Effect of artificial defoliation on growth and biomass of *Lantana camara* L. (Verbenaceae)

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Summary

Artificial defoliation techniques were used to examine the effect of frequency, timing and level of defoliation on *Lantana camara* L. (lantana). Every three months (spring, summer, or autumn), 0%, 50% or 100% of leaves were removed from plants. Changes in plant height, stem width and the number of stems were recorded one month after each episode of defoliation. At the end of the experiment all plants were harvested and the amount of biomass (dry weight) was calculated for the stems, roots, leaves and reproductive structures (buds, flowers and fruit).

There were no significant decreases in vertical height or the number of stems produced, but plants defoliated in spring produced more stems than those defoliated in spring and again in autumn. Similarly, there were no differences in root, stem, leaf or reproductive structure biomass. However, differences in the proportion of biomass allocated to reproduction were recorded. Plants that had been defoliated three times allocated a higher proportion of their biomass to reproduction than those defoliated once or twice. Overall, these results suggest that lantana compensates for defoliation.

Introduction

Artificial defoliation experiments simulate an individual plant's response to herbivory. Techniques involve the removal of portions of leaves, whole leaves, or reproductive structures such as pods (e.g. Poston *et al.* 1976, Talekar and Lee 1988, Peterson *et al.* 1992, Chen *et al*. 2002). These techniques have been criticized since they do not adequately simulate insect damage (Baldwin 1990) because, in addition to defoliation, insects may inject toxins or hormones, or introduce pathogens that affect the physiology of their host (e.g. Dyer and Bokhari 1976, Capinera and Roltsch 1980, Craig *et al.* 1986). A review by Baldwin (1990) concluded that though simulated and actual herbivory may produce the same physiological response, simulations are generally inferior to 'actual' experiments. Despite problems with the method, artificial defoliation experiments continue to be utilized in disciplines such as agriculture (e.g. Welter 1991, Singh and Sale 1997); animal, insect and plant ecology (e.g. Domínguez and Dirzo 1994, Harrison and Maron 1995); forestry (e.g. Hjältén and Danell 1993, Reichenbaker *et al.* 1996, Chen *et al*. 2002); and weed biocontrol (e.g. Cartwright and Kok 1990, Ang *et al.* 1994, Stamm-Katovich *et al*. 1999).

Several reasons explain the continued popularity of the artificial defoliation. Firstly, artificial defoliation allows an experimenter to accurately quantify damage since exact amounts of plant tissue can be removed (Baldwin 1990, Peterson *et al.* 1992). In contrast, natural insect populations are often unpredictable and may be difficult to manipulate, making replication of damage difficult, if not impossible (Higgins *et al.* 1984). Secondly, other effects of insect herbivory can be uncoupled from the effect of defoliation (Welter 1991). This is important if substances such as saliva, hormones or pathogens are introduced by the herbivore, or if plants vary in their susceptibility to herbivory (Baldwin 1990, Welter 1991, Shen and Bach 1997). For example, some cultivars are more susceptible to insect herbivory than others. Thirdly, the effects of timing of damage are important and easier to manipulate using artificial techniques than with insect populations (Welter 1991).

In this study, artificial defoliation was used to examine the response of *Lantana camara* L. (lantana) to defoliation. This technique was chosen in preference to actual herbivory because natural herbivory is due to five main insect species that feed on lantana leaves in Australia: two leaf-mining hispids (*Octotoma scabripennis* Guérin-Méneville and *Uroplata girardi* Pic), a leaf-mining agromyzid (*Calycomyza lantanae* (Frick)), a tingid (*Teleonemia scrupulosa* Stål) and a mealybug (*Phenacoccus parvus* Morrison) (Taylor 1989, Broughton 2000). Damage by these species is difficult to manipulate since they are active at different times of the year and damage different plant tissues (Harley *et al.* 1979, Cilliers 1982, 1987a,b, Broughton 2000). The objectives of this study were to determine the effect of timing, intensity of defoliation and frequency of defoliation on biomass partitioning and growth of lantana by defoliating lantana in spring, summer and autumn. Winter defoliation was not included as plants have few, if any, leaves at this time of the year.

