



Plant colonizers shape early N-dynamics in gopher-mounds

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Abstract

Disturbances by fossorial mammals are extremely common in many ecosystems, including the California annual grassland. We compared the impact of juveniles of four common plant colonizers (*Aegilops triuncialis*, *Cerastium glomeratum*, *Aphanes occidentalis* and *Lupinus bicolor*) on the pools and fluxes of N in mounds created by pocket gophers (*Thomomys bottae* Mewa). The mechanisms and magnitude of biotic N retention differed among plant species. In mounds colonized by *Cerastium*, *Aphanes* and *Lupinus*, the microbial N pool was significantly larger than the plant N pool, as is typical in California grasslands in the early spring, whereas in mounds colonized by *Aegilops*, there was a more equal distribution of biotic N between plant and microbial pools. A 1-day ¹⁵N pulse field experiment demonstrated that plant species significantly differed in their effects on the distribution of isotopic N, with the N-fixing *Lupinus* leaving most (82%) ¹⁵N as inorganic N in soil, whereas more ¹⁵N was immobilized in plants or otherwise removed from the available soil pool in mounds colonized by other species. The impacts of early colonizers on N dynamics suggest that the identity of plant species that initially colonize gopher mounds may have important consequences on the dynamics of the overall grassland community.

Introduction

The burrowing activity of fossorial mammals has strong effects on ecosystem and community dynamics (Huntly and Inouye, 1988). Since gophers disrupt up to 30% of the California grassland soil surface each year, their effects on plant communities and soil nutrient cycling may be of enormous importance to the overall dynamics of the ecosystem (Eviner and Chapin, 2003a; Hobbs and Mooney, 1985; Reichman and Jarvis, 1989; Reichman and Seabloom, 2002). The impact of these mammals on

nitrogen (N) dynamics is of particular interest because N availability strongly influences the productivity and community dynamics of grasslands (Burke et al., 1997; Sala et al., 1988). Recently created gopher mounds often experience an intense flush of inorganic N (Litaor et al., 1996) due to: (1) a stimulation of mineralization due to disruption of the soil structure that physically protects labile organic matter, (2) a stimulation of nitrifying activity, and (3) a decrease in plant N uptake and in root-enhanced microbial N-immobilization (Canals et al., 2003). In California annual grasslands, the intense activity of Botta's pocket gophers (*Thomomys bottae* Mewa) in late winter and early spring overlaps a time of intense plant demand and microbial

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retention (Jackson et al., 1988). Consequently the impact of gophers increasing the standing pools of inorganic N (Canals et al., 2003) is particularly significant due to the low levels of soil inorganic N occurring at this time of the year (Herman et al., 2003). This overlap in the timing of gopher activity with plant and microbial N demand is likely to be seen in other Mediterranean grassland ecosystems since many small mammal populations peak after periods of high cumulative rainfall, as in winter (Torre, 2004).

While gophers affect the amount and the type of N available in mound soil, the fate of this N may be influenced by the characteristics of species that colonize these mounds. Plant species differ in the amount and form of N they take up (Aerts and Chapin, 2000), and these species-specific patterns of uptake modify the pools of N available to soil microbes and to other plants (Jackson et al., 1989; Jaeger et al., 1999a; Stark and Hart, 1997). Plants also indirectly affect N dynamics through their influence on microbial activity (Bardgett and Shine, 1999; Hobbie, 1992; Jackson et al., 1988) *via* root exudation, above- and below-ground litter inputs, and effects on microclimate (Eviner and Chapin, 2003b; Hodge et al., 1998; Jaeger et al., 1999b). While the effects of litter quantity and quality are not apparent until litter accumulates and decomposes in the soil (Jingguo and Bakken, 1997; Vinton and Burke, 1995), root exudates and species effects on microclimate may affect the soil microbial community from the early stages of plant growth.

