



Survival and growth of *Acacia dealbata* vs. native trees across an invasion front in south-central Chile

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ABSTRACT

Tree invasions cause important conservation problems, such as changes in plant community composition, reduced regeneration rates of native species, and alteration in landscape structures. One of the most invasive tree genera in the world is *Acacia* (Fabaceae). In Chile, *Acacia dealbata* Link is distributed in the mediterranean zone, mostly associated with roadsides and anthropogenic disturbances. In this paper we address the following questions: How does *A. dealbata* perform across a gradient of native forest and invasive stands? Will it be capable of establishing itself in non-invaded native forests and regenerating under its own canopy in the absence of disturbances? From a contrasting viewpoint, will native species such as *Cryptocarya alba* (Molina) Looser and *Nothofagus obliqua* (Mirb.) Oerst be able to survive in an *A. dealbata* stand, allowing re-colonization of the invaded area? We conducted survival and growth experiments on *A. dealbata* seedlings in three sites near Concepción, Chile (36°S–72°W) under three conditions: under *Acacia* stand, in a close native forest and on an intermediate matrix between these two conditions. We compared this to the performance of two native trees (*Cryptocarya alba* and *Nothofagus obliqua*). Results showed that *A. dealbata* and *C. alba* have high growth and establishment capacities within the native forest, but on the intermediate matrix only *A. dealbata* can grow and survive. *C. alba* survives at significantly higher rates than *A. dealbata* within *Acacia* stand. *Nothofagus obliqua* only survive at a very low rate in the native forest. Without disturbances, *A. dealbata* would be successful on the intermediate matrix and within native forest, while *C. alba* seems capable of surviving and establishing itself in invaded areas, thereby contributing to recovery and restoration of natural spaces. The interplay between *Acacia dealbata* and the native vegetation may show us a larger picture of how invasive species are capable of expanding even into forested ecosystems and, furthermore, how we can restore native vegetation and avoid further invasion.

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1. Introduction

Tree invasions are spreading quickly and have been documented in several ecosystems world-wide (Richardson, 1998; Etienne, 2001; Weber, 2003; Martin et al., 2009). They can create conservation problems, such as changes in plant community composition, reduced regeneration rates of native species, and alteration in landscape structures (Di Castri et al., 1981; Groves and Di Castri, 1991; Richardson, 1998; Etienne, 2001). For example, *Acer platanoides*, L. has a negative impact on diversity and ecological performance of native species in secondary forests in New Jersey, USA, while *Ligustrum lucidum* W.T. Aiton is changing the landscape structure in the

central zone of Argentina (Aragón and Groom, 2002; Galbraith-Kent and Handel, 2008). Other invasive trees include widespread species such as *Ailanthus altissima* (Mill.) Swingle, *Spathodea campanulata* Beauv. and *Psidium guajava* L., which have shown important ecosystem impacts (Lugo, 2004). Most tree invasions have occurred through intentional introductions, originally for the forestry industry and for ornamental purposes, but now including other more diverse reasons/uses (Reichard and Hamilton, 1997).

The mechanism by which the natural vegetation of an area is invaded by non-native trees is still poorly understood. In some cases, a positive relationship between invasions and disturbance regimens has been reported (e.g. canopy gaps for light entrance, which allows the seed bank emergence) (Martin and Marks, 2006). Fires and cutting disturbances may also promote tree invasions because invasive species reproduction strategies are associated with such events (e.g. vegetation resprouting and fire-stimulated seed germination, Pauchard et al., 2008). Invasive tree species are generally early successors, with rapid-growth, easy reproduction,

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and high seed production (Bazzaz, 1979; Rejmánek and Richardson, 1996). Most of them are adapted to direct solar radiation and can endure long periods of drought (Bassuk et al., 2003). However, tree invasions occur under complex scenarios where temporal and spatial variation in disturbances and environmental factors makes it difficult to isolate the key mechanisms that promote invasions.

