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Traits of the invasive *Centaurea maculosa* and two native grasses: effect of N supply

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Abstract

The Eurasian forb *Centaurea maculosa* (Lam.; spotted knapweed) has invaded millions of hectares of semi-arid grasslands in western North America. It readily colonizes disturbed areas, but also invades pristine grasslands. *C. maculosa*'s success could be attributed to greater use, or more efficient use, of available soil nitrogen (N). Soil N often limits growth on semi-arid grasslands. Greater or more efficient use of soil N by *C. maculosa*, if this occurred, may inhibit establishment, survival, or reproduction of native grasses. In a glasshouse, *C. maculosa* and two native grasses, *Pseudoroegneria spicata* [Scribn. and Smith] A. Love and *Pascopyrum smithii* [Rybd.] A. Love, were grown in mixed- and monoculture for 8 weeks to determine growth response to two soil N supplies, which mimicked low and high N mineralization rates in semi-arid grasslands. At the end of the 8 weeks, plants were exposed to ^{15}N-labeled nitrate for 24 h, and harvested to compare uptake of NO_3^-. *C. maculosa's* growth response to N indicated that it was more competitive for N than the tussock grass *P. spicata*, but less competitive than the rhizomatous grass *P. smithii*. *C. maculosa* used nitrogen less efficiently than both of these native grasses. *C. maculosa* roots took up more ^{15}N per unit root mass than the grasses, but acquired less N than *P. smithii* because *P. smithii* had greater root mass than *C. maculosa*. Total biomass and ^{15}N uptake of *C. maculosa* varied depending on which species it was growing with. *C. maculosa*'s success cannot be explained wholly by greater or more efficient use of soil N than that of the native grasses with which it competes.

Introduction

The Eurasian forb *Centaurea maculosa* Lam. (spotted knapweed) was introduced to the Pacific Northwest (U.S.A. and Canada) in the late 1800s, and is spreading rapidly on semi-arid grasslands (Lacey et al., 1995). *C. maculosa* reduces the productivity of desirable forage plants (Watson and Renney, 1974), and floristic diversity (Tyser and Key, 1989). *C. maculosa*'s success in North America may reflect that it was introduced without its native enemies, it is not grazed by domestic large herbivores, it may be more competitive than native species, it may interfere with native species via allelopathy, or most likely some combination of these factors.

C. maculosa colonizes disturbed areas (Watson and Renney, 1974), which generally have a greater abundance of available (inorganic) nutrients, and less competition for resources (Davis et al., 2000; Pickett and White, 1985). Many ruderal, early-successional species have rapid nutrient-uptake rates on a per plant (e.g., Crick and Grime, 1987) or per root basis (e.g., Caldwell et al., 1996); rapid nutrient uptake allows plants to exploit elevated availabilities of nutrients associated with disturbance (Burke and Grime, 1996). Early-successional species grow rapidly during the first couple of years (Wedin and Tilman, 1993), presumably supported by rapid rates of nutrient uptake when nutrients are not limiting.

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Besides colonizing early-successional, disturbed sites, *C. maculosa* invades semi-arid grasslands dominated by native, late-successional grass species (Chicoine et al., 1985). Semi-arid grasslands are often characterized by low availability of nutrients, especially N (Charley, 1977). Most plant species that dominate late-successional, nutrient-poor environments tend to have high root mass ratios, high nutrient resorption efficiency, and low rates of ion-uptake, growth, and tissue turnover (Aerts, 1999; Lambers and Poorter, 1992), which may allow them to tolerate sites with limited resource availability.

C. maculosa's success may, in part, reflect its plasticity to colonize early-successional, disturbed sites by rapidly acquiring nutrients, and to compete with late-successional grasses for limited nutrients on undisturbed sites. We hypothesized that *C. maculosa* has a greater ability to acquire soil N than native grasses do when N is abundant. Alternatively, *C. maculosa* may take up more N or use N more efficiently than late-successional, native grasses when N is limited. Our objective was to compare nitrate uptake, nitrogen-use efficiency (NUE), and growth response (biomass, allocation) of *C. maculosa* and two native grasses grown with different N supplies in monoculture and mixed-culture species combinations.

Materials and methods

We conditioned *C. maculosa* and two native grasses, *P. smithii* [Rybd.] A. Love (western wheatgrass) and *P. spicata* [Scribn. and Smith] A. Love (bluebunch wheatgrass), to one of two N supply rates. These rates mimicked low and high rates of N mineralization in semi-arid grasslands of Montana (Neill, 1995). After 8 weeks, plants were exposed to ^{15}N-labeled nitrate (NO_3^-) for 24 h and then harvested. Root and shoot biomass and mg g^{-1}N, and whole plant NUE (total biomass (g)/total N (g)) reflected growth response to N supply over the 8 weeks. These tissues were analyzed for ^{15}N enrichment to determine atom % ^{15}N, ^{15}N-uptake per unit root mass (μmol g^{-1} h^{-1}), and percent ^{15}N acquired of applied which reflected the amount of ^{15}N taken up during the 24 h labeling period.

