viable offspring in a bottle was a consequence of an interspecific mating. After 6 days in the bottles, females were placed singly into vials, which were scored for larval activity after another 6 days. Only 2 of the 480 fertile females in the experiment produced viable offspring; one in a field allopatric population (Forster) and one in a field sympatric population (Eungella). This frequency of hybridization is about four times greater than that achieved with single heterotypic pairs (*13*).

22. Single 1-day-old *D. serrata* males were placed in bottles with either 20 1-day-old virgin *D. serrata* females (controls) or 20 1-day-old *D. serrata* females and 20 1-day-old sterilized *D. birchii* females and males (experimental sympatry). Five replicate bottles of each treatment were set up for each of the six geographic populations. After 2 days in the bottle, females were placed singly in vials, and after another 6 days were scored for larval activity, indicating the number of *D. serrata* females that had been inseminated in the 2-day period. The mean proportion of *D. serrata* females inseminated for each population was analysed in a split-plot ANOVA (*20*).
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30. We thank C. Moore and R. Diocares for GC technical advice and R. Brooks, P. Cassey, J. Endler, A. Hoffmann, I. Owens, C. Sgro, and two anonymous reviewers for comments on the manuscript. Supported by a grant from the Australian Research Council to M.W.B.

11 May 2000; accepted 6 July 2000

Invasive Plants Versus Their New and Old Neighbors: A Mechanism for Exotic Invasion

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Invading exotic plants are thought to succeed primarily because they have escaped their natural enemies, not because of novel interactions with their new neighbors. However, we find that *Centaurea diffusa*, a noxious weed in North America, has much stronger negative effects on grass species from North America than on closely related grass species from communities to which *Centaurea* is native. *Centaurea*'s advantage against North American species appears to be due to differences in the effects of its root exudates and how these root exudates affect competition for resources. Our results may help to explain why some exotic species so successfully invade natural plant communities.

Exotic plants threaten the integrity of agricultural and natural systems throughout the world. Many invasive species are not dominant competitors in their natural systems, but competitively eradicate their new neighbors. One leading theory for the exceptional success of invasive plants is that they have escaped the natural enemies that hold them in check, freeing them to utilize their full competitive potential. This perspective provides the theoretical framework for the widespread practice of introducing natural enemies as biological controls, which also are exotic, to suppress invasive plants (*1*). Plant communities are widely thought to be "individualistic," composed primarily of species that have similar adaptations to a particular physical environment (*2*, *3*). With few exceptions (*4*–*7*), plant communities are not thought to consist of coevolved species, nor to possess stable properties determined by plant-plant interactions. Here, we argue that some invasive plants may succeed because they bring novel mechanisms of interaction to natural plant communities.

We compared the competitive effects of an invasive Eurasian forb, *Centaurea diffusa* (diffuse knapweed), on three bunchgrass species that coexist with *C. diffusa* in Eurasia with the effects of *C. diffusa* on three bunchgrass species from North America that have similar morphologies and sizes, each of which is closely related to one of the Eurasian grass species. Seeds of *C. diffusa*, *Festuca ovina*, *Koeleria laerssenii*, and *Agropyron cristatum* were collected within an area of several hectares in the southern foothills of the Caucasus Mountains in the Republic of Georgia. Seeds of *F. idahoensis*, *K. cristata*, and *Pseudoroegneria spicata* were collected from grasslands in the northern Rocky Mountains in Montana. Until recently, *Pseudoroegneria* was included in the genus *Agropyron*. Each of the grass species made up more than 10% of the total cover at its respective site. At the study site in the Caucasus, the cover of *C. diffusa* was less than 1%, whereas at the Montana site, the cover of *C. maculosa* (which is closely related to *C. diffusa*) was 10 to 90%. Each of the seven species was planted alone and in all pairwise grass-*Centaurea* combinations. All combinations were grown in sand and mixed with activated carbon (*8*, *9*).

