ARTIGO | *ARTICLE*

The impact of flower head endophages on seed set of a native population of *Chromolaena odorata* (L.) King & Robinson (Asteraceae)

O impacto de endófagos de capítulos sobre a produção de sementes de uma população nativa de Chromolaena odorata *(L.) King & Robinson (Asteraceae)*

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ABSTRACT

Chromolaena odorata (L.) King & Robinson, also known as siam weed, has negatively affected the ecology of several tropical and subtropical regions of the world and has caused them economic losses. The biocontrol of *C. odorata* is a challenge for many countries; however, several phytophagous insects are natural enemies of *C. odorata*. Here we present the main flower head feeding insects associated with a native population of *C. odorata*. The aims of this study were: (1) to evaluate both individual and aggregated impacts of endophagous insects on *C. odorata* seed production, and (2) to provide information on host specificity of each endophagous species at local and regional scales. The study was conducted in the cerrado area of the *Reserva Biológica de Mogi-Guaçu, São Paulo*, Brazil. We found 17 endophagous species from seven genera. We estimated that the endophages damaged at least 22% of all of the seeds *C. odorata* produced. Tephritid species were only found on the plant species from the tribe Eupatorieae, whereas lepidopteran and agromyzid species were found on the plant species from two or more Asteraceae tribes.

Key words: Biological control. Brazilian Cerrado. Compositae. Fruit-flies. Invasive plants. Siam weed. *Xanthaciura*

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RESUMO

Chromolaena odorata *(L.) King & Robinson tem causado impactos negativos, tanto ecológicos quanto econômicos, em regiões tropicais e subtropicais de diversas partes do mundo. Embora já se conheçam vários insetos fitófagos de* C. odorata*, o controle biológico dessa planta ainda é um desafio em muitos países. Neste artigo são apresentados os principais insetos associados a capítulos de uma população nativa de* C. odorata*. Os objetivos desse estudo foram: (1) investigar os impactos dos insetos endófagos sobre a produção de sementes de* C. odorata*, e (2) fornecer informações sobre a especificidade de hospedeiras dos insetos endófagos. O estudo foi realizado na área de cerrado da Reserva Biológica de Mogi-Guaçu, São Paulo, Brasil. Foram encontradas 17 espécies de insetos endófagos de sete gêneros. A perda estimada de sementes não dispersas por insetos endófagos foi de, pelo menos, 22% do total produzido. As moscas da família Tephritidae foram encontradas somente em plantas hospedeiras da tribo Eupatorieae, enquanto mariposas (Lepidoptera) e moscas da família Agromyzidae foram encontradas em plantas hospedeiras de duas ou mais tribos distintas.*

Palavras-chave: *Cerrado. Compositae. Controle biológico. Moscas-da-frutas. Planta invasora.* Xanthaciura.

INTRODUCTION

Chromolaena odorata (L.) King & Robinson (=*Eupatorium odoratum* L.; Asteraceae) is listed in the World Conservation Union's 100 of the world's worst invasive species (Lowe *et al*., 2000). *C. odorata* is widely distributed across its native neotropical distribution range and has spread over several tropical and subtropical regions of the world (Kriticos *et al*., 2005; Raimundo *et al*., 2007). It is a perennial, polycarpic shrub that is highly variable in both size and architecture (Witkowski & Wilson, 2001). The main traits that contribute to its successful spread are its long distance dispersal through thousands of windborne cypselae, its resprouting ability, its allelopathic effects, shade tolerance, low seed dormancy and its apomictic reproduction (Coleman, 1989; Blackmore, 1998; Ambika, 2002; Almeida-Neto & Lewinsohn, 2004; Rambuda & Johnson, 2004).

Cruttwell's (1974) compilation of phytophagous fauna lists 240 species of insects and mites that are associated with *C. odorata*. Despite several insects being tested as candidates for biological control agents (Cock & Holloway, 1982; Zachariades *et al*., 2002; Kluge & Zachariades, 2006) a high demand exists to find the most effective biological control agent that would maintain the populations of *C. odorata* at manageable levels and that would decrease its spread in Africa and Asia.

