

Ingrid Parker
Department of Integrative Biology
University of California
3060 Valley Life Science Building
Berkeley, California 94720

And

William Harpole and Diana Dionne
Department of Botany
University of Washington
Seattle, Washington 98195

**Plant Community Diversity and Invasion of the Exotic Shrub *Cytisus Scoparius*:
Testing Hypotheses of Invasibility and Impact**

Ingrid Parker, William Harpole, and Diana Dionne

Abstract

Both the success and the consequences of invasion by an exotic are determined by the interaction between the invader and the host community. In this paper we couple a study of resident plant diversity with the results of a demographic study on invading *Cytisus scoparius* (Scotch or Scot's broom) populations at five sites, to ask questions about the relationship between invisibility and community characteristics. Population growth rate of the invader was positively (not negatively) correlated with species richness, failing to support the theory of biotic resistance. Population growth rate was negatively correlated with the proportion of total cover occupied by the other exotic species, suggesting that competition from previous aggressive invaders might play a role in reducing the success of an actively expanding population.

We also examined plant species richness and composition across a gradient of *Cytisus* density from 0% to 90% cover in five sites. We did not find evidence for a decline in total species richness in any site when both native and exotic species were considered together. Only two of the sites had considerable numbers of native species, and therefore only these glacial outwash prairies were used in analyzing the response of native plants to *Cytisus* invasion. Native species richness and native cover significantly declined with increasing *Cytisus* cover in one of the prairies but not the other; the proportion of total cover in native species declined significantly in both sites. The total cover of exotic species increased marginally significantly with *Cytisus* cover in both sites, suggesting that this nitrogen-fixing shrub might be facilitating the invasion of the exotic plants into the prairie. Cover of the prairie indicator species, *Festuca idahoensis* was dramatically negatively related to the presence of *Cytisus*. The result provides an example of how dominant or common species, by producing a strong "signal", may prove to be more useful than rare species for monitoring the environmental impact or degradation caused by invaders.

Introduction

The invasion of non-native species into natural areas has received increasing attention over the past decade, both from academic audiences and in the public arena. Some well-publicized case studies have demonstrated that the impacts of invaders can be dramatic (Vitousek et al. 1987, Thompson 1991), and several edited volumes (e.g., Krugre et al. 1986, MacDonald et al. 1986, Mooney and Drake 1986, Drake et al. 1989, Pysek et al. 1995) along with an important report by the Office of Technology Assessment (Office of Technology Assessment 1993) have recently compiled information on the state of our understanding of invasions – why and how they occur, and what their effects can be. Despite increasing public concern about biological invaders, there is surprisingly little published information on the interactions between invading and resident species for most introduced species (Parker and Reichard 1997). As one example, at the International Broom Symposium held in April of 1996, the speaker in charge of cataloguing the ecological impacts of *Cytisus* and *Genista* species was not able to cite a single study on the topic, this despite the fact that thousands of dollars and volunteer person-hours are spent controlling these plants throughout their range along the west coast of North America. Here we attempt to fill the lacuna by presenting data collected from the glacial outwash prairies of western Washington along with comparative information about *Cytisus* invasion in old fields in the Seattle area. We will also discuss the limitations of our data and suggest necessary future directions for research. Our investigation focuses on two spheres of inquiry: 1) What are

the effects of community characteristics on *Cytisus* invasion? And 2) What are the effects of *Cytisus* invasion on community characteristics?

What are the Effects of Community Characteristics on *Cytisus* Invasion?

A fundamental question in invasion biology is what influences the invasibility of communities (Orians 1986, Case 1991, Hobbs and Huenneke 1992). The issue of invasibility is interesting from a pure science point of view because it tells us something about how communities are formed and structured. It is important from an applied point of view because it bears directly on how we manage ecosystems to promote native species and discourage exotic ones. In 1958, Elton developed his idea of “biotic resistance” by considering the extreme invasibility of island communities. Island or other species-poor systems may have fewer competitors or natural enemies capable of excluding a potential invader (Elton 1958). Results from analytical and statistical models have sometimes but not always agreed with the biotic resistance hypothesis, and experimental tests are (Parker and Reichard 1997). Related to the idea of biotic resistance is that plant communities with more open space (reflecting greater availability of specific resources) are less competitive and therefore more invasible (Crawley 1987). This formulation is based more on overall vegetative cover than on species number. One can also focus on the identity of particular species and their competitive ability; one hypothesis is that invasion should be more difficult into communities made up of other exotic species, which are themselves

successful invaders (Simberloff and Boecklen 1991).

