

# Context-dependent pattern and process: the distribution and competitive dynamics of an invasive grass, *Brachypodium sylvaticum*

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**Abstract** *Brachypodium sylvaticum*, or false brome, a recent invader of North America, has spread rapidly following establishment in Oregon in 1939 and is now colonizing at least five US states. To understand how ecological processes and environmental context interact to facilitate invasion, we combined a GIS analysis of spatial patterns of invasion with a greenhouse competition experiment under two light and two nutrient levels, and a field competition-removal experiment. *Brachypodium sylvaticum* was concentrated along human-use corridors and in forests, where our experiments indicate it is a better competitor than co-occurring grasses. Forested areas near trails require

the greatest focus for detection and control because the species' dual propensities to establish and thrive in these locations may make them key source areas for further invasion. Our methodology demonstrates how understanding both the patterns and processes of invasion enables the prescription of context-specific remedial actions.

**Keywords** Competition · Exotic species · False brome · GIS · Invasion · Shade tolerance

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## Introduction

The degradation caused to native ecosystems by exotic plant invasions is well known (Vitousek et al. 1996; Pimental et al. 2005). Not all landscapes, however, are equally invaded. Whether a particular exotic plant species will be able to invade a specific site depends not only on the plant's life history characteristics, including dispersal ability (Wetzel and van der Valk 1998; Fréville and Silvertown 2005; DiVittorio et al. 2007), but also on qualities of the landscape, including the physical environment (Thomsen and D'Antonio 2007), existing plant communities (Hager 2004; Thomsen et al. 2006a), and the site's disturbance history (Hobbs and Huenneke 1992). Thus, the factors that are most important in a successful invasion can be highly context-specific (Higgins and Richardson 1998;

Jules et al. 2002; Lambrinos 2006; Thomsen et al. 2006b; Vila et al. 2006). Here we examine how a combination of environmental influences, landscape management, and plant competitive abilities may have fostered colonization by a recently arrived invasive grass species, *Brachypodium sylvaticum* (Huds.) Beauv.

*Brachypodium sylvaticum* is a perennial bunch grass native to Eurasia and North Africa that was first found in North America near Eugene, Oregon in 1939 (Chambers 1966), and was thoroughly naturalized in Oregon's Willamette Valley by 1966 (Chambers 1966; Kaye and Blakeley-Smith 2006). Unlike the native grasses of the Willamette Valley, this species is capable of forming a dense monoculture under a forest canopy, leading to concerns that it may decrease herbaceous diversity and tree seedling germination and alter forest fire dynamics (Roy *in press*). The grass establishes rapidly and readily from seeds, and plants begin to flower 1–2 years after germination (Roy et al. *in review*). Adult plants expand in size by increasing the number of tillers present each year but do not have rhizomatous growth (Hitchcock et al. 1969).

In its native range, *B. sylvaticum* occurs in habitats ranging from shaded forest understory to sunny open meadows (Holten 1980; Aarrestad 2000; Kirby and Thomas 2000). Landolt (1977) indicates that it is widely distributed in Europe, but that it avoids extremely continental climates and dry soils. It occurs across a wide elevation gradient, ranging from sea level up to 1,600 m in Europe (Long 1989) and up to nearly 4,000 m in the Himalaya (Roder et al. 2007). Similar to its distribution in Eurasia, *B. sylvaticum* occupies a diversity of habitats in Oregon, from full sun to full shade but most often in the shade, and across varying aspects and elevations, from sea-level to about 1,200 m (Rosenthal et al. 2008). *Brachypodium sylvaticum* appears to have first been reported as invasive in Oregon, but it is now known from four other states (Washington, California, Virginia and Missouri) (Roy *in press*). Based on its ability to live in diverse habitats and environmental conditions in the native range, *B. sylvaticum* appears likely to be able to spread throughout western Washington, Oregon and California, as well as along streams and in wet areas in the Intermountain West, and in deciduous woodlands in the rest of the country. Not surprisingly, this grass has been listed by WA,

CA and OR as a quarantined invasive species (CDFA 2009; NWCB 2009; ODA 2009).

#### *Brachypodium sylvaticum* at the Howard Buford Recreation Area

Parks and reserves are particularly important for plant invasions due to a combination of land management practices and high human use (Vitousek et al. 1996). Seeds and propagules can transfer across park boundaries along trails (human and wildlife), rivers, utility corridors and roads. Recreational use by hikers, bicyclists, equestrians and off-road vehicle users can create a high probability for propagules to enter the park and be distributed into even remote areas. Multi-use parks, such as city, county and state facilities often receive minimal management of natural vegetation due to large areas, low budgets, and a perception that “natural” areas should be unmanaged. In addition, there is a high likelihood of parks becoming sources of dispersal for invasive species when visitors leave and accidentally carry seeds with them. For these reasons, landscape designers, planners and managers who work with parks must increasingly pay attention to the issues of invasive exotic species.

We chose to analyze *B. sylvaticum* populations at the Howard Buford Recreation Area (HBRA, also known as Mt. Pisgah), a 956-hectare county park at the southern end of the Willamette Valley. The park supports regionally important native plant and wildlife habitat, and also serves as a public recreation destination and utility corridor access. The park also possesses a rapidly expanding population of *B. sylvaticum* that was first detected 15 years ago. Our hypothesis was that *B. sylvaticum* is dispersed along trails, roadsides, and other access corridors. It then establishes along the disturbed margins, and spreads into adjacent habitats, invading most successfully under the environmental conditions of shade and high nutrients. To test this hypothesis, we used a Geographic Information System (GIS) to analyze the plant's distribution in relation to plant communities and to trails or other potential dispersal routes. We also designed a paired set of field and greenhouse experiments to test *B. sylvaticum*'s competitive abilities under different environmental conditions. Our ultimate goal was to gain sufficient understanding of

the grass and how it invades to make recommendations for its control.

## Materials and methods

Howard Buford Recreation Area (lat. 44° 00' N, long. 122° 57' W) is located 7.5 km southeast of Eugene, Oregon. The park currently supports both pedestrian and equestrian recreation along an extensive trail system and has access roads for maintenance. For example, Bonneville Power Administration power line corridors transect the park along with associated vehicle right-of-ways. A survey of 10 people with extensive knowledge of the park and who were likely to be able to identify the species revealed that *B. sylvaticum* has been at the park since at least 1994 (Ed Alverson, TNC & Bruce Newhouse, Salix & Assoc., Eugene, OR, personnel communication). Respondents reported that it has expanded rapidly since it was first detected at HBRA.

