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PODA EXPERIMENTAL DE *Chromolaena pungens* (ASTERACEAE) E SEUS EFEITOS MULTITRÓFICOS

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“Ich habe keine besondere Begabung, sondern bin nur leidenschaftlich neugierig.”

Albert Einstein

Cecidochares connexa (Diptera: Tephritidae) sobre um capítulo de sua hospedeira *Chromolaena pungens* (Asteraceae:Eupatoriae) a lápis preto / por Débora Becker.

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RESUMO

Perturbações naturais ou antrópicas podem induzir mudanças fenotípicas nas plantas, que por sua vez podem influenciar herbívoros, predadores e polinizadores. Fatores abióticos, tais como nutrientes também podem influenciar a recuperação das plantas. Neste estudo investigamos o efeito de poda experimental em artrópodos associados a plantas rebrotadas em populações naturais de *Chromolaena pungens* (Asteraceae: Eupatoriae), uma planta subarbustiva, perene e nativa de cerrado. Os objetivos deste trabalho foram avaliar como o rebrote após corte raso ou poda parcial e o suprimento de nutrientes influenciam: (i) o crescimento vegetativo, (ii) a reprodução e os caracteres florais, (iii) a abundância de galhas, insetos folívoros, insetos sugadores e seus predadores; (iv) a comunidade de insetos endófagos associados e a incidência de seus parasitóides. O experimento seguiu um desenho de dois fatores em blocos, onde foram manipulados corte (controle, corte parcial e corte raso) e nutrientes (sem adição de nutrientes e com adição de nutrientes). Plantas cortadas na base foram menores, produziram menos folhas e capítulos, tiveram sua fenologia retardada em um mês em comparação com plantas controle ou de corte parcial. No entanto, a taxa de crescimento, a área foliar e o tamanho dos capítulos foram maiores em plantas submetidas a corte raso. Tais plantas sofreram maiores níveis de herbivoria foliar e destruição de sementes. Além disso, a abundância, a riqueza, a diversidade de espécies de endófagos associados a capítulos de plantas cortadas foram maiores do que em plantas controle ou parcialmente cortadas. Em conseqüência, a composição de espécies endófagas diferiu entre plantas submetidas a diferentes tipos de corte. Por isso, os resultados deste estudo são relevantes para o entendimento de interações inseto-planta em ambientes que sofrem perturbações naturais ou antrópicas recorrentes.

ABSTRACT

Natural or human-induced disturbances may promote plant phenotypic modifications, developmental and phenological changes which, in turn, may influence herbivores, predators and pollinators. Abiotic factors, especially nutrient availability, may also influence plant recovery. In this study, we evaluated plant regrowth and arthropod responses to experimental clipping plants in natural populations of *Chromolaena pungens* (Asteraceae: Eupatoriae), a perennial, native shrub in the Brazilian Cerrado. In particular, we assess how resprouting after severe or partial damage and nutrients influence: (i) vegetative regrowth; (ii) reproductive effort and floral traits; (iii) the abundance of galling, leaf-chewing and sap-sucking insects and their predaceous arthropods; (iv) endophagous insects and their parasitoids. The experiment followed a two-factor randomized block design, respectivelly clipping (control, partial clipping and basal clipping) and nutrients (no nutrient added and with nutrients added). Basally clipped plants were smaller, produced fewer leaves and flowerheads than partially clipped and control plants, moreover heir floral phenology was delayed by one month. However, the relative elongation rate, leaf area and flowerhead size were greater in basally clipped plants. These plants also suffered higher leaf herbivory and seed destruction. Moreover, the abundance, species richness and abundance of flowerhead endophages were higher in basally clipped plants than in the other treatments. Not surprisingly, species composition differed among clipping treatments. For this reason, these findings contribute to the knowledge of insect-plant interactions in recurringly disturbed habitats.

INTRODUÇÃO GERAL

Perturbações abióticas e bióticas exercem um papel importante na estruturação de comunidades (Sousa 1984, Menge & Sutherland 1987), no entanto poucos estudos examinaram seus efeitos diretos ou indiretos em interações bióticas (Spiller & Agrawall 2003, Nakamura et al. 2006). A destruição da parte aérea das plantas provocada por perturbações naturais ou antrópicas tem o potencial de estimular o crescimento vegetativo e reprodutivo de plantas, sendo esta resposta encontrada em vários sistemas (McNaughton et al. 1983, Stein et al. 1992, Bailey & Whitham 2002, Martinez & Wool 2003, Riipi et al. 2005, Nakamura et al. 2006). Porém, após serem severamente danificadas, as plantas podem responder positiva ou negativamente. As respostas compensatórias podem se situar em diferentes pontos de um contínuo que abrange desde a diminuição (subcompensação) até o aumento (sobrecompensação) da aptidão da planta após o dano (Maschinsky & Whitham 1989, Whitham et al. 1991). Este crescimento compensatório será determinado por certos fatores, tais como a quantidade de tecido removido, a inexistência de competidores, o estágio ontogenético, o período de floração, a quantidade de recursos estocados, e condições abióticas favoráveis para o crescimento subseqüente (Maschinsky & Whitham 1989). Embora a sobrecompensação de plantas tenha sido demonstrada em diversos experimentos em estufas e em sistemas agroecológicos, os mecanismos compensatórios de plantas em seus habitats naturais foram pouco estudados (Schoohoven et al. 2005).

A remoção da parte aérea pode modificar as características reprodutivas e vegetativas. Plantas rebrotadas podem sofrer mudanças em tamanho, arquitetura, podendo alterar seu período de floração, asssim como a produção de flores e/ou frutos (Maschinsky & Whitham 1989, Whitham et al. 1990, Freeman et al. 2003, Sharaf & Price 2004). Além disso, o dano severo pode induzir alterações morfológicas e químicas em componentes vegetativos e reprodutivos das plantas. Essas variações no número, qualidade, forma, tamanho e química de componentes estruturais podem modificar a atratividade de mutualistas e antagonistas (Root 1973, Bryant et al. 1893, Coley et al. 1985, Young & Stanton 1990, Johnson et al. 1995, Møller & Eriksson 1995, Brody 1997, Strauss et al. 1996, Ohashi & Yahara1998, Freeman et al. 2003, Sharaf & Price 2004). A morfologia das plantas pode ser um fator crítico nas interações tri-tróficas, podendo afetar o forrageamento e a eficácia de predadores e parasitóides. Recentemente, o número de estudos que demonstram a importância das características fisico-químicas da planta hospedeira sobre os inimigos naturais de herbívoros, tem crescido (Price et al. 1980, Clark & Messina 1998, De Moraes et al. 1998, Harvey et al. 2003).

Desta forma, plantas rebrotadas após a remoção de sua biomassa aérea por distúrbios naturais ou antrópicos podem desencadear efeitos multitróficos em cascata. No entanto, o conhecimento sobre os efeitos diretos ou indiretos das características diferenciais de plantas rebrotadas sobre suas entomofaunas associadas ainda é limitado. Por esta razão, o presente estudo propõe-se, primeiramente, a desenvolver uma pequena revisão sobre os efeitos de plantas rebrotadas sobre as interações planta-artrópodos (capítulo 1) apontando os principais resultado encontrados por estudos anteriores. No capítulo seguinte um experimento fatorial em blocos foi desenvolvido com o intuito de esclarecer as respostas de uma população nativa de *Chromolaena pungens* (Asteraceae: Eupatoriae) a diferentes intensidades de dano em sua parte aérea, avaliando ainda o efeito da disponibilidade de nutrientes na recuperação após o dano.

Como mencionado anteriormente, herbívoros e polinizadores respondem a variações morfológicas das plantas, porém o conhecimento do quão sensíveis são os herbívoros endófagos às variações nas estruturas florais ainda é escasso (Fenner et al. 2002, Masters et al. 2001). Sabe-se que esses insetos são geralmente muito especializados (Prado & Lewinsohn 2004). Os adultos depositam seus ovos nos botões florais e suas larvas sedentárias ficam extremamente dependentes dos recursos alimentares obtidos em um capítulo até se tornarem adultos. Por isso, acredita-se que estes herbívoros poderiam reagir a pequenas mudanças ocorridas em sua fonte alimentar. Além disso, a eficiência do forrageamento de seus parasitóides pode ser influenciada pelas características estruturais da planta de seu hospedeiro (Masters et al. 2001).

Portanto, o terceiro capítulo foi proposto com o intuito de esclarecer os efeitos das mudanças fenotípicas das plantas, após um dano severo, na abundância, riqueza e composição de insetos herbívoros associados à *C. pungens* e na incidência de seus inimigos naturais. Este estudo é especialmente importante para elucidar as conseqüências de perturbações bióticas ou abióticas em interações animal-planta.

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Capítulo I

Plant resprouting effects on arthropod-plant interactions: a review

ABSTRACT

Animal-plant interactions are inserted in complex webs of direct and indirect interactions and prone to environmental variation. Evaluation of factors that may disrupt these interactions is important to understand and to predict ecological and evolutionary outcomes of interactions. The destruction of plant aboveground structures may exert an important role altering the strength of mutualistic and antagonistic relationships, since the plant damage may set off cascading up effects to higher trophic levels. Here we review the evidence for changes in arthropod-plant interactions driven by plant resprouting induced by severe damage. First, we review the types of damage caused by human-induced disturbances, large-scale destruction or mammalian herbivory, leading to plant structural loss. Then we appraise plant traits that are modified after damage and their consequences for arthropods. Finally, we explore experimental studies reporting changes in animal-plant outcomes in response to plant regrowth. Several studies of the effects of plant resprouting on herbivore-plant interactions have revealed positive responses, increasing the performance, abundance and even species richness of herbivorous insects. Conversely, plant-pollinator interactions are generally disrupted after plant damage, which may impose a high cost to plants in lost pollination services. In contrast, in the relatively few studies assessing the effects of resprouting plant traits on the third trophic level, natural enemies of insect herbivores increased their abundance and performance after host-plant damage. We emphasize the importance of incorporating complexity in future studies to understand animal-plant responses to disturbances.

INTRODUCTION

Biotic interactions are inserted in complex webs of direct and indirect interaction embedded in the abiotic environment. As a consequence, interest on multispecies interactions or environmental variation has grown recently; factors may interact to determine both ecological and evolutionary outcomes of communities (Bailey & Whitham 2003, Strauss & Irwin 2004). For example, large-scale destruction caused by abiotic natural disturbances (e.g floods, fires and hurricanes), grazing, logging or even shoot cutting can modify indirectly the strength of animal-plant interactions by damaging plants. Damage promotes changes on plant resource allocation to vegetative and reproductive growth (Paige & Whitham 1987, Whitham et al. 1991, Irwin & Aarssen 1996). Therefore, plant responses to injury can result either in compensatory growth or reduced plant fitness (Maschinsky & Whitham 1989, Whitham et al. 1991), and compensatory growth will depend on how much resources a plant can acquire or reallocate to substitute lost tissue and/or the existence of favorable abiotic conditions to regrowth (Sharaf & Price 2004, Whitham et al. 1991, Maschinsky & Whitham 1989).

In response to loss of most or all aboveground biomass plants should either resprout or die (Bond & Midgley 2001). Resprouting is a key strategy for plants faced with unavoidable disturbances (Vesk et al. 2006). Studies of plant resprouting after damage have focused on species traits such as size (Paige & Whitham 1987, Irwin & Aarsen 1996, Juenger & Bergelson 1997), architecture (Huhta et al. 2000a), phenology (Juenger & Bergelson 1997, Freeman et al. 2003), foliage chemistry (Fahnestock & Detling 1999, Tong et al. 2003) and number of flowers, fruits and seeds (Paige & Whitham 1987, Maschinki & Whitham 1989, Juenger & Bergelson 1997, Kaitaniemi et al. 1999, Huhta et al. 2000b). Moreover, variation of these plant traits may alter the feeding behavior of herbivores (Fritz et al. 1987, Price 1991, Pittara & Katsoyannos 1992, Fenner et al. 2002), pollinators (Møller & Eriksson 1995, Ohashi & Yahara 1998), and also the performance of their natural enemies (Brody 1997, Clark & Messina 1998, Elle & Hare 2002, Teder & Tammaru 2002, Zvereva & Rank 2003, Harvey et al. 2003).

Although interactions between resprouting plants and arthropods are probably common, relatively few studies have documented them (Table 1, Fig. 1). Resprouting plants produce more young tissue, increasing nutritional quality for herbivores (Danell & Huss-Danell 1985, Stein et al. 1992, Olofsson & Strengbom 2000, Agrawal & Spiller 2004, Nakamura et al. 2006). Additionally, plants may induce direct and indirect effects on the associated arthropod community, which may cascade up to higher trophic levels (Schowalter 1994, Nakamura et al. 2005, Kagata et al. 2005, Nakamura et al. 2006). Consequently, large-scale destruction, mammalian herbivory and human-induced disturbances may initiate bottom-up cascading effects through multitrophic levels by altering the plants' aboveground biomass and/or structure.

This review explores changes in arthropod-plant interactions driven by plant resprouting after major damage brought about by various causes.

Plant damage producers

An individual plant can suffer small damages, such as the loss of a few leaves, up to severe damage, with the loss of most or even all of its aboveground biomass. Furthermore, most terrestrial ecosystems are prone to periodic disturbances that promote, at the community level, changes in competitive interactions among dominant plant species, which, in turn, can alter entire landscapes (Pickett & White 1985, Turner et al. 2001). For this reason, the role of natural disturbances in maintaining species composition, richness, diversity and succession has been considered an important ecological issue (Sousa 1984, Menge & Sutherland 1987, Walker 1991, Rieske 2002). Hurricanes, for example, are one of the most important natural disturbances affecting some tropical and sub-tropical regions; they can lead to extensive forest damage, structuring terrestrial and aquatic ecosystems for years thereafter.

Apart from the severe impact on vegetation composition caused by these climatically driven disturbances, they also affect plant traits by altering resource availability (Zimmerman et al. 1995, Carlton & Bazzaz 1998, Kwit & Platt 2000). Disturbance events profoundly alter resource levels promoting a patchy distribution of them across a landscape. For example, fire affects not only plant structural traits but also their biotic and abiotic environment and has often played an important evolutionary role, shaping fire-prone communities (Stein et al. 1992, Miranda et al. 2002). Changes in abiotic settings can modify the availability of light, and also the amount of carbon and nutrients, which are important components for structural metabolites and chemical defenses of plants (Bryant et al. 1983, Coley et al. 1985). Consequently, resource availability may determine plant chemical characteristics that are important for insect herbivores (Bryant et al. 1983, Coley et al. 1985).

Insects are important agents during the recovery of disturbed vegetation, mainly through decomposition (accelerating the rate of nutrient release), pollination (promoting gene flow), and herbivory (stimulating nutrient cycling). Apparently, insect communities may not suffer as much with large-scale destruction because they respond rapidly to disturbance. For example, Barberena-Arias & Aide (2002) showed that species richness returned to pre-disturbance levels in short periods. However, few studies have assessed the effects of natural abiotic disturbances on insect communities through changes in plants traits (Schowalter & Ganio 1999, Bailey & Whitham 2002). Herbivores can also alter plant phenotype, but their damage is usually less severe and in a different scale then those exert by large-scale abiotic disturbances. Hence, biotic and abiotic disturbances have the potential to initiate bottom-up effects that may cascade up in terrestrial arthropod food webs through changes in plant phenotypes.

Resprouting plant traits

Plant recovery after aboveground biomass removal involves resprouting from stems, main branches or underground organs (Schowalter & Ganio 1999, Bellingham & Sparrow 2000, Bond &

Midley 2001, Koptur et al. 2002, Bond & Midley 2003). Damage often changes nutritional status, production of defensive compounds, physical defense, architecture, morphology, or phenology of an individual plant (Dannell et al. 1985, Bergström & Dannell 1987, Basey et al. 1990, Karban & Baldwin 1997, Gadd et al. 2001, Gowda & Rafaelle 2004). Plant responses to severe damage can also be influenced by ecological factors (Whitham et al. 1991), and by plant architecture, which is in part associated to apical dominance; trees have higher apical dominance than shrubs (Irwin & Aarssen 1996, Martinez & Wool 2003). As a consequence of aboveground damage, plants lose their apical dominance and start producing a multi-stemmed resprouting architecture (Irwin & Aarssen 1996, Bellingham & Sparrow 2000).

Additionally, physiological responses may include the reduction of growth rate; augment the development of spines and thorns, and increase toughness of leaves (Hjältén 1999, Lucas et al. 2000, Massei et al. 2000, Gowda & Rafaelle 2004). However, plant responses to damage are plastic and vary according to biotic and abiotic conditions (Maschinski & Whitham 1989, Whitham et al. 1991). The compensatory continuum hypothesis states that the effect of damage on a plant can be detrimental or even beneficial to it (the extremes of the continuum), and a plant's ability to recover from damage will be influenced by several biotic and abiotic factors (Maschinski & Whitham 1989, Whitham et al. 1991). For example, experimentally clipped plants of *Ipomopsis arizonica* (Polemoniaceae) grew vigorously with supplemental nutrient addition and without competition (Maschinski & Whitham 1989). Nevertheless, nutrient availability has been found negatively associated with tolerance and compensation in other systems (Mutikainen & Walls 1995, Irwin & Aarssen 1996, Rautio et al. 2005).

Apart from changes in morphology and size in response to damage, plants can also show changes in their chemical compounds (Martinsen et al. 1998, Hunter & Forkner 1999, Schowalter & Ganio 1999, Radho-Toly et al. 2001, Shimazaki & Miyashita 2002, Strengbom et al. 2003, Agrawal & Spiller 2004, Nakamura et al. 2006). There are two mechanisms associated with the increase of foliage quality in severely disturbed sites. First, light availability in those areas is higher since most aboveground parts were destroyed. Light availability provides an increase in photosynthetic rate that results in higher concentrations of macronutrients in leaves. Second, disturbances may favor soil nutrient release, improving uptake by plants and hence increasing plant quality (Radho-Toly et al. 2001, Rieske 2002). Thus, severe damages that cause plant mortality can modify both light and nutrient availability for the remaining individuals, which in turn is likely to affect plant-insect interactions (Coley et al. 1985).

Resprouting plant effects on herbivore-plant interactions

The abundance of insect herbivores on plants is influenced by a range of factors, such as the presence of secondary compounds, the toughness of leaves, plant architecture, phenology, physical and chemical defense, plant size and abundance (Bryant et al. 1983, Coley et al. 1985, Schoonhoven et al. 2005). For flower and seed-eating herbivores flower and fruit availability are obviously important traits. The plant vigor hypothesis proposed by Price (1991) states that certain kinds of herbivores select fast-growing and younger plants and specific plant parts. In areas where natural fires are common, for example, herbivores may prefer resprouting plants because they produce more vigorously growing shoots. Resprouts may also have their nutritional quality increased, making them more attractive to herbivores (Radho-Toly et al. 2001, Table 1).

Furthermore, plants with differential defenses against mammals and insects may increase the abundance of insect herbivores when browsed (Danell & Huss-Danell 1985, Martinsen et al. 1998, Olofsson & Strengbom 2000, Martinez & Wool 2003). Nonetheless, insects will not invariably benefit from damage suffered by plants. Insect herbivores can be faced with lower quality food (Schowalter & Ganio 1999, Shimazaki & Miyashita 2002), higher resistance (Hunter & Forkner 1999) or a reduced number of niches for their colonization (Bailey & Whitham 2003).

