

Universidad de Chile
Facultad de Ciencias

ALELOPATÍA BIOLÓGICA Y SUS CONSECUENCIAS EN EL RECLUTAMIENTO DE PLÁNTULAS EN UN BOSQUE BOLIVIANO NEOTROPICAL

Tesis Entregada a la Universidad de Chile en cumplimiento parcial de los requisitos para optar al grado de Magister en Ciencias Biológicas con mención en Ecología y Biología Evolutiva

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INFORME DE APROBACIÓN

TESIS DE MAGÍSTER

Se informa a la Escuela de Postgrado de la Facultad de Ciencias que la Tesis de Magíster presentada por el candidato

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INTRODUCCIÓN GENERAL

La coexistencia de especies arbóreas en un bosque tropical depende de mecanismos asociados al reclutamiento de sus plántulas (Wright 2002). La depredación distancia-dependiente puede reducir el establecimiento de plántulas conespecíficas cerca de la fuente de propágulos (Janzen 1970, Connell 1971), generando espacios para el establecimiento de plántulas heteroespecíficas (Hubbell 1980, Condit *et al.* 1992, Harms *et al.* 2000). Tales plántulas se constituyen en potenciales individuos de reemplazo de los árboles adultos establecidos (Wright 2002). Sin embargo, además de la depredación, la distribución espacial de las plántulas puede ser influenciada por otros mecanismos tales como la alelopatía (Mongelli *et al.* 1997), es decir, por interacciones planta-planta donde una de ellas inhibe químicamente el crecimiento de la otra (Whittaker & Fenny 1971). Aunque la mayoría de los agentes alelopáticos son químicos y se encuentran en las hojas, la poda de plantas vecinas por hormigas residentes de plantas mirmecofíticas es considerada como un potencial agente de “alelopatía biótica”, ya que dicha poda impide el establecimiento o crecimiento de plantas vecinas, de manera análoga a los agentes alelopáticos químicos (Janzen 1969).

La mantención de una colonia de hormigas residentes representaría un costo energético para una planta mirmecofítica (e.g. producción de alimento)(Agrawal 1998), pero podría generarle beneficios al disminuir la herbivoría, actuando como defensas bióticas (Agrawal & Rutter 1998) y reduciendo la competencia intra- e interespecífica, al eliminar plantas vecinas (Janzen 1966, 1969).

La poda de plántulas por hormigas residentes en plantas mirmecofíticas podría incluir

la mantención de un claro basal alrededor de la planta hospedera (Davidson *et al.* 1988), originando espacios desprovistos de plántulas de cualquier especie. En este caso, la poda por las hormigas podría actuar como un agente alelopático en contra de potenciales plantas competidoras de la planta adulta establecida (Janzen 1969, Davidson *et al.* 1988). El comportamiento de poda sería una consecuencia de la defensa de la colonia. La poda de plántulas bajo el dosel del árbol hospedero eliminaría sustratos de forrajeo y rutas de acceso de hormigas enemigas que podrían invadir a la planta hospedera y dominar a la colonia residente (Davidson *et al.* 1988, Heil *et al.* 2001, Federle *et al.* 2002). El comportamiento de poda sería una consecuencia de la inferior habilidad competitiva de la hormiga residente, lo que causa su extrema fidelidad a la planta huésped (Federle *et al.* 2002). Por ello, la poda de plántulas podría beneficiar directamente a la colonia de hormigas residentes e indirectamente a la planta huésped al eliminar plántulas competidoras.

La defensa de la colonia podría afectar los patrones de reclutamiento arbóreo. La eliminación de plántulas implica remover los individuos de reemplazo para las plantas adultas establecidas, originando pequeños claros desprovistos de reclutas. La evidencia empírica sobre esta posibilidad es particularmente escasa. Los estudios se han dirigido a evaluar las diferencias intra- o interespecíficas del comportamiento de poda por la hormiga (Davidson *et al.* 1988, Federle *et al.* 2002) o a los beneficios de la poda para el éxito reproductivo de la planta huésped (e.g. defensas bióticas) (Janzen 1966, 1969, Oliveira *et al.* 1987, Agrawal & Rutter 1998, Heil *et al.* 2001), pero no a las posibles consecuencias comunitarias de la poda por las hormigas residentes.

En esta tesis evalué cómo la poda de plántulas por la hormiga residente de una planta mirmecofítica influiría en la dinámica del reclutamiento de plántulas en un bosque Neotropical en Bolivia, sugiriendo que la interacción hormiga-hormiga (e.g. defensa de la colonia) podría resultar en modificaciones en la diversidad y abundancia local de plántulas, generando un caso extremo del modelo de Janzen-Connell donde la depredación distancia-dependiente afecta tanto a plántulas con- y heteroespecíficas.

CAPÍTULO I. BIOLOGICAL ALLELOPATHY IN ANT-PLANTS AND ITS CONSEQUENCES ON SEEDLINGS RECRUITMENT IN A TROPICAL BOLIVIAN RAINFOREST

ABSTRACT

Distance-dependent predation reduces the presence of conspecific seedlings near parental trees originating free spaces for seed arrival and heterospecific seedling establishment. However, seedling survival near adult trees can be related with other mechanisms such as allelopathy. *Triplaris americana* (Polygonaceae) is a tree species characterized by presenting a scarce con- and heterospecific seedlings recruitment under its canopy, which suggests the existence of chemical or biological allelopathic agents. We evaluated the allelopathic effects of both aqueous extracts of mature leaves and defensive activities of resident ants (*Pseudomyrmex triplarinus*, Pseudomyrmecinae) on seed

removal and seedlings survival. We considered distance to *T. americana* tree, exclusion of seed consumers and seedling predators, and habitat fragmentation as study variables. Aqueous extracts did not inhibit seed germination. Resident ants did not remove the seeds under the canopy of host plant. The main seed consumer was the leaf-cutting ant *Atta sexdens* (Myrmicinae). In contrast, seedling leaves under the canopy of *T. americana* were partial or totally pruned by the resident ant species. Results suggest that scarce seedlings recruitment under the canopy of *T. americana* may be consequence of active defense by the resident ants, acting as a biological allelopathic agent. Ecological consequences of defense by ants are discussed.

Key words: *Triplaris americana*, local diversity, ants colony, fragmentation.

INTRODUCTION

Seedling recruitment in tropical forests is related to seed dispersal and seedling predation (Hubbell 1980, Howe & Smallwood 1982, Augspurger 1984, Clark & Clark 1984). The Janzen-Connell model suggests that recruitment of conspecific individuals increases as a function of distance from parental trees, allowing the establishment of heterospecific seedlings under the canopy of these trees (Janzen 1970, Connell 1971). A prediction of the model is that under the canopy of a given tree species, recruitment of heterospecific seedlings should be higher than recruitment of conspecifics (Hubbell 1980, Condit *et al.* 1992, Burkey 1994, Harms *et al.* 2000). For example, seedlings of 27 species growth under the canopy of *Astrocaryum murumuru* (Palmae) (Simonetti *et al.* 2001).