Also related to but distinct from biotic resistance is the idea that invasion is directly correlated with disturbance. Many have noted a relationship between non-native species and disturbed habitats (Fox and Fox 1986, Orians 1986, Hobbs 1989, Case 1991, Hobbs and Huenneke 1992, D'Antonia et al. 1997), and several studies have demonstrated an empirical correlation between the abundance of particular invaders and levels of disturbance (Cowrie and Werner 1993, Parker et al. 1993, Knops et al. 1995). In this study rather than documenting the presence/absence and distribution of an invader, we look at variation in the actual dynamics of populations invading under different conditions. Combining data on the community composition of a series of sites with rates of population growth estimated from those sites (see Parker 1996), we evaluate the support for the following hypotheses:

- a. Invasion should occur more rapidly into communities with fewer species (less "biotic resistance").
- b. Invasion should occur more rapidly into communities with lower vegetative cover.
- c. Invasion should occur more slowly into communities with higher percent of cover of exotic species (strong preemptive competitors).
- d. Invasion of *Cytisus* should occur more rapidly into more disturbed communities (greater anthropogenic influence).

What are the effects of *Cytisus* invasions on community characteristics?

Separate from the issue of what factors promote invasions in a community is what occurs after a successful invasion has begun. Some introduced species seem to have large effects on the surrounding community, while the others do not. Just as with invisibility, there is wide speculation about what characteristics determine the impact of an exotic species (Kareiva et al. 1991). Species that occupy a "novel niche" in the community, such as nitrogen fixing *Myrica faya* in Hawai'i (Vitousek et al. 1987) or large fish in lake systems (Carpenter and Kitchell 1993), are thought to be more likely to cause changes in native species abundance and distribution. *Cytisus* is one of the only woody species, with Douglas-fir (*Pseudotsuga menzeisii*), that readily invades the prairies of western Washington. Other shrub species such as snowberry (*Symphoricarpos albus*) are only found as isolated individuals or small patches. Like many legume species, *Cytisus* fixes nitrogen (Wheeler et al. 1979), a trait which may in fact contribute to its great success in the nutrient-poor soils of the glacial outwash prairies. Native nitrogen fixers in the prairie include *Lupinus lepidus* and *Lotus purshiana*, but these species are not abundant (Harpole, Dionne, and Parker, personal observation). Therefore *Cytisus* may play a functionally unique role in these prairies, which would cause us to predict that it should have a large effect on species composition.

In other systems, adding nutrient inputs above natural levels has resulted in declines in species diversity (Gurevitch

and Unnasch 1989, Inouye and Tilman 1995). This result is unintuitive because one might expect the ameliorated conditions to instead allow more species to persist at a site. However, a decline occurs because the few species that are best able to exploit the additional nitrogen (i.e., those least constrained by other limiting factors) outgrow and displace the rest (Gurevitch and Unnasch 1989). If such a mechanism is at work when *Cytisus* invades prairies, we might expect the seemingly contradictory result that total plant cover (with *Cytisus* cover excluded) would increase while species number declines. We would also expect the composition of the remaining plants to change, with the “winners” being species well adapted to taking advantage of high-nutrient situations, rather than resident species adapted to surviving on the gravelly prairie soils. It has been suggested that broom invasion may facilitate the invasion of other aggressive species, specifically nitrogen-loving, do-forming exotic grasses. If this is the case, the long-term impact of *Cytisus* on prairies could extend far beyond the tenure of individual plants.

Alternatively, if the impact of *Cytisus* is not primarily through nitrogen dynamics but is an effect of competition, we would expect to see a different pattern. In this case total cover of other species should decline. The species composition might still change but would be skewed toward species more shade-tolerant and/or more tolerant of low nutrient conditions.

We compare plant diversity patterns across a gradient of *Cytisus* abundance in several sites, focusing particular attention on two prairie sites at Fort Lewis. We evaluate the evidence for the following hypotheses:

- a. *Cytisus* invasion is associated with a simple decline in species richness.
- b. *Cytisus* invasion is associated with an increase in total cover.
- c. *Cytisus* invasion is associated with a decline in native prairie species diversity.
- d. *Cytisus* invasion is associated with the loss of particular native indicator species
- e. *Cytisus* invasion facilitates the invasion of other exotic plant species.

Methods

Five sites were used in the current study, two prairies and three urban old fields. Johnson Prairie and Weir Prairie are both found in the southwest section of the Fort Lewis Military Reservation. They are high quality remnants of the glacial outwash prairies that used to cover large expanses in western Washington (Kruckeberg 1991). The prairie are characterized by coarse-textured soils and low levels of soil nutrients (Franklin and Dyrness 1988). They are burned periodically to control the invasion of *Cytisus* and also of Douglas-fir (*Pseudotsuga menziesii*). Burning is also thought to have been an important management tool used in the prairies by Native Americans (Franklin and Dyrness 1988, Giles 1970). Discovery Park, Magnuson Park, and Montlake Fill sites are urban old fields and landfills. These habitats have high levels of both past and current anthropogenic influence. We sampled all sites in August/September of 1995, and then again in May/June of 1996. The

second sampling was done because native species in these prairies seem to have earlier phenologies than exotic species (S. Harpole, D. Dionne, and I. Parker, personal observation), and we wanted to be sure that there was no systematic bias in the patterns seen. The cover estimates presented here are from the spring 1996 census.

