

Leaf litter of *Kageneckia angustifolia* D. Don (Rosaceae) inhibits seed germination in sclerophyllous montane woodlands of central Chile

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Abstract Leaf litter accumulation can have either positive, negative or neutral effects on seed germination and seedling recruitment. In montane woodlands of the Mediterranean zone of central Chile, large amounts of leaf litter accumulate beneath the crowns of the summer semi-deciduous tree *Kageneckia angustifolia* and no regeneration of this or other plant species has been observed beneath this tree throughout the year. In a sample plot of 5000 m² we selected ten *K. angustifolia* trees and measured (1) leaf litter accumulation beneath and outside canopy; (2) the effects of time elapsed since burial on viability of *K. angustifolia* seeds with and without a leaf litter cover; (3) field seed germination with presence or absence of leaf litter and (4) the possible chemical effects of *K. angustifolia* leaf litter leachates on

seed germination of its own seeds and of other two co-occurring native shrubs species (*Guindilia trinervis* and *Solanum ligustrinum*). Our results show that a considerable accumulation of leaf litter occurred beneath *K. angustifolia*, and litter negatively affected seed viability and germination of this species in the field. Under laboratory conditions, *K. angustifolia* leaf litter leachates inhibited seed germination of its own seeds and of the two native shrub species. Chemical effects are likely involved in the negative effects of leaf litter on the recruitment of *K. angustifolia* in the montane sclerophyllous woodland of central Chile.

Keywords Leachate · Leaf litter inhibition · Montane sclerophyllous woodland

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Introduction

Leaf litter accumulation is an important factor involved in the regeneration dynamics of many plant communities (Facelli and Pickett 1991a; Xiong and Nilsson 1999). The recruitment of new individuals is very sensitive to the presence of leaf litter (Xiong and Nilsson 1997; 1999; Suding and Goldberg 1999) because leaf litter accumulation may modify the physical, chemical, and biological environment in which seeds germinate and

seedlings establish (Facelli and Pickett 1991a). The effects of leaf litter accumulation on plant recruitment can be positive, negative or neutral, direct or indirect, and can vary among species and seasons (Facelli 1994; Hastwell and Facelli 2000). For example, leaf litter negatively affects seed germination acting as a mechanical barrier for radicular growth (Clark and Clark 1989; Fowler 1986; Boserup and Reader 1995) and shoot emergence (Hamrick and Lee 1987; Green 1999). Leaf litter may also modify the quantity and quality of the light received by a seed in the ground, transmitting wavelengths that may be strongly inhibitory for seed germination (Vasquez-Yañes et al. 1990; Facelli and Pickett 1991a, b; Yirdaw and Leinonen 2002). Additionally, leaf litter can have negative effects on recruitment through phytotoxins that are leached to the soil, a phenomenon known as allelopathy (Rice 1979; Williamson 1990; Facelli and Pickett 1991a; Boserup and Reader 1995; Hilhorst and Karssen 2000). Leaf litter phytotoxins leached into the soil can impede either seed germination, seedling recruitment or both (Myster 1994; Al-Humaid and Warrag 1998; Preston and Baldwin 1999; Vellend et al. 2000). For instance, the bare zones around Californian shrubs such as *Adenostoma fasciculatum* and *Arctostaphylos glandulosa* are produced by phytotoxins that are leached from live and dead leaves after each rain, accumulating in the soil and inhibiting the germination and growth of herbaceous species (McPherson and Muller 1969; Chou and Muller 1972; Christensen and Muller 1975). Although the generality of the allelopathic effect of leaf litter in the Californian chaparral has been doubted (Keeley et al. 1985), similar patterns have been proposed for other Mediterranean-type climate zones such as the Mediterranean basin (Ballester and Vieitez 1979; Li and Romane 1997; Blondel and Aronson 1999) and Australia (del Moral et al. 1978; May and Ash 1990; Hobbs and Atkins 1991; Barrit and Facelli 2001), although there are also studies that do not support it (e.g., Hastwell and Facelli 2000; Harris et al. 2003). The importance of the allelopathic effect of leaf litter in species from the Mediterranean-type climate zone of central Chile has been seldom evaluated (see Montenegro et al. 1978; Fuentes et al. 1987).

Kageneckia angustifolia D. Don (Rosaceae) is the dominant tree species in the montane sclerophyllous forest of the Mediterranean-type climate zone of central Chile, growing from 1000 to 2100 m elevation. Above 1600 m elevation, it forms open woodlands where it is the only tree species present (Rundel 1981; Rodriguez et al. 1983). *K. angustifolia* is a summer semi-deciduous species that loses part of its foliage in order to endure the strong summer drought that characterizes central Chile (León 1993; Peñaloza 1996). The shed leaves accumulate mainly below the canopy, completely covering the soil beneath trees (Peñaloza 1996). Field observations indicate that beneath the canopy of *K. angustifolia* trees there is poor regeneration of this and other plant species throughout the year, even when native and introduced herbivores are excluded (Peñaloza 1996). The absence of plants below the canopy could be related with the negative effects of leaf litter accumulation on these sites. Chemical analyses of leaves of *K. angustifolia* have shown the occurrence of several compounds that can have inhibitory effects on seed germination (e.g., cucurbitacins and triterpenoids; Muñoz et al. 2002), suggesting that chemical inhibition of leaf litter is likely to be involved.

