Selective gopher disturbance influences plant species effects on nitrogen cycling

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Plant species effects on ecosystem processes are mediated by traits such as litter quality and exudation. These same traits also influence the activity and distribution of animals that play key roles in regulating ecosystem dynamics. We planted monocultures of eight plant species commonly found in California grasslands to investigate the relative importance of plant species direct effects on nitrogen cycling, versus their indirect effects mediated by plant interactions with gophers. Plant species differed in their litter C:N ratio, which closely related to species effects on rates of net mineralization and nitrification in undisturbed soil. However, the effect of selective gopher disturbance on N cycling greatly altered these species effects.

Plant species differed in their effects on the type and timing of gopher disturbance. Small feeding holes were formed in late spring in plots containing species with high tissue quality. These feeding holes minimally disturbed the soil and did not alter N cycling rates over the short term. Large gopher mounds were formed in the winter and early spring, primarily in plots containing the grass, *Aegilops triuncialis*, and to a lesser extent in plots containing *Avena barbata*. These large mounds significantly disturbed the soil and greatly increased net nitrification rates, but had no consistent effects on net N mineralization. In undisturbed soil, *Aegilops* had the highest litter C:N ratio and one of the lowest rates of net nitrification. However, gophers preferentially built large mounds in *Aegilops* plots. Once the effects of gopher burrowing were considered, *Aegilops* had one of the highest rates of net nitrification, indicating that the indirect effects of plant species on N cycling can be more important than the direct effects alone. This experiment indicates that it is vital to consider interactions between plants and other organisms in order to predict the ecosystem effects of plant communities.

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It is well established that plant species can differ in their effects on many ecosystem processes, including decomposition (Melillo et al. 1982, McClaugherty et al. 1985, Hobbie 1996), nitrogen cycling (Wedin and Tilman 1990, Hobbie 1992), and carbon cycling (Vinton and Burke 1995, Chen and Stark 2000). These effects of plants on biogeochemical cycles are mediated by multiple plant traits, and these same plant traits can have indirect ecosystem effects by altering the distribution and activity of other organisms that strongly influence ecosystem processes (reviewed by Eviner and Chapin 2003a).

Gophers selectively burrow in areas with high plant density and biomass, in fertilized plots (Huntly and Inouye 1988), and in patches containing certain plant species (Tilman 1983, Benedix 1993, Ferguson 1999). Burrowing consists of two types of disturbances that can be detected aboveground: laterals and popholes (Vleck 1981). Laterals are offshoots of main tunnels used to access food and to deposit soil from the tunnels on to the

soil surface, and result in the large mounds that are most often associated with gopher activity. Popholes are small holes filled with a soil plug and result in minimal soil disturbance. These are used by gophers to access above-ground vegetation for feeding. While selective gopher disturbance is usually attributed to food quality and availability, the production of large mounds is often not related to food preference (Bandoli 1981, Andersen 1990). Vleck (1981) suggests that gophers preferentially build mounds in areas with higher soil cohesion, which lowers the energetic costs of burrowing because cohesive soils allow gophers to make shorter, more vertical tunnels to the soil surface. Soil cohesion is primarily determined by plant roots (Waldron 1977, Selby 1993), suggesting that plant species can mediate gopher activity through both their rooting structure and their tissue quality.

The local distribution of patches of plant species may influence patterns of gopher activity, and these effects of plant species on gopher disturbance could potentially have larger ecosystem impacts than the direct effects of plants. This is particularly likely because gopher disturbance is extensive (approximately 26% of the soil surface annually in California grasslands, Hobbs and Mooney 1991), and alters many aspects of ecosystems including plant community composition, soil formation, nutrient availability, microtopography, and the behavior and abundance of other species (Huntly and Inouye 1988).

Our goal was to determine: 1) the direct effects of plant species on nitrogen cycling, 2) the mechanisms by which plant species affect gopher activity, 3) the effects of selective gopher activity on nitrogen cycling, and 4) the relative importance of the direct and indirect effects of plant species on nitrogen cycling.

Methods

Field site

This research took place in the California annual grass-land (Huenneke and Mooney 1989) at the University of California Hopland Research and Extension Center in the northern coastal mountains of Mendocino County (160 km north of San Francisco, $39°00'$N latitude, $123°04'$W longitude). This area of California experiences a Mediterranean climate, with hot dry summers and cool wet winters. Mean annual precipitation is 960 mm, which occurs October through May, with 75% of that falling between November and February. Temperatures also vary seasonally, with a mean temperature of $7.5°C$ in December through February, while summer temperatures (July through September) average $21°C$, with a mean daily maximum temperature of $33°C$. The growing season begins in the fall with the first germinating rains and continues until late spring, when the rains cease and most plants senesce. The plots were established at an elevation of 395 m on a west-facing slope of approximately $13°$, on a Sutherlin soil (a medium texture loam derived from hard sandstone and shale, classified as an ultic haploxeralf, Gowans 1958). This site is dominated by annual vegetation, including *Avena barbata*, *Bromus hordeaceus*, *Aegilops triuncialis*, *Taeniatherum caput-medusae*, *Bromus diandrus*, *Erodium botrys*, *Lupinus bicolor*, and *Trifolium subterraneum*.

Experimental setup

In the summer of 1997, we established 1 m² monoculture plots of eight species common in northern California grasslands. These included four species of grasses: barbed goatgrass (*Aegilops triuncialis* L.), slender wild oats (*Avena barbata* Link.), soft chess (*Bromus hordeaceus* L.), and medusahead (*Taeniatherum caput-medusae* L.), two forbs: filaree (*Erodium botrys* (Cav.) Bertol.) and fiddleneck (*Amsinckia douglasiana* A. D.C.), and two legumes: dove lupine (*Lupinus bicolor* Lindey) and maiden clover (*Trifolium microcephalum* Pursch). Nomenclature follows Hickman (1993). Eighteen replicate plots of each species, as well as nine replicates of an unvegetated treatment were planted in a randomized block design with a 0.5 m buffer between plots. In addition, a set of ten 4 m² control plots were established in the natural grasslands surrounding the experimental site.

In order to establish the experimental plots, the seed bank was minimized over a 30×60 m area. The area was mowed, and litter was removed and autoclaved at $200°C$ for 4 h. Germination of the soil seedbank was stimulated prior to autumn rains by irrigating with 6.35 cm of water. The resident seedbank was allowed to germinate, as it would in a typical fall germinating rain, and then was killed with glyphosate (Roundup Original Herbicide™, Monsanto Company, St. Louis, Missouri, USA). This procedure was then repeated once more. Seeds of *Avena*, *Bromus*, *Aegilops*, *Taeniatherum* and *Erodium* were collected from the field site, while seeds were purchased from California sources for *Trifolium*, *Lupinus* (S & S Seeds Inc., Carpinteria, California, USA) and *Amsinckia* (Valley Seed Service, Fresno, California, USA). Seeds were raked into the soil, covered with the autoclaved litter, and allowed to germinate naturally with the fall rains. Seeds of each species were planted at a density predicted to achieve constant end of season biomass among the species (based on preliminary greenhouse data; V. Eviner, unpubl.). Despite this, these plots differed substantially in peak plant biomass. There was no further attempt to maintain constant density or biomass among treatments since all undisturbed plots had 100% vegetation cover and these plants naturally grow at different densities. Species composition was

maintained by weeding of unwanted species throughout the duration of the experiment. At the end of the 1997–1998 growing season, seed screens were placed around each plot to minimize seed movement into or out from other plots. These seed screens were made of 6 mm hardware cloth, and were 1 m in height.

Plot measurements

Plots were allowed to establish during the first growing season and intensive sampling was initiated in the second (1998–1999) growing season.

Gopher disturbance in each plot (n = 18 replicates per species treatment, n = 9 for unvegetated controls, n = 10 for natural grassland controls) was monitored in December 1998, March 1999, and May 1999. The percent of soil disturbed was estimated visually, and the type of mound was noted.