Centaurea diffusa had much stronger negative effects on North American species than it had on Eurasian species. When grown with *Centaurea*, the biomass of North American grasses decreased 85.7 ± 0.3%; whereas in Eurasian species, biomass decreased by only 50.0 ± 4.7% (Fig. 1) (*10*). Correspondingly, none of the North American grass species (nor all species analyzed collectively) had a significant competitive effect on the biomass of *C. diffusa*, but the Eurasian species *K. laerssenii*, and all Eurasian species analyzed collectively, significantly reduced *C. diffusa* biomass (Fig. 2) (*11*). *Centaurea diffusa* had no effect on the amount of ^{32}P acquired by Eurasian grass species (*12*), but significantly reduced ^{32}P uptake of all North American species (Fig. 3) (*13*). Correspondingly, North American grasses had no competitive effects on ^{32}P uptake of *C. diffusa*, but all Eurasian species demonstrated strong negative effects on the amount of ^{32}P acquired by *C. diffusa* (Fig. 4) (*14*).

Activated carbon was added to ameliorate chemical effects (*8*), and it had contrasting effects on the interactions between *C. diffusa* and grass species from the different continents. The biomass of two North American species, *F. idahoensis* and *P. spicata*, when grown with *C. diffusa*, increased significantly in soil mixed with activated carbon; the overall effect of car-

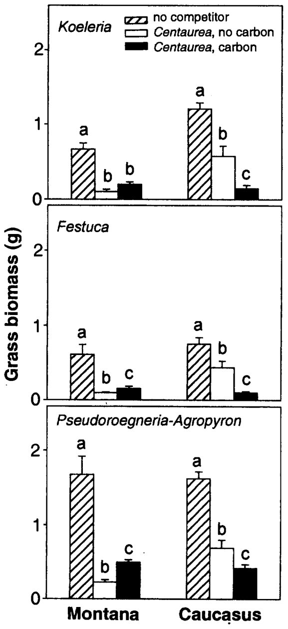

Fig. 1. Total biomass for related Eurasian and North American bunchgrass species grown alone, or with the invasive plant, *C. diffusa*, either with or without activated carbon in the soil. Error bars represent S.E.M. Means with different letters were significantly different in pairwise comparisons.

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bon on North American species in competition with *C. diffusa* was positive and significant (Fig. 1) (*10*). In contrast, the biomass of all Eurasian grass species growing with *C. diffusa* was reduced dramatically in the presence of activated carbon. Correspondingly, activated carbon gave *C. diffusa* a competitive disadvantage against North American grasses (*Centaurea* biomass was reduced) but a competitive advantage in the presence of Eurasian grasses (*Centaurea* biomass increased) (Fig. 2) (*12*). Unlike its effect on total biomass, the effect of activated carbon was not to enhance the uptake of ^{32}P of North American grasses in the presence of *C. diffusa*, indicating that allelopathic effects were manifest somewhat independently from competition for this particular resource (Fig. 3) (*13*). However, having activated carbon in the soil was a strong disadvantage for Eurasian grasses competing for ^{32}P with *C. diffusa*. In all cases, ^{32}P uptake by Eurasian grasses growing with *C. diffusa* decreased in the presence of activated carbon. The effects of activated carbon on ^{32}P uptake by grasses corresponded with the effects of activated carbon on ^{32}P uptake by *C. diffusa*. Activated carbon enhanced uptake by *C. diffusa* in the presence of Eurasian grasses but reduced uptake in the presence of North American grasses (Fig. 4) (*14*). We interpret the effects of activated carbon as evidence for allelopathy, as have others (*15–17*); however, activated carbon may also affect other soil properties, as well as the soil microbial community.

In a separate experiment (*9*), activated carbon did not have any significant direct effect on the total biomass of any of the six grass species when they were grown alone, nor was the effect of carbon significant when all species were tested together [ANOVA, treatment, $F(1,97) = 0.53$, $P = 0.471$]. As found in the first experiment, the Eurasian grass species were larger than North American grass species [region, $F(1,97) = 13.11$, $P < 0.001$].

