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Propagule Pressure and Disturbance Drive the Spread of an Invasive Grass, *Brachypodium sylvaticum*

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Propagule Pressure and Disturbance Drive the Spread of
an Invasive Grass, *Brachypodium sylvaticum*

by

Laura Alayna Vician Taylor

A thesis submitted in partial fulfillment of the
requirements for the degree of

Master of Science
in
Biology

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ABSTRACT

The invasibility, or susceptibility of an ecosystem to biological invasion is influenced by changes in biotic and abiotic resistance often due to shifts in disturbance regime. The magnitude of invasive propagule pressure interacts with an ecosystem's invasibility to determine the extent of a biological invasion. I examined how propagule pressure, forest community structure and disturbance interact to influence the invasibility of temperate Pacific Northwest forests by the newly-invasive grass, *Brachypodium sylvaticum*. My goal was to identify which of these factors is most instrumental in enabling the shift from establishment to population growth in *B. sylvaticum* at the edge of its expanding range.

Both observational and experimental studies were employed to identify the many ecological components of this problem. Ecological sampling methods were used to identify trends in *B. sylvaticum* habitat preference and signs of habitat disturbance. In addition, an experimental study was performed to test the effects of soil and vegetation disturbance on *B. sylvaticum* seedling propagation. I found that while soil disturbance did not have a significant effect on seedling propagation, vegetation disturbance was implicated in *B. sylvaticum* spread. Higher propagule pressure and coniferous forest type were also strong predictors of increased *B. sylvaticum* seedling propagation and survival within established sites. My study demonstrates how propagule pressure and plant community dynamics interact to shift the invasibility of Pacific Northwest forests and facilitate the transition from establishment to spread in the invasion of *B. sylvaticum*.

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INTRODUCTION

Invasibility is the complex, context-dependent susceptibility of an ecosystem to biological invasions (Lonsdale 1999). The ability of non-native species to establish in native communities may be influenced by multiple ecological processes. The composition and structure of the biotic community and abiotic environment may exert resistance to invasion, which can shift with changing disturbance regimes. On the other hand, each introduced species may vary in the expression of invasive traits and will have varying levels of propagule pressure (the amount and frequency of reproductive units entering a site) throughout the course of an invasion (Lockwood et al. 2007). The invasibility of an ecosystem can be different at each stage in an invasion (colonization, establishment, population growth and range expansion) such that greater resistance at any given stage can prevent invasion while the weakening of resistance at a given stage will enable the introduced species to progress to the next stage in the invasion (Dietz and Edwards 2006). The widespread phenomenon of introduced species invading many habitats around the world has prompted ecologists to search for the underlying mechanisms that influence ecosystem invasibility and species invasiveness.

Biotic interactions play a large role in determining the composition and structure of plant communities (Barbour et al. 1998) and so also influence an ecosystem's invasibility (Richardson and Pysek 2006). One mechanism hypothesized to influence an ecosystem's invasibility is the diversity-invasibility hypothesis which proposes that more diverse ecosystems will be more resistant to invasion (Elton 1958). There has been conflicting evidence for and against the diversity-invasibility hypothesis, but studies

focusing on small-scale neighborhood interactions more often show support, whereas large scale eco-region studies more often show a positive correlation between native and invasive species richness (Stohlgren et al. 2003, Davies et al. 2005). The reason for these different patterns likely results from the increased competition for resources and low habitat heterogeneity experienced by neighboring individuals at small scales versus the relaxed competition and greater habitat heterogeneity found at larger spatial scales (Davies et al. 2005). Based on the idea that competition is a driving force in biological resistance at the community scale, Elton's hypothesis has expanded into other useful permutations including resistance by a greater diversity of functional groups (Symstad 2000), resistance by more competitive or dominant species (Prevey et al. 2010), or varying relative resistance of different ecosystem types (eg dry vs wet prairie, Peters et al. 2006). One major implication of the biological resistance hypothesis is that if the community composition or structure conferring the resistance is disrupted, the ecosystem's invasibility will increase.