Besides distance-dependent predation, other mechanisms such as allelopathy can influence the spatial distribution and recruitment of seedlings under canopy trees (Wright 2002). In most cases, the allelopathic agents are chemical compounds found on leaves, flowers or fruits that inhibit the survival or establishment of an adjacent plant (Whittaker & Feeny 1971). However, leaves pruning of neighboring plants by resident ants of mirmecophytic plants could act as a potential biological allelopathic agents by producing the same effect as chemical allelopathic agent, the elimination of competitors for host plant (Janzen 1969).

Triplaris americana (Polygonaceae), a myrmecophytic tree, exhibits a scarce recruitment of both con- and heterospecific seedlings under its canopy, suggesting that it is an unsafe sites for seedling recruitment (Simonetti *et al.* 2001). In general, species richness and seedlings abundance is lower under the canopy of *T. americana* than far away from them. The absence of seedlings under the canopy may be a consequence of chemical and/or biological allelopathic agents that could reduce seed germination and/or seedling establishment (*sensu* Janzen 1969, Whittaker & Feeny 1971). In fact, aqueous extracts of *T. americana* leaves reduce in 16% the growth of wheat (*Triticum aestivum*) roots (Mongelli *et al.* 1997). This suggests that allelochemicals from *T. americana* could inhibit seeds germination of native plants and reduce the presence of seedlings under or close to adult trees. Therefore, if leaves have allelopathic substances, seeds watered with aqueous extracts of *T. americana* leaves should germinate in smaller

proportion than seeds watered with only water.

The scarce seedlings recruitment coincides with the home range of *Pseudomyrmex triplarinus* (Pseudomyrmecinae), the ant species that colonizes the trunks of *T. americana* (Oliveira et al. 1987, Simonetti et al. unpubl. data), which suggests that ants could be responsible for the low recruitment under *T. americana* because they could be pruning seedlings (sensu Davidson et al. 1988).

The defense of host plants by resident ants may act as a biotic allelopathic agent (Janzen 1966, 1969). Resident ants might affect different phases of the life history of plants like seeds and seedling survival. Many ant species gather seeds in order to transport them to their nests (Leal & Oliveira 1998, Farji-Brener & Medina 2000), modifying seedling diversity in understories (Fonseca 1999). Seed transport is infrequent in *Pseudomyrmex* (Hölldobler & Wilson 1990); however, it is necessary to experimentally evaluate whether resident *P. triplarinus* ants remove the seeds that arrive under *T. americana* canopies, there by reducing the establishment of seedlings. If seed removal accounts for the low recruitment under *T. americana* canopies, seed removal by ants should be distance-dependent (Janzen 1970, Connell 1971), with seed survival being lower near *T. americana* trees than far from them.

Pruning the leaves of *T. americana* trees as well as the leaves of the neighboring trees, in order to avoid any contact between canopies precluding the invasion of enemy ants (Oliveira et al. 1987, Davidson et al. 1988). Pruning of leaves could also include the elimination of any plant growing under or the host plant, in order to eliminate substrate of foraging and access routes of enemy ants (Davidson et al. 1988). If this occurs, *P. triplarinus* could reduce the local diversity of seedlings near to *T. americana* trees, influencing the dynamic of seedlings recruitment as a result of their nest defense. Therefore, if seedling pruning by ants accounts for the low recruitment under *T. americana* canopies, it should be distance-dependent (Janzen 1970, Connell 1971). Therefore, seedlings survival would be nil near *T. americana* trees increasing far away from them, coinciding with the pruning activity of resident ants.

Forest fragmentation can modify the intensity of plant-animal interactions (e.g. Aizen & Feinsinger 1994, Murcia 1995, Ledezma 1999, Lorini 2000, Rico 2000); however, it is unknown whether ant-plant interactions, such as the potential biological allelopathy produced by *P. triplarinus*, can be modified by habitat fragmentation. *Triplaris americana* grow either in fragments and continuous forest. In both places, conspecific and heterospecific seedlings recruitment under their canopy trees is low, with a tendency to greater recruitment under the canopy trees that grow on continuous forest (Simonetti et al. 2001). This field observation suggests that allelopathic agents either chemical or biological, can be influenced by habitat fragmentation by increasing their effectiveness in forest fragments compared to continuous forest in order to reduce the seedling growth near adult trees.

In this paper, we experimentally evaluated two factors - chemical and biological allelopathy - that could account for the low recruitment under *T. americana* canopies, rendering it as an unsafe recruitment focus, under two ecological scenarios: fragmented and continuous forest.

STUDY AREA

This study was carried out at the Beni Biological Station Biosphere Reserve (EBB)(Bolivia)(14°30'–14°50'S, 66°00'–66°40'W). This Reserve covers roughly 135,000 ha. Average temperature is 26°C with 1,927 mm of annual average precipitation. Vegetation is a mosaic of different forest types alternating with water bodies and humid savannas. In the savanna occurs forest fragments in different regeneration phases (Simonetti *et al.* 2001). We chose two areas of continuous forest (Campo Mono and Marimonos) and two forest fragments (Mid and Taita A). Continuous forest zones are separated by 8 km. The fragments have smaller surface (< 5 ha) and 1.2 km distant.

METHODS

We used a combination of natural, field and laboratory manipulative experiments. Allelopathic effects of leaves were analyzed by a laboratory experiment, while the potential effect of the resident ant as biological allelopathic agent was evaluated by field experiments. The effect of habitat fragmentation upon allelopathic agents was analyzed through a natural experiment, given that fragments were already present in the study zone (Moraes 2000, Simonetti *et al.* 2001).

Chemical allelopathy

To evaluate the allelopathic effect of *T. americana* leaves upon seed germination rate of heterospecific seedlings, we obtained 450 seed from fifteen fruits of *Theobroma cacao* (Sterculiaceae) that we collected from ten adult trees. We placed the seeds in 90 Petri dishes (5 seeds/Petri dish). Seeds of sixty Petri dishes were watered every two days with 2 cc of an aqueous extract elaborated with fresh leaves of *T. americana*. To prepare the extract, crushed leaves were soaked in water during 48 hrs at 6°C (Mongelli *et al.* 1997). Seeds of the remaining 30 Petri dishes acted as control and they were watered with 2 cc of water. To evaluate whether fragmentation influenced the allelopathic effect of *T. americana* leaves on seed germination rates, we obtained extracts from leaves of trees growing in continuous forest, as well as from leaves of trees from forest fragments. Of the 60 Petri dishes, 30 were watered with solutions from the continuous forest and 30 with the extract from forest fragments.

We evaluated seed germination rate every two days recording the number of seeds germinated by each Petri dish. A seed was germinated if it exhibited an emerged radicle at least 2 mm long. Differences in germination rate were evaluated through a Multivariate Analysis of Variance (MANOVA). We used MANOVA test instead of repeated-measures analysis of variance because its use is recommendable when $N - M > k + 9$, where N is

number of subjects observed, M is number of levels from factor design, and k is number of time observations is true (Scheiner 1993, von Ende 1993).

Biological allelopathy: Seed removal

We evaluated seed removal rate near and far from *T. americana* trees to determine whether defensive activities of resident ants could act as biotic allelopathic agent reducing seed survival under their canopy. In each area (two sites of continuous forest and two forest fragments) we selected 10 *T. americana* trees and 10 trees of another species, located 15 to 20 m from the focal *T. americana* tree. Under the canopy of each tree, we set exclusion types for: a) vertebrates, b) ants, and c) vertebrates & ants, and a control site. On each of them, we deposited 10 seeds of *T. cacao*.