Gathering information on the effects that natural enemies have in a weed's native range is one of the first steps to successful biological control (Briese, 2004). However, to our knowledge, no studies have reported the impacts that flower head endophages have on *C. odorata*. We present the main flower head endophages associated with a native population of *C. odorata* and evaluate both individual and aggregate impacts on seed production. Additionally, we examine host specificity and discuss the potential use of some endophagous species as biological control agents.

MATERIAL AND METHODS

Study site

This study was conducted in the *Cerrado* sensu stricto area (a sparse arboreal savanna) located in the Reserva Biológica de Mogi-Guaçu, in the state of São Paulo (22°15'-16'S, 47°08'-12'W), Brazil, at an average elevation of 650m above sea level. The regional climate is characterized by wet summers and dry winters. Details pertaining to the region's climate and soil types can be found in De Vuono *et al.* (1982). Asteraceae is the second largest plant family found in the Brazilian *Cerrado* (Sano *et al.*, 2008) and at least 15 *Chromolaena* species have been recorded in this biome (Almeida *et al.*, 2005; Sano *et al.*, 2008). We have found five *Chromolaena* species, in addition to *C. odorata,* in the study area: *Chromolaena chaseae* (B.L. Robins) King & Robinson; *Chromolaena laevigata* (Lam.) King & Robinson; *Chromolaena pedunculosa* (Hook., Arn.) King & Robinson; *Chromolaena pungens* (Gardner) King & Robinson and *Chromolaena squalida* (DC.) King & Robinson. *C. odorata* has often been misidentified as *Chromolaena maximilianii* (Schrader ex A.P. De Candolle) King & Robinson, because they are morphologically very similar (Esteves, 2001). Thus, while many studies report *C. maximilianii* as a common species in the Brazilian *Cerrado*, we believe that *C. odorata* was often misidentified and is probably more common and widespread in the *cerrado* biome than previously reported.

Data collection

The study was conducted in two phases. The first phase was conducted during the *C. odorata* flowering period (March to June 2001; Almeida-Neto & Lewinsohn, 2004 for details on flowering phenology). We sampled 65 individual plants (from a total of 96) within an area of 60 x 50m to ascertain the impact that each endophagous species had on seed loss in the individual flower heads and seed loss at the population level. Every week we sampled 30 pre-dispersal flower heads per plant (or fewer if 30 were not available). In the laboratory, the flower heads were stored separately in cellulose capsules to facilitate the recording of the endophages and their impact on seed production. Since the majority of endophages had emerged before sampling, we often used the distinctive puparia and the kinds of damage we found on the flower heads to identify the insect species.

We dissected each flower head and counted the number of intact and predated achenes (hereafter referred to as seeds) under a stereomicroscope. Two measures of seed damage were obtained for each endophagous species: the mean number of predated seeds per flower head and the aggregate percentage seed loss from the *C. odorata* population. Aggregate seed damage was calculated as the weighted mean of the proportion of predated seeds, using as the weight factor the total number of flower heads from all sampled plants per sample date.

We categorized the seeds into four classes to estimate the impact that the flower head endophages had on the total number of apparently viable seeds produced by each plant: (1) viable (i.e. apparently undamaged and developed); (2) predated (i.e. totally or partly damaged by endophagous insects); (3) empty (i.e. with a non-fertilized ovule); and (4) others (i.e. predated by exophages, damaged by fungi or undeveloped). We assumed that the percentage of predated seeds, excluding categories 3 and 4, was a reasonable estimate of the loss of the plant reproductive investment caused by herbivores.

The level of damage caused by some endophagous species could not be evaluated with confidence because these insects were either extremely scarce or their identification was problematic. We pooled seed predation caused by all lepidopteran species because they were relatively rare and their damage and/or puparia could not be associated with their adult forms. Cecidomyiid species, however, were relatively frequent but their identification was not possible because their larvae and adults are very uncommon in post-anthesis (pre-dispersal phase) flower heads. Thus, we grouped together any damage caused by the cecidomyiid species of the genera *Asphondylia* Loew and *Dasineura* Rondani.