When grown with *C. diffusa*, the proportion of total pot biomass made up of grasses was greater for Eurasian (38%) than North American (11%) species. Concomitantly, proportional biomass of *C. diffusa* was less when it was grown with Eurasian than with North American grasses. Activated carbon increased the dominance of *C. diffusa* with Eurasian grasses (84% from 62%) but decreased its dominance with North American grasses (78% from 89%). Significant biogeographical differences also existed for the total biomass and total resource uptake by both individuals combined within a pot. Pots with Eurasian grass species combined with *C. diffusa* produced 12% more total biomass and took up 63% more total phosphorus than pots with North American species planted with *C. diffusa* (*18*), suggesting that long-term association among plant species may enhance productivity and total resource utilization.

The strong effects of biogeographical place of origin on the competitive ability of grass species against *C. diffusa*, as well as the contrasting effects of activated carbon on competition, suggest that *C. diffusa* produces chemicals to which long-term and familiar Eurasian neighbors have adapted, but to which *C. diffusa*'s new North American neighbors have not. Chemical allelopathy has long been suspected as a mechanism by which invasive plant species eliminate natives (*19–21*). The competitive ability of Eurasian grass species against *C. diffusa* is greatly reduced by activated carbon, suggesting that the natural advantage of Eurasian species is, at least in part, also chemically mediated. In our experiments, the root systems of competing plants were constricted in pots, preventing any spatial root niche partitioning that might reduce competitive interactions.

Contrasting interactions among plants from different biogeographical regions have several implications for community ecology. First, they suggest that natural plant communities may be more tightly knit entities than generally thought. Second, these biogeographical effects conflict with the theory that plant competition is not species-specific (*22*, *23*). Third, they suggest that interactions among plant species may drive natural selection in communities. Fourth, they imply that natural biological communities may evolve in some way as functionally organized units (*24*, *25*). Finally, our results indicate that some exotic invasive plants may use competitive mechanisms that are not present in the natural communities that they invade to disrupt inherent, coevolved interactions among long-associated native species.

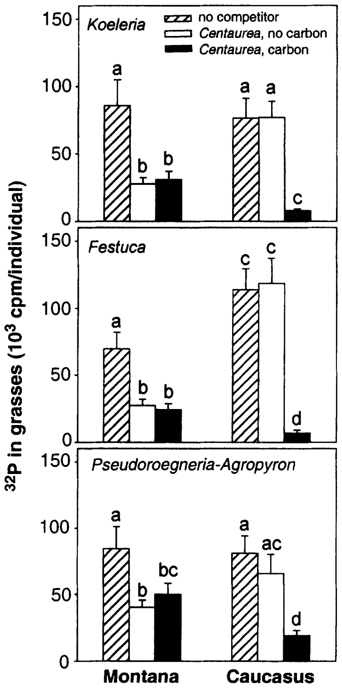

Fig. 2. Total biomass for *C. diffusa* plants grown alone, or with Eurasian or North American bunchgrass species, either with or without activated carbon in the soil. Error bars represent S.E.M. Means with different letters were significantly different in pairwise comparisons.

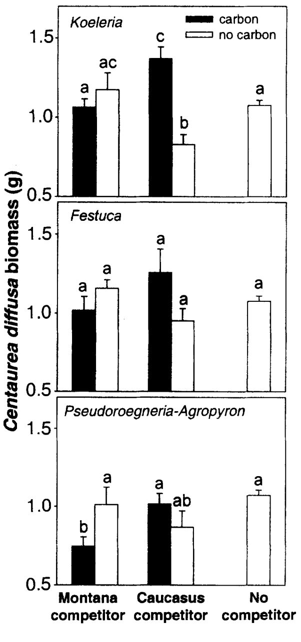

Fig. 3. Total counts per minute for related Eurasian and North American bunchgrass species grown alone, or with the invasive plant, *C. diffusa*, either with or without activated carbon in the soil. Error bars represent S.E.M. Means with different letters were significantly different in pairwise comparisons.