Plant species

C. maculosa is a perennial, tap-rooted Eurasian forb introduced to the Pacific Northwest in the late 1800s. *P. smithii* (western wheatgrass) is a native, perennial rhizomatous grass. *P. spicata* (bluebunch wheatgrass) is a native, perennial bunchgrass. These late-successional native grasses are associated with N-limiting, semi-arid grasslands in the northwestern United States (Charley,1977).

C. maculosa co-occurs with these three native grasses, although usually on different sites because these native grasses seldom co-occur. *P. spicata* grows primarily on well drained, upland soils, whereas *P. smithii* grows on swales and bottomlands. Rooting depths of all three species are similar, however, the fibrous-rooted grasses tend to have greater root mass in the upper soil layers compared with the tap-rooted *C. maculosa* (unpublished data).

Experimental design

Combinations of *C. maculosa/P. spicata*, *C. maculosa/P. smithii,* and monocultures of each species were grown in columns in a glasshouse and conditioned to low or high N supplies (after Cui and Caldwell, 1997). Because *P. spicata* and *P. smithii* seldom co-occur in the field, growing *P. spicata* and *P. smithii* together in columns was not relevant to testing our hypotheses; therefore, the design was an incomplete factorial. Treatments were replicated nine times and the experiment was arranged as a randomized complete block design.

The columns were constructed of polyvinylchloride (PVC) pipe, 10 cm in diameter and 40 cm in height, with perforated end caps as bottoms. The columns were filled to within 2 cm of the top with pasteurized (~80 °C for 1 h) sand (<2.0 mm in diameter). This common protocol is used to kill weed seeds, insect eggs, and pathogens, yet has minimal effect on the soil microbial community. Soil microorganisms have the potential to compete for soil N, at least in the short term (Hodge et al., 2000a). However, such competition is minimal when soil C:N ratios are less than 12.5 (Hodge et al., 2000b). C:N ratios of rangeland soils in Montana average 9:1 (Neill, 1995) so it is unlikely that microbial competition for N in such soils or our sand cultures would have been significant. Further, our focus was on relative differences in growth and N uptake among the three species in mixed- and monoculture, not absolute differences.

Seeds of each species were sterilized in a 2% NaOCl solution for 2 min and inserted 1 cm into the sand in two groups of three per column. Seed groups were spaced 6 cm apart, and each group consisted of the same species. Mixed culture columns received three seeds of two species; monoculture columns received six seeds of the same species. Seeded columns were placed in a cold room (2 °C) for an 8-week vernalization period to enhance germination. The sand surface was misted with water three times per week during vernalization. Columns were then moved to a glasshouse where they were watered with a dilute solution of commercial fertilizer (Miracle-Gro, Stern's Nurseries, Geneva, New York, USA; 30:30:30 NPK) until seedlings were established.

N availability

Established seedlings were thinned to two per pot, one from each group. Then these columns were watered daily for 8 weeks with a nutrient solution using an automated watering system. Plants in the low- and high-N treatments received 200 mL of dilute (0.1x) modified Hoagland stock solution (KH_2PO_4, KNO_3, $Ca(NO_3)_2$, $MgSO_4$, micronutrients; Cui and Caldwell, 1997) containing 0.75 and 1.5 mm N, respectively. These N supply rates (0.15 mmol N day^{-1}, 0.3 mmol N day^{-1}) to our sand-filled columns (approximately 5 kg dry weight) mimicked low and high levels of N mineralization rates in semi-arid grasslands of Montana (0.42 and 0.84 μg N g^{-1} soil day^{-1}; Neill, 1995). N was supplied as NO_3^-; most N mineralized from seven different Montana rangeland soils is in the form of NO_3^- (97.7–99.3%; Neill, 1995).

Glasshouse temperatures averaged 20 °C during the day and 15 °C at night. Grow lights (GE Multi-Vapor MVR1000/C/U, GE Lighting, General Electric Company, Cleveland, Ohio, USA) were on between 0700 and 2100 h each day during the experiment, which began in March and continued until the end of May. Natural daylength averaged 11.9, 13.5 and 14.9 h in March, April, and May, respectively. Photosynthetically active radiation (PAR) was recorded hourly in a nearby glasshouse without grow lights; daily maxima ranged from 108 to 798 μmol m^{-2} s^{-1} at bench height.

^{15}N Labeling and harvest

After 8 weeks of conditioning plants to the two N levels, ^{15}N-labeled nitrate ($K^{15}NO_3$; 99 atom %; Isotec, Inc. Miamisburg, Ohio, USA) in an aqueous solution (150 mL per column) was substituted for the daily watering of nutrient solution. Each column received the same amount of N (as $^{15}NO_3$) that had been supplied daily during the treatment period. Plants were harvested 24 h later.