### GIS mapping analysis

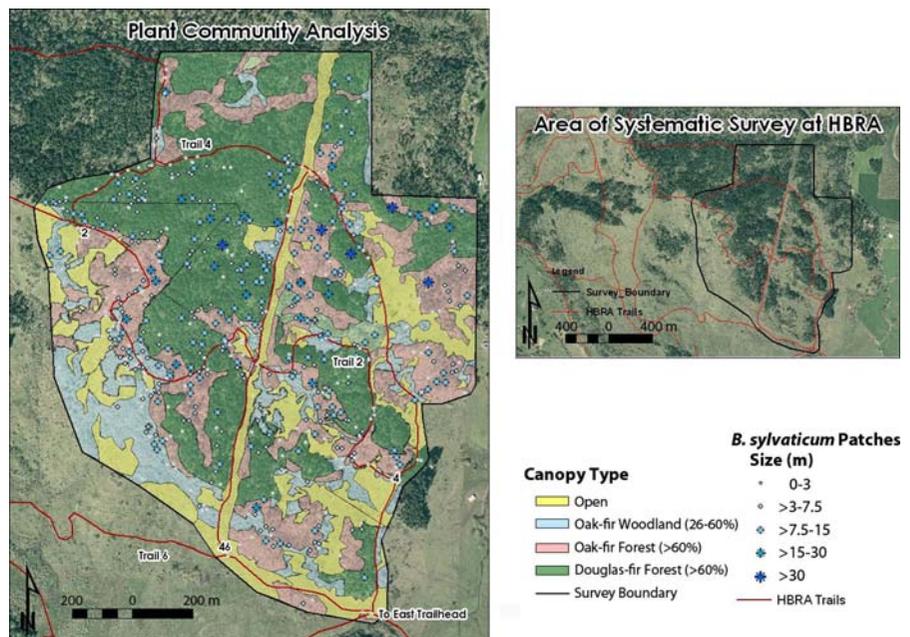
To examine the spatial dimensions and environmental context of *Brachypodium sylvaticum* invasion at HBRA, all *B. sylvaticum* patches were mapped in a 190-hectare study area. Locations were recorded with

handheld GPS units from 2005–2008 using a systematic search pattern. Data recorders were able to view their GPS tracks during the survey to ensure adequate coverage. Patch diameters were estimated in classes of 0–3 m, >3–7.5, >7.5–15, >15–30, and >30 m (Fig. 1). We then analyzed the distribution of *B. sylvaticum* using GIS to test the hypothesis that patch distribution and patch size were associated with plant community type and proximity to human-use corridors, as described below. All spatial data were derived using spatial analyst buffer and proximity tools in ArcMap 9.2 (ESRI 2006).

### Plant community analysis

Four community types were delineated and classified from aerial photos using ocular estimates of tree canopy cover (Fig. 1): open (0–25% canopy cover), mixed oak-fir woodland (>25–60% canopy cover), mixed oak-fir forest (>60% canopy cover, predominantly oak) and coniferous forest (>60% canopy cover); in all cases the principal conifer was Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and the oak was *Quercus garryana* Dougl. ex Hook. Categories were ground-truthed by a site visit to verify map-based estimates. The observed frequency of *B. sylvaticum* patches within the four plant community types was tested for significance using a *G*-test (Sokal and Rohlf

**Fig. 1** Map of GIS study field site and distribution of *Brachypodium sylvaticum* showing corridors (roads, trails and utility corridors) and patches by community type



1981) against the null hypothesis that they would be distributed proportionally to the total area occupied by each community type.

### Corridor proximity analysis

Trails, roads, and power line corridors were mapped and categorized as “corridors” in the GIS data layer because they potentially represent similarly functioning routes for seed dispersal. To investigate the possible role of these features in facilitating *B. sylvaticum* invasion, we used a *G*-test to examine the spatial distribution of *B. sylvaticum* in relation to corridors. We first established four corridor buffer zones in GIS. Buffer widths were based on anecdotal data on rates of spread (30 m in 5 years) taken from the False Brome Working Group ([www.appliedeco.org/invasive-species-resources/FBWG](http://www.appliedeco.org/invasive-species-resources/FBWG)). A buffer width of 0–30 m on each side of a corridor was used to determine whether there was a significantly higher concentration of *B. sylvaticum* patches in proximity to corridors or outside this buffer zone. As with community type, the observed frequency of *B. sylvaticum* patches was tested against the expected

frequency of occurrence in each respective buffer area. A further analysis of buffer bands at 30–60, 60–90, and 90–120 m was performed to examine a distance-from-corridor effect. Buffers beyond 120 m were not included because they comprised only 4% of the study area.

### Field experiment

Four field sites were selected within 80 km of each other in the Willamette Valley. Two sites were located outside Eugene, OR in Lane County approximately 16 km apart: Howard Buford Recreation Area, managed by Lane County Parks (E Aspect, 28% Slope, 213 m) and a private overgrown conifer tree farm outside Jasper, OR (WNW Aspect, 26% Slope, 335 m). Two sites were located outside Corvallis, OR in Benton County approximately 5 km apart: Philomath Prairie, managed by The Nature Conservancy (SW Aspect, 28% Slope, 122 m) and Bald Hill Park, managed by City of Corvallis Parks and Recreation (ENE Aspect, 14% Slope, 122 m). All sites consisted of mixed oak-Douglas-fir forest, with similar vegetation, soils, canopy cover and precipitation (Table 1).

**Table 1** Vegetation and environmental characteristics of the four field sites: Howard Buford Recreation Area (HBRA), Jasper, Philomath Prairie, and Bald Hill Park

Site	Clipped% grasses	Clipped% woody	Clipped% forbs	Rel. cover % <i>B. sylvaticum</i>	Rel. cover % other grasses	Rel. cover % poison oak	Soil series	Canopy cover %	Precipitation (cm)
HBRA	79 ± 6	8 ± 4	13 ± 5	85 ± 6.0	3 ± 2.9	4 ± 1.4	Witzel very cobble loam <sup>a</sup>	66.4 ± 2.6	114.9 <sup>c</sup>
Jasper	92 ± 6	0.2 ± 0.2	8 ± 6	67 ± 4.8	10 ± 8.5	10 ± 7.6	Philomath cobble silty clay <sup>a</sup>	70.1 ± 2.8	114.9 <sup>c</sup>
Philomath	77 ± 7	8 ± 4	16 ± 4	64 ± 0.2	1 ± 1.2	16 ± 4.4	Witham silty clay loam <sup>b</sup>	75.2 ± 3.6	104 <sup>d</sup>
Bald hill	65 ± 11	22 ± 10	13 ± 3	51 ± 2.7	7 ± 1.7	37 ± 3.4	Philomath silty clay <sup>b</sup>	66.6 ± 1.5	104 <sup>d</sup>

Clipped% (mean ± 1 s.e.) indicates the fraction of total biomass that were grasses, woody or forbs removed from the eight clipped plots/site during first clipping treatment. Relative cover data (mean ± 1 s.e., adjusted to 100% total cover) were taken from two 1 m<sup>2</sup> plots randomly placed within 15 m of the competition plots at each site in 2005 using point intercept methods. Poison oak (*Toxicodendron diversilobum*) was the dominant shrub. Percent canopy cover (mean ± 1 s.e.) was measured with a spherical densiometer

<sup>a</sup> USDA Soil Conservation Service with USDI Bureau of Land Management, Oregon Agricultural Experiment Station, and Lane County (1981) Soil Survey of Lane County Area, Oregon

<sup>b</sup> USDA Soil Conservation Service with Oregon Agricultural Experiment Station (1975) Soil Survey of Benton County Area, Oregon

<sup>c</sup> Precipitation data from [www.wrcc.dri.edu](http://www.wrcc.dri.edu), long-term average at the Eugene airport, 12/1/1939 to 12/31/2008