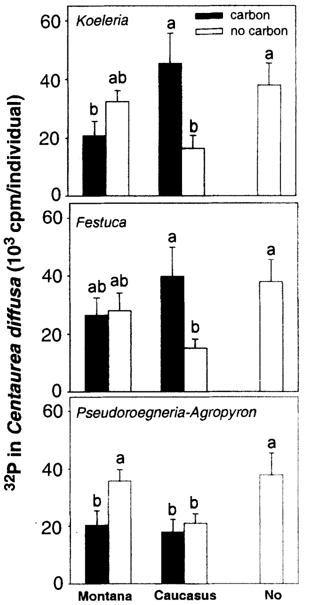

Fig. 4. Total counts per minute for *C. diffusa* plants grown alone, or with Eurasian or North American bunchgrass species, either with or without activated carbon in the soil. Error bars represent S.E.M. Means with different letters were significantly different in pairwise comparisons.

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8. Each of these seven species was planted alone and in all pairwise grass-*Centaurea* combinations in pots 20 cm tall and 6 cm in diameter (300 cm^2 volume) with 20 replicates per individual or species combination. The pots were filled with a 50:50 mixture 20 grit (mean diameter 0.85 mm), and 30 grit (mean diameter 0.60 mm) pure silica sand thoroughly mixed with 20 ml of soil from local Montana grasslands (to introduce microbes) in which all North American bunchgrasses and *C. maculosa* (a closely related species to *C. diffusa*) were present. Finely ground activated carbon (20 ml, without phosphorus) per 1 liter of sand was added to half of the pots with solitary grasses and with grass-*Centaurea* combinations. By mixing activated carbon into the sand in half of the pots, we established an experimental environment in which the effects of organic root exudates were reduced. Activated carbon has a high affinity for organic compounds, such as potentially toxic or "allelopathic" chemicals, and a weak affinity for inorganic electrolytes such as are found in nutrient solution (*26*), and it has previously been shown to reduce the negative effects of root exudates from other species (*15–17*). Other *Centaurea* species have been suspected to be allelopathic, and *C. maculosa*, which is very similar to *C. diffusa*, has been shown to have allelopathic root exudates [W. L. Ridenour, thesis, University of Montana, Missoula, MT, USA]. A separate experiment was conducted to examine the direct effects of activated carbon on the grasses. All plants were grown in a naturally lit growth room and supplemented with 12 hours of artificial light at $\sim$500 μmol m^{-2} s^{-1}. Pots were watered approximately every 3 days with distilled water or a dilute nutrient solution. All plants were started from seed, and 3 months after planting seeds, the roots and shoots of all plants were harvested, dried at 60°C, and weighed.
9. We conducted a second experiment designed to test the direct effects of activated carbon on the total biomass produced by the six grass species used in the competition experiment. Each grass species was planted alone in sand with activated carbon and in sand without activated carbon (n = 7 to 9). Protocol was as in the competition experiment (*26*).
10. Analysis of variance was conducted in which the effects of region, grass genus, and carbon treatment were tested. The dependent variable was the biomass of individual grasses grown with *C. diffusa* as a percentage of the mean biomass for each species when grown alone. Region, $F(1,120) = 23.7$, $P < 0.001$; grass genus, $F(2,120) = 18.22$, $P < 0.001$; carbon, $F(1,120) = 8.35$, $P = 0.005$; region × grass genus, $F(2,120) = 0.21$, $P = 0.813$; region × carbon, $F(1,120) = 39.93$, $P < 0.001$; grass genus × carbon, $F(2,120) = 2.06$, $P = 0.132$.
11. Analysis of variance was conducted in which the effects of region (grass origin), grass genus, and carbon treatment were tested. The dependent variable was the biomass of individual *C. diffusa* grown with grasses as a percentage of the mean biomass of *C. diffusa* when grown alone. Region, $F(1,120) = 0.13$, $P = 0.719$; grass genus, $F(2,120) = 6.45$, $P = 0.002$; carbon, $F(1,120) = 2.30$, $P = 0.133$; region × grass genus, $F(2,120) = 0.17$, $P = 0.841$; region × carbon, $F(1,120) = 24.05$, $P < 0.001$; grass genus × carbon, $F(2,120) = 2.57$, $P = 0.082$.
12. To examine the effects of species and the effects of activated carbon on resource competition, we added radioactive ^{32}P to the soil in all treatments 12 days before harvesting the plants. HCl (5 ml, 0.02 M) containing 0.1 μCi of ^{32}P-labeled $KH_2{}^{32}PO_4$ as the radiation source [after M. M. Caldwell *et al.*, *Science* **229**, 384 (1985)] was injected by using a hypodermic needle into each pot 10 cm below the surface and either halfway between a single plant and the pot edge or halfway between neighbors.
13. Analysis of variance was conducted in which the effects of region, grass genus, and carbon treatment were tested. The dependent variable was the total count for ^{32}P in individual grasses grown with *C. diffusa* as a percentage of the mean count for each species when grown alone. Region, $F(1,106) = 8.46$, $P = 0.005$; grass genus, $F(2,106) = 0.71$, $P = 0.50$; carbon, $F(1,106) = 59.44$, $P < 0.001$; region × grass genus, $F(2,106) = 2.87$, $P = 0.062$; region × carbon, $F(1,106) = 69.16$, $P < 0.001$; grass genus × carbon, $F(2,106) = 1.45$, $P = 0.239$.
14. Analysis of variance was conducted in which the effects of region (grass origin), grass genus, and carbon treatment were tested. The dependent variable was the total count for ^{32}P of individual *C. diffusa* grown with grasses as a percentage of the mean biomass of *C. diffusa* when grown alone. Region, $F(1,98) = 0.01$, $P = 0.939$; grass genus, $F(2,98) = 0.18$, $P = 0.834$; carbon, $F(1,98) = 1.75$, $P = 0.190$; region × grass genus, $F(2,98) = 0.81$, $P = 0.449$; region × carbon, $F(1,98) = 18.18$, $P < 0.001$; grass genus × carbon, $F(2,98) = 1.90$, $P = 0.156$.
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18. Analysis of variance testing for the effects of region (origin of grasses), grass genus, and carbon treatment on total biomass produced in pots with grasses and *C. diffusa* together. Region, $F(1,120) = 4.71$, $P = 0.032$; grass genus, $F(1,120) = 0.51$, $P = 0.611$; carbon, $F(1,120) = 0.29$, $P = 0.589$; no interactions were significant (all $P > 0.30$).
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31 July 2000; accepted 21 August 2000

