Effects of *Agathis australis* (New Zealand kauri) leaf litter on germination and seedling growth differs among plant species

Sarah V. Wyse* and Bruce R. Burns

School of Biological Sciences, The University of Auckland, Private Bag 92019, Auckland 1142, New Zealand
*Author for correspondence (Email: sarah.wyse@auckland.ac.nz)

Abstract: *Agathis australis* (*A. australis*, New Zealand kauri, Araucariaceae) exerts a substantial influence on soil properties and nutrient cycling, and mature specimens form an acidic organic soil layer beneath them that can be up to 2 m deep. We investigated whether phytotoxic compounds occurred in *A. australis* leaf litter and organic soil, and whether allelopathy may explain the distinctiveness of plant communities surrounding *A. australis*. We extracted water-soluble compounds from fresh litter, and conducted bioassays of seed germination and seedling growth in these extracts on both *A. australis*-associated and non-associated species. Germination of all species except *A. australis* was inhibited by extracts from *A. australis* litter, which probably contains phytotoxic compounds. Germination of a forest species that is not associated with *A. australis* was inhibited by the low pH organic soils collected from beneath mature *A. australis*, but when these soils were neutralised using lime, its germination was not inhibited. *Lactuca sativa*, a species highly sensitive to phytotoxic compounds, was negatively affected by both the low pH of the organic soil and the presence of phytotoxic compounds. In contrast, there was no effect of the organic soil on the germination and growth of *A. australis*-associated species. These results suggest that the high acidity of *A. australis* organic soil plays a considerable role in structuring the composition of plant communities associated with *A. australis*, and also that *A. australis* litter probably contains unidentified phytotoxic compounds that may exert additional direct allelopathic effects on sensitive species.

Keywords: allelopathy; Araucariaceae; organic soils; phytotoxicity; soil pH

Introduction

Agathis australis (D. Don) Lindl. ex Loudon (*A. australis*, New Zealand kauri, Araucariaceae) is endemic to the lowland warm temperate rainforests of northern New Zealand. Commonly attaining diameters of 1 m, rarely up to 3–7 m (Allan 1961), and with a lifespan of up to 1700 years (Ahmed & Ogden 1987), *A. australis* is the largest and longest lived tree species in New Zealand forests. *Agathis australis* exerts a considerable influence on the soil environment beneath its canopy as the litter shed by the species, high in phenolic compounds and tannins, decomposes slowly (Enright & Ogden 1987) to form an organic soil layer that can be up to 2 m deep beneath mature specimens (Silvester & Orchard 1999; Silvester 2000). This deep organic layer contains high levels of stored carbon and nitrogen (values of up to 225 t C ha^{-1} and 6.54 t N ha^{-1} have been recorded), and typically has pH values of around 4 (Silvester & Orchard 1999; Silvester 2000; Wyse 2012).

In forests across its range, *A. australis* is distributed in patches surrounded with forest dominated by broadleaved angiosperm species (Ogden & Stewart 1995). The species composition of the vegetation communities found in association with these *A. australis* stands is distinct from that of the flora beneath the surrounding broadleaved forest canopies (Cockayne 1908; Bieleski 1979), and abrupt changes in composition can be observed across the boundary of canopy types (Burns & Leathwick 1996). Research has shown that plant communities dominated by mature *A. australis* are highly homogeneous on the scale of a few hectares, and that stands containing similar vegetation composition, in addition to *A. australis*, can be widely separated geographically (Ahmed & Ogden 1987; Ogden & Stewart 1995). Along with the underlying edaphic

conditions of the sites where these stands are located, the vegetation composition of these plant communities may be influenced by factors such as allelopathic chemicals, including the phenolic compounds within *A. australis* leaf litter (Verkaik et al. 2006), and the low pH of the soils that develop beneath *A. australis* (Silvester & Orchard 1999; Silvester 2000; Wyse 2012). These factors could affect the germination and growth of *A. australis* and co-occurring plant species.

