Agricultural and Forest Entomology

Agricultural and Forest Entomology (2011), **13**, 191–196 DOI: 10.1111/j.1461-9563.2010.00515.x

Potential impact of the leaf-cutting ant *Acromyrmex lobicornis* on conifer plantations in northern Patagonia, Argentina

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Abstract

1 The economic losses associated with crop damage by invasive pests can be minimized by recognizing their potential impact before they spread into new areas or crops.

2 We experimentally evaluated the preferences of the leaf-cutting ant *Acromyrmex lobicornis* (Hymenoptera: Formicidae) for the most common conifer species commercially planted in northern Patagonia, Argentina. The areas of potential forest interest in this region and the geographical range of this ant overlap. We performed field preference tests and monitored the level of ant herbivory on planted conifer seedlings next to nests.

3 *Acromyrmex lobicornis* preferred some conifer species and avoided foraging on others. *Pseudotsuga menziesii* and *Austrocedrus chilensis* were the less preferred species, *Pinus ponderosa* and *Pinus contorta* were the most preferred by *A. lobicornis*.

4 The item mostly selected by ants was young needles from *P. contorta*. This species was also the pine mostly defoliated. Seedlings without ant-exclusion showed a mean ± SE of 60 ± 5% defoliation during the sampling period. *Pinus ponderosa* was less defoliated; control seedlings showed a mean ± SE of 8.5 ± 1% of leaf damage in the sampling period.

5 The present study shows how the use of simple field tests of leaf-cutting ant preferences could allow an improved selection of appropriate conifer species for future plantations in areas where leaf-cutting ants are present.

Keywords Ants, foraging preferences, forest pests, forestry, *Pinus* spp.

Introduction

Forest insects are an important factor limiting forestry production. Insects can affect tree growth and survival through defoliation or by damaging important tissues. Specific studies on pest ecology and control methods are usually carried out once the pest is recognized as such. Yet, the economic costs related to tree damage and pest management efforts can be reduced by evaluating the impact of such potential pests (i.e. before these reach outbreak or economic injury levels or before they establish in new areas or crops). In the present study, we experimentally evaluated the potential impact of the leaf-cutting ant *Acromyrmex lobicornis* (Hymenoptera: Formicidae) on conifer plantations in north-west Patagonia.

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Leaf-cutting ants *Atta* and *Acromyrmex* spp are amongst the most important forest pests in South America and a limiting factor for softwood forestry (Cherrett, 1986, 1989; Fowler *et al*., 1986). These ants have been reported to defoliate between 14% and 50% of conifer seedlings in plantations in Brazil and Venezuela (Jaffé, 1986; Vilela, 1986; Antunes & Della, Lucia, 1999; Da Silva Araújo *et al*., 2002; Cantarelli *et al*., 2008). Leafcutter damage to young trees (<6 months) can cause reductions of 32% in height, 25% in girth and up to a 60% loss in wood production (Della Lucia, 1993). Accordingly, leaf-cutting ant control methods may involve up to 5% of total planting costs and encompass 75% of the costs of overall pest management efforts (Jaffé, 1986; Vilela, 1986). Because not all conifer species and not all types of leaves of these species are equally susceptible to ants (Barnola *et al*., 1994), recognizing which tree species are more likely to be affected by them is central to forestry planning.

Softwood forestry is an increasing activity in many developing countries. In Patagonia, a region located in the South of Argentina, the area planted with conifers, mostly North American species, is steadily increasing and currently covers almost 68 000 ha. Forestry development in dry areas is strongly encouraged by government agencies because they could provide a substantial improvement to the local and regional economies and may also allow better options for arid environments compared with current activities such as sheep farming (Schlichter & Laclau, 1998). The species mostly planted in the drier areas are *Pinus contorta* (var. latifolia) and *Pinus ponderosa*, whereas, towards the west, and in wetter sites, *Pseudotsuga menziesii* grows (Loguercio & Deccechis, 2006). The areas with potential forest interest overlap with the expanding geographical range of *Acromyrmex lobicornis*, the only leaf-cutting ant species that is found in Patagonia (Farji-Brener & Ruggiero, 1994; Farji-Brener & Corley, 1998).