Exclusions for vertebrates were circular with approximately 35 cm of diameter and 30 to 35 cm height, built with galvanized wire mesh with hexagonal openings of $\frac{3}{4}$ inches. Exclusions for walking ants were built with sticky traps. Combined exclusions for vertebrates & ants were built with a sticky trap, which was covered with the galvanized wire mesh. We evaluated seed removal daily during one week. Differences in seed removal rates as a function of the distance to *T. americana* tree, exclusion type, and habitat fragmentation were evaluated through a Multivariate Analysis of Variance of 3-way (MANOVA)(Scheiner 1993, von Ende 1993) and Newman-Keuls *a posteriori* test. Due to low replicates number for evaluate effect of habitat fragmentation (n=2) we considered the *T. americana* trees as independent samples; therefore, pseudoreplication is included in the results interpretation (Hurlbert 1984).

Biological allelopathy: Seedling survival

We evaluated the pruning rate of seedling leaves and seedling survival growing under and far from to *T. americana* trees to determine whether the defensive activities of resident ants could act as a biotic allelopathic agent, reducing seedlings survival under the canopy of it host plant. We prepared three exclusion types: a) exclusions for vertebrates, b) ants, and c) vertebrates & ants, and a control site in the same trees we selected to evaluate seed removal. Each exclusion comprised by two *T. cacao* nursery-grown seedlings with 15 to 20 cm height, and 3 to 5 leaves (a month old, approximately).

Exclusions for vertebrates had circular form with 35 cm of diameter approximately, with 30 to 35 cm of height and were build with a galvanized wire mesh with hexagonal opening of $\frac{3}{4}$ inches. These exclusions allowed to reduce the potential effect of vertebrate folivores. Exclusions for ants consisted of putting around the seedling stem a 3 x 3 cm piece of pressed cardboard, covered with a thick larger of a sticky trap in order to minimize insect arrival to seedlings leaves. These exclusions attempted to minimized the potential effect of folivore ants. Combined exclusions for vertebrates & ants were build covering seedlings that had an ant enclosure with the galvanized wire mesh. These exclusions simultaneously minimized the potential effect of vertebrate and folivore ants. We counted every day the number of leaves pruned and the number of surviving seedling during a seven day period. We registered the number of pruned leaves over the number of

total leaves considering as pruned leaves those who were separated from the main stem through a cut in the petiole.

Differences in pruning rates as a function of distance to *T. americana* tree, exclusion type, and habitat fragmentation were evaluated through a Multivariate Analysis of Variance of 3-way (MANOVA)(Scheiner 1993, von Ende 1993) and Newman-Keuls a *posteriori* test. Due to low repliques number for evaluate effect of habitat fragmentation (n=2) we considered the *T. americana* trees as independent samples; therefore, pseudoreplication is included in the results interpretation (Hurlbert 1984). Differences in seedling survival as a function of habitat type (continuous forest & fragments), and *T. americana* trees distance (near & far) was evaluated through a Kaplan-Meier survival analysis test.

RESULTS

Chemical allelopathy

Aqueous extract of *T. americana* leaves did not inhibit the germination of *T. cacao* seeds (Wilk's Lambda=0.91; d.f.=10, 166; P=0.68). A 98% of the seeds watered with aqueous extracts of *T. americana* leaves (either from continuous forest: 4.9 ± 0.3 seed/Petri dish out of 5 (mean \pm SE) or forest fragments: 4.9 ± 0.3) germinated after 10 days (Fig. 1), while a 99.3% of the seeds watered with plain water germinated to the tenth day of experimentation (4.9 ± 0.2)(Fig. 1).

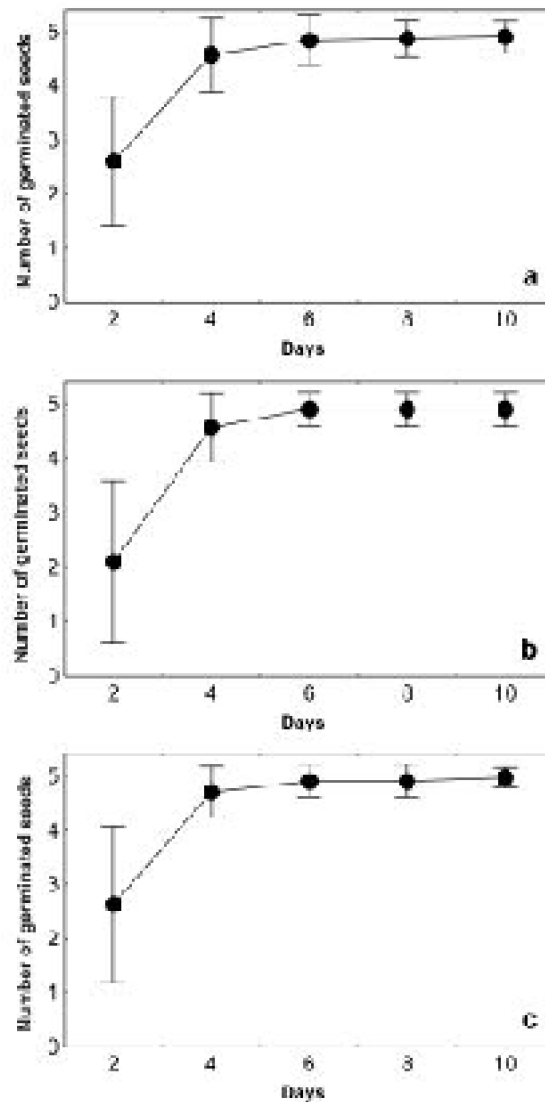


Fig. 1. Chemical allelopathy of *Triplaris americana* (Polygonaceae). Germination of *Theobroma cacao* (Sterculiaceae) seeds watered with aqueous extracts of *T. americana* leaves from trees growing in a) Continuous Forest, b) Fragments, and c) Controls (watered with plain water)(mean \pm SE).

Biological allelopathy: Seed removal

Overall, seed removal was independent of the distance to a *T. americana* tree (Table 1). After seven days, the number of seeds removed close to *T. americana* trees (3.6 ± 0.3)(mean \pm SE, n=160) does not differ from the number seeds removed far away from *T. americana* (3.5 ± 0.3)(Table 1, Fig. 2).

Seed removal was dependent on the consumer type (Table 1). After seven days, the number of seeds removed was significantly greater in control sites (4.7 ± 0.5)(mean \pm SE, n=80) and exclusions for vertebrates (4.5 ± 0.5), that on exclusions for insects (2.9 ± 0.4),

and combined exclusions (2.2 ± 0.4) (Newman-Keuls $P < 0.0001$), strongly suggesting that the main consumers were ants. In fact, we observed individuals of *Atta sexdens* (Myrmicinae) transporting complete or partially destroyed *T. cacao* seeds. We captured individuals of *A. sexdens* in the sticky trap of 47.5% of exclusions for insects (38/80 sticky traps), and 35% of the combined exclusions (28/80 sticky traps). No single individual of *Pseudomyrmex* was recorded removing seeds in any exclusions (0/80 sticky traps).

Table 1. Multivariate Analysis of Variance (MANOVA) evaluating the relationship between the number of seed removed with *Triplaris americana* distance, exclusion type and habitat fragmentation.