The aim of the present study was to quantify the accumulation of leaf litter below and outside the canopy of *K. angustifolia* trees and to evaluate its effect on the viability and germination of its seeds. The experiments were designed to answer the following questions: (1) Does leaf litter decrease seed viability? (2) Does leaf litter affect seed germination under field conditions? and (3) Do leachates of *K. angustifolia* leaf litter inhibit seed germination of its own seeds and other co-occurring shrub species?

Methods

Study area

Field work was conducted at Santuario de la Naturaleza Yerba Loca, located 50 Km east of the city of Santiago (33°20' S, 70°20' W, 1600 m a.s.l.). On the study area, mean monthly temperatures varies from a maximum of 22.9°C in

January (summer) to a minimum mean of 1.2°C in July (winter) (Peñaloza 1996). The summer drought period extends from October to March, while rains are concentrated during the south hemisphere winter months with an annual average of 445 mm (Santibáñez and Uribe 1992).

For measurements and experiments, we selected a monospecific stand of *K. angustifolia* on a gentle northeast-facing slope. To avoid browsing and destruction of the experiments by livestock, an exclusion plot of 5000 m² was built inside the stand.

Studied species

Kageneckia angustifolia D. Don (Rosaceae) is a dioecious tree, endemic to the Mediterranean-type climate zone of central Chilean (Rodríguez et al. 1983). At 32°–33°S latitude, this species occupies an ecotonal position between the montane forest, in which it is the single tree species present, and the high Andean vegetation, forming the treeline at 2200 m elevation (Rundel 1981; Piper et al. 2006). *K. angustifolia* can be described as a small tree species that forms open woodlands, with open canopies that do not produce sharp microclimatic differences between open areas and beneath canopy (Peñaloza et al. 2001). Additionally, this species undergo partial foliage loss during the summer season (León 1993; Peñaloza 1996). *K. angustifolia* flowering period occurs between November and December, whereas seed dispersal begins in February and it is extended until the end of April (León 1993). Seeds are small (6.3 mg) and wind-dispersed, with germination in the field occurring from July to October (Peñaloza et al. 2001). Unpublished seed germination trials at laboratory conditions indicated that this species is not light-demanding, and can germinate either at dark or light conditions with very high percentages in both cases (> 90%).

Leaf litter accumulation

To quantify spatial differences in leaf litter accumulation, 10 individual trees of *Kageneckia angustifolia* were selected at random. At each tree, two microhabitats were defined: (1) below

canopy, defined as the area comprised between the trunk and the projection of its crown border; and (2) open spaces, defined as the area between the external limit of the crown border to a distance of five times the radius of the crown, without contact with neighboring trees. At each selected tree, and at each microhabitat, four plastic trays of 500 cm² each were placed at random during the summer (February 1–April 31, 1993). The leaf litter accumulated at each tray was collected monthly and carried to the laboratory where it was dried in stoves at 70°C for 48 h, and weighed in a digital balance (precision 0.0001 g). Additionally, at the end of the growing season (April 2004) we measured the leaf litter remaining on the ground in both microhabitats. We randomly selected other ten *K. angustifolia* individuals and beneath each individual we collected all the leaf litter inside a quadrat of 1 m². This procedure was repeated in a paired sample taken in open spaces for each individual. Differences in the quantity of leaf litter accumulated between the two microhabitats as well as differences in the leaf litter remaining on the ground were analyzed with a paired samples *t*-test.

Viability of buried seeds that remain ungerminated

To monitor the viability of *Kageneckia angustifolia* seeds that remain ungerminated according to the elapsed time buried in soil with and without leaf litter cover, at the beginning of the seed dispersal season (end of February 1993) six burial sites (1 m² each) were chosen at random outside canopies. At each burial site the scarce leaf litter present was completely removed and 16 nylon-mesh envelopes with 100 seeds each were buried at 5 cm depth, and distanced 5 cm from each other. The eight buried envelopes placed in the left-hand side of each burial site were covered with a layer of 3 cm depth of *K. angustifolia* leaf litter, while the remaining eight envelopes (placed in the right-hand side) were covered with a wire mesh to exclude subsequent litterfall. Leaf litter employed in this experiment was a mixture of the leaf litter found in a 0.5 m² plot placed beneath each of the 10 adult trees used in the evaluation of leaf

litter accumulation. The layer of 3 cm depth corresponded to the average depth of *K. angustifolia* leaf litter beneath that adult trees. Since March, and during the eight subsequent months, an envelope from each burial site and treatment was recovered monthly. The viability of the seeds that remained ungerminated within the envelopes was assessed by germination trials in standard conditions of light and temperature during 30 days (12 h light, 25°C). Seeds remaining ungerminated after the trials were subjected to the tetrazolium test in order to verify their viability. The comparison of germination between months and treatments was carried out with a two-way repeated measures ANOVA.

