

Allelopathic effect of the invasive *Acacia dealbata* Link (Fabaceae) on two native plant species in south-central Chile

Efecto alelopático de la invasora *Acacia dealbata* Link (Fabaceae) en dos especies de plantas nativas del centro-sur de Chile

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ABSTRACT

Plant species that growth close to or under the canopy of *Acacia dealbata* Link (Fabaceae, subfamily: Mimosoideae) within its non-native range, survive with difficulty or not at all, especially if they are native. This phenomenon has been attributed to allelopathy; one of the strategies used by *A. dealbata* to trigger an invasion process. Native species *Quillaja saponaria* Molina (tree) and *Helenium aromaticum* (Hook.) H.L. Bailey (herb), share *A. dealbata*'s range in South-central Chile. This study was performed on the Mediterranean Biobío Region of Chile. We evaluated the effect of leaves, flowers, pods and seeds of *A. dealbata* on the germination and early growth of these native species. Biological assays were carried out under laboratory conditions, based on aqueous extracts and the direct effect of plant material. Leaf litter prevented the germination of both species and seeds of the invasive species impeded the germination of *Q. saponaria*. Other plant parts from *A. dealbata* also induced reductions of hypocotyl and radicle lengths in the native species, reaching over 50 % in some treatment values. All plant parts caused radicle necrosis, preventing the formation of root hairs and, consequently, jeopardizing the survival possibility of the recipient species. The results show that *A. dealbata* can interfere with the establishment of pioneer herbaceous species in ecological succession and can also affect trees if they are reached by the invasion front.

KEYWORDS: Allelochemicals, aqueous extracts, *Helenium aromaticum*, *Quillaja saponaria*, invasive plants.

RESUMEN

Las plantas que crecen cerca o bajo el dosel de *Acacia dealbata* Link (Fabaceae, subfamilia: Mimosoideae), cuando esta se encuentra en el rango no nativo, sobreviven con dificultad o no lo logran, especialmente si son nativas. Este fenómeno se ha atribuido a la alelopatía; una de las estrategias utilizadas por *A. dealbata* para promover su proceso de invasión. Las especies nativas *Quillaja saponaria* Molina (arbórea) y *Helenium aromaticum* (Hook.) H.L. Bailey (herbácea) comparten el rango de distribución de *A. dealbata* en el centro-sur de Chile. El presente trabajo se realizó en la Región del Biobío y se evaluaron los efectos de hojas, flores, vainas y semillas de *A. dealbata* en la germinación y crecimiento temprano de las especies nativas mencionadas. Los ensayos biológicos se llevaron a cabo en condiciones de laboratorio, basados en extractos acuosos y efectos directos del material vegetal. Nuestros resultados indicaron que las hojas impidieron la germinación de ambas especies nativas, pero las semillas impidieron sólo la germinación de *Q. saponaria*. Otras partes de la planta de *A. dealbata* también indujeron fuertes reducciones de las longitudes del hipocótilo y radícula en las especies nativas, superándose el 50% en algunos tratamientos. Todas las partes de la planta causaron necrosis en la radícula, evitando la formación de pelos radicales y, por consiguiente, comprometiendo la posibilidad de supervivencia de las especies receptoras. Estos resultados muestran que *A. dealbata* puede interferir en el establecimiento de especies herbáceas pioneras en la sucesión ecológica y también puede afectar especies arbóreas secundarias si son alcanzadas por el frente de invasión.

PALABRAS CLAVE: Aleloquímicos, extractos acuosos, *Helenium aromaticum*, *Quillaja saponaria*, plantas invasoras.