Positive responses

Plants of *Populus* spp. are frequently cut down by beavers and vigorously resprout from their stumps or roots. Martinsen et al. (1998) found that browsed plants were more attractive to the leaf beetle *Chrysomela confluens*. Browsed host leaves (*Populus fremontii* and *P. angustifolia*) contained twice the level of phenolic glycosides than those from unbrowsed hosts. These secondary chemical compounds act as defenses against mammalian herbivores, but have an opposite effect on the leaf beetle, which sequesters and uses it for its own defense against predators (Martinsen et al. 1998). Additionally, human-induced disturbances, such as artificial cutting, may change plant quality, promoting positive responses of subsequent insect herbivores (Nakamura et al. 2006). In willows, plant trunk cutting indirectly increased the abundance and species richness of the associated arthropod community, because rapid regrowth promoted bottom-up cascading effects through changes in plant quality (Nakamura et al. 2006).

Similarly, after fire, species of eucalyptus in Western Australia started producing better quality foliage (higher macronutrient levels) that was more palatable to herbivorous insects, resulting in higher leaf damage levels and increasing the abundance of canopy arthropods, which are associated to nutrient-richer foliage (Radho-Toly et al. 2001). In willows, fire stimulated plant regrowth; consequently, grasshoppers fed voraciously on resprouted burned plants (Stein et al. 1992). Therefore, changes in herbivore preference between resprouted burnt and unburnt plants may influence plant growth, plant population dynamics, and even the structure of the entire plant community.

Hurricanes can also cause changes in herbivore-plant interactions. Hunter & Forkner (1999) reported the influence of Hurricane Opal on both red maple and red oak trees. The foliar astringency of both species increased on damaged plants, and condensed tannin levels were greater on damaged red oaks trees (Hunter & Forkner 1999). Although the defensive plant compounds increased on damaged plants, these individuals suffered higher subsequent herbivory. Similarly, leaves from damaged *Conocarpus erectus* (Combretaceae) plants were larger and contained more nitrogen; this increased herbivores preference, which were 4.6 times more abundant on exposed sites than on protected ones, promoting an increase of 80% on foliar damage compared to pre-hurricane damage levels (Spiller & Agrawal 2003). In Japan, the majority of *Salix* trees responded vigorously to flood damage (Nakamura et al. 2005). The flood knocked down trunks and partly removed aboveground parts, such damage ended apical dominance, enhancing the plants' regrowth and increasing their quality; therefore they attracted more herbivores which, in turn, caused higher foliar damage (Nakamura et al. 2005).

Negative responses

In contrast, other studies have reported some, although less common, negative responses of herbivores to resprouting plants (Pascarella 1998, Koptur et al. 2002, Angulo-Sandoval et al. 2004, Table 1, Fig. 1). Folivory by insects decreased after hurricane damage, returning to pre-hurricane levels only a few months later (Koptur et al. 2002). Similar findings were reported on populations of a specialist flower galling moth on *Ardisia escallonioides* (Myrsinaceae), which declined after the hurricane, and some local populations took almost two years to recover (Pascarella 1998). Koptur et al. (2002) suggested that for most resprouting species there is a window in time where they are relatively free from herbivore pressure, since substantial insect damage appeared months later, while leaves from undamaged sites are often damaged in the first few months after disturbance. However, this difference could be a consequence of insect local extinction.

Furthermore, a shared host plant (*Viburnum dilatatum*) mediated a negative indirect interaction between its herbivores (Shimazaki & Miyahita 2002). Mammalian damaged plants had harder leaves and had lower tannin concentrations than those from a browser exclusion area. As result, leaf damage by insects was reduced in areas that harbored high densities of browser herbivores (Shimazaki & Miyahita 2002). In fact, even oak seedlings leaves have higher nitrogen and water content in burnt sites. However, the feeding behavior of the gypsy moth caterpillar did not differ between burned and unburned areas (Rieske 2002).

Finally, disturbances have the ability to modify herbivore-plant interactions through changes in plant characteristics. The interaction outcome may be strong and positive for the herbivore in most of the cases, and this outcome is often driven by a plant quality increase (Table 1, Fig. 1).

Plant resprouting effects on pollinator-plant interactions

As discussed above, damaged plants may change their morphology and phenology; and then they are liable to changes in pollinator behavior and pollen movement as well. Pollinators are known to respond to natural variation in flower size (Young & Stanton 1990, Ohara & Higashi 1994, Ohashi & Yahara 1998) as well as experiment manipulated petal length (Johnson et al. 1995). Furthermore, they do not only respond to attributes of individual flowers, but also to the number of flowers *per se*, although in general the proportion of flowers visited decreases as flower number increases (R. D. Loyola, unpublished data). Besides, mutualistic relationships may respond differentially from plant-herbivore interactions, since the decrease of a mutualistic population can affect its partner in a deleterious way, and it should be more pronounced on obligate interaction. Surprisingly, the obligate fig-wasp interaction did not suffer such catastrophic effect. This species-specific mutualism showed remarkably fast recovery from Hurricane Andrew damage, reestablishing within five months to pre-hurricane levels (Bronstein & Hossaert-McKey 1995).

Additionally, pollinators may have the ability to discriminate damaged from undamaged plants (Strauss et al. 1996), and their responses may differ from insect foliar herbivores that frequently find damaged plants more attractive (see section above). Fewer pollinator visits may result in fewer flowers that receive pollination service and, as consequence, lead to lower plant fitness. Herbivore damage may alter floral display (total number of flowers, numbers of flowers open at a given period, floral morphology or pollinator rewards) influencing pollinator effectiveness or the overall attractiveness of a damaged plant (Karban & Strauss 1993, Strauss et al. 1996). Leaf damage affected negatively plant attractiveness to pollinators in the wild radish *Raphanus raphanistrum*, decreasing the availability and size of flowers (Strauss et al. 1996, Lehtilä & Strauss 1999). However, how pollination services are altered on resprouting plants has long been ignored (Table 1). A key component of plant tolerance to herbivory may be the ability to maintain high levels of pollination after experiencing damage (Juenger & Bergelson 1997).

Mimicking natural ungulate browsing damage by clipping aboveground plant parts of *Ipomopsis aggregata*, Juenger & Bergelson (1997) reported that clipped plants delayed their reproductive phenology and altered their architecture (decreasing height and increasing branch production). Clipped plants responded negatively to damage by producing fewer flowers, which decreased pollination rates, consequently the number of fruits and seeds were reduced. However, they found that damaged plants could compensate, but only under a restrictive set of environmental conditions. Clipped plants that received fertilizer produced as many flowers as did control plants and when these plants received hand-pollination they set nearly the same amount of fruits and seeds, even without supplemented nutrient (Juenger & Bergelson 1997).

In fire-prone communities the dynamic between plants and their pollinators has been poorly investigated (Ne'eman et al. 2000), and most studies have been carried out in the last decade (Ne'eman et al. 2000, Potts et al. 2001, Potts et al. 2003). Ne'eman et al. (2000) studied the effect of fire on flower visitation rate and subsequent fruit set of four species in Mediterranean scrubland. All four flowering species (*Asphondelus ramosus*, *Salvia fruticosa*, *Satureja thymbra*, and *Phlomis viscosa*) received higher bee visitation rate at unburned than at burned area, and the higher pollinator frequency promoted a higher seed set in unburned area. They also showed that the less effective pollinator, *Bombus terrestris*, was the main visitor in burned area, while solitary bees, more effective pollen agent, were more frequent in undamaged areas. In *Satureja thymbra*

(Lamiaceaea), higher availability of nectar and consequently higher pollinator diversity and abundance were reported for unburned areas (Potts et al. 2001). However, the fruit set remained similar in unburned and burned areas. In contrast, Potts et al. (2003) compared the changes in plant-pollinator community from freshly burned areas until full regeneration of the vegetation. The most severe effect was found immediately after fire, however, the community reestablished rapidly and both flower and bee diversity reached their peak in the first two years. All nectar attributes were greater immediately after plants were exposure to the flames, decreasing consistently along the recovery.

Hence, pollination is an important ecological service to many plants and changes in the strength of mutualistic interaction can decrease the reproductive success. Damage often acts in a deleterious way on plant-pollinator interaction. There are only seven studies about this subject, and five of them showed decreased in pollination service after plant damage (Table 1, Fig. 1). Frequently, right after experiencing severe damage, plants can not produce as many flowers as undamaged ones, whereas the plant-pollinator interaction can reestablish to pre-damage levels in relatively short-term periods (months).

Resprouting plant effects on the third trophic level

The direct effects of plant volatiles, released after damage, and architectural structures have been documented as important factors for the searching behavior and attack efficiency of natural enemies of herbivores (Clark & Messina 1998, De Moraes et al. 1998, Thaler 1999, Legrand & Barbosa 2003). Parasitoids utilize plant morphology as a guide to localize their hosts, or they can follow the chemical compounds released by damaged plants to find the host (De Moraes et al. 1998, Thaler 1999). Moreover, changes in plant quality after damage may indirectly influence parasitoids and predators through changes in herbivore performance and susceptibility (Cole 1997, Zvereva & Rank 2003). For example, trunk cuttings of willows (*Salix eriocarpa*) affected the performance of the leaf beetle *Plagiodera versicolora*, and of its predator, the ladybird beetle *Aiolocaria hexaspilota* in laboratory experiments (Kagata et al. 2005). The performance, measured as survival rate, developmental time and adult mass, was higher when the leaf beetle was fed with cut willow leaves. The predatory ladybird also performed better when feeding on larvae that were fed with cut willow leaves (Kagata et al. 2005). After flood, the same leaf beetle, *Plagiodera versicolora*, fed preferentially on shoots of heavily damaged plants causing greater leaf damage (Nakamura et al. 2005). Resprouts following flood damage promoted bottom-up cascading effects, since larvae of the predatory ladybird *Aiolocaria hexaspilota* and webs of the spider *Agelena opulenta* were more abundant on heavily damaged plants.

Till now, few studies have reported the effects of severely damaged plants on the third trophic level; apparently, natural enemy performance is often increased, driven by the enhancement of herbivore fitness after feeding on damaged plants (Table 1, Fig. 1).

CONCLUDING REMARKS

As highlighted by some studies, our knowledge about multispecies plant-animal interactions has been sketchy, and when summed with environmental conditions our understanding becomes negligible (Strauss & Irwin 2004). In fact, diversity is not controlled by a single trophic level or abiotic variables; but by complex interactions among trophic levels, and indirect effects produced by disturbances and environmental variation (Bailey & Whitham 2003). Thus, one should forgo a markedly reductionistic approach in favor of incorporating complexity in future studies, because many ecosystems are shaped by large-scale and human-induced disturbances. Therefore, it is important to understand and to evaluate how severe disturbances can modify the outcome of arthropod-plant interactions through changes in plant traits, since relatively few studies have evaluated them. In addition, highly disturbed habitats will impose new selective forces on the evolution of plant tolerance to herbivory, as well as on the coevolution of pollinator-plant relationships.

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Table 1 – Summary of studies that evaluated plant damage effects on plant-arthropod interactions.

Type of interaction	Type of damage	Regional climates	Plant species (family)	Plant traits measured	Arthropod guild	Damage effect on insect	Reference
Plant-herbivore	Clipping	Boreal	*Three Salix species*	Height, shoot mass, root mass, number of leaves	Galler	Positive	Hjältém 1999
Plant-herbivore	Clipping	Temperate	*Salix lasiolepis* (Salicaceae)	Number, size and mass of shoots	Galler	Positive	Hjältém & Price 1996
Plant-herbivore	Clipping	Tropical	*Combretum apiculatum* (Combretaceae)	Shoot number, shoot lenght, shoot biomass, leaf area	Leaf chewer	Negative	Bergström et al. 2000
Plant-herbivore	Clipping	Tropical	*Conocarpus erectus* (Combretaceae)	Leaf toughness, leaf trichomes, nitrogen and carbon concentration	Leaf chewer	Positive	Agrawal & Spiller 2004
Plant-herbivore	Fire	Sub-tropical	*Eucalyptus* (Myrtaceae)	Shoot lenght, number of new leaves and leaf macronutrient	Leaf chewer, galler, miner	Positive	Radho-Toly et al. 2001
Plant-herbivore	Fire	Temperate	*Salix lasiolepis* (Salicaceae)	Number of shoots, shoot lenght	Leaf chewer	Positive	Stein et al. 1992
Plant-herbivore	Fire	Temperate	*Adenostoma fasciculatum* (Rosaceae)	Number of resproutings, resprout height	Leaf chewer	Positive	Moreno & Oechel 1991
Plant-herbivore	Fire	Tropical	*Aspilia foliacea* (Asteraceae)	Number of flowerheads	Seed predator	Positive	Prada et al. 1995
Plant-herbivore	Hurricane	Sub-tropical	Eight species	Leaf production and size	Leaf chewer	Negative to neutral	Koptur et al. 2002
Plant-herbivore	Hurricane	Temperate	*Quercus rubra* (Fagaceae) and *Acer rubrum* (Aceraceae)	Chemical compounds	Leaf chewer	Positive	Hunter & Forkner 1999
Plant-herbivore	Hurricane	Tropical	Many species	Chemical compounds	Leaf chewer	Negative	Schowalter & Ganio 1999
Plant-herbivore	Hurricane and clipping	Tropical	*Conocarpus erectus* (Combretaceae)	Leaf size, nitrogen content, leaf toughness, leaf trichomes	Leaf chewer	Positive	Spiller & Agrawal 2003
Plant-herbivore	Hurricane	Tropical	Eight species	Leaf production and number	Leaf chewer	Negative	Angulo-Sandoval et al. 2004

Type of interaction	Type of damage	Regional climates	Plant species (family)	Plant traits measured	Insect guild	Damage effect on insect	Reference
Plant-herbivore	Mammalian herbivory	Boreal	*Populus balsamifera and Salix novae-angliae* (Salicaceae)	Number and size of shoots	Galler	Positive	Roininen et al. 1997
Plant-herbivore	Mammalian herbivory	Boreal	*Betula pubescens* (Betulaceae)	Number and size of shoots, leaf size and chemistry	Leaf chewer, galler and miner, sap feeder and predator	Positive	Danell & Huss-Danell 1985
Plant-herbivore	Mammalian herbivory	Boreal	*Betula pendula and B. pubescens* (Betulaceae)	none	Leaf chewer	Positive	Neuvonen & Danell 1987
Plant-herbivore	Mammalian herbivory	Temperate	*Viburnum dilatatum* (Caprifoliaceae)	Leaf hardness, tannin concentration	Leaf chewer	Negative	Shimazaki & Miyashita 2002
Plant-herbivore	Mammalian herbivory	Temperate	*Populus fremontii* and *P. angustifolia* (Salicaceae)	Chemical compounds	Leaf chewer	Positive	Martinsen et al. 1998
Plant-herbivore	Mammalian herbivory	Temperate	*Pistacia atlantica* and *P. palaestina* (Anacardiaceae)	Number of shoots, number of lateral shoots, shoot lenght, number of leaves	Galler	Positive or neutral	Martinez & Wool 2003
Plant-herbivore	Mammalian herbivory	Tundra	*Salix lanata* (Salicaceae)	Shoot lenght, leaf size, leaf nitrogen content C:N ratio	Galler	Positive	Olofsson & Strengbom 2000
Plant-herbivore	Mammalian herbivory	Tundra	*Salix phylicifolia* (Salicaceae)	Height, shoot number and size, number of flowers	Leaf chewer and galler	Negative	Den Herder et al. 2004
Plant-herbivore	Mammalian herbivory and clipping	Temperate	*Ipomopsis aggregata* (Polemoniaceae)	Initiation of flowering, floral display, nectar volume and sugar concentration	Seed predator	Negative	Freeman et al. 2003
Plant-herbivore	Mammalian herbivory, fire and clipping	Temperate	*Populus tremuloides* (Salicaceae)	Aboveground biomass, number of resprouting ramets	Leaf roller, chewer and miner, galler, and sap feeder,	Neutral and negative	Bailey & Whitham 2002
Plant-herbivore	Mammalian herbivory and clipping	Temperate	*Populus tremuloides* (Salicaceae)	none	Galler	Negative	Bailey & Whitham 2003
Plant-herbivore; Plant-pollinator	Hurricane	Sub-tropical	*Ardisia escallonioides* (Myrsinaceae)	Flowering, inflorescence and seed production	Galler, seed predator and pollinator	Negative (gall), positive (seed predator) neutral (pollinator)	Pascarella 1998

Type of interaction	Type of damage	Regional climates	Plant species (family)	Plant traits measured	Insect guild	Damage effect on insect	Reference
Plant-herbivore; Plant-pollinator	Hurricane	Tropical	*Bourreria succulenta* (Boraginaceae)	Nectar production and fruit set	Seed predator; pollinator	Positive (herbivore) and negative (pollinator)	Rathcke 2001
Plant-herbivore; Predator-herbivore	Flood	Temperate	*Salix eriocarpa* (Salicaceae)	Trunk angle, number of shoots, shoot lenght, basal trunk diameter number of leaves	Leaf chewer; predator	Positive	Nakamura et al. 2005
Plant-herbivore; Predator-herbivore	Hurricane	Tropical	Five species	none	Leaf chewer; predator, sap feeder	Negative, neutral or positive	Schowalter 1994
Plant-herbivore; Predator-herbivore	Trunk cutting	Temperate	*Salix eriocarpa* and *S. gilgiana* (Salicaceae)	Number of lateral shoots, shoot lenght, number of leaves, leaf toughness, nitrogen and water content	Leaf chewer, galler, predator, sap feeder, borers, shelter marker	Positive	Nakamura et al. 2006
Plant-herbivore; Predator-herbivore	Trunk cutting	Temperate	*Salix eriocarpa* (Salicaceae)	none	Leaf chewer, predators	Positive	Kagata et al. 2005
Plant-pollinator	Fire	Temperate	Four species	Fruit set	Pollinator	Negative	Ne'eman et al. 2000
Plant-pollinator	Fire	Temperate	*Satureja thymbra* (Lamiaceae)	Fruit set, nutlet mass and nectar volume and concentration	Pollinator	Negative or neutral	Potts et al. 2001
Plant-pollinator	Fire	Temperate	Many species	Nectar volume, nectar water content, nectar concentration and pollen energy	Pollinator	Negative to positive	Potts et al. 2003
Plant-pollinator	Mammalian herbivory	Temperate	Many species	Number of flowers	Pollinator	Positive	Vulliamy et al. 2006
Plant-pollinator	Hurricane	Sub-tropical	*Ficus aurea* (Moraceae)	Flowering frequency, floral synchrony	Pollinator	Negative (short-term period) to neutral (long-term period)	Bronstein & Hossaert-McKey 1995

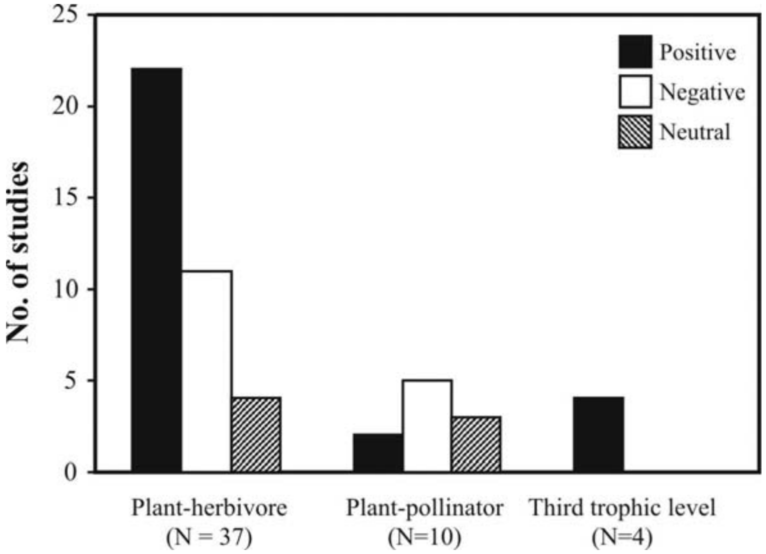

Fig. 1 – Number of studies reporting positive, negative or neutral effects of plant damage on its interactions with herbivores, pollinator or herbivores natural enemies.