Plant quality
Litter C:N ratio was used as the index of litter quality. In July 1998, a 10 cm × 1 m strip of aboveground litter was harvested 10–20 cm from the left edge of each plot. Live tissue C:N was also measured to relate to gopher feeding preferences. Aboveground plant material was harvested from a 10.2 cm diameter ring in February and April of 1999. Both litter and live tissue samples were taken from eight replicate plots, dried at $60°C$ for 48 h, and then weighed. Samples were ground in a Wiley mill, milled to a powder with a rolling mill, and analyzed for C and N on a CHN autoanalyzer (Carlo Erba Instruments, Milan, Italy).

Soil cohesion
Soil shear strength was used as an indicator of soil cohesion. This is a valid approach because the main way plants influence soil shear strength is by their root effects on soil cohesion (Waldron 1977, O'Loughlin and Ziemer 1982). Soil shear strength is a function of cohesion, total normal stress, pore water pressure, and the angle of internal friction (Sidle 1991). The normal stress and angle of internal friction should be constant among these plots because the plots are all on the same soil type, depth and slope. Pore water pressure should be similar among all plant treatments because measurements were taken under saturated soil water conditions. Thus differences in shear strength among vegetation treatments should be an indicator of soil cohesion.

In late January 2000, a torsional vane shear tester (mid-sized vane, 1 rotation = 1 kg cm^{-2}) (Forestry Suppliers, Inc., Jackson, Mississippi, USA) was used to determine if plant species affected soil cohesion. Subsurface soil was exposed using a shovel to make a sharp vertical slice in the corner of each plot. Shear strength measurements were taken on this vertical surface at a depth between 3 cm and 6 cm on eight replicate plots. We were not able to directly measure soil shear strength associated with *Aegilops* because all plots had been disturbed by gophers. To get an indication of the effects of *Aegilops* on soil structure, we measured shear strength in *Aegilops*-dominated areas in the field just outside the experimental plots. We also took measurements in the same field in areas naturally dominated by *Avena* and *Bromus*.

Soil nitrogen and water

Toward the end of the second growing season (April 1999), soil was harvested for determination of moisture and nitrogen cycling. Two 3.7 cm diameter by 15 cm deep soil cores were collected, bulked, mixed, and subsampled for soil moisture and nitrogen. These soil cores were taken from the undisturbed areas of eight replicate plots per treatment, as well as on soil that had been disturbed by gophers in that growing season. Since the degree of gopher disturbance differed among treatments (Fig. 1), there were an unequal number of replicates of mound soil samples for each treatment (*Avena* n = 3, *Bromus* n = 1, *Aegilops* n = 7, *Taeniatherum* n = 0, *Amsinckia* n = 1, *Erodium* n = 2, *Lupinus* n = 2, *Trifolium* n = 8).

Potential net N mineralization and nitrification rates were determined in 1-week laboratory aerobic assays (modification of Hart et al. 1994). Immediately after harvesting the soil, it was returned to the lab, and a 20 g subsample (wet mass) was extracted into 100 ml of 0.5 M K_2SO_4. This extract was used as the time zero measurement for the determination of net N cycling rates and also to determine soil inorganic nitrogen pools. At the same time, another 20 g subsample of soil was brought to constant moisture (14%) and incubated at room temperature (22°C). After a seven-day incubation, these soils were extracted into 0.5 M K_2SO_4. All soil-K_2SO_4 mixtures were shaken on a mechanical shaker for one hour, then allowed to sit in the cold room (4°C) over night. Extracts were then filtered the next day using pre-leached Whatman No. 1 filter paper. The extracted soil was then wet-sieved to determine rock content greater than 2 mm diameter. Extracts were frozen ($-20°C$) for approximately 2 months, then analyzed for NH_4^+ and NO_3^- concentrations on a Lachat autoanalyzer (Lachat Instruments, Milwaukee, Wisconsin, USA). Inorganic nitrogen concentrations of the soil were determined by correcting the extracted soil mass for moisture and rock content. Net rates of N mineralization and nitrification were calculated according to Hart et al. 1994.

Soil moisture content was determined gravimetrically by weighing 20–30 g (wet mass) of soil before and
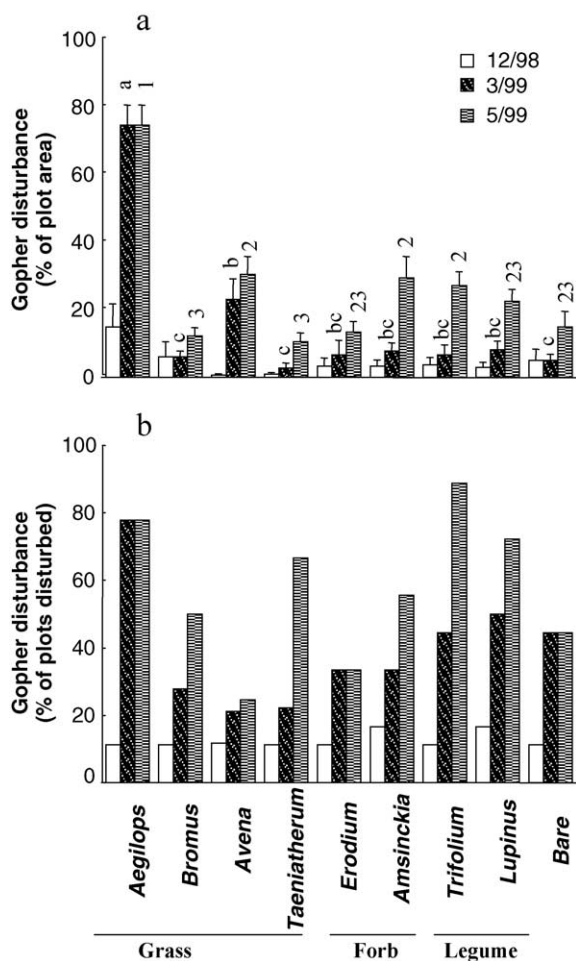
Fig. 1. Effects of plant species and season on gopher disturbance. Data are means±standard error. (a) Average % area of plots disturbed by gophers (repeated measures MANOVA: species p <0.0001, F(8,141) =17.4; season p <0.0001, F(2,140) =37; species × season p <0.0001, F(16,344) =5.9), n =18. Different letters (for March) and numbers (for May) indicate significant differences among species treatments (Tukey–Kramer posthoc test p ≤0.05). (b) The percent of plots within each treatment that were disturbed.

after being dried in a 105°C oven until constant mass (24 h). Soil temperature was measured with a Barnant hand-held thermometer using a K-type thermo-couple (Barnant Company, Barrington, Illinois, USA) placed at a depth of 5.3 cm. Temperatures were measured in the mid-afternoon at the end of the hottest part of the day in order to look at the maximum treatment effect on soil warming. Soil temperatures were measured in both disturbed and undisturbed areas of 20 randomly selected plots of varying species composition. Bulk density was measured on these same 20 plots using the cylinder approach (Campbell and Henshall 1991).

Statistical analyses

All statistics were performed using JMP software (SAS Institute, Inc., Cary, North Carolina, USA). Analysis of variance (ANOVA) was used to determine plant species effects on N cycling and inorganic N concentrations, using plant species as the main effect. Differences among species were determined using the Tukey–Kramer post-hoc test. A repeated measures ANOVA was used to determine the effects of plant species on gopher dis-turbance and tissue C:N over the growing season (using plant species and time as main effects). Because of significant species × time interactions, these repeated measure tests were followed by ANOVAs testing species effects at each individual time point (Zar 1999). MANOVAs were used to determine the effects of plant species and gopher disturbance on soil properties, and these were followed by paired t-tests to compare nitrogen cycling rates in undisturbed versus disturbed soil within each plant treatment.

In order to determine the direct + indirect effect of plant species on N cycling, rates were calculated per m^2 in the top 15 cm of soil. For each plot this was calcula-ted by: (% area disturbed × mound N values × soil bulk density of mounds × cm^3 m^{-2}) + (% area undis-turbed × undisturbed N values × undisturbed soil bulk density × cm^3/ m^{-2}). On the plots where mound N values were not determined, the mean values of mound N for the appropriate species were used in the calcula-tions. MANOVAs, followed by paired t-tests were used to determine how plant species effects (on an area basis) varied when considering or ignoring gopher disturbance.