The historical or endogenous disturbance regime of an ecosystem plays a fundamental role in its ecology (Connell 1979, Barbour et al. 1998). Humans produce many types of environmental disturbance that native ecosystems may not be adapted to, such as removal of vegetation, mixing and exposure of mineral soil, change in fire regime and alteration of river flow or tidal activity among others. By removing plant competition, an exogenous disturbance can make resources such as soil nutrients available for introduced species to take advantage of, creating an "invasion window" (Johnstone 1986, Davis et al. 2000). Daehler (2003) points out that while disturbance

does not necessarily facilitate invasion over native recolonization, the further the departure from the natural disturbance regime and the further the departure from the natural level of resource availability, the more invulnerable the ecosystem will become. A good example of this was recently demonstrated by Otfinowski and Kenkel (2010) who showed that prairies disturbed by simulated pocket gopher mounds experienced nitrogen levels equivalent to control plots and had lower levels of invasive *Bromus* establishment, whereas treatments where vegetation was killed with herbicide experienced a sharp increase in soil nitrogen and an accompanying increase in *Bromus* invasion. Although the dynamic interplay between community composition, structure and disturbance shapes the resistance of ecosystems, it is ultimately the interaction between invasion resistance and propagule pressure that will determine the invasibility of the ecosystem and subsequent success and extent of invasion (D'Antonio et al. 2001).

Propagule pressure, or the number, frequency and condition of reproducible units of an organism (often seeds in plant biology) introduced to a location, is a primary predictor of establishment success for many introduced species, sometimes surpassing the importance of many other biological parameters of invasiveness and invasibility (Von Holle and Simberloff 2005, Lockwood et al. 2009, Simberloff 2009). However, not all studies account for propagule pressure, and many traits associated with invasiveness can covary with propagule pressure, which could lead to confounding interpretations of the factors driving invasions (Colautti et al. 2006). Recent studies have revealed how propagule pressure interacts with variables affecting site invasibility such as diversity and disturbance of native communities to determine the outcome of exotic plant

establishment. For example, Eschtruth and Battles (2009) found that forest canopy disturbance and propagule pressure showed a significant positive interaction in promoting the invasion of two plant species. Similar results have also been found in seaweed (Britton-Simmons and Abbott 2008) and marine invertebrates (Clark and Johnston 2009). Yet McGlone et al. (2011) have shown that even a combination of propagule pressure and disturbance may not always be enough to overcome the resistance of established vegetation. The intricate context-dependence of interactions between ecosystem invasibility and propagule pressure and their effects on invasion success warrants further study.

The invasion process can be understood as three successive steps beginning with dispersal of propagules from the donor range and colonization in the novel habitat. These propagules must then establish in the new site and develop a self-sustaining population, a stage often referred to as naturalization. Finally the population can spread to new sites expanding its range (Vermeij 1996). The mechanism(s) underlying a given ecosystem's level of invasibility may be primarily defined by a greater resistance at only one of these stages. For example, an introduced plant species may be able to disperse and establish incidentally into a forest ecosystem, but may not be able to achieve high population growth due to competition with native vegetation. Furthermore, even in successful invasions, the relative importance of propagule pressure and the many factors influencing biotic and abiotic resistance may be different for each developmental life stage of an introduced species as well as for each stage in the invasion process (Dietz and Edwards 2006). For example, both Villalobos et al. (2010) and Averill et al. (2010) found that

disturbance affected invasive plant seedling emergence differently than plant survival and growth, and that these effects were also dependent on habitat type. Many studies have focused on the factors influencing the success of invasive plant establishment, but it is also important to understand how factors of ecological resistance and propagule pressure interact to influence the transition between establishment and population expansion. In this study, I evaluated the effects of propagule pressure and disturbance regimes on the population expansion of a newly-invasive grass, *Brachypodium sylvaticum*.

Many invasive plants such as English ivy (*Hedera helix*) and Scotch broom (*Cytisus scoparius*) threaten the Pacific Northwest; however, most of them have already moved beyond the initial phase of colonization and now reside in much of their potentially exploitable habitat. These species provide limited opportunities to observe the process of invasion. In contrast, the Eurasian bunchgrass *Brachypodium sylvaticum* (slender false brome) is a relatively recent introduced species to Oregon's Willamette Valley that demonstrates the ability to invade deciduous and coniferous forests. In sites where it has fully colonized, it has substantially replaced native vegetation but populations are often small and sparsely distributed at the edge of its expanding range (False Brome Working Group 2009).