To test hypotheses, regarding invisibility, we used *Cytisus* population growth rates estimated as the expanding edge of an infestation at each site. Population growth rates were calculated analytically from matrix models, which were constructed for marked individuals followed from 1994 to 1995 in permanent plots (see Parker 1996). Matrices were based on a seven-stage life cycle, with stage classes delimited by a combination of life history and size criteria.

Within each of these permanent plots at the edge of an invading front, we identified all vascular plant species present. We then estimated cover of each species in the following manner. We identified a 4m x 6m subplot inside each plot in order to equalize the total area covered by our sampling procedure among sites and stages of invasion (see Parker 1996). Within this subplot we randomly selected coordinates for the placement of 15 quadrats, 0.5m x 0.5 m in size. We estimated percent cover by eye, with no constraint on total cover to sum to less than or equal to 100%. Cryptogams (mosses, lichens) were a common component of the plant community at all sites; however, we were unable to identify individual species of cryptogams and could not classify them as native or exotic. Therefore, we have left them out of the

analyses of total cover and richness and the calculations of percent cover.

To assess the impacts of *Cytisus* invasion on species composition, we used the same site as above. Adding to the information from the edge of the front, we censused subplots of Parker's (1996) plots at intermediate (all populations) and late (Johnson Prairie and Discovery Park only) stages of invasion. Again 15 quadrats per subplot were sampled for vascular species richness and cover, as above. As there was no clearly interpretable pattern between *Cytisus* cover and cover of cryptogams, and the individual species of moss and lichen were not identified, we have again left these out of the analyses.

Results

Identifying all species in the plots, combined within sites, revealed 41 species at Johnson Prairie (22 native), 22 species at Weir Prairie (12 native), 28 species at Discovery Park (4 native), 25 species at Magnuson Park (1 native), and 31 species at Montlake Fill (3 native).

What are the Effects of Community Characteristics on *Cytisus* Invasion?

Rate of population growth in *Cytisus* positively correlated with the number of species recorded from a site (Fig. 1A, $r=0.95$, $P<0.01$). Controlling for the area censused, population growth was marginally positively correlated with mean species richness per quadrat (Fig. 1B, $r=0.86$, $P=0.06$).

Population growth rate declined with increasing total vascular plant cover, but

this relationship was not significant (Fig. 1C, $r=0.78$, $P=0.14$).

Population growth rate was significantly negatively correlated with the proportion of total cover occupied by exotic species (Fig. 1D, $r=-0.94$, $P=0.01$).

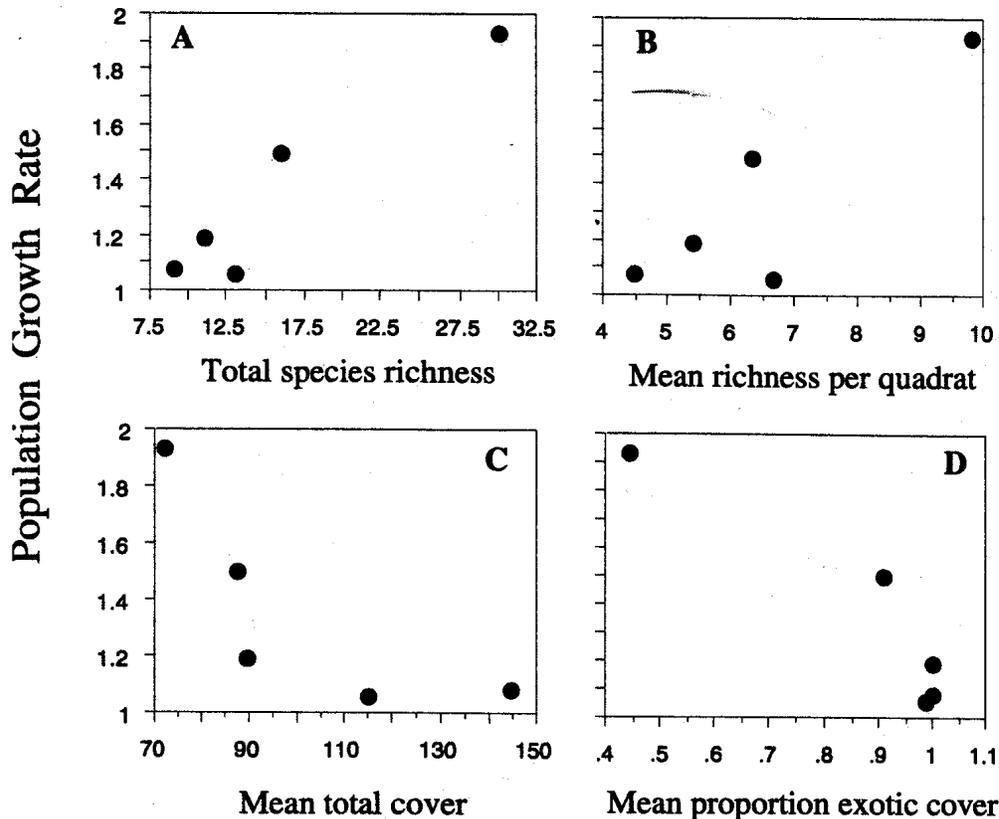


Figure 1. The relationship between various plant community characteristics and the population growth rate of *Cytisus scoparius* as estimated using matrix models (see Parker 1996). A. Total species richness within the uninvaded area of that site, B. Mean species richness per 0.25 m² quadrat, C. Mean total cover of vascular plants per quadrat, D. Mean proportion of total cover represented by exotic species. Each data point represents one population.

