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Litter effects of two co-occurring alpine species on plant growth, microbial activity and immobilization of nitrogen

William D. Bowman, Heidemarie Steltzer, Todd N. Rosenstiel, Cory C. Cleveland and Courtney L. Meier

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We measured the litter chemistry of two co-dominant alpine species, *Acomastylis rossii*, a forb characterized by a low growth rate and N uptake capacity, and *Deschampsia caespitosa*, a grass characterized by a high growth rate and N uptake capacity, and examined the effect litter of these two species had on the growth of *Deschampsia* phytometers in a greenhouse. We also examined the influence of litter from the two species on microbial respiration and immobilization of N, in two separate laboratory microcosm experiments and in the field. We hypothesized that *Acomastylis* litter would reduce plant growth more than *Deschampsia* litter, corresponding with either 1) suppression of microbial activity and thus a decrease in N mineralization, or 2) by stimulation of microbial biomass and increasing microbial immobilization of N. Relative to *Deschampsia* litter, *Acomastylis* litter had higher total water soluble organic carbon (DOC), and higher total phenolic concentration. *Deschampsia* litter had 30 times higher carbohydrate (primarily glucose and fructose) concentrations than *Acomastylis* litter. Soil respiration, microbial biomass N, and consumption of DOC and N were higher with the *Acomastylis* litter treatment than the *Deschampsia* litter treatment in experimental microcosms, and both respiration and microbial biomass N were higher in field soils under canopies dominated by *Acomastylis* relative to those dominated by *Deschampsia*. These results indicate that phenolics in *Acomastylis* are a C source for soil microorganisms, rather than an inhibitor of microbial activity. *Deschampsia* phytometers grew significantly less, had higher root: shoot biomass ratios, and acquired less nitrogen in the *Acomastylis* litter treatment relative to the control and *Deschampsia* litter treatments. The results of these experiments indicate that *Acomastylis* litter influences soil N cycling by increasing microbial activity and N immobilization, which may influence N supply to neighboring plants. This mechanism has the potential to influence competitive interactions between *Acomastylis* and its neighbors.

W. D. Bowman, T. N. Rosenstiel, C. C. Cleveland and C. L. Meier, Mountain Res. Stn, Inst. of Arctic and Alpine Research and Department of Ecology and Evolutionary Biology, Univ. of Colorado, Boulder, CO 80309-0334, USA (bowman@spot.colorado.edu). – H. Steltzer, Dept of Forest Sciences, Colorado State Univ., Fort Collins, CO 80523, USA.

Plants of resource poor environments are generally characterized by low growth rates, low rates of tissue turnover, and small size (Chapin 1980, Aerts and Chapin 2000). Such characters facilitate tolerance of low resource availability, that may in part be promoted by the low quality litter produced by these plants. Plant litter may influence the growth of neighboring plants, and can be an important mediator of plant-plant interactions in communities (Xiong and Nilsson 1999). Litter effects may include shading (Knapp and Seastedt 1986, Foster and Gross 1997), nutrient availability through alteration of soil biogeochemistry (Taylor et al. 1989), or direct inhibition of growth through allelopathy (Mahall and Callaway 1992, Wardle et al. 1996).

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Litter can influence soil nutrient supply by affecting soil organic matter quality (C:N, lignin) or by secondary compounds that may influence soil microbial activity or bind with available forms of nutrients (Northup et al. 1998, Schimel et al. 1998, Souto et al. 2000). By restricting resource supply to neighbors via litter effects, and by tolerating low resource availability through conservative growth and resource use, plants may maintain dominance in a competitive environment despite a low capacity to sequester and use resources for their own growth (Van Breemen and Finzi 1998).

We measured the effect of litter from two alpine moist meadow co-dominants on the growth of phytometers, to determine the potential influence of the litter of these species on neighboring plants. We also measured the litter effects on microbial N immobilization and soil respiration, to estimate the potential for soil microbial activity to mediate the interaction between the plants and their neighbors. The species we used were *Deschampsia caespitosa* (L.) P. Beauv., a tillering grass and *Acomastylis rossii* (R. Br.) Greene, a rhizomatous forb (hereafter referred to by their generic names). *Deschampsia* has a higher growth rate, higher rate of N uptake, and a higher capacity to alter biomass allocation in response to variation in resource supply relative to other alpine plants (Theodose et al. 1996, Bowman and Bilbrough 2001). *Acomastylis* has a relatively slow growth rate, related in part to preformation of vegetative primordia (Meloche and Diggle 2001), and a lower N uptake rate than *Deschampsia* (Theodose et al. 1996). Despite its more conservative resource acquisition potential, *Acomastylis* is common and widely distributed across the alpine landscape, reaching its peak abundance in moist meadow communities, which are the most resource rich and productive alpine communities (Fisk et al. 1998). Additionally *Acomastylis* has been shown to reduce the biomass of neighbors as well as *Deschampsia* in experimental field plots, despite its lower resource uptake capacity (Suding et al. in press). The relative abundance of *Deschampsia* and *Acomastylis* are associated with a large amount of the spatial variation in N cycling in moist meadow soils (Steltzer and Bowman 1998). The effects of each species on N cycling are associated with higher total phenolic concentrations in *Acomastylis*, correlating with lower rates of net N mineralization and nitrification, and higher fine root turnover in *Deschampsia*, correlating with higher rates of net N mineralization and nitrification (Steltzer and Bowman 1998).

