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GOPHER–PLANT–FUNGAL INTERACTIONS AFFECT ESTABLISHMENT OF AN INVASIVE GRASS

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Abstract. Many attempts have been made to link invasions of exotic plants to specific plant traits and key attributes of invaded ecosystems. While these factors play a role in determining the potential for invasion, they are often inadequate in predicting the success of a specific invasion. We show that interactions of an invasive grass with other members of the community determine the local pattern of invasion. A fungus, *Ulocladium atrum*, aids the establishment of barbed goatgrass (*Aegilops triuncialis*) by weakening the grass's tough seed head, thereby accelerating germination and seedling establishment. In contrast, gophers, *Thomomys bottae*, decrease establishment of this invader by selectively burying patches of goatgrass seedlings under mounds. Plants that survive these gopher disturbances produce seeds that are uninfected by *Ulocladium atrum*, which may further decrease the establishment of the next generation of goatgrass. A field survey indicated that goatgrass achieves dominance in areas with minimal gopher disturbance, but has limited establishment in pastures with high gopher activity, indicating that the landscape pattern of gopher activity influences patterns of goatgrass invasion by manipulating gopher–plant–fungal interactions.

Key words: Aegilops triuncialis; *California (USA) annual grasslands; disturbance; fungus; germination; goatgrass; plant invasion; pocket gophers; species interactions, role in plant invasion;* Thomomys bottae; Ulocladium atrum.

INTRODUCTION

The invasion of exotic plant species can have major impacts on natural and managed systems, with large negative consequences for conservation of native species, diversity, and the economy (Mack 1996, Mooney and Hobbs 2000). The globalization of trade and travel has dramatically increased the introduction of exotic species, and consequently the invasion of these species has become one of the most pressing global-change issues (Lovel 1997, Mooney and Hobbs 2000). In order to stem this influx of invasive species, it is critical to determine the mechanisms responsible for successful invasions. Most research has focused on predicting invasions based on plant traits that characterize successful invaders (e.g., high growth rate, high allocation to reproduction [Newsome and Noble 1986, Noble 1989, Hobbs and Humphries 1995, Rejmanek 1995]), and characteristics of invaded ecosystems (e.g., disturbance [Orians 1986, Hobbs and Huenneke 1992, Hobbs and Humphries 1995] and diversity [Tilman 1997, Levine 2000]). Any of these factors can determine the *potential* of a species to invade, but often cannot be used to predict if a species will actually invade (Mack et al. 2000). Here we argue that, when a species has the potential to invade a site, its successful establishment ultimately is determined by its interactions with other members of the community. The success of some invasive species due to release from natural enemies is a clear example of the importance of biological interactions in invasions (Mack et al. 2000), but other types of species interactions can be important as well.

Aegilops triuncialis (barbed goatgrass) is an aggressive exotic annual grass that is invading central and northern California (USA) annual grasslands. This grass is capable of establishing in a variety of sites, ranging from deep fertile soils to shallow rocky soils. It is even capable of invading serpentine soils (California Exotic Pest Plant Council 1999), which have largely resisted invasions by many exotic plants due to their low nutrients, high Mg/Ca ratio, low water-holding capacity, and possible heavy metal toxicity (Huenneke et al. 1990). Although goatgrass is capable of establishing in a wide variety of sites, its ability to dominate a site varies greatly, even among neighboring fields (V. T. Eviner, *personal observation*). The mechanisms responsible for determining patterns of invasion of the same species across different sites in the same ecosystem could be critical additions to the current framework for predicting invasion success. Since patterns of goatgrass invasion vary locally, they are unlikely to be determined by coarse-scale environmental factors or dispersal limitation. However, there are differences in the local environment or distribution of other organisms that might influence the establishment of goatgrass. In particular, there is considerable spatial variability associated with the presence of a fungus, *Ulocladium atrum*, which infects the seed head of this

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invasive grass. Furthermore, the distribution of pocket gophers varies across the landscape due to variation in soil depth (Howards and Childs 1959). We propose that these other organisms might determine the local invasion patterns of goatgrass.