Soil disturbance has been reported to play a role in the colonization of *B. sylvaticum* however this has not been empirically tested. While the exposed soils of river banks and trail edges are indeed a common substrate for its growth, *B. sylvaticum* also seems able to colonize and spread in the relatively thick duff litter of conifer forests (pers. obs.). It is not known if this progression into the forest has been facilitated by

disturbance, community dynamics, propagule pressure, or some combination thereof. *Brachypodium sylvaticum* thus serves as an effective organism to study factors contributing to ecosystem invasibility while also elucidating critical species-specific information which could be useful in future management efforts.

In this study, I examined the individual and combined effects of propagule pressure, forest community structure and disturbance on the invasibility of temperate Pacific Northwest forests by the newly-invasive grass, *Brachypodium sylvaticum*. My goal was to reveal what role, if any, each of these factors is playing in enabling the shift from establishment to population growth in *B. sylvaticum* at the edge of its expanding range. Both observational and experimental studies were employed to explore the many ecological components of this problem. I hypothesized that propagule pressure would positively affect seedling propagation in established sites (Colautti et al. 2006). Additionally, I hypothesized that native vegetation would confer resistance to invasion by *B. sylvaticum*, and that disturbance of vegetation and soil structure would contribute to increased propagation of *B. sylvaticum* seedlings in established sites.

METHODS

Study Site: Milo McIver State Park, Estacada, Oregon

Milo McIver State Park is a 951 acre park situated along the Clackamas River near Estacada, OR, about 28 miles southeast of Portland, OR. The park supports a number of recreational activities, including hiking, biking, horse-back riding, dog walking, fishing, boating, disc golf, camping and picnicking (oregonstateparks.org 2011). The landscape is made up of river terraces composed of clay-sandstone soils, which frequently experience small to large landslides in wet winter months (pers. obs.). Forest stands of varying age and successional development exist throughout the park ranging from young even-aged stands estimated to be 40-60 years old to later-successional stage forests of over 100 years old (estimates based on personal observations of tree diameters, density and forest structure). Large remnant stumps with springboard notches, characteristic of pre-1935 logging practices are widespread in the older forest stands (pers. obs.). These forests are primarily composed of the coniferous species *Pseudotsuga menziesii* (Douglas fir), *Tsuga heterophylla* (western hemlock), and *Thuja plicata* (western red cedar), and the deciduous species *Populus balsamifera* (black cottonwood), *Acer macrophyllum* (big-leaf maple), and *Alnus rubra* (red alder). There are also some tree species introduced to the park, presumably planted by humans as they exclusively border roadways, including *Acer platanioides* (Norway maple) and an unidentified Pine species (*Pinus sp.*). Forest stands range from predominantly deciduous to predominantly coniferous throughout the park. The park is experiencing impacts from several invasive plant species including *Rubus armeniacus* (Himalayan blackberry), *Phalaris*

arundinaceae (reed canray grass), *Cytisus scoparius* (scotch broom) and *B. sylvaticum*, which grows in many of the forest stands throughout the park. No management plan existed at the time of this study for controlling *B. sylvaticum* at Milo McIver, making it possible to perform studies on the plant's populations with fewer confounding influences.

Study species: Brachypodium sylvaticum (Hudson) Beauv (slender false brome)

Brachypodium sylvaticum is a perennial bunch grass native to Eurasia (Catalan and Olmstead 2000). It was first collected in Oregon in 1939 and has been expanding its range rapidly since at least the 1960's (Chambers 1966, Kaye and Blakeley-Smith 2006). There is evidence from chloroplast sequence and nuclear microsatellite analysis suggesting multiple introductions and intraspecific hybridization of Oregon populations (Rosenthal et al. 2008). Its foliage tufts can reach ~0.5 m tall and wide, with multiple flowering culms extending ~0.5 m above the foliage tuft (Hitchcock et al. 1969). It spreads exclusively through seed dispersal and becomes sexually mature after the first or second year of growth (Kaye and Blakeley-Smith 2006). Seed dispersal may be either local through its tall flowering culms falling over and releasing the seeds at the end of the season, or via long-distance animal transport as the seeds' barbed awns likely become caught in animal fur and human clothing and equipment (personal observation, Heinken and Raudnitschka 2002). In both its native and introduced ranges it tends to live in coniferous or deciduous forest understory but can also tolerate higher light levels (Holten 1980, Grime et al. 1988). In both forests and prairies it can form large monotypic stands, substantially displacing native plant species and degrading wildlife habitat such as that of

the endangered Taylor's checkerspot butterfly (*Euphydryas editha taylori*, Severns and Warren 2008).