Capítulo II

Plant responses to clipping and nutrient addition in Brazilian Cerrado

ABSTRACT

The destruction of plant aboveground biomass disrupts apical dominance, promoting the activation of dormant meristems from the remaining tissues or resprouting from underground organs, subject to resource availability. For this reason, we conducted an experiment in a natural population of *Chromolaena pungens* (Asteraceae), in cerrado vegetation, to investigate plant responses to moderate and severe damage, as well as the effect of nutrients on these responses. From November 2005, at then of the dry season, plants were manipulated in a two-factor randomized block design where treatments were: clipping (control, partially clipped, and totally clipped) and nutrients (without and with nutrient addition). Plants were measured and followed until July 2006, when they started to dry in early winter. Severely damaged plants (totally clipped) were shorter, had fewer shoots and leaves and produced fewer flowerheads than partially clipped or control plants. However, totally clipped plants had higher relative elongation rates and produced larger leaves and flowerheads than the other plants. The growth of *C. pungens* shrubs was not limited by nutrients and the recovery process was not influenced by added fertilizer. This study clearly demonstrated that plants could not compensate damage in short-term periods and most of the measured traits were strongly affected by total clipping. Changes in plant morphology due to mechanical damage or removal may have important implications on animal-plant interactions.

INTRODUCTION

Large-scale destruction, human-induced disturbances and herbivores can initiate bottom up cascade effects through multitrophic level by damaging plants' aboveground biomass (Agrawal & Spiller 2004, Nakamura et al. 2006). After severe damage, plants can either die or resprout (Bellingham & Sparrow 2000, Bond & Midley 2001). Recovery from losing most aboveground biomass and disrupting apical dominance entails the release of new modular units from lateral meristems or from underground plant structures (Irwin & Aarsen 1996). Removal of apical shoots promotes the activation and growth of dormant meristems, since apical shoot stop inhibiting other meristems to receive nutrients from underground organs (Husain & Linck 1966). Thus, the consequence of removal or drastic reduction of aboveground biomass is the production of a multi-stemmed resprouting architecture (Bellingham & Sparrow 2000).

Apart from changes in architectural morphology, damaged plants can alter their biomass, size, number, quality of structures and also their phenological pattern (Turner et al. 1993, Olofsson & Strengbom 2000, Gadd et al. 2001, Bailey & Whitham 2002, Freeman et al. 2003, Spiller & Agrawal 2003, Agrawal & Spiller 2004, Rooke et al. 2004). However, plant responses to severe damage are plastic and can result in an increased, neutral or reduced plant growth (Maschinsky & Whitham 1989, Whitham et al. 1991). Compensatory growth will depend on how much resources the plant can reallocate or acquire to substitute the lost tissue, and the external resource availability to sustain regrowth (McNaughton 1983, Maschinsky & Whitham 1989, Whitham et al. 1991, Sharaf & Price 2004). Nevertheless the hypothesis that nutrients can predictably promote plant compensation after damage has been equivocal (Hilbert et al. 1981, Hawkes & Sullivan 2001). Apparently, monocots are influenced positively by nutrients whereas woody and dicots plants are not (Hawkes & Sullivan 2001).

Besides nutrient effects on plant recovery, the ability to resprout is also dependent on timing, frequency and intensity of damage (Riba 1997, Riba 1998, Huhta et al. 2000). The timing of damage is relative to phenological stage, when damage occurs later in the growing season its effect can be detrimental (Maschinski & Whitham 1989), whereas it can be beneficial when occurs at the beginning of growing season, when the nutrient uptake is most intense (Maschinski & Whitham 1989). Moreover, some studies have shown that, the more severe the damage, the smaller will be the compensation growth (Alados et al. 1997, Huhta et al. 2000, Tong et al. 2003), although such response has not been found in other studies (Riba 1998, Kotanen & Bergelson 2000).

We carried out a study on the shrub *Chromolaena pungens* (Asteraceae) to elucidate the importance of nutrient and intensity of damage in altering plant traits. Thus, we aimed to answer the following questions: (i) how do increasing levels of severe damage and nutrient affect plant architecture? (ii) Do plant size and relative elongation rate (RER) change after damage? (iii) How do damage and nutrients affect leaf morphology? (iv) Do resprouting plants change their phenological pattern? (v) Do damage and nutrient addition affect total reproductive effort and flowerhead size?

METHODS

Study System

The study was carried out in the Estação Ecológica de Itirapina, in the county of Itirapina (22º13'09"S; 47º54'04"W), State of São Paulo, Brazil. The regional altitude varies from 700 to 830 meters. The area of the reserve is ca. 2300 ha of natural, little disturbed cerrado vegetation, including different cerrado formations, such as campo limpo (grassland), campo sujo (shrubby grassland), campo cerrado (shrubby grassland with trees), gallery forest, and swampy areas and the study area encloses a savanna vegetation of “campo cerrado”. The campos and campos cerrados of the Estação Ecológica de Itirapina are one of the last fragments of these types of cerrado in the State of São Paulo. These formations represented only 2% of the cerrado areas in the São Paulo State. Furthermore, in the last two decades over 95% of the campos and campos cerrados of the state were destroyed, mainly for cattle raising and agriculture. Therefore, the vegetation of Estação Ecológica de Itirapina is extremely important for its potential to gather knowledge on the fauna and flora typical of these formations. The Brazilian Cerrado is also denominated as Neotropical savanna and covers ca. of 2 million km^2, which represents approximately 22% of all Brazilian territory (Oliveira-Filho & Ratter 2002). Similar to other savanna-like ecosystem, Cerrado is also a fire-prone biome (Miranda et al. 2002).

The fire is considered one of the main components that determine the cerrado vegetation. This abiotic factor often removes all plants aboveground biomass and it may also kill plants, however not only plant structural traits are affected but also its biotic and abiotic environment. Different from other savannic ecosystem, Brazilian cerrado plants have not been damaged by large browsing mammals. However, recently, many cerrado non-protected areas are prone to clearcuts. Thus, cerrado plants can be damage by fire and clearcuts. It is important to emphasize that our plant damage manipulation was similar to that exerted by the factors mentioned above, when almost all plant aboveground biomass are lost or damaged and plants should resprout from underground organs. Then, our study is important to improve our understanding about plant responses to differences damage intensities, and how nutrients are involved on recovery process in disturbed and restored communities.

We selected a natural population of *Chromolaena pungens* (Gardner) R. King & H. Rob. because this species is an important plant compounding the vegetation of Brazilian savanna and it can be found in both protected and non-protected areas. Moreover, *C. pungens* is a perennial abundant shrub, therefore, amenable to experimental manipulation.

Experimental design

The experiment follows a two-factor, randomized block design. The two experimental factors were clipping (unclipped, partial clipped and total clipped) and nutrient (addition and no addition of nutrients). Thirty-two blocks, each containing the six combinations between factors, were positioned in an area of 5000 m^2, were all *C. pungens* plants were marked, but only 192 were selected to the experiment. Inside of each block, plants were minimum spaced of 1,5 m to prevent sampling the same individual, up to 6 m from their nearest neighbor. In August 2005, 192 individuals of *C. pungens* were grouped to compose blocks. Plants were grouped by proximity and similarity of size (height and crown size) and each individual was randomly assigned to one of the six treatments by previous random draw.

Plants assigned to the treatment "*partially clipped*" had from half of the shoots (randomly selected) all leaves and apical meristems removed, thus, plants had ca. of 50% of all leaves removed. Individuals of the treatment "*clipped*" suffered basal stem cutting; at 20 cm height; "*unclipped*" plants did not receive any manipulation. Plants assigned to group "*no nutrient added*" grew under natural soil conditions of nutrients, whereas plants assigned to "*nutrient added*" treatment received 80 g/m^2 of nitrogen (N), phosphorus (P_2O_5), potassium (K_2O), (concentrations 10:10:10) and micronutrients of Planalto Agrosciences Ltda (SP, Brazil) in an area of 25 cm of ray around the plant basis according to previous study (Dias 2003). All the experimental manipulations were done in the beginning of November 2005, and nutrients were re-added each 45 days.

Data collection

Starting in March of 2006, vegetative traits of plants, such as height (from ground to the apical meristem of the plant), main stem length (up to first bifurcation of stem), and crown size were measured. The height:crown ratio was calculated as the plant height divided by crown size and the relative elongation rate (RER) was estimated as $(FH - IH)*100/IH$, where FH is final height and IH is initial height. Concomitantly, we recorded the number of leaves and flowerheads of each plant. Flowerheads were counted and classified according to the following classes of development stage: (0) bud; (1) pre-anthesis; (2) mature; (3) dispersion. We used as phenology index the modal developmental stage of flowerheads of an individual plant in each census, thus we have a good estimative from the plant's phenological phase, because the phenolgy index is the most common flowerhead development stage. However, we did not discriminate infested and non-infested flowerheads by endophagous insects, since this estimative was done in the field. Therefore the phenology index varies from zero, when most or all flowerheads are buds, to three, when most or all flowerheads of an individual plant are in the dispersion stage.

In the third census (June), five flowerheads were randomly selected in each plant. Their length, diameter and achene length were measured to the nearest millimeter, and the number of achenes per flowerhead was registered. The flowerhead volume (roller) was estimated according its length and diameter. After being measured, flowerheads were dried at 70°C until reaching constant mass and weighed on an analytical scale with a precision of 10^{-4}g.; the mass of entire flowerhead and achenes set were measured. For analyses the mean number of the five flowerheads was used. In the same census, two branches were randomly selected per plant from we collected the oldest three leaves fully expanded. The leaves were scanned, and later they were dried at 70°C and weighted with a precision of 10^{-4}g. Foliar area was recorded to nearest millimeter, by the software Scion Image (Scion Image 2000, for Windows 4.0.2 - Scion Corporation, Frederick, Maryland USA). Specific leaf area (SLA) was estimated by dividing leaf area by its weight. For analyses the mean number of the three leaves was used.

In the beginning of July 2006, totalizing 9 censuses, the experiment was concluded, because some plants had started to dry, losing their leaves and flowerheads in response to the onset of dry season.

Statistical analysis

Discriminant analysis (DA) was used to show the plant traits that best discriminate the treatments, since DA is a method of choice to separate predefined groups (Legendre & Legendre 1998). The analysis was carried out using plant height, main stem length, relative elongation rate, leaf area and crown size ($\log_{10}$-transformed variables) and conducted on clipping groups (unclipped, partially clipped and clipped). The variables used in the DA were defined after a forward stepwise procedure (confirmed by a backwards procedure, which converged to the same set), and the excluded variables were number of flowerheads, number of leaves, height:crown ratio and specific leaf area (SLA). For this analysis data were standardized.

Multivariate analysis of variance (MANOVA) were used to analyze the effects of treatments on vegetative dependent variables: plant height, crown size, relative elongation rate, height:crown ratio, main stem length, number of shoots, number of leaves, leaf area and specific leaf area. A further MANOVA was performed on reproductive trait variables: number of flowerheads, flowerhead volume and weight, number of achenes, achene mass and length. Subsequently, univariate Factorial ANOVAs of two treatments in blocks were conducted to investigate the effect of independent factors (clipping and nutrient) on the dependent variables: plant height, crown size, relative elongation rate, height:crown ratio, main stem length, number of shoots, number of leaves and flowerheads, leaf area, specific leaf area, flowerhead volume and weight, number of achenes per flowerhead, achenes mass and length. This approach of perfoming ANOVAs after a significant result of MANOVA is referred to as a protected ANOVA (Scheiner 2001)

Multiple statistical tests to address the same hypothesis can increase the Type I error rate (Scheiner 2001). Therefore, we used the conservative Bonferroni correction because dependent variables were correlated. We applied Bonferroni correction separately for vegetative characters, including the number of flowerheads, and for flowerhead morphology variables. When appropriate, Fisher's least (LSD) significant difference tests were applied to compare means within or between treatment comparisons. Continuous dependent variables were $\log_{10}(x+1)$ transformed, whereas discrete dependent variables, were square root $(x+0.5)$ transformed to meet parametric assumptions.

To examine the effects of treatments (clipping and nutrient) on the dependent variable flowering onset we performed an exact logistic regression (Mehta & Patel 1990). To assess the effects of treatments on the flowerhead phenology index we used the repeated-measures factorial ANOVA, excluding the first census where there was no variation in our data. All statistics were done in Systat version 10, excluding the logistic regression, which was performed in LogXact version 5.

RESULTS

From the 64 plants subjected to full clipping, only 4 plants did not resprout. From the other 128 plants, one individual dried before the beggining of data collection. Of the 64 partially clipped plants, only 26 substituted the lost tissues for new ones. At the end of the experiment, from the 192 plants 31 had dried (unclipped N=9, partially clipped N=13, clipped N=9). Dead plants were not included in the analyses.

Multivariate analysis

The clipped plants were clearly distinct from unclipped and partially clipped plants, as shown by the discriminant analysis (Table 3, Fig. 1). However, the analysis did not discriminate between unclipped and partially clipped plants. The first canonical variable (factor 1) was positively correlated with height, main stem length and crown size, indicating that the first discriminant function is a measure of the overall size of the plant; moreover, it was negatively correlated with relative elongation rate and leaf size area (Table 3, Fig. 1). The first discriminant function extracted 98% of the variance associated to the plant traits (eigenvalue = 3.1). The second canonical variable (factor 2) was positively related to all variables excluding crown size, but did not contribute to discriminate groups (eigenvalue = 0.1). The analysis classified correctly 95% of clipped plants, but was much less effective in separating control and partially clipped plants (64% and 58% respectively classified correctly by the discriminant functions).

Multivariate analysis of variance (MANOVA) indicated differences among clipping treatments in vegetative traits (height, crown size, height:crown ratio, relative elongation rate, main stem length, number of leaves, leaf area size, specific leaf area), whereas there was no evidence for effects of nutrient addition or of a nutrient x clipping interaction (Table 1). Subsequently, the effects of treatments on some vegetative variables were studied by performing univariate analysis of variance (see below). However, according to MANOVA, clipping treatment did not affect the reproductive performance parameters (number of flowerheads, flowerhead volume, flowerhead weight, number of achenes and achene length; Table 2). The effects of treatments on main reproductive traits were further evaluated by carrying out univariate ANOVAs (see further results).

Plant size

Chromolaena pungens clipped plants started the reproductive season with an overall mean (± SE) height of 75.0 ± 3.9 cm, almost half that of unclipped plants ($\bar{x}$ = 137.7 ± 3.3 cm) and partial clipped ones ($\bar{x}$ = 136.9 ± 3.2, Fig. 2A). A factorial ANOVA showed that clipping treatment was highly significant, whereas nutrient addition did not affect plant height (Table 4). A similar pattern was found for plant crown size (Table 4, Fig. 2B), which was not affected by nutrient addition and highly affected by clipping treatment. However, the mean (± SE) relative elongation rate (RER) of clipped plants ($\bar{x}$ = 13.35 ± 1.6 cm) was more than twice the RER showed of partial clipped ($\bar{x}$ = 5.92 ± 1.0 cm) and unclipped plants ($\bar{x}$ = 5.44 ± 1.1 cm). Accordingly, the factorial ANOVA showed a highly significant effect of clipping treatment for RER (Table 4, Fig. 2C).

Plant architecture

Resprouting plants, after being clipped, have their architectural traits changed. The main stem length was significantly smaller in clipped plants (Table 4, Fig. 3A), indicating a multi-stemmed architecture. However, the plants were not able to produce many shoots; the mean (± SE) number of main shoots from clipped plants was only 8.1 ± 0.9, whereas unclipped ($\bar{x}$ = 15.4 ± 1.0) and partially clipped ($\bar{x}$ = 14.0 ± 1.6) plants had almost twice the number of shoots of clipped individuals (Table 4, Fig. 3B) The height:crown ratio was also affected by clipping intensity, but in a positive way (Table 4, Fig. 3C). Clipped plants had mean (± SE) height:crown ratio of 3.3 ± 0.2 cm, 1.5 times greater than unclipped plants ($\bar{x}$ = 2.1 ± 0.2).

Leaf number and size

The mean number of leaves (± SE) of unclipped plants ($\bar{x}$ = 610.9 ± 49.6 leaves), was 1.3 times higher than the number of leaves exhibited by partial clipped ones ($\bar{x}$ = 440.0 ± 44.6 leaves), and almost 3.5 times higher than the number displayed by clipped plants ($\bar{x}$ = 175.9 ± 33.2 leaves) (Table 4, Fig. 4A). The relative leaf biomass (leaves/shoots) was almost higher on control and partially clipped plants than in clipped plants. Despite the lower number of leaves in resprouting plants, the mean individual leaf area (± SE) of severe damaged plants ($\bar{x}$ = 501.5 ± 33.4 mm^2) was twice that of leaves of partial clipped ($\bar{x}$ = 232.3 ± 22.8 mm^2), and 2.5 times higher that of unclipped plants ($\bar{x}$ = 196.4 ± 8.9 mm^2) (Fig. 4B). Similarly to leaf area, mean specific leaf area (SLA) (± SE) was higher in clipped plants ($\bar{x}$ = 9531.2 ± 184.1 mm^2/g) than the SLA of unclipped ($\bar{x}$ = 8770.1 ± 124.1 mm^2/g) and partial clipped plants ($\bar{x}$ = 8952.0 ± 163.6 mm^2/g) (Fig. 4C). Factorial ANOVA showed that clipping treatment was highly significant for the number of leaves, number of leaves per shoot, leaf size and specific leaf area, but nutrient addition did not cause any significant effect on those variables (Table 4).

Flowering phenology and reproductive effort

Flowering onset also differed among clipping levels (odds ratio = 0.001; clipped plants flowered later than partially clipped and unclipped plants (Table 5, Fig. 5A). The proportion of clipped plants with and without flowerheads was reduced in the second census (Fig. 5B) and became similar to unclipped or partially clipped plants levels, only in the third census, when there was no significant difference among clipping levels. Nutrient addition affected marginally on flowering onset (Table 5). Apparently, clipped plants with nutrients added flowered earlier than clipped plants without nutrient addition (odds ratio = 14.770). The logistic regression showed a marginally effect of clipping x nutrient interaction. Clipping caused a significant reduction on the number of flowerheads per plant (Table 4, Fig. 5C). Fewer flowerheads were produced by clipped plants ($\bar{\times}$ = 106.6 ± 22.0 flowerheads) than by partially clipped ($\bar{\times}$ = 410.0 ± 54.1 flowerheads) or unclipped plants ($\bar{\times}$ = 658.1 ± 72.2 flowerheads).

Flowerhead phenological pattern was highly affected by clipping, as shown by a repeated-measures factorial ANOVA (Table 6). The phenology index of flowerhead development was similar among treatments in the first census, since all flowerheads were buds. However, the phenology index in the following censuses was highly affected by the clipping treatment (Fig. 6). In the second, third and fifth censuses the phenology index was lower for clipped plants, showing that the flowerhead development of severely damaged plants was delayed. In the fourth census, however, there was no discernible effect of treatments on the phenology index.

Flowerhead morphology

Flowerhead size (i.e volume) was significantly affected by clipping intensity (Table 7, Fig. 7A). The mean (± SE) flowerhead volume was greater in clipped plants ($\bar{\times}$ = 89.6 ± 2.1 mm^3) than in partial clipped ($\bar{\times}$ = 81.5 ± 1.3 mm^3) and unclipped plants ($\bar{\times}$ = 81.7 ± 1.8 mm^3). Nonetheless, flowerhead mass was not influenced by treatments (Table 7). However, clipping treatment had a negative effect, marginally significant, on the number of achenes per flowerhead (Table 7, Fig. 7B, $F_{2,127} = 3.874$, $P = 0.023$). Unclipped ($\bar{\times}$ = 23.9 ± 0.6 flowers) and partially clipped ($\bar{\times}$ = 23.7 ± 0.4 flowers) plants produced more achenes than clipped plants ($\bar{\times}$ = 22.3 ± 0.6 flowers), although the difference was only one achene. Treatments caused no effect on achene morphology (Table 7), since achene length and mass were similar among all treatments. Moreover, there was no evidence for nutrient or nutrient x clipping interaction effects on flowerhead morphology (Table 7).