Results

Plant species effects on gopher activity

Although a majority of plots experienced some gopher activity (Fig. 1b), both the extent and seasonality of gopher disturbance varied among plots planted with different plant species (Fig. 1a, repeated measures ANOVA: species p <0.0001, F(8,141) =17.4; season p <0.0001, F(2,140) =37; species × season p <0.0001, F(16,344) =5.9). Simple effects ANOVA tests indicated that the extent of gopher disturbance significantly changed (p <0.05) over the growing season for all treatments except *Bromus* and *Erodium*. Within time points, gopher disturbance was low from the beginning of the growing season through December, and there were no significant differences in gopher disturbance among species at this time (Fig. 1a, ANOVA p =0.17, F(8,141) =21.1). By looking at both the % area dis-turbed (Fig. 1a) and % of plots disturbed (Fig. 1b), we can get an indication of the size of the gopher mounds. For example, in May, nearly all *Trifolium* plots were disturbed (Fig. 1b), but the percent area disturbed was

relatively low (Fig. 1a), indicating that nearly all of these plots had small gopher disturbances. Between December and March, most *Aegilops* plots (Fig. 1b) experienced large disturbances (Fig. 1a). This disturbance consisted of large soil mounds covering most of the plot area (Vleck's (1981) "laterals"; Plate 1). Visual inspection under the mounds indicated that the vegetation was buried underneath the mounds and killed, but gophers did not remove this vegetation from the plot. This same type of disturbance was also seen in approximately 20% of *Avena* plots (Fig. 1), and infrequently in plots of *Bromus* and *Erodium*. Disturbance area on *Aegilops* plots was significantly greater than on all other plot types (Fig. 1a, ANOVA $p < 0.0001$, $F(8,149) = 34.2$, followed by Tukey–Kramer posthoc test), while disturbance area associated with *Avena* was significantly greater than disturbance on the *Bromus* and *Taeniatherum* treatments. While many other plots showed signs of gopher disturbance between December and March (Fig. 1b), these were very small disturbances (Fig. 1a).

Between March and May, the percent area disturbed increased on *Amsinckia*, *Lupinus*, and *Trifolium* plots (Fig. 1a). These plots (Fig. 1b) experienced disturbance that consisted of a number of small holes with earthen plugs (Vleck's "popholes"), and most vegetation was removed from around these holes (Plate 2). None of these plots experienced large gopher mounds. *Taeniatherum*, *Bromus*, *Erodium* and unvegetated plots experienced gopher disturbance (Fig. 1b), but the percent area disturbed was low compared to other vegetation treatments (Fig. 1a, ANOVA $p = 0.0055$, $F(8,149) = 3.4$, followed by Tukey–Kramer posthoc test). Control plots in the natural grassland did not provide a good estimate of gopher disturbance. These randomly placed plots were subject to virtually no gopher disturbance, while adjacent areas received significant gopher disturbance.

PLATE 1. Typical large mound found in *Aegilops* plots. These mounds deposited substantial soil on the soil surface and vegetation, and covered most of the 1 m² area of the plot.

PLATE 2. Typical gopher feeding disturbance pattern on plots containing *Trifolium*, *Lupinus* or *Amsinckia*. These plots had many small holes that were plugged with soil, and most of the aboveground vegetation was removed.

Mechanisms that might determine gopher activity

Tissue and litter C:N ratios

The live tissue C:N ratio of plant species changed through the season (Fig. 2, repeated measures ANOVA species $p < 0.0001$, $F(7,56) = 61$; season $p < 0.0001$, $F(2,56) = 84$; species × season $p < 0.0001$, $F(7,56) = 4.2$). Simple effects ANOVA tests indicated that time significantly affected tissue C:N in all species except *Lupinus*. Within time points, in February, the tissue C:N ratio was significantly lower in the two legume species *Trifolium* and *Lupinus*, and the forb *Amsinckia* (ANOVA $p < 0.0001$, $F(7,63) = 27$, followed by Tukey–Kramer
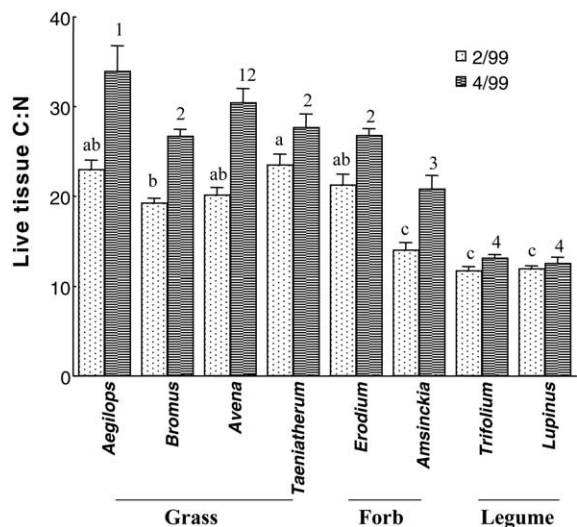

Fig. 2. C:N ratio of live plant aboveground biomass in February (shaded bars) and April (solid bars). In both February (ANOVA $p < 0.0001$, $F(7,63) = 27$) and April (ANOVA $p < 0.0001$, $F(7,63) = 27$, $n = 8$), tissue C:N significantly differed among species. Different letters (February) and numbers (April) indicate significant differences among species treatments (Tukey–Kramer posthoc test $p \leq 0.05$). Data are means ± standard error.

posthoc tests) than in the grass species and *Erodium*. By April, all forbs and grasses increased their C:N. *Trifolium*, *Lupinus* and, to a lesser extent *Amsinckia*, continued to be the species with the lowest live tissue C:N ratio (ANOVA $p < 0.0001$, $F(7,63) = 27$, followed by Tukey–Kramer posthoc test). Plots containing these low C:N species had abundant feeding holes (popholes) but infrequent mounds.

Litter C:N ratios were significantly different among species treatments (ANOVA $p < 0.0001$, $F(7,63) = 13.8$, Fig. 4a). The legume species (*Trifolium*, *Lupinus*) had lower litter C:N ratios than all other species, while *Aegilops* litter had a higher C:N than all species except for *Bromus* (Tukey–Kramer posthoc test at significance level $p = 0.05$).

Soil shear strength

Soil shear strength was used as an indicator of cohesion, which can influence gopher mound formation. Since most *Aegilops* plots were disturbed, we were unable to determine its effect on soil cohesion solely with our experimental setup. Instead, we compared soil cohesion in natural grassland plots dominated by *Avena* and *Bromus*, *Aegilops*-dominated patches within this grassland, and the experimental plots planted with other species. Vegetation treatments significantly differed in their effects on soil shear strength (ANOVA $p < 0.0001$, $F(8,90) = 6.2$, Fig. 3). Soil shear strength was greater in
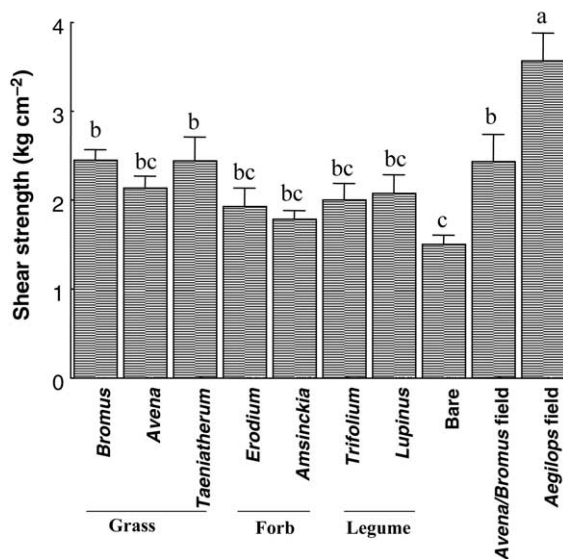

Fig. 3. Soil shear strength associated with different plant species treatments. *Aegilops* plots could not be tested since gophers disturbed them all. Instead, patches of *Aegilops* in the field outside these plots were tested and compared with areas of the grassland dominated by *Avena* and *Bromus*. *Aegilops* patches had much higher soil shear strength than the other treatments (ANOVA $p < 0.0001$, $F(8,90) = 6.2$, $n = 8$). Data are means ± standard error. Different letters indicate significant differences among species treatments (Tukey–Kramer posthoc test $p \leq 0.05$).