Allelopathy can be defined as a biological phenomenon whereby a plant or microorganism produces biochemicals that affect the ability of other plants to grow, survive, and reproduce (Whittaker & Feeney 1971; Rice 1984). This phenomenon has a role in the vegetation dynamics of a variety of forest types ranging from boreal forests to tropical rainforests, affecting seedling establishment and survival, and thereby influencing vegetation patterns (Pellissier & Souto 1999). Traditionally, the definition of allelopathy has described direct plant–plant chemical interference; however, some reviewers have expanded this to incorporate the indirect effects of allelochemicals on plants through their influence on ecosystem-level processes, such as nutrient availability and soil pH (Wardle et al. 1998; Inderjit & Weiner 2001). Such indirect effects of phytotoxins may be more important within plant communities than the direct effects of phytotoxic compounds released by one plant on another plant (Inderjit & Weiner 2001). The indirect effects of plant secondary metabolites may also act to confound the direct allelopathic effects of these compounds on neighbouring species. Phenolic compounds are present in the litter of *A. australis* (Bloomfield 1957; Verkaik et al. 2006) and these are phytotoxic (Blum 1996). Extracts of leaves from the Australian species *Agathis robusta* contain α-pinene, germacrene-D, and spathulenol and these have been shown to inhibit germination and growth of other plants (Seal et al.

2010). However, the phytotoxic potential of *A. australis* plant material has not been examined.

Soil pH is a factor that is influenced by the chemistry of plant litter, with secondary metabolites in recalcitrant litter acting to lower soil pH (Finzi et al. 1998). This low soil pH in turn acts to inhibit plant growth via multiple mechanisms. For example, low pH increases the concentrations of H^+, Al^{3+}, and Mn^{2+} and leads to toxicity of these ions. In contrast, low pH also acts to decrease the concentrations of cations such as magnesium and calcium, and reduce phosphorus and molybdenum solubility, resulting in plant nutrient deficiencies (Marschner 1995). In addition, inhibition of root growth and water uptake results in further nutrient deficiencies, drought stress and increased nutrient leaching (Marschner 1995). In very acid (pH < 4) organic soils H^+ toxicity may be the major growth-inhibiting factor for non-tolerant plants, while in acid mineral soils (pH 4.0–5.0) aluminium toxicity and/or phosphorus deficiency can dominate (Kidd & Proctor 2001). Previous studies have examined the role of the low pH of the *A. australis* organic layer on soil processes and podzolisation (e.g. Jongkind et al. 2007), but there have been no studies investigating the potential effects of this low pH on plant communities.

The present study investigates the phytotoxic potential of *A. australis* leaf litter, and determines whether the *A. australis* organic soil formed from this litter could have an allelopathic effect that may explain the vegetation patterns associated with the species. We examine the potential direct allelopathic effects of secondary metabolites within the organic soil on seed germination and early seedling growth, as well as indirect effects through their influence on soil pH. We use a series of bioassays that quantify the effects of *A. australis* litter extracts and organic soil on the seed germination and early seedling growth of four plant species, including *A. australis*.

Methods

Extract preparation

Freshly fallen leaf litter was collected from beneath five *A. australis* individuals in the University of Auckland scientific reserve at Huapai, West Auckland (36º47.7′ S, 174º29.5′ E). Any bryophytes and lichens were removed from the samples and the combined litter samples were dried at 60°C for 24 h. Samples were chopped to pass through a 2-mm sieve and mixed with filtered water at a concentration of 120 g L^{-1} to extract water-soluble compounds. The homogenised samples were stored in the dark at 25°C for 24 h before being filtered through a 2-mm mesh and then LabServ© medium retention qualitative filter paper. Extracts were diluted with filtered water to obtain additional solutions at concentrations equivalent to 40 and 80 g L^{-1}. To determine whether any phytotoxic effect of the extracts could simply be attributable to their low pH, a sample of the full-strength extract solution was brought up to a neutral pH with the addition of $NaHCO_3$. The pHs of all extract solutions were measured using a benchtop pH/mV meter (860031, Sper Scientific, Arizona, USA). All solutions were stored in the dark at 4°C until use.

