

Effect of aboveground litter on belowground plant interactions in a native Rough Fescue grassland

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Abstract

Chemical compounds from plants may exhibit stimulatory and/or inhibitory effects on surrounding organisms. However, research on belowground biochemical interactions among plants has focused more effort on elucidating negative effects. Moreover, the effect of shoot litter on belowground plant–plant interactions has remained relatively unexplored. In a field experiment with four target plant species (*Artemisia frigida* Willd., *Solidago missouriensis* Nutt.), *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths and *Poa pratensis* L.) interacting with intact grassland neighbours, we manipulated root competition using PVC tubes and shoot litter, and belowground chemical interaction by adding activated carbon (AC) to the soil. In *A. frigida*, shoot litter significantly interacted with root competition and root chemicals. Plants grown plus AC were larger than those minus AC when shoot litter was left intact suggesting inhibitory effects from neighbours and/or decomposing products. However, when shoot litter was removed, plants grown minus AC were larger suggesting stimulatory effects of root exudates. *B. gracilis* showed a similar trend but results were non-significant. Results demonstrate that the effects of neighbours can be inhibitory or facilitative depending on the presence or absence of shoot litter and mediation through AC.

Zusammenfassung

Die chemischen Inhaltsstoffe von Pflanzen können stimulierende und/oder inhibitorische Auswirkungen auf die umgebenden Organismen haben. Die Forschung zu den biochemischen Interaktionen zwischen Pflanzen im Boden hat sich stärker darauf konzentriert, die negativen Auswirkungen zu beleuchten. Darüber hinaus blieb der Einfluss der oberirdischen Streu auf die Pflanze–Pflanze-Interaktion im Boden bisher relativ unerforscht. In einem Freilandexperiment mit vier Zielpflanzenarten (*Artemisia frigida* Willd., *Solidago missouriensis* Nutt.), *Bouteloua gracilis* (Willd. ex Kunth) lag. ex Griffiths und *Poa pratensis* L.), die mit ihren intakten Grünlandnachbarn interagierten, manipulierten wir die Wurzelkonkurrenz indem wir PVC-Röhren und Triebstreu benutzten, und die chemische Interaktion im Boden indem wir dem Boden Aktivkohle (AC) zusetzten. Bei *A. frigida* interagierte die Triebstreu signifikant mit der Wurzelkonkurrenz und den Wurzelchemikalien. Pflanzen, die mit AC wuchsen, waren größer als die ohne AC, wenn die Triebstreu intakt gelassen wurde. Dies lässt inhibitorische Effekte der Nachbarn und/oder der sich zersetzenden Produkte vermuten. Wenn jedoch die Triebstreu entfernt wurde, waren die Pflanzen ohne AC größer, so dass sich stimulatorische Effekte der Wurzelausscheidungen vermuten lassen. *B. gracilis* zeigte einen ähnlichen Trend, die Ergebnisse waren jedoch nicht signifikant. Die Ergebnisse zeigen, dass die Auswirkungen auf Nachbarn inhibitorisch oder fördernd sein können, abhängig von der An- oder Abwesenheit der Triebstreu und der Mediation durch AC.

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Introduction

Interactions among plants can be positive or negative, each generated by a number of ecological mechanisms. For example, interference, the negative effect of one plant on the growth of another can be due to both competition and allelopathy (Harper 1961). As a result, plant removal experiments often attribute the negative effects surrounding neighbours impose on target plants to competition for limiting resources (Wilson & Tilman 1991; Cahill 1999), ignoring other factors for example root exudates. Although separating these two forms of interference is critical to understand their ecological role, they do not occur in isolation and it is nearly impossible to separate them in nature (Harper 1977; but see Weidenhamer, Hartnett, & Romeo 1989; Nilsson 1994). On the contrary, it may be more useful to estimate the effect of both types of interference in plant interaction studies (Hoffman, Weston, Snyder, & Regnier 1996).