The second phase of this study was conducted from August 2001 to August 2002. We recorded all Asteraceae individuals found within 20 randomly located transects (transects were 5m x 30m within an area of 6 ha; 200m x 300m). We sampled flower heads once every two weeks (n=26 sample days). The flower heads were collected randomly from plants we found in the 6 ha study area. We sampled up to 80mL of flower heads from each Asteraceae individual and up to 30 individuals from each Asteraceae species. Endophages were reared in the laboratory and all samples were kept in plastic pots with wide lids that had ventilation openings covered by a fine mesh screen. Samples were inspected every three days over a period of two months.

We examined data collected from other *cerrado* areas (Diniz, 2003; Fonseca *et al*., 2005; Almeida *et al*., 2006; Almeida-Neto, 2006) to obtain the number of host plants for each endophagous insect recorded in *C. odorata* on a regional scale.

With the data that we collected from the two study phases, we examined if the impact that the endophagous species had on seed production at the plant population level was related to their level of specialization, measured by the number of local host-plants. We also evaluated the relationship between the mean number of damaged seeds per flower head and the estimated proportion of seed damage at the population level of each endophagous species. Correlations were analyzed using Spearman's rank coefficient.

RESULTS

We found 17 endophagous species associated with *C. odorata* flower heads (species are listed in Tables 1 and 2; an unidentified microlepidoptera is not listed). Forty-three percent of the flower heads we dissected (n=5238) had one or more endophages. Two congeneric tephritid species, *Xanthaciura chrysura* Thomson and *Xanthaciura* sp. near *chrysura*, represented 71% of all of the endophagous individuals we found (Table 1), whereas two cecidomyiid species (*Asphondylia* sp. and *Dasineura* sp.) accounted for 27% of the total abundance.

Endophagous insects reduced by 38% the number of apparently viable seeds produced by the 65 sampled individuals of *C. odorata* (Table 1). The mean number of predated seeds per flower head ranged from less than 2 to 11 seeds at the end and at the beginning of the fruiting period, respectively (Figure 1).

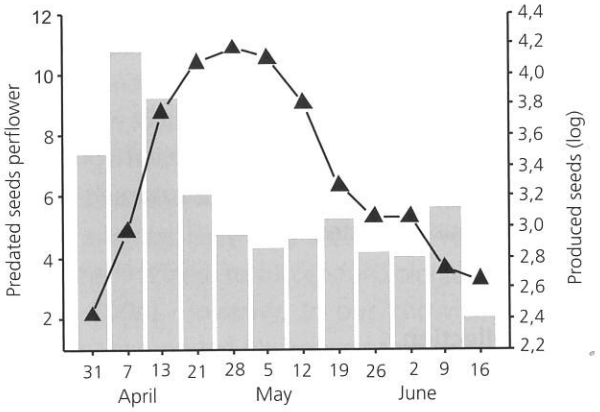

Figure 1. Mean number of predated seeds (achenes) per flower head (gray bars) and total number of produced seeds (black triangles) pooled for the 65 sampled plants from March 31 through June 16 (2001).

Table 1. Impact on seed production and the prevalence of the major flower head endophages found on a native population of Chromolaena *odorata* in Southeastern Brazil.

Species/group	Reared individuals*	Damaged flower heads (%)	Individuals per flower head	Damaged seeds per flower head	Total seed damage (%)
Xanthaciura chrysura	1 859	27.50	1.4	6.5	18.30
Xanthaciura sp.	620	10.80	1.2	8.8	7.60
Cecidomyiids	934	8.00	2.8	1	1.40
Xanthaciura mallochi	6	0.11	1	10.2	< 0.10
Cecidochares connexa	7	0.13	1	12.6	< 0.10
Cecidochares sp.	12	0.23	1	18	< 0.10
Melanagromyza bidentis	24	0.46	1	7.6	< 0.10
Melanagromyza neotropica	20	0.38	1	11.3	< 0.10
Lepidopterans	7	0.13	1	17.3	< 0.10
Apion sp.	14	0.27	1	16	< 0.10
Indeterminate	-	–	-	-	10.40

* reared in 5239 flower heads of 61 plants throughout the flowering/fruiting period in 2001.