Most work on plant species effects on N cycling has focused on species in well-established stands (Epstein et al., 1998; Hook et al., 1991; Hungate et al., 1996; Wedin and Tilman, 1990), and the role of pioneer species has been less studied. Because nutrients are frequently susceptible to loss after disturbance, attributes of plant colonizers may play a critical role in the N dynamics of disturbed ecosystems. In a species-rich grassland, disturbances may favor some plant species over others. Plant species that colonize disturbed areas are often non-dominant and non-competitive species in undisturbed sites (Bonis et al., 1997, Canals and Sebastià, 2000). These species can rapidly make use of the resources released by disturbance (space, light, N) to develop and reproduce

before being out-competed. In other cases, disturbed areas may be colonized by the dominant species in the community due to high propagule availability. In this manuscript, we investigate the patterns of N availability associated with different species of mound colonizers and the mechanisms responsible for these patterns.

Materials and methods

Experimental site and design

The experiment was performed in a California annual grassland located at the University of California's Hopland Research and Extension Center, in Mendocino County (39°00' N, 123°4' W). The area experiences a Mediterranean climate, with hot dry summers and wet cold winters and a mean annual precipitation of 960 mm. The growing season begins with the fall rains and lasts until late spring, when the soil dries out. Intense plant growth occurs at the end of the winter, favored by the rising temperatures and the frequent rainfall.

The site is characterized by a Sutherlin soil, derived from hard sandstone and shale (classified as ultic haploxeralf). The surface soil is a moderately aggregated, medium texture loam, while the subsoil (>28 cm depth) is a clay loam or gravelly clay (Gowans, 1958). Grasses such as *Avena barbata*, *Bromus hordeaceus*, *Bromus diandrus*, *Aegilops triuncialis* and *Taeniatherum caput-medusae* dominate the natural herbaceous vegetation. Common forbs are *Erodium botrys*, *Lupinus bicolor* and *Trifolium subterraneum*.

In 1997, a 30 m × 60 m grassland area was fenced and mowed, and 360 1 m² plots were established as plant monocultures and mixtures by planting seeds of the desired species composition in each plot (see Eviner, 2004, for details). Botta's pocket gophers (*Thomomys bottae* Mewa) were extremely active in the area. A survey of vegetation composition on the mounds in late winter 1999 revealed that recently created gopher mounds were most frequently colonized by *Cerastium glomeratum* Thuill. (introduced Caryophyllaceae forb), *Aphanes occidentalis* (Nutt) Rydb. (native Rosaceae forb), *Aegilops triuncialis* L. (exotic grass

selectively disturbed by gophers, Eviner and Chapin, 2003a), and *Lupinus bicolor* Lindley (native legume that is a preferred food for gophers, Chase et al., 1982, Eviner and Chapin, 2005). We focused on mounds colonized by these four plant species. *Lupinus bicolor* and *Aegilops triuncialis* were frequent colonizers of mounds created in plots that had been previously planted as monocultures of each of these species. In contrast, there were no planted monocultures of *Cerastium glomeratum* and *Aphanes occidentalis*, but both species were widespread on mounds throughout the fenced area, and were frequent mound colonizers in these grasslands.

N pools and ¹⁵N tracer field experiment

We compared N pools and followed the flow of N into the soil and the plants on 32 gopher mounds colonized by juveniles of *Cerastium glomeratum* (nine mounds), *Aphanes occidentalis* (eight mounds), *Lupinus bicolor* (eight mounds) and *Aegilops triuncialis* (seven mounds). We performed a ¹⁵N tracer field experiment in March 1999, after a period of peak gopher disturbance and at a time when moisture and temperature conditions favored the rapid growth and development of the seedlings established on mounds.