On the other hand, some invasive tree species, which form closed stands, may play an important role for the recruitment and growth of native shade-tolerant species which live under the invasive canopy or by those that do not endure low temperatures (Callaway, 2007). In both cases the understory species can benefit from the invader presence (Peng et al., 2005). In south China, some invasive *Acacia* species can act as nurse plants for native tree species, improving their performance in terms of photosynthetic efficiency, buffering against extreme temperatures and allowing for faster growth (Yang et al., 2009). A simultaneous assessment of the interplay between invasion and re-colonization has scarcely been explored. Invasion fronts could be an important landscape element to test these mechanisms and to better understand the restoration potential of areas invaded by native tree species. Thus, we should expect a relationship between the invasion spread process and the native re-colonization dynamic, which can lead to the recovery and conservation of natural communities (Ens and French, 2008). In recent years, much attention has been paid to the invasive potential of exotic species and the opportunity for them to act as nurse plants for ecosystem restoration purposes (Ewel and Francis, 2004). However, little has been done in order to address the potential re-colonization of native tree species into invaded stands.

Acacia, of the Fabaceae family, is one of the most invasive tree genera (Henderson, 1995; Le Maitre et al., 2002; Samways and Taylor, 2004; Turner and Pharo, 2005). It includes approximately 1300 species of trees and shrubs, mostly originating in Australia and Tasmania (Maslin, 2001). The invasion of the *Acacia* genus poses a threat to natural habitats through competition and replacement of native species, decreasing the native biodiversity and homogenizing the community (Lorenzo et al., 2010; Fuentes-Ramírez et al., 2010). Furthermore, it has a high colonization capacity, taking over sites that have been disturbed by fire, harvesting or other types of anthropogenic disturbance. *Acacia dealbata* has been documented as an invasive tree in several parts of the world, such as Portugal, Spain, South Africa and Madagascar (Henderson, 1991; Aguiar et al., 2001; Tassin et al., 2009; Lorenzo et al., 2010).

In Chile, *Acacia dealbata* was introduced for ornamental purposes and currently is widely distributed in mediterranean ranges. It has a strong association with riparian habitats, roadsides and anthropogenic disturbances (Matthei, 1995; Pauchard and Maheu-Giroux, 2007; Peña et al., 2007). The mediterranean area in Chile is a "Biodiversity Hotspot" (Myers et al., 2000) with a high rate of endemism and threatened species. Therefore, the invasive spread of *A. dealbata* may threaten remnant native forest fragments, causing a loss in their overall biodiversity (Fuentes-Ramírez et al., 2010). Some characteristics which make this species a successful invader are (a) its phenotypic plasticity, which allows it to adapt and be successful in changing environments (Carr, 2001; Pholman et al., 2005), (b) its high capacity for vegetative regeneration from rhizomes after disturbances (e.g. fire, cutting) (Sheppard et al., 2006), (c) its allelopathic properties (Carballeira and Reigosa, 1999; Lorenzo et al., 2008), which inhibit the growth and performance of neighboring native species, and (d) its positive relationship with anthropogenic disturbances, which is considered one of the most important factors for the invasive spread of *A. dealbata* in mediterranean areas (Cheal, 2002; Spooner, 2005; Lorenzo et al., 2010). In this paper, from the perspective of the invasive tree species and independent of disturbances, we ask: How does *A. dealbata* perform across a native forest–invasive stand gradient? Will it be capable

of establishing itself in non-invaded native forests and regenerating under its own canopy in the absence of disturbances? In contrast, we ask how native tree species such as *Cryptocarya alba* and *Nothofagus obliqua* perform across the native forest–invasive stand gradient. Would they be able to survive in an *A. dealbata* stand, allowing re-colonization of the invaded area?

Acacia dealbata in central-south Chile is a good model to understand how tree invasions can spread into semi-natural forests. In this area, we hypothesize that *A. dealbata* has a high survival and growth capacity, as much within the native forest and on the intermediate matrix as it does under its own canopy, even in the absence of disturbances. On the contrary, native species will only be successful within their native forests. In this scenario, the *A. dealbata* success could pose a serious threat to the native forest remnants in south-central Chile. This study explores the probability of re-colonization of the invaded areas by native species and their contributions to the recovery and conservation of natural communities.