Aegilops-dominated patches than in any other vegetation treatments (Tukey–Kramer posthoc test, at significance level $p = 0.05$). Shear strength in the *Avena-Bromus* dominated grassland was not significantly different from *Avena* and *Bromus* plots, indicating that testing of field patches outside the established plots is a valid approach. In the plots, there were no significant differences among the species, but most species plots tended to have higher soil cohesion than the bare plots, although this pattern was not always significant.

Direct plant effects on N cycling

Net N mineralization rates on undisturbed soil were not significantly different among species, but did display a strong trend towards higher rates in legume-dominated plots (ANOVA $p = 0.08$ $F(8,69) = 1.8$). The patterns of species effects on net mineralization were closely related to the litter C:N of each species (Fig. 4; $r^2 = 0.79$ $p = 0.0031$, $n = 8$), with most rapid N mineralization in plots of species with low C:N ratios. *Erodium* was a notable exception to this trend.

Net nitrification rates on undisturbed soil were significantly different among species (Fig. 4c, ANOVA $p = 0.002$, $F(8,70) = 3.0$). These were also closely related to species litter C:N ($r^2 = 0.70$ $p = 0.0091$, $n = 8$). One notable exception to the relationship of litter C:N ratio with rates of net N cycling was *Erodium*, which had much lower rates of net nitrification and mineralization than would be expected based on its C:N ratio. If *Erodium* was taken out of the regressions, the relationship between species litter C:N and N cycling became stronger (net mineralization $r^2 = 0.9$ $p = 0.001$, $n = 7$; net nitrification $r^2 = 0.93$ $p = 0.0004$, $n = 7$).

Effects of gophers on soil microclimate

Mounds did not alter species effects on soil temperature (Table 1, species × mound interaction), but soil temperature was significantly higher on gopher mounds ($15.0 \pm 0.3°C$) than in undisturbed soil ($12.0 \pm 0.2°C$; paired t-test $p < 0.0001$). While MANOVA indicated that gopher mounds influenced plant species effects on soil moisture, only *Avena* showed significant differences in percent soil moisture between undisturbed (11.7 ± 0.3) and mound (9.0 ± 1.2) soils (paired t-test $p = 0.05$).

Effects of gophers on N cycling

A comparison of N cycling in disturbed soil versus undisturbed soil indicated that while gophers tended to alter rates of net N mineralization (Table 1), the effects of most plant species on N mineralization did not differ
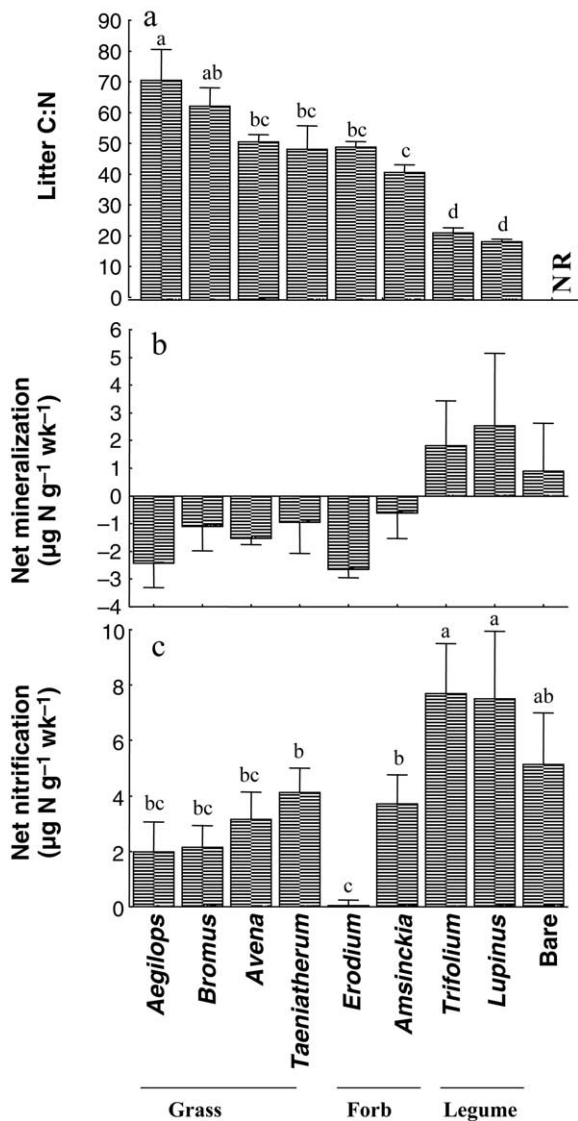
Fig. 4. Effect of plant species on litter quality and nitrogen cycling in undisturbed soil. Data are means ± standard error. Different letters indicate significant differences among species treatments (Tukey–Kramer posthoc test $p \leq 0.05$). (a) Plant species litter quality (C:N) (ANOVA $p < 0.0001$, $F(7,63) = 13.8$) (NR = not relevant) compared to (b) rates of net mineralization (ANOVA $p = 0.08$, $F(8,69) = 1.8$), and (c) net nitrification (ANOVA $p = 0.002$, $F(8,70) = 3.0$). Species mean values of litter C:N were closely related to mean values of net mineralization ($r^2 = 0.79$, $p = 0.0001$) and net nitrification ($r^2 = 0.70$, $p = 0.009$).

with disturbance (Fig. 5a). Disturbance only tended to increase rates of net N mineralization in *Avena* (t-test $p = 0.0003$) and *Bromus* (t-test $p = 0.08$) plots.

In contrast, an overall MANOVA for net nitrification indicated that gopher disturbance significantly altered plant species effects on net nitrification rates (Table 1). In particular, net nitrification rates (Fig. 5b) increased in

response to gopher disturbance in the plots that had experienced gopher mounds [*Aegilops* (t-test $p = 0.02$), *Bromus* (t-test $p = 0.006$), *Avena* (t-test $p = 0.02$) and *Erodium* (t-test $p = 0.0003$)]. Rates of nitrogen cycling did not change in disturbed areas of *Amsinckia*, *Trifolium* and *Lupinus*, indicating that the gopher pop-holes did not significantly affect net nitrification or mineralization rates.

Gopher-induced changes in soil inorganic nitrogen concentrations reflect both changes in net N cycling rates, and the absence of plant uptake in disturbed soil. Both species and gopher disturbance impacted soil nitrate (Table 1). Nitrate concentrations were significantly higher on large mounds than on undisturbed soil for all species, but were not affected by the small feeding-hole disturbances (Table 2). The dominant form of inorganic nitrogen, NH_4^+, also changed in response to gophers (Table 1). However, only *Erodium* plots had higher NH_4^+ on mounds than in undisturbed soil.

Indirect effects of plants on N cycling

Rates of N cycling were calculated on a per m^2 basis in order to compare the direct effects of plants (disturbance-free area of plots) with the overall effect of plant species in the top 15 cm of soil (including disturbed and undisturbed areas of each plot. An overall MANOVA indicated that only plant species significantly impacted net N mineralization (Table 3). A closer look within species indicated that the direct versus overall effects of plant species on net mineralization were not different for any species other than *Avena*. Rates of net mineralization in *Avena* plots were significantly higher when gopher disturbance was taken into account, than when just considering its direct effect (t-test $p = 0.03$, Fig. 6a).

When considering plant species effects on gopher disturbance, net nitrification rates were significantly greater than the direct plant effect in *Aegilops* (t-test $p = 0.04$) and *Erodium* (t-test $p = 0.02$, Fig. 6b) plots. Plant species effects on net nitrification were substantially altered when considering the overall effect of individual plant species compared to just the direct effect (Table 3, species × disturbance interaction). *Aegilops* had one of the lowest rates of net nitrification when considering only its direct effect. When including the effects of selective gopher disturbance on this species, *Aegilops* shifted from having one of the lowest nitrification rates, to one of the highest. When these indirect effects were taken into account, rates in *Aegilops* plots were not significantly different from the legume plots (Fig. 6b, ANOVA $p = 0.02$, $F(8,71) = 2.5$, followed by a Tukey–Kramer posthoc test).