Goatgrass seeds normally germinate by breaking through their intact seed head (Peters et al. 1996), which is thick and woody. This seed head substantially delays germination, compared with germination of seeds removed from their spike (Peters 1994). The fungus, *Ulocladium atrum*, is often associated with the seed head of goatgrass. *Ulocladium* fungi produce cellulolytic enzymes (Srivastav and Srivastav 1986) and break down lignin (Almendros and Martinez 1987) and may weaken the seed head and possibly quicken germination of goatgrass. Alternatively, this fungus could act as a pathogen and decrease the establishment of goatgrass by decreasing seed size and survival.

Gophers are an important component of California grasslands. On average they disturb 26% of the soil surface annually (Hobbs and Mooney 1991). Soil disturbance by gophers can have large effects on plant community composition (Hobbs and Mooney 1985, 1991, Huntly and Inouye 1988, Martinsen et al. 1990, Huntly and Reichman 1994) and may increase invasion by creating sites for establishment of exotic species (Hobbs and Mooney 1991, Kotanen 1997). Gophers can also exert their effects on plant community composition by selectively disturbing patches of certain plant species (Tilman 1983).

The purpose of this study was to investigate the roles of *U. atrum* and gophers on the establishment of goatgrass and to determine if these biotic interactions could account for the spatial variability in the invasion success of this grass.

METHODS

Field site

This research took place in the California (USA) annual grassland 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).

Study organisms

Barbed goatgrass (*Aegilops triuncialis* L. [nomenclature according to Hickman 1993]) is an aggressive invasive species and has been classified as a noxious weed in California and Oregon, USA (USDA Agriculture Research Service, USDA Invader Database System: Noxious weeds in the US and Canada).[4] This grass is native to Northern Africa, Asia, the Middle East, and Europe (van Slageren 1994). Its tough seed heads decrease the number and delay the timing of germinating seeds (Peters 1994), but may provide a number of advantages in the native habitat of goatgrass. The seed head is responsible for dormancy of some goatgrass seeds (Peters et al. 1996), which can be critical for the persistence of annual species (Foley 2002). In addition, this tough seed head protects seeds from fire (Hopkinson et al. 1999) and ingestion by animals (Lyon et al. 1992), both of which are prevalent in the native habitat of goatgrass.

Ulocladium atrum (nomenclature according to IMI [1995]) is a dematiaceous hyphomycetes that is found in a wide variety of geographic areas, including Africa, North America, South America, Asia, the Middle East, Australia, and Europe (IMI 1995). It is a very common fungus throughout these regions, and can be found on the leaves (Abdel-Hafez 1985, Kohl et al. 1995), twigs (Agarwal et al. 1993), seeds (Hashmi 1988, Hashmi et al. 1990, Lilja et al. 1995) and roots (Taheri et al. 1994, Hashem and Al-Farraj 1995) of a variety of plants, as well as in the soil (Eastburn and Butler 1988) and in airborne dust (Abdel-Hafez et al. 1993, IMI 1995). It is likely that this fungus is associated with *Aegilops triuncialis* in its native habitat since the geographic ranges of these species overlap, and *Ulocladium atrum* is frequently found on many plants, including on the roots (Taheri et al. 1994) and straw (Almendros et al. 1987) of wheat, whose close relation to *Aegilops* allows these species to hybridize (Crampton 1974). The dark fungal lesions of *U. atrum* that we observe on *A. triuncialis* seed heads are common on *Aegilops* species in Japan, and are often a key attribute in the classification of these grasses (H. Tsujimoto, *personal communication*).

Infection of *A. triuncialis* seed heads with *U. atrum* was evident in California grasslands, but there were no visible signs of fungal presence associated with seeds of other grassland species. There are two distinct characteristics of *A. triuncialis* that may account for its unique association with *U. atrum* in our system. *A. triuncialis* has tough glumes that form a woody seed head, which is a likely substrate for *U. atrum*, a competitive saprobe (Kohl et al. 1995) with cellulolytic capabilities (Almendros and Martinez 1987). This fungus is known to establish on similar tough seed heads, including sunflower seeds (Shtienberg 1994). There was no visible evidence of *U. atrum* infection on the other dominant plants in our system, which have seeds surrounded by very thin glumes. The unique association of *A. triuncialis* with *U. atrum* may also be attributed to the structure of this plant. The culms of young *A. triuncialis* plants are solid, but become hollow with age (Kennedy 1928). As the plant senesces, this dark fungus spreads up to the seed head from the soil through the inside of this hollow culm (V. T. Eviner, *personal observation*; see Plate 1).