2. Materials and methods

2.1. The species

Acacia dealbata Link (Fabaceae) is an introduced evergreen tree without thorns, which reaches between 4 and 20 m tall. It has compound bipinnate leaves between 10 and 20 cm in length, some of which are glaucous or silver. Its yellow flowers, which are arranged in dense groups of panicles, flower during the winter season. Its fruit is a dry legume between 4 and 10 cm in length, flat and slightly narrowed between seeds (Matthei, 1995; Rodríguez et al., 2005). It regenerates through seeds, but often through vegetation sprouting, after cutting or fires. It forms a permanent seed bank, which rapidly germinates after a fire or other type of disturbance (Sanz-Elorza et al., 2004; Gómez-Vigide et al., 2005).

Cryptocarya alba (Molina) Looser (Lauraceae) is a shade-tolerant evergreen native tree, between 15 and 20 m in height and 1 m in diameter. It is endemic in Chile, distributed from the Coquimbo Region to Los Ríos Region, principally in streams and humid shady valleys, occurring up to 1500 m above sea level. It is considered a threatened species in some areas of Chile, mainly due to overexploitation and habitat destruction (Benoit, 1989).

Nothofagus obliqua (Mirb.) Oerst. (Nothofagaceae) is a shade-intolerant, deciduous native tree, with a maximum height of 40 m and diameter of 2 m, found in the forests of central-south Chile, distributed in the valleys from Curicó to Llanquihue in both mountain chains (Cordillera de Los Andes and Cordillera de la Costa), up to 1500 m above sea level. (Rodríguez et al., 2005). We selected *N. obliqua* and *C. alba* because they are among the most abundant native trees in the study area and represent two distinct functional strategies (deciduous and evergreen trees, respectively).

2.2. Study area and study conditions

The study site is located near Concepción city, Bio-Bio Region, Chile (36°S; 73°W). The climate is warm-temperate, with a mediterranean influence (Csb₂), winter rain and an extended dry season (Köppen, 1948). The study was conducted in the 2008–2009 growing season. This year (May 2008 to April 2009) was normal in precipitation (1188.1 mm, historic mean = 1175.6 mm), but it was particularly dry in the months of the experiment (September–March, ca. 63% deficit).

The native vegetation in this area is the mediterranean deciduous forest, including *N. obliqua* and *C. alba*. *Acacia dealbata* appears as a common ruderal species associated with waterways, roadsides, and other anthropogenic disturbances (Gajardo, 1995; Luebert