First, shoots were separated from roots. Then, roots from different species in the mixed-culture columns were separated based on color, thickness, pliability, and branching architecture. *C. maculosa* roots were golden brown, relatively thick, brittle, and had fewer bifurcations, whereas roots from both grasses were white, fine, pliable, and had many bifurcations. Thus, roots from mixed-culture columns were readily separated in a water bath even though roots were intermingled in the columns. For monoculture columns, all roots could not be readily identified to a particular plant in the column, thus we averaged the response of the two plants for statistical analyses. Roots and shoots were dried at 70 °C for 72 h, and then weighed to determine root and shoot biomass. All variables are presented on a dry weight basis.

Using root and shoot mass to determine root mass ratio is subject to experimental error because: (1) there is no clear boundary between roots and shoots, (2) total root mass, especially fine roots, may not be recovered, and 3) roots are short-lived and some may decompose before recovery (Stulen and den Hertog, 1993). We were consistent in assessing the boundary between roots and shoots, and in time spent washing and separating roots, so loss of fine roots from one column or plant would not be exaggerated relative to another. Root mass ratios from these columns are similar to root mass ratios of these species in the field (unpublished data). Technically, rhizomes of *P. smithii* are underground stems. We combined rhizomes with roots because they assist the spread of a genotype, like lateral roots, although they do not take up water or nutrients.

Dried plant material was fine-ground using a Cyclone Sample Mill (UDY Corporation, Fort Collins, Colo. USA). Plant tissue N concentrations, atom % ^{15}N, and δ^{15}N were measured with a Europa mass spectrometer (PDZ Europa Ltd., U.C. Davis, Stable Isotope Facility, Davis, Calif. USA).

^{15}N-uptake rate by roots per unit root mass (μmol g^{-1} h^{-1}) during the 24 h labeling was calculated using root mass, % N, and fractional abundance (F). The amount of ^{15}N acquired relative to applied for the entire plant was the sum of the product of root mass, % N, and F, and the product of shoot mass, % N, and F. Fractional abundance and atom % ^{15}N were determined by the following steps (Boutton, 1991; Shearer and Kohl, 1993):

$$\delta^{15}\mathrm{N}(‰) = [(R_{\mathrm{sample}} - R_{\mathrm{std}})/R_{\mathrm{std}}] \times 10^3 \qquad (1)$$

where R represents the absolute ratio ($^{15}N/^{14}N$) of the plant sample and standard gases. The absolute ratio for the standard gas (R_{std}) is 0.0036765. The absolute ratio of a sample (R_{sample}) can be determined by rearranging (1).

$$R_{sample} = {}^{15}N/{}^{14}N = [(\delta^{15}N/1000) + 1] \times R_{std} \tag{2}$$

R_{sample} is used to calculate F, fractional abundance:

$$F = {}^{15}N/({}^{15}N + {}^{14}N) = R_{sample}/(R_{sample} + 1) \tag{3}$$

Atom % ^{15}N is related to F as follows:

$$\text{Atom } \%^{15}N = F \times 100. \tag{4}$$

Data analysis

The experiment included 2 N levels and 5 species combinations, and was analyzed as a complete randomized block design ($n = 9$). Atom %^{15}N, ^{15}N uptake by roots per unit root mass (μmol $g^{-1}h^{-1}$), ^{15}N acquired of applied (%), total biomass (g), root mass ratio, and NUE (total biomass (g) / total N (g)) were analyzed with ANOVA (SAS 1988). Atom %^{15}N and ^{15}N acquired of applied (%) were transformed with arcsine, whereas root mass ratio and NUE were transformed with natural log. Non-transformed least square means and standard errors are presented in figures. Pre-treatment plant height and number of tillers (grasses) or leaves (*C. maculosa*) were used as covariates for total biomass and NUE. Plant responses within columns were not independent of one another, thus we used planned contrasts to compare plant responses within different species combinations at each N supply, e.g., *C. maculosa*'s response in monoculture versus *C. maculosa*'s response when grown with one of the grasses at low N. *P*-values less than 0.05 were considered significant.

Results

At low and high N supply, ^{15}N enrichment (atom & ^{15}N) was greater for roots and shoots of *P. spicata* in monoculture than roots and shoots of *P. spicata* grown with *C. maculosa* (Figure 1a). At high N, ^{15}N enrichment of shoots of *C. maculosa* grown with *P. spicata* was greater than enrichment of *C. maculosa* grown with *P. smithii*. Overall, ^{15}N enrichment was greater at high than at low N.