Field germination

In March 1993, ten sites outside canopies were chosen in order to evaluate the effect of leaf litter on field seed germination. At each site, four bottomless plastic trays of 500 cm² each were placed on the soil. Two hundred seeds of *K. angustifolia* were deposited per tray and buried at 5 cm of depth using a homogeneous mixture of soil obtained from several areas inside the plot in order to avoid uncontrolled effects of the soil composition on seed germination. Two of the trays were covered with *K. angustifolia* leaf litter while the other two were left as a control. As in the previous experiment, trays were covered with a 3 cm depth layer of leaf litter, which corresponded to the average depth of the leaf litter found beneath adult trees. All the trays were buried at soil level, and were covered with a wire mesh in order to prevent the entrance or exit of seeds. This way, at each site, a total of 400 seeds m⁻² was obtained per treatment, a density that corresponded with the normal seed rain of this species in the area (León 1993). The number of germinated seeds was registered monthly during seven months. Germination phenology of control and leaf litter covered trays was compared with a Kolmogorov–Smirnov goodness of fit test, whereas differences in the mean germination per tray were assessed with a non-parametric Mann–Whitney *U* test.

Leaf litter leachate effects

Germination trials in the laboratory (bioassays technique *sensu* Inderjit and Dakshini 1995) were carried out in order to test possible chemical effects of *K. angustifolia* leaf litter on germination of *K. angustifolia*, and two native shrub species, *Guindilia trinervis* (Sapindaceae) and *Solanum ligustrinum* (Solanaceae), the most common native shrubs at the study site, which grow only on open areas away from *K. angustifolia* canopy (León 1993; Peñaloza 1996). For each species, 10 petri dishes with 50 seeds were prepared using wet filter paper as substratum in order to avoid the loss of humidity. Five petri dishes were watered with a leached extract of *K. angustifolia* leaf litter, whereas the remaining five petri dishes (control) were watered with distilled water. The leached extract was obtained following a similar procedure to that used in other studies (e.g., Noor et al. 1995, González et al. 1995, Al-Humaid and Warrag 1998). We soaked 150 g of dry *K. angustifolia* leaf litter, which corresponded ca. 1/3 of the leaf litter remaining on the ground at the end of summer, in 2 liters of distilled water for 36 h. In our study area, rains mainly occur during the fall (during winter precipitation occurs as snow; Santibáñez and Uribe 1992), and rain events can last up to 36 h with an accumulated total precipitation of ca. 6 mm (6 L m⁻², op. cit.), indicating that 150 g of leaf litter can be exposed to 2 liter of water during 36 h. All petri dishes were watered once at the beginning of the experiment and placed in a growth chamber with 12 hours of light and 25°C constant temperature. Germination was registered daily during a 30 days period. The statistical analyses were carried out with one-way Anova for each species, previous arcsin transformation of seed germination percentage.

Results

Leaf litter accumulation

The average dry weight of the leaf litter accumulated during the summer season below *K. angustifolia* was 7556.5 g/m² (± 353.5 g/m²),

while away from trees this figure was significantly lower ($t = 26.6$; $df = 9$; $P < 0.001$), with $88.8 \text{ gr/m}^2 (\pm 9.2 \text{ g/m}^2)$. This indicates that only 1.2% of leaf litter accumulation was deposited outside the canopies, while the rest remained below the canopy of *K. angustifolia*. This difference in the distribution of leaf litter was reinforced with the comparison of the leaf litter remaining on the ground at a single day. While 514.9 g/m^2 were found beneath *K. angustifolia* trees, 63.9 g/m^2 were found outside ($t = 16.7$; $P < 0.01$).

Viability of buried seeds that remain ungerminated

The presence of leaf litter significantly reduced the viability of seeds that remain ungerminated in the field ($F_{1,10} = 67.5$; $P < 0.001$), specially during the first four months of burial (Fig. 1, *a posteriori* Tukey's test, $P < 0.05$). Overall, viability of buried seeds, regardless of leaf litter treatment, varied significantly with time ($F_{3,30} = 114.2$; $P < 0.001$). For a given treatment, no differences in viability among the first three months after burial were observed, however an abrupt decay was observed at the fourth month (Fig. 1). Nonetheless, independently of the presence of leaf litter, buried seeds completely lost their viability after the fifth month of burial (Fig. 1). For those seeds that did not germinate in the labora-

tory, the tetrazolium test showed that they were unviable.

Field germination

Leaf litter reduced field germination at each date (Fig. 2, mean ± 2 SE were 45.5 ± 4.1 without litter and 20.7 ± 2.2 with litter, Mann–Whitney $U = 0.01$, $P < 0.001$). Seed germination in the field extended from July 31 through October 12, with a maximum on September 13 (Fig. 2). The first record of seed germination corresponded to trays not covered with leaf litter (Fig. 2), but overall germination phenology was not significantly affected by leaf litter (Kolmogorov–Smirnov, $D = 14$, $P = 0.079$; Fig. 2).