We tested the hypothesis that *Acomastylis* litter reduces plant growth more than *Deschampsia* litter, and that the difference in growth reduction would be associated with a higher amount of leachable dissolved organic carbon (DOC) in *Acomastylis*, made up primarily by phenolics (up to 20% tissue dry weight, Dearing 1996, Steltzer and Bowman 1998). We also examined the effect of the litter of the two species on microbial biomass in laboratory microcosms and in the field, to determine if the effect of the litter on plant growth could be mediated through its influence on microbial activity, and subsequently on N mineralization or immobilization. We hypothesized that the higher DOC in *Acomastylis* may influence N supply by either inhibiting microbial activity, lowering net N mineralization, or by providing a C substrate for soil microorganisms, thus enhancing N immobilization (Schimel et al. 1998, Fierer et al. 2001, Castells et al. 2003).

Methods

Field collections and litter chemistry determinations

Acomastylis and *Deschampsia* leaf litter, and *Deschampsia* plants were collected from an alpine moist meadow community at 3500 m on Niwot Ridge, Colorado, a long-term ecological research site, in September of 1998. The litter was air-dried and stored in paper bags.

Sub-samples of the field collected litter were analyzed for total phenolic and carbohydrate concentration, two potential sources of labile C in litter (Vance and David 1991, Kögel-Knabner 2002). Total phenolic concentrations were analyzed using the Folin-Ciocalteau assay (Waterman and Mole 1994), using both water and 85% methanol extractions. The values of total phenolic concentrations were standardized with gallic acid. Carbohydrate analyses were made on approximately 25 mg of ground leaf tissue extracted in 1.5 ml of 80% ethanol. Samples were centrifuged (10 000 × g, 15 min, 4°C), the supernatant decanted, and pellets resuspended in 80% ethanol. Ethanol extraction was repeated a total of five times, fractions pooled, and the ethanol removed with a centrifugal evaporator. To remove pigments, dried fractions were resuspended in 1.5 ml of 2: 1 water: chloroform. Ethanol insoluble material from the original pellet was resuspended in 1 ml of water, briefly sonicated, autoclaved, and hydrolyzed as described in Schulze et al. (1991). Glucose released from hydrolyzed starch and all additional soluble carbohydrates were measured by high-performance anion-exchange chromatography-PAD as described by Moore et al. (1997).

Litter experiments

Deschampsia phytometers were planted in pots to determine the effect of litter of the two study species on plant growth. *Acomastylis* plants were not used as phytometers, because they have slow growth rates, don't respond significantly to resource manipulations within a single growing season (Bowman et al. 1995), and have high mortality rates when transplanted from the field into a greenhouse environment. Field collected

Deschampsia plants were grown in a greenhouse for two months prior to the start of the experiments. The plants were subsequently divided into units of 2–4 interconnected tillers, the dead roots and shoots removed, the leaves trimmed to 1 cm length, and the fresh mass and number of tillers recorded (0.3–0.8 g). The plants were planted in 15 cm diameter × 20 cm depth pots, containing a mix of acid-washed autoclaved sand, approximately 2 g of fresh moist meadow soil (microbial inoculum), collected from under both the study species and composited, and 3.6 g dry mass of either *Acomastylis* or *Deschampsia* litter, or no litter (control). The mass of litter added was determined based on the annual net production of the species in the moist meadow (Bowman et al. 1995). The litter was coarsely ground and passed through a 4-mm sieve prior to mixing it into the sand.

Twelve replicate pots of each of the 3 litter treatments were maintained in the Univ. of Colorado greenhouse facility. The pots were watered to saturation every other day. After 2 weeks of growth the plants were given $\frac{1}{4}$-strength Hoaglands nutrient solution weekly. This level of nutrient addition is sub-optimal for *Deschampsia* growth, allowing us to assess the degree to which immobilization of N by the microbial biomass may influence phytometer growth. Without addition of external nutrients there would not be enough net N mineralization in the sand-litter culture to support plant growth. Temperatures in the greenhouse varied between 8 and 15 °C, and lighting was augmented with HID lamps to produce a 16 h day/8 h night cycle. The plants were harvested after 47 days. The roots were carefully removed from the growing medium and washed thoroughly with tap water. Shoots and roots were separated and dried at 70°C for 48 hours. Following oven drying the masses of the tissues were recorded and analyzed for total Kjeldahl N following acid digestion using a Lachat autoanalyzer. N accumulation in biomass was calculated as the product of the tissue N concentrations and the biomass values.

To address litter effects on soil microbial activity and immobilization of N, soil respiration and soil microbial biomass N were measured in 5.5 cm diameter × 20 cm length PVC tubes containing the same potting medium, soil inoculum, and litter treatments described above, but without phytometers. Six tubes per treatment were used. The tubes were watered every other day with tap water only. Soil respiration was measured as net CO_2 efflux, using a Li-Cor LI6200 gas exchange system, 5, 8, 10, 17, and 19 days after initiation of the treatments. The net flux of CO_2 in the headspace of the tubes was measured for 45 s after capping the tubes with a PVC top. The headspace volume in each of the tubes was measured and used in the calculation of net CO_2 flux. Measurements made with tubes containing only autoclaved sand showed no net CO_2 flux, indicating methodological problems associated with evaporation and boundary layer formations were minimized (Hooper et al. 2002). Microbial biomass N in the potting medium was measured in a separate set of identically maintained tubes using the chloroform-fumigation extraction technique (Brookes et al. 1985). Soil microbial biomass N was measured 6 days after initiating the treatments, when peak respiration rates were measured. A correction factors of 0.54 was used to convert the chloroform labile N to microbial N (Brookes et al. 1985).