The effect of Ulocladium atrum *on goatgrass*

In order to determine the effects of the fungus *U. atrum* on goatgrass we investigated how this fungus

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[4] URL: ⟨http://invader.dbs.umt.edu/noxious_weeds⟩

PLATE 1. (Left) *Aegilops* seed heads with (top) and without (bottom) the fungus *Ulocladium atrum* (scale bar shows 1 cm). This fungus is detectable as dark lesions on the seed head. *U. atrum* weakens the seed head and enhances germination rates, while germination of seeds without the fungus is significantly delayed. (Right) In a California annual grassland, 360 1-m^2 plots containing 24 different plant treatments were established. Gophers selectively disturbed plots containing *Aegilops triuncialis.* Photographs by Valerie Eviner.

altered seed number, mass, and germination, as well as the overall establishment of goatgrass. Infections of this fungus are visible as black lesions on the surface of the seed head, allowing visual determinations of infection rates (Kennedy 1928). Each culm of goatgrass produces one seed head (spike) that typically contains 3–6 seeds. At maturity, the seeds within a spike are dispersed as a single unit, and they germinate from within this intact seed head. Because of this, most of these experiments were performed using individual seed heads as the experimental unit, rather than individual seeds.

Fungal effects on seed number and mass.—Seed heads were collected from the field in order to plant plots of *Aegilops* for a separate experiment. Over 300 000 seed heads were collected, and of these we randomly selected fifty from each of three categories: (1) no visible fungal infection, (2) intermediate rates of fungal infection (fungal presence, but no obvious weakening of the seed head), and (3) high fungal infection (most of the seed head covered with fungal lesions, which substantially weakened the seed head). It is likely that many of the seed heads without visible infection carried some fungal innoculum, since traces of fungi were detectable once seeds were wet up for germination. Seeds were removed from the seed head, counted, and individually weighed.

Fungal effects on seed germination.—Germination rates were determined in the laboratory for seed heads with an intermediate rate of infection by *U. atrum*, uninfected seed heads, and seeds removed from uninfected seed heads (200 of each treatment). The latter treatment utilized the two seeds at the base of the seed head, which are the seeds that are most likely to germinate within the seed head. We only used seed heads infected at an intermediate rate, since this is almost exclusively the observed infection level in the field, and we did not have enough heavily infected seed heads to include them in this experiment. Seed heads were germinated separately for each treatment in order to minimize fungal contamination. Fifty seed heads were placed on a 2-mm sieve lined with moist paper towels (four sieves per treatment). High seed moisture was maintained by continuously dripping water onto the paper towels. Germinating seed heads were counted each day.

Fungal effects on establishment of goatgrass in the field.—In order to determine the net effect of *U. atrum* on seedling establishment and growth, seed heads that were uninfected or were infected at an intermediate rate were planted in the field in 0.5 × 0.5 m plots ($n = 5$ replicate plots with 100 seed heads per plot) in September 1999. Since we planted seed heads rather than individual seeds, this experiment accounts for the effects of the fungus on both seed germination rates, and seed number and mass, allowing us to determine the overall net effect of this fungus on goatgrass establishment. These plots were arranged in a randomized block design and there was a 0.5-m border between plots. Plots were established in rodent exclosures, because all seeds were harvested by rodents in previous experiments in plots outside of exclosures. Establishment was determined by measuring goatgrass biomass at the end of the growing season (June 2000). Aboveground biomass was clipped, dried at 60°C for 48 h, and weighed.