INTRODUCTION

The major negative impacts of plant invasions within the host communities include the alteration of successional dynamics, decline of diversity and relative abundance of native species, disruption of important ecosystemic functions and heavy economic costs to limit their proliferation (Inderjit 2005). In addition, one of the main recent developments in invasion biology is the recognition that many invasive species affect entire ecosystems, often through modifying nutrient cycles or physical structure (Ehrenfeld 2011, Simberloff 2011). Particularly when nutrient cycles are modified (as by introduction of a nitrogen-fixing plant into a nitrogen-poor system lacking such a species), the long-term effects may be enormous, but these are subtle and can be slow (Simberloff 2014). Several hypotheses have been proposed to explain the success of introduced plants in their non-native range (Hierro *et al.* 2005). However, a recent meta-analysis attributes great importance to the novel weapons hypothesis in regards to the phenomenon of invasion (Lamarque *et al.* 2011). This proposal is based on the idea that plants can release chemical compounds into the environment, and that these chemicals may suppress the growth and development of other surrounding plants; a process known as allelopathy (Inderjit *et al.* 2011). The main reason to consider this phenomenon as an important mechanism that contributes to the success of invasive plants is based on two premises. First, invasive species tend to form monocultures stands in places where diverse communities once thrived. Secondly, allelopathy may be more important in the host communities than in the origin communities, because the former are more sensitive to chemical compounds released by non-native species that did not co-evolve (Hierro & Callaway 2003). In this context, to assess the allelopathic potential of a given plant species over other surrounding species (e.g. native trees or herbs), different types of biological assays have habitually been used. Apparently, the most successful are based on the use of aqueous extracts from the donor plants (Wardle *et al.* 1996, Lin *et al.* 2004, Mutlu & Atici 2009, Zhu *et al.* 2009, Goodall *et al.* 2010, Chon & Nelson 2013) to simulate field conditions (Scognamiglio *et al.* 2013), or even by placing the host seeds in direct contact with the plant structures of the donor species in an aqueous environment (Aguilera *et al.* 2015a).

The largest number of bioactive secondary metabolites affecting insects, fungi and plants has been found in the Lamiaceae, Asteraceae and Fabaceae families (Boulogne *et al.* 2012). In the Fabaceae family we find the cosmopolitan genus *Acacia* (subfamily: Mimosoideae), which includes about 1380 species (Lorenzo *et al.* 2010). It has been shown that members of *Acacia-sensu lato* contain amines, simple cyanogenic glycosides, cyclitols, essential oils, diterpenes, fatty acids in oilseeds, fluoroacetate, gums, non-protein amino acids, triterpenes, phytosterols, saponins, flavonoids

and tannins; however, the identification of these compounds results from the study of a small number of species within this genus (Seigler 2003). Some of the above secondary metabolites have been associated with phytotoxic or inhibitory activity, for example alkaloids (Elakovich & Yang 1996, Hornoy *et al.* 2012, Goyal 2013), cyanogenic glycosides (Carlsen & Fomsgaard 2008, Ambika 2013), terpenes (Ens *et al.* 2009, Macias *et al.* 2010), flavonoids (Carlsen & Fomsgaard 2008, Ambika 2013) and tannins (Carlsen & Fomsgaard 2008). *Acacia dealbata* Link (silver wattle, aramo) one of the most widely distributed species of the genus *Acacia*. It is native to Australia (Lorenzo *et al.* 2010), but it has been reported as invasive in Southeastern Europe (Rodríguez-Echeverría *et al.* 2013), South Africa and South America (Richardson *et al.* 2011); specifically in Chile (Fuentes-Ramírez *et al.* 2011), where it was introduced in 1881 (Fuentes *et al.* 2013) and occupies about 100.000 hectares in the Biobío Region (Pauchard & Maheu-Giroux 2007). Several studies have shown evidence that *A. dealbata* has inhibitory effects on the germination of other plant species (Carballeira & Reigosa 1999, Lorenzo *et al.* 2008, 2011); most of them are native understory shrubs and herbs (e.g. *Hedera hibernica* and *Dactylis glomerata*). These effects, for instance, induce changes in net photosynthesis and the respiration rates of several native understory species in northwestern Spain (Lorenzo *et al.* 2011). The absence or scarcity of vegetation under the canopy of *A. dealbata* is often attributed to an allelopathy phenomenon (Fuentes-Ramírez *et al.* 2011), and consequently, the inhibitory effects from the secondary metabolites released by this species (Lorenzo *et al.* 2013). So far Aguilera *et al.* (2015a) have identified biomolecules present in leaves, flowers, pods and bark of *A. dealbata* and those involved in this process, attributing a great importance to resorcinol, lupanine and stigmasterol, among others.

Many native species are thought to be threatened by *A. dealbata* in Chile, from Valparaíso province to Los Lagos province (Fuentes *et al.* 2013), representing a serious ecological problem (Fuentes-Ramírez *et al.* 2011). *Quillaja saponaria* Molina (Rosaceae: Spiraeoideae), endemic to the Chilean coastal Mediterranean sclerophyllous forest (Fuentes *et al.* 2013), is a tree strongly affected by *A. dealbata* invasion from the Limarí to the Biobío province (Rodríguez *et al.* 2005). *Helenium aromaticum* (Hook.) L.H. Bailey (Asteraceae), an annual or biennial native herb widely distributed throughout the Mediterranean region in Chile (Bierner 1978). It is a pioneer species (Gómez-González *et al.* 2011) that is also threatened by *A. dealbata* in the same area (Aguilera, personal observation). Seeds and roots of these native species are in close contact with the plant material from *A. dealbata* that is deposited directly under its canopy or through rainwater that passes down through the litter into the soil. The invasive plant parts that persist over the time in this environment and throughout

the phenological cycle are the leaves and pods, which continuously release allelochemicals into the soil (Aguilera *et al.*, 2015a, 2015b). The aim of the present study is to determine the effect that different plant parts of the invasive species *A. dealbata* may have, through direct contact or aqueous natural extracts on the germination process and early growth of the native species *Q. saponaria* and *H. aromaticum* in the central-south Chile.