Table 1. MANOVA results: soil characteristics compared across plant species and on or off gopher mounds.

Soil characteristic	Variable	Degrees of freedom	Sum of squares	F-statistic	P value
Soil temperature	species	7	79.0	2.5	0.07
	mound	1	32.4	7.1	0.02
	sp ×mound	7	61.6	1.9	0.14
Soil moisture	species	7	0.0039	3.31	0.004
	mound	1	0.0002	1.11	0.29
	sp ×mound	7	0.0024	2.37	0.03
NH_4	species	7	319.4	4.19	0.17
	mound	1	21.3	1.95	0.0006
	sp ×mound	7	148.7	1.95	0.073
NO_3	species	7	416.5	8.2	<0.0001
	mound	1	166.7	23.0	<0.0001
	sp ×mound	7	54.5	1.07	0.39
Net mineralization	species	7	158.1	1.39	0.22
	mound	1	55.7	3.42	0.07
	sp ×mound	7	66.5	0.58	0.77
Net nitrification	species	7	145.5	1.66	0.13
	mound	1	233.6	18.7	<0.0001
	sp ×mound	7	294.9	3.37	0.0031

Discussion

Plant species can have multiple effects on ecosystem processes. In our study, litter C:N ratios were closely related to the direct effects of plant species on net N mineralization and nitrification. As litter C:N increased, rates of net mineralization and nitrification decreased. This is expected since higher C:N ratios are generally correlated with decreased decomposition rates (Taylor et al. 1989) and increased microbial immobilization of nitrogen (Rosswall 1982, Paul and Clark 1996). *Erodium* was a notable exception to this trend, having substantially lower rates of net nitrification and mineralization than expected based on its C:N ratio. *Erodium botrys* has a high concentration of phenolics (K. Johnson, pers. comm.), like other species in its genus (Lamaison et al. 1993). These compounds can decrease rates of decomposition, net mineralization and nitrification (Kuiters 1991, Siqueira et al. 1991), and plant species containing these compounds may depress rates of nitrogen cycling through effects on microbial immobilization (Schimel et al. 1996), or inhibition of microbial activity (Lodhi and Killingbeck 1980, Thibault et al. 1982, Palm and Sanchez 1991). Many other studies have also indicated that litter chemistry is an important mechanism determining plant species effects on N cycling (e.g. C:N; Wedin and Tilman 1990, Hobbie 1992, Steltzer and Bowman 1998, lignin:N; Stump and Binkley 1993, Scott and Binkley 1997, Maithani et al. 1998).

Although it is important to understand the direct effects of plants on ecosystems, it is ultimately most important to understand the overall impact of vegetation on N dynamics. Plant species can affect the activity and distribution of other organisms that play key roles in ecosystem dynamics. In this study we found that different types of gopher activity were concentrated in plots of particular plant species. Feeding holes with soil plugs (popholes) were formed in the late spring in plots containing species that were the most nutritious at that time of year, specifically the legumes and the forb species that had a lower C:N ratio. Multiple feeding holes were found in plots of these species. This type of gopher activity caused relatively little soil disturbance, but nearly all of the surrounding vegetation was removed. The gut contents of gophers confirm that these species are the preferred food of *Thomomys bottae* (Hunt 1992). This gut content study also indicated that *Erodium* is a preferred food species, but we saw no evidence of preferential gopher activity or vegetation removal in *Erodium* plots. This discrepancy is likely an artifact of our experimental design. In our study plots, gophers had access to large quantities of species that were more nutritious than *Erodium*. At our field site, however, these nutritious species usually have lower abundances, whereas *Erodium* abundance can be relatively high. In the natural grassland, with low availability of these highly palatable species, gophers probably select *Erodium*.

In contrast to the feeding holes which occurred exclusively in forb and legume plots, the substantial surface deposition of soil as large mounds due to tunnel excavation (laterals) occurred earlier in the growing season and was associated with different plant species (primarily *Aegilops*). Production of large mounds peaked in the late winter and early spring. Miller (1948) saw a similar temporal pattern in the production of gopher mounds by *T. bottae* in California grasslands. The timing of mound production relates to active burrowing associated with peak breeding time of *T. bottae*, when males are building tunnels in search of females, and females are building nest chambers (Howards and Childs 1959, Hunt 1992), and this burrowing at breeding time is independent of food preference (Bandoli 1981).
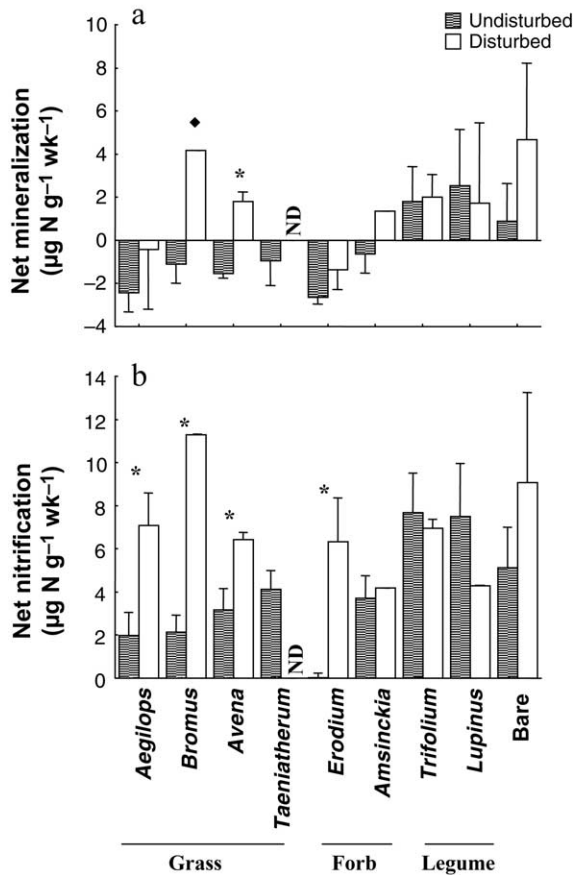
Fig. 5. Gopher effects on nitrogen cycling. Data are means ± standard error. ND indicates no data for that species (no mounds to test at sampling time). Asterisks indicate significant differences between disturbed and undisturbed N cycling rates within a species treatment, as determined by a paired t-test (* p ≤ 0.05, ◆ p < 0.10). (a) Rates of net N mineralization for each plant treatment in undisturbed (solid bars) versus disturbed areas (open bars) of the plots. Mound soil tended to have higher net mineralization rates in *Avena* (t-test p = 0.0003), and *Bromus* (t-test p = 0.08). (b) Rates of net nitrification for each plant treatment in undisturbed areas versus disturbed areas of the plots. All species with large mounds showed significantly higher net nitrification rates associated with gopher disturbance: *Aegilops* (t-test p = 0.02), *Bromus* (t-test p = 0.006), *Avena* (t-test p = 0.02), *Erodium* (t-test p = 0.0003).

We hypothesize that gophers make large mounds in *Aegilops* plots because of plant species effects on soil cohesion. Gopher burrowing is energetically expensive, using 360–3400 times more energy than traveling the equivalent distance aboveground (Vleck 1979). Soils with high cohesion have both negative and positive effects on gopher energetics. Gophers may need to expend more energy digging into soils with high shear strength, but can build shorter vertical tunnels to the soil surface in cohesive soils. It has been estimated that overall, it takes 30% less energy to build mounds in soils that are cohesive (Vleck 1981). *Aegilops* patches in the natural

grasslands had higher shear strength than patches without this species and any of the planted monoculture plots of other species. This magnitude of difference is comparable to differences between soil types that span the range of uncohesive to extremely cohesive (Peck et al. 1973), and it is extremely unlikely that soil type varied this dramatically in small (<1 m² patches). In contrast, this magnitude of difference in shear strength is typical of differences imposed by plant species (Waldron et al. 1983), which frequently differ in their effects on soil cohesion and shear strength (Chan and Heenan 1996, Angers and Caron 1998) primarily due to differences in the strength of the root–soil bond (Waldron 1977, Selby 1993). Fine root length density (Angers and Caron 1998), rooting length, and root hairs (Waldron and Dakessian 1981) are the key plant traits that regulate soil cohesion. Thus, the high soil cohesion associated with patches of *Aegilops* is likely due to the high root biomass V. T. Eviner unpubl.) and surface area (Peters 1994) of *Aegilops* compared to other species that we studied.