Leaf litter leachate effects

Seeds of *Kageneckia angustifolia* watered with distilled water germinated at a higher rate than seeds watered with the leached extract of leaf litter (Table 1; Fig. 3). Although germination percentage of seeds of *Guindilia trinervis* and *Solanum ligustrinum* were lower than those found in *K. angustifolia* (Fig. 3), the same negative effects of the *K. angustifolia* leaf litter leachate were observed on seeds of these species (Table 1; Fig. 3).

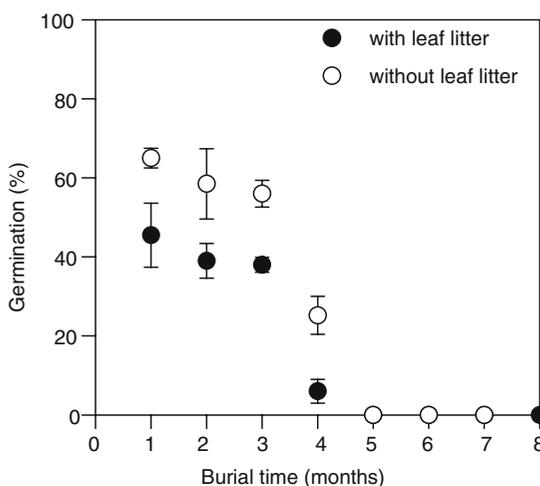


Fig. 1 Viability of *Kageneckia angustifolia* seeds after different time buried in soil with and without cover of *K. angustifolia* leaf litter. Means are shown with 2 SE

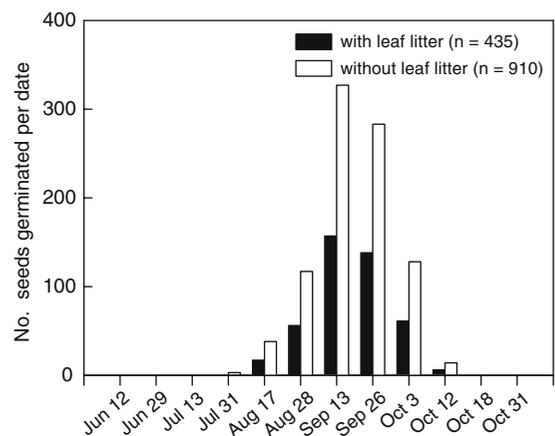
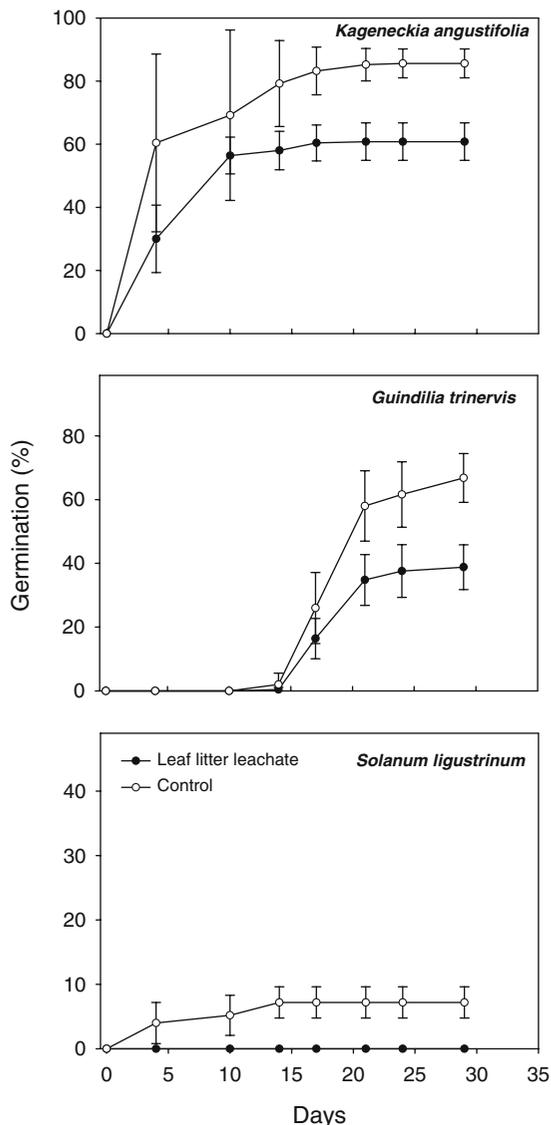


Fig. 2 Number of *Kageneckia angustifolia* seeds germinated at different dates with and without cover of *K. angustifolia* leaf litter. Numbers in the legend indicate the total number of seeds germinated at the end of the experiment