Some species recorded in the second phase of this study were not reared in the dissected flower heads We used the number of flower heads per sample date as a weighting factor to estimate the proportion of predated seeds.

Almost 95% of the seed damage at the plant population level was caused by the two most abundant species: *X. chrysura* and *Xanthaciura* sp.. The number of damaged seeds per flower head varied from zero, for some cecidomyiid species, to all seeds for some lepidopteran species. The intensity of seed damage caused by the endophagous species at the flower head level was not significantly correlated with their aggregate damage at the population level (*rs*=-0.310, *p*=0.417).

The number of additional host-plant species used by the endophagous species associated with *C. odorata* ranged from 0 to 9 and from 2 to 46 on the local and regional scales, respectively. Tephritid species were only found in plant species from the tribe Eupatorieae, whereas both lepidopteran and agromyzid species were found in plant species from two or more tribes (Table 2). The local specialization level of the endophagous species, measured as the number of local host-plants, was not related to their aggregate impact on seed production from the *C. odorata* population (*rs*=0.352, *p*=0.238).

DISCUSSION

Assessing the impact caused by releasing an insect species into a weed's native range is a critical step in improving the success of biological control agents; however, it is often difficult to accomplish. We report the impact that flower- and seed-feeding endophagous insects have on a native population of *C. odorata*. At least six of the species we found had not been previously listed as flower head endophages of *C. odorata* (Agromyzidae: *Melanagromyza bidentis* Spencer, *Melanagromyza neotropica* Spencer; Pyralidae: *Unadilla erronella* (Zeller); Tephritidae: *Xanthaciura chrysura*, *Xanthaciura mallochi* Aczel; Tortricidae: *Saphenista squalida* Raz. & Becker). The undescribed *Xanthaciura* sp. was mixed with *X. chrysura* but their puparia morphologies were easily distinguishable. *Xanthaciura* sp. is an undescribed species (Allen Norrbom; USDA, USA).

Seed-predating insects have been widely utilized in weed biocontrol programs (Julien, 1992) and there is evidence that they may be effective in

Table 2. Local and regional host-plants of the flower head endophagous species recorded on *Chromolaena odorata* in the State of *São Paulo*, Brazil.

Family Species	Species		Genus		Subtribe		Tribe	
	L	R	L	R	L	R	L	R
Agromyzidae								
Melanagromyza bidentis	7	8	3	3	3	3	3	3
M. neotropica	3	3	3	3	3	3	1	2
Melanagromyza sp.	4	5	3	4	3	4	2	2
Tephritidae								
Cecidochares connexa	3	7	1	1	1	1	1	1
Cecidochares fluminensis	2	5	1	1	1	1	1	1
Cecidochares sp.	1	9	1	1	1	1	1	1
Neomyopites paulensis	4	9	2	2	1	2	1	1
Xanthaciura biocellata	3	12	3	7	2	5	1	1
X. chrysura	8	17	5	8	4	7	1	1
X. mallochi	2	4	2	3	2	2	1	1
Xanthaciura sp.	6	10	3	3	2	3	1	1
Pyralidae								
Unadilla erronella	9	47	7	19	6	14	3	5
Tortricidae								
Saphenista squalida	10	22	7	15	6	12	4	5

L: number of Asteraceae hosts at the *Reserva Biológica de Mogi-Guaçu*; R: pooled number of Asteraceae hosts for several *cerrado* remnants in the State of *São Paulo*.

limiting plant recruitment (Louda, 1982; Louda & Potvin, 1995). Among Asteraceae, pre-dispersal seed predation is common, but its impact varies greatly among different species (e.g. Louda, 1982; Fenner & Lee, 2001; Pickering, 2009). In this study, we found that flower- and seed-feeding endophages reduced the number of apparently viable seeds of a native population of *C. odorata* by 38%.