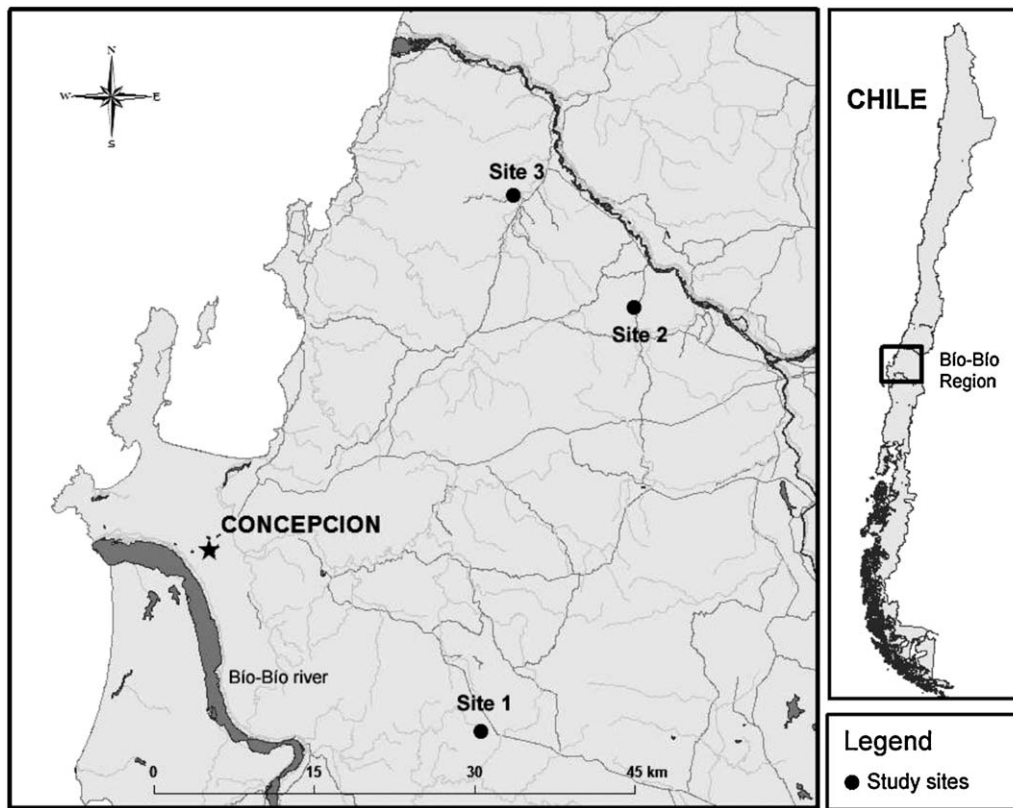


Fig. 1. Study area in the Bío-Bío Region, Chile (36°S–72°W). Site 1: El León, site 2: Palomares, and site 3: Coelemu.

and Pliscoff, 2006). In addition to the native vegetation, there are different land uses associated with human activities, such as forestry plantations (e.g. *Pinus spp.* and *Eucalyptus spp.*), agricultural production and livestock trade. In the study area, *A. dealbata* stands present a common structural pattern, in which DBH and height decrease from the interior to the stand edge. Furthermore, greater vegetative regeneration is observed along the edge, even within native forest, while a negative relation exists between DBH and the density of individuals (Claudio Novoa, unpublished data).

We selected three sites near Concepción (Fig. 1), using satellite images taken from Google™ Earth, where we conducted experiments to test seedling survival and growth rate for two native trees (*C. alba* and *N. obliqua*) and one alien invasive tree (*A. dealbata*) under three study conditions: (a) inside of an invaded stand by *Acacia*, (b) inside of a contiguous native forest (two patches of similar size, ca. 2 ha), and (c) on the intermediate matrix (open area) between both conditions (Fig. 2). Canopy photographs taken from ground level in November of 2008 show that *Acacia* stands have a cover of $71.2\% \pm 2.7\%$ (\pm SE, $n=9$) while native forests only $52.8\% \pm 1.8\%$ (\pm SE, $n=9$) ($t=-5.703$; $p<0.001$, Software Scion Image).

Adjacent native forest fragments have a medium disturbance level due to selective logging. However, these forests maintain important features such as high content of organic matter and moisture. Between these two conditions there is an anthropogenic matrix, generally consisting of artificial grasslands in highly degraded soils, exposed to direct sunlight and with a high proportion of introduced species. For this study we have called this condition “intermediate matrix”. These sites have not been recently disturbed and only show evidence of historic disturbances such as logging. The sites have similar plant communities as well as topography (see Fuentes-Ramírez et al., 2010).

2.3. Experiments

In each of the three study sites, we identified three conditions (*Acacia* stand, native forest and intermediate matrix). In each condition, we planted 20 seedlings of each species (*A. dealbata*, *C. alba* and *N. obliqua*) in random order. Seedlings were acquired at a local nursery and were ca. 10 cm tall. Planting was conducted during the middle of September. We planted a total of 540 seedlings in the three study conditions and in the three study sites (20 seedlings \times 3 species \times 3 conditions \times 3 sites = 540). Each seedling was planted 45 cm apart from any other to avoid direct competition effects. In



Fig. 2. Study conditions showing the invasion gradient: (a) *Acacia dealbata* stand, (b) contiguous native forest and (c) intermediate matrix between both conditions. Picture was obtained from Google™ Earth.