DISCUSSION

Damage intensity

Chromolaena pungens plants were very resistant to moderate levels (partial clipping) of damage. The removal of half the apical meristems and half the leaves did not change plant traits, since partially clipped plants were equally tall, had similar elongation rates and their phenology was in phase with unclipped plants. Only the number of leaves and flowerheads were affected; partially damaged plants did not have as many leaves and did not produce as many flowerheads as did undamaged ones. Therefore, *C. pungens* plants showed no plasticity after moderate damage. In most cases the plants did not substitute the lost structures. Since fire is a common feature in the cerrado, and there is evidence that this abiotic disturbance often remove the plants' entire aboveground parts (Stein et al. 1992), cerrado plants may be able to alter their phenotypes only after severe damage. Thus, our results showed no evidence of overcompensation of damage at moderate levels, as reported in other studies (McNaughton 1983, Belsky 1986, Paige & Whitham 1987, Huhta et al. 2000). For instance, in *Gentianella campestris* (Gentianaceae), the highest plant performance was achieved at intermediate damage levels (50%), clipping strongly induced the growth of lateral shoots, which resulted in a high number of fruits and seeds and greater aboveground biomass (Huhta et al. 2000). Monocarpic plants, such as *G. campestris*, are prone to invest more in their reproductive effort when damaged, since they reproduce only once during their lifetime. However, perennial plants, when damaged, decrease their reproductive output, investing in vegetative recovery from damage and postponing their reproduction to the next reproductive season (Verkaar et al. 1986). This may apply to *Chromolaena pungens*, also a perennial.

In contrast with the non-significant effect of moderate damage on plant performance, plants were strongly affected by severe damage as was to be expected. Similar to previous studies (Whitham et al. 1991, Bailey and Whitham 2002, Nakamura et al. 2006) severely damaged *C. pungens* plants resprouted rapidly and vigorously after aboveground biomass removal, but they did not achieve the same height nor produce as many flowerheads as did partially clipped or control plants. Clipped plants did not compensate in height, crown size, or number of leaves and flowerheads; on the other hand, they produced larger flowerhead and leaves. However, even these individually larger structures did not compensate the structural loss incurred by clipped plants, because their foliar and reproductive biomasses were not as large as partially clipped and unclipped plants.

Several mechanisms have been proposed to explain the responses of plants to damage. First, the degree of compensation can be determined by the ability of plant to acquire resources (increased nutrient uptake by roots) and to reallocate them (translocation of reserves stored in underground organs) in order to support the substitution of lost tissue. Physiological responses may also include the increase of photosynthetic rates in remaining tissue. With increasing damage levels, the amount of photosynthetic tissue decreases, and so does the number of meristems required for resprouting, which can limit compensatory growth. According to the compensatory continuum concept, plant responses to damage will be dependent on the timing and level of damage, resource availability, and intensity of competition (Maschinski & Whitham 1989, Lennartsson et al. 1998). Defoliation history can also play an important role (Turner et al. 1993). Although in our experiment plants received nutrient supplementation, and the experimental clipping was done at the end of the dry season, when many Cerrado plants metabolism is generally low. However, *C. pungens* probably did not have enough time to regrow to pre-damage levels, since its vegetative growth normally ends at the onset of the reproductive period (personal observation). Alternatively, underground reserve organs are commonly found in many species of Asteraceae from the Brazilian Cerrado (Esteves 2001, Figueiredo-Ribeiro et al. 1986, Tertuliano & Figueiredo-Ribeiro 1993). Some of these organs have been considered as an evolutionary response to environmental adversities (e.g. drought, fire, aluminium toxicity) (Eiten 1972). However, *C. pungens* resource storage in underground organs may not be sufficiently large to promote full compensation

Numerous studies have documented that the removal of apical meristems enhances the release of lateral buds, increasing the growth rate and performance of a plant (Maschinski & Whitham 1989, Irwin & Aarssen 1996, Bergström et al. 2000) since there is no more suppression of lateral meristems by apical meristems (Husain & Linck 1966). The end of apical dominance has been considered an important component for overcompensatory growth in several plant species (Irwin & Aarssen 1996, Huhta et al. 2000, Bergström et al. 2000). In our plants, clipping disrupted apical dominance, clearly stimulating plant growth, which could be seen in the higher elongation rate of clipped plants, however this stimulus was not enough to compensate damage. Similarly, in partially clipped plants the removal of half of apical meristms did not stimulate plant growth.

Developing larger structures

The production of larger leaves and/or higher specific leaf area (leaf area to weight ratio) after severe physical damage has been noted in other trees and shrubs (Danell & Huss-Danell 1985, Danell et al. 1985, Price 1991, Koptur et al. 2002, Shimazaki & Miyashita 2002, Spiller & Agrawal 2003, Rooke et al. 2004). In *Betula pendula* and *B. pubescens* (Betulaceae) damage promoted the production of larger leaves, which had higher nitrogen content (Danell & Huss-Danell 1985). Similar, in *Salix*, water and nitrogen content were significantly higher in severely damaged plants, whereas leaf toughness decreased (Nakamura et al. 2006). Therefore, specific leaf area, leaf nitrogen content and photosynthetic capacity may be closely associated (Reich et al. 1995). Changes in leaf toughness, water content and chemical constituents of an individual plant have been reported as important components influencing herbivorous feeding behavior and performance (Bryant et al. 1983, Faeth 1985, Coley et al. 1985).

Most studies of floral morphological changes have explored the effect of slight damage (e.g., foliar herbivory) on floral reproductive traits, such as petal size, male and female gamete production and nectar production (Lehtilä & Strauss 1997, 1999). However, less is known about the effect of severe damage effects on floral attributes (but see Potts et al. 2001, Potts et al. 2003). In this study, we found that severe damage caused an increase in mean flowerhead size. Changes in floral attributes may promote changes in pollinator visitation patterns (Møller 1995, Møller & Eriksson 1995, Lehtilä & Strauss 1997). Moreover, increasing flowerhead size may induce higher pre-dispersal seed predation rates in Asteraceae, since flowerhead feeders are attracted to larger capitula (Fenner et al. 2002). Apart from changes in floral morphology, we found no difference in the number of achenes, achene mass or length among treatments. In contrast, clipped *Ipomopsis aggregata* plants produced fewer seeds, and their total seed mass was lower than in unclipped individuals (Juenger & Bergelson 2000).

Nutrient effects

According to the compensatory continuum hypothesis, compensation to damage can be enhanced by increasing resource availability. Thus, overcompensation is more likely to occur under nutrient-rich conditions (Maschinski & Whitham 1989, Whitham et al.1991, Huhta et al. 2000, Li et al. 2004), because the increase of resource availability can counteract the negative effects of damage. Nonetheless, some studies have reported the opposite effect; compensatory responses are improved under low nutrient supply or under stressful conditions (Hilbert et al. 1981, Irwin & Aarssen 1996, Hawkes & Sullivan 2001). However, we did not detect a significant effect of nutrient addition by itself, or any clipping x nutrient interaction. It has been well documented the effect of soil nutrients in cultivated species, however the knowledge about the requirement of native species of Brazilian Cerrado are still scarce (Cuzzuol et al. 2003). The few studies about the subject have found that the species responded positively to the increase of nutrient supply (Vilela & Haridasan 1994, Melo 1999, Cuzzuol et al. 2003, Dias 2003). Melo (1999) suggested that even the native plants being adapted to nutrient-poor soils; they are able to absorve nutrients when these are available. Thus, plants growing on nutrient-poor soils, such as the soils of the Brazilian Cerrado may be nutrient-limited (Medina & Silva 1990, Melo 1999, Mota 2002). However, contrary to the assumption of resource limitation, *C. pungens* plants were not limited by nutrients. Probably, plants can benefit from fertilization when soil nutrients are a limiting factor for growth. *C. pungens* plants may be tolerated to the low levels of nutrients in Cerrado soils. Therefore, other abiotic factors (e.g. water) may be limited to these plants and may influence plant nutrient uptake.

Flowering phenology

Damage can modify plant reproductive traits, such as flowering phenology, number of flowers, nectar and pollen availability, which, in turn, may affect the attractiveness to pollinators (Juenger & Bergelson 1997, 2000, Sharaf & Price 2004). The delay in flowering may impose a high cost after damage (Juenger & Bergelson 2000). Late flower opening may reduce pollinator visitation rates and their effectiveness, hence reproductive performance, since plants will produce fewer seeds (Sharaf & Price 2004). In *Ipomopsis aggregata*, clipping delayed flowering, which led clipped plants to miss the peak of pollinator activity, and reduced their visitation rates (Sharaf & Price 2004). Our results are consistent with previous studies in which flowering phenology is modified by damage; clipped plants delayed their flowering onset and the development of flowerheads was also affected, since flowerhead production of clipped plants lagged a month behind partially clipped and unclipped plants. The effects of phenology on insect-plant interactions have been investigated before (Juenger & Bergelson 1997, Freeman et al. 2003, Sharaf & Price 2004). In *Ipomopsis aggregata* (Polemoniaceae), damage negatively affected plant reproductive success through changes in flowering phenology (Freeman et al. 2003). The flowering delay decreased the synchrony between plants and pollinators, resulting in a large reduction of seed set (Juenger & Bergelson 1997, Freeman et al. 2003). However, the negative effect of damage can be ameliorated when the phenological delay leads to lower seed-predation rates (Freeman et al. 2003) or when the delay in flowering decreases intra or interspecific competition for pollinators.

CONCLUSIONS

Plants often suffer severe damages, being faced with the loss of most their aboveground biomass. For this reason, understanding mechanisms and abiotic factors underlying plant tolerance, resistance, and plasticity is extremely important to predict plant responses to damage. *Chromolaena pungens* showed much less plasticity and compensatory growth than other plant species; however, there were difference among some of the studied traits, modulated by damage level. These differential responses may have ecological and evolutionary consequences for the plants themselves as well as for their interactions with other plants or with animals. These will be examined in the next chapter.

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Table 1- Wilks' lambda value and *F*-statistic of generated by MANOVA of vegetative plant traits (plant height, crown size, main stem height, height:crown ratio, relative elongation rate, number of leaves, number of shoots, leaf area, specific leaf area); treatments are clipping (unclipped, partially clipped and clipped) and nutrients (nutrients added and nutrients added). Subscript in F-value indicates hypothesis df and error df. Note that all variables were transformed see methods for details.

Source of variation	Wilks' lambda value	F	P
Block	0.083	$1.599_{310,1152}$	0.000
Clipping	0.176	$17.031_{20,236}$	0.000
Nutrient	0.937	$1.778_{10, 118}$	0.072
Clipping*Nutrient	0.897	$0.884_{20,236}$	0.608

Table 2 - Wilks' lambda and *F*-statistic MANOVA of reproductive plant traits (number of flowerheads, flowerhead volume, flowerhead mass, number of achenes, achene length and achenes mass); for treatments see Table 1. Subscript in F-value indicates hypothesis df and error df. Note that all variables were transformed; see methods for details.

Source of variation	Wilks' lambda	F	P
Block	0.186	$1.283_{186,722}$	0.186
Clipping	0.612	$5.618_{12,242}$	0.612
Nutrient	0.986	$0.217_{6,121}$	0.986
Clipping*Nutrient	0.935	$0.691_{12,242}$	0.935

Table 3 - Discriminant analysis on vegetative measures. F statistics and two canonical discriminant functions to separate plants subjected to three clipping treatments.

	F	1	2
Height (log)	15.83	0.872	1.115
Main stem height (log)	14.02	0.600	0.425
Crown size (log)	5.11	0.229	-1.467
Relative elongation rate (log)	8.45	-0.425	0.138
Leaf area (log)	15.63	-0.629	0.120
Eigenvalue		3.105	0.077

Table 4 – Summary of F-values generated by factorial ANOVAs on plant-size, plant architecture, leaf number and size, and flowerhead number; for treatments see Table 1. Note that all variables were transformed, see methods for details. Bonferroni correction was applied to probability levels.

Source of variation	df	Height	Crown size	RER†	Main stem height	No. of shoots	Height:Crown ratio	No. of Leaves	No. of leaves/shoot	No. of flowerheads	df	Leaf area	SLA‡
Block	31	1.455	1.112	0.691	0.757	0.940	0.991	1.167	1.288	2.300***	31	3.937***	2.656***
Clipping	2	105.109***	56.562***	20.733***	55.118***	17.748***	12.973***	40.957***	6.252*	43.601***	2	101.603***	6.614*
Nutrient	1	1.974	0.318	0.329	0.125	1.610	0.404	0.052	0.248	0.280	1	1.631	0.785
Clipping*Nutrient	2	0.620	0.930	0.059	0.619	2.926[a]	1.753	0.325	0.328	1.581	2	0.947	1.628
Error	150										130		

* $P < 0.005$; ** $P < 0.001$; *** $P < 0.0001$. (a) $P = 0.057$

† Relative elongation rate

‡ Specific leaf area

Table 5 - Summary of t-ratio and P-values generated by exact logistic regression performed on flowering onset of *Chromolaena pungens* in the first census; treatments are clipping (partial clipping and clipping contrasted with controls; nutrient (no nutrient added and nutrients added). Block was used as stratum variable.

Parameter	Beta Coefficient	p-value 2*1 - sided
Partial clipping	-0.704	0.993
Clipping	-5.065	0.000
Nutrient	-1.471	0.356
Partial clipping*Nutrient	0.617	1.000
Clipping level*Nutrient	2.692	0.096

Exact Likelihood ratio = 80.843, P-value < 0.001

Table 6 - Summary of F-values and p-values of repeated-measures ANOVA of flowerhead index of phenology of *Chromolaena pungens*; for treatments see Table 1.

Source of variation	df	F	P
Between subjects			
Block	31	2.154	0.002
Clipping	2	15.977	0.000
Nutrient	1	1.982	0.162
Clipping*Nutrient	2	4.194	0.017
Error between subjects	126		
Within subjects			
Time	3	1188.379	0.000
Time*Block	93	1.536	0.003
Time*Clipping	6	1.313	0.250
Time*Nutrient	3	1.386	0.247
Time*Clipping*Nutrient	6	0.893	0.500
Error within subjects	378		

Table 7 – Summary of F-values of factorial ANOVAs of flowerhead morphology; for treatments see Table 1. Note that all variables were transformed and Bonferroni correction was applied to probability levels, see methods for details.

Source of variation	df	Volume	Mass	No. of achenes	Achene length	Achene mass
Block	31	1.113	1.099	1.347	1.924	0.914
Clipping	2	5.915*	0.284	3.874	0.787	1.749
Nutrient	1	0.063	0.179	0.427	0.261	0.005
Clipping*Nutrient	2	0.348	1.614	1.069	0.338	0.253
Error	127					

* $P < 0.01$; ** $P < 0.002$; *** $P < 0.0002$

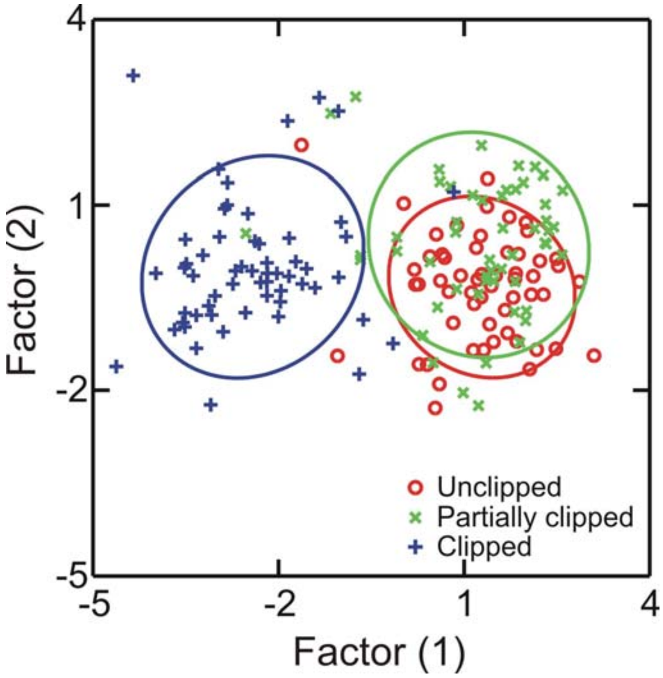

Fig. 1 – Relationship between scores on factor 1 and factor 2 for the discriminant analysis of plant traits. Ellipses encompass 95 % confidence limits for each clipping intensity. Values were standardized.

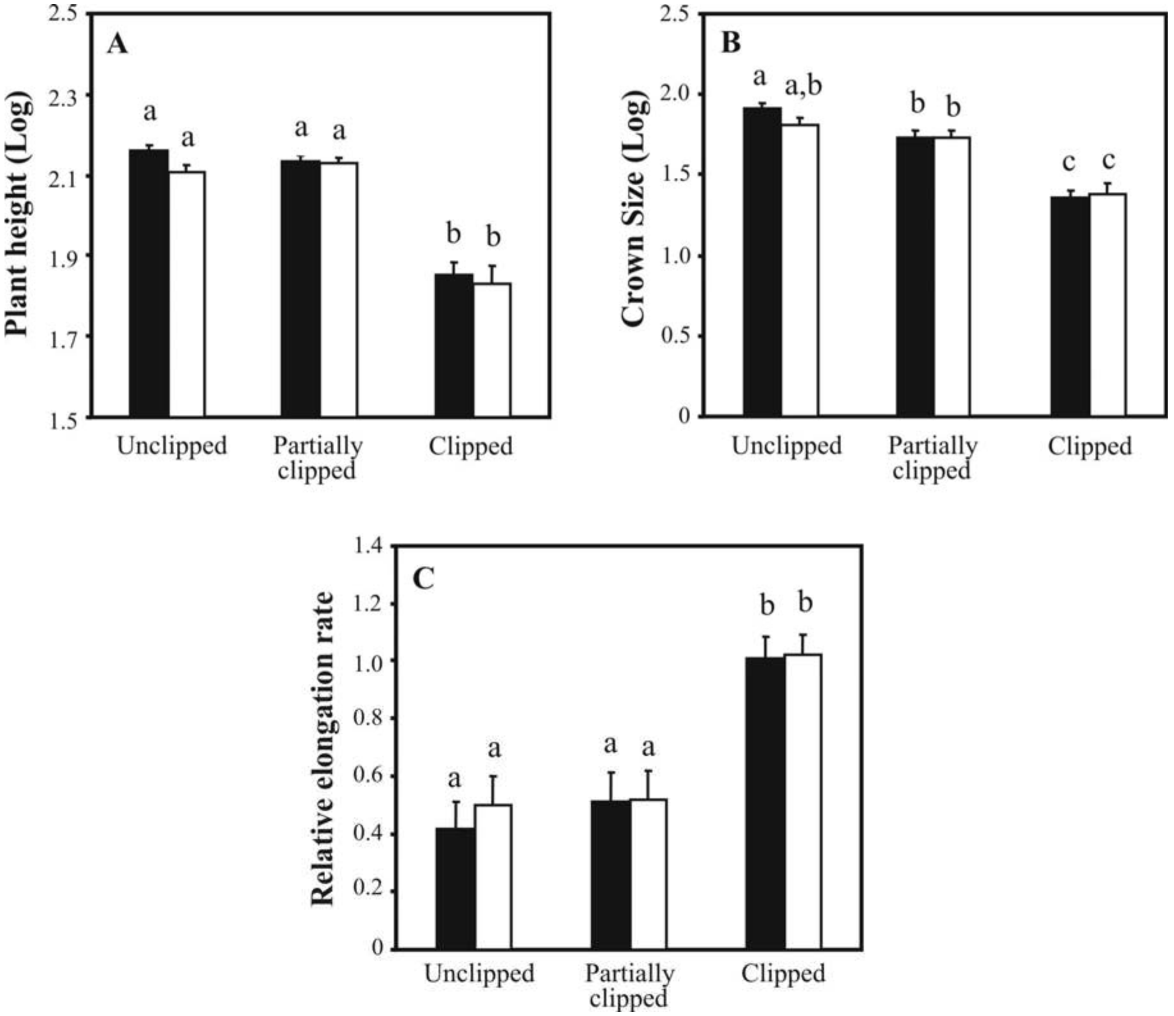

Fig. 2 – Plant size (mean ± SE) of *Chromolaena pungens* before reproductive season. Values, excluding relative elongation rate, were $\log_{10}$-transformed and originally measured in centimeters. (A) Plant height. (B) Plant crown size. (C) Plant relative elongation rate. Treatments are clipping (unclipped, partial clipped and clipped); no nutrient added (solid bars) and nutrients added (open bars). Letters indicate significant differences ($P<0.05$) between means compared using LSD multiple comparisons test.