<sup>d</sup> Precipitation data from [www.wrcc.dri.edu](http://www.wrcc.dri.edu), long-term average at the Oregon State University, 1/1/1890 to 12/31/2008

Similar to the experiments in Pfeifer-Meister et al. (2008), competition treatments were set up by removing adjacent vegetation by a specific level (0, 50, and 100%, see Fig. 4a) around a target *B. sylvaticum* plant inside 23-cm diameter plots. We made the assumption that conditions aboveground would affect those belowground. Each treatment was replicated four times at each of the four sites, for a total of 48 plots. At each site, similar amounts of graminoids, forbs and woody plants were removed from the plots, the large majority of which were graminoids (Table 1). Although clipped graminoids were not identified to species prior to drying, they were primarily *B. sylvaticum* as supported by cover measurements nearby (Table 1). The sites were visited every two weeks to re-clip the treated areas to control competition. At the beginning and end of the experiment (early April and early July, respectively) we estimated the height of each target plant by measuring the longest leaf, and plant width by measuring basal diameter. At the end of the experiment we counted the number of spikelets (grass flowers) per target plant to estimate fitness. It was possible to use spikelets as a fitness measure because demographic work at the same sites showed that abortion rates were almost zero and seed germination rates were near 100% (Halbritter 2009).

Because one of the main effects of the competition treatment was a change in plant morphology, we analyzed how competition affected the height: diameter ratio of the plants as well as the number of spikelets using ANCOVA (Analysis of Covariance). We used initial diameter as a covariate in all analyses because initial diameter, a plant size measurement, varied significantly within and among the sites. The statistical model included treatment as a fixed effect, site as a random effect, and the interaction of site by treatment. Both initial diameter and number of spikelets were square-root transformed to normalize the residuals (Zar 1996). All analyses were performed in the program JMP (SAS 2003).

### Greenhouse experiment

To determine whether the competitive ability of *B. sylvaticum* was context-specific, we performed a greenhouse experiment in which competition was fully crossed with light (sun and shade) and nutrients (low and high). *Brachypodium sylvaticum* was tested against

itself in monocultures and in mixtures with the three other perennial grasses that co-occur with it in the Willamette Valley: exotic *Schedonorus arundinaceus* (Schreb.) Dumort, native *Festuca roemerii* (Pavlick) E.B. Alexeev, and native *Elymus glaucus* Buckley.

All three species are perennial, caespitose, non-rhizomatous bunchgrasses. *Schedonorus arundinaceus* (= *Festuca arundinacea*), or tall red fescue, is a tussock-forming European perennial common in fields, meadows, roadsides, and other disturbed areas (Gibson and Newman 2001). It is abundant at low to mid elevations across much of North America (Hitchcock et al. 1969; Pojar and MacKinnon 1994) and is widely used for pastures and forage. This grass occurred with *B. sylvaticum* in the sunnier areas of three of the four sites used in the competition experiment. *Festuca roemerii* (synonym = *Festuca idahoensis* spp. *roemerii*), or Roemer's fescue, is a native species found principally in upland prairies west of Cascade Range of Oregon and Washington (Wilson 1996). It is thought to have been common in historic Pacific Northwest prairie ecosystems (Ewing 2002; Jones et al. 2008). *Festuca roemerii* was present only at one of the sites, HBRA, and was the only grass we used in the competition experiment that was not found in close proximity to *B. sylvaticum* at the field sites. *Elymus glaucus*, or blue wildrye, is a native species common in dry to moist prairies, open woodlands and gaps in forests. It usually forms tall, small-diameter clumps. This species co-occurred with *B. sylvaticum* at all four of our field sites.

To determine the response of *B. sylvaticum* to competition, we tested it in pots with the three other species, forming all pair-wise combinations. Because we were interested in the role of the environment (light and nutrients) as well as competition, we used a single density in pots to make the experiment tractable. In each pot there were four plants, two individuals of *B. sylvaticum* plus two individuals of one of the other species to form interspecific treatments, and four individuals of *B. sylvaticum* to form the intraspecific treatment. In the field, the grasses grow in conditions ranging from full sun to dense shade (66–75% canopy cover, see Table 1) and likely under a range of nutrient conditions. We thus fully crossed the competition treatment with a light treatment (shade cloth that reduced ambient by 70% to emulate the field conditions vs. ambient) and a nutrient treatment (high and low). The high-nutrient treatment was a recommended

application of a nitrogen, phosphorus and potassium fertilizer, Down To Earth (DTE) 5-5-5 All Purpose Blend. The low-nutrient treatment was a 10% dilution of the high nutrient treatment. Every combination of species, competition, light, and nutrients was replicated five times. Pots were randomly placed into sun and shade treatments, and replicates were manually randomized in the greenhouse twice during the experiment to minimize micro-environmental effects of placement in the greenhouse (Potvin et al. 1990).

We used wild-collected seeds from the HBRA study site (see field experiment), stored at 4°C until use. Competition hierarchies may be set up very early if different species germinate at different times (Stanton et al. 2000). Since we performed this experiment in a greenhouse (12 h days, max 27°C, min 4°C) and did not know in advance whether there were differences in the field among species' germination times, we controlled germination so that all plants started at the same time. Seeds were germinated in Petri dishes using 1,000 mg/l gibberellic acid (Stanton et al. 2000). All seedlings were transplanted on the same day into 17.5 cm pots containing sand. We used sand to make the differences in nutrient inputs large, and so that we could separate the roots later. Seedlings were placed 5 cm away from each other in a square formation in the center of the pot and kept moist until established (at least 2.5-cm tall). After establishment, the pots were watered as needed to maintain constant soil moisture. Plants in the sun required more frequent watering than those in the shade. Nutrient treatments (100 ml) were applied every two weeks post-establishment. Plants were harvested at 125 days when they began to become root bound. Roots of individual plants were gently teased apart from the sand substrate in water baths. Each plant was separated into above-ground and belowground biomass, placed into drying ovens at 60°C for 48 h, and weighed.

A full factorial ANOVA was performed to test the effects of light, nutrients, and competition on the total biomass and root:shoot ratios of *B. sylvaticum*. We used a priori planned contrasts (*B. sylvaticum* vs. *E. glaucus*, *S. arundinaceus*, and *F. roemeri*) to determine whether *B. sylvaticum* in competition with itself had more or less biomass than when in competition with the three other species. The dependent variables were transformed as needed to conform to the assumptions of ANOVA. All ANOVAs were performed in the program JMP (SAS 2003).

We also estimated the relative yield per plant (RYP) for *B. sylvaticum* in response to each of the other species for each treatment. Relative yield per plant is an integrative measure of interspecific versus intraspecific competition and is calculated by:

$$\text{RYP}_{ij} = Y_{ij}/Y_i$$

where  $Y_{ij}$  is the mean of *B. sylvaticum* grown with another species and  $Y_i$  is the mean biomass of *B. sylvaticum* in monoculture for that treatment (Harper 1977; Wetzel and van der Valk 1998; Pfeifer-Meister et al. 2008). In this analysis, a value of one is always obtained for the monoculture. To determine whether growth in the mixtures within each treatment was significantly different from one, we used one-sample *t* tests (Pfeifer-Meister et al. 2008).