In addition to living plants, other factors such as plant litter are known to affect plant–plant interactions. Plant litter can directly impact the performance of plants by physically altering microenvironmental conditions (Facelli & Pickett 1991; Foster & Gross 1997), indirectly by releasing nutrients and phytotoxic substances that affect the chemical environment (Facelli et al. 1991; Facelli & Pickett 1991) as well as influence plant community structure (Facelli & Pickett 1991). Chemical interference can occur through various avenues: litter decomposition (Patrick & Koch 1958; Guenzi, McCalla, & Norstadt 1967), leaching after rainwash or fog drip (Moral & Muller 1969), volatilization (Weaver & Klarich 1977) or exuded from living plant roots (Overland 1966). Evidence on the negative effects of litter leachates on germination and plant growth is extensive (Patrick & Koch 1958; Rice 1979; Dejong & Klinkhamer 1985; Zackrisson & Nilsson 1992; Bonanomi, Sicurezza, Caporaso, Esposito, & Mazzoleni 2006). Although, the allelopathic effects of litter is well known, to our knowledge no study has looked at the potential effects of shoot litter physically, allelopathically or both changing belowground plant–plant interactions. Chemical interference by living plants by itself may have been given more attention because it has mostly been alluded to as a mechanism by which some plants establish monocultures, especially alien species (Callaway & Aschehoug 2000). However, overlooked in chemical ecology is the notion that chemically mediated plant interactions can be beneficial among native plants. In this regard, it has recently been shown that some root-exuded compounds facilitate nutrient acquisition in plants (Uren 2007), and at least in one scenario that was the case in addition to the chemical compound being phytotoxic to neighbours (Tharayil et al. 2009). Other context-dependent interactions in plants have been observed, for example conditionality for competition (Connell 1983) and allelopathy (Pollock, Callaway, Thelen, & Holben 2009), whereby they varied depending on environmental condition. However, whether belowground chemical interactions among plants can switch from facilitative to inhibitory depending on

the presence or absence of shoot litter and its potential allelopathic effects are unknown. In different studies, litter has been shown to have both positive (e.g. Willms, Smoliak, & Bailey 1986) and negative (e.g. Goldberg & Werner 1983) effects on plant growth depending on the productivity of the site as well as allelopathic effects (e.g. Putnam & DeFrank 1983). The goal of this study was to address two specific questions:

- (1) Does the presence or absence of shoot litter alter the outcome of root competition?
- (2) Does the presence or absence of shoot litter alter the outcome of belowground chemical interactions?

To accomplish this goal, we transplanted naturally co-occurring target plant species into experimental plots in which we manipulated litter (intact or removed), root competition (with or without) and the soil chemical environment (plus or minus activated carbon).

Materials and methods

Study site and target species

We conducted the experiment in a 50-ha field at the University of Alberta Research Ranch near Kinsella, Alberta, Canada (53°05'N, 111°33'W), located in the Aspen Parkland Ecoregion (Sims & Risser 2000). The study site is a savanna-type habitat containing a mixture of trembling aspen (*Populus tremuloides*) stands and rough fescue (*Festuca hallii*) prairie. Historically cattle have grazed this area; however, grazing was halted four years prior to the start of the experiment allowing recovery of the plant community. The soils are classified as thin Orthic Black Chernozems with thin organic-matter-enriched topsoil horizons and moderately drained, over glacial till (Howitt 1988; Soil Classification Working and Group 1998).

Four native target species were selected based on their historic presence at this field site and/or because they have been reported to contain chemicals that inhibit growth of other plants (e.g. Bokhari 1978; Lipinska & Wanda 2005). Two perennial forbs (*Artemisia frigida* Willd., *Solidago missouriensis* Nutt.) and two perennial grasses (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths, *Poa pratensis* L.) were chosen because they exhibit large differences in their competitive abilities (Cahill, Kembel, Lamb, & Keddy 2008).