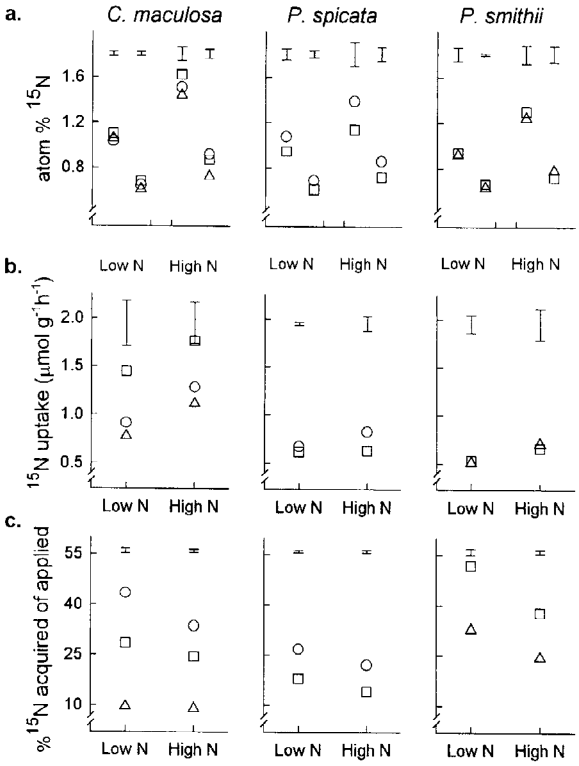

Figure 1. Atom % ^{15}N in roots and shoots (a), root uptake of ^{15}N-labeled nitrate (b) and percent ^{15}N-label acquired of applied (c) by target species *C. maculosa*, *P. spicata* and *P. smithii* when growing with *C. maculosa* (□) or *P. spicata* (○) or *P. smithii* (△), and conditioned to low N or high N. Bars indicate standard error of least square means within treatment.

At low and high N, *C. maculosa* in monoculture had greater ^{15}N uptake (μmol g^{-1} h^{-1}) than when grown with *P. smithii* and *P. spicata* (Figure 1b). Overall, *C. maculosa* had greater ^{15}N-uptake rates than the grasses.

C. maculosa grown with *P. spicata* acquired more of the applied ^{15}N (%) than *C. maculosa* in monoculture at low and high N, whereas *C. maculosa* grown with *P. smithii* acquired less ^{15}N than *C. maculosa* in monoculture (Figure 1c). *P. spicata* in monoculture acquired more ^{15}N than *P. spicata* grown with *C. maculosa*, whereas *P. smithii* in monoculture acquired less ^{15}N than *P. smithii* grown with *C. maculosa*. *P. smithii* grown with *C. maculosa* acquired more ^{15}N than *P. spicata* grown with C. maculosa; conversely, *C. maculosa* grown with *P. smithii* acquired less ^{15}N than *C. maculosa* grown with *P. spicata*.

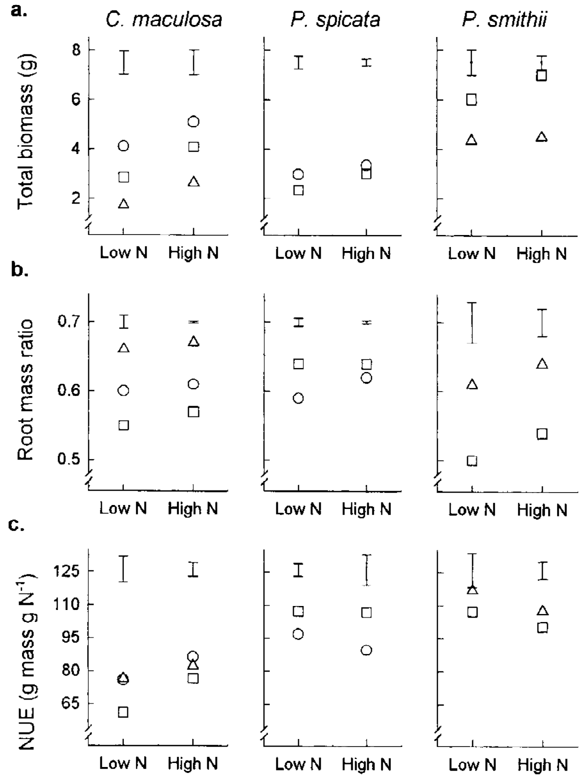

Figure 2. Biomass (a) root mass ratios (b), and nitrogen-use efficiency (c) of target species *C. maculosa*, *P. spicata* and *P. smithii* when growing with *C. maculosa* (□) or *P. spicata* (○) or *P. smithii* (△), and conditioned to low N or high N. Bars indicate standard error of least square means within treatment.

C. maculosa grown with *P. spicata* had greater biomass than *C. maculosa* in monoculture, whereas *C. maculosa* grown with *P. smithii* had lower biomass than *C. maculosa* in monoculture (Figure 2a). *P. smithii* in monoculture had lower biomass than when grown with *C. maculosa*. *P. smithii* grown with *C. maculosa* had greater biomass than *P. spicata* grown with *C. maculosa*. Conversely, *C. maculosa* grown with *P. smithii* had less biomass than *C.* maculosa grown with *P. spicata*.

Root mass ratios varied depending on the neighbor (Figure 2b). For example, *C. maculosa* had greater root mass ratios when grown with *P. smithii* than when grown in monoculture; conversely *P. smithii* had much greater root mass ratios when grown in monoculture than when grown with *C. maculosa*.