Effects	Wilks' Lambda	d.f. 1	d.f. 2	P
Distance	0.983	7	298	0.63
Exclusion	0.857	21	856	0.001
Fragmentation	0.819	7	298	<0.001
Distance*Exclusion	0.918	21	856	0.21
Distance*Fragmentation	0.955	7	298	0.06
Exclusion*Fragmentation	0.924	21	856	0.31
Distance*Exclusion*Fragmentation	0.960	21	856	0.94

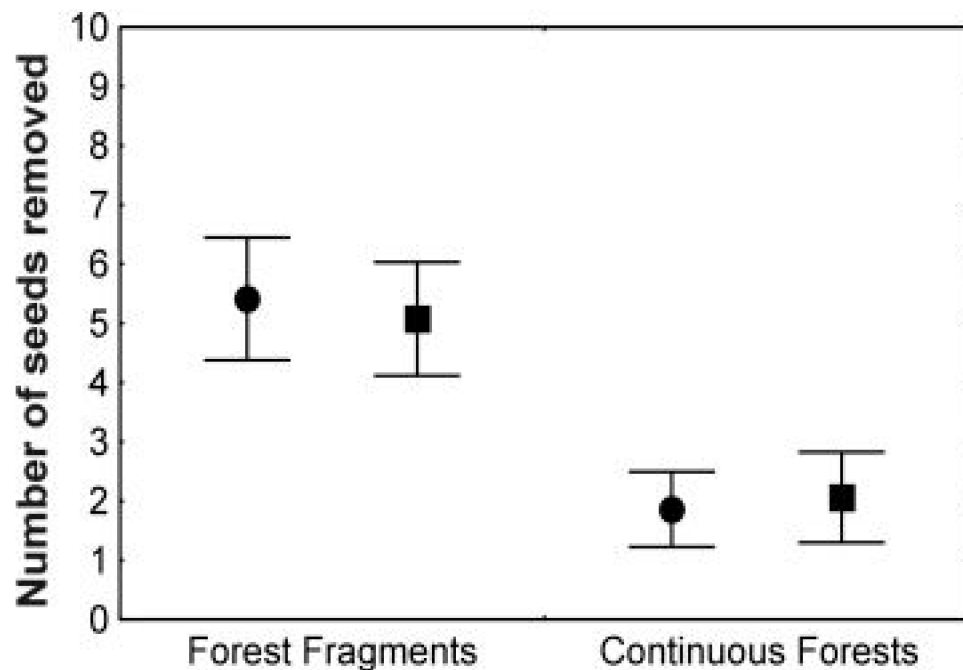


Figure 2. Seed removal under Triplaris americana (Polygonaceae). Removal of Theobroma cacao (Sterculiaceae) seeds near (n) and far (g) of T. americana trees that grow in a habitat fragmented (mean ± SE).

After seven days, the number of seeds removed was significantly higher in forest fragments (5.1 ± 0.4) (mean ± SE, $n = 160$) than in continuous forest (1.9 ± 0.3) (Table 1), regardless of exclusion type (Newman-Keuls $P \leq 0.002$). In forest fragments, the number of seeds removed in control sites and exclusions for vertebrates, insects, and combined

exclusions was in 1.9, 2.0, 4.5 and 6.1 times bigger than the number of seeds removed in continuous forest, respectively (Fig. 3). In fragments, we captured individuals of *A. sexdens* in 62.5% of exclusions for insects (25/40 sticky traps), and 47.5% to combined exclusions (19/40 sticky traps), while in the continuous forest we registered *A. sexdens* only in 32.5% of exclusions for insects (13/40 sticky traps), and 22.5% of combined exclusions (9/40 sticky traps). In no case, we registered *Pseudomyrmex* individuals.

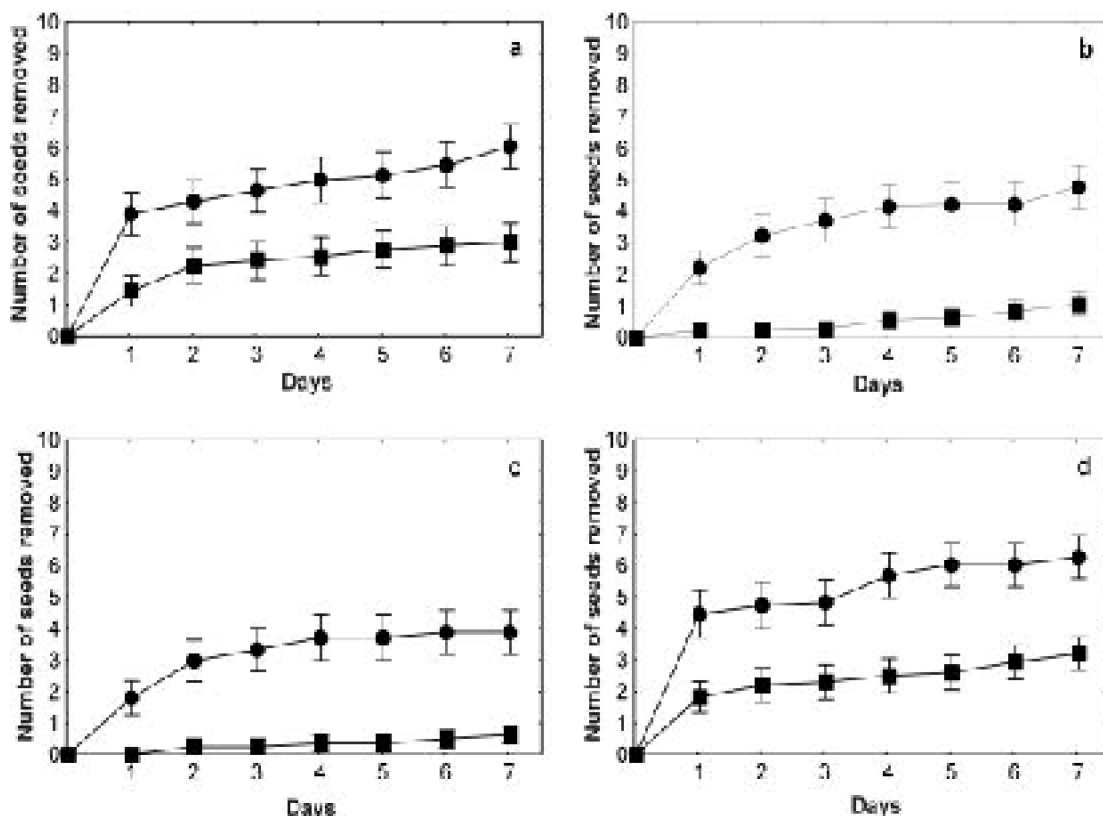


Fig. 3. Intensity of seed removal under *Triplaris americana* (Polygonaceae) canopies. Removal of *Theobroma cacao* (Sterculiaceae) seed by a) ants, b) vertebrates, c) without granivores, and d) vertebrates and ants (nFragments, gContinuous Forest)(mean \pm SE).

Biological allelopathy: Seedling survival

Pruning of leaves was dependent on the distance of *T. americana* tree. After seven days, the proportion of pruned leaves was significantly larger near to *T. americana* trees (41.2 ± 3.8)(mean (%) \pm SE, $n=152$) than far from them (9.8 ± 2.0)(Fig. 4, Table 2).