Several characteristics suggest that this leaf-cutting ant species could become an important pest of pine plantations in Patagonia. First, *A. lobicornis* is known to be major pest of agriculture and forestry in other regions of Argentina (Bonetto, 1959; Pilati *et al*., 1997; De Coll, 2003). Their defoliation rates are in the range 2.5–8.5 kg/colony/year, and are higher than in other *Acromyrmex* species (Pilati *et al*., 1997). Second, the area with highest nest density in north-west Patagonia (up to 54 nest/ha) is close to existing and probable future forest plantations (Schlichter & Laclau, 1998; Farji-Brener, 2000). Finally, as has been shown for other regions of Argentina, *A. lobicornis* shows an increase in nest density and a change in foraging habits at sites where naturally-occurring vegetation is replaced by conifer plantations (De Coll, 2003). Thus, it is important to study the capacity of this pestiferous ant species to affect conifer forestry in Patagonia. This information can help recommend forestry practices and select those tree species that are likely to be less affected by ants. The aim of the present study was to assess the potential impact of the leaf-cutting ant *A. lobicornis* on conifer plantations in north-west Patagonia. Accordingly, we determed experimentally the preferences of *A. lobicornis* for different conifer species and needle ages.

Materials and methods

Study area and conifer species

The study was carried out in the Patagonian steppe, 25 km east of the city of SC de Bariloche (41°S, 71°W). This is a region where *A. lobicornis* has only recently established (approximately 50 years), and includes areas of forest interest (Schlichter & Laclau, 1998). The dominant vegetation is a mix of native species typical of the Patagonian steppe (e.g. *Stipa speciosa*, *Mulinum spinosum*, *Imperata condensata*, *Plagiobothrys tinctoreus* and *Baccharis pingraea*) and exotics (e.g. *Bromus tectorum*, *Onopordon acanthium*, *Carduus nutans* and *Verbascum thapsus*). For our experiments, we selected the three most common conifer species cultivated in Patagonia: *Pinus ponderosa* Dougl. Ex Laws, *Pseudotsuga menziesii* Mirb. Franco and *Pinus contorta* var. *murrayana* Dougl. ex Loud. (Schlichter & Laclau, 1998). We also included in our field experiments the native species tree *Austrocedrus chilensis* (D. Don) Pic. Ser. et. Bizzarri. This is a common tree species in north-west Patagonia, which is frequently harvested because of the value of its wood (Villacide & Corley, 2008).

Acceptability bioassays

We used standard 'pick-up' assays to determine the influence of leaf age and species on leafcutter preferences. Field bioassays were carried out during the summer season of 2005–2006, when leaf-cutting ants forage actively. Pick-up assays are designed to determine ant preferences among leaf types based on their chemical defenses or nutritional quality, and have been frequently used in studies with leaf-cutting ants (Farji-Brener, 2001). Groups of five pine needles (length 3 cm) per species and per leaf age (mature or young) were presented to ants simultaneously along with needle-shaped bran flakes (Best Bran '3 Arroyos'; Laso S.A., Argentina). Bran flakes were used as a control for differences in ant trail activity among bioassays because of their known high acceptability to leaf-cutting ants (Farji-Brener, 2001). Pine needles were collected from randomly selected branches of three to five different plants per species. Mature and young needles were easy to differentiate from each conifer species because of their different colour. All field assays were initiated within 2 h and completed within 5 h after collection, before the appearance of observable changes in leaf acceptance by ants (Howard, 1987). A group of five bran flakes and a group of five needles per species/age, were placed in a single row, next to an active ant trail (approximately 5 cm) at 2–5 m from the nest entrance. Individual needles and bran flakes were replaced as ants harvested them, to maintain constant availability. To eliminate possible position effects, the order of the needles belonging to different treatments was changed in each trial with respect to the nest entrance. The acceptability of needles was expressed as the number needles removed from each species/age group divided by the number of bran flakes (control) removed during 30 min. This preference index thus ranged from 0 (rejection; no needles removed) to 1 (maximal preference, equal number bran flakes removed as needles) (Farji-Brener, 2001). This test was carried out eight times per colony and on six different colonies (48 trials). Variations in preferences regarding plant species and needle age were examined using a factorial blocked analysis of variance. Before the analysis, we tested dependent variables for normality and, where necessary, used arcsine transformations. Although the preference index was the response variable, nests were considered as blocks, and the age of the leaves (mature or young) and the plant species as fixed factors.