An additional laboratory experiment was performed to investigate the effect of the litter on soil microbial activity and N uptake. Six samples of 50 g dry senesced litter of *Acomastylis* and *Deschampsia* were extracted for 1 h in 1 l deionized water at 25°C. Following extraction, the leachate was first filtered through a 0.5-mm mesh sieve and then sterile filtered using 0.45-μm glass filters to remove microorganisms and particulate matter from the sample. Pairs of leachate were pooled, resulting in three leachate samples of ~1.8 l for each of the species. The leachate was immediately sampled for initial DOC and total soluble N using a Shimadzu TOC 3201 combustion analyzer. After initial sampling, the leachate was transferred to 2.4 l amber brown bottles equipped with an air intake port and outlet vent. Samples were inoculated with 1 ml of a water-diluted (1: 10^{-3}) recently collected field soil sample. The inoculated bioreactors were capped and aerated using atmospheric air and an airstone to prevent anoxia within the bioreactors during the experiment. The bioreactors were kept at room temperature in the dark, to prevent autotrophic C fixation. At regular intervals, reactors were sampled for DOC and total soluble N after filtering to 0.45 μm to exclude microorganisms. Concurrently, total sample volume was checked to ensure no moisture loss via evaporation, and volume losses due to evaporation were replenished prior to sampling.

Field measurements

Soil respiration and microbial biomass N and C were measured in an alpine moist meadow under canopies of *Deschampsia* and *Acomastylis*, to examine the association between these species and microbial activity in the field. Soil respiration was measured using a LiCor 6200 gas exchange system in 5.5 cm diameter × 20 cm depth PVC tubes placed into the soil (ca 120 cm^3 headspace). Ten tubes for each species were inserted into soil lacking aboveground plant tissues but surrounded by the study species, immediately after snowmelt, and 1 week prior to taking initial measurements. We assumed root respiration in the tubes was negligible, as the tubes severed the roots during insertion into the soil, and greater than 80% of the root mass in the alpine is in the top 15 cm of soil (Webber and May, 1977). Compari-

son of soil respiration in the study tubes with tubes installed the previous year indicated that any increase in respiration due to root excision declined after the 1 week period. Respiration measurements were made at 1–2 week intervals until plant senescence, in mid-August, and then once again in mid-September, 1999. Soil temperature at 5 cm depth was measured in each tube immediately following the respiration measurements. A small soil core was taken adjacent to the tubes at each sampling period to determine gravimetric soil moisture.

Table 1. Components of litter chemistry in *Acomastylis* and *Deschampsia*. Values are means ± se. See Methods for details of analyses. Although the units are the same, the values are not comparable among the variables, as extraction procedures differed and phenolics are expressed relative to a Gallic acid equivalent (GAE).

litter type	*Acomastylis*	*Deschampsia*
C:N ratio*	70.3 ± 2.8	56.8 ± 3.8
N concentration (mg N/ g dry weight)*	7 ± 0.3	8 ± 0.6
DOC (mg/ g dry weight)	29.61 ± 1.13	7.34 ± 0.28
soluble N (mg/g dry weight)	0.50 ± 0.02	0.53 ± 0.01
total phenolics (mg GAE/g dry weight)		
85% methanol extract	42.12 ± 1.19	1.05 ± 0.13
water extract	62.87 ± 1.07	2.48 ± 0.66
carbohydrates (mg/g dry weight)		
raffinose	0	Trace
starch	0	Trace
myoinositol	0	0.87 ± 0.27
glucose	4.00 ± 0.49	42.73 ± 4.42
fructose	1.33 ± 0.14	116.18 ± 7.02
sucrose	0.20 ± 0.15	11.50 ± 2.63
total	5.53 ± 0.71	170.57 ± 13.57

* from Steltzer 1999

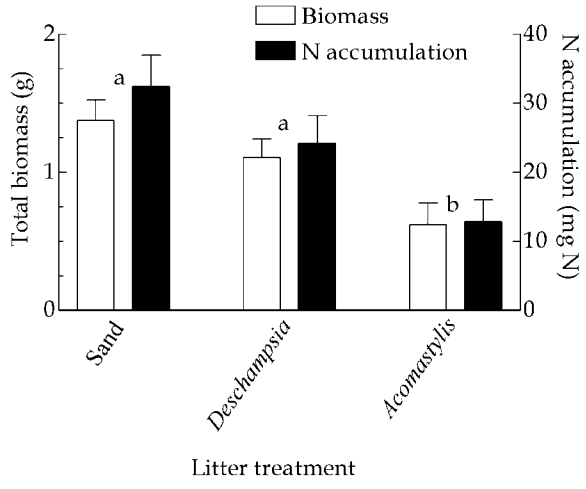

Fig. 1. Biomass (open bars) and N accumulation (shaded bars) for *Deschampsia* tillers grown in autoclaved sand with no litter, *Acomastylis* litter, or *Deschampsia* litter, and a small amount of alpine soil to provide inoculum. Bars are means ± 1 se, n = 12. Letters above the bars indicate significant differences among treatments ($P < 0.05$) using a Tukey multiple range test.

Microbial biomass N and C were estimated in field soils collected in early August 1998. The soils were sieved (2 mm) and processed within 3 hours of collection, and analyzed for chloroform labile C and N following the procedure described in Brookes et al. (1985). Ten samples each from *Acomastylis* and *Deschampsia* dominated soils were collected. Correction factors of 0.54 for N and 0.45 for C were used to convert the chloroform labile N and C to microbial N and C (Brookes et al. 1985).

Statistical analyses

The biomass accumulation, root: shoot ratios, plant N concentrations and N accumulation, and soil microbial biomass N and C data were analyzed using one-way analysis of variance, with litter treatment as a categorical variable. The use of initial fresh weights as a covariate were not significant with any of the biomass measures, and thus were dropped from the models. Tukey multiple range tests were used to compare means among the treatments for the biomass and N accumulation measurements. Soil respiration data from the greenhouse and field were analyzed using repeated measures analysis of variance.