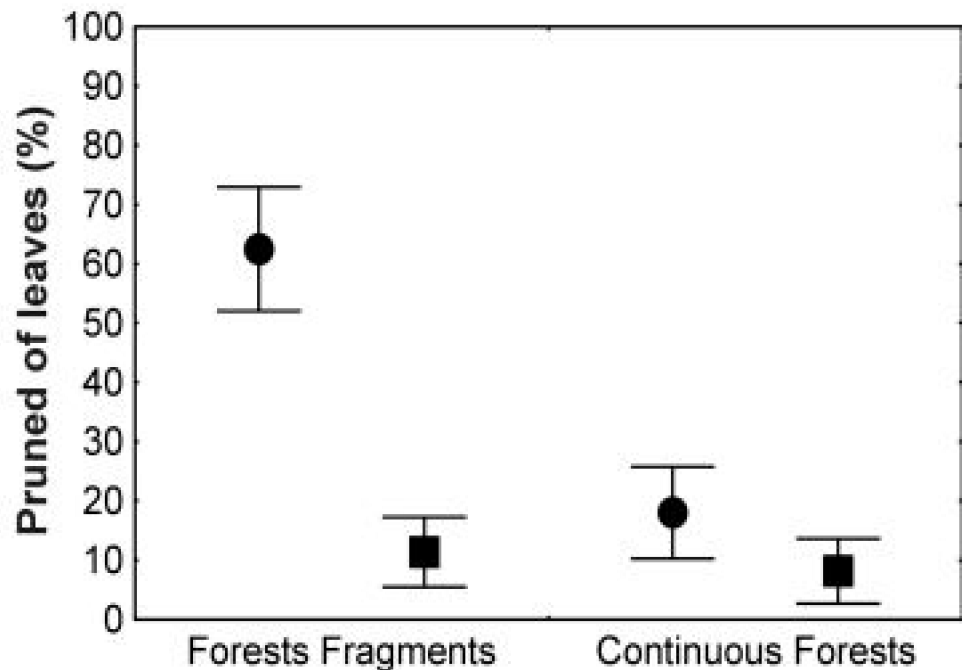


Figure 4. Leaves pruned under *Triplaris americana* (Polygonaceae). Pruned of *Theobroma cacao* (Sterculiaceae) leaves near (n) and far (g) of *T. americana* trees that grow in a habitat fragmented (mean \pm SE).

Table 2. Multivariate Analysis of Variance (MANOVA) evaluating the relationship between the proportion of leaves pruned with *Triplaris americana* distance, exclusion type and habitat fragmentation.

Effects	Wilks'Lambda	g.l. 1	g.l. 2	P
Distance	0.825	7	282	<0.001
Exclusion	0.913	21	810	0.23
Fragmentation	0.793	7	282	<0.001
Distance*Exclusion	0.929	21	810	0.46
Distance*Fragmentation	0.846	7	282	<0.001
Exclusion*Fragmentation	0.925	21	810	0.39
Distance*Exclusion*Fragmentation	0.947	21	810	0.80

Under the canopy of *T. americana* trees, 74 of 152 seedlings presented pruned leaves (48.7%). All leaves were pruned by *P. triplarinus* who cut seedlings leaves at the petiole base (27.1%). However, in most cases the ants cut the seedlings stem, provoking all leaves falling (72.9%)(Fig. 5). The number of ants that we observed patrolling the leaves or fallen seedlings varied from 1 to 7 individuals (3.9 ± 0.4)(mean \pm SE, n=20). Ants did not use leaves pruned to any purpose. However, ants patrolled the leaves or fallen seedlings by 3 to 4 hours (23.6% of total cases). Far of *T. americana* trees, 25 of 152 seedlings presented pruned leaves (16.4%). Leaves were cut by *A. sexdens* who cut leaves on the petiole base (71.9%), and pruning all the leaves of a seedling was not very frequent (28.1%).

Pruning of the seedling leaves was independent of exclusion type (Table 2). After seven days, the proportion of leaves pruned in the control sites (30.1 ± 4.9) (mean (%) \pm SE, $n=76$) did not differ of the exclusions for vertebrates (27.1 ± 4.8), insects (22.7 ± 4.3), and combined exclusions (22.7 ± 4.5). This fact is due a reduced effectiveness of the sticky trap. Exclusion for insects and combined exclusions were unable to preclude the arrival of ants to the seedling. Near *T. americana* trees, we recorded *P. triplarinus* in 44.7% of exclusions for insects (17/38 sticky traps), and 42.1% of combined exclusions (16/38 sticky traps).

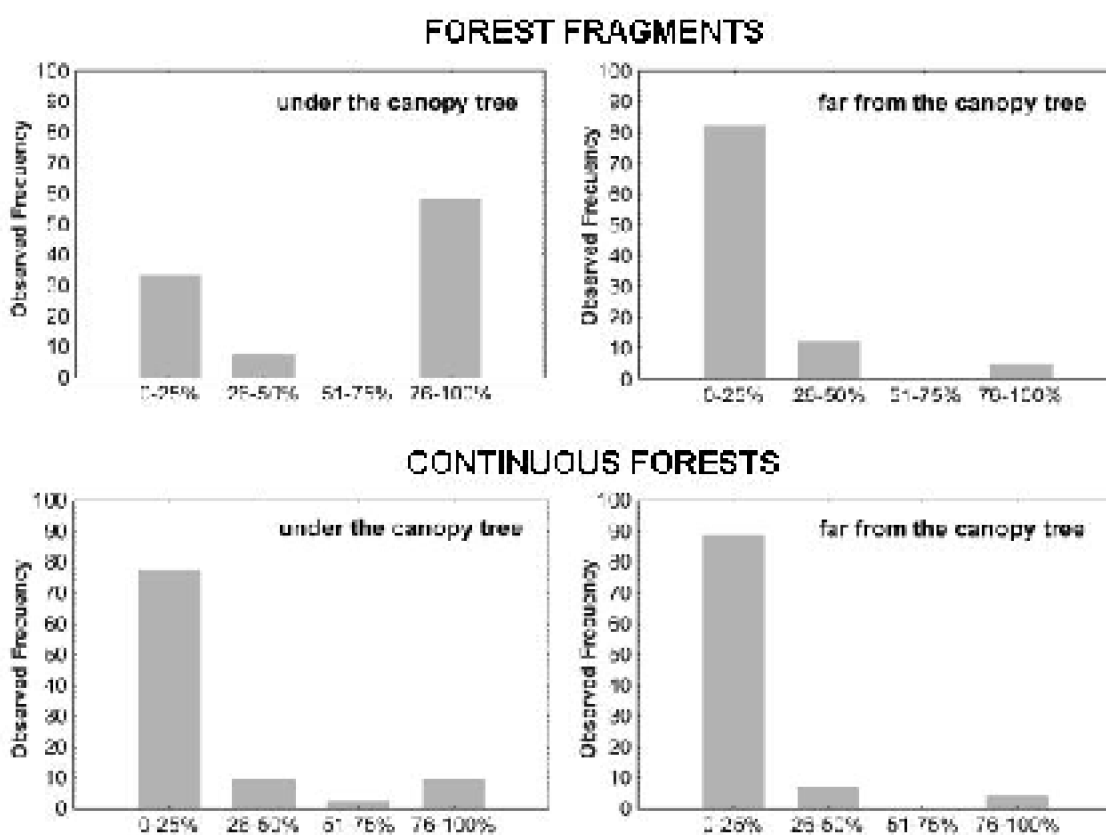


Fig. 5. Frequency distribution of pruned leaves under the canopy of Triplaris americana (Polygonaceae) trees.