## Results

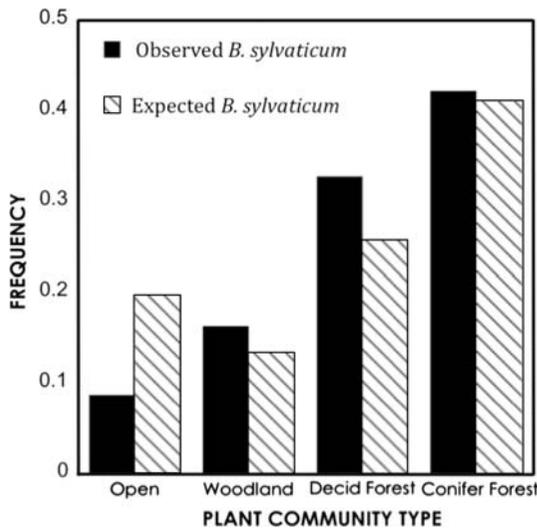
### GIS mapping analysis

#### *Plant community analysis*

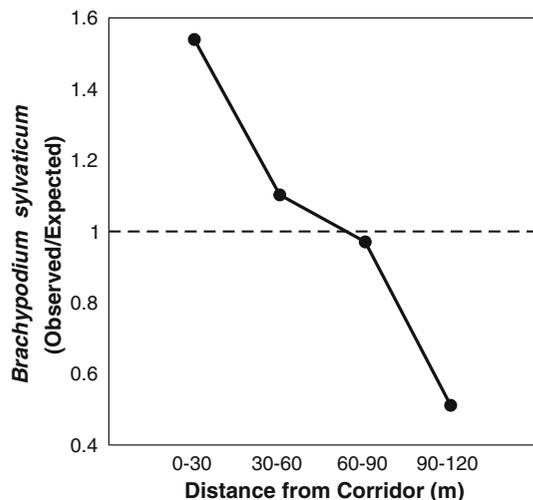
*Brachypodium sylvaticum* was significantly under-represented in open areas compared to more shaded community types ( $G_3 = 55.17$ ,  $P < 0.001$ ). Twenty percent of the area mapped was open habitat, yet only 9% of patches were found there (Fig. 2). In contrast, oak-fir forest showed the highest degree of *B. sylvaticum* patch over representation, with 33% of the patches located in 26% of the study area (Fig. 2). Not only were there more patches in the forested communities, the patches were also larger ( $G_6 = 52.14$ ,  $P < 0.001$ ). Patch size distribution shifted from smaller patches to larger patches as a function of canopy cover class (open < woodland < forest) and there was no difference between mixed-oak/fir and Douglas-fir forests.

#### *Corridor proximity analysis*

*Brachypodium sylvaticum* patches were concentrated within 30 m from corridors ( $G_3 = 41.22$ ,  $P < 0.001$ ). In addition, when we examined the proportional representation of patches for each successive 30-m buffer band from a route, *B. sylvaticum* patch density declined rapidly with distance (Fig. 3).



**Fig. 2** Observed versus expected frequencies of *Brachypodium sylvaticum* by community types. Expected frequency was based on the frequency of each community type



**Fig. 3** Proportional representation of *Brachypodium sylvaticum* in buffer bands for trails/routes. Frequency equals proportional area of each community type

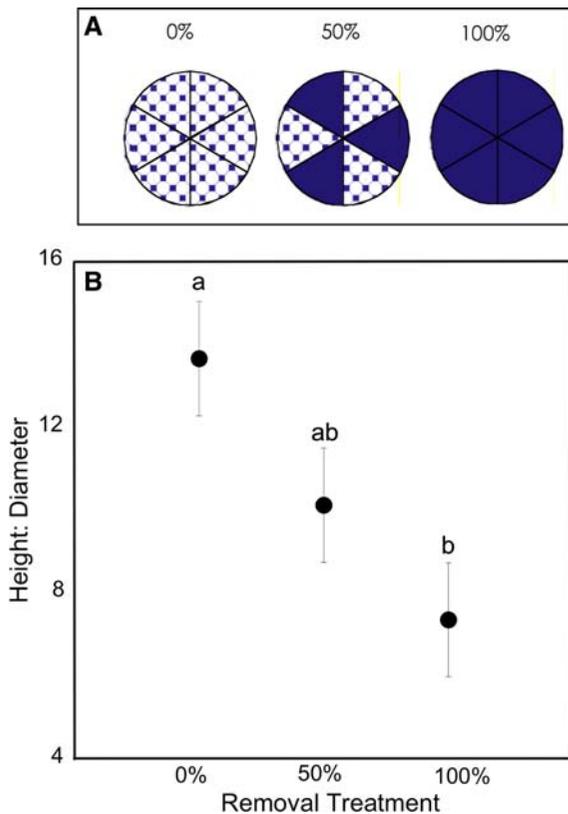
Because both the community type and corridor proximity results were significant, we performed two additional sets of  $G$ -tests to examine whether either the community type effect or corridor effect could be an artifact of a disproportionate representation of the community types in the two corridor buffer zones. For the former issue, we determined that there is a strong and consistent community type effect both near corridors ( $G_3 = 32.47$ ,  $P < 0.001$ ) and distant

from corridors ( $G_3 = 57.53$ ,  $P < 0.001$ ). In both cases the effect was driven by the disproportionately low number of *B. sylvaticum* patches in the open habitat type. Moreover, because open habitat was over-represented in the 0–30-m corridor buffer (largely due to the presence of the BPA powerline which created a wide swath of open habitat) the lower occurrence of *B. sylvaticum* patches in open habitat was actually underestimated by the single factor  $G$ -test for community type. For the latter issue, we used an interaction  $G$ -test (Sokal and Rohlf 1981) to take into account the proportions of each community type located in each buffer zone. We found there was a strong overall corridor effect ( $G_4 = 52.78$ ,  $P < 0.001$ ) that was driven both by divergence from the expected patch frequencies for the pooled community type data ( $GP_1 = 41.81$ ,  $P < 0.001$ ) and by heterogeneous responses among the community types ( $GH_3 = 10.97$ ,  $P < 0.05$ ). An examination of individual community types showed a consistent overabundance of patches near corridors, with the two forest types exhibiting the strongest effects (open habitat  $G = 7.14$ ,  $P < 0.01$ ; woodland  $G = 8.41$ ,  $P < 0.01$ ; mixed oak-fir forest  $G = 20.28$ ,  $P < 0.001$ ; Douglas-fir forest  $G = 22.83$ ,  $P < 0.001$ ;  $df = 1$  for all individual tests). Similar to the community type analysis, the overabundance of open habitat in the 0–30-m buffer band caused an underestimate of the trail effect in the single factor  $G$  test.