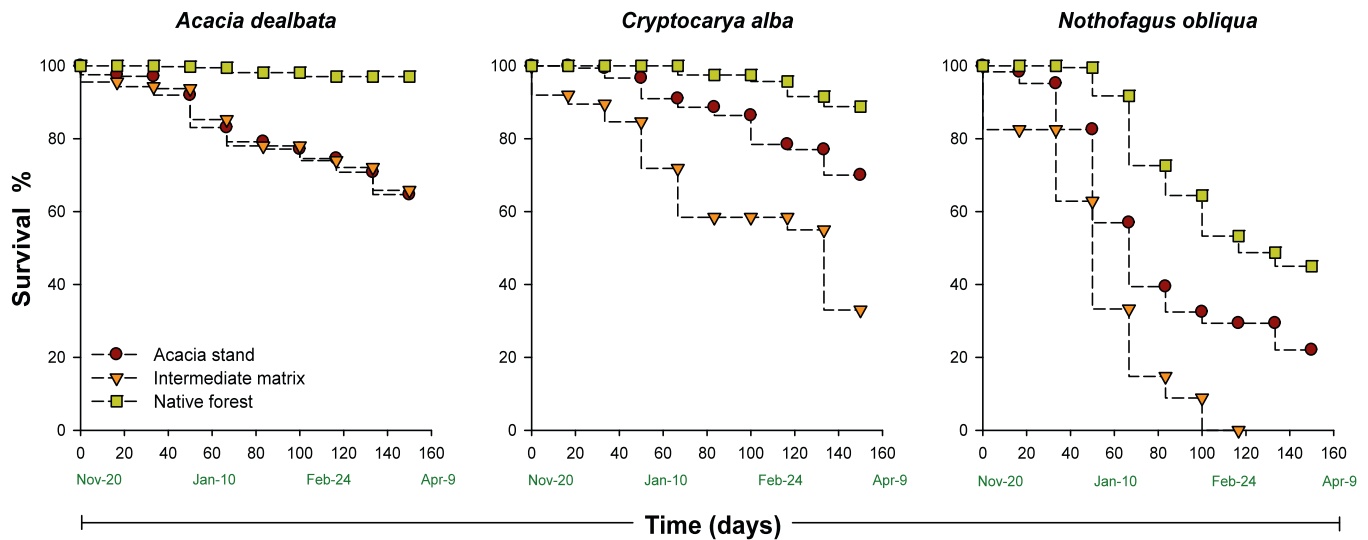


Fig. 3. Kaplan–Meier survival curves for seedlings of *Acacia dealbata*, *Cryptocarya alba* and *Nothofagus obliqua* in three study conditions (*Acacia* stand, intermediate matrix and native forest). Monitoring was conducted for five months starting in late spring (November 2008).

addition, we enclosed every seedling individual within a metallic mesh in order to avoid loss or damage through herbivory from the start to the finish of the study. We irrigated during the first three weeks to ensure initial seedling establishment. One month after the experiment began we started the survival assessment recording the number of living seedlings in each condition and in the three study sites every 15 days for a period of 5 months. We also recorded the monthly height of each seedling to get the differences on the growth rates. In order to evaluate the seedling performances during the first drought season in summer 2008–2009, the most critical stage of the plant development (Isselstein et al., 2002), we monitored these experiments from November 2008 through the first rains of April 2009 (fall season).

2.4. Data analysis

For the seedling survival analysis, we used Kaplan–Meier survival curves (1958) and the Cox–Mantel test to check the significances among the survival curves among species and conditions. We evaluated monthly growth rates using *t*-tests taken among the initial and final heights of the surveyed seedlings. Data showed homoscedasticity (Kolmogorov–Smirnov) and no site effects were detected (ANOVA, $F = 2.8$; $p = 0.067$). Growth rates were only recorded for *A. dealbata* and *C. alba*. *N. obliqua* was not considered because there were some cases of total seedling mortality in five months of assessment. Due to this mortality, we balanced comparisons by randomly selecting the same number of individuals in the initial condition as those surviving at the end of the experiment. Analyses were run in STATISTICA and SPSS.

3. Results

3.1. Survival

The highest survival rate for the three species was in the native forest. *A. dealbata* survived significantly more in the native forest than it does in the intermediate matrix and under its own canopy ($p < 0.001$). No significant differences were detected in these last two conditions. For *C. alba* higher survival also occurred in the native forest ($p < 0.001$), but in the *Acacia* stand, it survived significantly more than *A. dealbata* (70% and 64.7% respectively, $p < 0.05$). Its lowest survival occurred in the intermediate matrix, with only

33% survival ($p < 0.001$). *N. obliqua* mortality reached 100% at three months on the intermediate matrix, having its higher survival in the native forest (45%, $p < 0.001$) (Fig. 3; Table 1).