At low N, NUE was greater for *C. maculosa* when grown with each grass (mixed-cultures) than when grown in monoculture (Figure 2c). *P. smithii* in monoculture had greater NUE than *P. smithii* grown with *C. maculosa*. At high N, NUE was greater for *P. spicata* grown with *C. maculosa* than *P. spicata* in monoculture.

Discussion

N uptake

Overall, ^{15}N enrichment (atom % ^{15}N) was similar among species, except roots and shoots of *P. spicata* in monoculture had greater ^{15}N enrichment than roots and shoots of *P. spicata* grown with *C. maculosa*, indicating that *C. maculosa* was a stronger sink for ^{15}N than *P. spicata*.

^{15}N enrichment (atom % ^{15}N) was greater at high than at low N, which simply reflects that high N plants received twice as much ^{15}N as low N plants during the labeling period. As expected, roots were more enriched in ^{15}N than shoots; plants had access to the label for only 24 h so there was not much time for ^{15}N movement to shoots. Atom % ^{15}N of shoots ranged from 0.61 to 0.92; atmospheric background atom % ^{15}N is 0.366 indicating that some ^{15}N moved to the shoots.

C. maculosa took up ^{15}N (μmol g^{-1}h^{-1}) more rapidly than *P. spicata* and *P. smithii* during the 24 h labeling period, which helps explain *C. maculosa's* ability to colonize disturbed areas with high N mineralization rates (Burke and Grime, 1996). The late-successional grasses' slower N-uptake rate was expected; plants from low-nutrient environments often rely on extensive root systems, not rapid uptake, to capture nutrients in limited supply (Aerts et al., 1991).

C. maculosa took up more ^{15}N (μmol g^{-1}h^{-1}) at high N than at low N, whereas this difference in uptake rates at the two N supplies was much lower for the grasses. This suggests *C. maculosa* has a more plastic response to take advantage of high N supplies, whereas the slow-growing semi-arid grasses have a relatively fixed response to N availability. This may reflect selection for extensive root systems, not flexible uptake patterns, to capture nutrients normally in limited supply.

In our study, plants supplied with low N during the study acquired a greater percent of the applied ^{15}N during the labeling period. In other studies, plants supplied with low N also had a greater capacity to absorb N under N-limiting conditions (Lee, 1982; Robinson, 1996). Plants supplied with low N tend to have more extensive root systems, i.e. greater allocation to root systems. Percent acquired of applied $^{15}NO^{-}_3$ is a function of ^{15}N uptake per unit root mass and root mass. Unlike our results, alpine grasses conditioned to a high N supply acquired more of the applied $^{15}NO^{-}_3$ than grasses conditioned to a low N supply, which primarily reflected greater root biomass of high-N plants (Bowman and Bilbrough, 2001). Their high- and low-N plants received the same amount of $^{15}NO^{-}_3$; therefore, it was not surprising that their high-N plants acquired more of the label. In contrast, our high- and low-N plants received the amount of N ($^{15}NO^{-}_3$) they were exposed to during the 8 week conditioning period because we were interested in relative differences between species conditioned to high and low N supplies.

As expected, *C. maculosa* acquired more of the applied ^{15}N when grown with *P. spicata*, whereas *P. spicata* grown with *C. maculosa* acquired less ^{15}N than *P. spicata* in monoculture. This reflects *C. maculosa*'s more rapid uptake of N and greater root mass than those of *P. spicata*. In contrast, *P. smithii* grown with *C. maculosa* acquired more of the applied ^{15}N, whereas *C. maculosa* grown with *P. smithii* acquired less of the applied ^{15}N. This reflects *P. smithii*'s greater root mass, offsetting its slower uptake of ^{15}N compared with *C. maculosa*. Thus, each grass species responded differently when growing with *C. maculosa*. Similarly, N-uptake rates and allocation patterns of *Quercus douglasii* seedlings differ depending on whether they are competing with other *Quercus* seedlings, the perennial grass *Stipa pulchra*, or the annual grass *Bromus mollis* (Welker et al., 1991). *Poa pratensis* captures more N from nitrogen-rich organic matter when growing with *Lolium perenne* than in monoculture (Hodge et al., 2000c).

In our study, percent ^{15}N acquired of applied differed considerably between the early-successional *C. maculosa* and our late-successional grasses. In contrast, total ^{15}N uptake of the early-successional annual *Ambrosia artemisiifolia* and the late-successional perennial *Achillea millefolium* were similar (Kosola and Gross, 1999). However, both of those species are erect forbs and related (Asteraceae), unlike our fibrous-rooted grasses and the tap-rooted *C. maculosa*. In their study, different neighbors did not affect 15N acquired; in our study, ^{15}N acquired by all three species was greatly affected by neighbor identity. Their plants had access to ^{15}N for 40 days; ours had access for only 24 h.

