

Plant Population Structure and Insect Herbivory on *Solanum mauritianum* Scopoli (Solanaceae) in Southern Brazil: a Support to Biological Control

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ABSTRACT

Solanum mauritianum Scopoli (Solanaceae), a native Brazilian shrub, has become naturalized and invasive in several countries. In South Africa, where invasions are severe, herbivorous insects that attack *S. mauritianum* in its native area have been considered for introduction as biological control agents. To assess the action of such herbivores on the plant, studies were carried out on a population of *S. mauritianum* in an area undergoing regeneration in southern Brazil. An analysis of the structure of that population was performed, as well as of herbivory by insects, in particular of *Anthonomus* (Curculionidae). The population structure showed an “inverted J” pattern in diameter classes, but not in height classes. Individual plants showed an aggregate distribution. The damage caused by *Anthonomus* did not amount to the loss of a large leaf area, but since it was inflicted on young leaves and in a large proportion, could lead to the survival decrease.

Key words: Population structure, *Solanum*, *Anthonomus*, Herbivory, Biological control

INTRODUCTION

Solanum mauritianum Scopoli (Solanaceae), commonly known as “cuvitinga” or “fumo-bravo” (Kissman and Groth, 1995), is a native plant from southern Brazil that has become naturalized in Africa, Australasia, India and islands of the Atlantic, Indian and Pacific Oceans, probably through the Portuguese trade routes in the 16th century (Roe, 1972). In South Africa, the plant has invaded croplands, forestry plantations, riparian

and conservation areas, particularly in the higher rainfall regions of the country (Olckers, 1999). Although chemical control methods have proved effective in South Africa, biological control using herbivorous insects has been investigated as a more sustainable, long-term solution (Olckers, 2000; 2003).

Solanum mauritianum in its native country displays many ecological features that are typical of pioneer species. Some of these features include: (i) colonization of disturbed habitats that

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are in the initial stages of ecological succession; (ii) the production of small, abundant seeds that are spread by birds and bats; (iii) germination under conditions of high temperature or light; and (iv) the ability of seeds to persist in a soil seed bank until conditions for their establishment are favorable (Denslow, 1980; Brokaw, 1985; Swaine and Whitmore, 1988). Due to these characteristics, the species is able to grow and to reproduce in human made habitats and this aggravates the biological invasion problem.

The structure of a plant population is determined by abiotic and biotic factors which influence the spatial arrangement, age group and genetic structure of the plants in the population (Hutchings, 1997). These factors also cause temporal and spatial changes in the number of plants within the population (Watkinson, 1997). Information on the population's regeneration ability (i.e., the recruitment of new plants relative to local mortality) or on the occurrence of prior disturbances can be obtained from assessments on the size distribution of plants in a population, if carefully interpreted (Harper, 1977). This kind of study has been carried out for some tropical plant species (Swaine et al., 1987, Marques and Joly, 2000), in which the size distribution has provided information on the local and point stability of the relevant population. Population structure also incorporates the spatial distribution of plants that, according to Janzen (1970), depends on their seed dispersal pattern and on the probability of seedling survival.

Herbivory can play a major role in determining the structure of a plant population and can vary according to the density and distance of the individuals from the parent plant (Janzen, 1970). In particular, leaf-feeding herbivorous insects often have a high reproductive capacity and can periodically reach high densities, causing defoliation, decreased plant growth and reproduction, and increased mortality (Hartley and Jones, 1997). Considering that plant reproductive success is dependent on a high production of leaves (Solbrig, 1981) of good quality (Gramacho et al., 2001), sporadic or sustained instances of herbivory can significantly lower the regenerative capacity of plant populations (Howe, 1990; Doyle et al., 2002). Indeed, the exploitation of insect herbivores to lower the growth rates and reproductive capacity of invasive plants is the primary function of biological control. Several insect herbivore species have been identified as

potential biological control agents for release against *S. mauritianum* in South Africa (Olckers, 1999; Pedrosa-Macedo et al., 2003). Besides several leaf-feeding insect species that have potential for reducing the plant's high growth rates, species that reduce flowering and fruiting have been given high priority (Olckers, 2003). In particular, flowerbud-feeding weevils of the genus *Anthonomus* (Curculionidae), which also feed on young leaves on the tips of the branches, have been studied on natural *S. mauritianum* populations around Curitiba in Brazil because of their abundance and importance as candidate agents.