Effects of gophers on goatgrass

In order to determine the effects of pocket gophers, *Thomomys bottae* Mewa, on goatgrass, we used three different approaches: (1) comparing the effects of gophers on eight plant species dominant in the northern California grasslands, (2) comparing establishment of goatgrass inside and outside of gopher exclosures, and (3) performing a field survey to look for linkages in

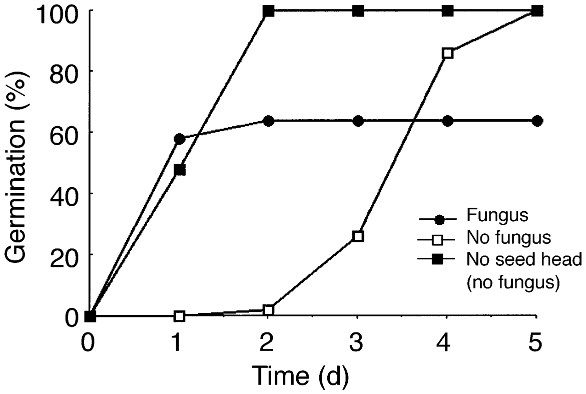

FIG. 1. Effect of *Ulocladium atrum* on germination of goatgrass. Germination rates of fungal-infected (solid circles) and uninfected (open squares) seed heads ($n = 200$ seed heads per treatment) and of seeds removed from their woody, uninfected seed head (solid squares; $n = 200$ seeds per treatment).

spatial variability of gopher activity and establishment of goatgrass.

Gopher disturbance of different plant species.—In the fall of 1997, monocultures were established of eight different plant species commonly found at our field site, including four grasses (*Aegilops triuncialis* L., *Avena barbata* Link, *Bromus hordeaceous* L., *Taeniatherum caput-medusae* L.), two forbs (*Erodium botrys* (Cav.) Bertol., *Amsinckia douglasiana* A. DC.), and two legumes (*Lupinus bicolor* Lindley, *Trifolium microcephalum* Pursh) (nomenclature according to Hickman [1993]). These species were also grown in two- or three-species mixtures (total of 14 mixture treatments). Eighteen replicates of each plant monoculture, and nine replicates of each species mixture were planted in 1-m^2 plots in a randomized block design, with 0.5-m borders surrounding each plot (see V. T. Eviner and F. S. Chapin [*unpublished manuscript*] for complete experimental design; also see Plate 1). Species composition was maintained for two years by weeding all nontarget plants from each plot. In March of 1999, the percentage area of the plots disturbed by gophers was visually determined.

Effects of gophers on the establishment of goatgrass.—In September 1999, goatgrass seed heads (690 g/m^2) were planted in 0.5 × 0.5 m plots, inside and outside of a gopher exclosure. Eight pairs of replicate plots were established along the perimeter of a 20 × 20 m gopher exclosure that was surrounded with 1-m-deep aluminum sheeting. At the end of the growing season (June 2000) plots were harvested for biomass, and visual determinations were made of fungal infection of seeds. Aboveground biomass was clipped, dried at 60°C for 48 h, and weighed.

Field survey of goatgrass establishment.—In April 1999 we conducted a field survey of the University of California's Hopland Research and Extension Center. We surveyed 21 different pastures over 1009 ha of grassland for the presence of gopher mounds (high, medium, or low numbers of mounds), establishment of goatgrass (dominant, co-existing, or sparse to absent), and soil depth. The presence of gopher mounds and goatgrass was determined visually. Soil depth (greater or less than 30 cm) was determined by a 2-cm diameter soil probe. Gophers are usually not active in soils shallower than this 30-cm depth (Howards and Childs 1959).

Statistical analysis

The chi-square test was used to determine differences in percentage germination among treatments, as well as differences in *Aegilops* establishment in fields with and without gophers. We used ANOVAs to determine differences in percentage gopher disturbance among plant treatments, and fungal effects on seed number and mass; and *t* tests to determine differences in *Aegilops* establishment with and without the fungus, and inside and outside of gopher exclosures.