Ecological characterization of B. sylvaticum habitat

Past ecological disturbance could leave traces that can be discerned through quantitative differences in ecosystem structure and composition. For example, vegetation abundance, composition and maturity, soil profile and compaction and organic litter depth may be affected by and thus indicate a disturbance event. These hypothesized indices of disturbance were thus regressed with *B. sylvaticum* density to test the hypothesis that *B. sylvaticum* is associated with disturbed habitats and to gain a general understanding of this grass' habitat preferences in northern Oregon.

Ten populations of varying size and density were chosen in the Clackamas watershed at Milo-McIver State Park near Estacada, Oregon (Fig. 1 top). In each population, density and total area occupied by *B. sylvaticum* was characterized using a stratified random sampling design as follows. A 50 meter tape was extended through the longest axis of the population to points on either side where *B. sylvaticum* no longer existed (referred to as the baseline). Four transects then perpendicularly crossed the baseline at even intervals, but with the starting point of the interval chosen randomly. Each transect extended through the width of the *B. sylvaticum* patch at that point. Population area was calculated as the average length of the four transects multiplied by the length of the baseline. *B. sylvaticum* density was estimated by placing three one-by-one meter quadrats randomly along each transect for a total of 12 samples per population.

Within each quadrat, the percent cover, and number of tillers and seed-bearing culms of *B. sylvaticum* were counted. *B. sylvaticum* density was calculated as the mean number of tillers or culms per m².

For characterization of *B. sylvaticum* habitat preference, an additional quadrat was added to each transect just beyond the extent of *B. sylvaticum*, resulting in 16 sample quadrats per population covering a range of *B. sylvaticum* densities. In each quadrat, the following variables were estimated: percent cover of herbs, non- *B. sylvaticum* grasses, ferns, shrubs, woody debris, bare ground, and rocks. Litter depth (from the surface of the leaf litter to the beginning of the mineral soil layer) was measured at five points within each quadrat; at the center, and at a point equidistant between the center and each corner. Mean litter depth for each quadrat was calculated by averaging these five measurements. Percent canopy cover was measured using a spherical densiometer (model-C, Robert E. Lemmon, Forest Densimeters, Bartlesville, Oklahoma, U.S.A.). Mean percent canopy cover was calculated by averaging four readings taken facing North, East, South and West, and then multiplying by 1.04, following standard methods.

Data were analyzed using R 2.8.1 statistical analysis software (R Development Core Team 2009). Response variables (% cover false brome, number of tillers, and number of culms) were checked for normality and equal variance, and were subsequently transformed to better satisfy assumptions of linear regression. A Box-Cox analysis was used to determine the most appropriate coefficient with which to transform each variable: $\ln(\text{Tillers}+1)$, $(\text{Culms}+1)^{-0.13}$, and $(\% \text{Brachy}+1)^{-0.25}$. The variance inflation factor (VIF) was calculated for each of the predictor variables (% cover of herbs, vines, other grasses,

ferns, shrubs, rocks, woody debris, average litter depth and average canopy cover) to check for collinearity. In all cases $VIF < 1.45$ (mean $VIF = 1.24$), indicating that there was not a significant amount of standard error inflation due to collinearity (O'Brien 2007).

My objective was to determine the relative influence of each predictor variable on the abundance of false brome. Given the geographically structured nature of the study design, the most appropriate model to use was mixed effect regression. This way, I could account for variation due to site differences as well as variation due to the predictor variables within each site. To determine the most influential variables, a full model was specified with site as a random group effect, and all predictor variables (% cover of herbs, vines, other grasses, ferns, shrubs, rocks, woody debris, average litter depth and average canopy cover) included as fixed effects. Step selection based on the Akaike information criterion (AIC) identified the most influential predictor. This predictor was then used to begin a forward stepwise selection model construction, with the predictor with the next highest t-value from the full regression model added at each step. At each step, the growing model was compared to the full model using ANOVA. The null hypothesis for this test states that there is no difference between the two models. If the null hypothesis was accepted, then this model was considered the minimum adequate model, and the variables it contained were deemed more influential in adult *B. sylvaticum* ecology. I also developed models with only the most influential predictor, and allowed slope to vary as a random effect. These models were compared to the corresponding fixed effect single predictor models using ANOVA to test the null hypothesis that the two

models did not differ significantly. For each response variable (culms, tillers and percent cover), the null hypothesis was accepted, therefore varying slope models were not considered for less influential variables.