Seeds of *A. frigida*, *S. missouriensis* and *B. gracilis* were purchased from a local native seed supplier (Bedrock seeds, Edmonton, Canada) while seeds of *P. pratensis* were purchased from Apache Seeds Ltd. (Edmonton, Canada). Seeds of *A. frigida* and *S. missouriensis* were wet and cold stratified at 4 °C for 3 weeks, and sown into seedling trays filled with sterilized seedling starter (Sunshine Professional Peat Light Growing Mix, Sun Gro Horticulture Canada Ltd.) on April 5th and 6th 2009. All seedlings were grown in the greenhouse for approximately 4 weeks and then hardened to withstand

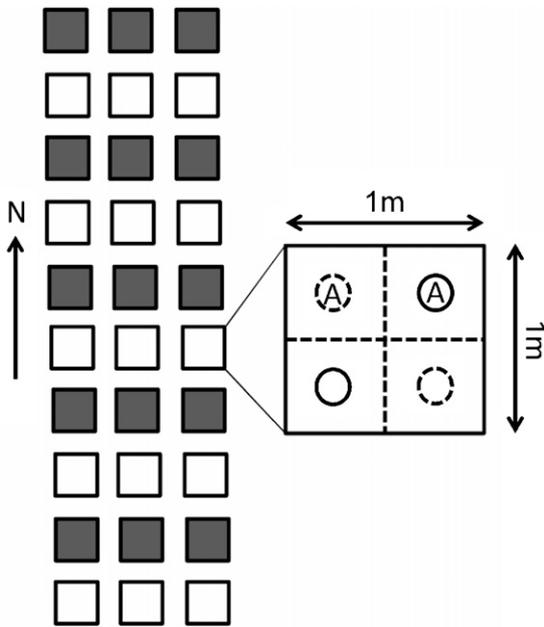


Fig. 1. Experimental layout for each species separately. Plots were alternately assigned to two litter treatments defined by intact litter (dark squares) and removed litter (white squares). The plots were further divided into four contiguous 25 cm × 25 cm subplots (indicated by dashed lines) that were each randomly assigned one of the four root competition (dashed circles) × activated charcoal (AC) treatment combinations. Root exclusion tubes (PVC tubes diameter: 10 cm, depth: 15 cm) were used to manipulate root interactions between target plants and their neighbours.

field conditions by placing them outside for 2 weeks before transplanting them into the field. Similar-sized seedlings of each species were randomly selected and transplanted (one seedling per plot) into experimental plots between May 26 and May 28, 2009.

Experimental design

We established 120 1 m × 1 m plots in a 24 m × 20 m area on a dry south-facing slope at the field site. A 1 m buffer zone separated plots in each direction. We then assigned plots (30 per species) to two litter treatments in stripes (Fig. 1). The two litter treatments were applied in May, 2009, whereby litter was either left intact or removed from plots. Litter removal was done by hand using a garden rake, taking care to minimize plot disturbance. Plots were further divided into contiguous four 25 cm × 25 cm subplots, with each subplot randomly assigned one of the four root competition × activated carbon treatment combinations (see section ‘Root competition and chemical interaction treatments’). We used this split-plot design because litter removal can alter local micro-environmental conditions (Facelli & Pickett 1991), and a litter removed subplot adjacent to a litter intact subplot may not maintain the integrity of the treatments.

Plots were initially watered by hand at a rate of 7.5 L per plot every other day to assist with seedling establishment. After 1.5 weeks, the amount was reduced to 3.75 L per plot every two days. Supplemental watering ended on June 9, with the exception of two watering events in late June (3.75 L per plot) due to an extended drought. In total, each plot received 26% more water than the mean natural rainfall (190 mm) recorded for the months of June, July and August at the nearest weather station, Viking, Alberta (53°16′N, 111°46′W) during the same period (Environment Canada National Climate Archive; <http://www.climate.weatheroffice.gc.ca>).