MATERIALS AND METHODS

STUDY AREA AND PLANT MATERIAL

Plant material from *Acacia dealbata* was collected in the Quillón, approximately 67 km north of the city of Concepción in the Biobío Region, Chile (36°50'58.81"S, 72°32'4.91"W at 140 m a.s.l), characterized by its Mediterranean climate. This area is characterized by a temperature of 12.4 °C, 87.0% relative humidity and 827.0 mm average rainfall. The relief is undulating. Moreover, the natural predominant vegetation is woodland dominated by *Quillaja saponaria* Molina, *Lithrea caustica* (Molina) Hook. et Arn. and *Peumus boldus* Molina, with a rich understory consisting of herbs and leguminous shrubs. This type of forest in the study area is frequently observed being invaded and overcome by the greater competitiveness of this invasive species. The sizes of the stands of *A. dealbata* were highly variable, and in none of the cases native or non-native species were observed growing under the stands.

Plant material was collected under *A. dealbata*'s canopy after natural deposition in 2013. The litter sampling was conducted in January for pods and seeds, in May for leaves and in August for flowers (glomerulus globular inflorescence). Additionally, fresh leaves were collected directly from trees in May. After this, the plant material was stored in closed plastic bags, and carried back to the lab and refrigerated (~8 °C) until we used it in the bioassays (about a week). As regards the native species involved in this study, we used seeds from seed banks due to the lag in flowering times between *A. dealbata* and native species. Seeds of *Q. saponaria* were collected in San Carlos de Apoquindo, Santiago de Chile (33°27'S; 70°42'W at 900 m a.s.l) at the Mediterranean Ecological Research Station (EDIEM, Pontificia Universidad Católica de Chile), which is located in the foothills of the Andes. This area is characterized by a temperature of 13.9 °C, 72.0% relative humidity and 356.0 mm average rainfall. The relief is relatively undulating and there is abundant presence of grasses, shrubs and stands of *A. dealbata*. Seeds of *Helenium aromaticum* were obtained in Quebrada de La Plata (33°30'10.42"S; 70°55'21.73"W at 488 m a.s.l), in the municipality of Calera de Tango, in the Metropolitan Region of Santiago de Chile. This area is characterized by a temperature of 12.9 °C, 60.0% relative humidity and 623.2 mm average rainfall. In addition, the

relief is from flat to undulating and there is widespread presence of monocotyledonous and dicotyledonous herbs; as well as isolated tree and short stands of *A. dealbata*. A sample of each species was deposited in the Herbarium of the University of Concepción (CONC).

BIOASSAY WITH AQUEOUS EXTRACTS

The amount of plant material per square meter deposited naturally from *A. dealbata* was calculated by using 25 quadrats of 0.24 m² that were randomly distributed under its canopy. Predominant plant material inside these quadrats was collected, weighed and used to calculate a biomass fall rate; based on the average of the 25 quadrants. On average, approximately 32 g/m² of pods and leaf litter, 48 g/m² of flowers and 32 g of fresh leaves were collected. In the study region, the annual historical average rainfall is 827 L/m² (Santibáñez & Uribe 1993) and the average daily rainfall is about 2 L/m². In accordance to this and in order to mimic natural conditions, aqueous solutions of each plant material were established, soaking (72 h at 10 °C) the collected plant material per square meter with the amount of rain fallen in one day per square meter: pods, leaf litter and fresh leaves 32 g/2L, flowers 48 g/2L. The pH of the mother solutions was measured with a TESTO portable pH meter PH-206 (Lenzkirch, Germany), and ranged from 6.5 to 7, an adequate value for the germination and seedling growth of *Q. saponaria* (Rodríguez *et al.* 2005).