What are the Effects of *Cytisus* invasion on Community Characteristics?

Cytisus cover in the individual quadrats varied from 0% to over 90% in all sites,

although the values were more evenly distributed across this range in some sites than others (Fig. 2). The maximum species richness per quadrat also varied among sites, and was highest in Johnson

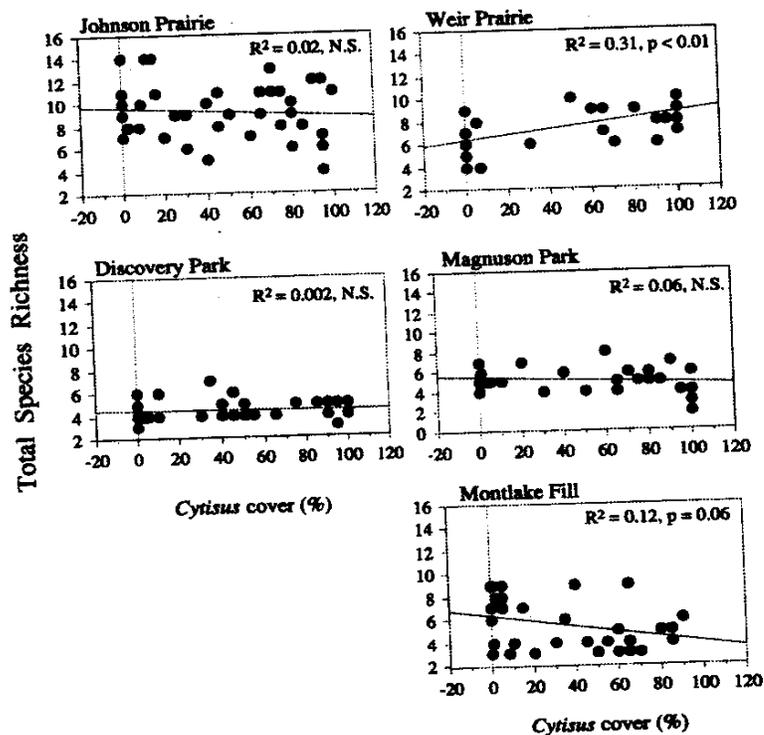


Figure 2. Total species richness (including both native and exotic species) as a function of the cover of *Cytisus scoparius* in five sites, two prairies and three urban parks. Sample size represents the number of 0.25 m² quadrats sampled per population: Johnson Prairie and Discovery Park, N = 45, Weir Prairie, Magnuson Park, and Montlake Fill, N = 30.

Prairie and lowest in Discovery Park (Fig. 2).

Total species number did not decline significantly with increasing *Cytisus* in *Cytisus* cover ($r^2=0.31$, $P<0.01$). Total cover (other than *Cytisus* cover) did not show a significant increase in either prairie or urban sites. In prairie sites there was no trend ($r^2=0.04$, $P=0.1$), and urban sites showed a significant decline in plant cover ($r^2=0.14$, $P<0.001$).

There are too few native species present in the urban field sites to comment on the relationship between native diversity and broom invasion at these sites; therefore we will focus only on prairie sites from here on.

any site (Fig. 2), although the relationship was marginally significant for Montlake Fill ($r^2=0.12$, $P=0.06$). In Weir Prairie, total species number actually increased significantly with

In contrast to the results from total species richness, the decline of native species richness was significant in Johnson Prairie (Fig. 3, $r^2=0.26$, $P<0.001$), although not significant in Weir Prairie ($r^2 = 0.06$, $P = 0.2$). Percent native richness ($100 \times \# \text{ native species} / \text{total } \# \text{ species}$) declined significantly with increasing *Cytisus* cover in both Johnson Prairie and Weir Prairie (Fig. 3; Johnson Prairie $r^2 = 0.36$, $p = 0.001$, Weir Prairie $r^2 = 0.30$, $P = 0.002$).