#### Field experiment

The competition-reduction treatment (Fig. 4a) changed plant morphology and size, as measured by the ratio of plant height to diameter (treatment  $F_{2,5.59} = 5.20$ ,  $P = 0.0530$ ). Target plants with 100% removal treatments grew broader and lower than controls (Fig. 4b). There was no significant effect of site ( $F_{3,9.36} = 1.89$ ,  $P = 0.1985$ ), nor was there a significant treatment by site interaction ( $F_{6,35} = 0.72$ ,  $P = 0.6388$ ), indicating that the same processes were acting at all four sites. The larger the initial size of the plant, the larger the removal effect, as was indicated by a significant ( $F_{1,47} = 7.84$ ,  $P = 0.0082$ ) positive slope of the covariate, initial diameter.

The competition-reduction treatments did not significantly alter seed production ( $F_{2,5.5} = 2.32$ ,  $P = 0.1852$ ), but there was a significant site effect;



**Fig. 4** *Brachypodium sylvaticum* height:diameter growth response to removal treatments. **a** Diagram of the removal treatments. **b** Response to treatments. Significant treatment differences ( $P < 0.05$ ), determined by Tukey's test, are indicated by different letters; means  $\pm 1$  s.e.

spikelet production was lower at Philomath than the other three sites ( $F_{3,9.7} = 6.88$ ,  $P = 0.0091$ ). There was no treatment by site interaction ( $F_{6,35} = 0.65$ ,  $P = 0.6860$ ), so the lack of a competition effect held across all four sites. Larger plants made more spikelets, as indicated by a significant positive slope of the covariate, initial diameter ( $F_{1,35} = 7.19$ ,  $P = 0.0111$ ).

#### Greenhouse experiment

There were main effects of light and nutrients on the total biomass and root:shoot ratios of *B. sylvaticum* (Table 2, compare means in Table 3). Nutrient concentration influenced growth differently in the sun and shade, as indicated by significant light by nutrient interactions (Table 2; Fig. 5). *Brachypodium sylvaticum* was larger in the sun than in the shade under both treatments; the interaction with the light treatment arose because plants were much larger in the sun under high nutrients but tended to be larger in the shade under low nutrients. On the other hand, root-to-shoot ratios tended to be highest in the sun, low nutrient treatments, and lowest in the shade, high nutrient treatments (Table 3).

There was a significant main effect of competition on *B. sylvaticum* total biomass and on root:shoot ratios (Tables 2, 3). *Brachypodium sylvaticum* had smaller biomass when grown with the invasive *S. arundinaceus* (contrast,  $F_{1,213} = 5.71$ ,  $P = 0.0177$ ) than when

**Table 2** Effects of competition, shade and nutrients on total biomass (=shoots + roots) and root:shoot ratios of *Brachypodium sylvaticum*

Variable	Source	df	Sum of squares	F ratio	Prob > F
Total biomass (log transf)	Competition	3	1.500	2.97	<b>0.0328</b>
	Light	1	29.919	177.68	<b>&lt;.0001</b>
	Nutrients	1	2.563	15.22	<b>0.0001</b>
	Light*competition	3	2.684	5.31	<b>0.0015</b>
	Light*nutrients	1	4.625	27.46	<b>&lt;.0001</b>
	Nutrients*competition	3	0.247	0.49	0.6907
	Light*nutrients*comp	3	0.088	0.17	0.9138
Root:shoot (sqrt transf)	Competition	3	0.527	6.05	<b>0.0006</b>
	Light	1	2.792	96.10	<b>&lt;.0001</b>
	Nutrients	1	1.449	49.87	<b>&lt;.0001</b>
	Light*competition	3	0.186	2.13	0.0972
	Light*nutrients	1	0.391	13.47	<b>0.0003</b>
	Nutrients*competition	3	0.213	2.44	0.0651
	Light*nutrients*comp	3	0.176	2.02	0.1121

All factors with  $P < 0.05$  are bolded

**Table 3** Total biomass (root + shoot) and root:shoot ratios (mean  $\pm$  1 s.e.) from the greenhouse experiment

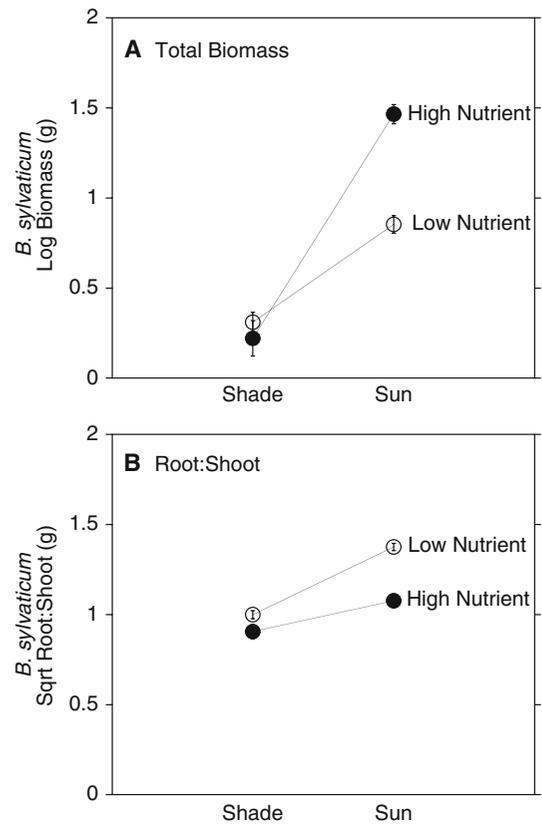
Competition	Light	Nutrients	Biomass	Root:shoot
BS	Sun	High	5.00 $\pm$ 0.85	0.67 $\pm$ 0.07
BS	Sun	Low	2.14 $\pm$ 0.20	1.26 $\pm$ 0.13
BS	Shade	High	0.09 $\pm$ 0.01	0.37 $\pm$ 0.09
BS	Shade	Low	0.41 $\pm$ 0.05	0.65 $\pm$ 0.05
EG + BS	Sun	High	3.49 $\pm$ 0.66	0.72 $\pm$ 0.07
EG + BS	Sun	Low	1.27 $\pm$ 0.29	1.40 $\pm$ 0.20
EG + BS	Shade	High	0.35 $\pm$ 0.07	0.29 $\pm$ 0.08
EG + BS	Shade	Low	0.49 $\pm$ 0.13	0.40 $\pm$ 0.08
SA + BS	Sun	High	2.41 $\pm$ 0.37	0.72 $\pm$ 0.09
SA + BS	Sun	Low	0.85 $\pm$ 0.12	2.21 $\pm$ 0.20
SA + BS	Shade	High	0.35 $\pm$ 0.10	0.40 $\pm$ 0.05
SA + BS	Shade	Low	0.31 $\pm$ 0.04	0.65 $\pm$ 0.09
FR + BS	Sun	High	6.16 $\pm$ 1.03	0.58 $\pm$ 0.04
FR + BS	Sun	Low	2.03 $\pm$ 0.24	1.00 $\pm$ 0.09
FR + BS	Shade	High	0.24 $\pm$ 0.08	0.26 $\pm$ 0.08
FR + BS	Shade	Low	0.36 $\pm$ 0.09	0.38 $\pm$ 0.07

BS *B. sylvaticum*, EG *Elymus glaucus*, SA *Schedonorus arundinaceus*, FR *Festuca roemerii*

grown alone. There were no significant differences in *B. sylvaticum* biomass when grown with either of the natives, *E. glaucus* (contrast,  $F_{1,213} = 1.15$ ,  $P = 0.2854$ ) or *F. roemerii* (contrast,  $F_{1,213} = 0.55$ ,  $P = 0.4588$ ), though it tended towards being larger when grown with *F. roemerii*. *Brachypodium sylvaticum* had significantly larger root:shoot ratios when grown with *S. arundinaceus* than by itself (contrast,  $F_{1,213} = 6.90$ ,  $P = 0.0092$ ), and significantly smaller ones when grown with *F. roemerii* (contrast,  $F_{1,213} = 4.26$ ,  $P = 0.0427$ ).