Root competition and chemical interaction treatments

Root exclusion tubes (PVC tubes 10 cm diameter × 15 cm deep) were used to manipulate root interactions between target plants and their neighbours (e.g. Wilson 1993). Eliminating root competition using root exclusion tubes however does not allow full separation of the effects of chemical interference and competition. The tubes were pressed into the soil until the upper surface was flush with the soil surface (in and outside the tube), and then we dug and pulverized the soil inside the tubes. To control for this disturbance we did this procedure in all four subplots but left the PVC tube in place for no-root competition treatment and removed the PVC tube in root competition treatment. Although shoot competition intensity is low compared to root competition at this field site (Lamb, Shore, & Cahill 2007), we wanted to ensure that plant interactions were confined belowground. We eliminated plant neighbour shading by installing plastic deer netting (2 cm × 2 cm mesh size; 1 mm thick), tying back neighbour shoots in all treatments. A 50 cm × 50 cm of netting was centred over the plot, its centre fastened to the soil surface using steel pins, and the outer four corners anchored approximately 10 cm above the soil surface. The centre of the netting was cut (6 cm × 6 cm) to allow transplants to grow uninhibited. The netting was installed between June 24 and June 25, 2009. Neighbouring plants beneath the netting were pulled toward the netting edges and the integrity of this shade elimination was maintained by periodically pulling the growing neighbours beneath the netting and away from the target plants.

To alter plant chemical interactions, we used finely ground activated carbon (Reef Carbon, Kent Marine, Franklin, WI, USA). Care was taken to select a brand of carbon that did not leach phosphates. In the plus carbon treatment, we thoroughly mixed carbon at a rate of 20 mL carbon/L of soil (Callaway & Aschehoug 2000) with an excavated volume of soil (diameter: 10 cm, depth: 15 cm) which was equal to the volume of the root exclusion tubes (see above). Activated carbon (AC) has a high affinity for organic compounds and can reduce the negative effect of suspected allelopathic chemicals (e.g. Mahall & Callaway 1991; Nilsson 1994). While side effects of activated carbon are a concern (e.g. Lau et al. 2008), activated

carbon is still one of the only methods available to potentially manipulate allelopathic chemicals in the field.

Target plant harvest

All target plants were harvested in the last week of August 2009, after 13 weeks of growth. At harvest, only *Bouteloua* plants had started to flower in significant numbers. Plants were harvested by clipping shoots at the soil surface, dried at 65 °C for 72 h, and weighed. Root data was not analyzed as it was not reliable.

Data analysis

Each species was analyzed separately to reduce the complexity of our statistical models. We analyzed the effects of activated carbon, root competition and litter on shoot biomass for each species using a linear mixed model procedure in R version 2.12.0 (R Development Core Team 2010) using nlme library package (Pinheiro, Bates, DebRoy, Sarkar, & the R Development Core Team 2010).

Shoot mass data for all species was tested for normality and log transformed ($x+1$) prior to analysis whenever necessary. Each model included activated carbon (\pm), root competition (without/with), litter (intact/removed) and their interactions as fixed effects. Plots (nested in litter treatment) were included as a random variable. A significant root competition \times litter interaction would indicate that litter influences the outcome of belowground competition. A significant carbon \times litter interaction would also indicate that litter influences belowground plant–plant chemical interactions.

Results

Generally, *A. frigida*, *S. missouriensis* and *B. gracilis* plus activated carbon plants (+AC) had similar final shoot biomass as minus activated carbon plants (–AC), without root competition and when litter was either left intact or removed (Fig. 2E–G). For *P. pratensis* however, –AC plants were 25% larger than +AC plants without root competition, and when shoot litter was present (Fig. 2H). Contrary, +AC plants were 29% larger than –AC plants for *P. pratensis* in the absence of both shoot litter and neighbour roots (Fig. 2H). However, these findings were non-significant (Table 1). These findings together with the similarity of final shoot biomass for +AC and –AC plants' final shoot biomass in no-competition treatments for the other three species is a strong indication but not proof that fertilizing side effects of AC were limited.

Root competition significantly reduced shoot biomass by 15–75% for *A. frigida*, *S. missouriensis* and *B. gracilis* focal plants (Fig. 2A–C), and by 31–42% for *P. pratensis*, although this was non-significant (Table 1 and Fig. 2D). These results are a strong indication for intense root competition in this

system. On average, litter removal reduced the biomass of *A. frigida*, *S. missouriensis*, *B. gracilis* and *P. pratensis* plants by 14%, 6%, 6% and 9%, respectively. The effects of neighbour removal, litter and AC were intertwined in two-way interactions as described below.