Materials and methods

Plants

In April 1993, seeds were collected from 10 naturally growing *L. camara* plants of the cultivar pink-edged red (Smith and Smith 1982) at Samsonvale (27.20°S, 152.82°E). Seeds were planted into tubs filled with seed raising mix and germinated seeds were planted singly into 10 cm pots filled with a mixture of 4 parts sand, 1 part peat moss and 0.01 part of a slow-release fertilizer, (Osmocote®). Plants were watered daily and fertilized with Osmocote® at 12 and 18 months. After six months, plants were repotted into 15 cm plastic pots and transferred from the glasshouse to a prepared plot of land at the Alan Fletcher Research Station, Sherwood, Queensland, Australia (27.52ºS, 152.98ºE). To prevent root interaction, pots were placed 1.5 m apart on plastic sheeting. After 24 months, plants were repotted into 45 cm plastic pots.

Five grams of the granular insecticide/nematicide Furadan® were incorporated into the soil to discourage insect feeding. Furadan® contains 100 g kg^{-1} carbofuran as the active ingredient and is absorbed by the roots. Although the direct effects of Furadan® on lantana were not investigated, all pots received the same amount of insecticide and no phytotoxic effects were observed.

The experiment was laid out as a randomized complete-block design with ten replicate blocks. Pots were randomly assigned to each block; four columns and four rows comprised a single block.

Defoliation

Plants were defoliated at three-month intervals on the weeks beginning 22 September 1995 (spring), 22 December 1995 (summer) and 20 March 1996 (autumn) (Table 1). Since defoliation of all treatment plants took one week to complete, defoliation always commenced with the same block. Leaves were removed from the apex of the main stems and lateral stems first, lower branches were defoliated last. All terminal leaf pairs were left intact as earlier experiments had indicated that removal of these causes multiple branching (M. Hannan-Jones personal communication 1995). Whole leaves were removed by cutting through the leaf petiole with a scalpel blade. All leaves were removed from every branch in the 100% treatment, one leaf in each pair in the 50% treatment. Season combinations, defoliation levels and frequency of defoliation gave a total of 16 treatments with three levels of defoliation (0, 50 or 100%), seasonal defoliation combination (e.g. autumn, spring and

summer) and frequency of defoliation (1×, 2× or 3×) (Table 1).

Measurement of plants

Before the start of the experiment and six weeks after each episode of defoliation, the vertical height of each plant (cm), total number of branches and diameter of the main branch (cm) were recorded.

In September 1995, December 1995 and March 1996, five control plants (treatment 2) were randomly selected and harvested for biomass measurement. These plants were replaced by ones of the same age and grown under the same conditions to ensure an even distribution of pots within each block. In June 1996, all plants were harvested. The leaves, stems and reproductive structures (buds, flowers, and seed-heads) were separately collected into paper envelopes. Envelopes and their contents were dried in an oven at 70ºC until a constant dry weight was recorded (approximately 12 hours).

Roots were removed from their pots and the entire root-mass shaken to remove excess soil. The root masses were broken up and washed through a series of sieves to remove soil and collected and sun dried for 1–2 days to remove excess moisture. They were then dried until a constant weight was recorded.

Statistical analysis

Changes in plant dimensions. Changes in plant dimensions were calculated for each variable (number of stems, stem diameter, vertical height) using the equation:

Change in plant dimension (e.g. vertical height) = Final measurement–initial measurement/Initial measurement

Values were transformed prior to analysis to increase the homogeneity of variance and normalize distribution of the data (Fowler and Cohen 1990). Changes in plant dimensions were analysed using a randomized block three-way ANOVA. The three factors were defoliation level (0, 50 or 100%), seasonal defoliation combination (e.g. summer and spring, autumn and spring) and frequency of defoliation (1×, 2× or 3×).

Analysis of biomass partitioning. Biomass of the leaves, root, stem and reproductive structures (buds, flowers and fruit) was analysed separately. These values were also combined to derive a total biomass per plant. Above ground biomass was calculated by combining leaf, stem and reproductive structure biomass. An index of reproductive effort was calculated by dividing reproductive structure biomass by total biomass (Bazzaz and Reekie 1985). The effects of defoliation level, frequency of defoliation and seasonal combinations on biomass partitioning were analysed using three separate ANOVAs.