Besides uptake per unit root mass and root mass, nutrient uptake may be related to specific root length (root length/unit mass; Aerts and Chapin, 2000) or root length density (root length/patch volume; Robinson et al., 1999). In general, grasses have finer roots than forbs (Glimskar, 2000), which we noticed while separating roots of our grasses from those of *C. maculosa*. Yet specific root length may not be the dominant factor that affects nitrate uptake. At least in nutrient-rich patches, nitrate uptake may reflect physiological plasticity rather than morphological plasticity (Fransen et al., 1998; Hodge et al., 1998; Jackson and Caldwell, 1996).

Growth response

We thought our late-successional grasses would grow slower and produce less biomass than the invasive *C. maculosa*. Plants may grow slowly to reduce their demand for nutrients; slow-growing plants may also have low tissue turnover rates and high nutrient-resorption efficiency, or some combination of these factors (Aerts, 1999). Such characteristics are common for plants that evolved in low-nutrient environments, such as our grasses. Slower growth rates of native grasses, if observed, could also reflect interference via allelopathy associated with root exudates or decomposition. Two potentially allelopathic compounds, sesquiterpene lactones and polyacetylenes, have been isolated from *C. maculosa* species (Stevens, 1986; Kelsey and Locken, 1987). In sand culture, activated charcoal (which adsorbs organic compounds) reduced the apparent allelopathic effect of *C. maculosa* on *Festuca idahoensis* Elmer, a North American tussock grass (Ridenour and Callaway 2001).

As expected, *C. maculosa* produced more biomass than *P. spicata*. Plants that initiate growth early or grow fast are able to rapidly occupy space and resources, which may be an advantage when competing for limited resources (Robinson et al., 1999). If allelopathy were a significant factor between growth of *C. maculosa* and our two native grasses, *C. maculosa* should have reduced growth of both grass species. Unlike *P. spicata* though, *P. smithii* produced more, not less, biomass when growing with *C. maculosa* than when growing with a conspecific. *P. smithii* did not have greater uptake of ^{15}N than *C. maculosa* during our 24 h label, but it did have an extensive root system (greater root mass, data not shown), which is not congruent with interference via allelopathy. Our sand medium was similar to Ridenour and Callaway's (2001), who reported an apparent allelopathic effect of *C. maculosa* on another native grass (*F. idahoensis*).

Lacking organic matter, a sand medium should accentuate allelopathic effects, but it did not in our study, at least not between *C. maculosa* and *P. smithii*. Such differences in grass response when growing with *C. maculosa* may explain *C. maculosa*'s ability to create monospecific stands on pristine grasslands historically dominated by *P. spicata* and *F. idahoensis* (Ridenour and Callaway 2001), but not those dominated by *P. smithii*.

Root mass ratios varied depending on the neighbor, especially for *C. maculosa* and *P. smithii*. When grown in monoculture, *C. maculosa*'s lower root mass ratio is typical of an early-successional, ruderal species, although its root mass ratios were considerably greater when grown with the grasses. Rapid nutrient uptake, observed with our ^{15}N label with *C. maculosa*, may offset relatively low allocation to root systems, or plants may compensate for lower root mass ratios by having greater length per unit mass (specific root length; Aerts and Chapin, 2000). Herbaceous monocots invest more in roots and less in leaves than herbaceous dicots with similar relative growth rates (Garnier, 1991).

Root mass ratios are often greater when N availability is low (Aerts and De Caluwe, 1989; Fichtner and Schultze, 1992; Poorter and Nagel, 2000; Reynolds and D'Antonio, 1996; Robinson, 1996; Van der Werf et al., 1993). In contrast, root mass ratios of *C. maculosa, P. smithii*, and to a slight extent *P. spicata,* were greater at the high N supply. Allocating a greater percentage of resources to root growth increases the ability to compete for soil nutrients, whereas allocating more resources to leaves maximizes growth rate (Gleeson and Tilman, 1990). The latter may be problematic when available nutrients, not solar radiation, limit above-ground growth in semi-arid grasslands. However, greater root mass does not necessarily increase root absorption capacity because absorption capacity generally declines as roots age (Chapin, 1980).

Nitrogen-use efficiency

Overall, *P. smithii* and *P. spicata* had greater NUE than *C. maculosa*. Plant species that evolved in nutrient-poor environments tend to have low tissue N concentrations, thus high NUE (Gleeson and Tilman, 1990). Relative to the grasses, *C. maculosa*'s low NUEs would be expected where minerals are readily abundant such as on disturbed sites. Low NUEs may reflect N storage to help initiate growth when N may not be readily available (Aerts, 1997), such as in the spring or fall when soils are cool and mineralization rates are slow. Low NUEs may also reflect the presence of large amounts of cell wall material, lignin, and protective compounds in leaves and stems which may deter herbivory (Lambers and Poorter, 1992). *C. maculosa* contains the bitter tasting cnicin, a sesquiterpene lactone, which may partly explain why large ungulates avoid the plant. Further, high levels of *C. maculosa* in the diet reduce activity of rumen microorganisms (Olson and Kelsey, 1999).