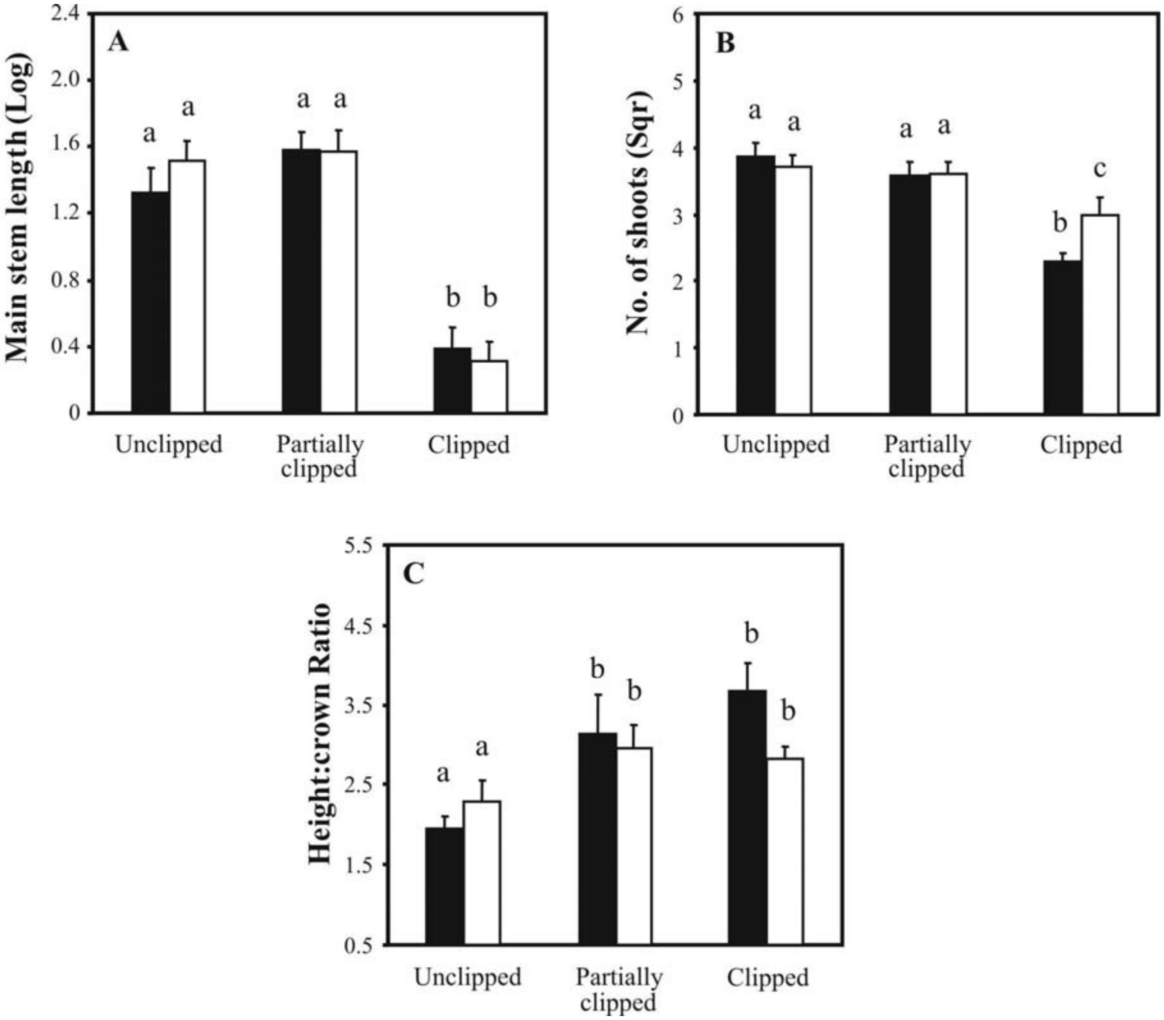

Fig. 3 – Architecture traits (mean ± SE) of *Chromolaena pungens* plants before the reproductive season. (A) Plant main stem height size (originally measured in centimeters). (B) Number of main shoots. (C) Plant height:crown ratio. Treatments are clipping (unclipped, partial clipped and clipped); no nutrient added (solid bars) and nutrients added (open bars). Letters indicate significant differences ($P<0.05$) between means compared using LSD multiple comparisons test. Continuous values were $\log_{10}$-transformed and discrete values were square root transformed (See Methods for details).

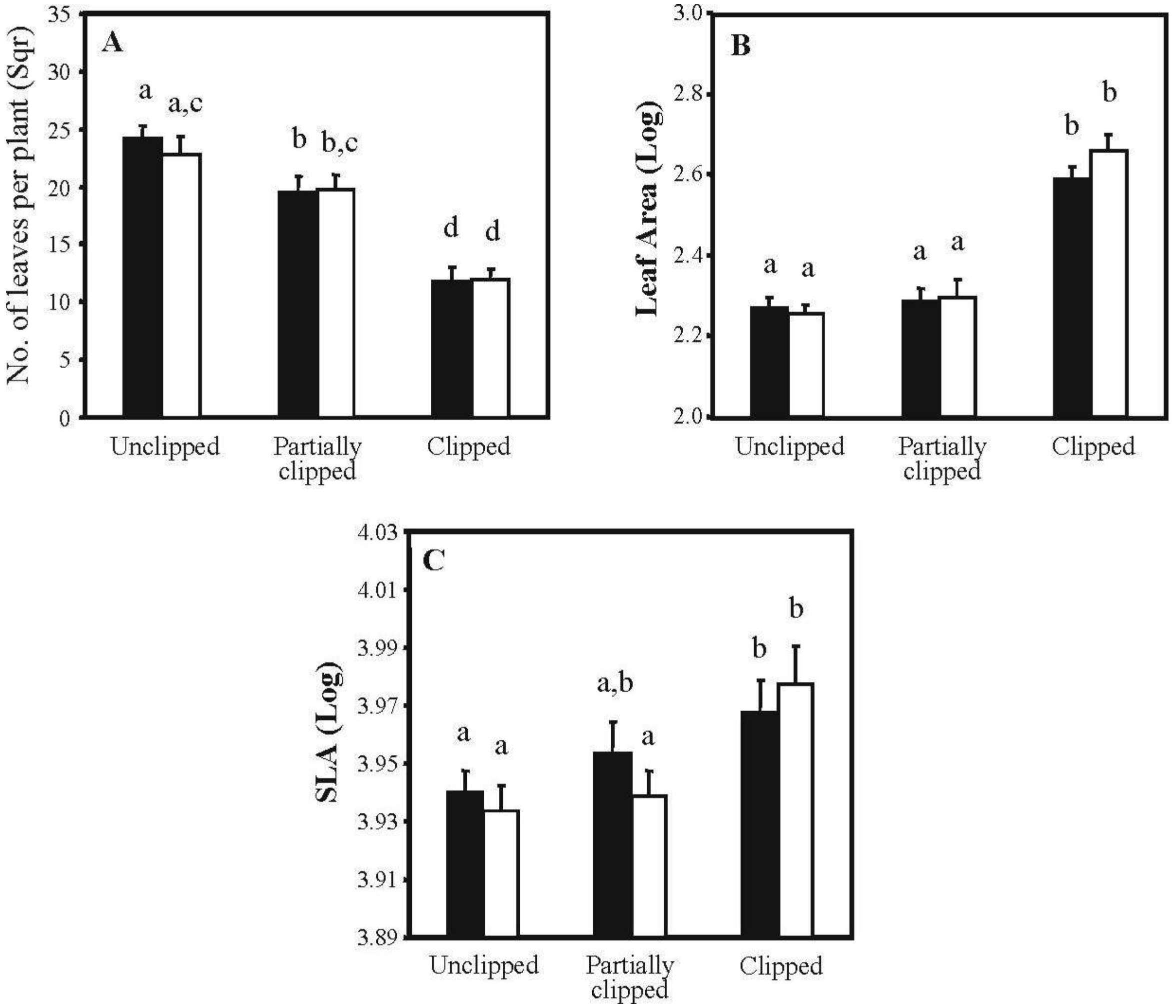

Fig. 4 – Number of leaves and leaves attributes of *Chromolaena pungens* plants. Values are mean (± SE) and were $\log_{10}$-transformed except in panel A, which was square-root transformed. (A) Total number of leaves. (B) Leaf area, originally measured in mm^2. (C) Specific leaf area measured in mm^2/g. Treatments are clipping (unclipped, partial clipped and clipped); no nutrient added (solid bars) and nutrients added (open bars). Letters indicate significant differences ($P<0.05$) between means compared using LSD multiple comparisons test.

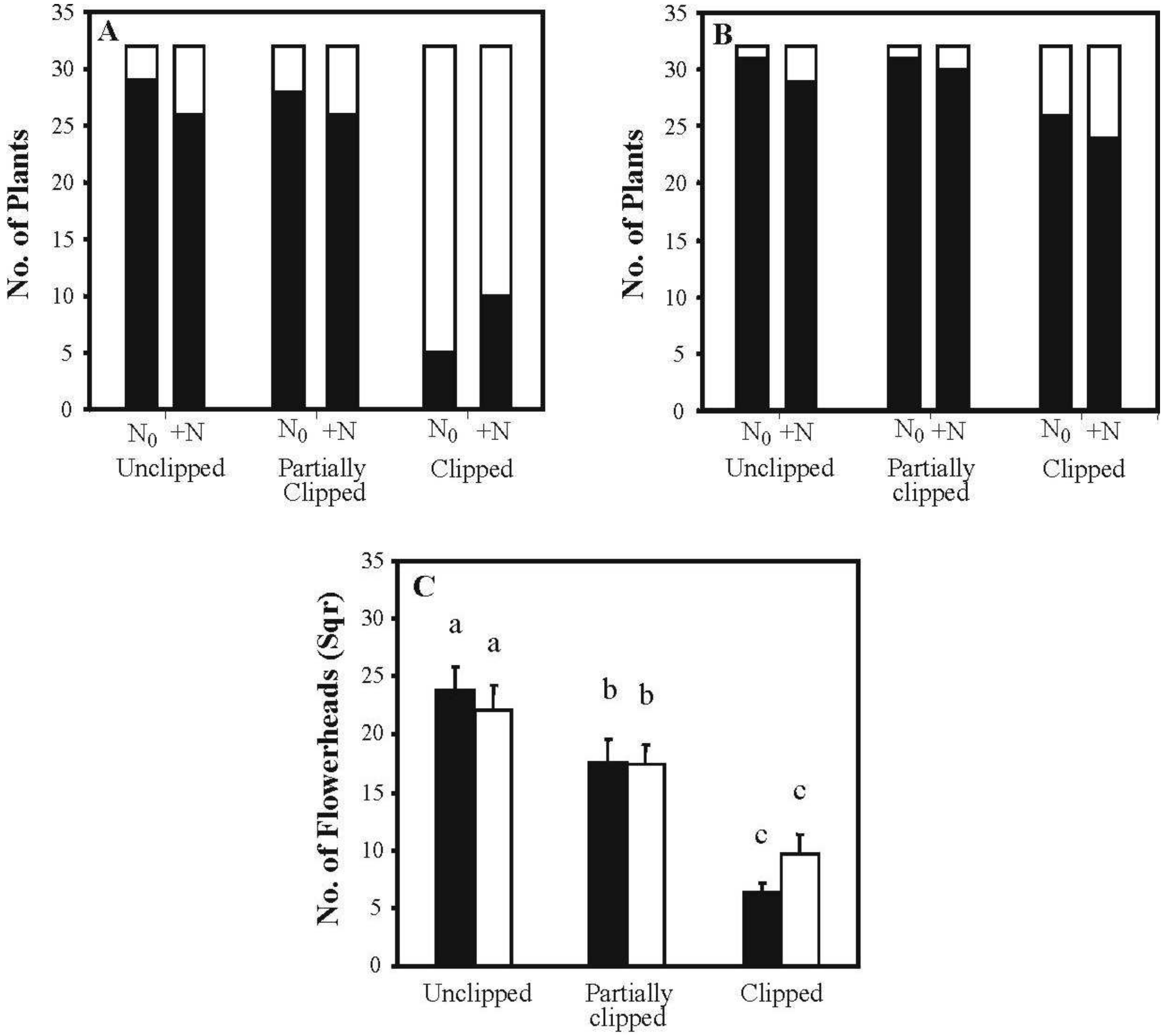

Fig. 5 – Reproductive effort of *Chromolaena pungens* plants. (A) Flowering onset, number of plants with flowerheads in the first census (March 2006). (B) Number of plants with flowerheads in the second census (April 2006). (C) Total number of flowerheads produced by *Chromolaena pungens* plants (square-root transformed). Treatments are clipping (unclipped, partial clipped and clipped); no nutrient added (N_0) and nutrients added (+N). Letters indicate significant differences ($P<0.05$) between means compared using LSD multiple comparisons test.

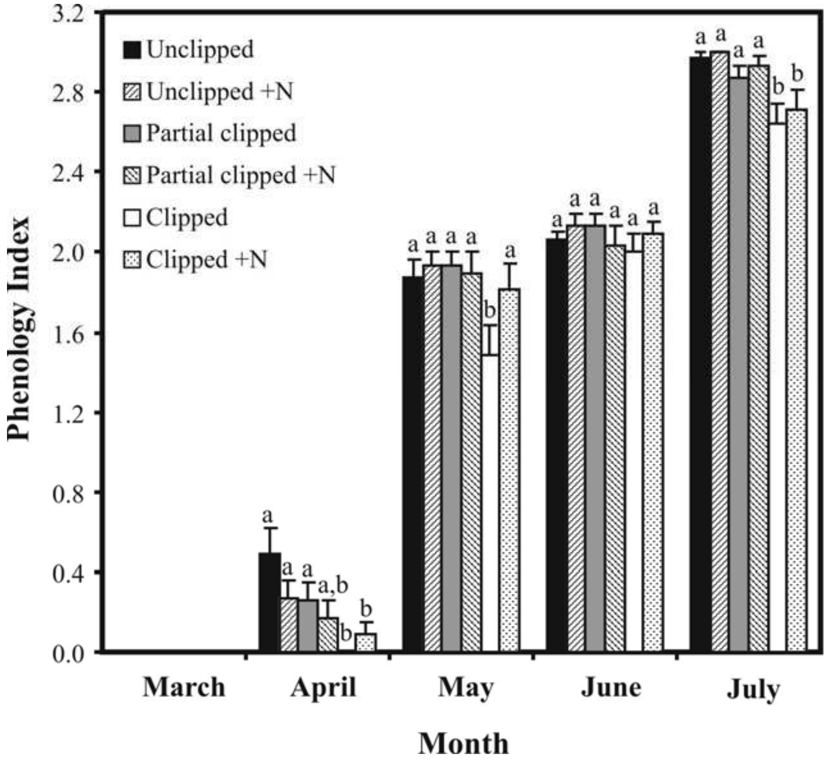

Fig. 6 – Flowerhead development phenology index of *Chromolaena pungens* plants along the 5 months of experiment. Values are mean ± SE.

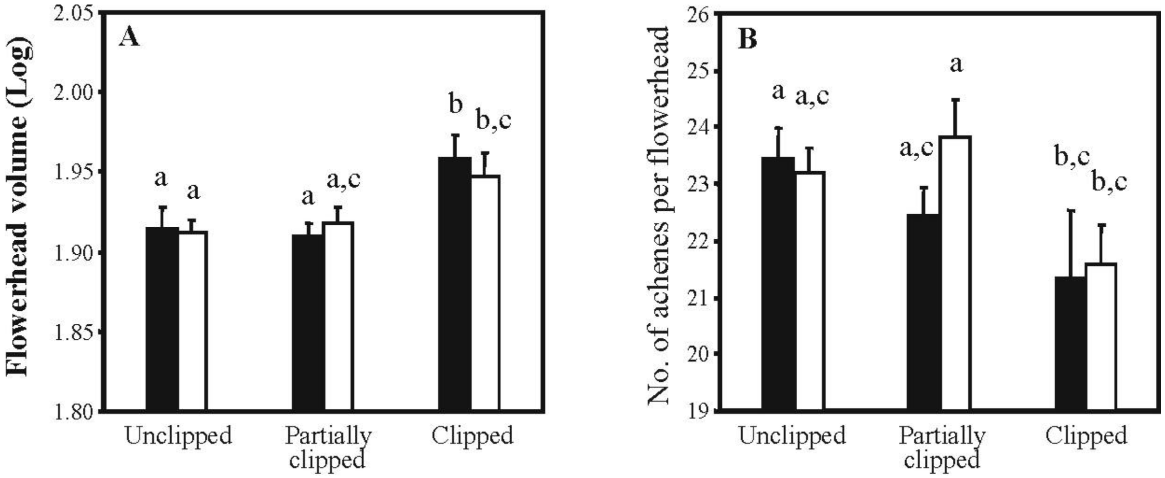

Fig. 7 – Flowerhead morphology of *Chromolaena pungens* plants. (A) Flowerhead volume, originally measured in mm^3 (log$_{10}$-transformed). (B) Number of achenes per flowerhead. Values are the mean (± SE) from five flowerheads measured. Treatments are clipping (unclipped, partial clipped and clipped); no nutrient added (solid bars) and nutrients added (open bars). Letters indicate significant differences ($P<0.05$) between means compared using LSD multiple comparisons test.

Capítulo III

Bottom-up cascading effects on multitrophic interactions initiated by plant damage and nutrient availability

ABSTRACT

Large-scale destruction or human-induced disturbances often damage severely the aboveground plant parts. Thereafter, plants can modify their morphological, phenological and structural traits. Such changes may enhance plant susceptibility to herbivores. Abiotic factors, such as nutrients, may also exert an important role on herbivore attractiveness. This study aims to evaluate the responses of insect community to changes in plant traits on natural occurring populations of *Chromolaena pungens* (Asteraceae). We carried out an experiment to test the hypothesis that plant resprouting indirectly promotes bottom-up cascading effects up to higher trophic levels. In particular, we evaluate how clipping and nutrients influence: (i) the abundance of galls, leaf-chewers and sap-suckers; (ii) the incidence of their predaceous arthropods; (iii) the species composition, richness, diversity and abundance of the endophagous insects associate to flowerheads; and additionally, (iv) the incidence of their parasitoids. The experimental design follows a two-factor randomized complete blocks design. The results indicated that severe damage on plants increased the achenes damaged, the abundance, richness and diversity of flowerhead endophages, even the species composition was altered on clipped plants. However, the number of galls decreased on severely damaged plants, and the abundance of sap-sucking and leaf-chewing insects was not affected. Moreover, the leaf consumption was almost 4 times higher on resprouted plants. Additionaly, the incidence of predaceous arthropods and parasitioids were also influenced by the treatments but in a less pronounced way. Then, our findings improve the ecological understanding of the effect of disturbances on animal-plant interactions.