Comparative study of forests with and without *B. sylvaticum*

To gain a clearer picture of the differences in vegetation and soil structure between forest habitats with and without *B. sylvaticum*, a comparative observational study was performed in the summer of 2010. The same *B. sylvaticum* populations at Milo McIver State Park were used with the exception of Site Mc10, resulting in a total of nine sites surveyed. At each site, one transect was extended through the longest axis of the *B. sylvaticum* population. Another transect of equal length was extended through an area of vegetation that contained no *B. sylvaticum* for at least the entire length and a two-meter width from the transect. This second transect was located by finding the closest area qualified by *B. sylvaticum* absence in a random direction from the first transect. Five one-by-one meter quadrats were placed evenly but with a random starting point along each of these transects. In each quadrat, the following variables were measured: the height of the understory vegetation was measured at five points, the center and at a point equidistant between the center and each corner and averaged to find mean understory height, the number of *B. sylvaticum* reproductive culms and seedlings were counted and percent canopy cover was estimated in the same manner as for the habitat characterization study above.

For soil analysis, a 10x10 cm sub-sample area was placed at the center of each quadrat and the following variables were measured. Percent cover of moss, coniferous

tree litter, deciduous tree litter and grass litter were estimated. Litter depth was measured as above. All litter within the 100 cm² area was collected into paper bags, dried and weighed to determine litter biomass. Litter density was calculated by dividing the litter dry mass by litter depth. Beneath the litter layer, soil compaction was measured at five points (the center and a point equidistant between the center and each corner) using a penetrometer, then averaged to find mean soil compaction. Next, the soil within the 100 cm² was collected to a depth of 10 cm and transported to the lab for composition analysis. In the lab, each soil sample was suspended in a 1:1 soil: distilled water- detergent solution in a Pyrex 250 ml cylindrical beaker, then allowed to settle for 24 hours. Once settled, the volume of each soil component: sand, silt, clay and organic mater was measured, and the relative percent of each calculated. Unfortunately, a number of samples were misplaced, resulting in an incomplete data set for soil composition.

Data were analyzed in SAS 9.1 using a mixed model which controlled for differences among sites. Each variable (understory height, soil compaction, % canopy cover, % moss cover, % cover of litter types, litter depth and density, and organic, sand, silt and clay soil fractions) was tested for differences between areas with and without *B. sylvaticum*. To avoid type I errors due to multiple tests, a Bonferroni adjustment was made to the standard α of $P \leq 0.05$. The effect of each variable was considered significant if the adjusted experiment-wide α' was $P \leq 0.0038$ ($\alpha/13$ tests; Gotelli and Ellison 2004). Within sites where *B. sylvaticum* was present, understory height, soil compaction, canopy cover, moss cover and coniferous, deciduous and grass litter cover were tested for their effects on *B. sylvaticum* seedling density using an ANCOVA model. The response

variable, *B. sylvaticum* seedling density was natural-log transformed to satisfy assumptions of normality and equal variance based on a Box-Cox transformation analysis.

Disturbance experiment

From April through June of 2009, a disturbance experiment was initiated to test the effects that soil and vegetation disturbance have on *B. sylvaticum* seedling establishment. Four 2x2m permanent plots were established in the North, East, South and West quadrants of each population, placed a random distance between the center and edge of the population in each given direction (Fig 1). Some populations were too narrow to allow this type of arrangement (< 5m wide), and so were arranged with plots extending at intervals along the longest axis of the population with the beginning of the interval chosen at random. Each 2x2m plot was divided into four 1x1 m subplots, and assigned one of four disturbance treatments: 1) Control - unaltered, 2) Tilled - organic soil layer tilled into mineral layer 6 cm deep, 3) Mulched - Organic soil layer tilled into mineral layer 6 cm deep, then covered with 2.7 cm (1 ft³, or 0.027m³) of Rexius Hemlock Bark®, 4) Bare - organic leaf litter layer completely removed exposing mineral soil layer. Treatment position within plots alternated systematically with respect to the center of the population.

Before treatments were implemented, the following ecological parameters were estimated for each subplot: Percent cover of total vegetation, herbs, ferns, shrubs, non-*B. sylvaticum* grass, and *B. sylvaticum* were estimated. Litter depth was measured at four

points equidistant between the center and each corner of the subplot as above. Each plant species present was recorded. Treatments were then installed and left to natural field conditions for the remainder of the year.