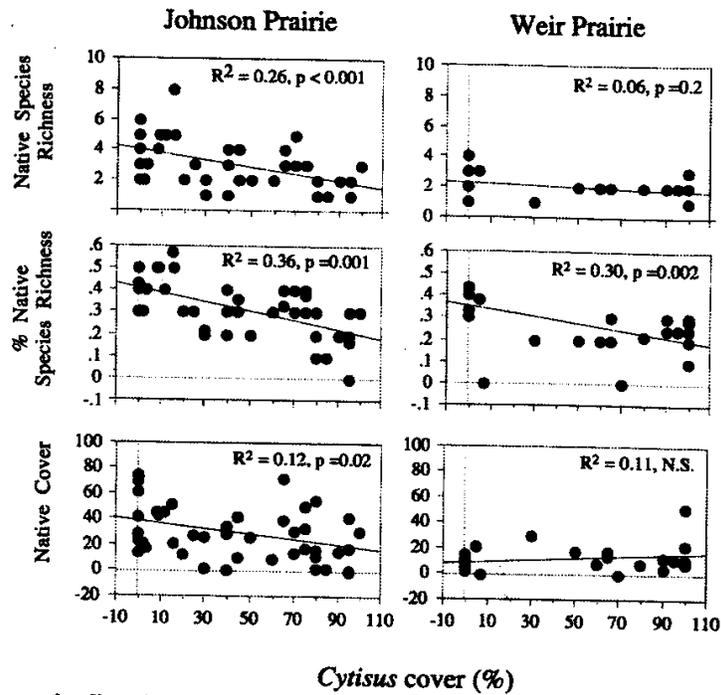


Figure 3. Native species diversity as a function of the cover of *Cytisus scoparius* in two prairie sites. Three diversity measures are shown: native species richness per quadrat, proportion of species that are native per quadrat, and total cover of native species. Johnson Prairie, N = 45; Weir Prairie, N = 30

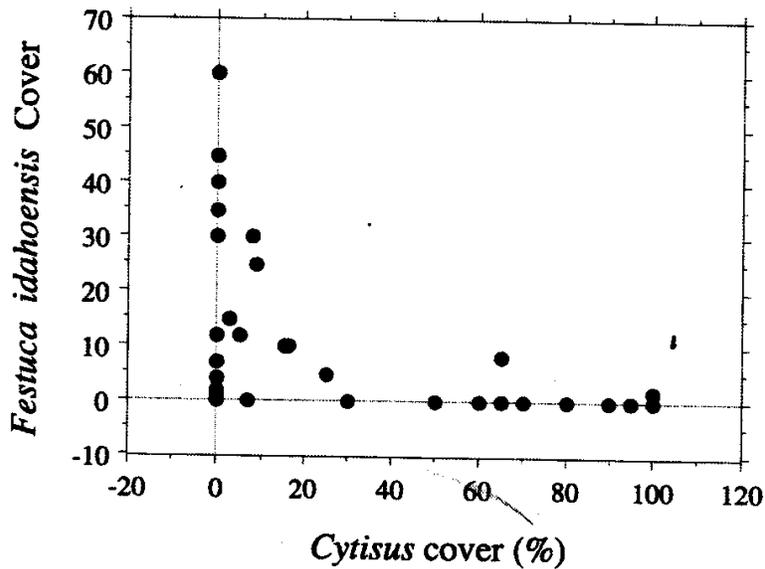


Figure 4. Estimated cover of *Festuca idahoensis* (Idaho fescue), an important prairie indicator species, as a function of the cover of *Cytisus scoparius*. Only plots that contained some individuals of both species are included in the analysis.

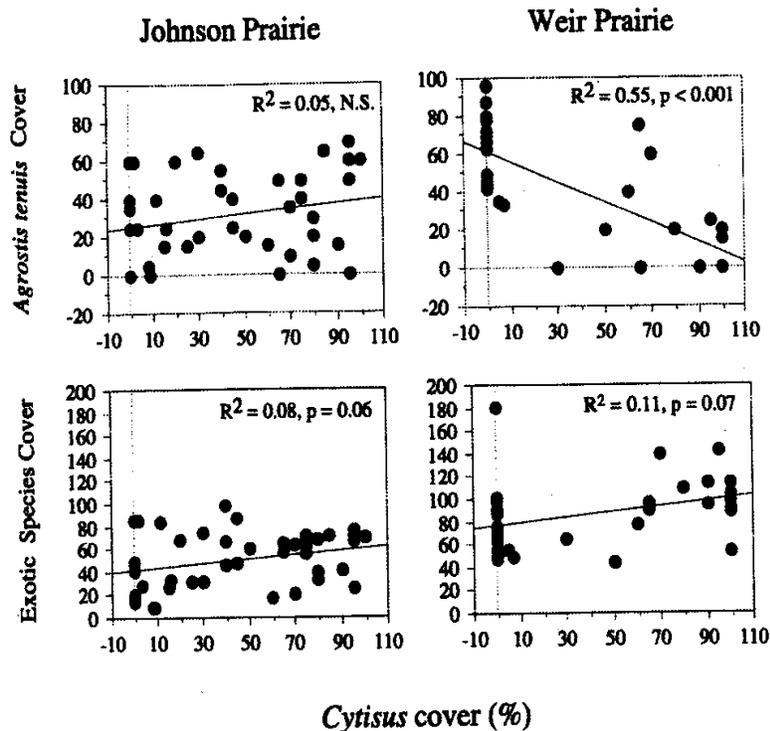


Figure 5. Cover of A) the exotic grass *Agrostis tenuis* and B) all exotic species combined, as a function of the cover of *Cytisus scoparius*. Johnson Prairie, N = 45; Weir Prairie, N = 30.