Despite considerable information on the insect natural enemies associated with *S. mauritianum* in its native countries (Olckers et al., 2002; Pedrosa-Macedo et al., 2003), little is known about the auto-ecology of the target plant. Studies on the structure of *S. mauritianum* populations in its natural environment could help to elucidate the plant's population behavior and assess its susceptibility to attack by insect herbivores. The aim of this study was, thus, to describe the structure of a *Solanum mauritianum* population in an early successional area in the Metropolitan Area of Curitiba, Paraná, Brazil, and relate it with the degree of leaf damage. In particular, the following issues were addressed: (i) the size and spatial structure of the plant population; (ii) the amount of herbivory (in particular by *Anthonomus* species); and (iii) whether insect herbivory is related to plant size. On the basis of the above information, an attempt was made to define the stages in which the plants were more susceptible to insect attack as this could influence the selection of agents and proceedings for biological control.

MATERIALS AND METHODS

The study was carried out at the Centro de Estações Experimentais do Canguiri of Universidade Federal do Paraná, located in the county of Pinhais, Paraná State (49°06'15"W and 25°24'30"S, 1000m altitude). The study area was previously used for agriculture and was abandoned approximately two years before the work started, thus being in the process of natural regeneration, with abundant pioneer species. The soil in the region is rarely deep (from 30 to 90 cm) and has good drainage, an organic to clayey structure,

typical of humic Cambisol and Xanthic Acric Ferralsol (Fupef, 2002) and has a soft relief that slopes slightly to the west. The study was carried out in the spring (September to November of 2003) when plants were flowering and fruiting.

A 3,200-m² area was subdivided into 32 adjacent 10x10 m plots. All *S. mauritianum* plants that were more than 20 cm tall were marked and their height and diameter at soil level was recorded. This minimum height was selected because of the difficulty in distinguishing between smaller individuals of *S. mauritianum* and the related *S. granuloso-leprosum*. The data were analyzed to estimate the size structure of the population, based on the frequency distribution in the height and diameter classes. A Kolmogorov-Smirnov test was carried out to determine if size structure was different from homogeneity (Zar, 1999). The spatial distribution of individual plants was evaluated by preparing maps of the density classes and using Morisita's index of dispersion (Brower and Zar, 1984), which determined whether the pattern was random (MI<1), aggregate (MI>1) or uniform (MI=1).

Leaf damage was assessed on each marked plant by sampling 30 leaves on three different branches (10 leaves per branch). For younger and smaller plants with less than three branches, 30 leaves from the existing branches were sampled. All leaves were sampled on plants with less than 30 leaves. Sampling started with the most basal leaf in each branch. Sampled leaves were recorded as: (i) whole (or undamaged); (ii) damaged solely by *Anthonomus* weevils; (iii) damaged by all other insects and (iv) damaged by *Anthonomus* weevils and all other insects. The damage caused by *Anthonomus* species was assessed because the weevils were frequent and had considerable potential as biological control agents (Pedrosa-Macedo et al., 2003). Feeding damage of the weevils was evidenced by small holes that were circular in the leaf lamina or semi-circular on the leaf borders, and leaf veins were all that remained after the intense feeding.

To estimate the leaf area lost by herbivory on the sampled branches, one leaf (the most basal) was collected for each of the four damage categories (see above). Branches that were not subject to all damage categories were sampled according to the categories represented. The leaves were taken to

the laboratory for oven drying and measurement. The leaf area assessments were facilitated by Sigma Scan Pro 5.0 software, in which the leaves were glued to white A4 size paper and then scanned in black and white. Once the total area damaged by insects (i.e. the perforated area) was calculated, then all the leaf perforations were colored-in with felt-tipped pens and the leaves were scanned again to calculate to total leaf area. The differences between the second and first area measurements for each of the leaves were recorded as the percentage of the total leaf area lost to herbivory. The means and standard deviations of the leaf areas lost in each category were obtained from these data.