Experimental design

The effects of the extract solutions on the germination and growth of four plant species were investigated. Plant species were *A. australis*, *Melicytus macrophyllus* (large-leaved māhoe), *Melicytus ramiflorus* (māhoe) and *Lactuca sativa*

(lettuce). *Lactuca sativa* is a species highly sensitive to the presence of phytotoxins and is frequently used in laboratory bioassays examining phytotoxicity and allelopathy (Braine et al. 2012). Its use here is as an indicator species to show the presence of phytotoxins, should all the forest species prove tolerant of the potential chemicals. *Melicytus macrophyllus* is commonly found under the canopies of mature *A. australis*, whereas *M. ramiflorus* is generally absent from *A. australis* stands but occurs abundantly in the surrounding forest (Cockayne 1908; Wardle 1991). To break seed dormancy, *Melicytus macrophyllus* and *M. ramiflorus* were cold-stratified at 4°C for 4 weeks prior to the onset of the experiment. *Agathis australis* and *Lactuca sativa* seed do not exhibit dormancy, so such measures were not necessary with them.

The extract bioassays were carried out in Petri dishes containing a layer of filter paper. Five replicates, consisting of 15 seeds each, were used for each combination of seed species and extract type, and a filtered water control. Initially, 2 ml of extract or filtered water was added to each dish, and the filter paper was kept moist with filtered water for the course of the experiment.

To investigate whether any phytotoxic compounds present in the extract solutions could be present in the organic soil formed beneath *A. australis* at sufficient concentrations to have a biological effect, we carried out further bioassays to examine the effects of this organic soil on seed germination and early seedling growth. These bioassays were undertaken concurrently with the extract bioassays, and using the same four species. The organic litter horizons (A_o) beneath mature *A. australis* can be differentiated into three layers: the upper (L) layer of largely intact material, the middle (F) layer of fermenting partially decomposed material, and the lower (H) layer of black friable humus (Silvester & Orchard 1999). Three soil samples were taken from the F horizon of the organic soil beneath each of three mature (diameter at breast height > 1 m) *A. australis* individuals also at the University of Auckland scientific reserve at Huapai, West Auckland. At the sites where samples were taken, the F layer was located between depths of approximately 2–5 cm. Any roots were removed from the soil samples, and they were bulked and dried at 60°C for 48 h, before being passed through a 2-mm sieve and homogenised. Oven-drying the samples allowed equal volumes of soil, and therefore concentrations of potential chemicals, to be applied per replicate for the two soil treatments without variation in soil moisture leading to variations in the actual amounts applied, and thereby potentially confounding the results.

To determine whether any inhibitory effect of the organic soil on seed germination and early seedling growth could simply be the result of the low pH, assays were also carried out using organic soil where the pH was neutralised with the addition of lime ($CaCO_3$). Lime was ground to pass through a 2-mm sieve and mixed with the dried and sieved organic soil at a dry-weight ratio of two parts soil to one part lime, which adjusted the pH to approximately neutral. Both the pure and limed organic soils were mixed with filtered water at a ratio of 1:2 (soil weight excluding lime to water), then placed in Petri dishes to entirely cover the dish with a layer approximately 5 mm thick. Again, five replicates, consisting of 15 seeds each, were used for each species and soil-type combination. Seeds were placed directly on the soil, and watered with 2 ml of filtered water. The soil was kept moist with additions of filtered water during the course of the experiment. Soil pH was assessed with a 1:5 suspension of dry soil in water, shaken vigorously, and measured with the benchtop pH meter.

Assessment of germination and early seedling growth

As germination times differed considerably among species, the time at which germination was assessed was individual to each species and was determined by the time taken for seeds to germinate within the water control treatments. Germination success of a species was assessed at the time when no new seeds of that species had germinated in the control treatments after a period of 10 days. Seeds were considered germinated once they produced a 2-mm-long radical. Per cent germination was then calculated for each Petri dish. For every species, germination success was compared among treatments using analysis of variance (ANOVA).

The effect of the extracts on early seedling growth was assessed by measuring the lengths of 10-day-old seedlings from the shoot apex to the apex of the primary root, using a Vernier calliper. Where present, secondary roots were not included. In some instances, particularly with *Melicytus ramiflorus*, the few seeds that were able to germinate in some treatments did not survive to reach 10-day-old seedlings. For the species and treatments in which this occurred, or in which germination rates were very low, these treatments were excluded from the analysis. For each species, seedling length was compared among treatments using ANOVA, and pairwise comparisons were made using Tukey's HSD tests ($\alpha = 0.05$). Analyses were performed in R v. 2.13.0 (R Development Core Team 2011).