Results

Acomastylis litter was characterized by a high C:N ratio, high DOC and total phenolic concentrations, and low carbohydrate concentrations (Table 1). Conversely, *Deschampsia* litter had a lower C:N ratio, DOC and phenolic concentrations, but higher carbohydrate concentrations than *Acomastylis* litter. Litter N concentrations did not differ between the 2 species. Because different extraction techniques were used and the phenolic assay relies on binding to hydroxyl groups rather than measurement of C concentrations, we were not able to account for the composition of DOC in the study species. However, it appears that the majority of the DOC leached from *Acomastylis* is made up of phenolics, while carbohydrates are a greater proportion than phenolics of the DOC leached from *Deschampsia*.

Biomass production of *Deschampsia* was 44% lower and N accumulation was 46% lower with *Acomastylis* litter than with *Deschampsia* litter ($F = 6.24$, $P < 0.01$ for biomass production, $F = 6.54$, $P < 0.01$ for N accumulation; Fig. 1). Plants in the *Acomastylis* litter treatment had significantly higher root: shoot ratios than the other treatments ($F = 10.48$, $P < 0.001$; Fig. 2). Tissue N concentrations did not differ among the treatments (data not shown), and thus differences in N accumulation among treatments were due to differences in biomass accumulation.

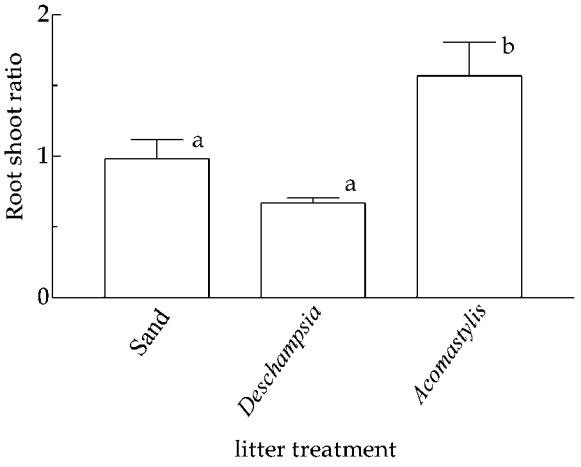

Fig. 2. Root: shoot biomass ratios for *Deschampsia* tillers grown in autoclaved sand with no litter, *Acomastylis* litter, or *Deschampsia* litter, and a small amount of alpine soil to provide inoculum. Bars are means ± 1 se, n = 12. Letters above the bars indicate significant differences among treatments ($P < 0.05$) using a Tukey multiple range test.

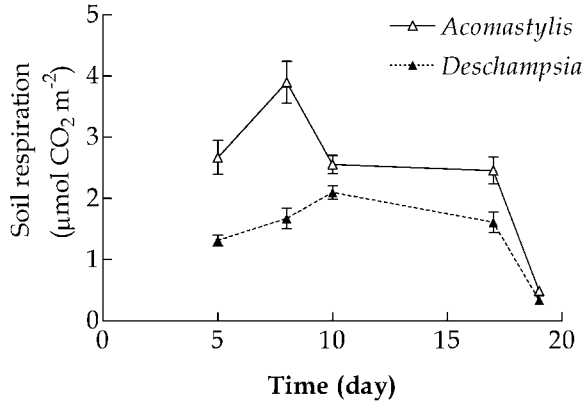

Fig. 3. Soil respiration in PVC tubes containing autoclaved sand, *Acomastylis* litter or *Deschampsia* litter, and ca 2 g of alpine soil to provide inoculum. Soil respiration rates in tubes with no litter (control) and soil inoculum were not different from zero throughout the experiment (data not shown). Symbols are means ± 1 se, n = 6.

Soil respiration in the microcosms differed significantly among the litter treatments ($F = 88.26$, $P < 0.001$, Fig. 3). Respiration rates in the control (no litter) treatment were not significantly different from zero. During the first 3 weeks of the experiment soil respiration rates in the *Acomastylis* litter treatment were as much as two-fold higher than the *Deschampsia* litter treatment; following this period respiration rates declined and there were no differences between the *Acomastylis* and *Deschampsia* litter treatments. Soil microbial biomass N in the microcosms measured 1 week into the experiment was significantly related to the litter treatments ($F = 11.8$, $P < 0.01$; Fig. 4a), with the lowest in the control treatment, intermediate in the *Deschampsia* litter treatment, and highest in the *Acomastylis* litter treatment. Soil respiration measurements made the same day the soils were harvested were significantly correlated with microbial biomass N (Fig. 4b).

The consumption of DOC by microorganisms in the bioreactors was greater for *Acomastylis* litter extract than for *Deschampsia* litter extract, although greater than 90% was consumed for both species leachates (Fig. 5a). Total soluble N concentrations were initially similar in leachate from both litter types despite a 4-fold difference in DOC, but declined to a greater extent in the *Acomastylis* litter extract than the *Deschampsia* litter extract (Fig. 5b), indicating greater consumption of N by microorganisms in the *Acomastylis* litter extract. Similar results were found for extracts of dried non-senesced tissues of the two species collected during the growing season (data not shown).

Soil respiration measured in the field was higher in *Acomastylis* dominated soils than in *Deschampsia* dominated soils ($F = 19.6$, $P < 0.001$), while soil moisture and soil temperature did not differ consistently between the two patch types (Fig. 6). Microbial biomass N and C measured in early August were higher in *Acomastylis* dominated soils than in *Deschampsia* dominated soils ($F = 5.76$, $P < 0.05$ for N, $F = 8.12$, $P < 0.01$ for C; Fig. 7).