Seedling defoliation

Defoliation of conifers by *A. lobicornis* was assessed by placing seedlings in the vicinity of ant nests. Field experiments were carried out between November 2005 and May 2006. We employed healthy commercial seedlings, 2–3 years old (approximate height 10–20 cm) of *P. ponderosa* and *P. contorta*, the most preferred pines for leaf-cutters, as determined by the pick-up assays (see results). Eight seedlings

of each species (*P. ponderosa* or *P. contorta*) were planted next to four main, active foraging ant trails (two per trail). Five active ant nests were randomly selected for each conifer species. Each ant nest was thus considered as a replicate. In each nest, half of the seedlings (one per trail) were randomly selected to exclude them from ant attack. This was achieved by the used of grease that physically deters ants from climbing up shoots (Farji-Brener & Sierra, 1998). In all cases (treatments and controls), seedlings were protected with a metallic wire mesh against mammalian and/or beetle herbivory. The mesh size avoided the access of beetles and mammals and allowed free access of leaf-cutters to the plants. Thus, we established two treatments (ants exclusion versus control), which were replicated five times each ($n = 5$ nests), involving a total of ten ant nests and 80 conifer seedlings (40 per species). Because both the surrounding vegetation and colony size can affect leaf-cutting foraging impact on our experimental design (Folgarait *et al*., 1996; Farji-Brener, 2001), we set our experiments in similar habitats (i.e. sites with similar plant assemblage composition), measured the availability of naturally occurring vegetation around each nest and estimated colony size. The ground cover of surrounding plants was measured by locating four square plots (1 × 1 m), each subdivided into 10 × 10 cm cells, in the area surrounding a nest. The percentage plant cover was estimated as the number of cells with vegetation divided by the total number of cells. To estimate colony size, we measured the size of the ant nest mound, a good estimator of colony size (Fowler *et al*., 1986, 1990). To evaluate defoliation by ants, we marked 20 needles in each seedling. This amount represented approximately 30% of the estimated number of needles per seedling. The damage of leafcutters to the conifer seedlings was then tallied as the number of marked needles removed by ants divided by the total number of needles marked. We visually confirmed that leaf-cutting ants were solely responsible for needle harvesting. We monitored percent herbivory, and remarked needles to compensate for those harvested, each week during 20 weeks. We examined differences in defoliation and in its timing, for each conifer species separately using one-way, repeated measures analysis of covariance. Before analysis, we tested dependent variables for normality and, when necessary, used arcsine transformations. Each ant nest was considered as a block because the foraging activity of each colony may influence defoliation. The size of the nest mound and the cover of surrounding vegetation were considered as covariables. Ant exclusion was considered as a fixed factor, and timing as the repeated measure. In all analyses, Tukey's post-hoc comparisons were performed when main factors were statistically significant $P < 0.05$). All data analyses were performed using the R software environment (R Development Core Team, 2008).

Results

Acceptability bioassays

The preference of leaf-cutting ants depended on conifer species and needle age (Fig. 1). Overall, younger needles were more preferred than mature needles (0.30 ± 0.12 versus 0.13 ± 0.07, mean ± SE, $F_{1,40} = 7.7$, $P = 0.008$), and preferences differed between conifer species ($F_{3,40} = 3.9$, $P = 0.01$). *Pseudotsuga menziesii* and *A. chilensis* were less preferred (mean preference indices in the range 0.01–0.23) than *P. ponderosa* and *P contorta* (preference indices in the range 0.2–0.6) by leafcutters. The item mostly selected by ants was young needles from *P. contorta* (mean preference index of 0.6).