Cover of all native species combined also decreased significantly with increasing *Cytisus* cover in Johnson Prairie (Fig. 3, $r^2 = 0.12$, $P = 0.02$) but not in Weir Prairie (Fig. 3). Cover of the indicator species *Festuca idahoensis* declined dramatically as *Cytisus* cover increased (Fig. 4, $r^2 = 0.13$, $P = 0.01$).

The exotic turf-forming grass, *Agrostis tenuis*, was common in many of the plots at both Johnson Prairie and Weir Prairie (Fig. 5). There was no discernible positive relationship between *Cytisus* invasion and cover of *Agrostis*; in fact, in Weir Prairie *Agrostis* cover declined significantly with increasing *Cytisus* cover ($r^2 = 0.55$, $P < 0.001$). Total cover

of exotic species, however, did increase in both Johnson Prairie and Weir Prairie (Fig. 5), although this increase was only marginally significant in both sites (Johnson Prairie $r^2 = 0.08$, $P = 0.06$; Weir Prairie $r^2 = 0.11$, $P = 0.07$).

Discussion

Invasibility: What are the Effects of Community Characteristics on *Cytisus* Invasion?

We found little support for the biotic resistance hypothesis. That is, rates of population growth were not negatively correlated with species richness, either on a whole-plot level or as mean

richness per quadrat. If anything, then number of resident species was *positively* associated with invasiveness. Most investigations corroborating the importance of biotic resistance have been analytical or statistical models (e.g. Drake, 1983, 1988; Post and Pimm, 1983; Drake, 1988; Case, 1990; Moulton and Pimm, 1983, 1986). Only recently have field studies been done specifically to address biotic resistance, and these have not provided support for the idea. Plant-Tabacchi et al. (1996) found that riparian zones in France and the Pacific Northwest of the U.W. showed a positive relationship between plant species richness and the percentage of exotic species. In an experimental test using the native herb *Eschscholzia californica* (California poppy) as an “invader”, Robinson, Quinn and Stanton (1995) introduced individuals into plots of California grassland and obtained higher establishment rates in the plots with greatest species richness. In these cases, as with our study, invasion occurred more easily in more diverse communities.

However, *Cytisus* does seem to invade more slowly in plots with higher total plant cover, suggesting that competition from resident species may impact the dynamics of the spreading populations. The slowest-growing populations also have the highest proportion of total cover in exotic species, lending support to the idea that previous invaders are likely to be strong competitors and have preempted the available resource space (Simberloff and Boecklen 1991). Consistent with this interpretation is the observation that resource managers at Discovery Park, Seattle, have found intense fertilization with dense seeding of exotic grasses to be an effective way

to slow *Cytisus* invasion (D. Vorecamp, pers comm.).

Underlying the observed relationships between invasion rate and community characteristics is the fact that population growth is significantly faster in glacial outwash prairies than in urban fields. The prairies are very hospitable places for *Cytisus* germination and growth (Parker 1996), a result that contradicts the way we usually think about the natural history of successful invasive species.

Impact: What are the Effects of *Cytisus* Invasion on Community Characteristics?

It does not appear that nitrogen fixation by *Cytisus* results in a pattern of decline in total species number or of increase in total plant cover in either urban or prairie sites. This contradicts our expectations based on the nitrogen enhancement experiments performed in other grasslands (Inouye and Tilman 1995, Gurevitch and Unnasch 1989). Each site showed a different pattern, suggesting that patterns of response are variable and complex, and may reflect a balance between the influences of nitrogen addition and competition for other factors. Some species appear to drop out but are replaced by other species, as will be discussed below.

Several lines of evidence point to a negative relationship between *Cytisus* invasion and native species diversity, however. We found a nearly exclusive relationship between *Cytisus* and the important prairie indicator species, *Festuca idahoensis*. In Johnson Prairie, which is by far the most diverse site for native plants and the only prairie site

with a comparison plot in the center of a dense *Cytisus* infestation, increasing cover of the invader was associated with significant declines in native species, richness, percent of native richness, and native species cover. Weir Prairie showed a significant decline for percent native richness. An important characteristic of Weir Prairie is a high mean cover of cryptogams (74%, compared to 57% for Johnson Prairie). An analysis of species composition within this guild might reveal interactions between diversity and *Cytisus* invasion as well.

As it had been suggested that *Cytisus* might promote the invasion of nitrogen-loving exotic grasses, we looked for evidence of this sort of facilitation. We focused on *Agrostis tenuis* as a common invader in many habitats of western Washington, including both Johnson and Weir Prairies. We found no significant positive relationship between cover of *Agrostis* and *Cytisus*, and in fact at Weir Prairie the relationship was significantly negative. Cover of all exotic grasses combined shows the same relationship as *Agrostis* alone (unpublished data). However, the increase of total cover of other exotic species with *Cytisus* cover (though only marginally significant) does imply that a facilitation effect may be occurring. Maron and Connors (1996) recently showed that patches of dead *Lupinus arboreus* act as sites for colonization of exotic species in a coastal grassland system mediated by local high pulses of nitrogen. Such an effect has not been shown for *Cytisus scoparius*, but could be possible. A detailed experimental study is needed to confirm the pattern we observed and ascertain the mechanism for facilitation.