Pruning of leaves was also dependent on habitat fragmentation (Table 2). After seven days, the proportion of leaves pruned was significantly higher in forest fragments (36.9 ± 3.6) (mean (%) \pm EE, $n=160$) that on continuous forest (13.1 ± 2.4 , $n=144$). Likewise, in forest fragments the proportion of leaves pruned was significantly greater close to *T. americana* trees (62.5 ± 5.2 , $n=80$) than far from them (11.4 ± 2.9) (Newman-Keuls

$P < 0.0001$) (Fig. 6a), while on continuous forest we did not find differences in the proportion of leaves pruned as near (18 ± 3.9 , $n=72$) as far from *T. americana* trees (8.2 ± 2.7) ($P=0.22$) (Fig. 6b). The significant interaction among distance and fragmentation is accounted for by the low pruning intensity in the continuous forest and its independence of distance (Table 2).

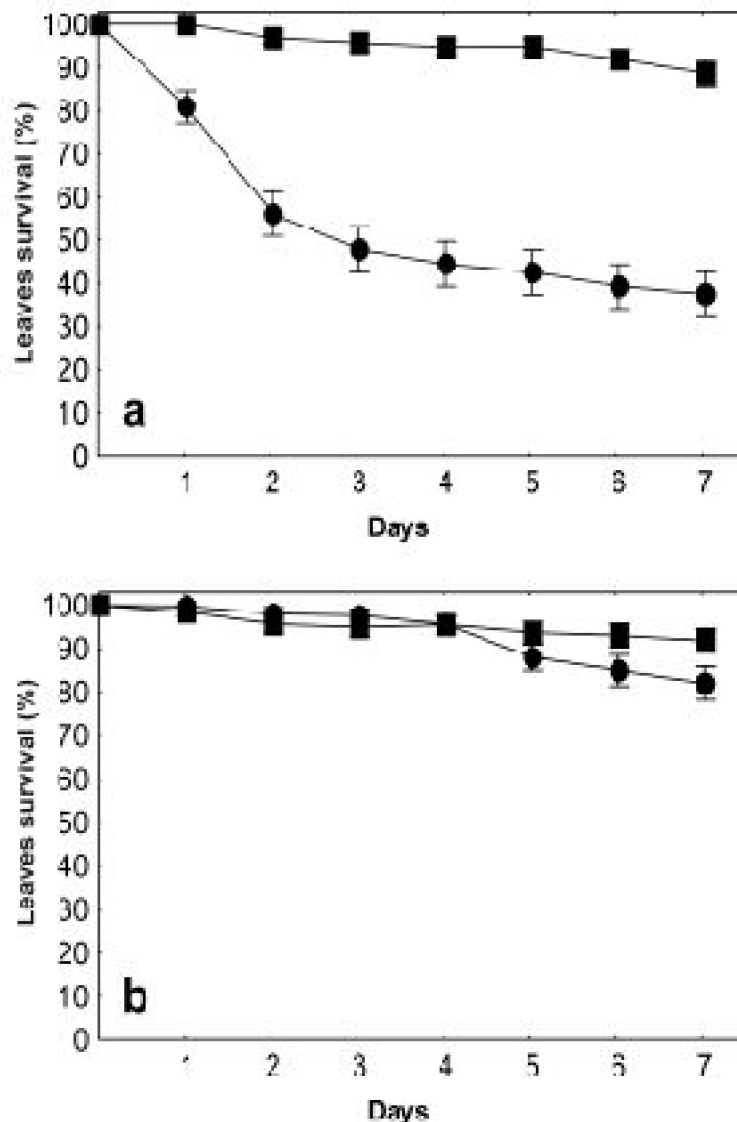


Fig. 6. Pruning of leaves under Triplaris americana (Polygonaceae) trees growing in fragments and continuous forests. Cut leaves of Theobroma cacao (Sterculiaceae) seedlings in function of time, habitat (a: Fragments, b: Continuous Forest), and T. americana trees distance (nNear, gFar)(mean \pm SE).

In forest fragments, the proportion of leaves pruned near and far from *T. americana* trees, was 3.5 and 1.4 times larger the pruning of leaves in continuous forests. Close to *T. americana* trees that grew in fragments, we recorded *P. triplarinus* in 60% of exclusions for insects (12/20 sticky traps), and 65% of combined exclusions (13/20 sticky traps). While near to *T. americana* trees that grew in continuous forest, we registered *P. triplarinus* in 27.8% to exclusions for insects (5/18 sticky traps), and 16.7% of the

combined exclusions (3/18 sticky traps).

Overall, survival of *T. cacao* seedlings was significantly higher in the continuous forest (93.7%) than in forest fragments (68.1%)($Z=-7.443$; $P<0.0001$). Seedling survival on fragments was significantly larger farther from *T. americana* (95%) than near them (41.3%)($Z=-9.674$, $P<0.0001$), while on continuous forest zones we did not find an effect of *T. americana* trees distance over seedlings survival ($Z=-1.162$, $P=0.091$).

DISCUSSION

Density- or distance-dependent response of species-specific seeds and seedling predators and pathogens can reduce the recruitment of conspecific individuals near parental trees (Janzen 1970, Connell 1971, Clark & Clark 1984), allowing establishment of heterospecific seedlings (Hubbell 1980, Condit *et al.* 1992, Harms *et al.* 2000). These seedlings are the replacement individuals of the established trees, increasing local diversity (Wright 2002). However, seedling survival near mature trees could be related to other mechanisms such as chemical (Wright 2002) and biological allelopathy (Janzen 1969).

Tree recruitment under the canopies of *T. americana* is lower than under the canopies of other trees. This reduced recruitment includes both conspecific and heterospecific individuals. Aqueous extracts of *T. americana* leaves did not inhibit seed germination of *T. cacao* a tree that occurs in the same forests, strongly suggesting that the reduced recruitment is not accounted for by chemical allelopathic agents.

Furthermore, the lack of inhibitory effects of *T. americana* leaf extracts germination does not support the claimed role that allelopathy could have upon tropical forest diversity (Mongelli *et al.* 1997). The assertion that chemical allelopathy is a factor enhancing forest diversity is based on the inhibitory effects of aqueous extracts of several tree species upon germination and growth of domesticated plants (e.g. Mongelli *et al.* 1997), an inadequate surrogate for native species, as cultivars and native species often react differently to potential allelochemicals (see Anexo).

The scarce recruitment under *T. americana* canopies could be an epiphenomenon of the defensive activities of *P. triplarinus*. Ant attempts to preclude the invasion of the host tree by other ant species thus reducing the access routes for competing ants. This is achieved by cutting leaves and twigs of the canopies of neighboring trees that reach and overlap *T. americana* canopies (Davidson *et al.* 1988, Heil *et al.* 2001, Federle *et al.* 2002). Similarly, as shown here, ants also could be either avoiding the establishment of vegetation under the canopies either by preying upon seeds or pruning seedlings.