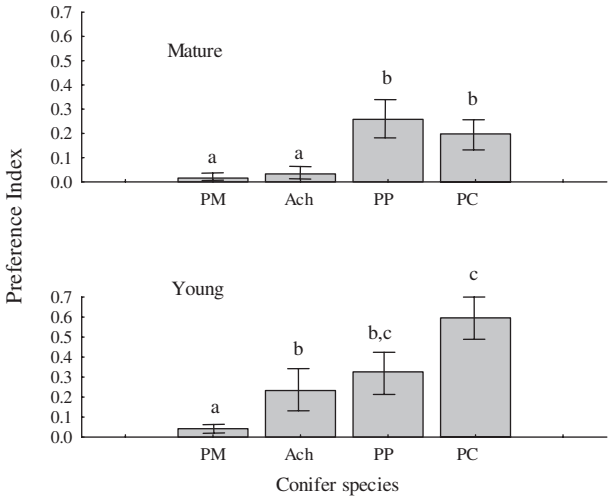

Figure 1 Mean ± SE preference indices (0 = rejection, 1 = maximal preference) for leaf-cutting ants in field pick-up assays on leaves of different age (mature and young) from the most commonly cultivated conifer species of north-west Patagonia. PM, *Pseudotsuga menziesii*; Ach, *Austrocedrus chilensis*; PP, *Pinus ponderosa*; PC, *Pinus contorta*. Different superscript letters denote statistically significant differences (Tukey's post-hoc test, $P < 0.05$).

Defoliation of conifer seedlings

Conifer seedlings of both species were defoliated by *A. lobicornis*. Although seedlings excluded from ants showed almost no signs of ant herbivory, control seedlings showed mean values of ant defoliation in the range 8–60% (Fig. 2). *Pinus contorta* was the pine mostly defoliated. Seedlings without ant exclusion showed a mean ± SE of 60 ± 5% defoliation during the sampling period ($F_{1,74} = 112.4$, $P < 0.0001$). In only 3 weeks, more than 50% of the marked needles were defoliated (Fig. 2; *P. contorta*). *Pinus ponderosa* were also defoliated but less so; control seedlings showed a mean ± SE of 8.5 ± 1% of leaf damage in the sampling period ($F_{1,74} = 29.2$, $P < 0.0001$). This pine species showed more homogeneous herbivory over time (Fig. 2; *P. ponderosa*). In both conifer species, neither the cover of surrounding plants (range 50–75%), nor the size of the colony affected defoliation (i.e. both covariables were statistically nonsignificant, all $P > 0.34$).

Discussion

Leaf-cutting ants are considered as a serious pest of forestry in South America. In the present study, we show that the strength of their negative impact depends on tree species. These findings demonstrate that simple field tests of leaf-cutting ant preference