RESULTS

Effect of Ulocladium atrum *on establishment of goatgrass*

Infection by *Ulocladium atrum* enhanced the germination rate of goatgrass (*Aegilops triuncialis*). In the laboratory, seed heads with intermediate infection rates (the infection rate most commonly seen in the field) germinated earlier than uninfected seed heads, and germinated just as rapidly as seeds taken out of the seed head (Fig. 1, day 2: $\chi^2 = 191.5$, $P < 0.0001$). Fungal infection, however, decreased the percentage of germinable seeds (Fig. 1, day 5: $\chi^2 = 92.3$, $P < 0.0001$), the average mass of seeds (ANOVA $P = 0.0001$), and the number of seeds per seed head (ANOVA $P = 0.003$, Table 1). To determine the net effect of this fungus on *Aegilops* establishment, we planted a fixed number of seed heads with and without fungus. Since each culm of goatgrass produces an individual seed head, this gives us the net effect of fungal infection on *Aegilops*, accounting for both fungal-induced decreases in seed number and size, and increases in germination rate. When goatgrass seed heads with and without the fungus

TABLE 1. Fungal effects on seed number and mass.

Degree of fungal infection	No. seeds per seed head	Seed mass (mg/seed)
None	5.1 ± 0.316^a	13 ± 2^a
Intermediate	4.4 ± 0.242^a	9 ± 1^b
High	3.0 ± 0.414^b	4 ± 1^c

Notes: Increasing infection rates of the fungus *Ulocladium atrum* decreases seed number (ANOVA, $P = 0.0031$, $n = 50$ seed heads per treatment) and mass (ANOVA, $P = 0.0001$, $n = 50$ seed heads) of goatgrass. Data are means ± 1 SE. Column entries with the same lowercase letter are not significantly different between levels of infection at $P = 0.05$ (Tukey-Kramer test).

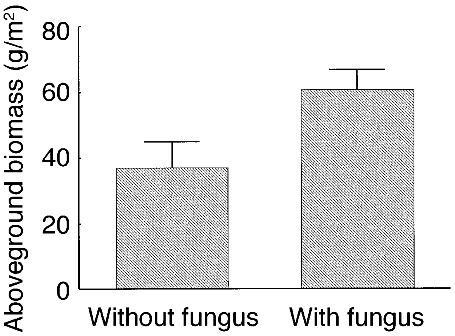

FIG. 2. Effect of *Ulocladium atrum* on goatgrass establishment. End-of-season aboveground biomass of goatgrass in plots sown with seeds uninfected or infected by the fungus *U. atrum*. Fungal infection increased aboveground biomass of this grass (*t* test, $P = 0.04$, $n = 5$ plots per treatment). Data are means and 1 SE.

were planted in the field, end-of-season aboveground biomass of goatgrass was 65% greater in plots planted with infected seed heads than in plots with uninfected seed heads (*t* test, $P = 0.04$; Fig. 2), indicating that fungal effects on germination rate had a greater effect on final biomass than did fungal effects on seed size and number.

Effect of gophers on establishment of goatgrass

In planted monoculture plots of eight dominant plant species in northern California grasslands, gophers selectively disturbed goatgrass plots (ANOVA $P < 0.0001$, Fig. 3), leading to high mortality through burial of these plants. This vegetation had not been removed by the gophers, but was simply buried intact under the mounds. This preference to build mounds in areas with goatgrass was also seen in mixed-species plots planted with goatgrass. High levels of gopher disturbance were found in seven out of eight mixed-species treatments containing goatgrass, while very little disturbance was associated with plots that did not contain goatgrass (ANOVA, $P < 0.0001$, Fig. 4). Aboveground biomass of goatgrass was 3.5 times higher inside gopher exclosures than in areas exposed to gophers (Fig. 5) (*t* test $P = 0.01$), where gopher mounds completely covered vegetation in six of eight plots. This gopher-exclosure treatment also significantly altered fungal infection of goatgrass seed heads ($\chi^2 = 9.3$, $P = 0.002$). In plots disturbed by gophers, all surviving plants produced seeds without fungal infection, whereas 60% of the

