Light availability influences patterns of leaf production (hypothesis 2). Leaf production was continuous in the canopy and seasonal in saplings, but the degree of seasonality depended on the light environment in the understorey. Saplings in gaps had broader peaks, while saplings in the lower light environments produced most of their leaves during a peak in June following the annual peak in light intensity (Angulo-Sandoval 1998). These results support previous observations that patterns of leaf phenology are associated with light availability (Angulo-Sandoval 1998, Coley & Aide 1991, van Schaik *et al.* 1993, Wright & van Schaik 1994; but see Reich 1994). Variation in leaf phenology in the vertical profile occurs because light decreases from the canopy (100%) toward the understorey (2%) (Chazdon & Fetcher 1984), but there can also be sufficient variation in light in the understorey (gaps vs. shade) to affect sapling leaf phenology (Augspurger 1984). Contrary to other studies (Aide 1993, Lowman 1992), differences in leaf production in *M. bidentata* had no affect on levels of herbivory. Levels of herbivory were similar between the leaves produced during the peak of leaf production and leaves produced out of the peak (hypothesis 3). Constant levels of herbivory throughout the year for each size class may occur because *Acrocercops* sp. populations can track changes in food availability as has been observed in other herbivore species (Basset 1991, Wolda 1978).

Herbivory in the vertical and horizontal profile

In the vertical profile, levels of herbivory varied and increased (hypothesis 4) from the canopy (1.3%) to the understorey (35.6%). Even when comparing leaves produced by saplings located in high light environments (e.g. gaps) and leaves produced in the canopy, herbivory was higher in gaps in comparison with the canopy. Other studies have documented similar patterns (Basset *et al.* 1992, J. L. Brown *et al.* 1997, Carroll & Luck 1984, Connor *et al.* 1983, Hinckley 1972, Lowman 1985, Phillipson & Thompson 1983) and have suggested that changes in the microclimate and leaf characteristics are the major factors affecting herbivores. Canopy leaves of *M. bidentata* had lower water content and were tougher in comparison with leaves from saplings, providing lower quality resources for larvae. High light in the canopy results in the development of thicker palisade parenchyma and thicker epidermal cells (Raven *et al.* 1992). *Acrocercops* sp. feed on parenchymal cells and it is possible that thicker parenchyma inhibits feeding. In addition, thicker epidermal cells may hinder larvae from reaching the parenchyma. Microclimate factors may also contribute to the low levels of herbivory in the canopy. Females of *Acrocercops* sp. may not reach the canopy because of high winds and high temperatures (Barbosa & Wagner 1989), and even if mines are established, larval survivorship would be low due to higher leaf temperatures in comparison with saplings. Nevertheless more research is necessary to determine female oviposition behaviour.

In the horizontal profile, levels of herbivory in saplings of *M. bidentata* were similar for plants in different light environments as has been found in other studies (Aide & Zimmerman 1990). However, some studies have found higher levels of herbivory in areas of low light and have suggested that herbivores cannot survive in high light environments (Maiorana 1981, Niesenbaum 1992, Papaj & Rausher 1983, White 1984). In contrast others have found that herbivores prefer plants in high-light environments (Harrison 1987, Lincoln & Mooney 1984) because leaves have a higher nutrient content. The lack of statistical difference in levels of herbivory in the horizontal profile is due to the high variation in damage rates. High variation in leaf damage to young leaves could occur if there is only a short period when leaves are vulnerable (Aide & Londoño 1989, Hunter & Lechowicz 1992). If ovipositing females discover young leaves while they are still tender, leaves may be completely eaten. In contrast if females lay eggs on slightly older leaves, larvae may not be able to develop on these tougher leaves.

Effects of herbivory on sapling growth

Although some saplings received high levels of herbivory, there was no detectable effect on growth (hypothesis 5: for height, diameter and new leaves). Other studies have demonstrated a negative effect of herbivory on plant growth (Aide & Zimmerman 1990, Fowler & Rausher 1985; Marquis 1984, 1992; Mendoza *et al.* 1987, Schierenbeck *et al.* 1994), even when levels of herbivory were lower than those observed in the present study. The lack of effect of herbivory on above-ground growth in *M. bidentata* may be due to the use of below-ground resources or it may be that reduced growth will only be detected over longer periods (Crawley 1983, Mambry & Wayne 1997, Trumble *et al.* 1993, Vranjic & Gullan 1990). Another possible explanation is that variation in herbivory reflects variation in defenses and although herbivory may be low, the cost of defense could limit the plant's growth (Coley 1983).

Plant density can influence levels of herbivory, but this study demonstrated that the spatial scale chosen for the analysis was crucial. If the study had only been done at the smaller scale (20-m × 20-m) we would not have detected an effect of plant density. In addition, the extreme variation in herbivory in the vertical profile demonstrates that plant/herbivore interactions are complicated and data from all size classes and different spatial scales are needed to understand patterns of herbivory at the population level.

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