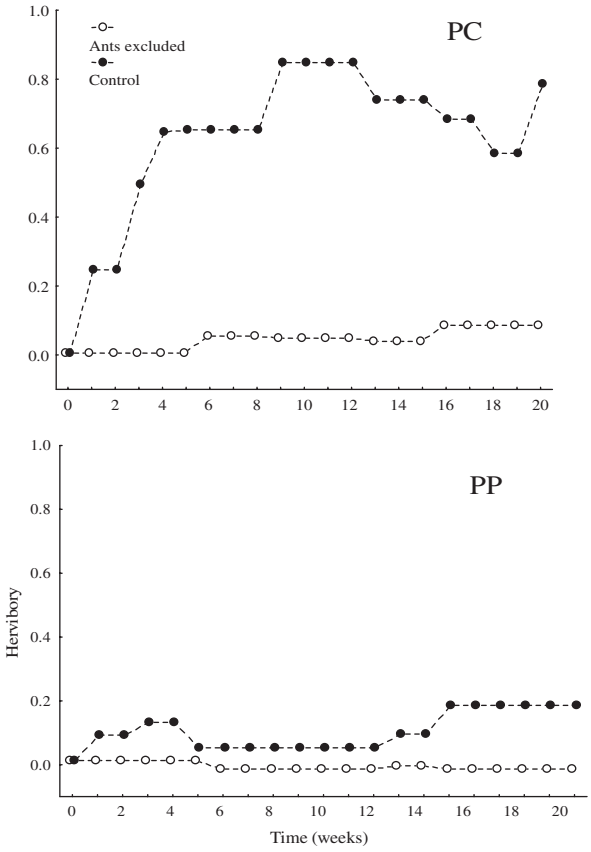

Figure 2 Mean leaf-cutting ant herbivory on seedlings located around nests with (white circle) and without (black circles) ant exclusion. Defoliation is shown as a proportion where 1 (= 100%) indicates maximum defoliation. PC, *Pinus contorta*; PP, *Pinus ponderosa*.

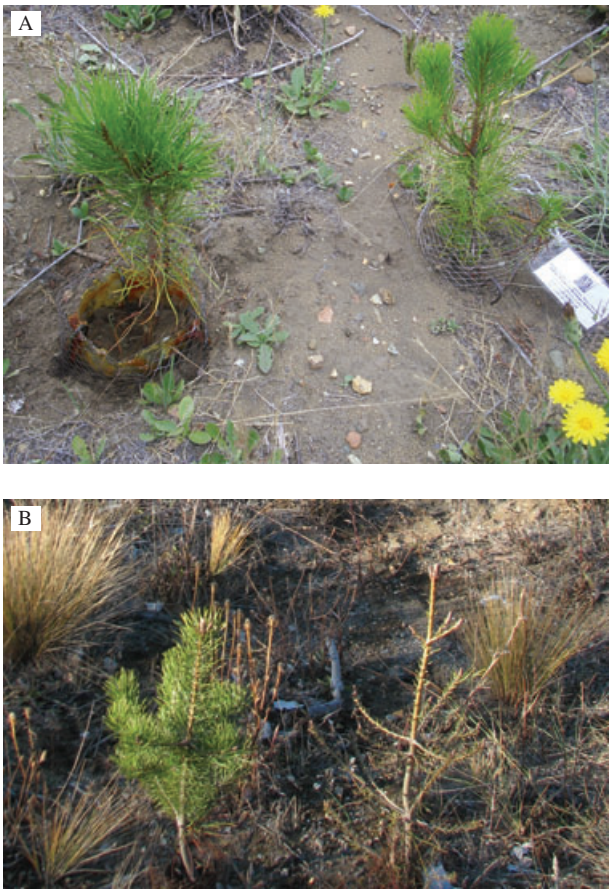

Figure 3 Conifer seedlings of *Pinus contorta* planted at both sides of an active foraging trail of the leaf-cutting ant *Acromyrmex lobicornis* at the beginning of the field experiment (A), and 5 weeks later (B). Left: seedling with ant exclusion. Right: seedling without ant exclusion.

may allow improved selection of appropriate conifer species for future plantations in areas where leaf-cutting ants are present.

In Patagonia, the leaf-cutting ant *A. lobicornis* may be regarded as a potential pest for pine afforestation. Some species were highly preferred by leaf-cutting ants but others were almost completely ignored. Although *P. menziesii* leaves were not selected by leafcutters, needles from *P. ponderosa*, and especially from *P. contorta*, were preferred by these ants. In only a few weeks, more than 50% of the marked needles of *P. contorta* were harvested by the ants and it was common to observe complete defoliation of unprotected seedlings of this pine tree (Fig. 3).