Effect of litter on root competition and belowground chemical interaction

Shoot litter altered root competition and belowground chemical interaction only in *A. frigida* as indicated by a significant litter by root competition interaction, and litter by carbon interaction (Table 1). Average shoot biomass for *A. frigida* increased by 21% with root competition, and when litter was left intact and AC added to the soil (Fig. 2A). This result suggests an allelopathic effect on *A. frigida* target plants from surrounding neighbours. In contrast, when litter was removed and with root competition, AC suppressed shoot biomass production by 18% (Fig. 2A). This suggests that root chemicals potentially adsorbed by AC reduce the strength of competition, implying a facilitative effect when litter is removed. *B. gracilis* showed a similar trend when litter was removed. Adding AC decreased shoot biomass by 36% in the presence of root competition, although this was not significant (Table 1 and Fig. 2C). *S. missouriensis* and *P. pratensis* showed no significant litter interactions.

Competitive effect increased from 25% when litter was intact to 42% when it was removed for *A. frigida* which suggests that litter ameliorates stress on target plants.

Discussion

Shoot litter significantly influenced the net outcome of belowground plant interactions only for *A. frigida*. With root competition, belowground interactions switched from negative (allelopathic) when litter was present (+AC plants' shoot mass was larger than –AC plants') to positive (facilitative) when litter was removed (+AC plants' shoot mass was smaller than –AC plants', Fig. 2A). Similarly, addition of AC to the soil with root competition suppressed *B. gracilis* shoot mass production when shoot litter was removed. However, this result was non-significant. These results demonstrate context-dependency of belowground plant interactions. Although, the role that litter plays in interaction among plants has been investigated before (Ladd & Facelli 2008), to our knowledge this is the first time that an attempt has been made to link litter effects to both belowground chemical interaction and resource competition.

Interactions in plant communities may assume a positive or a negative nature depending on a number of factors including habitat type and the species involved. Negative effects of one plant on another can occur through competition or chemical interference (Harper 1961; Fuerst & Putnam 1983). However, this tends to look at net effects, which