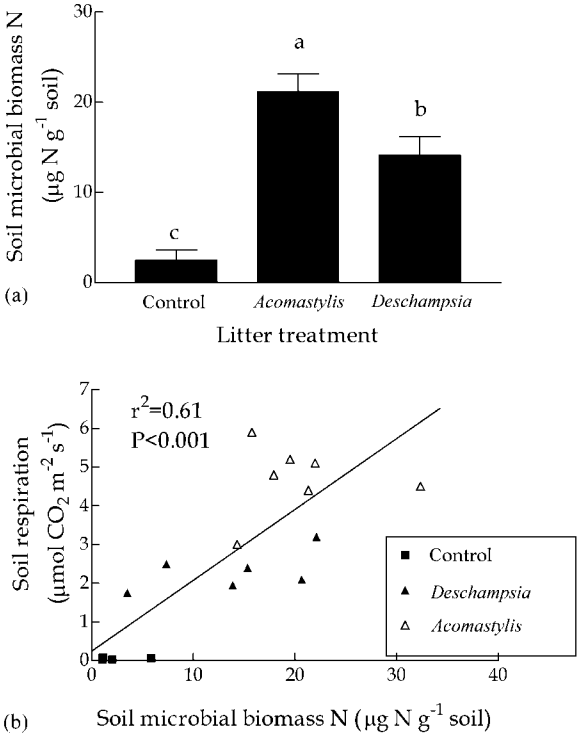

Fig. 4. (a) Microbial biomass N measured after one week in PVC tubes containing autoclaved sand with no litter, *Acomastylis* litter, or *Deschampsia* litter, and ca 2 g of alpine soil to provide inoculum. Bars are means ± 1 se, n = 6. (b) Correlation between soil respiration and microbial biomass N in these same tubes.

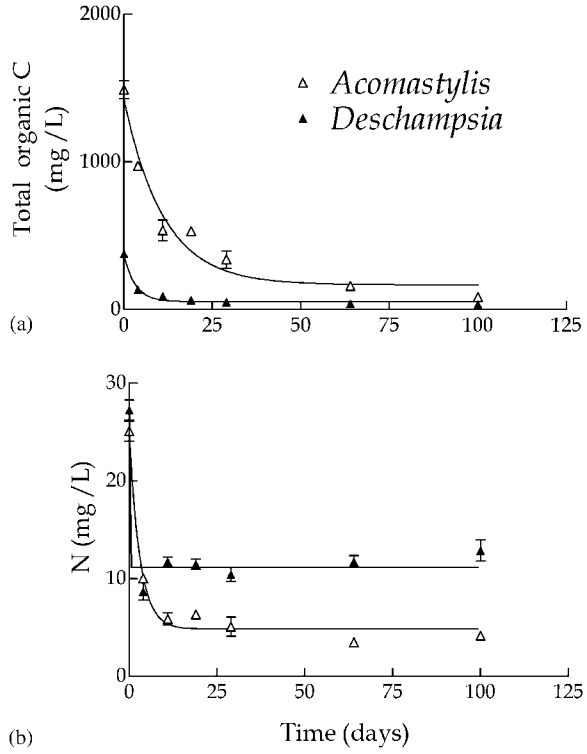

Fig. 5. Consumption of DOC (a) and total N (b) by microorganisms in bioreactors containing leachate from *Acomastylis* (△) and *Deschampsia* (▲) litter. See text for experimental procedures. Lines fit using one phase exponential decay function ($r^2 > 0.95$ for all data-sets).

Discussion

Acomastylis litter significantly reduced the growth of *Deschampsia* phytometers more than the control and *Deschampsia* litter treatments, and had a concomitant, and possibly related, stimulatory effect on soil microbial immobilization of N. The higher allocation to root biomass over shoot biomass in the *Deschampsia* plants in the *Acomastylis* litter treatment was symptomatic of a N constraint on *Deschampsia* growth (Bowman and Bilbrough 2001), potentially resulting from lower N availability due to higher microbial N immobilization. Higher microbial respiration and N immobilization were observed both in laboratory microcosms with *Acomastylis* litter and in field plots dominated by *Acomastylis*. A previous study documented a ten-fold lower net N mineralization rate in soils dominated by *Acomastylis* relative to those dominated by *Deschampsia* (Steltzer and Bowman 1998).

The results from this study, in combination with previous results, are consistent with the hypothesis that *Acomastylis* litter influences soil N biogeochemistry by enhancing microbial growth through its high DOC content, rather than inhibiting microbial enzyme activity. This mechanism may facilitate the persistence of *Acomastylis* in the relatively productive N-limited alpine moist meadows, despite its low growth and N uptake capacities. N fertilization of this community results in increased growth of *Deschampsia*, but not *Acomastylis* (Bowman et al. 1995), indicating that constraints on N supply can control the relative abundance of the two co-dominants. The abundances of these two co-dominant species are negatively spatially correlated with each other (Steltzer 1999), indicating each has effective mechanisms to exclude the other. By lowering N availability and growth of neighbors, and by tolerat-