The findings of the present study confirm that leaf-cutting ants can discriminate among plant species and leaf ages (Howard, 1987, 1988, 1990; Folgarait *et al*., 1996). Choice among conifer species and needle ages is probably related to both nutritional and secondary chemical traits. Species and leaves with fewer secondary compounds and better nutrition status are often preferred by leaf-cutting ants (Berish, 1986; Howard, 1987, 1988, 1990; Barnola *et al*., 1994; Farji-Brener, 2001). For example, the concentration of secondary compounds such as myrcene and caryophyllene determines the rejection of certain types of *Pinus caribaea* trees (Barnola *et al*., 1994). Water content is also a good predictor of leaf-cutting ant preferences because leaves with greater water content are a better substrate for the ants' fungus culture (Bowers & Porter, 1981). This may be particularly important in dry areas such as the Patagonian steppes. Accordingly, the conifers least preferred by leafcutters in our field assays were those with lower leaf water content (P. Pérez, unpublished data). Future studies should investigate whether the choices of *A. lobicornis* for certain conifer species depend on chemical defences, physical leaf traits, nutritional quality and/or leaf water content.

From an applied perspective, the results of the present study indicate which conifer species among those of commercial interest in the region are more likely to be attacked by ants. Because the areas with forest interest overlap with the geographical range of *A. lobicornis* (Farji-Brener & Ruggiero, 1994; Farji-Brener & Corley, 1998; Schlichter & Laclau, 1998; Loguercio & Deccechis, 2006), understanding which conifer species are less preferred by leaf-cutting ants is of practical significance.

The success of afforestation strongly depends on the success of seedlings (Jaffé, 1986; Vilela, 1986). In Patagonia, pine plantations are typically initiated by planting the seedlings in the matrix of natural vegetation. In the present study, we have shown that seedlings may be heavily defoliated by leaf cutters

over a short time span. It is thus likely that planting unprotected seedlings of preferred species in areas where *A. lobicornis* is common will yield unsuccessful tree establishment. In other areas, leafcutter damage to conifer seedlings during the early stages of plantation can cause up to 30% reduction in height at logging age (Della Lucia, 1993). Although the information provided in the present study originated from field preference tests, these bioassays can well represent the diet preferences of leaf-cutting ants in natural conditions (Farji-Brener, 2001).

Overall, the results of the present study provide useful information for reducing environmental and economic costs associated with tree loss and pest management practices in conifer plantations of northern Patagonia. Because of the observed preferences, the conifer species investigated in the present study should not be considered as equivalent candidates for plantation purposes. *Pinus contorta* appears to be the pine species most affected by established *A. lobicornis* populations. Leaf-cutting ants showed high preference for both young and mature needles of this species and their seedlings were almost completely defoliated in a few weeks. Therefore, the success of *P. contorta* plantations in areas where *A. lobicornis* nests occur will necessarily involve further research on management practices aimed at reducing the impact of ants.

Insect pests such as leaf-cutting ants are important limiting factors for forest plantations in several regions of South America (Blanton & Ewel, 1985; Cherrett, 1986; Jaffé, 1986; Vilela, 1986; Fowler *et al*., 1986; Della Lucia, 1993; Folgarait *et al*., 1996). These ants, however, do not feed on all plants with the same intensity (Howard, 1987, 1988; Farji-Brener, 2001). An evaluation of their preferences before the establishment of plantations, may help to minimize economic losses. The results of the present study support the view of including preference studies of herbivorous insects, such as inexpensive, simple field assays on leaf-cutting ants, in the list of factors to be considered when determining which forest species to grow in given areas. Finally, the present study points towards the use of a preventive approach for forest pest management. In this way, we may reduce the environmental and economic costs involved in managing forest insects.

Acknowledgements

This study was supported by PICT (Proyecto de Investigacion Científica y Tecnológica) 2004, #25314 to A.G.F.B. and PNFOR (Proyecto Nacional de Forestales) 2212 (*INTA*) to J.C.C.

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Accepted 8 August 2010
First published online 19 December 2010