Results

All litter extract solutions had pH values around 4, with more concentrated solutions having slightly lower pH values (Table 1). With a value of approximately 3, the pH of the organic soil taken from the F horizon was lower than that of the extract solutions. The addition of the $NaHCO_3$ to the 120 g L^{-1} extract solution and the $CaCO_3$ to the organic soil raised these pH values to near-neutral.

There was no effect of treatment on the germination success of *A. australis*, which was between 30% and 40% for all treatments (Fig. 1a). For *Lactuca sativa*, there was no significant difference between the water control and the 40 g L^{-1} litter extract solution, but there was significantly lower germination success in the 80 g L^{-1} solution and both the pH 4.4 and pH 6.9 120 g L^{-1} extract solutions than in the water control treatment (Fig. 1b). Germination success of this species in both the untreated organic soil and the limed organic soil was significantly lower than the 98% mean germination success of the water control (Fig. 1b). However, this effect was greatest for the untreated organic soil where germination success was reduced to a mean of 37%, compared with the limed organic

soil where it was only lowered to 73% (Fig. 1b). Germination successes of both *Melicytus macrophyllus* and *M. ramiflorus* in all litter extract solutions were significantly lower than in the water controls for these species (Fig. 1c, d). There was no significant difference between germination successes in the *Melicytus ramiflorus* water control and that in the limed organic soil, but there was a significant inhibitory effect of the untreated organic soil on *M. ramiflorus* germination, where germination success dropped from a mean of 87% in the water control to 23% in the untreated organic soil (Fig. 1d). In contrast, there was no effect of either soil treatment on the germination of *Melicytus macrophyllus* (Fig. 1c).

Ten-day-old seedlings of *A. australis* grown in 40 g L^{-1} extract were longer than those grown in untreated organic soil, but there were no differences among the other treatments (Fig. 2a). In contrast, 10-day-old seedlings of *Lactuca sativa* grown in the water control and limed organic soil were much longer than any other treatment (Fig. 2b). Among the remaining treatments, *Lactuca sativa* seedlings grown in 40 g L^{-1} extract were longer than in 80 g L^{-1} extract and 120 g L^{-1} extract (pH 4.4 and 6.9), all of which had negligible growth (Fig. 2b). There were no differences in *Melicytus macrophyllus* seedling lengths among the water control and any other treatment, nor between the two organic soil treatments (Fig. 2c). However, the seedlings in the 40 g L^{-1}, 80 g L^{-1}, and pH 4.4 120 g L^{-1} extract solution treatments were significantly shorter than those in the limed organic soil (Fig. 2c). For this species, there was insufficient survival of seedlings in the pH 6.9 120 g L^{-1} extract solution treatment for seedling lengths from this treatment to be included in the analysis. For *Melicytus ramiflorus*, there was only sufficient seedling survival in the water control, 40 g L^{-1} extract solution and limed organic soil treatments for these treatments to be included in the analysis. For these treatments, the seedlings in the 40 g L^{-1} extract solution were significantly shorter than the water control and limed organic soil seedlings (Fig. 2d).

Discussion

Effects of phytotoxic compounds within *Agathis australis* leaf litter and organic soil

The results of the leaf-litter-extract component of this study indicate the presence of phytotoxic compounds in the *A. australis* leaf litter. As with previous investigations into the phytotoxicity of extracts made from litter or plant parts of other species (e.g. Seal et al. 2010; Li et al. 2011; Braine et al. 2012), a dose-dependent response was observed where the more concentrated extract solutions had a greater inhibitory effect on seed germination and early seedling growth. This response, coupled with continued toxicity of the extract solution when the pH was adjusted to near-neutral, strongly suggests that the negative effects of the litter extracts on germination and growth were caused directly by the action of phytotoxic compounds in *A. australis* leaf litter and not only by low pH. The specific phytotoxic chemicals in *A. australis* leaves and litter remain to be determined.