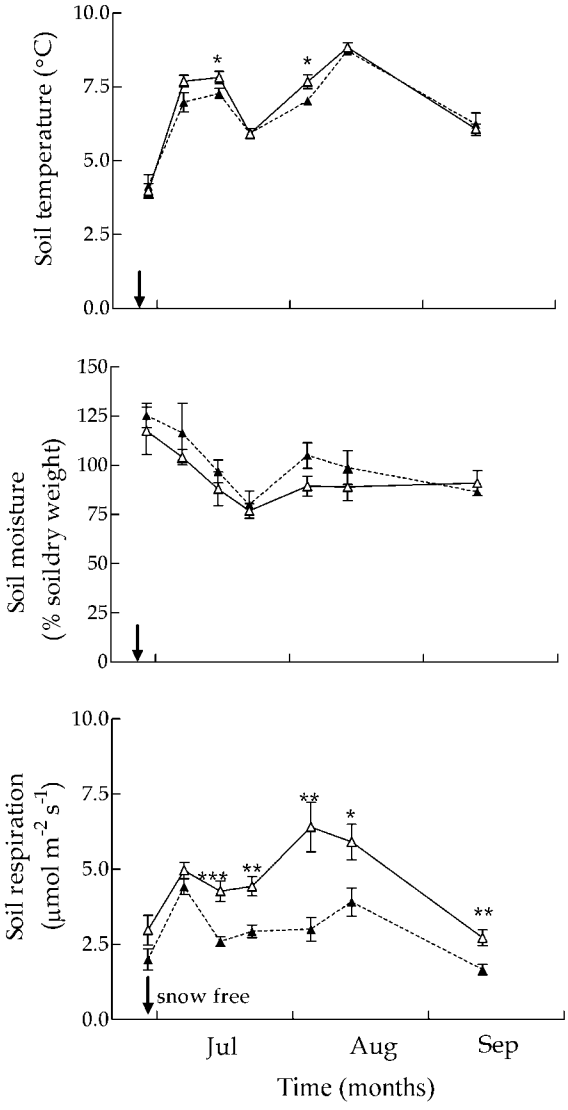

Fig. 6. Soil temperature, moisture, and respiration measured under canopies dominated by *Acomastylis* (△) and *Deschampsia* (▲) in a moist meadow community on Niwot Ridge, Colorado during the summer of 1999. Arrows indicate initiation of snow-free period. Asterisks denote significant differences between the soils (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, based on ANOVA; n = 10).

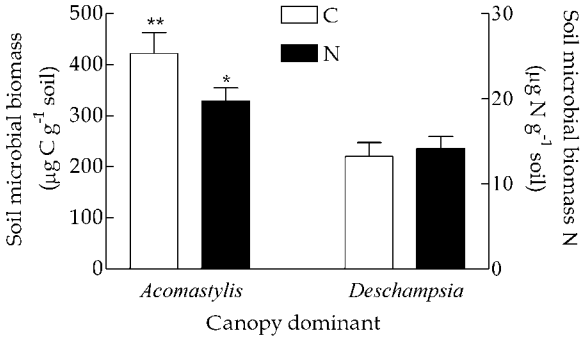

Fig. 7. Soil microbial biomass C and N from soils dominated by *Acomastylis* and *Deschampsia* measured from Niwot Ridge, Colorado, in September 1998. Bars are means ± 1 se, n = 10. Asterisks denote significant differences between the soils (* = $P < 0.05$, ** = $P < 0.01$ based on ANOVA).

ing these conditions through slow growth and conservative N use, *Acomastylis* may be able to dominate patches within the relatively resource rich alpine moist meadows. The same mechanism has been proposed for heathland ecosystems in the Netherlands (Berendse 1998) and for boreal forest understory species (Castells et al. 2003).

The importance of litter chemistry in mediating interactions between neighboring plants has been supported in studies using other plants from infertile communities, particularly for ericaceous shrubs (Berendse 1998, Nilsson et al. 1999, 2000). In general, plants from nutrient poor-communities tend to lower rates of N cycling relative to plants from more fertile communities (Wedin and Tilman 1990, Van Vuuren et al. 1992, Van der Krift and Berendse 2001). High phenolic concentrations in litter are thought to influence N-supply primarily by inhibiting soil microbial activity (Bradley et al. 2000, Souto et al. 2000) or by enhancing uptake of inorganic N by recalcitrant soil polyphenolic compounds (Northup et al. 1998, Hättenschwiler and Vitousek 2000). However, there is also evidence that plants may enhance microbial immobilization of N when they provide C to soil microorganisms in the form of low molecular weight phenolics. Schmidt et al. (2000) found that biomass of salicylate-mineralizing microorganisms increased in association with alpine willows, and suggested that simple phenolic compounds were a potentially important carbon source for soil microorganisms in the alpine. Schimel et al. (1996, 1998) and Fierer et al. (2001) demonstrated that balsam poplar influences N availability during primary succession in taiga floodplains through production of both low molecular weight phenolics that stimulated microbial N immobilization, as well as high molecular weight phenolics that lowered N availability by binding to microbial exoenzyme substrates in the soil. Thus individual plants may contain a diverse array of phenolic compounds that may influence microbial activity and soil biogeochemistry via different mechanisms.

While the influence of the litter on microbial activity and subsequent N dynamics may have been sufficient to explain the differential growth of the phytometers in this experiment, the influence of litter on vegetation dynamics in alpine moist meadows is less clear. Litter stimulated microbial activity in the soil microcosms and bioreactors approximately 3 weeks, while respiration rates in the field were higher in *Acomastylis* dominated patches than in *Deschampsia* dominated patches throughout the summer and into early fall. Field soils contain much higher amounts of organic matter (ca 30%, Seastedt 2001) than were present in the experimental microcosms, where it appeared that the majority of the labile C was consumed during the 3-week period. Temperature, and in some communities moisture, are important controls on microbial degradation of organic matter in the alpine (Fisk et al. 1998, Seastedt et al. 2001); such constraints were presumably absent in the experimental microcosms. Thus labile C may last longer in soils under alpine field conditions than in our greenhouse and laboratory microcosms.