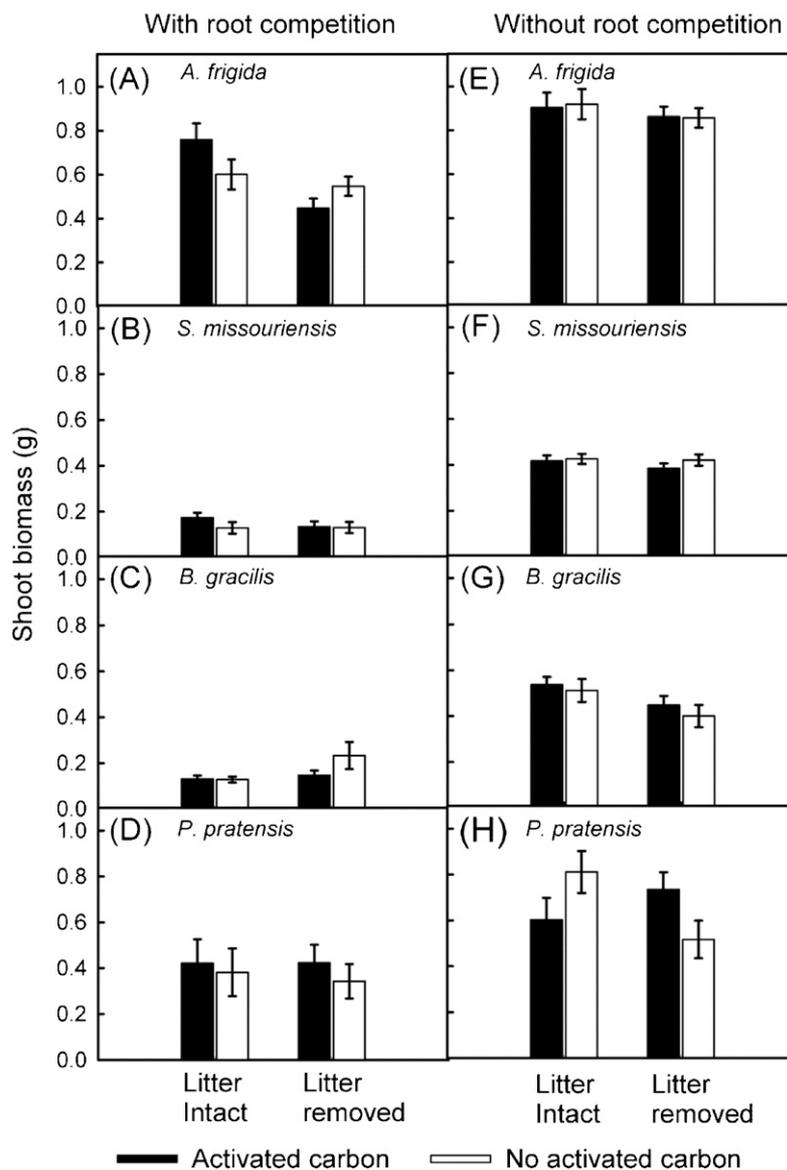


Fig. 2. Shoot biomass (means \pm SE) of *A. frigida*, *S. missouriensis*, *B. gracilis*, and *P. pratensis* when litter was left intact or removed, grown in soil amended with (dark bars) or without (white bars) activated carbon, and with or without root competition, panels A–D and E–H, respectively.

really are combinations of potentially opposing effects. This study showed variation in belowground interaction and that conditional interference is contingent on the presence of aboveground litter, although this was in a quarter of the species studied. In nutrient limited systems such as the University of Alberta Research Ranch near Kinsella (Lamb et al. 2007), reduced performance in the presence of AC could imply sequestration of root exudates involved in nutrient acquisition (Tharayil et al. 2009). Increased performance by –AC plants suggests that resource competition is mitigated by root exudates when microclimatic conditions possibly become stressful after litter removal. Litter in this system is likely to alter microclimatic conditions and have little shading effect on surrounding plants because more than 80% of the biomass in this site is belowground (Lamb et al. 2007).

Although, not the focus of the present study, we found evidence for strong root competition in this system, an attribute that has been shown before (Lamb et al. 2007). The increased performance of plants in +AC, with root competition and intact litter treatments (Fig. 2A) imply allelopathic effects from litter, neighbours or both. However, since we only see this response in one out of four species that we tested, this could be a phenomenon that is not widespread across species.

Litter can mediate positive plant interactions by mitigating stressful environmental conditions especially in unproductive environments (Willms et al. 1986). We found that, at least for one species (*A. frigida*), removing litter significantly increased the competitive effect. Additionally, root exudates are known to mediate positive interactions in the rhizosphere through beneficial symbiotic associations with microbes such

Table 1. Results of linear mixed model testing the effects of activated carbon (AC), root competition (RC) and litter (L) on target plants' shoot biomass. Degrees of freedom are numerator degrees of freedom followed by denominator degrees of freedom.

Effect	<i>A. frigida</i>		<i>S. missouriensis</i>		<i>B. gracilis</i>		<i>P. pratensis</i>	
	<i>F</i> _{df}	<i>P</i>	<i>F</i> _{df}	<i>P</i>	<i>F</i> _{df}	<i>P</i>	<i>F</i> _{df}	<i>P</i>
AC	3.3184 _{1,81}	0.0722	2.3522 _{1,77}	0.1292	0.0043 _{1,74}	0.9477	0.2030 _{1,74}	0.6536
RC	3.9241 _{1,81}	0.0510	52.8566 _{1,77}	<0.0001	56.9831 _{1,74}	<0.0001	1.8836 _{1,74}	0.1741
L	14.0769 _{1,28}	0.0008	1.4335 _{1,28}	0.2412	0.1124 _{1,28}	0.7399	0.0000 _{1,28}	0.9973
AC × RC	2.3769 _{1,81}	0.1270	1.9151 _{1,77}	0.1704	0.0982 _{1,74}	0.7549	2.1290 _{1,74}	0.1487
AC × L	5.5195 _{1,81}	0.0212	1.2272 _{1,77}	0.2714	1.3858 _{1,74}	0.2429	0.0463 _{1,74}	0.8302
RC × L	6.7788 _{1,81}	0.0110	0.1719 _{1,77}	0.6796	1.8287 _{1,74}	0.1804	0.5603 _{1,74}	0.4565
AC × RC × L	3.2523 _{1,81}	0.0750	0.2679 _{1,77}	0.6062	1.1036 _{1,74}	0.2969	2.4537 _{1,74}	0.1215