RESULTS

Plant population structure

A total of 222 *S. mauritianum* plants was recorded in the study area (0.32 ha), indicating a population density of 694 plants.ha⁻¹. Plant heights ranged from 20 to 270 cm (mean=136.1±68.5). The height class distribution (Fig.1a) was not uniform ($D=84.6$; $P<0.05$), with a prevalence of individuals in classes 2 to 4 (from 45.5 to 121.5 cm) and 7 to 8 (from 173 to 223.5 cm). Individual stem diameters ranged from 0.32 cm to 9.23 cm (mean=2.5±1.5). The diameter class distribution (Fig. 1b) was not uniform ($D=26.6$; $P<0.05$) and showed a prevalence of individuals in classes 2, 3 and 4 (from 0.92 to 3.66 cm), with a smaller number of individuals in classes 1, 5, 6 and 7. The distribution of individual plants in the population was not uniform (Fig. 2), showing groupings as confirmed by Morisita's Index (MI=2.09).

Insect herbivory: In addition to the damage caused by *Anthonomus* species, *S. mauritianum* leaves were damaged by leaf-cutting ants of the genus *Acromyrmex* (Hymenoptera: Formicidae), which caused semicircular cuts on the leaf borders. In addition, damage was caused by leaf-mining larvae of the flea beetle *Acallepitrax* sp. (Coleoptera: Chrysomelidae) and the moth *Acrolepia* sp. (Lepidoptera: Acrolepiidae) and by the leaf-sucking lace bugs *Corythaica cyathicollis* and *Gargaphia decoris* (Hemiptera: Tingidae) that caused chlorotic speckling of the leaves.

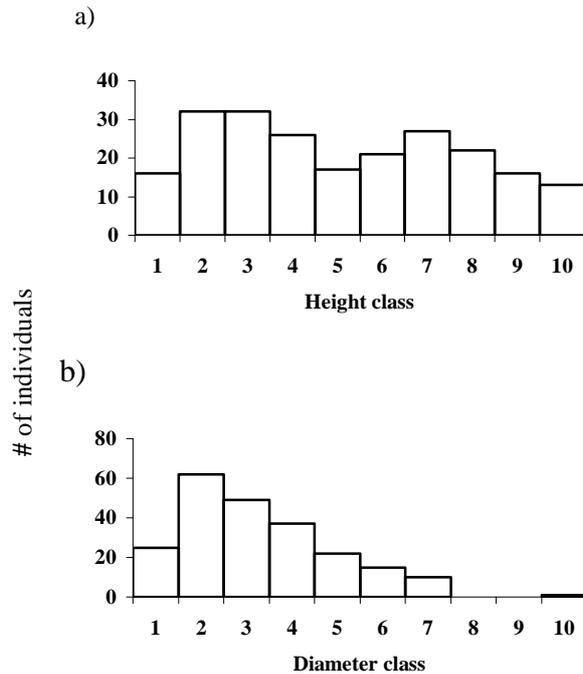


Figure 1 - The frequency of plant height class (a) and stem diameter class (b) within a *Solanum mauritianum* population in an area of regeneration in southern Brazil. Height classes (cm): 1= 20<x≤45; 2= 45<x≤70; 3= 70<x≤95; 4= 95<x≤120; 5= 120<x≤145; 6= 145<x≤170; 7= 170<x≤195; 8= 195<x≤220; 9= 220<x≤245; 10= 245<x≤270. Diameter classes (cm): 1= 0.001<x≤0.923; 2= 0.924<x≤1.846; 3= 1.847<x≤2.769; 4= 2.770<x≤3.692; 5= 3.693<x≤4.615; 6= 4.616<x≤5.538; 7= 5.539<x≤6.461; 8= 6.462<x≤7.384; 9= 7.385<x≤8.307; 10= 8.308<x≤9.230.

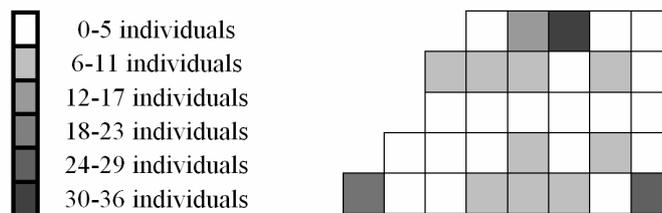


Figure 2 - Spatial distribution of *Solanum mauritianum* plants, according to six density classes, in 32 plots marked in an area of regeneration in southern Brazil.