Analysis 1. Differences between control plants (five sets of plants destroyed in September 1995, December 1995 and March 1996) were analysed using a one-way ANOVA. Differences between treatment means were assessed using Tukey's test (SAS 1989, Zar 1996).

Analysis 2. Differences between treatments were determined by randomized blocks one-way ANOVA. The group means of the 14 treatments were compared with the mean for the control treatment (Treatment 1) using Dunnett's test (Zar 1996).

Analysis 3. Differences in biomass partitioning between treatments were further divided into three factors: defoliation level (0, 50 or 100%), seasonal defoliation combination (e.g. summer and spring, autumn and spring) and frequency of defoliation (1×, 2×, 3×). These factors were analysed by three-way ANOVA.

Results

Defoliation effects on plant architecture

No significant pre-treatment differences in height, stem diameter or total number of stems were detected (Table 2). All plants increased in height, stem diameter

Table 2. Effects of level, season, and frequency of defoliation on vertical height, stem diameter and stem number (n = 140).

Factor	Source		Pre-treatment		Treatment	
		DF	MS	*F*	MS	*F*
Vertical height	Block	9	251.40	0.88 ^{NS}	0.004	0.82 ^{NS}
	Treatment	14	355.42	1.25 ^{NS}		
	Level	1	-	-	0.007	1.37 ^{NS}
	Season	4	-	-	0.007	1.36 ^{NS}
	Level*Frequency	2	-	-	0.006	0.95 ^{NS}
Stem	Block	9	0.013	2.48 ^{NS}	0.012	1.48 ^{NS}
	Treatment	14	0.013	0.94 ^{NS}		
	Level	1	-	-	0.002	0.25 ^{NS}
	Season	4	-	-	0.008	1.01 ^{NS}
	Level*Frequency	2	-	-	0.017	2.10 ^{NS}
Number of stems	Block	9	0.017	1.15 ^{NS}	0.013	1.79 ^{NS}
	Treatment	14	0.017	1.48 ^{NS}		
	Level	1	-	-	0.0005	0.06 ^{NS}
	Season	4	-	-	0.022	2.98 **
	Level*Frequency	2	-	-	0.017	2.10

^{NS} = not significant (P >0.05); ** P <0.001.

Table 1. Defoliation and destruction treatments

Treatment #	Defoliation level % and (season)	Treatment #	Defoliation level % and (season)
1	Control – no defoliation	9	50% (spring and summer)
2	Destruction (collection of all leaves, stems, flowers and fruit for biomass measurement) in spring, summer, autumn and winter	10	50% (summer and autumn)
3	50% (spring)	11	50% (spring and autumn)
4	50% (summer)	12	100% (spring and summer)
5	50% (autumn)	13	100% (summer and autumn)
6	100% (spring)	14	100% (spring and autumn)
7	100% (summer)	15	50% (spring, summer and autumn)
8	100% (autumn)	16	100% (spring, summer and autumn)

and produced more stems irrespective of treatment (Figure 1). Significant treatment effects were observed for changes in the number of stems only ($F = 2.98$, $df = 4$, $P = 0.001$, Table 2). Plants defoliated in spring (September 1995) (treatments 3 and 6) produced 2–4 times more stems than those defoliated in spring and autumn (March 1996) (treatments 11 and 14) (Tukey's test, $P = 0.05$, Figure 1).

Biomass partitioning

Non-defoliated plants. There were significant differences in the biomass allocated to different plant structures between seasons ($P < 0.05$, Table 3). The exception was above ground biomass which was not significantly different between seasons ($F = 1.97$, $P > 0.05$). Plants harvested in spring had accumulated less biomass (stem and root) than plants harvested later in the year (spring < summer, autumn, winter) (Table 3). However, plants harvested in winter were also nine months older than those harvested in spring. Seasonal differences in biomass allocation were better illustrated by differences in leaf and reproductive structure biomass. In spring and summer plants bore more leaves, and in spring,