There was a significant light by competition interaction for total biomass, but only a nearly significant trend for root:shoot ratios (Table 2; Fig. 6). In Fig. 6a, it can be seen that in the shade treatment there were no differences in *B. sylvaticum* biomass as a result of competition; it grew poorly under all treatments in the shade. However, in full sun, the biomass of *B. sylvaticum* was significantly reduced by the presence of *S. arundinaceus* and by *E. glaucus* but not by the native *F. roemerii*.

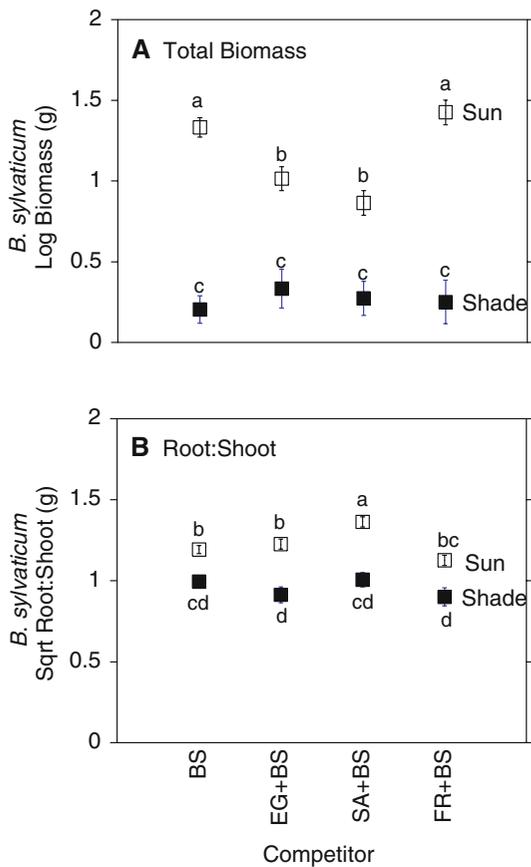
There was a nearly significant nutrient by competition interaction for *B. sylvaticum* root:shoot ratios (Table 2; Fig. 5b). Under high nutrients, *B. sylvaticum* had somewhat larger root:shoot ratios when grown



**Fig. 5** Responses of *Brachypodium sylvaticum* to light and nutrient levels. **a** Total biomass, **b** Root:shoot ratios. Significant treatment differences ( $P < 0.05$ ), determined by Tukey's tests, are indicated by different letters; means  $\pm$  1 s.e.

with *S. arundinaceus* than with itself or the two natives. There were no significant three-way interactions for biomass or root:shoot ratios (Table 2).

We calculated the relative yield per plant (RYP) for *B. sylvaticum* against each of its competitors under each light and nutrient combination, as summarized in Fig. 7. RYP values  $>1$  indicates that *B. sylvaticum* was bigger when grown with other species than with itself (smaller effects of interspecific competition than intraspecific competition on biomass) and values  $<1$  indicate that there is a disadvantage of growing in a mixture with other species (larger effects of interspecific competition than intraspecific competition on biomass). Under shady conditions with high nutrients (Fig. 7d), the RYC was  $>1$ , which means the other species decreased the biomass of *B. sylvaticum* less than competition with *B. sylvaticum* plants did (e.g., intraspecific competition had a larger effect than interspecific competition on the growth of *B. sylvaticum*).



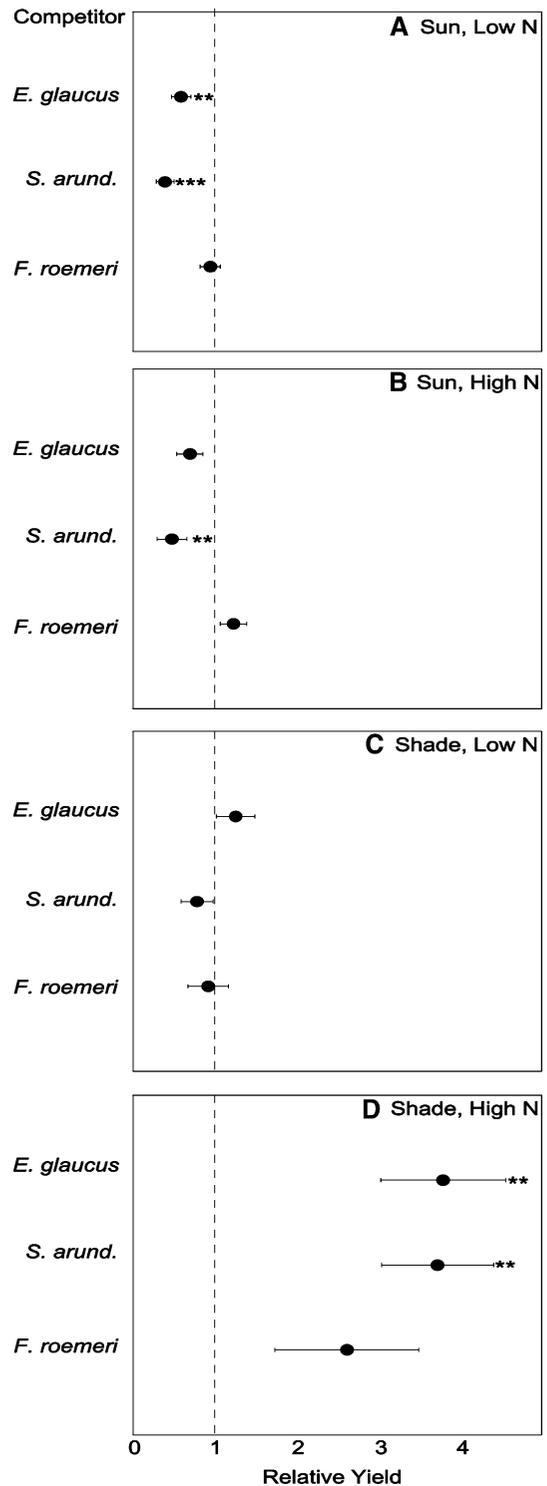
**Fig. 6** Response of *Brachypodium sylvaticum* to competition and light. **a** Total biomass, **b** Root:shoot ratios. Significant treatment differences ( $P < 0.05$ ), determined by Tukey’s tests, are indicated by different letters; means  $\pm$  1 s.e. Species Codes: BS *Brachypodium sylvaticum*, EG *Elymus glaucus*, SA *Schedonorus arundinaceus*, FR *Festuca roemerii*

The opposite extreme was under full sun with low nutrients (Fig. 7a) where the RYC was  $< 1$ . Under this environment, the other species decreased the biomass of *B. sylvaticum* more than competition with *B. sylvaticum* plants did (e.g., interspecific competition had a larger effect than intraspecific competition on the growth of *B. sylvaticum*).