Pseudomyrmex triplarinus did not affected the survival of *T. cacao* seeds, probably due to high nutritious dependence on their host plant (Davidson *et al.* 1988, Höllböbler & Wilson 1990). Therefore, seed removal by resident ants was not the mechanism that explains the scarce seedlings recruitment that characterizes *T. americana* trees. Nevertheless, due to the high aggressiveness of *P. triplarinus* and its stingent venom

(Hink *et al.* 1994), they probably influence on the arrival of zoocorial seeds by precluding the presence of animals under its canopies. The reduced branch growth of *T. americana* trees will benefit *P. triplarinus* defense activities reducing the arrival of medium and large size animals, or frugivorous birds perching (pers. obs.). Hence, seed arrival near *T. americana* will depend mainly on the neighbouring tree species (i.e. direct fall of seeds).

In contrast, the presence of seedlings close to host plant originated the defensive response of resident ants that partially or totally pruned seedlings growing under its canopies. Pruning diminishes seedlings survival near *T. americana* trees, suggesting that defensive activities of *P. triplarinus* are an effective allelopathic agent against establishment of seedlings close to the host plant, rendering *T. americana* trees as an unsafe site for seedling recruitment. Furthermore, the indifference of *P. triplarinus* to the presence of seeds, suggests that the area under the canopy of *T. americana* trees could originate a seed-seedling conflict (Schupp 1995, Jordano & Herrera 1995, Rey & Alcántara 2000), because seeds arrive in a safe place as others, but it becomes unsafe when seedlings emerge. Seed survival under the canopy of these trees would not assure the survival of future seedlings. Once the seedlings emerge will be pruned by resident ants reducing the diversity of seedlings in the understory.

The elimination of seedlings by resident ants could act over include the conspecific seedlings. The absence conspecific seedlings suggests that the allelopathic activity of *P. triplarinus* could affect the population recruitment of *T. americana*, originating areas that could not be occupied by any seedling species, including its own. The *T. americana* trees reflect that biological allelopathy is a process that can increase the distance-dependent predation effect, modifying the dynamics of seedlings recruitment in the forest, as an extreme case of Janzen-Connell model.

Habitat fragmentation increased the biotic allelopathic effects. Pruning of leaves was more intense under *T. americana* trees that grow in forest fragments that under conspecific trees that grow in continuous forests. Therefore, the character of unsafe site of *T. americana* trees could increase when this tree establish in forest fragments, affecting the dynamics of seedling recruitment in these habitats. The defensive activities of *P. triplarinus* could be enhanced in fragments due to the quick growth of seedlings in fragments. A significant fraction of those seedlings are shade-intolerant tree species (Simonetti *et al.* 2001), which might represent a more threatening scenario for resident ants as these seedlings of fast growth offer more opportunities to competing ants to invade host trees. Trees that grow in fragments could also house colonies more numerous than trees that grow in continuous forest. However, more precised measures are necessary to evaluate how colony defense by resident ants (e.g. biological allelopathy) is affected by habitat fragmentation.

Regardless of the precise mechanisms that increase ants activities in forest fragments, our results suggests that a defense mechanisms of an ant colony can strongly impinge upon forest dynamics. Cutting vegetation under tree canopies in order to avoid the arrival of competing ants, *P. triplarinus* is modifying the diversity and abundance of recruitmig trees as well as its spatial pattern of recruitment.

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ANEXO. ALELOPATÍA: ¿SON LAS ESPECIES EXÓTICAS BUENAS PREDICTORAS DE LA RESPUESTA DE LAS ESPECIES NATIVAS?

La alelopatía es una interacción planta-planta donde una de ellas inhibe químicamente el crecimiento de la otra. La mayoría de los agentes alelopáticos, tales como los ácidos felúrico y p-cumárico, se encuentran en las hojas y actúan luego de la abscisión foliar incrementando sus concentraciones en el suelo, inhibiendo la germinación de semillas y el crecimiento de las plántulas con- o heteroespecíficas (Whittaker & Feeny 1967). Usualmente, los estudios sobre alelopatía utilizan como sujeto de estudio especies exóticas, como el poroto *Phaseolus vulgaris* (Fabaceae) y el trigo *Triticum aestivum* (Poaceae), que se caracterizan por su rápida germinación y elevadas tasas de crecimiento, lo cual permite una rápida evaluación del posible efecto alelopático de las hojas de otras especies. El uso de especies exóticas supone que la respuesta de estas especies a los agentes alelopáticos es similar a la respuesta que tendrían las especies nativas a los mismos agentes alelopáticos. Sin embargo, este supuesto no ha sido contrastado empíricamente. Por ejemplo, Mongelli et al. (1997) evaluaron experimentalmente el efecto alelopático de extractos acuosos de sesenta especies de árboles tropicales y templados en el crecimiento de las raíces de trigo (*T. aestivum*). Entre

otras, extractos acuosos preparados con hojas de *Triplaris americana* (Polygonaceae) inhiben en un 16% el crecimiento de las raíces de trigo (*T. aestivum*), lo cual sugiere un potencial efecto alelopático de esta especie sobre el reclutamiento de plántulas. En efecto, los árboles de *T. americana* se caracterizan por presentar un escaso reclutamiento de plántulas bajo su dosel (Simonetti et al. 2001), lo cual podría ocurrir por la existencia de agentes alelopáticos que reducirían la germinación de semillas y el establecimiento de plántulas. Por lo tanto, basado en la inhibición del crecimiento del trigo (*T. aestivum*), se esperaría que las plantas nativas fuesen igualmente inhibidas por *T. americana*, lo cual explicaría el patrón de reclutamiento observado. De esta forma, si las hojas de *T. americana* poseen un efecto alelopático, extractos acuosos preparados de sus hojas deberían inhibir la germinación de semillas independientemente de si éstas se tratan de especies exóticas o de especies nativas. De ser así, la respuesta de las especies exóticas podría ser considerada como buena “predictora” de la respuesta de las especies nativas, y por tanto podrían usarse como sujetos sustitutos en evaluaciones de alelopatía. Para evaluar empíricamente este supuesto, estudié experimentalmente los efectos alelopáticos de las hojas de *T. americana* sobre la germinación de semillas de una especie nativa, el cacao (*Theobroma cacao*; Sterculiaceae), y una especie exótica, el poroto (*P. vulgaris*; Fabaceae).

Para ello, preparé 120 placas Petri con cinco semillas en cada una de ellas. La mitad de las placas (60) contenían semillas de cacao y la otra mitad, semillas de poroto. Las semillas de 30 placas por especie fueron regadas diariamente con 2 cm³ de un extracto acuoso preparado con hojas de *T. americana*. El resto de las semillas sirvieron como control y fueron regadas diariamente con 2 cm³ de agua. El extracto acuoso fue preparado triturando las hojas en un utensilio local análogo a un mortero (“tacú”) y almacenando los restos foliares en agua durante 48 hrs a 6°C (Mongelli et al. 1997). El experimento se llevó a cabo en el Laboratorio del Centro de Operaciones “El Porvenir” de la Reserva de la Biósfera Estación Biológica del Beni (Bolivia).

Como variable de respuesta, evalué la tasa de germinación de las semillas cada dos días, considerando el número de semillas germinadas por placa Petri en un período de diez días. Para evaluar la relación entre el número de semillas germinadas con el tipo de riego (agua o extracto acuoso) y el tiempo de germinación, utilicé un Análisis de Varianza Multivariado (MANOVA) con pruebas *a posteriori* Newman-Keuls (Zar 1998).