An alternative to the soil cohesion hypothesis is that gophers concentrate their activity in *Aegilops* plots because this species is an attractive food source. This hypothesis seems less likely to explain our observations because gophers usually do not consume grasses until the dry season (Hunt 1992), and aboveground tissues in these plots were buried beneath mounds with no evidence of consumption. Aegilops is an unlikely choice for preferential feeding in spring when large mounds are produced, because its aboveground tissue quality is lower than the forb and legume species (e.g. *Amsinckia*, *Lupinus* and *Trifolium*). These low C:N species are frequently observed in the guts of the gopher *Thomomys bottae* (Hunt 1992), but are not disturbed by large gopher mounds. It is unlikely that the formation of these large mounds is associated with root feeding because species patterns of root biomass are not consistent with these disturbance preferences. While *Aegilops* roots have the highest biomass, *Bromus* has a similar root biomass (V. T. Eviner unpubl.) but was rarely disturbed by gophers, and gophers formed large mounds in plots of *Avena*, which has half the root biomass of *Aegilops*. It is also unlikely this activity is mediated by root feeding since the fibrous roots of grasses such as *Aegilops* have not been observed in gopher food caches (Cortinas and Seastedt 1996).

Gopher mounds (both by *T. bottae* and *Geomys bursarius*) are generally concentrated in areas with high plant biomass or density (Tilman 1983, Reichman and Smith 1985, Behrend and Tester 1988, Benedix 1993). Increased disturbance by both *G. bursarius* and *T. bottae* has also been found in fertilized plots with increased plant biomass (Tilman 1983, Inouye et al. 1987, 1997, Hobbs et al. 1988). Although these results are often interpreted as evidence for optimal foraging, other studies have found that the pattern of gopher activity

Table 2. Effects of plant species and the presence and type of gopher disturbance on soil inorganic nitrogen. Data are presented as means (μg N per gram dry weight of soil)±standard error.

Species	Undisturbed soil			Mound soil			Paired t-tests on mound vs undisturbed (p values)	
	n	NH_4^+ μgN g^{-1}	NO_3^- μgN g^{-1}	n	NH_4^+ μgN g^{-1}	NO_3^- μgN g^{-1}	NH_4^+	NO_3^-
Large mounds								
Aegilops triuncialis	8	10.80±0.67	1.21±0.15	7	12.06±2.04	3.74±1.05	ns	0.01
Bromus hordeaceous	8	7.99±0.61	0.72±0.16	1	11.39	8.04	ns	<0.0001
Avena barbata	8	9.76±0.58	0.96±0.09	3	10.33±0.82	3.45±0.54	ns	<0.0001
Taeniatherum caput-medusae	8	9.44±0.95	0.76±0.17	0	–	–	–	–
Erodium botrys	8	6.05±0.28	0.92±0.19	2	14.07±1.41	4.17±0.78	0.002	0.0048
Bare	8	7.73±0.83	7.13±0.87	3	7.57±0.62	12.13±1.46	ns	0.02
Small mounds								
Amsinckia douglasiana	8	9.32±0.56	1.75±0.28	1	5.84	0.85	ns	ns
Trifolium microcephalum	8	12.89±1.11	3.46±0.79	8	12.64±1.51	4.98±1.38	ns	ns
Lupinus bicolor	8	10.53±0.79	4.01±1.09	2	12.65±2.48	9.89±2.65	ns	ns

cannot be explained by food availability or preference (Andersen 1990), particularly during times of reproduction by *T. bottae* (Bandoli 1981). The relative importance of soil cohesion and food abundance in determining burrowing behavior may differ among sites. Five of the seven studies that show preferential burrowing in high-biomass plots (Tilman 1983, Reichman and Smith 1985, Inouye et al. 1987, 1997, Behrend and Tester 1988) took place at Cedar Creek, Minnesota, on extremely sandy soils in which soil cohesion could be a major energetic constraint on gopher activity.

Regardless of the cause of gopher behavior, we have shown that plant species mediate the type and timing of gopher disturbance in a landscape with patchy distribution of species. Feeding holes, formed later in the season, were associated with the most nutritious plant species. Large mounds occurred as gophers actively tunneled during their breeding season and were concentrated in plots with fibrous roots and cohesive soils. Similarly, moles selectively burrow in different types of vegetation patches through the growing season. Burrowing patterns are dominated by breeding in the spring and by food preference in the fall (Edwards et al. 1999). This type of selective disturbance is possible in areas with a patchy distribution of species because gophers tunnel extensively, and can select favorable patches for feeding or soil

excavation while tunneling through vegetation patches. This type of plant species effect on gopher disturbance would be less likely in areas with large scale, homogenous shifts in vegetation.

Changes in vegetation clearly affect gopher activity, with important consequences for ecosystem processes. The small feeding holes caused minimal soil disturbance and showed no short term effects on net N mineralization, nitrification, or inorganic N availability. However, nearly all vegetation was cleared from these plots, and this could have important effects on nitrogen cycling in the next growing season due to lack of litter input. Large mounds had substantial soil deposition, disturbing most of the 1 m^2 area of the plots. These did not consistently affect net N mineralization rates, but substantially increased rates of net nitrification and inorganic N availability. Other studies have shown that gopher mounds increase inorganic N (Litaor et al. 1996), potential nitrification (Canals et al. 2003), and decomposition (Cortinas and Seastedt 1996).

The direct effect of plant species on nitrification is very different than their overall effect that incorporates plant–gopher interactions. When considering only the direct effect of *Aegilops*, it was one of the species with the lowest rates of net nitrification. Including the indirect effect shifted *Aegilops* to one of the species

Table 3. MANOVA table comparing plant species effects on N cycling (on a m^2 basis) when considering vs ignoring gopher disturbance.

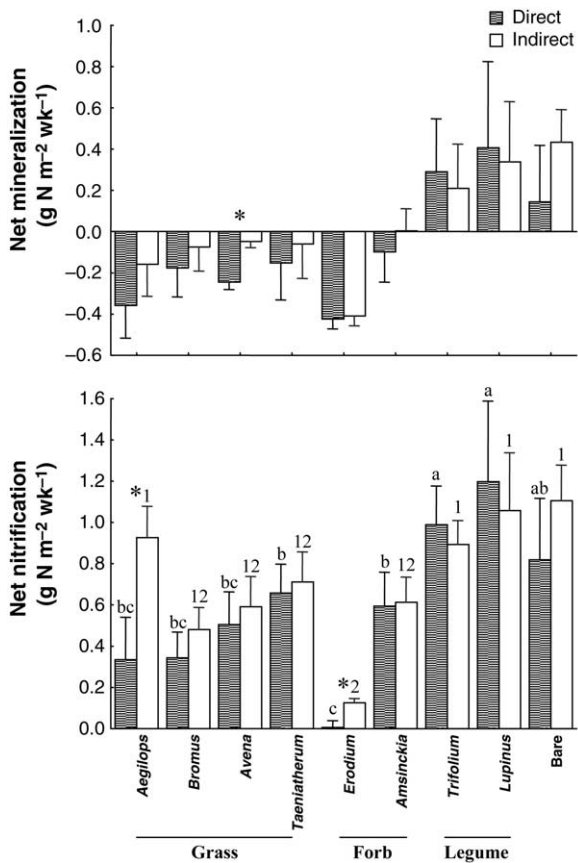| N cycling measure	Variable	Degrees of freedom	Sum of squares	F-statistic	P value
Net N mineralization	species	8	4.7	3.0	0.004
	disturbance	1	0.31	1.6	0.21
	species ×disturbance	8	0.44	0.28	0.97
Net nitrification	species	8	8.0	5.3	<0.0001
	disturbance	1	0.62	3.3	0.07
	species ×disturbance	8	3.1	2.11	0.04