3.2. Growth

We analyzed only the growth rates of *A. dealbata* and *C. alba*, due to *N. obliqua* having an extremely low survival rate. Initial heights of tree seedlings were significantly different between species ($t = 6.37$; $p < 0.0001$). However, within-species variation was not significant. *A. dealbata* started the experiment at 15.1 ± 0.3 cm and *C. alba* at 12.7 ± 0.2 cm. Across pooled conditions, *A. dealbata* grew more quickly ($\Delta 9.5$ cm) than *C. alba*, which only grew 1.5 cm on average after five months assessment. *A. dealbata* growth was significantly different from zero on the intermediate matrix and inside native forest ($t = -2.92$; $p < 0.01$ and $t = -9.38$; $p < 0.001$, respectively), while beneath its own canopy it did not grow. *C. alba* grew only in native forest ($t = -3.95$; $p < 0.001$) (Fig. 4).

4. Discussion

Tree invasions depend highly on disturbance regimes to be successful, because most invasive species are shade-intolerant and require a large liberation of resources for their establishment (Hickey, 1994; Martin et al., 2009; Lockwood et al., 2007). However, we found that in the absence of disturbance regimes, *A. dealbata* can successfully establish and grow into non-invaded areas, such as the intermediate matrix and adjacent native forests. On the contrary, native species perform poorly in invaded areas. Only *C. alba* had a high survival rate within invaded stands, but it had limited growth. With the observed high vegetative resprouting of the invasive species, our results confirm the observation that the invasive spread of *Acacia* into non-invaded areas seems to be a threat for the few remaining native fragments, which appear vulnerable to *A. dealbata* spread (Martínez et al., 2009) (Fig. 5). Nonetheless, the survival of one of the native trees inside the invaded stand opens the possibility of exploring restoration actions.

Results show that native forest is the best site for establishing *A. dealbata*; in this condition its survival reached 97.1%. In the intermediate matrix and the *Acacia* stand, it maintained a high survival rate, which shows its high capacity of tolerating long summer drought periods through high competition for water and light

Table 1
Cox–Mantel’s test for seedlings survival of three species under Acacia stand, intermediate matrix and native forest.

Conditions	<i>Acacia dealbata</i>		<i>Cryptocarya alba</i>		<i>Nothofagus obliqua</i>	
	I. Matrix	Native forest	I. Matrix	Native forest	I. Matrix	Native forest
Acacia stand	ns	–8793***	6502***	–5297**	5373***	–6472***
I. Matrix	–	–8973***	–	–12,059***	–	–12,205***

Asterisk means significant differences between plots: ** $p = 0.01$; *** $p = 0.001$; ns means non-significant differences.

(Lorenzo et al., 2010). In its native habit, *A. dealbata* is distributed mainly in arid and semi-arid areas, giving it the ability to withstand long drought periods (Maslin, 2001). Its higher growth was also seen in the native forest condition where, despite its status as shade-intolerant, it can adapt and grow quickly (Weber, 2003). In some cases, species typically considered light-demanding in their native ranges can become shade-tolerant in their introduced range (DeWalt et al., 2004). Across all conditions, *A. dealbata* grew an average of 7.71 cm in the entire assessment period. For this species, the literature does not provide similar records detailing survival and growth rates. However, for other Acacias, some results show that its development depends on several biotic factors, such as herbivory (Auld, 1995) and parasitism (Wiegand et al., 1999), and even abiotic factors, including altitude, humidity, temperature, soil type and light rates (Oginosako et al., 2005; Weber et al., 2005). *A. dealbata*

proved to be particularly resistant to the intense summer drought during the year of the experiment. Such drought resistance can have important implications in a scenario of climate change and increasing drought in central Chile.