Caveats

Several weaknesses of this study, to which we have already alluded, cause us to present these results with some qualifications. Like most currently published studies of the negative impacts of invasive species (see Parker and Reichard 1997 for a review), this research is correlational in nature. Although the sub-sampled plots were in close proximity and formed parts of the same expanding population in each site, they were likely to vary somewhat in microclimatic or compositional characteristics unrelated to *Cytisus* invasion. Differences between Johnson Prairie and Weir Prairie are difficult to interpret for several reasons. The discrepancy in detecting of a negative relationship between *Cytisus* cover and native diversity measures in the two prairie sites may be caused by the lack of a late invasion-stage plot at Weir Prairie (where impacts of *Cytisus* invasion would be most extreme), or could simply reflect the consequently smaller sample size of quadrats from that site. Weir Prairie also began with fewer native vascular plants suggesting that the sites may differ in other ways, such as fire or past invasion history. In addition, the use of percent cover as a metric for the influence of *Cytisus* in a quadrat may not have been as informative as alternatives such as the number and diameter of stems within a local neighborhood. A better measure would accurately reflect even the past history of *Cytisus* influence, such as how long *Cytisus* had inhabited the plot. We believe there is a great need for experimental work in these systems, and detailed long-term, mechanistic studies of the impact of *Cytisus* on soil nutrient characteristics and on plant community composition.

Implications For Management

Cytisus invasion does not diminish in habitats with high species richness or relatively high biotic “integrity” –i.e. those containing few exotic species. The management implication of this result is that we can not rely on the inherent high biodiversity of undisturbed western Washington prairies to act as a barrier to invasion by *Cytisus*.

The undisturbed prairie itself is not resistant to invasion either by virtue of filling all “available niches” or by virtue of its intact cryptogamic layer (Parker, in preparation). Therefore, restoration efforts will need to continue taking a direct, population-level approach to controlling *Cytisus*; indirect methods of bolstering ecosystem “health” (such as reducing disturbance levels) are not likely to slow the spread of this species. An exception to this rule is the re-establishment of regular fires as a technique for returning the prairies to a more natural state. However, even in this case, fire is an effective control measure for *Cytisus* because it kills *Cytisus* individuals, not because it makes the prairie more resistant to invasion *per se*. Despite our caveats, we feel there is good evidence that *Cytisus* invasion results in a decline in native species diversity. Whether this decline is an effect of competition for light, water, or nutrients, or results primarily from the facilitation of other aggressive species via nitrogen dynamics (or other factors) is unclear. A particularly distinctive pattern was obtained when analyzing the cover of *Festuca idahoensis*. This dominant prairie grass is often used as an indicator species for healthy prairie, and illustrates the point that common species may be more useful than rare species for quantifying environmental

degradation. Rare species will by definition be found only occasionally by a sampling regime, and therefore it is difficult to observe and demonstrate changes in abundance for these species. In contrast, a dominant species will produce a strong “signal” for evaluating changing conditions.

Prairie land managers will probably not be surprised by the finding that high *Cytisus* abundance is associated with a paucity of native species. Given the level of resources spent on exotic species control and eradication, what is more surprising is the current lack of published data demonstrating what we suspect to be the case; that aggressive invaders like *Cytisus scoparius* do have important negative effects on native biodiversity.

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Literature Cited

Carpenter, S.R. and J.F. Kitchell. 1993. The Trophic Cascade in Lakes. Cambridge University Press, Cambridge.