INTRODUCTION

Many ecosystems have been shaped by abiotic natural disturbances (e.g. fires, hurricanes and floods), and more recently by human-induced disturbances (logging and clipping, livestock grazing, and prescribed fires). Therefore, a current important ecological issue is to understand and to evaluate how these disturbances can alter biotic interactions (Agrawal & Spiller 2004). Abiotic natural or human-induced disturbances can damage an individual plant, promoting the loss of most or even all its aboveground biomass. Consequently, plants should either resprout or die (Bond & Midgley 2001). Resprouting is a key strategy for plants faced with unavoidable damage (Vesk et al. 2006). Moreover, plant responses to damage are plastic and vary according to biotic and abiotic conditions (Maschinski & Whitham 1989, Whitham et al. 1991). Some plants can present overcompensation in aboveground biomass after damage, producing larger structures, in higher number and even attaining greater total biomass (Whitham et al. 1991, Maschinsky & Whitham 1989).

Damage caused by abiotic natural disturbances, browsing by mammals and cutting often stimulates plant regrowth (Stein et al. 1992, Bond & Midgley 2001, Radho-Toly et al. 2001, Bailey & Whitham 2002, Spiller & Agrawal 2003, Nakamura et al. 2006). Additionally, damage will often enhance changes in nutritional status, production of chemical or physical defense, or cause changes in the architectural and morphological traits; the production of flowers and seeds and floral phenology of individual plants can also be influenced (Karban & Baldwin 1997, Radho-Toly et al. 2001, Freeman et al. 2003, Spiller & Agrawal 2003, Sharaf & Price 2004, Nakamura et al. 2006). All the above factors may profoundly affect herbivore performance and/or preference (Bryant et al. 1983, Coley et al. 1985, Fritz et al. 1987, Price 1991, Pittara & Katsoyannos 1992, Rathcke 2001, Fenner et al. 2002, Zvereva & Rank 2003, Schoonhoven et al. 2005).

Thus, resprouts may have their nutritional quality status increased being more attractive to herbivores (Dannell et al. 1985, Danell & Huss-Danell 1985, Radho-Toly et al.2001, Strengbom et al. 2003, Agrawal & Spiller 2004), influencing the entire associate arthropod community through bottom-up cascading effects (Nakamura et al. 2005, Nakamura et al. 2006). However, damaged plants may offer to herbivores lower quality food (Shimazaki & Miyahita 2002), higher resistance (Hunter & Forkner 1999) or a reduced number of free niches for their colonization (Bailey & Whitham 2003).

In the Asteraceae family, it was found that the incidence of pollinators, flower and seed predators is greater on larger flowerheads, both among species and among individuals (Fenner et al. 2002). In *Cirsium vulgare*, the egg number laid by fruit-flies in the flowerhead was positively correlated with its diameter (Zwölfer and Preiss 1983). Flowerhead endophagous herbivores are generally very specialized (Prado & Lewinsohn 2004). The females lay their eggs in floral buds and their sedentary larvae are extremely dependent of the food resources obtained from a flowerhead until become adults. Therefore, these flowerhead feeders may react even to the small morphological changes in their food source. Moreover, the foraging efficiency of natural enemies can be guided by host plant traits (Clark & Messina 1998, De Moraes et al. 1998, Thaler 1999), and consequently, changes in host plant traits can also influence parasitism and attack rate (Masters et al. 2001).

This study is an experimental investigation of responses of herbivore-plant interaction to plant aboveground damage. To our knowledge, this is the first study investigating the effect of resprouting plants on both exophagous and endophagous herbivores and their respective natural enemies. This study aims to clarify responses of the insect community to resprouting host plants in a naturally occurring population, which should help to elucidate the consequences of disturbed or restored communities on community organization.

We carried out an experiment within a cerrado naturally population to test the hypothesis that clipping promotes bottom-up cascading effects up to higher trophic levels. In particular, we aim to evaluate how clipping and nutrients influence: (i) the abundance of gall-forming, leaf-chewing and sap-sucking insects; (ii) the incidence of their predaceous arthropods; (iii) the species composition, richness, diversity and abundance of the endophagous insects associate to flowerheads of *Chromolaena pungens*; and additionally, (iv) the parasitism rate of flowerhead endophages.

METHODS

Study System

The study was carried out in the Estação Ecológica de Itirapina, in the county of Itirapina (22°13'09"S; 47°54'04"W), State of São Paulo, Brazil. The regional altitude varies from 700 to 830 meters. The area of the reserve is ca. 2300 ha of natural, little disturbed cerrado vegetation, including different cerrado formations, such as campo limpo (grassland), campo sujo (shrubby grassland), campo cerrado (shrubby grassland with trees), gallery forest, and swampy areas and the study area encloses a savanna vegetation of "campo cerrado". The campos and campos cerrados of the Estação Ecológica de Itirapina are one of the last fragments of these types of cerrado in the State of São Paulo. These formations represented only 2% of the cerrado areas in the São Paulo State. Furthermore, in the last two decades over 95% of the campos and campos cerrados of the state were destroyed, mainly for cattle raising and agriculture. Therefore, the vegetation of Estação Ecológica de Itirapina is extremely important for its potential to gather knowledge on the fauna and flora typical of these formations. The Brazilian Cerrado is also denominated as Neotropical savanna and covers ca. of 2 million km^2, which represents approximately 22% of all Brazilian territory (Oliveira-Filho & Ratter 2002). Similar to other savanna-like ecosystem, Cerrado is also a fire-prone biome (Miranda et al. 2002).

The fire is considered one of the main components that determine the cerrado vegetation. This abiotic factor often removes all plants aboveground biomass and it may also kill plants, however not only plant structural traits are affected but also its biotic and abiotic environment. Different from other savannic ecosystem, Brazilian cerrado plants have not been damaged by large browsing mammals. However, recently, many cerrado non-protected areas are prone to clearcuts.

Thus, cerrado plants can be damage by fire and clearcuts. It is important to emphasize that our plant damage manipulation was similar to that exerted by the factors mentioned above, when almost all plant aboveground biomass are lost or damaged and plants should resprout from underground organs. Then, our study is important to improve our understanding about plant responses to differences damage intensities, and how nutrients are involved on recovery process in disturbed and restored communities.

We selected a natural population of *Chromolaena pungens* (Gardner) R. King & H. Rob. because this species is an important plant compounding the vegetation of Brazilian savanna and it can be found in both protected and non-protected areas. Moreover, *C. pungens* is an abundant shrub that facilitated experimental manipulation. The responses of *C. pungens* to aboveground removal were evaluated before (see chapter 2). The severely damaged plants were considerably smaller, producing fewer leaves and flowerheads. However, the leaf and flowerhead size were larger in these plants, but the even producing larger structures the plants were not able to compensated vegetative and reproductive biomass. The damage also clearly promoted phenological changes, clipped plants delayed their flowering onset and the development of their flowerheads were lagged a month compared to flowerheads of partially clipped and unclipped plants.

Experimental design

The experimental design follows a two-factor randomized complete block design. We manipulated clipping (unclipped, partially clipped and total clipped) and nutrient (no nutrient added and nutrients added). Thirty-two blocks, each containing the six combinations between factors, were positioned in an area of 5000 m^2. Inside of each block, plants were minimum spaced of 1,5 m to prevent sampling the same individual, up to 6 m from their nearest neighbor. In August of 2005, 192 individuals of *C. pungens* were marked and grouped to compose blocks. Plants were grouped by similarity of size (height and crown size) and each individual was randomly assigned to one of the six treatments.

Plants assigned to the treatment "*partially clipped*" had 50% of their leaves and apical meristems removed. Individuals of the treatment "*clipped*" suffered basal stem cutting (at 20 cm height); "*unclipped*" plants did not receive any manipulation. Plants assigned to group "*no nutrient added*" grew under natural soil conditions of nutrients, whereas plants assigned to "*nutrients added*" treatment received 80 g/m^2 of nitrogen (N), phosphorus (P_2O_5), potassium (K_2O), (concentrations 10:10:10) and micronutrients of Planalto Agrosciences Ltda (SP, Brazil) in an area of 25 cm of ray around the plant according to previous study (Dias 2003. All the experimental manipulations were done in the beginning of November of 2005; nutrients were re-added each 45 days.

Data collection

Starting in March of 2006, vegetative traits of plants were measured (see chapter 2). Flowerheads and leaves were counted and the phenology index was estimated (for details see chapter 2). Biweekly, from March to June of 2006, visual censuses were performed for a minute per plant to register the abundance of different herbivorous guilds (leaf-chewers, sap-suckers and galls) and their predators (ants, spiders and hemipteran predators) per plant. All censuses were carried out in sunny days only. For each plant, the number of individuals per guild was registered by direct counting, excluding insects that arrived on plants after the beginning of counting. When necessary and possible, the individuals were collected for further identification.

Flowerhead assessment was focused on mature flowerheads (pre-dispersal), to obtain larvae in their last stages and to minimize the collection effects over the remaining flowerheads. In the laboratory, we randomly selected 50 flowerheads, which were conditioned individually in gelatin capsules to rear endophagous insects. The remaining flowerheads of each plant sample were maintained in transparent plastic pots covered with fine mesh screen for additional rearing. To evaluate flowerhead infestation rate, we dissected all flowerheads (from gelatin capsules up to 110 per plant. The endophagous insects were identified to the nearest taxonomic levels by their puparium or damage traces. In infested flowerheads the number of eaten and intact seeds was recorded.

In the third census (June) the level of herbivory of each plant was estimated. Two branches were randomly selected and the mean level of herbivory of the oldest 50 leaves was estimated. The leaf consumption level was visually estimated according to the following classes of foliar damage (0) 0%; (1) 1-5%; (2) 6-25%; (3) 26-50%; (4) 51-75%; (5) 76-99%, following Fonseca (1994). Thus, leaf consumption level is weighted mean of foliar damage classes and varies between 0 and 5.

In the beginning of July, after 9 censuses, the experiment was concluded, because several plants had started to dry, losing their leaves and flowerheads in response to the onset of the dry season.

Statistical analysis

Randomized block ANOVAs were used to investigate the effect of independent factors (clipping and nutrient addition) on the dependent variables: Leaf consumption level; density of leaf-chewers (insects per leaf), sap-suckers (insects per shoot), galls (insects per shoot) and predaceous arthropods (predators per leaf). When appropriate, Fisher's least significant difference (LSD) tests were applied to compare means within or between treatment comparisons.

A multiple-response permutation procedure (MRPP) was used to test the hypothesis of no difference among treatments in endophagous species composition. MRPP is a non-parametric method that compares the observed data with data generated by permutation (McCune & Grace 2002). To calculate the distance matrix we used Sørensen (Bray-Curtis). Nonmetric multidimensional scaling (NMDS) was performed in order to visualize pattern of species compositions among clipping intensities. For this ordination we also used Sørensen distance.

NMDS is an effective ordination method well suited to ecological community data (McCune & Grace 2002). Both analyses (MRPP and NMDS) used the abundance of endophagous species divided by the number of dissected flowerheads, so that abundances were scaled by sample size.

A randomized block analysis of covariance (ANCOVA) was used to analyze the effect of clipping intensity and nutrient addition, using the number of dissected flowerheads as a covariate to control for the effect of sample size on endophagous species richness and diversity (Simpon's index) and on the number of achenes eaten per plant. The number of achenes destroyed and dissected flowerheads were square-root transformed. These variables means shown on the text and on graphics are least square means provided by ANCOVAs. Factorial ANOVAs were also performed on the proportion of infested flowerheads; abundance of all endophagous insects; abundance of all tephritids, and of the more common taxa, with at least 100 individuals sampled (*X. chrysura*, *Xanthaciura* sp. 1, *Cecidochares connexa*, *Melanagromyza* sp., cecidomyiids, mirids, Lepidoptera, Coleoptera sp. 1 and Coleoptera, excluding Coleoptera sp. 1) per flowerhead. Data were not transformed and when appropriate, Fisher's least significant difference tests were applied to compare means within or between treatments comparisons. For all endophagous insects groups we calculated an infestation rate index according to the equation: $[(IR1*PF1) + (IR2*PF2) + (IR3*PF3)] / 3$, where IR is the infestation rate (number of individuals divided by dissected flowerheads and multiplied per 100) in the first (1), second (2) and third (3) census, and PF is the proportion of collected flowerheads in each census (the three *PF*s summed is equal to 1).

The parasitism rate was evaluated by the proportion of endophagous individuals which showed signs of parasitoids attack, and the total parasitism rate was estimated as the proportion of all individuals attacked by parasitoids. Factorial ANOVAs were carried out to assess treatment effect on parasitism rate. The proportions were arcsin transformed.

All statistics were conducted in Systat version 10, excluding MRPP and NMDS which were performed in PCord version 5.

RESULTS

Exophages

Leaf herbivory

Leaf consumption was clearly influenced by plant damage. A factorial ANOVA showed that clipping intensity enhanced the leaf consumption level (Table 1, Fig. 1). Mean (± SE) leaf consumption level of clipped plants ($\bar{x}$= 1.1 ± 0.1) was almost 4 fold greater than unclipped plants ($\bar{x}$= 0.3 ± 0.0) and almost 3 times higher than partially clipped plants ($\bar{x}$ = 0.4 ± 0.1). However our analysis failed to detect any nutrient addition effect (Table 1, Fig. 1).

Abundance of exophages

Sap-sucking herbivores, in the order Hemiptera, were the main apparent guild feeding on *Chromolaena pungens* plants. This guild totaled 11160 individuals, represented 95% of the all exophagous herbivores in the censuses (N=11745) on vegetative structures. We also registered 349 galls and 236 leaf-chewers. Factorial ANOVA showed a significant effect of clipping treatment on the total number of herbivores (Table 1, Fig. 2A). Partially clipped plants had on average 83.3 exophagous herbivores (± 19.9), unclipped plants had 73.8 (± 25.0) whereas on clipped plants we recorded only 29.9 exophagous herbivores (± 9.7) (data not corrected by plant size).

Clipping intensity and nutrient addition had no influence on the mean number of leaf-chewers per leaf or sap-sucking insects per shoot (Table 1, Fig. 2A and 2B). The main predators recorded on *C. pungens* were hemipteran-tending ants and the abundance of these predaceous arthropods per leaf was highly influenced by clipping (Table 3, Fig. 2D). The mean (± SE) number of predators per leaf recorded on clipped plants ($\bar{x}$ = 0.06 ± 0.01) was twice the number of predators on partially clipped ($\bar{x}$ = 0.03 ± 0.01) and 3.5 times those on unclipped plants ($\bar{x}$ = 0.02 ± 0.00).

Endophages

Gall density

Treatments significantly affected the mean number of galls per shoot. Clipped plants had fewer galls ($\bar{x} = 0.05 \pm 0.02$) than partially clipped ($\bar{x} = 0.23 \pm 0.03$) and unclipped plants ($\bar{x} = 0.22 \pm 0.03$) (Table 1, Fig. 2C). Therefore, factorial ANOVA showed that the clipping x nutrient interaction was highly significant, so that the effect of nutrients addition was different among clipping levels. The addition of nutrients interacted positively with partially clipped plants ($\bar{x}_{-N} = 0.15 \pm 0.03$, $\bar{x}_{+N} = 0.30 \pm 0.05$) and negatively with unclipped plants ($\bar{x}_{-N} = 0.27 \pm 0.06$, $\bar{x}_{+N} = 0.17 \pm 0.03$), whereas gall density on clipped plants did not respond to fertilization ($\bar{x}_{-N} = 0.05 \pm 0.02$, $\bar{x}_{+N} = 0.06 \pm 0.03$) (Fig. 2C).

Pre-dispersal seed predation by endophages

The number of achenes damaged per plant was highly affected by clipping intensity as shown by ANCOVA (Table 2, Fig. 3). The least square mean (± SE) number of achenes eaten in clipped plants was 15.7 (± 0.6), significantly higher than the number of achenes destroyed by endophagous insects in partially clipped ($\bar{x} = 13.4 \pm 0.5$) and unclipped plants ($\bar{x} = 11.5 \pm 0.5$). We did not correct the number of achenes eaten by the mean number of achenes per flowerhead that the plant had. This correction would increase among clipping levels by around 5% since clipped plants produced fewer achenes than partially and clipped plants (for details see chapter 2).

Flowerhead endophagous insect community

In the flowerheads of *Chromolaena pungens* we recorded 5484 individuals from at least 16 endophagous insect species: 7 Tephritidae (Diptera), 2 Agromyzidae (Diptera), 1 Apionidae

(Coleoptera), 3 unidentified Coleoptera, 1 Lepidoptera, 1 Cecidomyiidae (Diptera), 1 Miridae (Hemiptera). However, some groups could not be identified to species level (e.g. Lepidoptera, Coleoptera and Cecidomyiidae) (Table 3). Cecidomyiidae (Diptera) was the most abundant group of endophages attacking *C. pungens* flowerheads, with 2414 individuals representing 44% of the total number of endophagous insects recorded by dissection. Most of the cecidomyiids were found inside the floral tubes of flowerheads; hence the seeds were not visibly damaged. Predaceous cecidomyiids were not included in this total.

The second abundant group was the family Tephritidae (Diptera) which summed 960 individuals, represented 18% of the total number of herbivores recorded in flowerheads. From this family were separated seven species, *Xanthaciura chysura* (N=558), *Xanthaciura sp. 1* (N=183), *X. mallochi* (N=24), *X. biocellata* (N=45), *Neomiopytes paulensis* (N=11), *Cecidochares connexa* (N=133) and *Cecidochares* sp.1 (N=6) (Table 3). The other groups of endophagous insects associated with *C. pungens* flowerheads were less common: Coleoptera (N=407); Agromyzidae (N=305); Miridae (N=302); and Lepidoptera (N=286) (Table 3).

Endophagous species abundance, diversity and composition

Clipping intensity affected the endophagous richness and diversity as shown by factorial ANCOVAs (Table 4, Figs. 4A and 4B). Species richness of endophages was higher on clipped plants ($\bar{x}$ = 6.3 ± 0.3) than on partially clipped ($\bar{x}$ = 5.7 ± 0.2) and unclipped plants ($\bar{x}$ = 5.4 ± 0.2), however, the difference among clipping intensity was marginally significant. Similarly, species diversity also increased with damage level, Simpson's index was higher on clipped plants ($\bar{x}$ = 0.66 ± 0.03) than on partially clipped ($\bar{x}$ = 0.58 ± 0.02) and unclipped plants ($\bar{x}$ = 0.55 ± 0.02) (means are least square means). However, there was no evidence either for nutrient or for nutrient x clipping interaction effects on species richness and diversity of endophagous insects.

The number of infested flowerheads and the total number of individuals per flowerhead were significantly affected by the treatments. The mean (± SE) number of infested flowerheads of clipped plants ($\bar{x}$ = 21.6 ± 2.8) was twice the number of unclipped plants ($\bar{x}$ = 9.9 ± 0.6) and almost twice that on partially clipped ($\bar{x}$ = 13.7 ± 1.9) plants (Table 6, Fig. 4C). Moreover, the factorial ANOVA showed that the clipping x nutrient interaction was significant. Fertilized partially clipped plants showed a higher number of infested flowerheads ($\bar{x}$ = 17.6 ± 3.9) than unfertilized partially clipped ($\bar{x}$ = 10.2 ± 0.9) plants. In contrast, fertilized clipped plants had a lower number of infested flowerheads ($\bar{x}$ = 18.4 ± 3.3) than the unfertilized ones ($\bar{x}$ = 24.3 ± 4.5). A similar but less pronounced response was found for the number of endophages per flowerhead (Table 6, Fig. 4D).