Twenty five seeds of *Q. saponaria* were uniformly placed in Petri dishes (9 cm diameter) lined with a Whatman No 1 paper disc soaked with 3 mL of each aqueous solution or distilled water as control. Dishes were sealed with Parafilm® to prevent evaporation and randomly placed in a growth chamber (Bioref-Pitec, Santiago, Chile) at 70% to 75% relative humidity, 12 h light/dark (~80 µmol m⁻² sec⁻¹) and 20 °C for 15 days. Seven replicates were maintained for each treatment and the experiment was repeated four times. Germination was calculated according to Fernández *et al.* (2013) and the value was expressed as percentage (GP). Radicle length (RL) and hypocotyl length (HL) of each seedling were measured and expressed in mm. Additionally, necrosis of the radicle (RN) was assessed and classified according to five categories (see description in Table I).

BIOASSAYS: DIRECT CONTACT OF PLANT MATERIAL

Since bioassays were performed in Petri dishes (63.6 cm²), different plant material was collected in an equivalent area. Samplings of leaves, flowers, pods and seeds were collected as described in previous experiment. Litter averages of these plant parts for a Petri dish were 2, 3, 3.3 and 4.3 g, respectively. Each different plant material was placed into a Petri dish covered with a Whatman N° 1 paper disc and then watered with 20 mL (leaves and pods), 15 mL (flowers) or 8 mL (seeds) of distilled water. The volume of water was chosen based on previous experiments to ensure

the minimum amount of water to allow germination. Petri dishes with no plant material but lined with Whatman N° 1 paper discs soaked with 5 mL of distilled water were used as controls. Twenty five seeds of *Q. saponaria* or 30 seeds of *H. aromaticum* were sown in each Petri dish, which were sealed and randomly placed in a growth chamber. Seven replicates were maintained for each treatment and the experiment was repeated four times. Growth conditions and measurements were the same as in previous experiment. The pH was measured directly in Petri dishes at the beginning and end of the experiment by pH-indicator strips pH 0 - 14 (Acilit® MERCK, Darmstadt, Germany), similar to the values of previous experiments.

STATISTICAL ANALYSES

Bioassays were established on the basis of a completely randomized experimental design. To test the effect of aqueous extracts and the direct effect of plant parts from *A. dealbata* on GP, HL, RL and RN of *Q. saponaria* and *H. aromaticum*, a one-way ANOVA and a Tukey's test were carried out for each plant material, in order to determine differences between treatments. Data normality and homogeneity of the variances were respectively evaluated with Kolmogorov-Smirnov and Levene tests. When the homogeneity of the variances was not achieved, data were Log (n+1) or root⁴ transformed (Zar 1996, Xie *et al.* 2000). Kruskal-Wallis and Mann-Whitney *U* tests were applied when data or its transformations did not meet the assumptions for parametric statistics. The level of significance for all statistical analyses was fixed at $P \leq 0.05$. All statistical analyses were carried out using STATISTICA 8.0 for Windows (StatSoft 2007).

TABLE I. Description of the radicle necrosis degree (Aguilera *et al.* 2015a).

TABLA I. Descripción del grado de necrosis de la radícula (Aguilera *et al.* 2015a).

NECROSIS DEGREE	DESCRIPTION
0	Radicle without discoloration and with abundant root hairs
1	Radicle light brown and reduction of root hairs up to 50 % of their length
2	Radicle brown and 5 to 10 % necrosis. No root hairs observed
3	Radicle dark brown and <i>ca.</i> 50 % necrosis. No root hairs observed
4	Radicle dark brown and more than 75 % necrosis. No root hairs observed

RESULTS

EFFECT OF AQUEOUS EXTRACTS ON THE GERMINATION AND EARLY GROWTH OF *QUILLAJA SAPONARIA*

The GP was significantly affected by the aqueous extracts of all plant parts ($P \ll 0.001$) (Fig. 1a). Flowers and fresh leaves caused the greatest decrease in GP (*ca.* 50 to 60%). The response of HL (Fig. 1b) and RL (Fig. 1c) was similar. HL was significantly reduced compared to control in all treatments ($P \ll 0.001$). Leaf litter extract was the one which most inhibited the radicle elongation of *Q. saponaria*'s seedlings in comparison with other treatments. Overall, RL was respectively reduced by 50% and 90% due to the action of fresh leaves and leaf litter aqueous extracts. All aqueous extracts caused disruption of the normal coloration of the radicle (zero degree in Table I), so that the degree of RN was significantly higher than control in all treatments ($P \ll 0.001$) (Fig. 1d), with values near grade 2 (Table I) in the case of fresh leaves and the pods aqueous extracts.