The levels of herbivory were determined by an analysis of 5552 leaves. Of these, 5427 (97.8%) were damaged by insects and only 125 (2.2%) were intact. Of the damaged leaves, 81% were damaged by the other main insect groups (*Acromyrmex* spp., *Acallepitrax* sp., *Acrolepia* sp., *Corythaica cyathicollis* and *Gargaphia decoris*), while 14.5% were damaged by *Anthonomus* species and other insects, leaving only 2.3% (a low

level) that were only damaged by *Anthonomus* species alone.

Looking at the relationship between the number of damaged leaves and plant height (Fig. 3), it appeared that the damage caused in two of the categories, notably by other insects and by other insects and *Anthonomus* spp., tended to increase with increased plant height ($r^2 = 0.36$; $F = 56.23$; $P < 0.05$ and $r^2 = 0.03$; $F = 6.61$; $P < 0.05$,

respectively). By contrast, the damage caused by *Anthonomus* spp. was not influenced by plant height ($r^2 = 0.0044$; $F = 0.44$; $P = 0.64$).

The leaf area analysis indicated that leaves damaged by *Anthonomus* spp. were on average smaller than those attacked by other insects (Table 1), confirming observations that the weevils feed

on younger leaves at the shoot tips. As expected, the leaf area lost due to damage caused by *Anthonomus* spp. was considerably less than that caused by the feeding of other insects (Table 1).

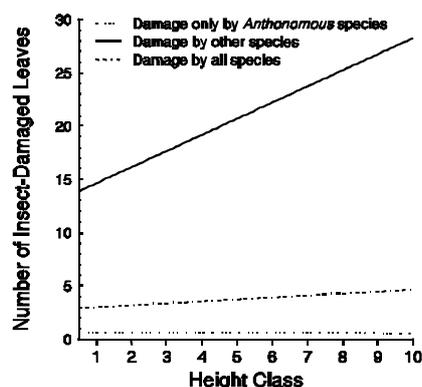


Figure 3 - Relationship between the number of insect-damaged leaves and plant height class (HC).
 Damage only by *Anthonomus* species = $13.933 + 1.7751HC - 0.3174(HC - 0.909)^2$.
 Damage by all species = $3.39 + 0.2838HC - 0.1710(HC - 4.909)^2$.

Table 1 - Mean (\pm standard deviation) area of leaves of *Solanum mauritianum* that were subject to different categories of insect feeding and the leaf area that was lost as a result. *Anthonomus* spp. $N=198$; All other species $N=586$.

Insect feeding	Leaf area (cm ²)	
	Total	Lost by damage (% of total)
<i>Anthonomus</i> spp.	20.34 \pm 12.17	0.24 \pm 0.20 (1.16%)
All other species	67.38 \pm 37.38	2.58 \pm 3.28 (3.83%)

DISCUSSION

In the *S. mauritianum* population under study, the stem diameter class distribution showed an “inverted J” pattern that suggested population stability (Agreen and Zackrisson, 1990; Marques and Joly, 2000). However, the different pattern observed with the plant height classes suggested that the stems might have been disturbed in some moments in the past.

Although the *S. mauritianum* population was recently established (2 years old), this provided sufficient time for all size classes of individuals to be represented and suggested that the population was stable at that time. This rapid growth and establishment was typical of pioneer species

(Brokaw, 1987), such as *S. mauritianum*. The disparity between the stem diameter and plant height patterns could be ascribed to the mechanical clearing of individual plants, which sprouted and continued to grow (personal observation). As a result, stem diameter continued to increase normally, giving rise to the stable “inverted J” pattern, while plant height increments were disrupted by differential levels of cutting, affecting some older plants that were shorter than younger ones. The presence of a comparatively smaller number of individuals in diameter class I could have been influenced by the exclusion of plants smaller 20 cm from the sampling.

The *S. mauritianum* population displayed an aggregate spatial distribution pattern, as shown by

the Morisita's indices. Studies on the structure and dynamics of plant populations have shown that the spatial distribution can be influenced by several biotic factors, including seed dispersal patterns and seedling survival, as well as abiotic factors like water and soil (Janzen, 1970; Hubbell, 1980; Marques and Joly, 2000). In *S. mauritanium*, the aggregate pattern might have been influenced by the aggregation of seeds under parental individual or by the vegetative propagation, since observations indicated several plants that were formed by vegetative "suckering". Though underground systems could be considered an additional problem to biological control (Kleinjan et al., 2004), plant aggregations might favor insect colonization and the subsequent build-up of large populations, because the plant populations provide an abundant and easily accessible food source.