MRPP showed clearly that there was a difference in herbivore species composition on plants submitted to distinct clipping treatments (Table 4, Fig. 5), as shown by the chance-corrected within-group agreement (A = 0.026) and test statistic ($T = -9.133$, $p < 0.001$). MRPP showed that the endophagous species composition of clipped plants differed from partially clipped and unclipped plants (Table 4, Fig. 5), however, the difference seems to be a species abundance effect, and not a community response, since the differences are mainly quantitative not qualitative. These last two treatments were not significantly different from each other. Even when the nutrient factor was incorporated in the model, the species composition remained different among clipping groups (A = 0.028, $T = -6.031$, $p < 0.001$). Clipping did modify endophagous assemblages, which is consistent with the pattern of separation of points in the nonmetric multidimensional scaling (NMDS). NMDS indicated a three dimensional solution for these data. The final stress for 3-dimensional solution was 0.14, with 63 iterations. The first axis better separated species composition among clipping intensities (Fig. 5). The endophagous species composition of clipped plants was more dispersed in ordination space, hence more variable than the composition of unclipped plants. Partially clipped and unclipped plants were very similar.

Responses of endophagous insect species

Tephritids responded positively to clipping intensity and nutrient addition (Table 6, Fig. 6A). The flowerheads of clipped plants ($\bar{x}$ = 6.2 ± 1.2) were almost 4 times more infested by tephritids than those on unclipped plants ($\bar{x}$ = 1.7 ± 0.2) and twice more than those on partially clipped plants ($\bar{x}$ = 2.6 ± 0.5). Moreover, the abundance of tephritids on unfertilized clipped plants ($\bar{x}$ = 7.7 ± 2.1) was twice the number on fertilized clipped plants ($\bar{x}$ = 3.4 ± 0.8). Thus, the clipping x nutrient interaction was significant for the number of tephritids per flowerheads. The most abundant species were *Xanthaciura chrysura*, *Xanthaciura* sp. 1 and *Cecidochares connexa*. *X. chrysura* responded consistently to clipping intensity, as shown by factorial ANOVA (Table 6, Fig. 6B). The mean (± SE) abundance of *X. chrysura* in clipped plants ($\bar{x}$ = 3.6 ± 0.7) was more than twice the number of individual in partially clipped ($\bar{x}$ = 1.7 ± 0.5) and 4 times that unclipped plants ($\bar{x}$ = 0.9 ± 0.1). For *C. connexa*, clipped plants were the main host, and they were also affected by the clipping x nutrient interaction, since unfertilized clipped plants showed 9.6 times more individuals then the fertilized clipped plants (Table 6, Fig. 6C). Apart from the treatment significance on both species mentioned above, the abundance of *X. sp. 1* was not significantly affected by any treatments (Table 6, Fig. 6D).

Clipping intensity was also an important factor for the infestation rate of *Melanagromyza* sp. (Agromizydae: Diptera) as shown by the significance of factorial ANOVA (Table 6, Fig. 6E). The mean (± SE) of *Melanagromyza* sp. infestation rate in clipped plants ($\bar{x}$ = 1.7 ± 0.3) was more than 3 times the infestation rate on unclipped ($\bar{x}$ = 0.5 ± 0.1) and almost twice on partially clipped ($\bar{x}$ = 0.9 ± 0.2) plants. However, no significant effect of nutrient supplementation was found. The abundance of lepidopterans was significantly affected by clipping intensity as shown by factorial ANOVA; the mean (± SE) number of lepidopterans was 2.0 ± 0.4 in clipped plants, 4 fold greater than the abundance on unclipped plants ($\bar{x}$ = 0.5 ± 0.1), and almost twice on partially clipped plants ($\bar{x}$ = 1.2 ± 0.4) (Table 6, Fig. 6H).

Cecidomyiids were more abundant on partially clipped plants ($\bar{x}$ = 12.0 ± 5.3) than on the other two clipping levels ($\bar{x}_{\text{unclipped}}$ = 5.4 ± 0.5, $\bar{x}_{\text{clipped}}$ = 7.8 ± 1.7), but this treatment was not significant in factorial ANOVA (Table 6, Fig. 6F). Finally, clipping had no detectable effect on the number of Coleoptera sp. 1, other coleopterans or Miridae (Hemiptera) found on plants (Table 6).

Parasitism rate

Factorial ANOVA showed that total parasitism rate was significantly influenced by the clipping x nutrient interaction (Table 7, Fig. 7). The addition of nutrients enhanced the parasitism rate on clipped plants ($\bar{x}_{-N}$= 0.319 ± 0.059, $\bar{x}_{+N}$ = 0.419 ± 0.027) but decreased it on unclipped plants ($\bar{x}_{-N}$= 0.386 ± 0.028, $\bar{x}_{+N}$ = 0.262 ± 0.037) and had no influence on the parasitism rate of endophages on partially clipped plants. *Melanagromyza* sp., *X. chrysura*, *Xanthaciura* sp. 1 and *C. connexa* were the most parasitized species (Table 3). However, neither clipping intensity nor nutrients enhanced the parasitism rate of these four species ($P > 0.05$).

DISCUSSION

Our findings indicated that plant traits affected by severe damage provoked a suite of bottom-up cascading effects across trophic levels. Resprouting plants affected differently the insect guilds studied, decreasing the densities of galls whilst increasing considerably the leaf consumption and flowerhead infestation rate. Furthermore, species diversity and composition of flowerhead endophagous insects were affected. Moreover, changes in host plant traits stimulated indirectly the increase of the densities of predaceous arthropods and the total parasitism rate of endophagous insects in flowerheads.

Responses of leaf chewing, gall-forming and sap-sucking insects to host plant damage

Aboveground destruction often stimulates plants to resprout, inducing changes in their nutritional status (Danell & Huss-Danell 1985, Radho-Toly et al.2001, Shimazaki & Myashita 2002), which in turn, alter the quality for herbivores that use them as food source (Danell & Huss-Danell 1985, Stein et al. 1992, Nakamura et al. 2006). Stein et al. (1992) reported that fire stimulated willow (*Salix lasiolepis*) regrowth, increasing grasshopper feeding rates. In our study, the leaf consumption level was very high on severely clipped plants, whereas there was no difference between partially clipped and unclipped plants. Damage enhances the production of new leaves (Stein et al. 1992, Nakamura et al. 2005), and it has been well demonstrated that as leaves grow old the water and protein contents decline, and digestible reducers increase (Feeny 1970). Thus, feeding on young leaves provides a temporal escape from plant defenses (digestible reducers), and it would be synchronized with high leaf water content, which promotes higher leaf consumption rates. The increase of leaf herbivory after the destruction of most aboveground parts of host plant has been well demonstrated (Hunter & Forkner 1999, Spiller & Agrawal 2003, Agrawal & Spiller 2004, Nakamura et al. 2005, Nakamura et al. 2006), however few studies have reported a negative effect of host plant resprouting on leaf damage (Olofsson & Strengbom 2000, Shimazaki & Miyahita 2002, Angulo-Sandoval et al. 2004). Apart from the increase in leaf consumption, we failed to detect clipping effects on the densities of leaf-chewing insects, in visual censuses. However, many leaf eaters have crepuscular or nocturnal habits in the tropics (Lewinsohn, unpublished) and can go undetected in diurnal surveys.

In *Anthyllis cytisoides* (Fabaceae), sucking insects showed a slightly tendency to decrease densities as damage rates increased (Alados et al. 1997). In contrast, in our study the densities of sap-sucking insects were also similar among partially clipped, unclipped and clipped individuals. The main sap-sucking insect recorded was an ant-tended hemipteran, which feeds on young tissues rather than on mature tissues, and apparently depends on a higher number of branches to increase its densities (M. F. Kersch unpublished observation). Clipped plants were smaller than the others plants, thus offering fewer structures on which the hemipterans could increase densities.

Clipping, browsing and fire damage increased the number of gall-forming insects in several systems (Danell & Huss-Danell 1985, Olofsson & Strengbom 2000, Martinez & Wool 2003). However, our results did not support these findings. The number of galls was much lower in severely clipped plants than on partially clipped and unclipped ones. The differences in gall densities can have three explanations. First, there could be an oviposition preference of gall-forming insects to avoid severely damage plants. Second, the oviposition peak period may occur before plants resprouted. Third, clipping could reduce the number adequate sites for their oviposition (Bailey & Whitham 2003).

Responses of endophagous community

Past studies have mainly focused on numerical changes on the second and third trophic levels in response to changes in host plant traits (but see Bailey & Whitham 2002 and Nakamura et al. 2006). In willows (*Salix eriocarpa* and *Salix gilgiana*), trunk cuttings increased plant biomass and quality, which, in turn, induced an increase in leaf consumption, relative abundance and species richness of herbivorous and predaceous arthropods (Nakamura et al. 2006). In this study, we clearly demonstrated, for the first time, that species diversity and composition are affected by severe damage. As we did not found a significant difference in species richness, species diversity could be mainly affected by species evenness. The common endophagous species found on *C. pungens* plants were *Xanthaciura chrysura*, *Cecidochares connexa* and *Melanagromyza* sp which had higher densities on clipped plants. We also documented higher flowerhead infestation rates on clipped plants than on plants that suffered partial or no damage.

As noted by previous studies, flowerhead infestation was higher on larger flowerheads, and this preference is found intra- and inter-specifically (Zwölfer & Preiss 1983, Prada et al. 1995, Fenner et al. 2002). In our study the highest infestations rates were on flowerheads from clipped plants, which produced the largest flowerheads (capítulo 2). Larger flowerheads may also produce bigger seeds which have been demonstrated to show greater viability (Harper et al. 1970, Lehtilä & Ehrlén 2005). However, in our case the differences in flowerheads among clipping treatments were only in total size, no differences in seed number, flowerhead weight or seed length or weight were found among treatments. Therefore, flowerhead endophages may be responding to changes in plant floral phenology, rather than to size of the floral structures.

Some insect herbivores that use ephemeral plants or plant parts are likely to suffer higher immature mortality rates due to seasonal changes in their food source (Schoonhoven et al. 2005). Several studies have highlighted the influence of biotic and abiotic factors on flowering phenology (Brody 1997, Pilson 2000, Almeida-Neto & Lewinsohn 2004, Sola & Ehrlén 2007). Floral phenological swifts may promote negative effects on plants; thus, pollinator peaks may be missed or else the flowering delay may compensate the loss of pollination through temporal escape from pre dispersal seed predators (Sharaf & Price 2004). In this study, however the delay in flowering maturation increased plant susceptibility to flowerhead feeders, since clipped plants offered young buds when control plants were displaying pre-anthesis or mature capitula. This may be the main reason why clipped plants were more attacked by endophagous insects. Plants that flower immediately after the peak are prone to suffer higher pre dispersal seed predation rates, as numbers of flowers decrease while the abundance of seed predators is still high (Honek & Martinkova 2005). Conversely, plants synchronized with the flowering peak production are less vulnerable to seed predation, since their effects are diluted.

Cascading effects on the third trophic level

In this study, we evaluated the indirect effect of plant damage on the densities of predaceous arthropods and on the parasitism rate of flowerhead endophagous insects. Several studies have revealed that a herbivore's host plant can dictate directly or indirectly the efficacy of natural enemies (Price et al. 1980, Clark & Messina 1998, De Moraes et al. 1998, Nakamura et al. 2005). The predaceous arthropods were more commonly found on clipped plants, supporting previous findings which have reported higher densities of predators on severely damaged plants (Kagata et al. 2005, Nakamura et al. 2005, Nakamura et al. 2006). In willows (*Salix eriocarpa*), resprouted plants increased consistently the performance of the leaf beetle (*Plagiodera versicolora*) whereas the effect of damaged plants on the predatory ladybird beetle (*Aiolocaria hexaspilota*) was significant but less pronounced (Kagata et al. 2005). Not only the quality of plants is modified after damage, but their architecture is also affected, in turn is likely to alter the effectiveness of predaceous arthropod against insect herbivores (Clark & Messina 1998). Main predators were hemipteran-tending ants, which were found closely associated to sap-sucking insects ($r_{\text{Pearson}} = 0.62$, df = 1, $P<0.001$). The sap-feeders were not significantly affected by plant damage intensity and differences in densities of a partner could provoke a positive effect on the ant-hemipteran mutualistic interaction in clipped plants. However, we were not able to test this idea directly.

Recent studies have documented that herbivore feeding can stimulate plants to release chemical substances to attract parasitoids (De Moraes et al. 1998, Thaler et al. 1999). Therefore, the detrimental effect of endophages on the production of seeds, damaged plant could be counter balanced if attract more parasitoids. However, the remarkable abundance and richness of tephritids in notwithstanding flowerheads of clipped plants, the effect of clipping intensity on their parasitoids was less pronounced, supporting previous findings which reported that parasitoids did not respond to the increase of host density (Zvereva & Kozlov 2000). We showed that the parasitism rate was influenced by the nutrient x clipping interaction; endophagous insects of control plants with no nutrient added were less parasitized, whereas in clipped plants the nutrient had the opposite effect, and endophages of plants with nutrients were more parasitized.

High quality host plants may improve herbivore performance that, in turn, can cause two different outcomes on parasitoid performance. First, healthier herbivores can increase parasitoid performance because they will feed on a high quality food source (Zvereva & Rank 2003). Second, parasitoids may be faced with higher host resistance, which lower their survival rates; healthier herbivores can encapsulate the parasite, stopping their development. Thus, in response to nutrient supplementation clipped plants may have their quality changed and they may assimilate their resources differently from undamaged ones, since their physiology may be altered in response to damage.

CONCLUSION

The removal of plant aboveground biomass can initiate bottom-up cascading effects up to higher trophic level through changes in plant traits. Thus, changes in ecological environments may alter or even disrupt animal-plant interaction. As a result, variation in the strength of interactions may modify evolutionary processes (Thompson 1994, 1999). Finally, the results presented here provide a clear demonstration that the destruction of plant's aboveground structure, contingent on nutrient availability, can considerably alter the incidence and effects of second and third trophic level organisms.

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Table 1 – Randomized block ANOVA on the number of leaf chewers per leaf, the number of sap-suckers per shoot, number of galls per shoot and predators per leaf; treatments are clipping (unclipped, partially clipped and clipped) and nutrients (nutrients added and no nutrient added). F-values and degrees of freedom (df) shown. (Leaf consumption levels N=172, arthropods N=186)

Source of variation	df	Leaf consumption level	df	Leaf chewers	Sap-suckers	Galls	Predators
Block	31	2.572***	31	1.639*	1.540*	2.000**	1.253
Clipping	2	84.753***	2	0.507	0.165	14.046***	11.112***
Nutrient	1	0.082	1	0.027	0.036	0.634	0.748
Clipping*Nutrient	2	2.292	2	0.821	0.545	6.207**	0.265
Error	135		149				

* $p < 0.05$, **$p < 0.01$, *** $p < 0.001$

Table 2 – Randomized block ANCOVA on the number of achenes destroyed by herbivores; and the number of dissected flowerheads as covariate; for treatments see Table 1. Sqr = square root transformed. (N=156).

Source of variation	df	Seeds eaten (Sqr)
Block	31	1.034
Clipping	2	10.567***
Nutrient	1	0.000
Clipping*Nutrient	2	0.523
Dissected Flowerheads (Sqr)	1	28.290***
Error	118	

*** $p < 0.001$

Table 3 – Flowerhead endophagous species associated to *Chromolaena pungens* in this study. Frequency (%) of the specie in *C. pungens* flowerheads and the total number of individuals recorded (N), number of plants where they were recorded and the number of parasitized endophages.

Order	Family	Species	N	Frequency (%)	No. of Plants	No. of Parasitized
Diptera	Agromyzidae	*Liriomyza* sp. 1	4	0.07	3	0
		Melanagromyza sp.	301	5.49	112	41
	Cecidomyiidae		2417	44.02	150	476
	Tephritidae	*Cecidochares connexa*	133	2.43	60	29
		Cecidochares sp. 1	6	0.11	3	1
		Neomyopites paulensis	11	0.20	8	0
		Xanthaciura biocellata	45	0.82	31	5
		Xanthaciura chrysura	558	10.18	131	91
		Xanthaciura sp. 1	183	3.34	82	27
		Xanthaciura mallochi	24	0.44	18	4
Coleoptera	Anthicidae	Anthicidae sp	20	0.36	17	1
	Apionidae	*Apion* sp	6	0.11	6	0
	Not identified	Coleoptera sp. 1	197	3.59	76	2
		Coleoptera sp2	37	0.67	27	0
		Damage trace	147	2.68	71	0
Heteroptera	Miridae	Miridae sp	302	5.5	70	30
Lepidoptera			286	5.21	91	15
Not identified			848	15.46	131	19
Total			5484		155	741

Table 4 - Summary of F-values generated by randomized block ANCOVA of endophagous species richness and diversity (Simpson's Index); and number of dissected flowerheads as covariate; for treatments details see Table 1. Sqr = square root transformed. (N=155)

Source of variation	df	Richness (Sqr)	Simpson's Index
Block	31	0.751	0.968
Clipping	2	2.381 [a]	3.459*
Nutrient	1	0.072	0.575
Clipping*Nutrient	2	1.554	0.064
Dissected flowerheads (Sqr)	1	53.453***	6.835**
Error	117		

* $p < 0.05$, **$p < 0.01$, *** $p < 0.001$, [a] $p = 0.09$

Table 5 – Summary statistics for multiple-response permutation procedure (MRPP). Multiple pairwise comparisons for the Sørensen distances between treatments (A) among clipping levels;, and (B) among clipping (control, partially clipped, clipped) and nutrient (without (N_0) with (N_+) nutrients added), overall chance-corrected within-group agreement, *A* = 0.028 (P<0.001). In bold p<0.001.

A

	Control	Partially Clipped	Clipped
Control			
Partially clipped	-0.614		
Clipped	**-13.828**	**-5.614**	

B

		Control		Partially clipped		Clipped	
		-N	+N	-N	+N	-N	+N
Control	N_0						
	N_+	0.607					
Partially clipped	N_0	-0.222	-1.423				
	N_+	0.076	0.420	-0.574			
Clipped	N_0	**-8.482**	**-4.223**	**-4.544**	**-4.222**		
	N_+	**-4.739**	**-5.657**	-1.219	-2.233*	-0.722	

* p<0.05

Table 6 – Randomized block ANOVA on the proportion of infested flowerheads, abundance of endophagous insects and endophagous species separately; for treatments see Table 1. F-values and degrees of freedom (df) shown (N=156).

Source of variation	df	Infested flowerheads	Abundance of endophages	Tephritids	*C. connexa*	*X. chrysura*	*Xanthaciura* sp. 1	*Melanagromyz*a sp.	Lepidoptera	Cecidomyiids	Coleoptera sp. 1	Coleoptera	Mirids
Block	31	1.309	1.227	1.522^{a}	0.966	1.588*	1.284	1.416^{a}	0.831	1.164	1.381	1.397	1.291
Clipping	2	9.825***	3.571*	9.631***	3.532*	58.958**	1.457	10.026***	4.462*	1.655	0.219	1.789	0.255
Nutrient	1	0.032	0.164	0.573	3.184^{a}	0.534	0.541	0.569	1.189	0.145	2.688	0.065	0.055
Clipping* Nutrient	2	3.609*	2.095^{a}	3.604*	3.191*	1.334	1.667	0.412	0.821	1.207	1.304	0.174	0.942
Error	119												

* $p < 0.05$, **$p < 0.01$, *** $p < 0.001$, (a) $p<0.09$.

Table 7 - Summary of *F*-values generated by randomized block ANOVA on the number total parasitism rate of endophages (arcsin transformed); for treatments see Table 1 (N=155).