The procedure used followed Jackson et al. (1989) and Hungate et al. (1996). In early March, we inserted PVC cylinders (7.6 cm diameter × 20 cm depth) to a depth of 19 cm in the gopher mounds recently colonized by the selected species. One week later, we collected soil samples around the PVC cores to measure initial inorganic N-pools. We then injected 12 ml of 6 mmol (NH₄)₂SO₄/L solution (99 atom% ¹⁵N) into the top 10 cm of each core. To obtain a uniform distribution of the label, we injected twelve 1-ml aliquots in a grid pattern using a sideport needle, gradually releasing the solution while pulling up and rotating the needle. The amount of ¹⁵N injected in each core produced an average enrichment of 5 μg ¹⁵N g⁻¹ soil. Twenty-four hours after labeling, we collected plant and soil samples to determine ¹⁵N partitioning. All aboveground vegetation inside the PVC cores was clipped. Roots were harvested by taking one soil core of 3.6 cm diameter × 10 cm depth, from inside each

PVC core. The remaining soil within the top 10 cm of the PVC core (corresponding to the zone of most active root growth) was harvested for the determination of the ¹⁵N enrichment of soil inorganic N and for the determination of microbial biomass N.

Laboratory analyses

We analyzed aboveground and belowground plant tissues for C, N and ¹⁵N. Living tissues were separated from necromass, dried at 60 °C to constant mass, weighed and ground to a fine powder. Plant percent carbon and N contents were determined with an automated combustion analyzer (Roboprep-CN, PDZ Europe, Crewe, UK) and plant ¹⁵N enrichment by mass spectrometry (Tracermass, PDZ Europe, Crewe, UK). Plant ¹⁵N uptake was calculated by multiplying excess ¹⁵N concentration (measured as atom % ¹⁵N – natural abundance % ¹⁵N in control samples) by N concentration and tissue mass.

We measured microbial N using chloroform-fumigation followed by direct extraction (Davidson et al., 1989). Twenty grams of fresh soil were extracted in 100 mL of 0.5 M K₂SO₄ (unfumigated samples). We then fumigated 15 g soil samples with chloroform for 24 h, and extracted this soil in 75 mL of 0.5 M K₂SO₄ (fumigated samples). We performed Kjeldahl digestion on the extracts, and measured the NH₄⁺ product using an automated flow-injection analyzer (model QC 8000, Lachat Instruments, Milwaukee, WI). We determined microbial biomass N by difference in the NH₄⁺ contents between fumigated and unfumigated samples, dividing by 0.54 to correct for extraction efficiency (Brookes et al., 1985). We determined soil NH₄⁺ and NO₃⁻ in the unlabeled extracts by flow-injection analysis, and prepared labeled extracts for mass spectrometry by diffusion (Herman et al., 1995).

Statistical analyses

Statistical analyses were performed using SPSS 11.5 (SPSS Inc., Chicago, IL). Variables were transformed to meet normality criteria: Plant ¹⁵N uptake, plant N and plant biomass values were log₁₀-transformed, and soil pools of NO₃⁻ and

$^{15}\text{N}\text{-NO}_3^-$ were arcsin-transformed. Analysis of variance for unequal sample sizes was performed to test for differences among species and least significant difference test was used for means comparisons.

Results

Standing stocks of biomass and N

Standing plant biomass represents the total growth since the gopher disturbance. *Cerastium*, *Aphanes* and *Lupinus* displayed similar, low standing biomass, which differed significantly from the larger shoots developed by *Aegilops* individuals (Figure 1). The total plant N content did not differ significantly among species, although *Aegilops* tended to accumulate the most N (Figure 2). The legume *Lupinus* exhibited the highest percent N and the lowest C:N ratios (Table 1).