Table 1 One-way ANOVAs for the evaluation of *Kageneckia angustifolia* leaf litter leachate effect on seed germination of *K. angustifolia*, *Guindilia trinervis* and *Solanum ligustrinum*

Species	Source of variation	SS	d.f.	MS	F	P
<i>Kageneckia angustifolia</i>	Treatment	0.361	1	0.361	34.36	0.000378
	Error	0.084	8	0.011		
<i>Guindilia trinervis</i>	Treatment	0.644	1	0.644	20.90	0.001821
	Error	0.246	8	0.031		
<i>Solanum ligustrinum</i>	Treatment	0.013	1	0.013	28.04	0.000732
	Error	0.004	8	0.001		

**Fig. 3** Rates of germination of seeds of *Kageneckia angustifolia*, *Guindilia trinervis* and *Solanum ligustrinum* watered with leachate of *K. angustifolia* leaf litter (black circles) and with distilled water (control, white circles). Means are shown with 2 SE

Discussion

Our results show that a considerable accumulation of leaf litter occurred beneath *Kageneckia angustifolia* in the montane matorral of central Chile, and that the presence of this leaf litter negatively affected viability and seed germination of this species in the field. In addition, seed germination assays under laboratory conditions show that *K. angustifolia* leaf litter leachates inhibited seed germination of its own seeds as well as other two co-occurring native shrub species. Therefore, our findings suggest that leaf litter is likely to have a role in the low regeneration observed beneath adult trees.

Previous studies performed on Chilean matorral species suggested that leaf litter does not play a significant role in the dynamics of matorral because they failed to find evidence of leaf litter inhibition in several dominant tree and shrub species of lower elevation forest (Montenegro et al. 1978; Fuentes et al. 1987). The only species previously reported with this kind of effect in the Chilean matorral was *Flourensia thurifera* (Fuentes et al. 1987), which is restricted to dry matorral sites. These authors found that leaf litter leachates of *F. thurifera* negatively affected seed germination of dominant tree species of the Chilean matorral such as *Quillaja saponaria*, *Acacia caven* and *Lithrea caustica*. These results contrast with the findings in the climatically similar Californian chaparral, where more evidence was found about inhibitory effects of leaf litter leachates on seed germination (see McPherson and Muller 1969; Chou and Muller 1972; Keeley et al. 1985; Preston and Baldwin 1999). Thus, according to our findings, *K. angustifolia* can exert an important role in structuring vegetation through its leaf litter as it has been observed in

other trees inhabiting Mediterranean-type climate areas (e.g., *Quercus ilex* in the Mediterranean Basin; Li and Romane 1997).

Causes of leaf litter inhibition on seed germination, both at intra and interspecific levels, can be physical, chemical, biological or produced by the interaction of these factors (Facelli and Pickett 1991a). In the physical aspect, leaf litter deposition can alter the microclimatic environment in the seed bank by controlling the light levels and the temperature of soil, usually key factors in the germination of several species (Sydes and Grime 1981a,b; Holland and Coleman 1987). For instance, soil temperature below litter is usually lower than sites without litter (Facelli and Pickett 1991b) hence, the lower *K. angustifolia* seed germination observed in treatments with its own leaf litter may be related with litter-driven decreases in soil temperature. However, Peñaloza et al. (2001) found no significant differences in soil temperature between areas beneath canopy (where leaf litter tends to accumulate) and areas outside the canopy (devoid of leaf litter), suggesting that litter effects mediated by temperature are unlikely to be involved in the observed results.

Leaf litter may also modify the quantity and quality of light received by a seed in the soil, inhibiting seed germination (Vasquez-Yañes et al. 1990; Yirdaw and Leinonen 2002). Unpublished results indicate that *Kageneckia angustifolia* is able to germinate both under light and dark conditions, suggesting that the modification of light environment created by its own leaf litter may not be important for seed germination in this species. Therefore, the faster loss of viability and the lower germination of seed covered with leaf litter suggest that the effect of *K. angustifolia* leaf litter is unlikely to be mainly related with physical changes.

Chemical inhibition of seed germination or seedling establishment has been attributed to diverse factors, such as the presence of associated organisms (e.g., fungi, nematodes, insects) that liberate allelochemicals from the leaf litter (de Jong and Klinkhamer 1985) and/or the accumulation of leached secondary metabolites in the soil (Williamson 1990; Facelli and Pickett 1991a). Considering the faster loss of viability of seed

covered with leaf litter, their lower germination in the field, and the lower germination of *Kageneckia angustifolia* seeds exposed to a leached extract of leaf litter under laboratory conditions, it seems likely that dead leaves possess one or more water-soluble chemical compounds that depress seed germination. The hypothesis of the existence of secondary metabolites in the dead leaves of *K. angustifolia* is reinforced by the strong negative effect observed in the seed germination of other native species (*Guindilia trinervis* and *Solanum ligustrinum*; this study) and introduced grass species (e.g., *Hordeum vulgare*; Peñaloza 1996) when watered with the leached leaf litter extract. However, although our evidence suggests that important effects of leached secondary metabolites in soil, we can not rule out the possibility that the activity of the soil microfauna liberates allelochemical compounds from the dead leaves.