Source of variation	df	Total parasitism rate
Block	31	1.571
Clipping	2	1.609
Nutrient	1	0.001
Clipping*Nutrient	2	4.384*
Error	118	

* $p < 0.05$

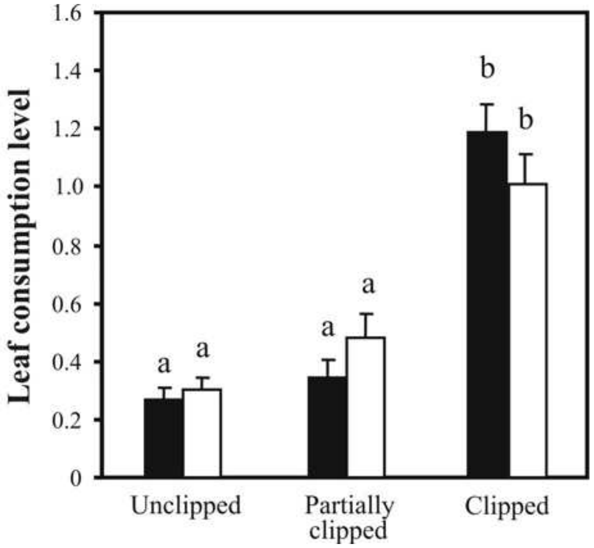

Fig. 1 – Leaf consumption level (mean ± 1SE) of *Chromolaena pungens*. Leaf consumption level measures the degree of leaf damage, varying between 0 (all leaves intact) to 5 (almost defoliated). Treatments are unclipped, partially clipped and clipped; no nutrient added (solid bars) and nutrients added (open bars). Letters indicate significant differences ($P < 0.05$) between means compared using LSD multiple comparisons test.

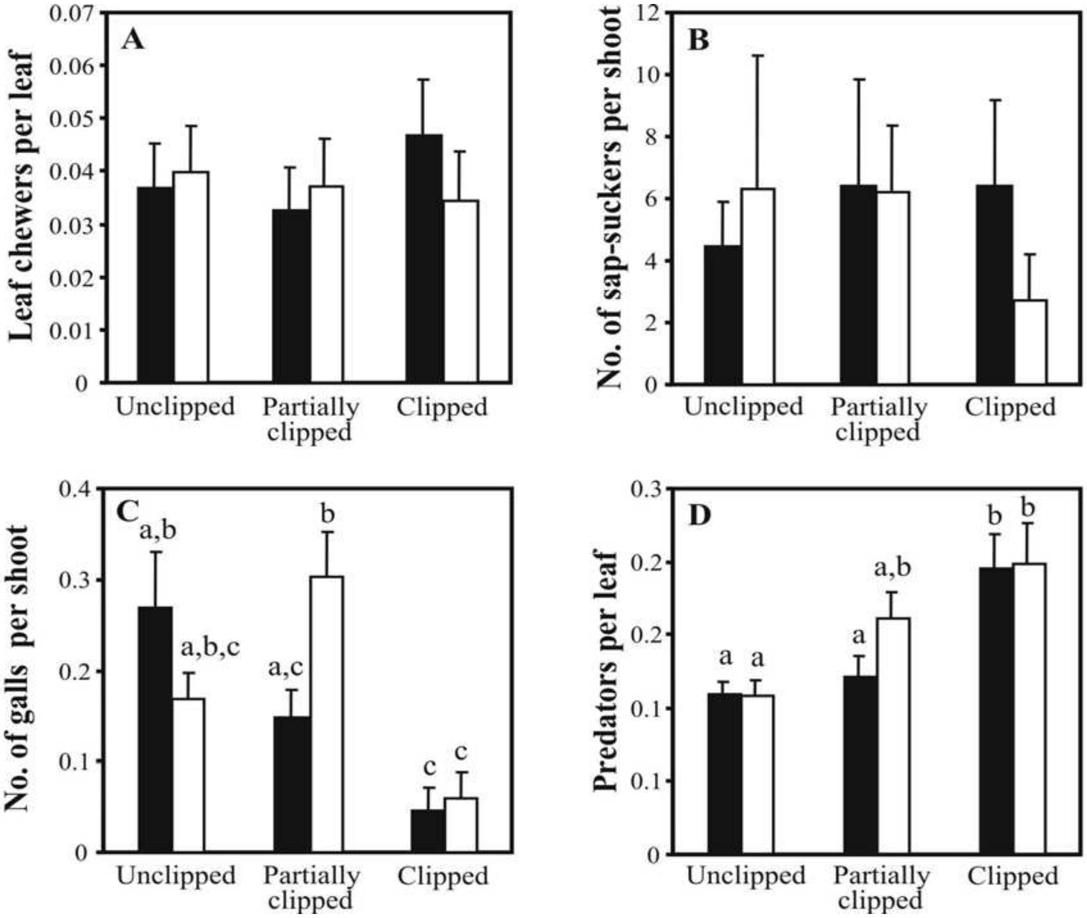

Fig. 2 – Abundances of exophagous herbivores of *Chromolaena pungens* subject to different treatments. (A) Number of leaf chewers per leaf. (B) Number of sap-sucking herbivores per shoots. (C) Number of galls per shoot (D) Number of predators per leaf. Treatments are unclipped, partially clipped and clipped; no nutrient added (solid bars) and nutrients added (open bars). Letters indicate significant differences ($P < 0.05$) between means compared using LSD multiple comparisons test. Values are means (± 1SE).

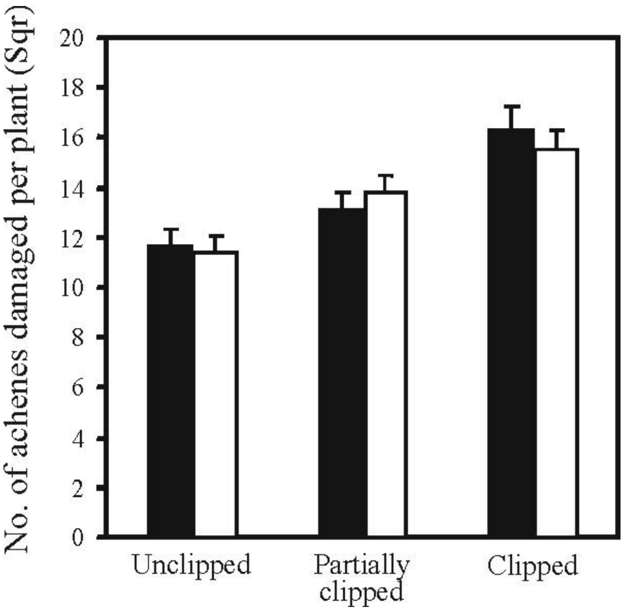

Fig. 3 – Number of achenes destroyed by endophagous insects on *C. pungens*. Values are least square means (± 1SE). Treatments are unclipped, partially clipped and clipped; no nutrient added (solid bars) and nutrients added (open bars).

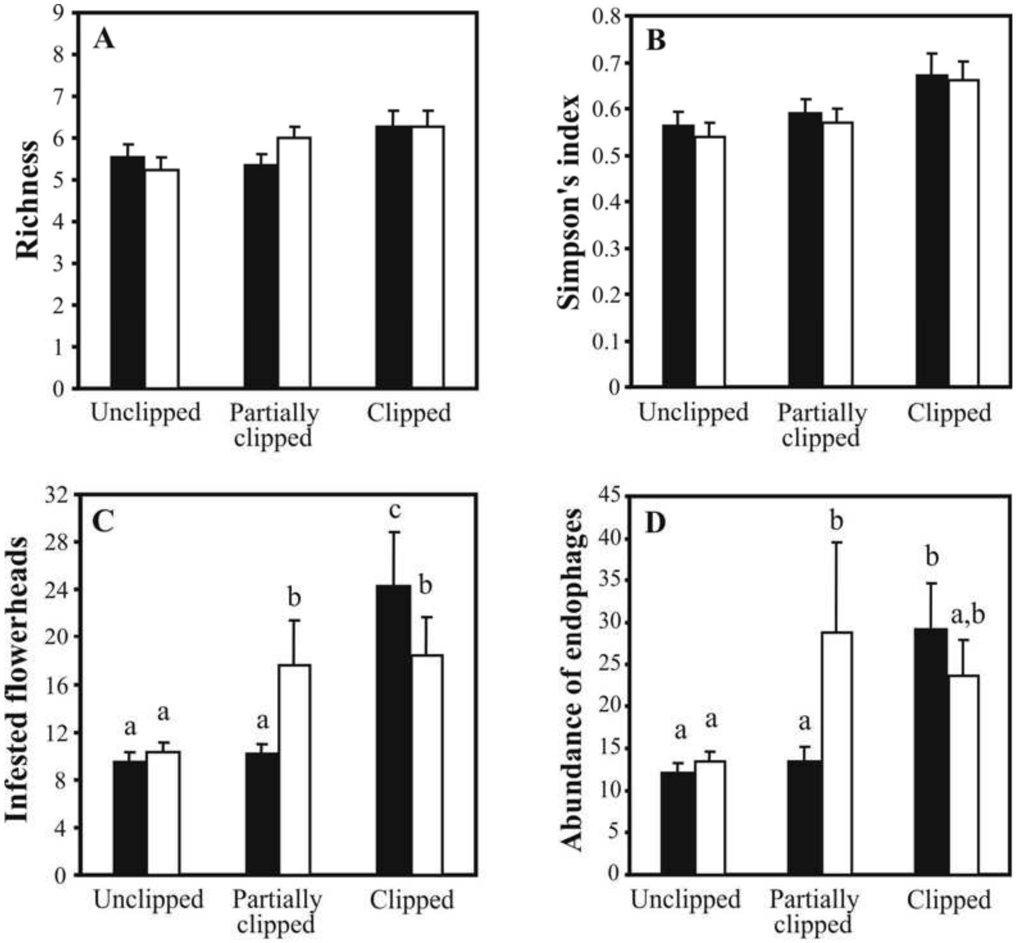

Fig. 4 – Response of the endophagous insect community. (A) Species richness. (B) Simpson's diversity index. (C) Number of infested flowerhead in 100 flowerheads. (D) Number of endophagous insects in 100 flowerhead. Data shown of species richness and diversity index are least-square means (± 1SE), and the values of infested flowerheads and endophagous abundance are means (± 1SE). Treatments are unclipped, partially clipped and clipped; no nutrient added (solid bars) and nutrients added (open bars). Letters indicate significant differences ($P < 0.05$) between means compared using LSD multiple comparisons test.

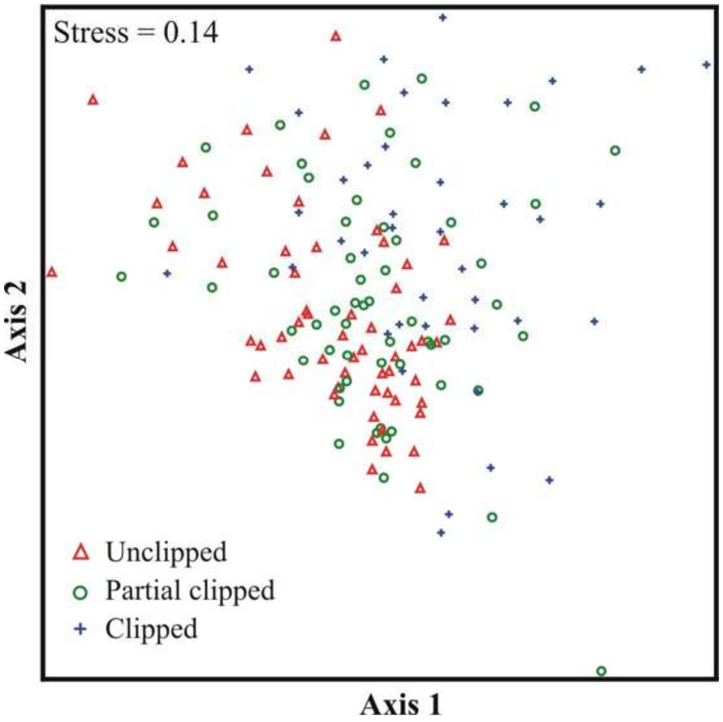

Fig. 5 - Nonmetric multidimensional scaling (NMDS) plot of endophagous species composition in each of the three clipping treatments. Each point represents the assemblage of insects on an individual plant combined over three censuses. In NMDS axes numbering is arbitrary.

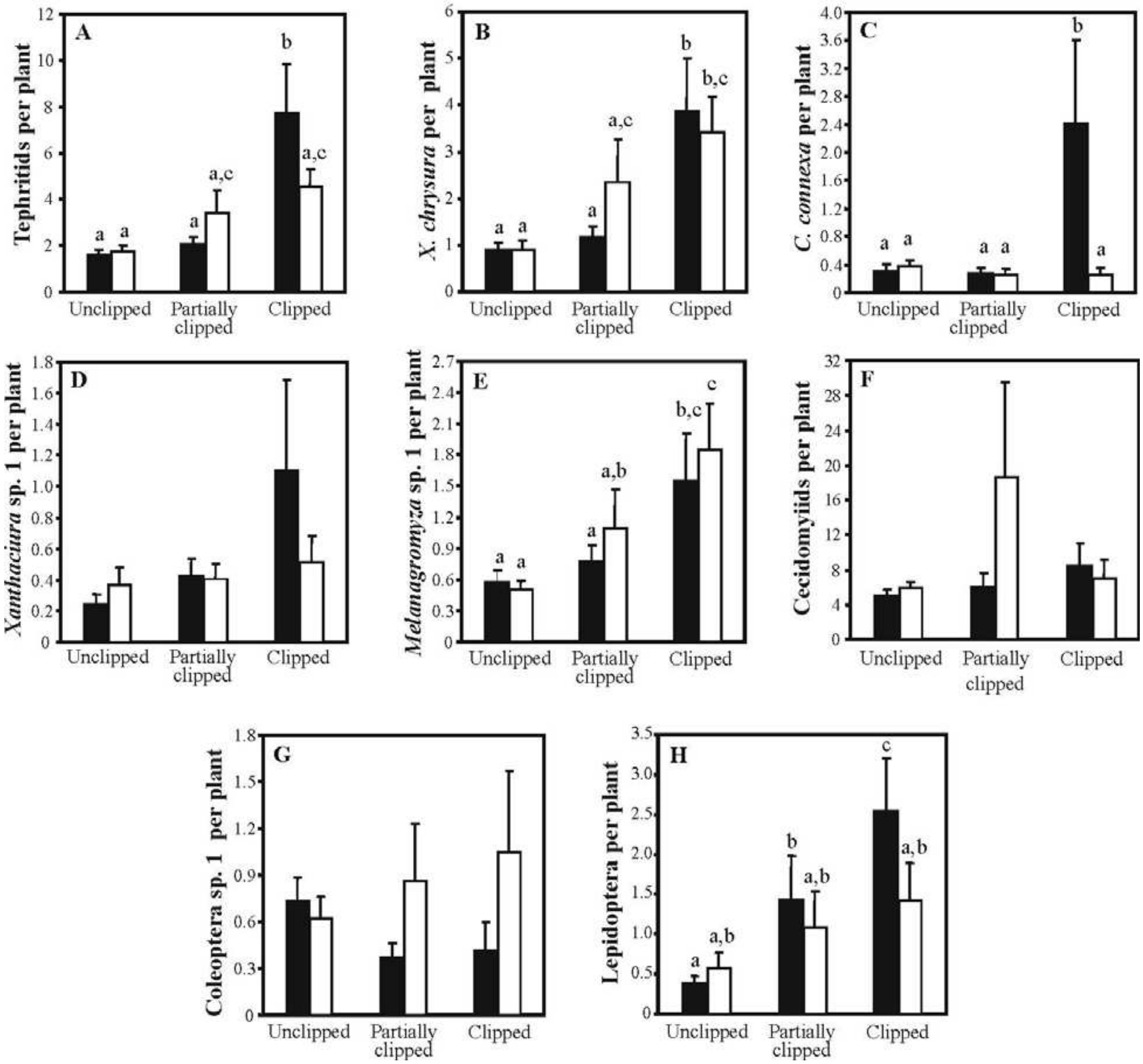

Fig. 6 – Infestation rates in 100 flowerheads per plant by endophagous taxa in different treatments. (A) Tephritids (all species) in 100 flowerheads. (B) Number of *Xanthaciura chrysura* individuals in 100 flowerheads. (C) Number of *Cecidochares connexa* individuals in 100 flowerheads. (D) Number of *Xanthaciura* sp. 1 individuals in 100 flowerheads. (E) Number of *Melanagromyza* sp individuals in 100 flowerheads. (F) Number of Cecidomyiids individuals in 100 flowerheads. (G) Number of Coleoptera sp. 1 individuals in 100 flowerheads. (H) Number of Lepidoptera individuals in 100 flowerheads. Treatments are unclipped, partially clipped and clipped; no nutrient added (solid bars) and nutrients added (open bars). Letters indicate significant differences ($P < 0.05$) between means compared using LSD multiple comparisons test. Values are means (± 1SE).

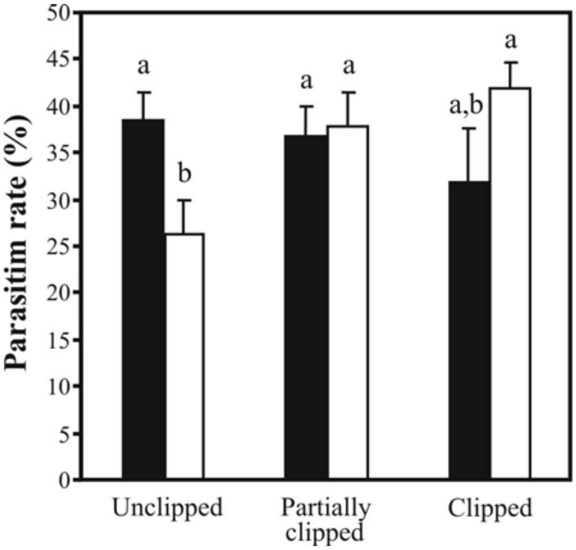

Fig. 7 – Total parasitism rate of flowerhead endophages. Values are means (± 1SE) after arcsine transformation. Treatments are unclipped, partially clipped and clipped; no nutrient added (solid bars) and nutrients added (open bars). Letters indicate significant differences ($P < 0.05$) between means compared using LSD multiple comparisons test. Probability level between clipped plants without nutrient added and clipped plants with nutrients added is marginally significant ($p = 0.09$).

CONSIDERAÇÕES FINAIS

No presente estudo, o corte da parte áerea da planta ocasionou mudanças fenotípicas em *Chromolaena pungens* (Asteraceae), e essas mudanças alteram a incidência de herbívoros exófagos e endófagos, predadores e parasitóides. Plantas cortadas foram menores, produziram menos folhas e capítulos, demoraram a produzir os primeiros capítulos, proporcionando um atraso na fenologia floral, as quais chegaram a estar atrasadas um mês quando comparadas com plantas controle ou de corte parcial. No entanto, plantas severamente danificadas obtiveram altas taxas de crescimento em altura, produziram áreas foliares e capítulos maiores. Porém, o aumento da área foliar e do tamanho dos capítulos não foi suficiente para compensar a biomassa foliar e reprodutiva produzida pelas plantas dos demais tratamentos. A remoção da parte aérea de *C. pungens* influenciou seus herbívoros associados. Essas plantas sofreram maiores níveis de herbivoria foliar e altas taxas de destruição de sementes. Além disso, a abundância, a riqueza, a diversidade de espécies endófagas associadas a capítulos de plantas cortadas foram maiores do que em plantas controle ou de corte parcial. Em consequência, a composição de espécies destes insetos diferiu entre plantas cortadas, controle e de corte parcial. Além disso, a abundância de predadores e parasitóides diferiram entre tratamentos. Por isso, este estudo evidenciou que a remoção da parte aérea iniciou efeito de cascata trófica através das mudanças nas características morfológicas das plantas hospedeiras. Estes resultados contribuem para o conhecimento de interações inseto-planta em ambientes que sofrem recorrentes perturbações naturais ou antrópicas.