as mycorrhizae (Badri & Vivanco 2009) or the chelation of limiting minerals (see Metlen, Aschehoug, & Callaway 2009 for review). Tharayil et al. (2009) found a conditional effect of phytotoxin 8-hydroxyquinoline (8HQ) from *Centaurea diffusa*; whereby its toxicity reduced when it complexed with metals. They concluded that 8HQ could primarily be an agent for resource foraging. Similarly, we show conditionality for chemical effects in *A. frigida*; the net outcome of this interaction switches from inhibitory to facilitative depending on the absence or presence of shoot litter. This implies that other factors (e.g. environmental condition) that influence the net outcome of plant interactions should be taken into consideration (Inderjit et al. 2005). Embracing the possibility of the existence of a stimulatory-inhibitory continuum ('allelopathy phenotype') – analogous to the mutualism-parasitism continuum in AMF (Johnson, Graham, & Smith 1997) – may improve our understanding of the role played by the array of chemical compounds plants exude. To our knowledge this is the first time that context-dependency of chemical effects (mediated through shoot litter) has been demonstrated in plants. However, since the context-dependency of chemical effects is exhibited only in one out of four species in this study, we underscore that this is a proof of concept and not the 'rule'. Additionally, the absolute magnitude of the results suggests that allelopathy and litter play only minor roles in this system.

To date, allelopathy research has mainly focused on negative effects of chemical compounds while tending to ignore the positive effects of plant-produced chemicals (Romeo & Weidenhamer 1998). It is known that root exudates (which include secondary metabolites such as allelochemicals) mediate both positive and negative interactions in the rhizosphere (Badri & Vivanco 2009) and are involved in vital soil processes (Zhang, Romheld, & Marschner 1991). However, it has not been explicitly established whether the production of secondary metabolites could be a mechanism by which plant species facilitate each other (Metlen et al. 2009). This observation implies that a narrow focus on negative effects may not capture the potential role that chemical compounds may play in mediating the outcome of plant–plant interactions. We believe new terminology that defines these

positive ecological interactions may be necessary. Here we coin the term 'allelarexis' for this potential ecological interaction, based on the Greek roots *allelo* meaning "one another" or "reciprocal" and *arexis* meaning "help", "aid" (Brown 1956). Since our study used plant species that naturally co-exist, we can argue that naturally coexisting plants species may have evolved mechanisms to tolerate and facilitate each other through chemicals exuded from roots. Recently, the role that positive interactions play in natural plant communities has reignited research interest (see Brooker et al. 2008). However, the focus is still on the traditional amelioration of stressful physical stress while ignoring the potential effects of chemical compounds. Incorporating chemical effects may shed light on an important potential mechanism that might further improve our understanding of coexistence among plants.

In conclusion, our results suggest a potential mechanism of positive interaction among plants that has not been given much attention in the discussions on plant facilitation. We have shown that shoot litter can significantly alter the net outcome of plant–plant interactions from inhibitory to facilitative although the size effect of this interaction is smaller compared to root competition. A similar trend was shown in *B. gracilis* though non-significant. Similar to 'mycorrhizal phenotype' in AMF-plant association we speculate the existence of 'allelopathy phenotype'. This is determined by a number of factors such as plant species identity and environmental factors including litter. We have argued that this context-dependency of chemical effects, if common in nature, may change how we view plant interactions and species coexistence. Finally we suggest that chemical effects be considered in discussions about facilitation in plants.

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