Fig. 6. Comparison of direct effects vs overall plant species effects (indirect+direct) on N cycling. Data are means± standard error. Asterisks (*) indicate significant differences in rates of N cycling within a species treatment when comparing direct versus overall effects (paired t-test $p \leq 0.05$). (a) Net N mineralization per m^2 considering only direct effects (solid bars), and direct and indirect effects (open bars). Including indirect effects significantly increased rates of net mineralization in *Avena* plots (t-test $p = 0.03$). (b) Net nitrification per m^2 considering only direct effects (solid bars), and direct and indirect effects (open bars). Including the indirect effects increased rates of nitrification for *Aegilops* (t-test $p = 0.04$) and *Erodium* (t-test $p = 0.02$). Different letters (direct effects) and numbers (indirect+direct effects) indicate significant differences among species treatments (Tukey–Kramer posthoc test $p \leq 0.05$). *Aegilops* changed from being one of the species with the lowest rates of net nitrification, to one of the highest (ANOVA $p = 0.02$, $F(8,71) = 2.5$).

with the highest rates of net nitrification, nearly as high as the legumes. The overall effect of this species was completely different than expected based on its litter C:N ratio, indicating that the indirect effect was much stronger than the direct effect. Despite the fact that many undisturbed samples were taken from the same plots as disturbed samples, we feel these undisturbed values are good indicators of the direct effects of plant species on N cycling. Most species had a number of plots that were not disturbed at all by gophers, and values of N cycling in these plots did not differ from

measurements taken from undisturbed areas of plots that had some gopher disturbance. In other studies, soil and plant N in undisturbed areas 10 cm from mounds were not affected by the changes that occurred on the mounds (Reichman et al. 1993).

Selective gopher activity can have other important ecosystem consequences. *Aegilops* is an aggressive exotic species in California grasslands, and this selective gopher disturbance leads to high mortality and can limit its invasion (Eviner and Chapin 2003b). Plant community shifts in response to gopher disturbance are widespread (Hobbs and Mooney 1985, 1991, Huntly and Inouye 1988, Stromberg and Griffin 1996) and may also have important ecosystem effects.

Conclusion

This study highlights two important ways in which plant species can affect nitrogen cycling. They can directly mediate rates of net mineralization and nitrification through their litter C:N ratio. They can also indirectly alter nitrogen cycling by mediating gopher disturbance, which greatly alters net nitrification rates.

Previous work on the role of plant species in ecosystems has focused on direct species effects. However, it is vital to broaden this perspective to include the interactions of plant species with other organisms. These species interactions can be important and widespread across ecosystems. For example, plant species rooting patterns (Springett and Gray 1997, Zaller and Arnone 1999) and canopy architecture (Zaller and Arnone 1999) can affect the distribution and activity of earthworms, which have large effects on nitrogen (Willems et al. 1996, Cortez et al. 2000, Cortez and Hameed 2001) and phosphorus (Thompson et al. 1993) cycling. Vegetation composition can also affect the distribution of small rodents, which can alter tree seedling establishment through their different feeding preferences (Ostfeld et al. 1997). These shifts in tree species can greatly alter decomposition (Geng et al. 1993).

Plant species are frequently associated with a specific suite of other organisms (Recher et al. 1996, Grayston et al. 1998, Bardgett et al. 1999, Schroth et al. 2000) that may play key roles in ecosystems. The indirect impacts of plant species through these associated organisms may be viewed as an "extended trait" of plant species, allowing us to mechanistically link plant traits with the activity and distribution of these other organisms. Since it is vital to look beyond the direct effects of plant species to their overall impacts (Hobbie 1995), this approach could be a powerful tool in predicting the consequences of vegetation change on ecosystem dynamics.

References

Andersen, D. 1990. Search path of a fossorial herbivore, *Geomys bursarius* foraging in structurally complex plant communities. – J. Mammal. 71: 177–187.

Angers, D. and Caron, J. 1998. Plant-induced changes in soil structure: processes and feedbacks. – Biogeochemistry 42: 55–72.

Bandoli, J. 1981. Factors influencing seasonal burrowing activity in the pocket gopher, *Thomomys bottae*. – J. Mammal. 62: 293–303.

Bardgett, R., Mawdsley, J. and Edwards, S. 1999. Plant species and nitrogen effects on soil biological properties of temperate upland grasslands. – Funct. Ecol. 13: 650–660.

Behrend, A. and Tester, J. 1988. Feeding ecology of the plains pocket gopher in east central Minnesota. – Prairie Nat. 20: 99–107.

Benedix, J. 1993. Area-restricted search by the plains pocket gopher (*Geomys bursarius*) in tallgrass prairie habitat. – Behav. Ecol. 4: 318–324.

Campbell, D. J. and Henshall, J. K. 1991. Bulk density. – In: Smith, K. A. and Mullis, C. E. (eds), Soil analysis. Marcel Dekker, Inc. pp. 329–366.

Canals, R. M., Herman, D. J. and Firestone, M. K. 2003. How disturbance by fossorial mammals alters N cycling in a California annual grassland. – Ecology 84: 875–881.

Chan, K. and Heenan, D. 1996. The influence of crop rotation on soil structure and soil physical properties under conventional tillage. – Soil Tillage Res. 37: 113–125.

Chen, J. and Stark, J. 2000. Plant species effects and carbon and nitrogen cycling in a sagebrush-crested wheatgrass soil. – Soil Biol. Biochem. 32: 47–57.

Cortez, J. and Hameed, R. 2001. – Simultaneous effects of plants and earthworms on mineralization of 15N-labelled organic compounds absorbed onto soil size fractions. – Biol. Fert. Soils 33: 218–225.

Cortez, J., Billes, G. and Bouche, M. 2000. Effect of climate, soil type and earthworm activity on nitrogen transfer from a nitrogen-15-labelled decomposing material under field conditions. – Biol. Fert. Soils 30: 318–327.

Cortinas, R. and Seastedt, T. 1996. Short- and long-term effects of gophers (*Thomomys talpoides*) on soil organic matter dynamics in alpine tundra. – Pedobiologia 40: 162–170.

Edwards, G., Crawley, M. and Heard, M. 1999. Factors influencing molehill distribution in grassland: implications for controlling the damage caused by molehills. – J. Appl. Ecol. 36: 434–442.

Eviner, V. T. and Chapin III, F. S. 2003a. The role of species interactions in invasions: gopher-plant-fungal interactions affect establishment of an invasive grass. – Ecology 84: 120–128.

Eviner, V. T. and Chapin III, F. S. 2003b. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. – Annu. Rev. Ecol. Syst. 34: 455–485.

Ferguson, D. 1999. Effects of pocket gophers, bracken fern, and western coneflower on planted conifers in northern Idaho–an update and two more species. – New For. 18: 199–217.

Geng, X., Pastor, J. and Dewey, B. 1993. Decay and nitrogen dynamics of litter from disjunct, congeneric tree species in old-growth stands in northeastern China and Wisconsin. – Can. J. Bot. 71: 693–699.

Gowans, K. 1958. Soil survey of the Hopland field station. – California agriculture experiment station, Berkeley

Grayston, S., Wang, S., Campbell, C. et al. 1998. Selective influence of plant species on microbial diversity in the rhizosphere. – Soil Biol. Biochem. 30: 369–378.

Hart, S. C., Stark, J. M., Davidson, E. A. et al. 1994. Nitrogen mineralization, immobilization, and nitrification. – In: Weaver, R. W. (ed.), Methods of soil analysis. Part 2: Microbiological and biochemical properties. Soil Sci. Soc. Am., Inc., Madison, Wisconsin, USA, pp. 985–1018.

Hickman, J. 1993. The Jepson manual: higher plants of California. – Univ. of California Press, Berkeley.

Hobbie, S. 1992. Effects of plant species on nutrient cycling. – Trends Ecol. Evol. 7: 336–339.

Hobbie, S. 1995. Direct and indirect effects of plant species on biogeochemical processes in arctic ecosystems. – In: Chapin, F. I. and Korner, C. (eds), Arctic and alpine biodiversity. Springer-Verlag, pp. 213–224.