- Case, T. J. 1991. Invasion Resistance, Species Build-up and Community Collapse in Metapopulation Models with Interspecies Competition. *Biological Journal of Linnean Society* 42:239-266.
- Cowrie, I.D. and P.A. Werner. 1993. Alien Plant Species Invasive in Kakadu National Park, Tropical Northern Australia. *Biological Conservation* 63:127-135.
- Crawley, M.J. 1987. What Makes a Community Invasible? Pp. 429-453 in A.J. Gray, M.J. Crawley and P.J. Edwards eds. *Colonization, Succession, and Stability*. Blackwell Scientific, Oxford.
- D'Antonio, C., T. Dudley and M. Mack. 1997. Biological Invasions and Disturbance: Correlations, Mechanisms, and Feedbacks. In press in L. Walker ed. *Ecosystems of Disturbed Ground*. Elsevier, Amsterdam.
- Drake, J.A., H.A. Mooney, F.D. Castri, R.H. Groves, F. J. Kruger, M. Rejmanek and M. Williamson. 1989. *Biological Invasions: A Global Perspective*. Wiley & Sons, New York.
- Elton, C.S. 1958. *The Ecology of Invasions by Animals and Plants*. Methuen, London.
- Fox, M.D. and B.J. Fox. 1986. The Susceptibility of Natural Communities to Invasion. Pp. 57-66 in R.H. Groves and J.J. Burdon eds. *Ecology of Biological Invasions: An Australian Perspective*. Australian Academy of Sciences, Canberra.
- Franklin, J.F. and C.T. Dyrness. 1988. *Natural Vegetation of Oregon and Washington*. Oregon State University Press, Corvallis.
- Gurevitch, J. and R.S. Unnasch. 1989. Experimental Removal of a Dominant Species at Two Levels of Soil Fertility. *Canadian Journal of Botany* 67:3470-3477.
- Hobbs, R. J. 1989. The Nature and Effects of Disturbance Relative to Invasions. Pp. 389-405 in J. A. Drake, H.A. Mooney, F. d. Castri, R. H. Groves, F. J. Kruger, M. Rejmanek and M. Williamson eds. *Biological Invasions: A Global Perspective*. Wiley & Sons, New York.
- Hobbs, R.J. and L.F. Huenneke. 1992. Disturbance, Diversity, and Invasion: Implications for Conservation. *Conservation Biology* 6:324-337.
- Inouye, R.S. and D. Tilman. 1995. Convergence and Divergence of Old-Field Vegetation after 11 Years of Nitrogen Addition. *Ecology* 76:1872-1887.
- Kareiva, P., M. J. Groom, I. M. Parker and J. Ruesink. 1991. Risk Analysis as a Tool for Making Decisions about the Introduction of Non-indigenous Species into the United States. United States Office of Technology Assessment Report.

- Knops, J.M.H., J.R. Griffin and A.C. Royalty. 1995. Introduced and Native Plants of the Hasting Reservation, Central Coastal California: A Comparison. *Biological Conservation* 71:115-123.
- Kruckeberg, A. R. 1991. *The natural History of Puget Sound Country*. University of Washington Press, Seattle.
- Kruger, F.J. , D. M. Richardson and B. W. van Wilgen. 1986. Processes of Invasion by Alien Plants. In I.A. W. MacDonald, F.J. Kruger and A. A. Ferrar eds. *The Ecology and Management of Biological Invasions in Southern Africa*. Oxford University Press, New York.
- MacDonald, I.A. W., F. J. Kruger and A.A. Ferrar. 1986. *The Ecology and Management of Biological Invasions in Southern Africa*. Oxford University Press, New York.
- Maron, J.L., and P.G. Connors. 1996. A Native Nitrogen-Fixing Shrub Facilitates Weed Invasion. *Oecologia* 105:302-312.
- Mooney, H.A. and J.A. Drake. 1986. *Ecology of Biological Invasions of North America and Hawaii*. Springer-Verlag, New York.
- Office of Technology Assessment. *Harmful Non-Indigenous Species in the United States*. U.S. Congress, 1993. OTA-F-565.
- Orians, G.H. 1986. Site Characteristics Favoring Invasions. Pp. 133-148 in H.A. Mooney and J.A. Drake eds. *Ecology of Biological Invasions of North America and Hawaii*. Springer-Verlag. New York.
- Parker, I.M. 1996. *Ecological Factors Affecting Rates of Population Growth and Spread in *Cytisus scoparius*, an Invasive Exotic Shrub*. Ph.D. Dissertation, University of Washington.
- Parker, I.M., S.K. Mertens and D.W. Schemske. 1993. Distribution of Seven Native and Two Exotic Plants in a Tallgrass Prairie in Southwestern Wisconsin: The Importance of Human Disturbance. *The American Midland Naturalist* 130:43-55.
- Parker, I.M. and S.H. Reichard. 1997. *Critical Issues in Invasion Biology for Conservation Science*. In press, in P. Fiedler and P. Kareiva, eds. *Conservation Biology for the Coming Decade*. Chapman Hall, New York.
- Pysek. P., K. Prach, M. Rejmanek and M. Wade. 1995. *Plant Invasions: General Aspects and Special Problems*. SPB Academic, Amsterdam.
- Simberloff, D. and W. Boecklen. 1991. Patterns of Extinction in the Introduced Hawaiian Avifauna: A Re-examination of the Role of Competition. *The American Naturalist* 138:300-327.

- Thompson, J.D. 1991. The Biology of An Invasive Plant: What Makes *Spartina anglica* so Successful? *Bioscience* 41:393-401.
- Vitousek, P.M. , L.R. Walker, L.D. Whiteaker, D. Mueller-Dombois and P. Matson. 1987. Biological Invasion by *Myrica faya* Alters Ecosystem Development in Hawaii. *Science* 238:802-804.
- Wheeler, C.T., D.A. Perry, O. Helgerson and J. C. Gordon. 1979. Winter Fixation of Nitrogen in Scotch Broom (*Cytisus scoparius*). *New Phytologist* 82:697-701.