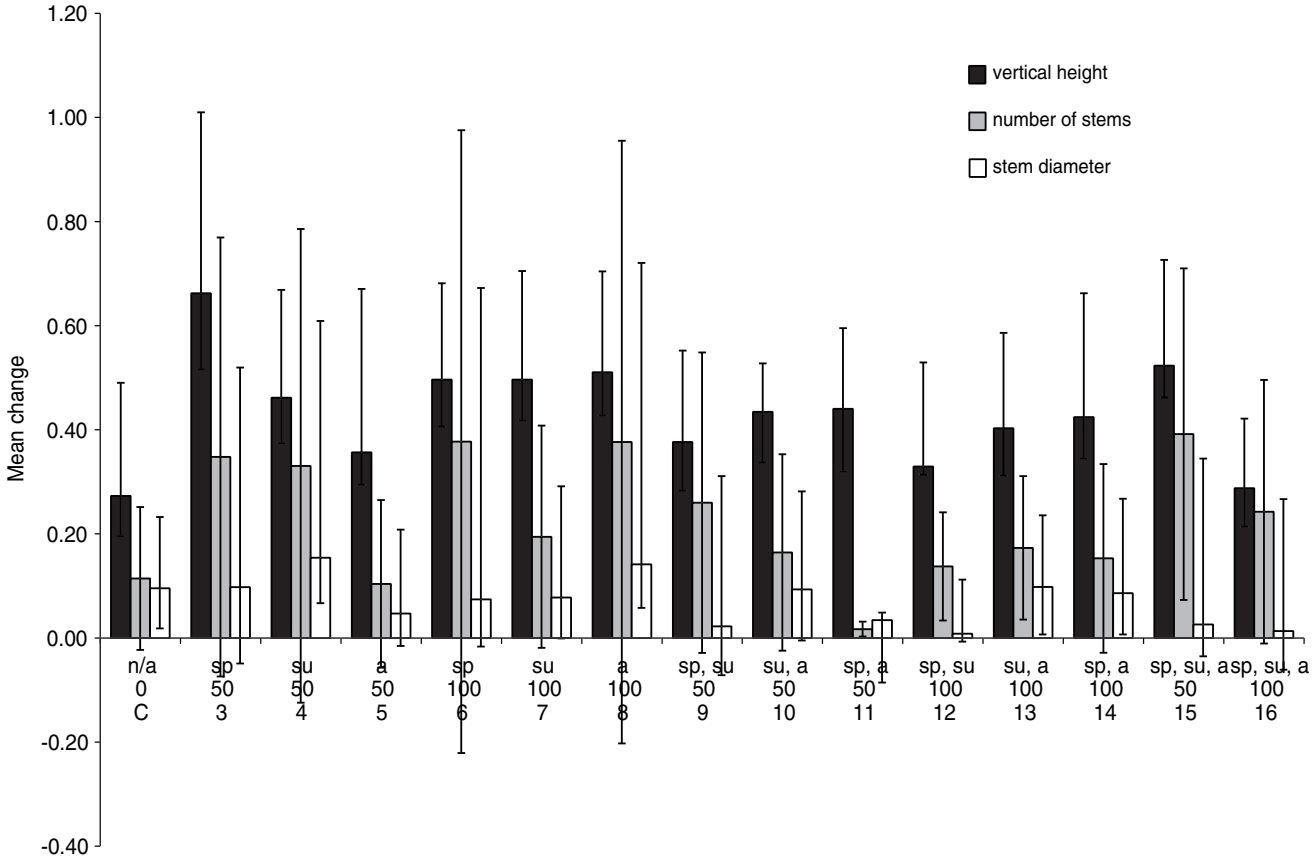

Figure 1. Mean changes (± SE) in vertical height, number of stems and stem diameter, for each treatment. Values on the X-axis show the season of defoliation (top line e.g. su = summer), level of defoliation (middle line: 0, 50 or 100) and treatment number (bottom line). See Table 1 for definitions.

Table 3. Biomass partitioning of destructively sampled plants. In any row, data followed by the same letter are not statistically different from each other (Tukey's test, P = 0.05).