The leaf-feeding insects recorded on *S. mauritanium* did not appear to display preferences based on the plants' developmental stage and attacked both young and adult plants. The high proportion of damaged leaves (98%) also suggested that insects could contribute to the regulation of *S. mauritanium* populations in native habitats, since the loss of photosynthetic area had been shown to reduce reproductive output by lowering the levels of flowering (Marquis, 1992b; Snow, 1994; Aizen and Raffaele, 1996) and seed production (Gramacho et al., 2001). Indeed, damage to leaves located in branches with flowers or flowerbuds was particularly destructive because these were the most important source of carbohydrates for the development of floral structures (Marquis, 1992a). Possibly the levels of herbivory on these leaves have a direct impact on the plant's reproductive capacity. Insects as *Anthonomus* spp. that attack floral tissues directly and also feed on younger leaves at the shoot tips, probably increase their impact on reproductive output.

The number of leaves damaged by *Anthonomus* spp. did not increase with increased plant height, despite the higher number of leaves available for feeding, confirming their preference for younger leaves at the shoot tips. By contrast, the number of leaves damaged by the other main insect herbivores increased with plant size, although this could be an effect of leaf damage that accumulated with time. Although the total leaf area that was estimated to have been lost by insect herbivory was low (around 5% for all species), this probably was under-estimated to a large extent. This was

because the evaluative method did not measure: (i) damage other than the leaf area that was missing at the time, (ii) reduced leaf vigour caused by leaf sucking and leaf mining, and, (iii) the levels of previous and future leaf abscission that would have resulted from high levels of feeding by the sap-sucking and leaf-mining insects. Indeed, the fact that only 2% of all leaves were not attacked by insects suggested that insect herbivory was much more significant than was suggested by the area loss table. Furthermore, this study did not consider the action of flower-feeding and stem-boring species that were known to be abundant in the area (Pedrosa-Macedo et al., 2003) and which would further increased the levels of herbivory reported.

In conclusion, although the results have not shown a strong relation among *S. mauritanium* population structure and insect herbivory, they suggested that leaf size and plant height was important for insect attack and must be considered to future biological control projects.

ACKNOWLEDGEMENTS

We thank to Agriculture Research Council - Plant Protection Research Institut (South Africa) for financial support, to Fundação de Pesquisas Florestais da Universidade Federal do Paraná (Brazil) for project administration and to Centro de Estações Experimentais do Canguiri of Universidade Federal do Paraná (Brazil) for field assistance. To João Renato Stemman for plant identification, to Maria Regina Torres Boeger for laboratory assistance and Augusta Karkow Doetzer for manuscript comments. We thank to Edgard Bredow, Luizimir Furmann, Thiago Granemann, Rafaela Sella and Lorena Stolle for field assistance.

RESUMO

Solanum mauritanium Scopoli (Solanaceae), um arbusto endêmico do sul do Brasil, naturalizou-se e tornou-se invasor em vários países do mundo. Na África do Sul, onde as invasões são severas, insetos fitófagos associados à planta no país de origem têm sido considerados para introdução como agentes de controle biológico. Para avaliar a ação de tais insetos no ambiente natural, foram conduzidos estudos em uma população de *S.*

mauritianum em uma área em regeneração no sul do Brasil. Foi realizada análise da estrutura populacional, bem como da herbivoria causada por insetos, em particular para uma espécie do gênero *Anthonomus* (Curculionidae), para subsidiar o trabalho sobre controle biológico. A estrutura da população mostrou um padrão “J invertido” nas classes de diâmetro, mas não nas classes de altura; a distribuição espacial dos indivíduos era agregada. O dano causado por *Anthonomus* sp. não refletiu na perda real de grande área foliar. No entanto, uma vez que foi detectada uma grande frequência de danos sobre indivíduos jovens, a herbivoria poderia levar à diminuição da sobrevivência da planta.

Palavras-chave: Estrutura populacional, *Solanum*, *Anthonomus*, herbivoria, controle biológico.

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Received: December 21, 2006;

Revised: September 18, 2007;

Accepted: December 20, 2008.