DIRECT EFFECT OF PLANT PARTS ON THE GERMINATION AND EARLY GROWTH OF *QUILLAJA SAPONARIA*

Except for pods, all other plant parts induced a significant reduction of germination of *Q. saponaria* compared to control ($P \ll 0.001$), with seeds and leaf litter having a complete inhibitory effect (Fig. 2a). HL of *Q. saponaria*'s seedlings significantly decreased due to the pods and flowers effects ($P \ll 0.001$) (Fig. 2b), respectively inducing reductions of 33% and 72%. Similarly, pods and flowers inhibited more than 70% of the RL, causing highly significant differences in respect to control ($P \ll 0.001$) (Fig. 2c). This growth reduction was accompanied by a significantly higher RN than the control ($P \ll 0.001$) (Fig. 2d) and an absence of root hairs caused by the resulting tissue necrosis, which prevented the formation of a radicle piliferous area (Fig. 3). In general, the effect of aqueous extracts and direct contact of plant parts with *Q. saponaria* seeds produced significant reductions in early seedling growth, but these effects were expressed more strongly when seeds were exposed directly to the plant material.

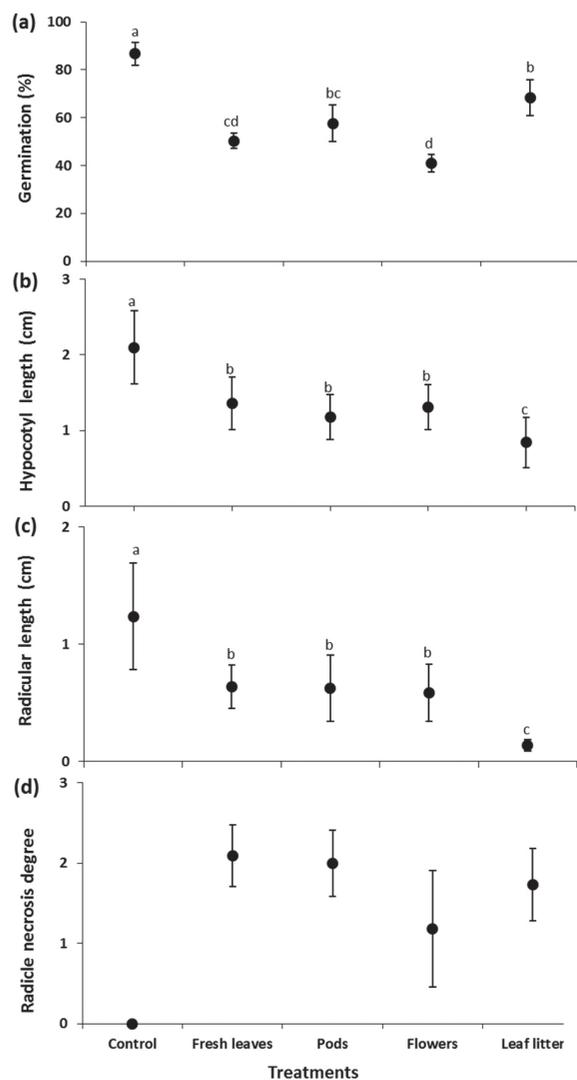


FIGURE 1. Effect of aqueous extract from different parts of *Acacia dealbata* on germination (a), hypocotyl length (b), radicle length (c) and radicle necrosis degree (d) of *Quillaja saponaria* seedlings. Mean \pm SD values ($n = 7$) followed by different letters indicate statistical significance according to Tukey *post hoc* test; in (d) nonparametric Kruskal-Wallis analysis was applied.

FIGURA 1. Efecto de extractos acuosos a partir de diferentes partes de *Acacia dealbata* en la germinación (a), longitud del hipocótilo (b), longitud de la radícula (c) y grado de necrosis radicular (d) de plántulas de *Quillaja saponaria*. Media \pm DE ($n = 7$) seguido por diferentes letras indica significación estadística de acuerdo con la prueba *post hoc* de Tukey; en (d) se aplicó el análisis no paramétrico Kruskal-Wallis.