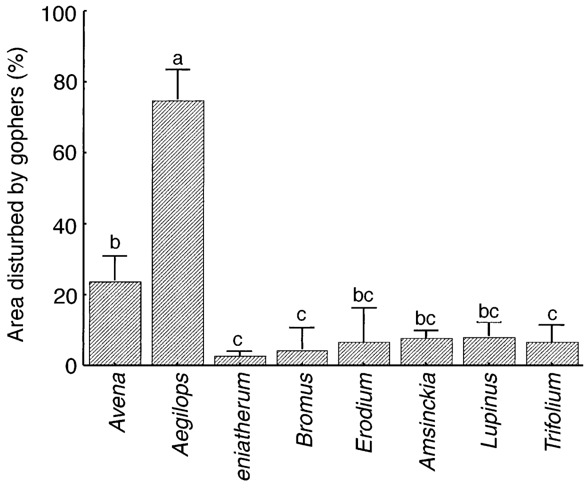

FIG. 3. Percentage area of planted monoculture plots disturbed by gophers. Gophers preferentially disturb monoculture plots of goatgrass (*Aegilops triuncialis*) (ANOVA, $P < 0.0001$, $n = 18$ plots per treatment). Data are means and 1 SE. Bars with the same lowercase letter are not significantly different between treatments at $P = 0.05$.

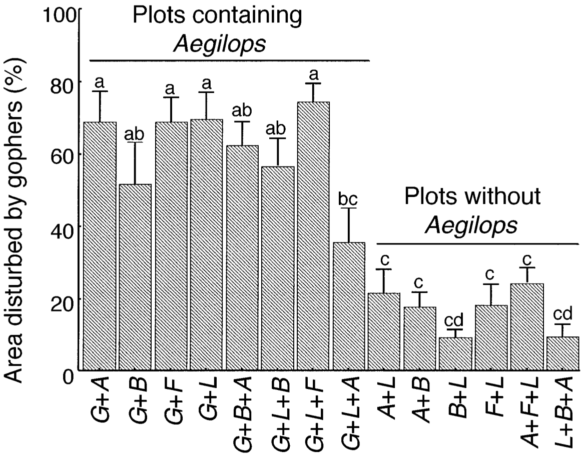

FIG. 4. Percentage area of plots planted as mixtures disturbed by gophers. Gophers preferentially disturbed mixed-species plots containing goatgrass (ANOVA, $P < 0.0001$, $n = 9$ plots per treatment). Species abbreviations are as follows: *A* = *Avena barbata*, *B* = *Bromus hordeaceous*, *G* = *Aegilops triuncialis*, *F* = *Amsinckia douglasiana*, and *L* = *Lupinus bicolor*. Data are means and 1 SE. Bars with the same lowercase letter are not significantly different between treatments at $P = 0.05$.

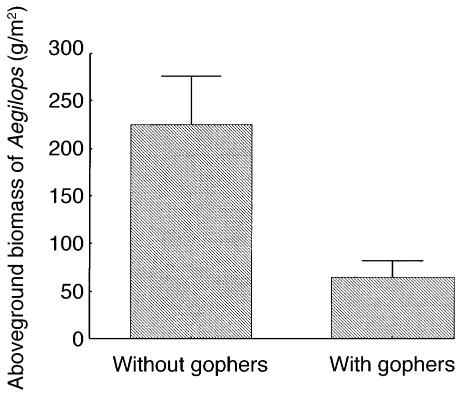

FIG. 5. Effect of gophers on goatgrass establishment. Plots inside of gopher exclosures had substantially higher biomass at the end of the growing season than plots disturbed by gophers (ANOVA, $P = 0.01$, $n = 8$ plots per treatment). Data are means and 1 SE.

gopher-exclusion plots produced seed heads infected by *U. atrum*. The field survey indicated that goatgrass dominated fields without gopher activity, and tended to have a minor presence where gophers were common ($\chi^2 = 10.5$, $P = 0.0012$). The survey also showed that sites with low gopher activity, and thus high amounts of goatgrass, tended to be areas with shallow soils or heavy grazing by sheep, while gopher disturbance was common in ungrazed pastures, where goatgrass coexisted with other plant species and failed to dominate the community (V. T. Eviner, *personal observation*).