Two–Amino Acid Molecular Switch in an Epithelial Morphogen That Regulates Binding to Two Distinct Receptors

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Ectodysplasin, a member of the tumor necrosis factor family, is encoded by the anhidrotic ectodermal dysplasia (EDA) gene. Mutations in EDA give rise to a clinical syndrome characterized by loss of hair, sweat glands, and teeth. EDA-A1 and EDA-A2 are two isoforms of ectodysplasin that differ only by an insertion of two amino acids. This insertion functions to determine receptor binding specificity, such that EDA-A1 binds only the receptor EDAR, whereas EDA-A2 binds only the related, but distinct, X-linked ectodysplasin-A2 receptor (XEDAR). In situ binding and organ culture studies indicate that EDA-A1 and EDA-A2 are differentially expressed and play a role in epidermal morphogenesis.

Members of the tumor necrosis factor receptor (TNFR) superfamily are involved in a number of physiological and pathological responses by activating a wide variety of intracellular signaling pathways. In a database search based on sequence similarity (*1*), XEDAR was initially identified as a member of the TNFR superfamily.

The deduced amino acid sequence of XEDAR contains three cysteine-rich repeats and a single transmembrane region (Fig. 1A). XEDAR lacks an NH_2-terminal signal peptide. The presence of an in-frame upstream stop codon in both human and mouse cDNA clones indicated that the sequence shown in Fig. 1A represents the full-length open reading frame (ORF) (*1*). To confirm that XEDAR was indeed a membrane protein, we transfected MCF7 cells with either an NH_2- or COOH-terminal Flag-tagged version of XEDAR (Fig. 1B). In permeabilized cells, the expression of both tagged proteins was readily detected by anti-Flag immunostaining. However, in the absence of permeabilization, cell surface staining

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