Some authors have questioned the relevance of the chemical effects of the leaf litter because the negative effects observed on seed germination could be related with the immobilization of nutrients, lack of O₂ in the soil and the toxic accumulation of CO₂ rather than leached, exuded or volatilized phytotoxins (de Jong and Klinkhamer 1985; Facelli and Pickett 1991a; Myster 1994; Xiong and Nilsson 1997). Although our field results do not permit us to rule out nutrient immobilization, lack of O₂ and/or CO₂ accumulation, laboratory results strongly suggest the existence of water-soluble allelochemicals in the leaf litter of *K. angustifolia* that affect seed germination. Together with the presence of cucurbitacins and triterpenoids in *K. angustifolia* leaves (Muñoz et al. 2002), Peñaloza and Muñoz (unpublished results) have recorded the presence of cyanogenic compounds such as cyanohidrin, which could act as inhibitors of seed germination at the embryo level, as it has been shown in other plant species (Bewley and Black 1994) or act in herbivory defense (Feeny 1991) (see below). The experiments with buried seeds germinated under laboratory conditions and with seeds watered with leaf litter leachates indicate that the loss of the seed germination in *K. angustifolia* would be related to embryonic death. The results of the bioassay suggest that this same mechanism could

affect the germination of the others plant species studied.

It has been suggested that allelopathy can be very important in the interference between plant species (Ridenour and Callaway 2001). The inhibition of germination by *K. angustifolia* leaf litter leachates may be interpreted as a mechanism mediated by allelopathic factors to reduce interspecific competition (Rice 1979) or as a strategy to avoid future competition (Inderjit and del Moral 1997). For example, Vandermast et al. (2002) suggest that leachate from *Castanea dentata* leaf litter could suppress germination and growth of competing shrub and trees species such as *Rhododendron maximum* and *Tsuga Canadensis* and that allelopathy was a mechanism whereby *C. dentata* may have controlled vegetative composition and dominated eastern forests. Likewise, several other studies have also found some inhibitory effects of leaf litter leachates on seed germination and growth of associated ground cover species (e.g., González et al. 1995; Noor et al. 1995; Barrit and Facelli 2001; Ibáñez and Schupp 2002; Dzwonko and Gawronski 2002). Therefore, it can be argued that the leaf litter of the dominant tree species *K. angustifolia* acts as a factor regulating the structure of the community such as it occurs in many plant communities ranging from grasslands to forests (Facelli and Facelli 1993; Inderjit and del Moral 1997; Nilsen et al. 1999). In addition, the negative effects of *K. angustifolia* leachates may be greater if we consider for example, phenolic acids leached from living parts of the adult trees that can have a significant additional allelopathic effect, which would be added to that being leached from litter. Experimental designs that include the effects of throughfall and stemflow from adult trees may shed light about the importance of these processes.

As well as *K. angustifolia*, there are many examples of autotoxic effects of leaf litter on seed germination (Grace 1983; de Jong and Klinkhamer 1985; Saxena et al. 1996; Li and Romane 1997). Some of these authors have suggested that these autotoxic effects may be a consequence of other processes such as nutrients and/or water immobilization (e.g., Grace 1983; de Jong and Klinkhamer 1985). Thus, the

negative effect of *K. angustifolia* on its own seeds (the intraspecific effect) may be interpreted for example, as a cost of reducing interspecific competition or herbivory. With respect to herbivory, Rice (1979) proposed that many of the molecules that confer anti herbivory properties to plants are the same as those that cause allelopathy. This could be the case of *K. angustifolia* where chemical cyanogenic compounds (a very well known deterrents against herbivores; Feeny 1991) such as cyanohidrin, cucurbitacins and prunasin have been isolated from its leaves (Muñoz et al. 2002).

Thus, based on the results of our experiments, we can conclude that the absence of natural regeneration beneath *Kageneckia angustifolia* trees is related with the accumulation of leaf litter of this species. Chemical effects are likely part of this phenomenon in the montane sclerophyllous woodland of the Mediterranean-type climate zone of central Chile.

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References

- Al-Humaid AI, Warrag MOA (1998) Allelopathic effects of mesquite (*Prosopis juliflora*) foliage on seed germination and seedling growth of bermudagrass (*Cynodon dactylon*). *J Arid Environ* 38:237–243
- Ballester A, Vieitez E (1979) The allelopathic potential of *Erica australis* and *E. arborea*. *Bot Gazette* 140:433–436
- Barrit AR, Facelli JM, (2001) Effects of *Casuarina pauper* litter and grove soil on emergence and growth of understorey species in an arid lands of South Australia. *J Arid Environ* 49:569–579
- Bewley JD, Black M (1994) *Seeds: physiology of development and germination*. 2nd edn. Plenum Press, New York
- Blondel J, Aronson J (1999) *Biology and wildlife of the Mediterranean region*. Oxford University Press, New York
- Bosy JL, Reader RJ (1995) Mechanisms underlying the suppression of forbs seedling emergence by grass (*Poa pratensis*) litter. *Funct Ecol* 9:635–639