DISCUSSION

Establishment of the invasive grass, *Aegilops triuncialis*, is greatly affected by its interactions with a fungus, *Ulocladium atrum*, and gophers, *Thomomys bottae*. Although fungal infection decreased the percentage of germinable seeds, the average mass of seeds, and the number of seeds per seed head of goatgrass, these seeds germinated earlier and the net effect of the fungus was to dramatically increase establishment of this invasive grass. The woody intact seed head of goatgrass significantly delays germination (Fig. 1, Peters 1994). In the field, uninfected goatgrass seeds germinated more than two weeks after all other dominant grass species at our site (V. T. Eviner, *personal observation*). *Ulocladium atrum* is a very competitive saprophyte (Kohl et al. 1995) that can degrade cellulose and lignin (Almendros and Martinez 1987). This allows it to decompose many recalcitrant substrates such as industrial polymers (Morgan-Jones and Jacobsen 1988), the shells of sunflower seeds (Shtienberg 1994), and the seed head of goatgrass (V. T. Eviner, *personal observation*). By breaking down the woody seed head of goatgrass, this fungus significantly decreases germination time. A number of other studies have shown that cellulytic enzymes from fungi promote the germination of hard seeds (reviewed in Egley [1989]; Mittal and Wang 1993). Differences in germination time of only a few days strongly influence the species composition of grassland communities (Harper 1961, Black and Wilkinson 1963), so this fungal-induced speeding of germination could significantly increase seedling establishment of goatgrass. When infected and uninfected goatgrass seed heads were planted in the field, the net effect of the fungus was to increase the end-of-season goatgrass biomass by 65% compared to plots with uninfected seeds. The infection of seeds with *U. atrum* thus substantially enhanced establishment and growth of goatgrass, most likely by speeding germination. *U. atrum* can also inhibit pathogens (Kohl et al. 1995), which may also have contributed to its enhancement of goatgrass establishment. These experiments were performed on seed heads with intermediate infection rates, which was the level most commonly observed in the field. It is likely that heavy infection decreases germination, but that level of infection is rare in the field.

We cannot rule out the possibility that these observed patterns are due to site or population differences in which smaller seeds, higher germination rates, and higher fungal infections co-vary in a non-causal manner. However, our observations suggest that these patterns are probably causal. The woody seed head clearly delays germination. This was established in a controlled experiment using seeds from the same population to compare germination rates of seeds inside and removed from the seed head. It is also clear that the fungus substantially weakens this seed head (V. T. Eviner, *personal observation*). Finally, seeds from the same population were planted in adjacent plots inside and outside of gopher exclosures, and fungal infection of the next generation of seeds was lower in gopher-disturbed plots.

Gophers also play an important role in the establishment of goatgrass, both by selectively disturbing patches of goatgrass, and by altering fungal infections of goatgrass seeds. Gophers disturbed ~70% of the area in plots containing goatgrass, and only 20% in plots without goatgrass. This was true in both the monoculture and mixed-species plots. This selective disturbance greatly decreases the establishment of goatgrass. Aboveground biomass of goatgrass was 3.5 times higher inside gopher exclosures than in areas exposed to gophers, where gopher mounds covered vegetation in six of eight plots. This disturbance behavior is unlikely associated with feeding. There was no evidence of removal of aboveground vegetation, and *Aegilops* has fibrous roots, which are an unlikely food source for gophers (Cortinas and Seastedt 1996). A related experiment at our site has shown that the disturbances associated with gopher feeding and with mound building are distinct, and gophers preferentially disturb different plant species for each of these activities. This selective mound building of gophers in areas dominated by goatgrass is likely related to its high rooting area, which stabilizes soil, making it more energetically efficient for gophers to burrow in patches of goatgrass (V. T. Eviner and F. S. Chapin, *unpublished manuscript*). A similar pattern has been observed in the alpine tundra, where gophers preferentially buried a perennial sedge with fibrous roots, with no evidence of gophers using this plant as a food source (Cortinas and Seastedt 1996). These studies confirm Huntly and Inouye's (1988) assertion that gophers interact with plants in a number of ways other than herbivory.

Gophers clearly decrease the establishment of goatgrass in experimental manipulations. These results are consistent with our field observations that goatgrass coexists with other plant species in areas where gophers are active, but almost completely eliminates other plant species in areas with no gopher activity. It is likely that, as goatgrass establishes local dominance, gophers selectively disturb those patches, leading to high goatgrass mortality through burial of these plants. This selective gopher activity can significantly decrease the establishment of goatgrass, preventing it from becoming a dominant member of the community. Gophers also selectively disturb certain species of tree seedlings (Ferguson 1999), and patches dominated by certain grass species (Tilman 1983), suggesting that species-specific effects of gophers are widespread.