Other variables hypothesized to be important covariates were measured later on in the summer of 2009 or 2010. To monitor the effects of proximity to reproducing adults and therefore propagule pressure, *B. sylvaticum* culm density was counted in the 8 m² bordering each subplot. The tree canopy species above each subplot were recorded, and canopy type classified as primarily coniferous or deciduous. Percent canopy cover was estimated at each subplot using a spherical densiometer following standard protocol. In addition, a higher resolution measure of canopy cover was acquired for each plot by taking a hemispherical fish-eye photograph of the canopy from the center of the plot using a Pentax K100D digital camera. The camera was oriented with the top directly at magnetic North, and the lens level for each photograph. Photographs were analyzed using Gap Light Analysis (GLA 2.0) software following methods outlined in the user manual (Frazer et al. 1999). The % canopy openness calculated from each photograph was scaled to account for differences between subplots by subtracting the difference between the densiometer reading for a given subplot and the mean value for all four subplots from the GLA derived % canopy openness value according to the following equation: Scaled subplot % canopy openness = GLA derived plot % canopy openness – (mean plot densiometer % openness – subplot densiometer % openness).

The following growing season, each subplot was revisited monthly from May through September 2010 to record the number of *B. sylvaticum* seedlings emerged.

Seedlings were counted up to ~ 500 in the entire m², or estimated in subplots where they were clearly greater than ~ 500 by selecting a random 10cm x 100cm width of the subplot, and then multiplying the resulting count by 10.

At the end of the second season, total vegetation percent cover was again estimated. The magnitude of impact that each disturbance treatment exerted on the existing vegetation was quantified by subtracting post-treatment vegetation cover from pre-treatment cover.

Data were analyzed in SAS 9.1 using two repeated measures nested ANCOVA models, one including soil disturbance treatment classes, and the other including the change in existing vegetation as the primary predictor. To test the effect of soil disturbance on seedling propagation, treatment, site, plot and forest type were included as class variables, with site and plot listed as random. The effect of each treatment on *B. sylvaticum* seedling number was tested over the five months (May – September) with site, plot, forest type, number of neighboring culms, percent open canopy, and percent cover of herbs, ferns, shrubs and other grasses included as covariates. The VIF was calculated for each covariate to test for collinearity, and was found to be ≤ 2 in all cases (mean VIF = 1.4) indicating relatively little variance inflation.

To test the effect of vegetation disturbance on seedling propagation, the same nested ANCOVA design was used as in the soil disturbance analysis, but with the post-treatment change in vegetation cover included as the predictor variable of interest. The treatment class variable and individual vegetation types were not included as they would confound the variable of interest due to collinearity. Initial vegetation percent cover was

included as a covariate to account for the large variation in vegetation between subplots. VIF scores were found to be < 2 for each covariate (mean VIF = 1.6).

The effect of population size on seedling number was tested with a logarithmic regression, using population area measurements from the ecological characterization study. Response variables, were natural-log +1 transformed to satisfy assumptions of normality and equal variance based on a Box-Cox transformation analysis. Variables shown to have a significant effect ($p < 0.05$) in the ANCOVA analyses were regressed against seedling number and correlation coefficients calculated in R 2.8.1 statistical analysis software (R Development Core Team 2009).

RESULTS

*Ecological characterization of *B. sylvaticum* habitat*

The abundance of perennial vegetation types (shrubs, ferns and other grasses), litter depth and canopy cover were significantly predictive of variation in *B. sylvaticum* abundance. The minimum adequate model for all *B. sylvaticum* response variables (percent cover, tiller number and culm number) contained the predictor variables percent cover of ferns, other grasses, shrubs, litter depth and canopy cover, and the final model for tillers additionally contained woody debris as a significant predictor (Table 1). All perennial vegetation types and litter depth were negatively correlated while canopy cover was positively correlated with *B. sylvaticum* (Table 1, Fig 2). Percent cover of herbs, bare soil, woody debris (for the most part), and rocks did not contribute predictive power to the final minimum adequate models of *B. sylvaticum* abundance.