Growing season inputs of DOC may result from phenolics leaching from live tissues of *Acomastylis*. Live aboveground shoots and underground rhizomes of *Acomastylis* both contain relatively high concentrations of total phenolics (up to 20%, Steltzer 1999), which are relatively water soluble (Table 1). Higher phenolic concentrations occur in soils dominated by *Acomastylis* than in those dominated by *Deschampsia* during the growing season (C.L. Meier, unpubl.), indicating that either phenolics leached from litter can remain in soils throughout the year, or that phenolics leach from live tissues. Schmidt et al. (2000) proposed that soil microbes consume most of the phenolics leached from alpine litter during the winter, and thus the soil phenolics measured during the growing season may be derived primarily from living tissues.

Functionally, the high DOC content of *Acomastylis* litter could represent several distinct categories of soluble compounds. As alpine plants contain significant quantities of soluble carbohydrates, up to 30% dry mass (Körner 1999), soluble carbohydrates could represent a significant fraction of DOC in the alpine litter system. However, although *Deschampsia* litter did contain 17% (dry mass) soluble carbohydrates, the relative absence of these compounds in *Acomastylis* litter cannot account for its relatively high DOC content. Furthermore, the fact that litter N content was not significantly different between the two species suggests that the differences in DOC content are not a result of high concentrations of leachable amino acids or amino sugars in *Acomastylis*. Although we were not able to quantitatively determine the composition of DOC leached from both species, our results strongly suggest that phenolics make up a large proportion of the extractable DOC in *Acomastylis*.

The existence of phenolics in plants is relatively widespread (Waterman and Mole 1994), but the functional classes of different phenolic compounds and their influence on soil biogeochemistry are not well known. Phenolics in *Acomastylis* may have several ecological roles, including protection from herbivores (Dearing 1997), attenuating harmful UV irradiance (Caldwell 1981), and deterring competitive encroachment by neighbors (Castells et al. 2003, this study). Thus there are multiple potential evolutionary histories that may have resulted in the high phenolic production in *Acomastylis* (Binkley and Giardina 1998, Van Breemen and Finzi 1998). However, the results from the present experiments indicate that in addition to the traditionally emphasized role of deterring herbivores, phenolic compounds may be important factors in plant interactions through their effect on soil biogeochemical processes mediated by soil microbial activity.

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References

Aerts, R. and Chapin, F. S. III. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. – Adv. Ecol. Res. 30: 1–67.

Berendse, F. 1998. Effects of dominant plant species on soils during succession in nutrient-poor ecosystems. – Biogeochem. 42: 73–88.

Binkley, D. and Giardina, C. 1998. Why do tree species affect soils? The warp and woof of tree-soil interactions. – Biogeochemistry 42: 89–106.

Bowman, W. D. and Bilbrough, C. J. 2001. Influence of a pulsed nitrogen supply on growth and nitrogen uptake in alpine graminoids. – Plant Soil 233: 283–290.

Bowman, W. D., Theodose, T. A. and Fisk, M. C. 1995. Physiological and production responses of plant growth forms to increases in limiting resources in alpine tundra: implications for differential community response to environmental change. – Oecologia 101: 217–227.

Bradley, R. L., Titus, B. D. and Preston, C. P. 2000. Changes to mineral N cycling and microbial communities in black spruce humus after additions of $(NH_4)(2)SO_4$ and condensed tannins extracted from *Kalmia angustifolia* and balsam fir. – Soil Biol. Biochem. 32: 1227–1240.

Brookes, P. C., Landman, A., Pruden, G. et al. 1985. Chloroform fumigation and the release of soil-nitrogen – a rapid direct extraction method to measure microbial biomass nitrogen in soil. – Soil Biol. Biochem. 17: 837–842.

Caldwell, M. M. 1981. Plant responses to ultraviolet radiation. – In: Lange, O. L., Nobel, P. S., Osmond, C. B. et al. (eds), Encyclopedia of plant physiology: physiological plant ecology I. Springer-Verlag, pp. 170–197.

Castells, E., Penuelas, J. and Valentine, D. W. 2003. Influence of the phenolic compound bearing species *Ledum palustre* on soil N cycling in a boreal hardwood forest. – Plant Soil 251: 155–166.

Chapin, F. S. III 1980. The mineral nutrition of wild plants. – Annu. Rev. Ecol. Syst. 11: 233–260.

Dearing, M. D. 1996. Disparate determinants of summer and winter diet selection in a generalist herbivore, *Ochotona princeps*. – Oecologia 108: 467–478.

Dearing, M. D. 1997. Effects of *Acomastylis rossii* tannins on a mammalian herbivore, the North American pika, *Ochotona princeps*. – Oecologia 109: 122–131.

Fierer, N., Schimel, J. P, Cates, R. G. et al. 2001. Influence of balsam poplar tannin fractions on carbon and nitrogen dynamics in Alaskan taiga floodplain soils. – Soil Biol. Biochem. 33: 1827–1839.

Fisk, M. C., Schmidt, S. K. and Seastedt, T. R. 1998. Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. – Ecology 79: 2253–2266.

Foster, B. L. and Gross, K. L. 1997. Partitioning the effects of plant biomass and litter on *Andropogon gerardi* in old-field vegetation. – Ecology 78: 2091–2104.

Hättenschwiler, S. and Vitousek, P. M. 2000. The role of polyphenols in terrestrial ecosystem nutrient cycling. – Trends Ecol. Evol. 15: 238–243.

Hooper, D. U., Cardon, Z. G., Chapin, F. S. III et al. 2002. Corrected calculations for soil and ecosystem measurements of CO2 flux using the LI-COR 6200 portable photosynthesis system. – Oecologia 132: 1–11.

Kögel-Knabner, I. 2002. The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. – Soil Biol. Biochem. 34: 139–162.

Körner, Ch. 1999. Alpine plant life: functional plant ecology of high mountain ecosystems. – Springer Verlag.

Knapp, A. K. and Seastedt, T. R. 1986. Detritus accumulation limits productivity of tallgrass prairie. – BioScience 36: 662–668.