In general, the grasses had greater NUE at low N than at high N. In contrast, *C. maculosa* had greater NUE at high N than at low N when growing with *P. spicata* and *C. maculosa*. We had expected that NUE of all three species would be greater at low N than at high N because the need to use N efficiently to produce biomass should increase with reduced N availability. A plant's ability to produce more biomass per unit of N may be an advantage in low-nutrient environments (Aerts et al., 1991). However, traits that reduce nutrient losses and/or increase retention time may be more important than NUE per se (Aerts, 1999).

C. maculosa's greater NUE at high than at low N supply when growing with *P. spicata* and *C. maculosa* suggests that *C. maculosa* requires relatively high levels of N. This would be expected for species such as *C. maculosa* that colonize disturbed areas with high N supply (McLendon and Redente, 1991). Alternatively, *C. maculosa*'s lower NUE with low N supply may reflect that *C. maculosa* retains N at low N (Aerts, 1999), ensuring that sufficient N is available for growth when growing conditions in semi-arid grasslands are more favorable.

Neighbors influenced NUEs of the grasses, although in different ways. *P. spicata* in monoculture had lower NUE than *P. spicata* grown with *C. maculosa*, whereas *P. smithii* in monoculture had greater NUE than *P. smithii* grown with *C. maculosa*. These results indicate that *P. spicata* growing with *C. maculosa* had to use limited N more efficiently than when growing with conspecifics, whereas *P. smithii* growing with conspecifics had to use N more efficiently than when growing with *C. maculosa*. This suggests a competitive hierarchy with *P. smithii* being the most and *P. spicata* the least competitive.

In conclusion, *C. maculosa* has certain traits that explain its ability to colonize early-successional, disturbed sites, including more rapid N uptake, lower root mass ratios, and lower NUEs than our two native grasses. Such traits may also allow it to colonize microdisturbances on late-successional, pristine grasslands (Davis et al., 2000; Tyser and Key, 1989), but do not explain *C. maculosa*'s ability to spread once established.

C. maculosa's growth response depended on the neighbor. *C. maculosa* was able to out-compete *P. spicata* for N, but was not able to out-compete *P. smithii* for N. This suggests that certain native species would have a greater chance of success when attempting to restore native grasses to *C. maculosa*-infested areas.

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References

Aerts R, Boots R G A and Van der Aart P J M 1991 The relation between aboveground and belowground biomass allocation patterns and competitive ability. Oecologia 87, 551–559.

Aerts R 1997 Nitrogen partitioning between resorption and decomposition pathways: a trade-off between nitrogen use efficiency and litter decomposibility? Oikos 80, 603–606.

Aerts R 1999 Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. J. Exp. Bot. 50, 29–37.

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, 5–55.

Aerts R and De Caluwe H 1989 Aboveground productivity and nutrient turnover of *Molinia caerulea* along an experimental gradient of nutrient availability. Oikos 54, 320–324.

Aerts R, Boot R G A and van der Aart P J M 1991 The relation between above- and below-ground biomass allocation patterns and competitive ability. Oecologia 87, 551–559.

Boutton TW 1991 Stable carbon isotope ratios of natural materials: I. Sample preparation and mass spectrometric analysis. *In:* Carbon Isotope Techniques. Eds. D C Coleman and B Fry. 155–171. Academic Press, San Diego.

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.

Burke M J W and Grime J P 1996 An experimental study of plant community invasibility. Ecology 77, 776–790.

Caldwell M M, Manwaring J H and Durham S L 1996 Species interactions at the level of fine roots in the field influence soil heterogeneity and plant size. Oecologia 106, 440–447.

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

Charley J L 1977 Mineral cycling in rangeland ecosystems. In: Rangeland plant physiology. Ed. R E Sosebee. pp 215–256. Soc. Range Manage., Denver.

Chicoine T K, Fay P K and Neilsen G A 1985 Predicting weed migration from soil and climate maps. Weed Sci. 34, 57–61.

Crick J C and Grime J P 1987 Morphological plasticity and mineral nutrient capture in two herbaceous species of contrasted ecology. New Phytol. 107, 403–414.

Cui M and Caldwell M M 1997 Growth and nitrogen uptake by *Agropyron desertorum* and *Psuedoregneria spicata* when exposed to nitrate pulses of different duration. Aust. J. Plant Physiol. 24, 637–642.

Davis, M A, Grime J P and Thompson K 2000 Fluctuating resources in plant communities: a general theory of invasibility. J. Ecol. 88, 528–534.

Fichtner K and Schultze E-D 1992 The effect of nitrogen nutrition on growth and biomass partitioning of annual plants originating from habitats of different nitrogen availability. Oecologia 92, 236–241.

Fransen B, de Kroon H and Berendse F 1998 Root morphological plasticity and nutrient acquisition of perennial grass species from habitats of different nutrient availability. Oecologia 115, 351–358.

Garnier E 1991 Above and below-ground resource capture in herbaceous plants: Relationships with growth and biomass allocation. Trends Ecol. Evol. 6, 126–131.