### Discussion

The environmental context of the invasion

The pattern we found of increased establishment along trails and other corridors is consistent with that found by many others working with invasive species



**Fig. 7** Relative yield per plant (RYP) of *Brachypodium sylvaticum* under competition. **a** Sun, Low nutrients, **b** Sun, High nutrients, **c** Shade, Low nutrients, **d** Shade, High nutrients. \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

(Tyser and Worley 1992; Reed et al. 1996; Parks et al. 2005; Leu et al. 2008). Two mechanisms are commonly cited for the abundance of weeds along roads and trails: dispersal and disturbance. Seeds are spread along trails and roads by animals, including people, and by equipment. *Brachypodium sylvaticum* has barbed awns that facilitate its dispersal by animals (Heinken and Raudnitschka 2002). Disturbance along corridors may also facilitate invasion by this grass by opening up space for plants to grow, and, once established, our field experiment suggests they will spread out to fill available space. However, we note that while disturbance may facilitate invasion, disturbed land is not essential habitat for the grass, either in its native range or in the invaded range. In Europe, *B. sylvaticum* is often found along the disturbed edges of trails and rivers and in recently logged forests, but it also occurs in less disturbed forests (Roy *in press*). In favorable habitat in Oregon, the plants grow and produce abundant seeds (Roy et al. *in review*). Subsequently, they are likely to be carried away from the trails and rivers that facilitated their initial dispersal by animals (Heinken and Raudnitschka 2002), including people, and vehicles (Hansen and Clevenger 2005).

Our GIS analysis showed that open habitats at HBRA are the least suitable for *B. sylvaticum*, while forested habitats contain both larger and greater numbers of patches. But why is this, especially when it can grow far larger in sun than in shade? Our greenhouse experiment results suggest that reduced competition from other grasses in shade and high nutrients vs. sun and low nutrients is likely to be one of the primary reasons for this effect, although perhaps not the only one, as we discuss below.

In its native range, *B. sylvaticum* is primarily a shade plant, although it also can be found in the open where soils are moist (Landolt 1977; Long 1989; Aarrestad 2000; Roder et al. 2007). Genotype may also matter. In the native range in England, there are two different types, hairy and non-hairy (NHE, Davies and Long 1991). Transplant experiments have shown that the hairy type grows best in the sun, but also does well in the shade, whereas the non-hairy type is more restricted to the shade (Long 1989; Davies and Long 1991). In Oregon, the plants are also found primarily in shaded habitats, although the only genotype identified to date is the phenotypically plastic hairy variety (Roy et al. *in review*, Cruzan and

Rosenthal personnel communication). Two pieces of data suggest why *B. sylvaticum* is most often found in the shade: it has better ability to photosynthesize under very low light conditions than many other species (Murchie and Horton 1998), and as demonstrated in our greenhouse experiment, it performs relatively better in the shade under competition from other species than under the same competition in the sun (Fig. 7).

The greenhouse experiment also revealed that the environmental context of *B. sylvaticum* invasion is likely to be associated with interactions between nutrients and light. It performed relatively better in competition with other species in the shade only under high nutrients—the conditions under which it produced the least biomass and lowest root:shoot ratios. In the Willamette Valley Ecoregion, where HBRA is located, these two conditions may be met most often under forested conditions, as shown by a recent study of four common successional habitats associated with historic oak savanna (Douglas-fir forest, mixed oak-fir woodland, edges, and prairie-oak savanna) (Murphy 2008). Nitrogen ( $\text{g/m}^2$ ) in the organic layer varied significantly by community types, and was, on average, significantly lower in prairie/savanna than forest across multiple sites. In the 0–20 cm zone, however, there was a highly significant site by community interaction, so the amount of nitrogen present in each community type varies by site. HBRA was one of the sites measured in the study; there the difference between prairie/savanna nitrogen ( $521 \pm 24 \text{ g/m}^2$ ) and forest ( $650 \pm 62 \text{ g/m}^2$ ) was large, but not significant due to high variation in both habitats. These measurements indicate that the nutrient environment is patchy even within community types. Wherever there is shady habitat with high nutrients, our greenhouse experiment suggests that *B. sylvaticum* is likely to have a competitive advantage.

Our GIS study results also suggest that, in terms of patch numbers, *B. sylvaticum* at HBRA was most over-represented relative to habitat area at HBRA in the mixed oak-fir forest. However, because patches were larger in the Douglas-fir forest, the overall proportion covered in the mixed oak-fir forest was only about 10% higher. While this difference is small, it is intriguing. We have two ideas as to how this pattern might have arisen: (1) mixed oak-fir forest favors *B. sylvaticum* over growth in open areas

or Douglas-fir forest, or (2) there are unaccounted site-specific factors contributing to this pattern. In the following paragraphs we evaluate these ideas.

Is there any other evidence that mixed oak-fir forest favors *B. sylvaticum*? This grass is often found in deciduous forest, both in its native range in Europe (Landolt 1977; Long 1989; Aarrestad 2000) and in its invaded range (pers. obs.). However, recent evidence suggests that it may perform better in conifer forests in both ranges. Roy et al. performed a demographic study in Oregon, USA and Switzerland. Two sites per country were located in deciduous forest (predominantly oak) and two per country were located in conifer forest. *Brachypodium sylvaticum* cover was significantly higher in conifer forests than in deciduous forests (33.54 vs. 18.91%) and there was no country by community type interaction, indicating that the same pattern held in both countries (Roy et al. [in review](#)). There also was no evidence that population growth rates were better in deciduous-dominated forests since of the eight sites, both the lowest (Bald Hill) and the highest population growth rates (HBRA) were found in deciduous-dominated forest patches. The success of *B. sylvaticum* patches in mixed oak-fir forests at HBRA, combined with the high population growth rate at the Park (Roy et al. [in review](#)) suggests there may be additional site-specific factors contributing to its success in this habitat at the HBRA.

We can gain further insight into the landscape-scale mechanisms for *B. sylvaticum* invasion at HBRA by examining the interactions of environmental variables and plant community succession, which is representative of a much broader trend in the Willamette Valley. Regardless of whether one forest type or another better facilitates *B. sylvaticum* invasion, both forest types were relatively uncommon in the Willamette Valley Ecoregion prior to Euro-American settlement (circa 1840). Around that time, indigenous landscape management practices of frequent burning to maintain open habitats ceased (Boyd 1999). Subsequently, the formerly dominant prairie and savanna communities that required periodic, low-intensity fires declined precipitously. Forest succession due to a lack of fire has been a major factor in prairie and savanna loss in the valley (Hulse et al. 2002; Johnson et al. unpublished data).