	Season				ANOVA	
	spring	summer	autumn	winter	MS	*F*
Leaves (g)	85.33 ± 18.83ab	148.44 ± 59.25a	76.31 ± 14.7ab	61.91 ± 10.61a	7295.22	3.42 *
Stems (g)	138.08 ± 48.76a	195.59 ± 41.79ab	244.0 ± 16.93ab	350.39 ± 153.34b	40511.66	3.63 *
Roots (g)	286.13 ± 104.92a	895.37 ± 281.55ab	1039.35 ± 287.26ab	1114.95 ± 577.39b	708379.93	3.83 *
Total biomass (g)	533.23 ± 152.46a	1267.51 ± 343.64ab	1389.93 ± 320.58ab	1536.77 ± 617.58b	995509.33	4.31 *
Above-ground biomass (g)	247.10 ± 59.76	372.14 ± 87.75	350.58 ± 33.33	421.81 ± 145.74	27031.51	1.97 NS
Reproductive structures (g)	23.68 ± 3.99a	28.11 ± 3.13a	30.25 ± 4.79a	9.51 ± 6.41b	435.21	11.43 *
Proportion of biomass allocated to reproduction	0.046 ± 0.011a	0.024 ± 0.010b	0.024 ± 0.007b	0.008 ± 0.010b	0.0001	14.23 ***

NS = not significant ($P > 0.05$); * $0.01 < P < 0.05$; *** $P < 0.001$.

summer and autumn, more biomass was allocated to reproductive structures than in winter (F = 14.23, P < 0.001, Table 3).

Defoliated plants. Analysis of the data for biomass partitioning indicated no differences between treatments or blocks, except reproductive biomass (F = 1.68, P = 0.06) and effort (F = 0.0004, P = 0.0004) (Table 4). The significance of this result is discussed in the following section.

Effect of level, timing and frequency of defoliation. Level and frequency of defoliation did not affect biomass partitioning (Figures 2, 3). There were significant block effects for reproductive structure biomass (F = 4.74, P = 0.0001) and reproductive effort (F = 2.10, P = 0.03, Table 5). Plants in block one had a higher reproductive biomass and reproductive effort than any other group, due to a slight slope allowing more water to collect in block one. When this block was excluded from analysis, significant differences were still detected between blocks for reproductive biomass (F = 3.86, P = 0.0003), but not for reproductive effort (F = 1.64, P = 0.11). Overall, plants defoliated three times (50%, 100%) had a higher proportion of their biomass allocated to reproduction than plants defoliated once or twice (F = 4.09, P = 0.02; Table 5).

Table 4. One-way ANOVA results for biomass partitioning (Model = treatment; test block = random).

Factors	Block			Treatment		
	n	MS	*F*	*n*	MS	*F*
Leaf	9	1285.27	1.27 ^{NS}	14	1417.14	1.4 ^{NS}
Root	9	81092.25	0.60 ^{NS}	14	118855.46	0.87 ^{NS}
Stem	9	18855.22	1.54 ^{NS}	14	9629.85	0.79 ^{NS}
Above ground biomass	9	23995.81	1.68 ^{NS}	14	13543.75	0.95 ^{NS}
Total biomass	9	153519.01	0.85 ^{NS}	14	191040.00	1.06 ^{NS}
Reproductive effort	9	0.002	2.1*	14	0.001	1.38 ^{NS}
Reproductive structure biomass	9	31.98	4.7***	14	31.98	3.03***

^{NS} = not significant (P > 0.05); * 0.01 < P < 0.05; *** P < 0.001.