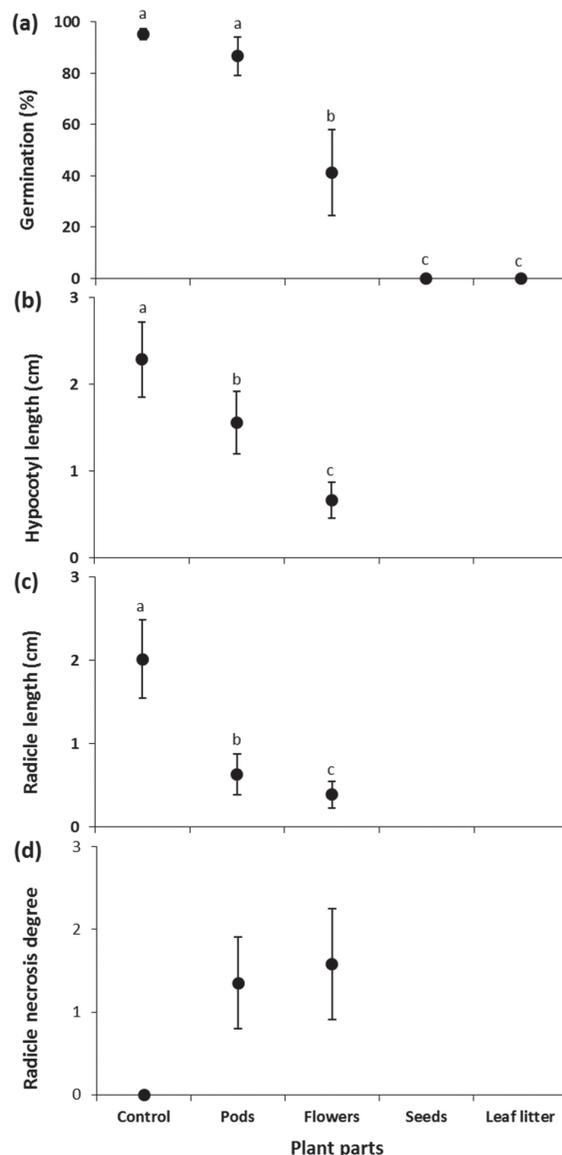


FIGURE 2. Direct effect of different parts of *Acacia dealbata* on germination (a), hypocotyl length (b), radicle length (c) and radicle necrosis degree (d) of *Quillaja saponaria* seedlings. Mean \pm SD values ($n = 7$) followed by different letters indicate statistical significance according to Tukey *post hoc* test; in (d) nonparametric Kruskal-Wallis analysis was applied.

FIGURA 2. Efecto directo de diferentes partes de *Acacia dealbata* en la germinación (a), longitud del hipocótilo (b), longitud de la radícula (c) y grado de necrosis radicular (d) de plántulas de *Quillaja saponaria*. Media \pm DE ($n = 7$) seguido por diferentes letras indica significación estadística de acuerdo con la prueba *post hoc* de Tukey; en (d) se aplicó el análisis no paramétrico Kruskal-Wallis.

DIRECT EFFECT OF PLANT PARTS ON THE GERMINATION AND EARLY GROWTH OF *HELENIUM AROMATICUM*

A. dealbata's pods did not affect the germination of *H. aromaticum*; however, the other plant parts significantly decreased the GP in comparison to control ($P << 0.001$) (Fig. 4a) in the case of values higher than 50%. Direct contact with leaf litter prevented the germination of this native herbaceous species. HL also significantly decreased compared to control in all treatments ($P << 0.001$), reaching the lowest values with the effect of pods and seeds (Fig. 4b). All plant parts dramatically prevented radicle growth (Fig. 4c), leading to values close to zero and significantly lower than control ($P << 0.001$). The pods reduced RL by 88%, while the flowers and seeds respectively caused a decrease of 94% and 96%. At the same time, growth inhibitions were accompanied by high levels of RN and it was significant different in all plant parts in respect to control ($P << 0.001$) (Fig. 4d). The pods were mainly induced to dark brown color rootlets, about 50% of which was necrotic; and the seeds led to the next RN degree 4 (Fig. 4d, Table I), which means that virtually all the radicle was necrotic.