Mahall, B. E. and Callaway, R. M. 1992. Root communication mechanisms and intracommunity distributions of 2 Mojave desert shrubs. – Ecology 73: 2145–2151.

Meloche, C. G. and Diggle, P. K. 2001. Preformation, architectural complexity, and developmental flexibility in *Acomastylis rossii* (Rosaceae). – Am. J. Bot. 88: 980–991.

Moore, D. B., Palmquist, D. E. and Seeman, J. R. 1997. Influence of plant growth at high CO_2 concentrations on leaf content of ribulose-1,5-bisphosphate carboxylase/oxygenase and intracellular distribution of soluble carbohydrates in tobacco, snapdragon, and parsley. – Plant Phys. 115: 241–246.

Nilsson, M. C., Wardle, D. A. and Dahlberg, A. 1999. Effects of plant litter species composition and diversity on the boreal forest plant-soil system. – Oikos 86: 16–26.

Nilsson, M. C., Zackrisson, O., Sterner, O. et al. 2000. Characterisation of the differential interference effects of two boreal dwarf shrub species. – Oecologia 123: 122–128.

Northup, R. R., Dahlgren, R. A. and McColl, J. G. 1998. Polyphenols as regulators of plant-litter-soil interactions in northern California's pygmy forest: a positive feedback? – Biogeochemistry 42: 189–220.

Schimel, J. P., VanCleve, K., Cates, R. G. et al. 1996. Effects of balsam poplar (*Populus balsamifera*) tannins and low molecular weight phenolics on microbial activity in taiga floodplain soil: implications for changes in N cycling during succession. – Can. J. Bot. 74: 84–90.

Schimel, J. P., Cates, R. G. and Ruess, R. 1998. The role of balsam poplar secondary chemicals in controlling soil nutrient dynamics through succession in the Alaskan taiga. – Biogeochem. 42: 221–234.

Schmidt, S. K., Lipson, D. A. and Raab, T. K. 2000. Effects of willows (*Salix brachycarpa*) on populations of Salicylate-mineralizing microorganisms in alpine soils. – J. Chem. Ecol. 26: 2049–2057.

Schulze, W., Stitt, M., Schulze, E. D. et al. 1991. A quantification of the significance of assimilatory starch for growth of *Arabidopsis thaliana* L. Heynh. – Plant Phys. 95: 890–895.

Seastedt, T. R. 2001. Soils. – In: Bowman, W. D. and Seastedt, T. R. (eds), Structure and function of an alpine ecosystem: Niwot Ridge, Colorado. Oxford Univ. Press, pp. 157–176.
Seastedt, T. R., Walker, M. D. and Bryant, D. M. 2001. Controls on decomposition processes in alpine tundra. – In: Bowman, W. D. and Seastedt, T. R. (eds), Structure and function of an alpine ecosystem: Niwot Ridge, Colorado. Oxford Univ. Press, pp. 222–236.
Souto, X. C., Chiapusio, G. and Pellissier, F. 2000. Relationships between phenolics and soil microorganisms in spruce forests: Significance for natural regeneration. – J. Chem. Ecol. 26: 2025–2034.
Steltzer, H. 1999. Plant species effects on spatial variation in nitrogen cycling in alpine tundra. – PhD thesis, Univ. of Colorado.
Steltzer, H. and Bowman, W. D. 1998. Differential influence of plant species on soil N transformations within moist meadow alpine tundra. – Ecosystems 1: 464–474.
Suding, K. N., Larson, J. R., Thorsos, E. et al. in press. Species effects on resource supply rates: do they influence competitive interactions? – Plant Ecol.
Taylor, B. R., Parkinson, D. and Parsons, W. F. J. 1989. Nitrogen and lignin as predictors of litter decay rates: a microcosm test. – Ecology 70: 97–104.
Theodose, T. A., Bowman, W. D., Schardt, J. C. et al. 1996. Uptake and allocation of ^{15}N by alpine tundra plants: implications for the role of competitive ability in predicting community structure in a stressful environment. – Oikos 75: 59–66.
Van Breemen, N. and Finzi, A. C. 1998. Plant-soil interactions: ecological aspects and evolutionary implications. – Biogeochem. 42: 1–19.
Van der Krift, T. A. J. and Berendse, F. 2001. The effect of plant species on soil nitrogen mineralization. – J. Ecol. 89: 555–561.
Van Vuuren, M. M. I., Aerts, R., Berendse, F. et al. 1992. Nitrogen mineralization in heathland ecosystems dominated by different plant species. – Biogeochem. 16: 151–166.
Vance, G. F. and David, M. B. 1991. Chemical characteristics and acidity of soluble organic-substances from a northern hardwood forest floor, Central Maine, USA. – Geochim. Cosmochim. Acta 55: 3611–3625.
Wardle, D. A., Nicholson, K. S. and Rahman, A. 1996. Use of a comparative approach to identify allelopathic potential and relationship between allelopathy bioassays and "competition" experiments for ten grassland and plant species. – J. Chem. Ecol. 22: 933–948.
Waterman, P. G. and Mole, S. 1994. Analysis of phenolic plant metabolites. – Blackwell.
Webber, P. J. and May, D. E. 1977. Magnitude and distribution of below ground plant structures in alpine tundra of Niwot Ridge, Colorado. – Arc. Alp. Res. 9: 157–174.
Wedin, D. A. and Tilman, D. 1990. Species effects on nitrogen cycling – a test with perennial grasses. – Oecologia 84: 433–441.
Xiong, S. and Nilsson, C. 1999. The effects of plant litter on vegetation: a meta-analysis. – J. Ecol. 87: 984–994.