Although native forest is the best condition for the establishment of both *C. alba* and *A. dealbata*, the native species has a higher survival rate than *A. dealbata* (70%, $p < 0.05$) within the *Acacia* invaded stands. This could demonstrate the success of *C. alba* despite allelopathic characteristics of *A. dealbata* and potential soil modification (Lorenzo et al., 2008). This evidence shows that native species, such as *C. alba*, are likely to re-colonize invaded areas, as it seems be able to “invade” the *Acacia* stands. These results contrast with the findings by Guerrero and Bustamante (2007), who conclude that *C. alba* has fewer germination and survival probabilities within pine plantations compared to within native forest. In *A. dealbata* invaded stands, at least in the short-term, *C. alba* appears as a successful re-colonizer species.

Like many native tree species, *C. alba* is a slow-growth tree, demonstrated by its average growth of 1.62 cm during the assessment period, across all conditions. It only grew significantly within the native forest ($p < 0.001$), but it did not grow within the *A. dealbata* stand. However, its shade and drought tolerance allow *C. alba* to survive under the *A. dealbata* dense stands. *Acacia* allelopathic characteristics could explain the limited growth (Lorenzo et al., 2008). For other *Acacia* spp., this seems to be the most important constraint that restricts the growth and development of many species under its canopy (Marchante et al., 2008, 2009). The allelopathic effects could even deter the establishment of new plants of *A. dealbata*. However, we cannot disregard other factors, such as intense competition for light and water under the dense invasive stands.

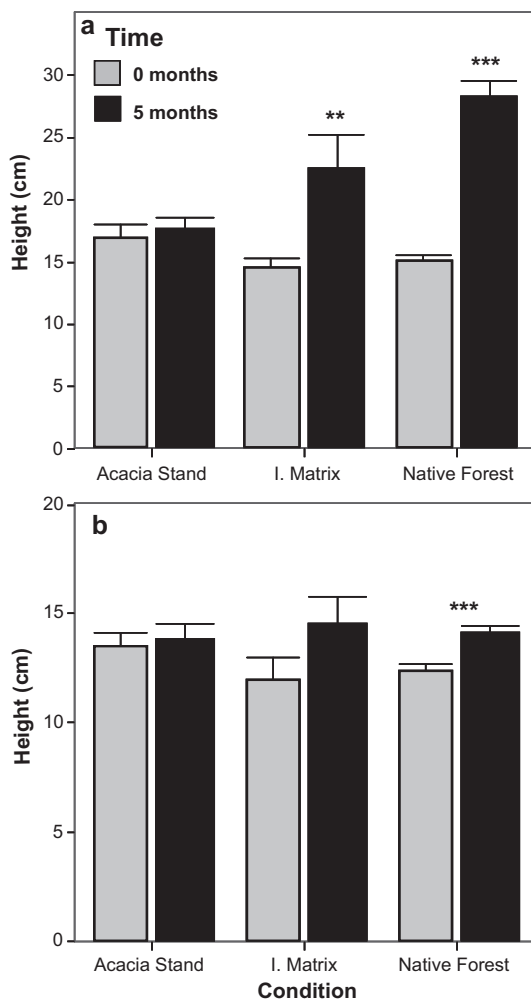


Fig. 4. Mean height of *Acacia dealbata* (a) and *Cryptocarya alba* (b) in each study conditions (under *Acacia* stand, intermediate matrix and within native forest) at the beginning of the experiment and after five months. Asterisk means significant differences between time: ** $p = 0.01$; *** $p = 0.001$. Bars means standard error.