*Comparative study of forests with and without *B. sylvaticum**

Significant differences existed in the habitat characteristics of forests with *B. sylvaticum* versus those without *B. sylvaticum*. There was lower litter depth and dry mass in sites with *B. sylvaticum* (Table 2). Sites with *B. sylvaticum* had denser litter and more compact soil than those with no *B. sylvaticum* present (Table 2, Fig. 3). The average height of understory vegetation was shorter in sites with *B. sylvaticum* (Table 2, Fig. 3). Finally, forests sites with *B. sylvaticum* present had denser canopy cover (Table 2, Fig. 3). Within forests where *B. sylvaticum* was present, there was a negative correlation between the density of *B. sylvaticum* seedlings and the percent cover of deciduous leaf

litter (Fig. 4).

Disturbance experiment

Soil disturbance treatments had no significant effect on the magnitude of seedling recruitment (Table 3). Several covariates, however did influence seedling recruitment, including forest type, the number of neighboring culms, and the percent cover of herbs, ferns, and shrubs (Table 3, Fig. 5 top). While the number of neighboring culms had a positive effect on seedling number (Fig. 6), all vegetation types were negatively correlated with seedling number. A plot effect was also detected (Table 3). These trends were fairly consistent throughout each month of the experiment, with minor variations. For instance, in May there was a significant forest-type by disturbance treatment interaction (Fig. 5 bottom), and in September, there was a significant soil disturbance treatment effect (Fig. 7). Many of these same variables, with the inclusion of a site effect, and the exclusion of percent shrub cover effects interacted with the model significantly over time (Table 3).

Soil disturbance treatments had a significant effect on the existing vegetation, with the 'control' (Mean Δ % cover \pm S. E. = 0.0 ± 5.86) and 'bare' (2.8 ± 4.38) treatments exerting the least, the 'till' (-7.25 ± 5.02) treatment intermediate, and the 'mulch' (-13.06 ± 4.98) treatment having the greatest impact on vegetation ($F=5.29$, $P=0.002$, 3/ 117 df). The reduction in percent cover of vegetation due to disturbance treatments significantly influenced seedling propagation; the greater the decrease in vegetation cover, the more seedlings germinated ($F=4.48$, $P=0.037$, 1/ 117 df ; Fig. 8).

There was a strong positive correlation between the number of flowering culms neighboring a subplot and the number of seedlings that emerged (Fig. 6). The extent of land area inhabited by each *B. sylvaticum* population displayed a positive logarithmic correlation with the number of seedlings emerged (Fig. 9).

DISCUSSION

The consistent inverse correlation between adult *Brachypodium sylvaticum* and native vegetation, the increased response of seedling propagation to vegetation disturbance, and the strong effect of propagule pressure on seedling density demonstrates how shifts in biotic resistance caused by vegetation disturbance interact with propagule pressure by an invasive grass to drive increases in its population density. While soil disturbance had little effect on *B. sylvaticum* seedling propagation overall, a significant effect developed by the end of the growing season. This effect was primarily due to increased survivorship of seedlings in mulched and tilled deciduous forest plots, suggesting that in this instance, invasibility of deciduous forests is influenced by different processes than coniferous forests.

The role of disturbance

Brachypodium sylvaticum appears to associate with disturbed habitats such as road and trail edges, stream sides and logged forests both in its native and invasive range. It was therefore surprising to find that a range of different soil disturbances had very little effect on the propagation of *B. sylvaticum* seedlings when tested in this study. It appears that soil disturbance *per se* may not be an important facilitator for *B. sylvaticum* invasion in the upland forests of northern Oregon studied here. Several other lines of evidence investigated in this study however, do implicate the role of some kind of habitat disturbance in the invasion of *B. sylvaticum* at Milo McIver State Park. In all three studies, a negative correlation was found between the relative abundance of perennial

vegetation types (ferns, shrubs, and other grasses) and that of established adult *B. sylvaticum*. Examined in isolation, this could be interpreted in two ways - either the disturbance of native vegetation is providing a window of opportunity for the invasion of *B. sylvaticum*, or *B. sylvaticum* is able to actively out-compete and displace established native vegetation. The results of the comparative study lend more support to the first hypothesis. For instance, un-invaded areas had significantly deeper, less dense litter, less compact soil and a taller understory vegetation layer than invaded forest despite the soil composition being indistinguishable in these two scenarios. The combination of a thinner litter layer, more compact soil and a reduced understory in *B. sylvaticum* invaded forests implicates a history of disturbance via human activity such as trail and road construction and maintenance, tree thinning, or off-trail hiking. This hypothesis is further supported by the correlation between magnitude of vegetation disturbance and *B. sylvaticum* seedling propagation observed in the disturbance experiment.