- Chou C, Muller CH (1972) Allelopathic mechanism of *Arctostaphylos glandulosa* var. *zacaensis*. *Am Midl Nat* 88:324–347
- Christensen NL, Muller CH (1975) Effects of fire on factors controlling plant growth in *Adenostoma* chaparral. *Ecol Monogr* 45:29–55
- Clark DB, Clark DA (1989) The role of physical damage in the seedling mortality regime of a neotropical forest. *Oikos* 55:225–230
- de Jong TJ, Klinkhamer PGL (1985) The negative effects of litter of parent plants of *Cirsium vulgare* on their offspring: autotoxicity or immobilization? *Oecologia* 65:153–160
- del Moral R, Willis RJ, Ashton DH (1978) Suppression of coastal heath vegetation by *Eucalyptus baxteri*. *Aust J Bot* 26:203–219
- Dzwonko Z, Gawronski S (2002) Influence of litter and weather on seedling recruitment in a mixed Oak-Pine woodland. *Ann Bot* 90:245–251
- Facelli JM (1994) Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. *Ecology* 75:1727–1735
- Facelli JM, Facelli E (1993) Interactions after death: plant litter controls priority effects in a successional community. *Oecologia* 95:277–282
- Facelli JM, Pickett STA (1991a) Plant litter: its dynamics and effects on plant community structure. *Bot Rev* 57:1–32
- Facelli JM, Pickett STA (1991b) Plant litter: light interception and effects on an old-field plant community. *Ecology* 72:1024–1031
- Feeny P (1991) The evolution of chemical ecology: contributions from the study of herbivorous insects. In: Rosenthal GA, Berenbaum MR (eds) *Herbivores. Their interactions with secondary plant metabolites*, Vol. II, 2nd edn. Academic Press, pp. 1–44
- Fowler NL (1986) Microsite requirements for germination and establishment of tree grass species. *Am Midl Nat* 115:131–145
- Fuentes ER, Espinoza G, Gajardo G (1987) Allelopathic effects of the Chilean matorral shrub *Flourensia thurifera*. *Revista Chilena de Historia Natural* 60:57–62
- González L, Souto XC, Reigosa MJ (1995) Allelopathic effects of *Acacia melanoxylon* R.Br. phyllodes during their decomposition. *Forest Ecol Manage* 77:53–63
- Grace JB (1983) Autotoxic inhibition of seed germination by *Thypha latifolia*: an evaluation. *Oecologia* 59:366–369
- Green P (1999) Seed germination in *Chrysophyllum* sp. nov., a large-seeded rainforest species in north Queensland: effects of seed size, litter and seed position. *Aust J Ecol* 26:608–613
- Hamrick JL, Lee JM (1987) Effects of soil surface topography and litter cover on germination, survival and growth of musk thistle (*Cardus nutans*). *Am J Bot* 74:451–457
- Harris MR, Lamb D, Erskine PD (2003) An investigation into the possible inhibitory effects of white cypress pine (*Callitris glaucophylla*) litter on the germination and growth of associated ground cover species. *Aust J Bot* 51:93–102
- Hastwell GT, Facelli JM (2000) Effects of leaf litter on woody seedlings in xeric successional communities. *Plant Ecol* 148:225–231
- Hilhorst H, Karssen C (2000) Effect of chemical environment on seed germination. In: Fenner M (ed) *Seeds. The ecology of regeneration in plants communities*. Cab International, Oxon, UK, pp. 293–309
- Hobbs RJ, Atkins L (1991) Interactions between annuals and woody perennials in a Western Australian nature reserves. *J Vege Sci* 2:643–654
- Holland AE, Coleman DC (1987) Litter placement effects on microbial and organic matter dynamics in an agroecosystem. *Ecology* 68:425–433
- Ibañez I, Schupp EW (2002) Effects of litter, soil surface conditions, and microhabitat on *Cercocarpus ledifolius* Nutt. Seedling emergence and establishment. *J Arid Environ* 52:209–221
- Inderjit, Dakshini KMM (1995) On bioassays in allelopathy. *The Bot Rev* 61:28–44
- Inderjit, del Moral R (1997) In separating resource competition from allelopathy realistic? *Bot Rev* 63:221–230
- Keeley JE, Morton BA, Pedrosa A, Trotter P (1985) Role of allelopathy, heat and charred wood in the germination of Chaparral herbs and suffrutescents. *J Ecol* 73:445–458
- Li J, Romane FJ (1997) Effects of germination inhibition on the dynamics of *Quercus ilex* stands. *J Vege Sci* 8:287–294
- León P (1993) Efecto del espaciamiento entre plantas en la producción de frutos y semillas en *Kageneckia angustifolia* Don., un árbol dioico del bosque esclerófilo montano de Chile Central. Master thesis, Universidad de Chile, Santiago
- May FE, Ash JE (1990) An assessment of the allelopathic potential of *Eucalyptus*. *Aust J Bot* 38:245–254
- McPherson JK, Muller CH (1969) Allelopathic effects of *Adenostoma fasciculatum*, “chamise”, in the Californian chaparral. *Ecol Monogr* 39:177–198
- Montenegro G, Rivera O, Bas F (1978) Herbaceous vegetation in the Chilean matorral. *Oecologia* 36:237–244
- Muñoz O, Estevez-Braun AM, Ravelo AG, González AG (2002) Cucurbitacin F in leaves of *Kageneckia angustifolia* (Rosaceae). *Zeitschrift fur naturforschung C-A J Biosci* 57:208–209
- Myster RW (1994) Contrasting litter effects on old field tree germination and emergence. *Vegetatio* 114:169–174
- Nilsen ET, Walker JF, Miller OK, Semones SW, Lei TT, Clinton BD (1999) Inhibition of seedlings survival under *Rhododendron maximum* (Ericaceae): could allelopathy be a cause? *Am J Bot* 86:1597–1605
- Noor M, Salam U, Khan MA (1995) Allelopathic effects of *Prosopis juliflora* Swartz. *J Arid Environ* 31:83–90
- Peñaloza AP (1996) Consideraciones microclimáticas en la sobrevivencia de semillas y plántulas de *Kageneckia angustifolia* Don., una especie del bosque esclerófilo montano de Chile Central. Master thesis, Universidad de Chile, Santiago.