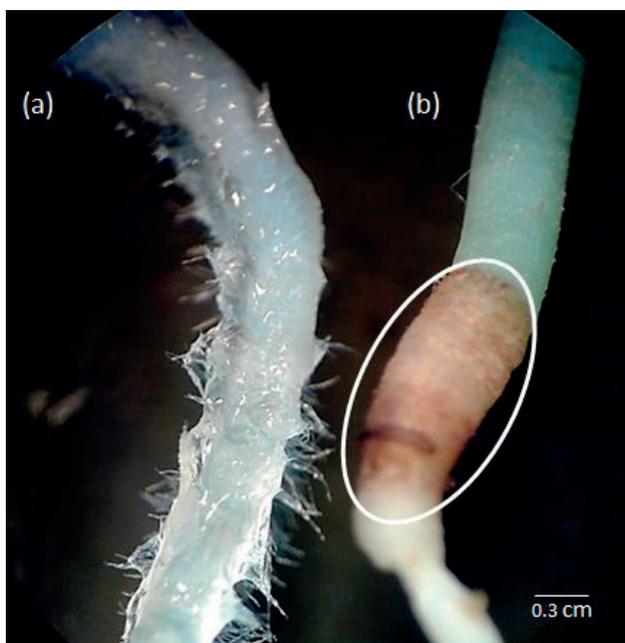


FIGURE 3. Direct effect of pods of *Acacia dealbata* on piliferous radicle zone of *Quillaja saponaria*. The abundant root hairs were shown in control (a) and root necrosis and lack root hairs were observed in affected radicle (b).

FIGURA 3. Efecto directo de vainas de *Acacia dealbata* en la zona pilifera de radícula de *Quillaja saponaria*. Se muestran abundantes pelos radicales en el control (a), y se observa necrosis radicular y ausencia de pelos radicales en la radícula afectada (b).

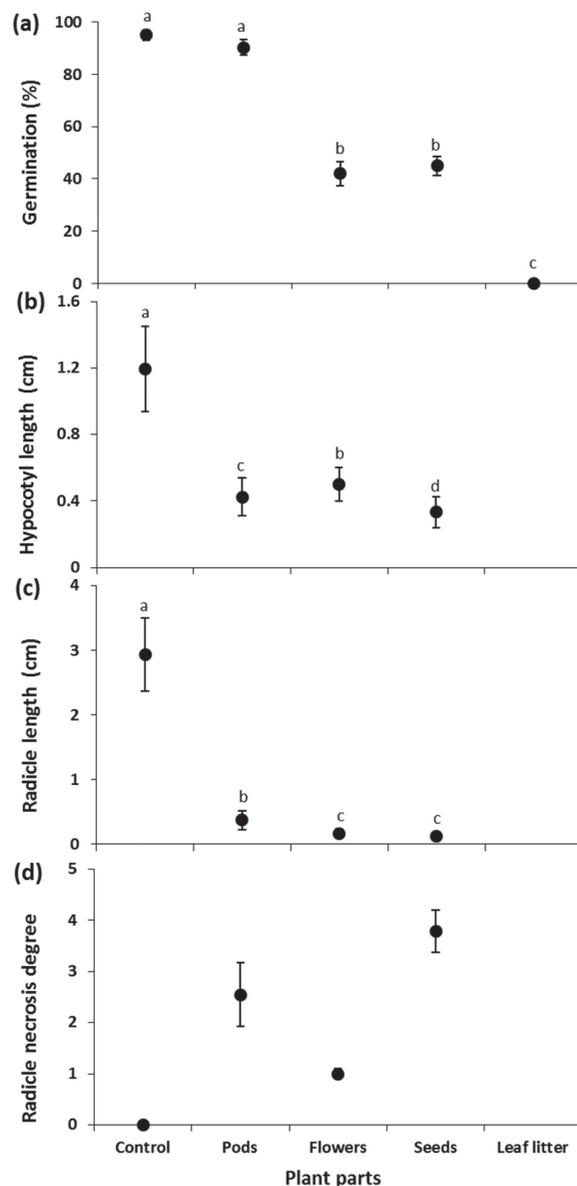


FIGURE 4. Effect of different parts of *Acacia dealbata* on germination (a), hypocotyl length (b), radicle length (c) and radicle necrosis degree (d) of *Helenium aromaticum* seedlings. Mean \pm SD values ($n = 7$) followed by different letters indicate statistical significance according to Tukey post hoc test; in (d) nonparametric Kruskal-Wallis analysis was applied.

FIGURA 4. Efecto directo de diferentes partes de *Acacia dealbata* en la germinación (a), longitud del hipocótilo (b), longitud de la radícula (c) y grado de necrosis radicular (d) de plántulas de *Helenium aromaticum*. Media \pm DE ($n = 7$) seguido por diferentes letras indica significación estadística de acuerdo con la prueba *post hoc* de Tukey; en (d) se aplicó el análisis no paramétrico Kruskal-Wallis.

DISCUSSION

Allelopathic compounds from *Acacia dealbata* significantly affected the germination and early growth of the two native target species. The responses obtained with aqueous extracts indicate *A. dealbata*'s ability to interfere with *Q. saponaria*'s germination process. In analogy, we can consider that the natural wetting of the leaves, flowers and pods deposited under its canopy must lead to the unleashing of biological activity that will negatively impact the establishment and survival of this species, from a competitive standpoint with *A. dealbata*. These effects were expressed more acutely through the bioassays that involved direct contact with the plant material, in which the interference of allelochemicals from leaves and seeds impeded germination absolutely.