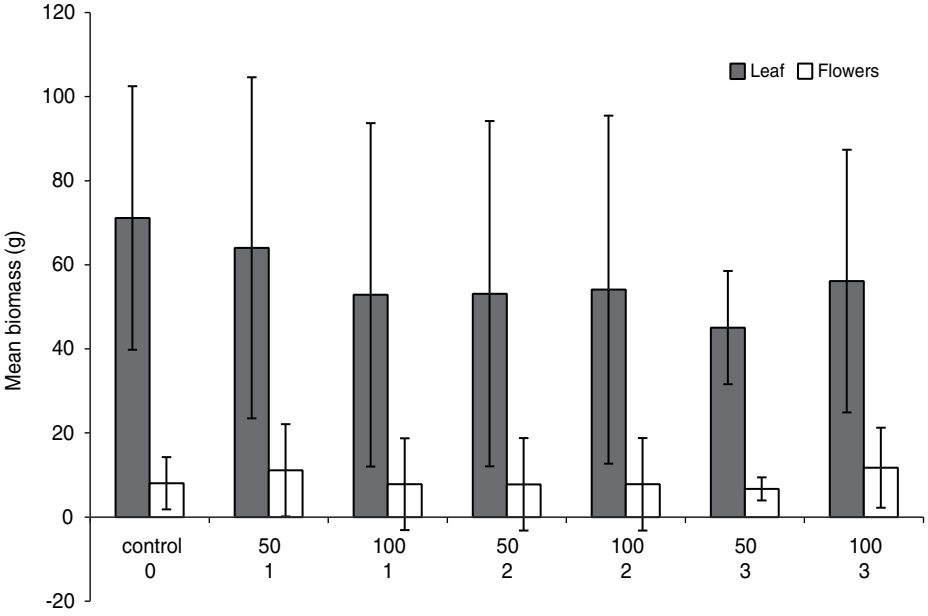

Figure 2. Effect of frequency and level of defoliation on leaf and reproductive structure biomass (± SE). Values on the X-axis show the level (top line e.g. 50 = 50%) and frequency of defoliation (bottom line). See Table 1 for definitions.

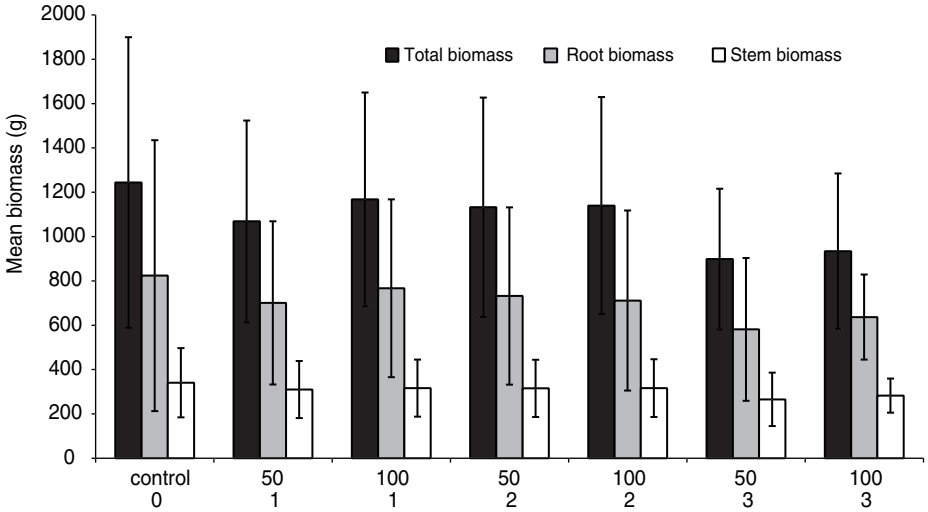

Figure 3. Effect of frequency and level of defoliation on total, stem and root biomass. Values on the X-axis show the level (top line, e.g. 50 = 50%) and frequency of defoliation (bottom line).

Discussion

Defoliation effect on plant growth

During the experiment, none of the treated plants died and all plants increased in height, stem width and produced more stems. Level of defoliation had no significant effect on biomass partitioning of the leaves, roots or stems. However, in response to increasing defoliation frequency, root and stem biomass gradually declined, though not significantly.

Leaf biomass was not significantly different between treatments, suggesting that *L. camara* compensated for damage by producing new leaves. Other possible compensatory mechanisms that were not assessed include increased efficiency of remaining leaf tissue (Reichenbacker *et al.* 1996), redistribution of assimilates (Bassman and Zwier 1993), reduction in shoot length (Craig *et al.* 1986), production of thinner, larger leaves (Winder 1980), or respiration of the stem (Pearson and Lawrence 1958, Winder 1980). Unfortunately, neither the time nor resources were available to collect the data to test these alternatives.

Defoliation had no effect on the production of reproductive structures or the amount of biomass allocated to reproduction, with the exception of plants defoliated three times. These plants had a higher proportion of biomass allocated to reproduction than plants defoliated once or twice. Other treatment differences may have been undetectable due to individual

Table 5. Three-way ANOVA F statistics for effects of blocking (B), level of defoliation (L), frequency of defoliation (F), seasonal defoliation combination (S) and their interactions on various measures of biomass partitioning. RE = reproductive effort.