HBRA typifies the oak and Douglas-fir infill that have occurred on historic prairie and savanna

throughout the Willamette Valley, and *B. sylvaticum* appears to have benefited as evidenced by its success in shaded habitats where infill has occurred. Douglas-fir infill has occurred on mostly north and eastern aspects, likely due to deeper soils and greater soil moisture availability whereas oak infill has occurred primarily in areas with shallower soils and lower soil moisture that have limited conifer invasion (Murphy 2008). Some areas that have remained treeless or nearly so may be unable to support dense tree canopies due to even shallower, drier soils, on hotter exposures (Murphy 2008). In other areas, succession has been held back by historic livestock grazing (Johnson et al. unpublished data). The fact that *B. sylvaticum* rarely occurs under full sun in the US, and, when it does, is in moist conditions such as riversides or wet prairie (pers. obs.) suggests that in addition to competition, reduced soil moisture may be contributing to *B. sylvaticum*'s sparse occupancy in most open areas.

In our greenhouse experiment, we controlled for moisture differences among the treatments by watering when needed. Thus we know that *B. sylvaticum* is less affected by competition in the shade, independent of moisture. It is likely, however, that moisture is also important in the field. Future experiments with *B. sylvaticum* should explore the effects of soil moisture in combination with shade, nutrients and competition.

The relative value of our three approaches

We used three kinds of data to evaluate the pattern and process of *B. sylvaticum* invasions: GIS mapping, a greenhouse competition experiment, and a field competition-removal experiment. All three were valuable. The GIS study yielded critical information on the pattern of invasion, and pointed to environmental variables that might be implicated: dispersal along corridors, and preference for shaded habitats. The greenhouse competition experiment suggested a potential contributing mechanism for this latter pattern: in deep shade under high nutrient conditions, *B. sylvaticum* was little affected by other species, but in the sun it was at a competitive disadvantage. The field competition-removal experiment showed that when competition is released, the plants change their morphology to fill the newly available space.

While we did not find a concomitant increase in fitness in the field competition-release experiment,

two things suggest an effect might not be measurable until a second growing season. First, we commenced clipping at the beginning of the growing season, but in perennial plants, reproductive effort is often set by growth conditions of the previous year (Grime 1979). This means that our clipping treatment would more likely have affected seed set in the following year. Second, competition removal increased plant size, and, in this species, larger plants have greater reproduction than smaller plants (Roy et al. in review). In the future, competition reductions in the field with perennial plants need to be run over two or more seasons to determine the true effects of the manipulation.

Our three-pronged approach yielded far more insight into the mechanisms of invasion than any one of the approaches would have alone. Managers and academics often must decide whether to use all available resources on a single study of an invasive species, or to perform smaller studies on a variety of potential causal mechanisms. Given that invasions are often context-dependent, and the environment is not uniform but instead varies in multifactorial ways, we advocate for a multidimensional approach, as long as reasonable replication can be maintained with the resources available for the study.

### Prescription

Together, the results of this combined GIS, field, and greenhouse study point to several direct management applications. By focusing removal efforts along corridors, where *B. sylvaticum* appears to establish, and in shadier environments, where it appears to thrive, land managers can target both areas of dispersal and initial establishment, and areas of population growth and patch expansion.

Prioritizing control efforts is a critical decision; we can focus management further using our combined results. Results from the field experiment show that when competition is removed, *B. sylvaticum* size increases, and it spreads out to fill available space. A recent study of several other grasses (Pfeifer-Meister et al. 2008) documented a similar response to reductions in surrounding competition. Our greenhouse results indicate that competition with other species regulates the biomass of *B. sylvaticum* in the sun whereas competition with itself is more important in the shade. Since *B. sylvaticum* fitness is highly

correlated with biomass, these results suggest that in the shade, small populations and patch edges will likely expand more rapidly than large, dense areas of *B. sylvaticum*. Thus, a key area to target for early detection and control are shady areas along corridors because the species' dual propensities to establish and thrive in these locations may make them key source areas for further invasion. Even if established at low densities along disturbed trail and roadsides, the grass will grow larger to fill available space and set more seeds as a consequence, thus accelerating rates of invasion. This suggests that disturbances along trails and roads should be minimized and that manual removal treatments should be followed by immediate re-vegetation with *E. glaucus* and other native species to prevent remnant plants or seeds from exploiting the openings caused by disturbance. This is especially true in full sun where *B. sylvaticum* has high potential growth rates but is at a competitive disadvantage relative to some other grasses.

Our results suggest that management of not only *B. sylvaticum* but also of human activities should be focused on shaded roads, trails and other corridors, and that new corridors in these habitats should be avoided. Our results support the idea that trails, roads and utility corridors serve as conduits through which invasive exotics can be dispersed (Baret and Strasberg 2005; Sutton et al. 2007; Wells and Lauenroth 2007). Thus, while trails and roads are often an essential component of recreational open spaces, their ecological implications must be considered.

One way to address the role of corridors in invasive plant management is to simply recognize them as vectors for dispersal and consider them as indicators, or areas for early detection. A useful approach would be to patrol corridors to prevent invasive exotics from becoming established (Tyser and Worley 1992). This could be done with both experts in plant identification, and educated users. However, it is also important to reduce invasive species transmission along corridors. Trail users can be educated about problematic species by posting interpretive signs that identify the plant of interest and problems associated with it (Tyser and Worley 1992). Additional measures could include boot-cleaning stations (comprised of boot brushes and seed catchments) at trailheads as these may help prevent hikers from contributing to further dispersal. Finally, the role of animals in carrying the seeds needs to be addressed. Horses (Wells and Lauenroth 2007)

and cattle (Molinillo and Brener 1993) are known to be weed-seed vectors in general, and wild ungulates are known to move *B. sylvaticum* seeds in particular (Heinken and Raudnitschka 2002). Not only do animals carry seeds on their legs, but they may also disperse them in their manure. Wells and Lauenroth (2007) recommend that equestrians feed their horses native seed before riding to prevent invasive seeds from being dispersed in their droppings.

From a broader conservation perspective, our results, in combination with knowledge about the background ecology of HBRA and the Willamette Valley, suggest a way to combine controlling *B. sylvaticum* with restoring an endangered ecosystem. If *B. sylvaticum* performs poorly in dry, open environments with other grasses, one management alternative would be to dramatically open forest canopies and restore Willamette Valley prairie and oak savanna grasslands, which have been identified as among the most endangered ecosystems in the United States (Noss et al. 1995). If *B. sylvaticum* dispersal and establishment can be controlled during restoration activities, and native species can be successfully established in its place, then the more open habitat may inhibit this invasive exotic grass. The next step would be to test this prescriptive treatment in a restoration, either at HBRA, or another site.

## Conclusions

Our methodology demonstrates how spatial analysis and experimentation can be combined to understand both the patterns and processes of invasion. By so doing, it provides an approach to prescribing context-specific remedial actions for a poorly understood invasive species while simultaneously investigating the mechanisms that may underlie the species' ability to invade. Based on its wide ecological tolerance (Roy *in press*), *B. sylvaticum* may spread well beyond the Pacific Northwest, into shaded moist habitats across much of the US. *Brachypodium sylvaticum* is only one example of how a newly arrived invasive plant species may rapidly lead to a conservation crisis that requires effective, rapid, and site-specific responses that themselves must be rooted in an ecological understanding of the mechanisms of invasion.

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