Total biotic N retention (plants plus microbes) was not significantly different among treatments, and ranged from $8.5 \pm 0.8 \text{ g N m}^{-2}$ in *Lupinus* to $12.4 \pm 1.3 \text{ g N m}^{-2}$ in *Cerastium*. Although total biological N uptake capacity did not vary significantly, the mechanisms of retention differed among species. The grass *Aegilops* supported a significantly lower microbial N pool than *Aphanes* and *Cerastium* (Figure 2). As a consequence, plant and microbial N pools were approximately equal for *Aegilops*, whereas in the

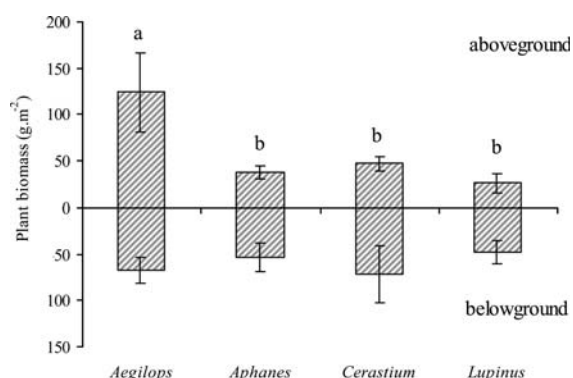


Figure 1. Aboveground and belowground biomass per unit of ground area for each species. Error bars are standard errors and values sharing a common letter are not significantly different by the LSD multiple-range test ($P < 0.05$).

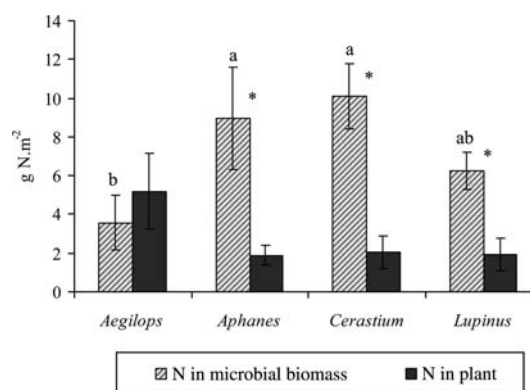


Figure 2. Total plant N and microbial biomass N per unit of ground area. Error bars are standard errors. Different letters indicate significant differences in soil microbial N by the LSD multiple-range test ($P < 0.06$). Asterisks indicate significant differences in N pools between plants and microbes ($P < 0.05$).

other species microbial N pools were significantly larger than plant N pools (Figure 2).

Before the labeling, soil NH_4^+ and NO_3^- pools averaged 896 and 119 mg N m^{-2} , respectively, and there were no significant differences among treatments (data not shown).

^{15}N fluxes

Twenty-four hours after the labeling, differences in ^{15}N uptake were observed among species. ^{15}N was barely detected in the shoots of *Lupinus*, and total shoot ^{15}N uptake was significantly lower in the legume than in the rest of species (Figure 3a). Short-term patterns of N uptake among species were not a simple function of the plant biomass present. *Cerastium* and *Aphanes* displayed as low biomass as *Lupinus* (Figure 1), but exhibited higher concentrations of ^{15}N , which was rapidly translocated to aboveground tissues (Figure 3b). Less than 7% of the applied N accumulated in plants of any species.

Twenty-four hours after ^{15}N was added to the soil, the proportion that remained in the soil fraction varied significantly among plant species (Figure 4). In *Lupinus*, most of the ^{15}N injected (82%) remained in the soil, whereas in *Aegilops*, *Aphanes* and *Cerastium* the ^{15}N recovered in the soil extractable fraction decreased to an average of 53% after one day. In all cases, most of the

Table 1. Contents of carbon, nitrogen and C:N ratios in the tissues of the juveniles in study

	<i>Aegilops triuncialis</i>	<i>Aphanes occidentalis</i>	<i>Cerastium glomeratum</i>	<i>Lupinus bicolor</i>
%C				
Belowground tissues	36.2 ± 1.3 a	26.8 ± 4.0 b	24.2 ± 1.3 b	25.4 ± 1.9 b
Aboveground tissues	39.6 ± 0.7 a	35.7 ± 1.4 b	31.4 ± 0.7 c	35.0 ± 1.7 bc
%N				
Belowground tissues	1.3 ± 0.1 b	1.4 ± 0.2 ab	1.0 ± 0.1 b	1.9 ± 0.2 a
Aboveground tissues	2.4 ± 0.3 ab	1.7 ± 0.3 b	2.0 ± 0.2 b	3.1 ± 0.1 a
C/N				
Belowground tissues	28.8 ± 2.7 a	19.3 ± 2.1 bc	24.2 ± 1.3 ab	14.0 ± 0.8 c
Aboveground tissues	17.6 ± 2.8 ab	21.6 ± 2.1 a	16.4 ± 2.1 ab	11.3 ± 0.3 b