Our field survey suggests that there is another important species interaction that influences goatgrass establishment. Areas with heavy grazing had little gopher activity and were dominated by goatgrass. Other studies in California grasslands confirm that gopher activity tends to decrease in grazed pastures (Hobbs and Mooney 1991, Hunter 1991, Stromberg and Griffin 1996), and goatgrass density increases with heavy grazing (Crampton 1974, Peters 1994). The formation of molehills also decreases in response to grazing (Edwards et al. 1999). Rangeland management practices may unintentionally facilitate the invasion of goatgrass through decreases in gopher activity associated with the presence of livestock. While gophers are often regarded as pests on rangelands, they are more desirable than the invasion of goatgrass. Goatgrass can have devastating economic effects on rangelands because its extremely low nutritional value decreases range capacity by 50–75%, and its sharp spikes can severely injure wildlife and livestock (Jacobson 1929).

Gophers may also reduce goatgrass establishment indirectly by reducing fungal infection rates. In plots with gophers, all surviving plants produced seeds without fungal infection, whereas 60% of the gopher-exclusion plots produced seed heads infected by *U. atrum*. It is not clear what the mechanism is for this decrease in fungal infection rates in the presence of gophers. *Ulocladium atrum* forms a hyphal network on rock (Gutiérrez et al. 1995) and likely does in the soil as well, particularly because at plant senescence the fungus moves along the inside of the hollow culm from the soil to the seed head (V. T. Eviner, *personal observation*). Gopher mounds (Koide and Mooney 1987) and soil disturbance (McGonigle and Miller 1996) decrease fungi, possibly by disrupting this hyphal network. Alternatively, gophers may decrease fungal infection by reducing goatgrass density to the point that it limits fungal spread (Burdon and Chilvers 1982) by decreasing host density and causing a ‘‘dilution effect’’ (Ostfeld and Keesing 2000). The likelihood of this mechanism depends on how this fungus spreads, and although *Ulocladium* spores can be dispersed by wind, by water, through the soil, by plant debris and by insects (IMI 1995, Shtienberg 1994), it is not clear which of these is dominant in our system.

This study suggests that the patterns of goatgrass invasion into California grasslands reflect a complex balance of interactions among multiple species. In the absence of gophers, *Aegilops* is an aggressive invader that dominates both deep and shallow soils. The enhancement of goatgrass germination by a fungus promotes goatgrass invasion and loss of local plant diversity. In deep soils, preferential disturbance and burial of goatgrass by gophers and an associated reduction in fungally promoted germination prevent goatgrass from attaining dominance. These observations suggest that gopher disturbance could enhance landscape-scale diversity by reducing the rate of spread of the exotic invader goatgrass across the grassland.

These observations suggest that species interactions can prevent or enhance plant invasion. Most of the research to predict the patterns of plant invasions has focused on plant traits and site characteristics. While these are important factors governing invasion, they are often inadequate to predict invasions (Mack et al. 2000). In addition to plant traits and environmental properties, species interactions are a vital component in predicting plant invasions and could lead to novel ways to manage ecosystems to prevent or control invasions. The roles of interactions in invasions are evident in the importance of natural enemies in regulating plant establishment (Guretzky and Louda 1997, Maron and Vila 2001), and the use of biocontrol to decrease establishment of invaders (Strong and Pemberton 2000). Invasion theory could benefit greatly by focusing on mechanisms by which plants can influence interactions with other organisms that are known to play a large role in vegetation community structure. By linking plant traits to the activity and distribution of these key organisms (e.g., Springett and Gray 1997, Bardgett et al. 1998, Zaller and Arnone 1999), we will be better able to predict local patterns of invasion. For example, selective mound building of gophers in areas dominated by goatgrass is likely related to its high rooting area that stabilizes soils, making it more energy efficient for gophers to burrow in patches of goatgrass (V. T. Eviner and F. S. Chapin, *unpublished manuscript*). While the characteristics of the plant and particular site likely dominate the *potential* of a plant to invade, if these conditions are met, the actual establishment patterns may be determined by the interactions of species at that site.

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