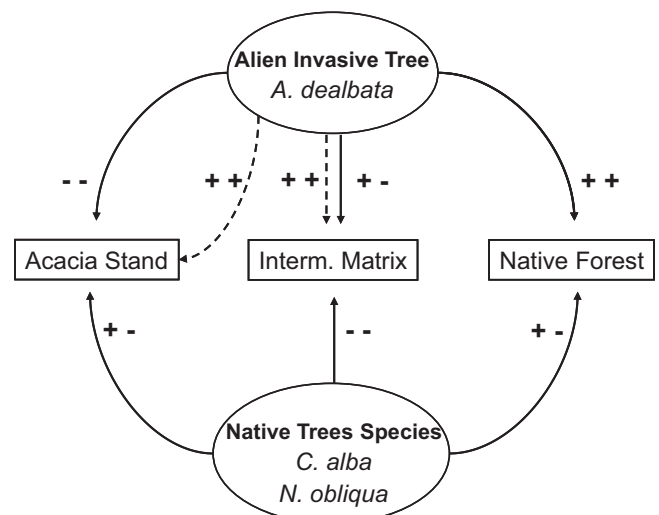


Fig. 5. Interaction model among *Acacia dealbata*, *Cryptocarya alba* and *Nothofagus obliqua* and the three study conditions (*Acacia* canopy, intermediate matrix and native forest). Solid lines show survival results after five months and dash lines represent observed vegetative resprouting after fire or cutting disturbance. Positive or negative signs (+, –) indicate possible outcomes for survival and growth of the species in each study conditions.

N. obliqua was the species with the lowest survival rate in the three study conditions, which may be explained by its ecological requirements. It is a shade-intolerant species and, therefore, would be unsuccessful under the canopy. On the intermediate matrix, where solar radiation is direct, *N. obliqua* survives only through the first three months. This species requires rainfalls around 1,500 mm; but in the study area it is common to have dry years with less than 1100 mm of rain (Donoso, 2008). Furthermore, *N. obliqua* do not resist more than a month of drought (Donoso, 2008), which may limit its ability to compete with non-native trees or other more drought-resistance native trees.

The specific ecophysiological mechanism by which *A. dealbata* is a successful invader in most environments of the study area, absent disturbance, remains as an open question. There is no evidence of its ability to germinate in these conditions. In the field, invasion spread is mainly observed through resprouting after fires, cutting and other disturbances. This leads us to consider some environmental constraints, which prevent *Acacia* germination and spreading into adjacent areas, despite high annual volume of seed production and its persistent seedling bank (e.g. dispersal, seedling herbivory, frugivory, and pre-germinating treatments). Clearly, the success of the *A. dealbata* to spread into non-invaded areas is not due to a single mechanism; apparently it would involve a group of interrelated processes (Shang, 2004). In this study, we demonstrate that *A. dealbata* has a high competitive ability for establishment and survival into non-invaded areas, such as the intermediate matrix. Although *A. dealbata* is able to successfully survive, mainly in the intermediate matrix and in native forest, *C. alba* seems to have the chance to establish within *Acacia*-invaded areas, even more than *A. dealbata*. Canopy cover plays a key role in this performance. While *C. alba*, a shade-tolerant species, grows better under the closed canopy of *Acacia* stands, *A. dealbata*, a shade-intolerant species, better perform under the open canopy of native forest.

The interplay between *A. dealbata* and native vegetation may reveal the process by which invasive species are capable of expanding into forested ecosystems. Clearly, invasive species develop highly mono-specific stands in areas where re-colonization by native species is extremely difficult. Competition for light, water and nutrients, and allelopathic mechanisms can be responsible for creating an extremely difficult environment for native tree species (Lorenzo et al. 2010; Carballeira and Reigosa, 1999). However, if we want to reclaim some of this land to restore native forests we need to better understand which species can re-establish in the invasive stands and under what specific conditions.

In addition, to stop invasion into the remaining fragmented forests, management actions should be aimed at detecting what conditions are particularly favorable for invasive species and under what conditions the species disperse into the fragments. Early detection and control in native forest edges should also be implemented, especially when the remaining forest has a particular environmental value.

Most of the studies conducted in alien plant invasions are based on observations without further experimental testing, while the few experimental studies focus mainly on grassland communities. Only a low percentage (5/63) is made in forests (Levine et al., 2003). Moreover, >85% of the studies assess annual plants or perennial grasses, while only 5.6% assess trees (Levine et al., 2004). Clearly, more research is needed on tree invasions into forest ecosystems to understand which mechanisms determine the invasion process. Furthermore, this study may be a first step for beginning discussion and exploring the probability of using native species as “recolonizers” of invaded areas for restoration purposes. A better understanding of the interaction between the invasion process and native species re-colonization can greatly contribute to the conservation of natural areas and the restoration of invaded ecosystems.

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