- Peñaloza A, Cavieres LA, Arroyo MTK, Torres C (2001) Efecto nodriza intra-específico de *Kageneckia angustifolia* D. Don (Rosaceae) sobre la germinación de semillas y sobrevivencia de plántulas en el bosque esclerófilo montano de Chile central. *Revista Chilena de Historia Natural* 74:539–548
- Piper FI, Cavieres LA, Reyes-Diaz M, Corcuera LJ (2006) Carbon sink limitation and frost tolerance control performance of the tree *Kageneckia angustifolia* D. Don (Rosaceae) at the treeline in central Chile. *Plant Ecology* 185:29–39
- Preston CA, Baldwin IT (1999) Positive and negative signals regulate germination in the post-fire annual, *Nicotiana attenuata*. *Ecology* 80:481–494
- Rice EL (1979) Allelopathy, an update. *Bot Rev* 45:15–109
- Ridenour WM, Callaway RM (2001) The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. *Oecologia* 126:444–450
- Rodríguez R, Matthei O, Quezada M (1983) Flora Arbórea de Chile. Universidad de Concepción, Concepción
- Rundel P (1981) The Matorral zone of Central Chile. In: Di Castri F, Goodall DW, Spetch RL (eds) Mediterranean-type shrublands. Elsevier, Netherlands, pp 175–201
- Santibañez F, Uribe JM (1992) Agroclimatología de Chile Central: Regiones V y Metropolitana. Universidad de Chile, Santiago
- Saxena A, Singh DV, Joshi NL (1996) Autotoxic effects of pearl millet aqueous extracts on seed germination and seedling growth. *J Arid Environ* 33:255–260
- Suding KN, Goldberg DE (1999) Variation in the effect of vegetation and litter on recruitment across productivity gradients. *J Ecol* 87:436–449
- Sydes C, Grime JP (1981a) Effects of tree litter on herbaceous vegetation in the deciduous woodlands: I. Field investigations. *J Ecol* 69:237–248
- Sydes C, Grime JP (1981b) Effects of tree litter on herbaceous vegetation in the deciduous woodlands: II. An experimental investigation. *J Ecol* 69:249–262
- Vandermaast DM, Van Lear DH, Clinton BD (2002) American chestnut as an allelopath in the southern Appalachians. *Forest Ecol Manage* 165:173–181
- Vázquez-Yanes C, Orozco-Segovia A, Rincón E, Sánchez-Coronado ME (1990) Light beneath the litter in a tropical forest: effect on seed germination. *Ecology* 71:1952–1958
- Vellend M, Lechowicz MJ, Waterway MJ (2000) Germination and establishment of forest sedges (*Carex*, Cyperaceae): test for home-site advantage and effects of leaf litter. *Am J Bot* 87:1517–1525
- Williamson GB (1990) Allelopathy, Koch's postulates, and the neck riddle. In: Grace JB, Tilman D (eds) Perspectives on plant competition. Academic Press, New York, pp. 143–162
- Xiong S, Nilsson C (1997) Dynamics of leaf litter accumulation and its effects on riparian vegetation: a review. *Bot Rev* 63:240–264
- Xiong S, Nilsson C (1999) The effects of plant litter on vegetation: a meta-analysis. *J Ecol* 87:984–994
- Yirdaw E, Leinonen K (2002) Seed germination responses of four afro-montane tree species to red/far-red ratio and temperature. *Forest Ecol Manage* 168:53–61