Gleeson S K and Tilman D 1990 Allocation and the transient dynamics of succession on poor soils. Ecology 71, 1144–1155.

Glimskar A 2000 Estimates of root system topology of five plant species grown at steady-state nutrition. Plant Soil 227, 249–256

Hodge A, Robinson D and Fitter A 2000a Are microorganisms more effective than plants at competing for nitrogen? Trends Plant Sci. 5, 304–308.

Hodge A, Stewart J, Robinson D, Griffiths B S and Fitter A H 1998 Root proliferation, soil fauna and plant nitrogen capture from nutrient-rich patches in soil. New Phytol. 139, 479–494.

Hodge A, Stewart J, Robinson D, Griffiths BS and Fitter A H 2000b Competition between roots and soil micro-organisms for nutrients from nitrogen-rich patches of varying complexity. J. Ecol. 88, 150–164.

Hodge A, Stewart J, Robinson D, Griffiths BS and Fitter A H 2000c Spatial and physical heterogeneity of N supply from soil does not influence N capture by two grass species. Funct. Ecol. 14, 645–653.

Jackson J B and Caldwell M M 1996 Integrating resource heterogeneity and plant plasticity: modeling nitrate and phosphate uptake in a patchy soil environment. J. Ecol. 84, 891–903.

Kelsey R G and Locken L J 1987 Phytotoxic properties of cnicin, a sesquiterpene lactone from *Centaurea maculosa* (spotted knapweed). J. Chem. Ecol. 13, 19–33.

Kosola K R and Gross K L 1999 Resource competition and suppression of plants colonizing early-successional old fields. Oecologia 118, 69–75.

Lacey C A, Lacey J R, Fay P K, Story J M and Zamora D L 1995 Controlling spotted knapweed on Montana rangelands. Mont. Sta. Univ. Ext. Serv. Pub. 311.

Lambers H and Poorter H 1992 Inherent variation in growth rate between higher plants: A search for physiological causes and ecological consequences. Adv. Ecol. Res. 23, 187–261.

Lee R B 1982 Selectivity and kinetics of ion uptake by barley plants following nutrient deficiency. Ann. Bot. 50, 429–449.

McLendon T and Redente E F 1991 Nitrogen and phosphorous effects on secondary succession dynamics on a semi-arid sagebrush site. Ecology 72, 2016–2024.

Neill K E 1995 Mineralization of nitrogen and carbon in adjacent crop-fallow and native range soils. M.S. Thesis, Mont. Sta. Univ., Bozeman, Mont., USA.

Olson B E and Kelsey R G 1997 Effect of *Centaurea maculosa* on sheep rumen microbial activity and mass in vitro. J. Chem. Ecol. 23, 1131–1144.

Pickett S T A and White P S (eds) 1985 The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, London.

Poorter H and Nagel O 2000 The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. Aust. J. Plant Phys. 27, 595–607.

Ridenour W M and Callaway R M 2001 The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. Oecologia 126, 444–450.

Reynolds H L and D'Antonio C O 1996 The ecological significance of plasticity in root weight ratio in response to nitrogen: opinion. Plant Soil 185, 75–97.

Robinson D 1996 Variation, co-ordination and compensation in root systems in relation to soil variability. Plant Soil 187, 57–66.

Robinson D, Hodge A, Griffiths B S and Fitter A H 1999 Plant root proliferation in nitrogen-rich patches confers competitive advantage. Proc Royal Soc (London) Ser B 266, 431–435.

SAS Institute, Inc 1988 Statistical analysis system. SAS Institute Inc, Raleigh, North Carolina. Shearer G and Kohl D H 1993 Natural abundance of 15N: Fractional contribution of two sources to a common sink and use of isotope discrimination. *In*: Nitrogen Isotope Techniques. Eds. R Knowles and T H Blackburn. pp 89–125. Academic Press, Inc. San Diego.

Stevens K L 1986 Allelopathic polyacetylenes from *Centaurea repens* (Russian knapweed). J. Chem. Ecol. 12, 1205–1211.

Stulen I and den Hertog J 1993 Root growth and functioning under atmospheric CO_2 enrichment. Vegetatio 104/105, 99–115.

Tyser R W and Key C H 1989 Spotted knapweed in natural area fescue grasslands: an ecological assessment. Northwest Sci. 62, 151–160.

Van der Werf A, van Nuenen M, Visser A J and Lambers H 1993 Contribution of physiological and morphological plant traits to species' competitive ability at high and low nitrogen supply. Oecologia 94, 434–440.

Watson A K and Renney A J 1974 The biology of Canadian weeds *Centaurea diffusa* and *C. maculosa*. Can. J. Plant Sci. 54, 687–701.

Wedin D A and Tilman D 1993 Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. Ecol. Monographs 63, 199–229.

Welker J M, Gordon D R and Rice K J 1991 Capture and allocation of nitrogen by *Quercus douglasii* seedlings in competition with annual and perennial grasses. Oecologia 87, 459–466.

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