Studies investigating seed and seedling responses to extracts can demonstrate a phytotoxic effect of extracts from the plant parts examined, but are not able to provide conclusive evidence of allelopathy (Inderjit & Callaway 2003; Ens et al. 2009). Such bioassays conducted in the absence of soil considerably exaggerate the occurrence of allelopathy, as within natural conditions soil acts to dilute
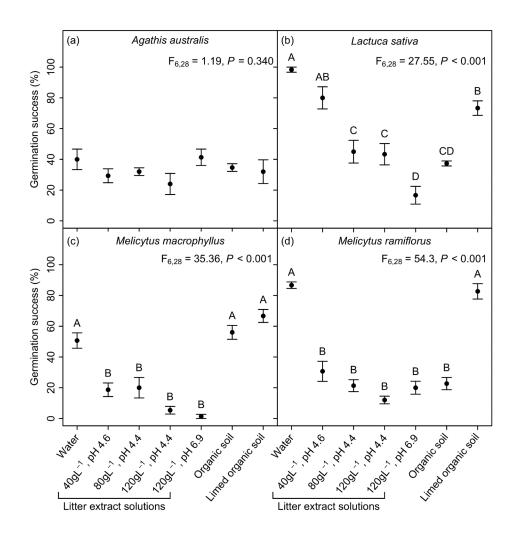
Table 1. pH values of the *Agathis australis* litter extract solutions and organic soil samples that made up the assay treatment groups.

Treatment	pH
Litter extract 40 g L^{-1}	4.56
Litter extract 80 g L^{-1}	4.42
Litter extract 120 g L^{-1}	4.37
Litter extract 120 g L^{-1} with $NaHCO_3$ addition	6.90
Organic soil	3.12
Organic soil with $CaCO_3$ addition	6.19

Figure 1. Mean germination success (±SEM) of seed of the four study species in the water control treatment, four water-extract solutions made from freshly fallen and dried *Agathis australis* leaf litter, and organic soil taken from the F horizon beneath mature *A. australis* specimens. The pH of the 120 g L^{-1} litter extract solution was increased from 4.4 to 6.9 with the addition of $NaHCO_3$. The pH of organic soil was 3.1, and with the addition of lime was 6.2. Different letters above data denote that differences among treatments are significantly different at $P < 0.05$ (post-hoc Tukey HSD tests).

and deactivate secondary metabolic compounds (Wardle et al. 1998). For *Lactuca sativa*, we found the negative effect of the *A. australis* untreated organic soil on germination rates to be considerably ameliorated with the addition of lime, yet it was still significantly lower than in the water control. This indicates a direct phytotoxic effect of compounds within the organic soil in addition to the pH effect. However, we did not find evidence for a direct allelopathic effect of the *A. australis* organic soil on seed germination or early seedling growth for the forest species investigated (*A. australis*, *Melicytus macrophyllus* and *M. ramiflorus*). The germination and early seedling growth of *Melicytus macrophyllus*, although inhibited by phytotoxins in the extract solutions, were unaffected by the untreated organic soil. In addition, the negative effect of the untreated organic soil on the germination and early seedling growth of *Melicytus ramiflorus* was dominated by the low pH of the soil, as it was ameliorated by the addition of lime. These results suggest the presence of low concentrations of phytotoxic compounds within the *A. australis* organic soil that have a significant impact on the sensitive indicator species (*Lactuca sativa*), but that are not present in sufficient concentrations to negatively affect the *Melicytus* species.

Potential role of pH in driving vegetation patterns

The negative effects of soil acidity on both the germination success and early seedling growth of *Lactuca sativa* and *Melicytus ramiflorus* demonstrated in this study have been shown by other authors for species such as sorghum (*Sorghum*

bicolor; Wilkinson & Duncan 1989) and Norway spruce (*Picea abies*; Abrahamsen et al. 1977). Wilkinson and Duncan (1989) found the reduction in sorghum germination in acidic conditions (pH < 4.5) resulted from the influence of H^+ on seed imbibition; an effect that may be a cause of the reduced germination rates in the *A. australis* organic soil. The results of the present study showing the sensitivity of *Melicytus ramiflorus* to soil acidity support those of a previous investigation (Wyse 2012) where this species was found to have reduced growth rates when grown in organic and mineral soil from beneath *A. australis* (pH < 4 in both soil types) compared with in mineral soil from beneath a nearby broadleaved-angiosperm-dominated canopy (pH = 6). The roots of *Melicytus ramiflorus* grown in both *A. australis* soil types did not penetrate the soil, forming a mat on the soil surface (Wyse 2012); a similar response to that observed by Abrahamsen et al. (1977) in Norway spruce when soil pH was below 4.0.