Data are means (±SE). Means in the same row sharing a common letter are not significantly different ($P < 0.05$).

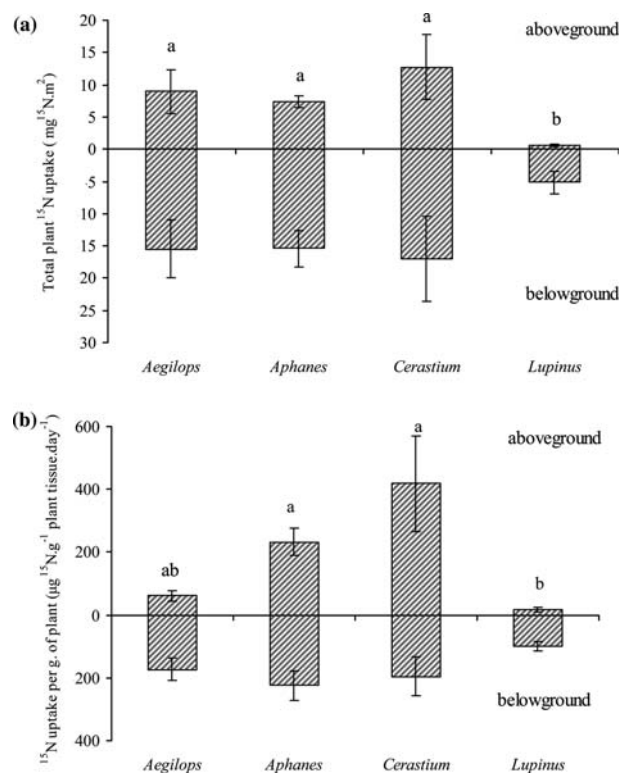


Figure 3. Percent recovery of ¹⁵N tracer as inorganic N in the soils of the mounds after 24 h of labeling. Values with different letters were significantly different by the LSD multiple-range test (for ammonium, $P < 0.01$).

soil ¹⁵N was in the form of NH_4^+ , only a small amount of NO_3^- was detected in the soil after the 24-h field incubation for all species.

Discussion

It has been well established that different plant species have distinct effects on N cycling

(Hobbie, 1992; Wedin and Tilman, 1990) but most of this work has focused on plant litter as the main determinant of plant species effects on N dynamics. Our study demonstrates that plant species identity can be a significant determinant of N dynamics at the early stages of plant development, well before litter inputs play a role. The magnitude of N retention differs across species, and plant species also differ in

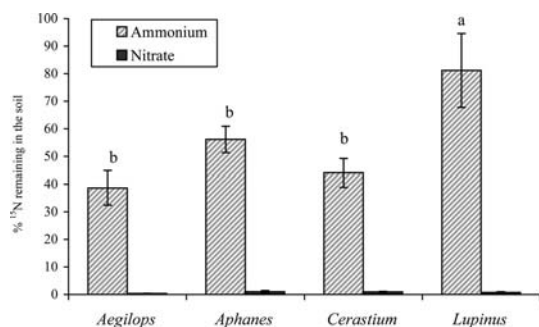


Figure 4. (a) Total plant ^{15}N uptake and, (b) plant ^{15}N tracer concentration after 24 h of labeling. Error bars are standard errors and values sharing a common letter in shoots are not significantly different by the LSD multiple-range test (a) $P < 0.05$; (b) $P < 0.001$.

whether N is retained in plant vs. microbial biomass.