Hobbie, S. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. – Ecol. Monogr. 66: 503–522.

Hobbs, R. and Mooney, H. 1985. Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. – Oecologia 67: 342–351.

Hobbs, R., Gulman, S., Hobbs, V. et al. 1988. Effects of fertilizer addition and subsequent gopher disturbance on a serpentine annual grassland community. – Oecologia 75: 291–295.

Hobbs, R. and Mooney, H. 1991. Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. – Ecology 72: 59–68.

Howards, W. and Childs, H. 1959. Ecology of pocket gophers with emphasis on *Thomomys bottae* Mewa. – Hilgardia 29: 277–358.

Huenneke, L. F. and Mooney, H. A. (eds). 1989. Grassland structure and function: California annual grassland. – Kluwer Academic Publisher.

Hunt, J. 1992. Feeding ecology of valley pocket gophers (*Thomomys bottae* sanctidiegi) on a California coastal grassland. – Am. Midl. Nat. 127: 41–51.

Huntly, N. and Inouye, R. 1988. Pocket gophers in ecosystems: patterns and mechanisms. – Bioscience 38: 786–793.

Inouye, R., Huntly, N., Tilman, D. et al. 1987. Pocket gophers, vegetation, and soil nitrogen along a successional sere in east central Minnesota. – Oecologia 72: 178–184.

Inouye, R., Huntly, N. and Wasley, G. 1997. Effects of pocket gophers (*Geomys bursarius*) on microtopographic variation. – J. Mammal. 78: 1144–1148.

Kuiters, A. 1991. Phenolic substances in forest leaf litter and their impact on plant grown in forest vegetation. – In: Rozema, J. and Verkleij, J. (eds), Ecological responses to environmental stresses. Kluwer Academic Publishers, pp. 252–260.

Lamaison, J., Petitjean-Freytet, C. and Carnat, A. 1993. Polyphenol levels and antioxidant activities in French Geraniaceae. – Plantes medicinales phytotherapie 26: 130–134.

Litaor, M., Mancinelli, R. and Halfpenny, J. 1996. The influence of pocket gophers on the status of nutrients in alpine soils. – Geoderma 70: 37–48.

Lodhi, M. and Killingbeck, K. 1980. Allelopathic inhibition of nitrification and nitrifying bacteria in ponderosa pine (*Pinus ponderosa* Dougl.) community. – Am. J. Bot. 67: 1423–1429.

Maithani, K., Arunachalam, A., Tripathi, R. et al. 1998. Influence of leaf litter quality on N mineralization in soils

of subtropical humid forest regrowths. – Biol. Fert. Soils 27: 44–50.

McClaugherty, C., Pastor, J., Aber, J. et al. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. – Ecology 66: 266–275.

Melillo, J., Aber, J. and Muratore, J. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. – Ecology 63: 621–626.

Miller, M. 1948. Seasonal trends in burrowing of pocket gophers (Thomomys). – J. Mammal. 29: 38–44.

O'Loughlin, C. and Ziemer, R. 1982. The importance of root strength and deterioration rates upon edaphic stability in steepland forests. Proceedings of an IUFRO workshop. – In: Waring, R. (ed.), Carbon uptake and allocation in subalpine ecosystems as a key to management. Forest Research Laboratory, Oregon State Univ., Corvallis, pp. 70–78.

Ostfeld, R., Manson, R. and Canham, C. 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. – Ecology 78: 1531–1542.

Palm, C. A. and Sanchez, P. A. 1991. Nitrogen release from the leaves of some tropical legumes as affected by their lignin and polyphenolic contents. – Soil Biol. Biochem. 23: 83–88.

Paul, E. and Clark, F. 1996. Soil microbiology and biochemistry. – Academic Press.

Peck, R. B., Hanson, W. E. and Thornburn, T. H. 1973. Foundation engineering, 2nd ed. – J. Wiley and Sons.

Peters, A. 1994. Biology and control of barb goatgrass (Aegilops triuncialis). – Oregon State Univ. Corvallis.

Recher, H., Majer, J. and Ganesh, S. 1996. Eucalypts, arthropods and birds: on the relation between foliar nutrients and species richness. – For. Ecol. Manage. 85: 177–195.

Reichman, O. and Smith, S. 1985. Impact of pocket gophers burrows on overlying vegetation. – J. Mammal. 66: 720–725.

Reichman, O. J., Benedix Jr., J. H. and Seastedt, T. R. 1993. Distinct animal-generated edge effects in a tallgrass prairie community. – Ecology 74: 1281–1285.

Rosswall, T. 1982. Microbial regulation of the biogeochemical nitrogen cycle. – Plant Soil 67: 15–34.

Schimel, J., Van Cleve, K., Cates, R. 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.

Schroth, G., Krauss, U., Gasparotto, L. et al. 2000. Pests and diseases in agroforestry systems of the humid tropics. – Agrofor. Syst. 50: 199–241.

Scott, N. and Binkley, D. 1997. Foliage litter quality and annual net N mineralization: comparison across North American forest sites. – Oecologia 111: 151–159.

Selby, M. J. 1993. Hillslope materials and processes, 2nd ed. – Oxford Univ. Press.

Sidle, R. 1991. A conceptual model of changes in root cohesion in response to vegetation management. – J. Environ. Qual. 20: 43–52.

Siqueira, J. O., Nair, M. G., Hammerschmidt, R. et al. 1991. Significance of phenolic compounds in plant-soil-microbial systems. – Critical Rev. Plant Sci. 10: 63–121.

Springett, J. and Gray, R. 1997. The interaction between plant roots and earthworm burrows in pasture. – Soil Biol. Biochem. 29: 621–625.

Steltzer, H. and Bowman, W. 1998. Differential influence of plant species on soil nitrogen transformations within moist meadow alpine tundra. – Ecosystems 1: 464–474.

Stromberg, M. and Griffin, J. 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers and grazing. – Ecol. Appl. 6: 1189–1211.

Stump, L. M. and Binkley, D. 1993. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. – Can. J. For. Res. 23: 492–502.

Taylor, B., Parkinson, D. and Parsons, W. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. – Ecology 70: 97–104.

Thibault, J., Fortin, J. and Smirnoff, W. 1982. In vitro allelopathic inhibition of nitrification by balsam poplar and balsam fir. – Am. J. Bot. 69: 676–679.

Thompson, L., Thomas, C., Radley, J. et al. 1993. The effect of earthworms and snails in a simple plant community. – Oecologia 95: 171–178.

Tilman, D. 1983. Plant succession and gopher disturbance along an experimental gradient. – Oecologia 60: 285–292.

Vinton, M. and Burke, I. 1995. Interactions between individual plant species and soil nutrient status in shortgrass steppe. – Ecology 76: 1116–1133.

Vleck, D. 1979. The energy cost of burrowing by the pocket gopher Thomomys bottae. – Physiol. Zool. 52: 122–135.

Vleck, D. 1981. Burrow structure and foraging costs in the fossorial rodent, Thomomys bottae. – Oecologia 49: 391–396.

Waldron, L. 1977. The shear resistance of root-permeated homogeneous and stratified soil. – Soil Sci. Soc. Am. J. 41: 843–849.

Waldron, L. and Dakessian, S. 1981. Soil reinforcement by roots: calculation of increased soil shear resistance from root properties. – Soil Sci. 132: 427–435.

Waldron, L., Dakessian, S. and Nemson, J. A. 1983. Shear resistance enhancement of 1.22 meter diameter soil cross sections by pine and alfalfa roots. – Soil Sci. Soc. Am. J. 47: 9–14.

Wedin, D. and Tilman, D. 1990. Species effects on nitrogen cycling: a test with perennial grasses. – Oecologia 84: 433–441.

Willems, J., Marinissen, J. and Blair, J. 1996. Effects of earthworms on nitrogen mineralization. – Biol. Fert. Soils 23: 57–63.

Zaller, J. and Arnone, J. I. 1999. Interactions between plant species and earthworm casts in a calcareous grassland under elevated CO_2. – Ecology 80: 873–881.

Zar, J. H. 1999. Biostatistical analysis, 4th ed. – Prentice Hall.