El extracto acuoso preparado con las hojas de *T. americana* no inhibió la germinación de las semillas de *L. ...*

T. cacao. Al décimo día de experimentación, un 98% de las semillas del tratamiento (regadas con extracto acuoso de las hojas) y del control (regadas solamente con agua) germinaron (Wilk's Lambda=0,918; g.l.=5, 54; P=0,45)(Fig. 1a). Sin embargo, los extractos acuosos inhibieron en un 43% la germinación de las semillas de *P. vulgaris*. Al décimo día, un 21% de las semillas que fueron regadas con agua germinaron, mientras que sólo el 12% de las semillas que fueron regadas con el extracto acuoso lo hicieron (Wilk's Lambda=0,756; g.l.=5, 54; P=0,008)(Fig. 1b). El efecto del extracto fue acumulativo en función del tiempo. Hasta el segundo día de experimentación, no hubo un efecto del extracto acuoso en la germinación de las semillas de *P. vulgaris* (Newman-Keuls P>0,05); sin embargo, a partir del cuarto día el número de semillas que

germinaron en los controles fue significativamente mayor a la germinación de las semillas del tratamiento (P£0,03).

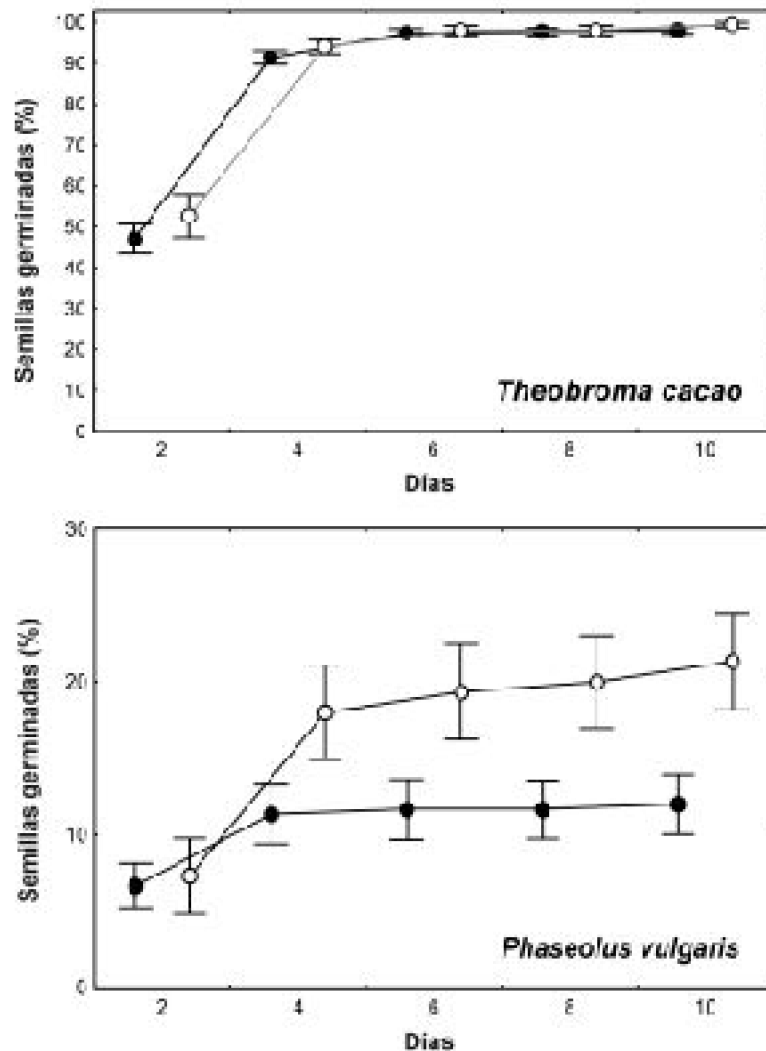


Figura 1. Alelopatía por *Triplaris americana* (Polygonaceae). Porcentaje de germinación de semillas de *Theobroma cacao* (Sterculiaceae)(a) y *Phaseolus vulgaris* (Fabaceae)(b) regadas con extractos acuosos de hojas de *Triplaris americana* (Polygonaceae)(n). Los controles fueron semillas regadas con solamente agua (j)(media \pm 1 EE).

La respuesta diferencial de ambas especies a los efectos del extracto acuoso demuestra que la germinación de las semillas de *P. vulgaris*, una planta exótica comúnmente usada en ensayos de alelopatía, no puede ser considerada como una buena “predictora” de la respuesta de las semillas de plantas nativas, como *T. cacao*. Por tanto, el valor heurístico de las especies exóticas puede ser limitado, por lo que su uso en ensayos de alelopatía para inferir efectos sobre especies nativas, debe ser considerado con cautela.

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DISCUSIÓN GENERAL

En los sistemas de plantas mirmecofíticas, la alta dependencia de la planta por la hormiga residente, origina que el ámbito de hogar de éstas hormigas se reduzca a algunos metros alrededor del tronco de la planta huésped (Hölldobler & Wilson 1990). Evidencia empírica sugiere que estas hormigas no buscan alimento lejos de la planta, debido a que ellas les proporcionan alimento y domicilio que asegura su permanencia en el tronco de la planta que los alberga (Heil *et al.* 2001). Por esta razón, el transporte o acarreo de semillas es una actividad poco frecuente en estas hormigas asociadas a plantas mirmecofíticas, debido a que las hormigas no tendrían la necesidad de buscar alimento fuera de la planta que los alberga. Ello sugiere fuertemente que la mantención de un claro basal alrededor de la planta huésped (e.g. eliminación de sustratos de forrajeo de hormigas enemigas) no incluye la remoción o destrucción de semillas que llegan bajo la copa de éstos árboles.

La presencia de plántulas cerca de la planta huésped, es decir, al interior del ámbito de hogar de la hormiga residente, desata la respuesta de la hormiga en defensa de su colonia, eliminando la potencial amenaza que ha detectado (Davidson *et al.* 1988, Federle *et al.* 2002). Esta diferencia en la respuesta de la hormiga frente a la presencia de semillas o plántulas define a los árboles de los sistemas mirmecofíticos como potenciales zonas de desacoplamiento semilla-plántula (Schupp 1995, Jordano & Herrera 1995), debido a que independientemente de los mecanismos por los cuales las semillas llegan bajo la copa de éstos árboles, una vez que las plántulas emergen su probabilidad de sobrevivencia es reducida.

Las actividades defensivas de las hormigas residentes estarían modificando la

dinámica del reclutamiento de plántulas en los bosques tropicales, principalmente al reducir la sobrevivencia de plántulas con- y heteroespecíficas que se establecen cerca de la planta huésped. Es decir, la defensa de la colonia por parte de la hormiga residente incrementaría la depredación distancia-dependiente cerca de la fuente de propágulos, donde ninguna especie de plántula, incluyendo las conespecíficas, encontrarían condiciones adecuadas para su sobrevivencia. Por ello, la dinámica de la interacción entre la colonia de hormiga residentes y sus hormigas enemigas podría influir en la diversidad local que se presenta en los bosques tropicales.

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