Similar results were obtained with aqueous extracts of leaves from *Phytolacca americana* L., which inhibited germination plant growth and root of *Cassia mimosoides* L. var. *nomame* Makino at a rate of 50%, an effect that was attributed to phenolic compounds (Kim *et al.* 2005). Coincidentally, Sodaiezhadeh *et al.* (2009) found various phenolic acids in aqueous extracts of leaves from *Peganum harmala* L. that decreased germination and root length in *Avena fatua* L. and *Convolvulus arvensis* L. Also, aqueous extracts of leaves and seeds of *Acacia cyanophylla* Lindl. significantly reduced the germination, shoot length and root of *Triticum aestivum* L., *Lactuca sativa* L. and two weed species (El Ayeub *et al.* 2013).

Although *Q. saponaria* seeds germinate, seedlings interacting with the invasive species plant litter will have limited chances of competing for resources (especially soil nutrients). This statement is based on the significant reductions observed in hypocotyl and radicle growth, in addition to varying degrees of necrosis in the latter that will prevent the formation of root hairs and result in the inability to absorb water and nutrients from soil (Steudle 2000). Similar responses occurred in *H. aromaticum*, reflecting strong affectation of GP, to the point that seeds were not able to germinate in the presence of *A. dealbata*'s leaf litter, while the radicle practically did not grow at all when exposed to either part of the plant and showed high levels of RN. These results are consistent with those previously obtained by Aguilera *et al.* (2015a, 2015b) that used *L. sativa* as model plant to test *A. dealbata*'s allelopathic effects. The same authors argue that the different plant parts interact with each other, in order to maintain the allelopathic potential under the canopy of *A. dealbata* during its phenological cycle. Thus, the native species are constantly in contact with allelochemical sources capable of interfering in its interspecific relationships in a non-native range.

Biological activity obtained from different parts of *A. dealbata* has been reported by Aguilera *et al.* (2015a,

2015b), mainly attributing the aforementioned to the presence of the phenolic compound resorcinol and the non-protein amino acid maculosin from leaves. In flowers, the anisal benzaldehyde was found, while in pods, quinolizidine alkaloid lupanine was identified. The resorcinol was found to exhibit a high allelopathic power within a group of rice varieties (Dayan *et al.* 2005); while maculosin is considered a phytotoxin capable of producing strong inhibitions in plant cell suspension (Jun *et al.* 2012). Benzaldehydes, for their part, have been described as having high biological activity in *Arabidopsis thaliana*, registering inhibitory effects on germination and radicle length (Reigosa & Pazos-Malvido 2007). On the other hand, quinolizidine alkaloid lupanine, is bioactive and characteristic of some Fabaceae tribes (Wink & Carey 1994, Wink *et al.* 2010).

It is important to consider that both native species share the range of *A. dealbata* in Chile (Bierner 1978, Rodríguez *et al.* 2005, Donoso 2006, Fuentes *et al.* 2013), and are potential candidates to interact with it, due to its progressive invasion process. Therefore, throughout the ecological succession process, *A. dealbata* can interfere with the establishment of an herbaceous pioneer such as *Helenium aromaticum* (Gutiérrez 1993), and can also cause an impact in woods or forest patches inhabited by *Q. saponaria*. The vulnerability of these two native species, so different from a biotypic point of view, suggest that several native species would face a similar risk concomitantly to the progress of *A. dealbata*, something that has been shown in studies involving other plant species (Orr *et al.* 2005). In consequence, it is possible to infer the jeopardizing effect that this invasive species may pose over the native biodiversity on a short and long term basis, as well as to help us to understand the mechanisms used by *A. dealbata* in the invasion process within the a non-native range. These findings should be taken into account in order to establish efficient prevention and management strategies for this species. Additionally, this paper provides a basis for studies that explore the changes that allelochemicals may cause in chemical, physical and biological soil properties. Such alterations have been documented as part of the competitive abilities of invasive species in their non-native range (Jordan *et al.* 2008, Kim & Lee 2011, Steinlein 2013).

ACKNOWLEDGMENTS

This research was supported by the CONICYT Project 79100025, the Vice-Rectoría for Research and the Development of the University of Concepción and by the CONICYT/National PhD/2013-fellowship folio 63130029 awarded to NA. The authors are grateful to Mrs. Melanie Belanger for revision of the English.

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Recibido: 31.07.14
Aceptado: 17.03.15