In gopher mounds colonized by the legume *Lupinus bicolor*, a large proportion (82%) of the added ^{15}N remained available in the soil as ammonium after 24 h and rates of plant ^{15}N uptake were very low. Despite the low uptake of ^{15}N , *Lupinus* accumulated a quantity of N similar to that found in other species, suggesting that most plant N came from symbiotic N_2 fixation. The high concentrations of soil inorganic N associated with *Lupinus* may be susceptible to rapid leaching loss or denitrification at this time of the year. However, over the longer term, the occurrence of the legume and its ability to fix N_2 is likely to replenish the potential loss of N from the system.

In contrast to the legume, mounds colonized by *Cerastium* and *Aphanes* demonstrated efficient uptake of N due to rapid plant ^{15}N uptake and large microbial N pools. In Europe, species from the same genera flourish in bare, nutrient-enriched soils, such as molehills and decline sharply at later stages of the revegetation process (Bonis et al., 1997; Canals and Sebastià, 2000). The behavior of *Cerastium* and *Aphanes* is consistent with that of fugitive nutritional colonizers, taking advantage of the flush of available N released in recently disturbed areas to develop rapidly and produce seeds before being replaced by more N-efficient species (Grime, 1977; Redente et al., 1992). These ephemeral patches likely track the pulses of inorganic N produced in disturbed areas of the grassland, and play an important role in ecosystem N dynamics,

through both rapid plant uptake and stimulation of microbial N immobilization.

Cerastium, *Aphanes* and *Lupinus* supported microbial communities with larger standing stocks of N than the plants themselves. This is a common pattern in California annual grasslands at this time of the year, when most N is retained by microbes (Jackson et al., 1988). However, soil microbes associated with *Aegilops* acquired less N than microbes associated with other plant species. We had expected that the high carbon allocation of *Aegilops* to its root system and the soil labile carbon fraction (Eviner, 2004) would result in high microbial N sequestration. However, the rapid accumulation of aboveground biomass in *Aegilops* suggests that the species can compete for N with microbes through its early growth and nutrient uptake. Plant effects on microbial N uptake are critical since microbial N represents a stock of biologically active N that can be mineralized and used by plants (Burger and Jackson, 2005). *Aegilops* is an aggressive invasive species in northern California grasslands (DiTomaso, 2000), and its reductions of microbial N stocks may partly explain its tendency to out-compete and displace other plant species. Similarly, a decline in the N supplied to microbial communities occurs in response to the invader *Bromus tectorum* (Evans et al., 2001). Other studies have also suggested that invasive plants may modify ecosystem properties, modulating the availability of resources to other species (D'Antonio and Vitousek, 1992; Gordon, 1998; Mack et al., 2000; Vitousek et al., 1996).

In the case of *Aegilops*, its long-term effects on California grassland communities and ecosystem processes may depend on its complex interactions with gophers. According to Eviner and Chapin (2003) pocket gophers display a preferential burrowing activity in patches of *Aegilops triuncialis*. Resulting mounds mostly bury and kill the vegetation underneath (Eviner and Chapin, 2005). These observations suggest that, although new propagules of *Aegilops triuncialis* may establish on the mounds and cause a reduction of microbial N stocks, contributing to its dominance, the recurrent and negative effects of burrowing on *Aegilops* patches, killing established individuals, may decrease the abundance of the invader in the long term. The net effect of

repeated cycles of gopher disturbance and *Aegilops* reestablishment remains unresolved.

Summarizing, the study demonstrates that the identity of early plant colonizers on gopher mounds can significantly alter N dynamics. Because plant species differ in their N demands and in the sources from which they most efficiently derive N (Aerts and Chapin, 2000), these post-disturbance effects on N pools may influence longer-term community and ecosystem dynamics. To evaluate the overall impact multifactorial, long-lasting studies must be implemented.

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