Flower- and seed-feeding endophagous insects may not be effective biological control agents for *C. odorata* due to the vast number of seeds produced by this weed (Zachariades *et al.*, 1999). Zachariades *et al.* (1999) propose that leaf-, stem- and root-feeding insects are better candidates for the biological control of *C. odorata* because they would remove growth and flowering tissue, whereas flower- and seed-feeding endophages could not reduce the seed production significantly. This assumption is based on the idea that plant damage at the fruit, individual and population levels is strongly correlated. However, we found that the intensity of seed damage in a single flower head was not correlated with the aggregate damage found at the individual and population levels. This finding illustrates the importance of evaluating the effects that natural enemies have in a weed's native range.

The selection of weed biocontrol agents has two major focuses: (1) effectiveness (i.e. the demographic effect of the agent on the target weed in non-native regions) and (2) specificity (i.e. the host species number or phylogenetic distance of additional plants consumed by the agents; see Briese, 2004). One of the chief goals is to minimize the economic cost. While high effectiveness reduces the need for other biological control agents or methods, high specificity reduces the risk of undesirable effects on non-target plants. Thus, it is necessary to use all of the available information when selecting which species would be the most appropriate agent for the biological control of weeds.

We provide novel ecological information on the impact that flower head endophages have on *C. odorata*. The endophagous insect *X. chrysura* damaged at least 14% of all apparently viable seeds and was responsible for 67% of all predated seeds; however, this tephritid species has never been cited as a phytophage of *C. odorata*. Although this impact may be small for biological control purposes, as far as we know it is the greatest seed loss measured at the plant population level during a complete flowering/fruiting period for this weed. McFadyen (1988) only found 10% of damaged flower heads in the first five weeks of the flowering season at three sites on the island of Trinidad and concluded that the total effect of seed destruction was insignificant. We have not measured the impact of other insect guilds in the field but we did not find frequent external herbivory in our study area. Thus, the demographic impact that *X. chrysura* had on the sampled population of *C. odorata* is probably the greatest among the phytophages. *Xanthaciura chrysura* occurs from southern Mexico to northern Argentina (Foote *et al.*, 1993) and specializes on Asteraceae from the tribe Eupatorieae (Prado *et al.*, 2002). We sampled flower heads from nine Asteraceae tribes (Astereae, Eupatorieae, Gnaphalieae, Helenieae, Heliantheae, Mutisieae, Plucheeae, Senecioneae and Vernonieae) but *X. chrysura* was reared only on Eupatorieae. Without its natural parasitoids *X. chrysura* would have had a greater demographic impact on *C. odorata*. *Xanthaciura chrysura* is a potential candidate for future tests as a biological control agent for *C. odorata*. Both *X. chrysura* and the undescribed *Xanthaciura* sp. near *chrysura* could improve the biological control of *C. odorata* if used in combination with other agents, such as the tephritid *Cecidochares connexa* Macquart and the arctiid *Pareuchaetes pseudoinsulata* Rego Barros (Siebert, 1989; McFadyen *et al.*, 2003).

There is a growing consensus that the choice of biological control agents must be based on the ecological interactions between the target weed and their natural enemies (Briese, 2000) instead of on an agent's ability to damage an individual plant with little consideration for its effects on population levels (Briese, 2004). More than three decades after McFadyen's (Cruttwell 1974) annotated list of 240 species that attack *C. odorata* and several subsequent studies of related, potential biological control agents

(Cock & Holloway, 1982; Kluge & Zachariades, 2006), *C. odorata* still causes large economic and ecological losses in its non-native range (McWilliam, 2000; Leslie & Spotila, 2001). The control of *C. odorata* requires an integrated approach involving proven methods (Ambika & Jayachandra, 1989). We suggest that *X. chrysura* should be evaluated further as a potential biological control agent for *C. odorata,* mainly in regions where there are few or no native Eupatorieae species, such as Southeast Asia and most tropical Pacific islands.

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