Factor	df	Leaf	Stem	Reproductive structures	Above-ground biomass	Roots	Total biomass	RE
B	9	1.27 ^{NS}	0.14 ^{NS}	4.74 **	1.68 ^{NS}	0.60 ^{NS}	0.85 ^{NS}	2.10 *
L	1	0.14 ^{NS}	0.78 ^{NS}	0.13 ^{NS}	0.03 ^{NS}	1.67 ^{NS}	1.22 ^{NS}	0.20 ^{NS}
S	4	1.73 ^{NS}	0.59 ^{NS}	4.29 ***	0.99 ^{NS}	1.21 ^{NS}	0.98 ^{NS}	2.12 ^{NS}
L X F	2	1.88 ^{NS}	0.55 ^{NS}	4.09 *	0.42 ^{NS}	0.11 ^{NS}	0.05 ^{NS}	2.39 ^{NS}
L X S (F)	4	1.47 ^{NS}	0.73 ^{NS}	2.9 *	0.57 ^{NS}	0.31 ^{NS}	0.65 ^{NS}	0.64 ^{NS}

^{NS} = not significant (P >0.05); * 0.01 < P <0.05; ** P <0.01; *** P <0.001.

plant variation. In particular, plants within certain areas of the experimental plot apparently flowered much earlier. This event had been observed in the field (personal observations), where it might have been due to differences in nutrient or water availability. However, in this experiment all plants received the same amount of water and nutrients, although there may have been small differences in the amount of water retained by the plant due to the slight slope of the plot.

Timing of damage

Biomass sampling of plants during spring, summer, autumn and winter (controls) demonstrated a seasonal growth trend. During autumn and winter, fewer leaves and reproductive structures were present and in spring, *L. camara* produced more leaves, flowers and fruit. Since plants were watered daily, temperature and changing day-length apparently influenced growth.

Stem production was the only variable affected by timing of damage. Plants defoliated once in spring (50 and 100% defoliation) produced 2–3 times more stems than those defoliated during spring and autumn (50 and 100% defoliation). This result supports the hypothesis that plants defoliated early during the growing season compensate for damage, whereas plants defoliated later in the growing season are less able to compensate (Crawley 1989). For *L. camara* in southeast Queensland, the growing season is from spring to autumn, with most growth occurring in summer/autumn (Broughton 2000).

Overview and implications for the lantana biological control program

The results of this study are similar to those of Winder and van Emden (1980). In Brazil, they showed that only 100% defoliation effectively prevented vertical growth and reduced leaf biomass of *L. tiliaefolia*; root and stem biomass were not recorded. They also recorded a significant decline in fruit production and seed size: defoliation levels of 75 and 100% reduced fruit production by about 90% compared with controls. The differences between my results and Winder and van Emden's (1980) are probably due to the greater number of episodes of defoliation (21) and the longer duration of the experiment (two years).

In a study of *L. camara* at six sites in south-east Queensland, introduced agents damaged 1–25% of the leaves (Broughton 2000). This is similar to levels recorded in South Africa (Cilliers 1982, 1987b, Cilliers and Neser 1991). Damage was found to be continuous, with most insect damage occurring in autumn in Queensland (Broughton 2000) and midsummer in South Africa (Cilliers 1987b). For insect herbivory to be an effective strategy in a weed biological control program, damage must result in either under compensation or no compensation (van der Meijden 1989). Insect destruction of 1–25% of the leaves, well below the artificial defoliation levels inflicted during this study, was insufficient to prevent growth or the production of flowers and fruit at any of the field sites (Broughton 2000). For these reasons, I suggest that insect herbivory is not an effective strategy for the lantana biological control program. Plants that are able to compensate for damage are thought to store reserves for regrowth in parts that are relatively free from insect attack, such as the roots or stems (van der Meijden 1989). Future programs should concentrate on these areas rather than the leaves.

Acknowledgments

This work would not have been possible without V. McRoberts, who helped defoliate lantana, M. Hannan-Jones who provided the lantana plants, and the staff of the Alan Fletcher Research Station (Sherwood). G. White, D. Panetta, G. Gordh, R. McFadyen and R. Randall provided useful comments on earlier drafts of the manuscript. J. Hendricks provided statistics advice. The Cooperative Research Centre for Tropical Pest Management generously provided funds for research.

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