Allelopathy could be a factor that explains the vegetation associations occurring with *A. australis* (e.g. Cockayne 1908; Bieleski 1979; Ogden & Stewart 1995). We predicted that species that commonly occur in association with *A. australis* would be less negatively affected by *A. australis* soil and litter extracts than the species most abundant beyond the zone of *A. australis* litterfall influence. Of the three native species investigated here, *A. australis* and *Melicytus macrophyllus* commonly establish in the soils beneath mature *A. australis*, whereas *M. ramiflorus* is a species common in the surrounding forest but typically absent from beneath *A. australis* canopies
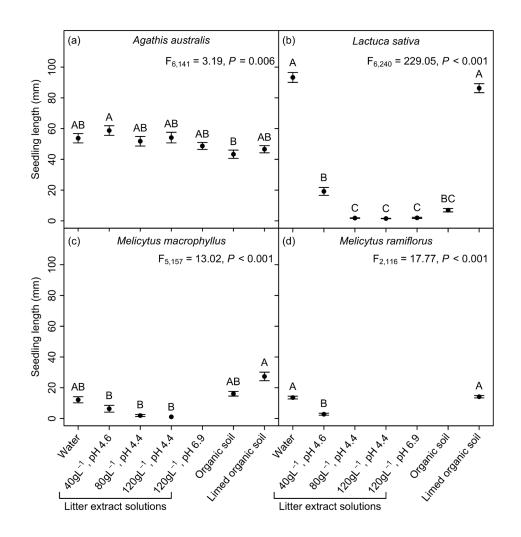
Figure 2. Mean length (±SEM) of seedlings of the four study species in the water control treatment, four water-extract solutions made from freshly fallen and dried *Agathis australis* leaf litter, and organic soil taken from the F horizon beneath mature *A. australis* specimens. The pH of the 120 g L^{-1} litter extract solution was increased from 4.4 to 6.9 with the addition of NaHCO$_3$. The pH of organic soil was 3.1, and with the addition of lime was 6.2. Seedling length was measured from the shoot apex to the apex of the primary root. Where values are missing, there was insufficient germination success or seedling survival in the treatment for it to be included in the analysis. Different letters above data denote that differences among treatments are significantly different at $P < 0.05$ (post-hoc Tukey HSD tests).

(Cockayne 1908; Wardle 1991). Unlike *Melicytus ramiflorus* and *Lactuca sativa*, the germination and seedling growth of the two species associated with *A. australis* were not inhibited in the untreated organic soil relative to the water control or the limed soil. These results indicate that soil pH is likely to be a dominant factor promoting the vegetation patterns associated with *A. australis*, as species sensitive to low pH are unlikely to be able to establish on these acidic soils. Further examination should be undertaken with additional species to determine the role of pH in the ecosystem as a whole; however, it is clear that the contrasting abilities of the two *Melicytus* species to tolerate low pH plays a substantial role in their opposing habitat preferences with respect to *A. australis*.

Many of the remaining *A. australis* stands tend to be distributed on sites with underlying low soil fertility and soil moisture, such as ridge crests and north-facing slopes (Ogden et al. 1992). In these situations, the composition of the associated vegetation will be partly influenced by the underlying edaphic conditions of the site. However, it is evident that additional to this, *A. australis* is likely to have a considerable effect on the plant community as, through its influence on soil pH, the species can be seen to have an indirect allelopathic effect on plants establishing on the organic soil formed beneath its canopies.

Conclusions

Under a broad definition of allelopathy, encompassing allelochemical interactions with soil ecological processes (Inderjit & Weiner 2001), *A. australis* can be seen to have an indirect allelopathic effect on forest plants in its vicinity through the low pH of the organic soil formed from *A. australis* litter. In addition, the results of *Lactuca sativa* show that phytotoxic compounds may be present in the soil in concentrations that directly affect sensitive species. However, we did not find any direct allelopathic effects of *A. australis* soil separate to a pH-mediated effect on the three forest species investigated here. To tease out the relative roles of direct and indirect allelopathic effects of *A. australis* within the ecosystem, future work should investigate the influence of these factors on further species, and in field conditions. Future work should also aim to identify the compounds involved in producing these allelopathic effects, and examine the modes of action by which the compounds may directly affect germination and plant growth (Inderjit & Callaway 2003).

Acknowledgements

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