Although soil disturbance treatments did not explain a significant portion of the variability in seedling density overall, month-by-month analysis revealed that the treatments did become significant by September, implying that treatments affected seedling survival but not germination. It is interesting to note that seedling survival was higher in the 'mulch' and 'till' treatments where vegetation was most impacted, while survival was lower in the 'control' and 'bare' treatments where vegetation was minimally impacted. This also lends support to the idea that *B. sylvaticum* seedling establishment is facilitated by vegetation disturbance and the accompanying release from competition more so than alteration of soil structure or texture. Many other studies have also shown

that releasing invasive plants from competition plays a key role in their establishment and spread (Averill et al. 2010, de Villalobos et al. 2010, Otfinowski and Kenkel 2010, Prevey et al. 2010). The positive response of seedling propagation to increased vegetation disturbance and negative correlation between native perennial vegetation and adult *B. sylvaticum* abundance observed in this study supports the hypothesis that the release of resources such as water, light and nutrients caused by vegetation disturbance is also instrumental in the invasion of *B. sylvaticum*.

The role of habitat

Surprisingly, in contrast to my hypothesis, mulching soil tended to improve *B. sylvaticum* seedling establishment, while exposing bare soil marginally discouraged seedling establishment. This result is opposite to that found by Blakeley-Smith and Kaye (2008) when they tested mow-mulch treatments along *B. sylvaticum* infested road-sides and found that mulching significantly suppressed its abundance. There are many possible reasons for the contrasting results found in these two studies. There were fundamental differences in the study design, particularly in that Blakeley-Smith and Kaye mowed *B. sylvaticum* flowering culms prior to mulching, which was not done in this study. There were also differences in mulch composition and depth as well as the habitat in which the studies took place, theirs occurring in a ruderal habitat versus this study taking place in upland forests.

Examination of the role of forest type provides some further elucidation of why mulching and tilling mildly enhanced *B. sylvaticum* seedling propagation in this study.

Brachypodium sylvaticum seedling germination was much greater under coniferous trees (mostly Douglas fir and western hemlock) than under deciduous trees (primarily big-leaf maple, red alder and black cottonwood). Abundance of *B. sylvaticum* seedlings was negatively correlated with increasing deciduous litter cover, however the coniferous hemlock bark mulch and tilling treatments increased seedling abundance in deciduous but not coniferous forest plots. These patterns suggest that *B. sylvaticum* has greater difficulty germinating and surviving in the loose large-leaved litter of deciduous forests, and exhibits some amount of habitat preference toward coniferous forests and their more fine-textured litter type. Perhaps tilling and mulching in coniferous forests did not change the composition of the plant's growing substrate substantially (especially considering the constant rain of new needles onto the ground), whereas these same actions disturbed deciduous leaf litter enough to provide the seedlings with root access to the soil while keeping enough organic matter present to retain soil moisture (Schramm and Ehrenfeld 2010). While other environmental influences may also have played a role in *B. sylvaticum*'s different germination ability in deciduous versus coniferous forests such as soil acidity or moisture, these variables most likely covary strongly with forest type and thus would require study under controlled green house conditions to disentangle. This study was able to demonstrate that litter texture may be one component of the mechanism underlying *B. sylvaticum*'s coniferous forest habitat preference.

Deciduous canopy enabled higher light levels and greater amounts of other grasses to exist in the forest understory (data not shown). Holmes et al. (2010) found that *B. sylvaticum* was a weaker competitor against other grasses under high light levels,

which may be one mechanism influencing the large differences in seedling germination between deciduous and coniferous forests. However, due to the collinearity between deciduous canopy type and other grass abundance, it is difficult to dissect which factor is driving this pattern. Holmes et al. (2010) also found that *B. sylvaticum* patch number and size increased with greater canopy cover and coniferous tree component. In their study however, *B. sylvaticum* was most over-represented in oak-Douglas fir mixed forests, which do not occur at Milo McIver State Park and were not included in this study. Peters et al. (2006) demonstrate another example where the extent of colonization and patch expansion of an invasive woody shrub depended upon ecosystem type. This increasingly frequent finding that invasion depends on habitat type seen throughout the invasion biology literature as well as in the case of invasive *B. sylvaticum* provides support to the emerging understanding that invasions are highly context dependent.

Understory vegetation had a complex influence on *B. sylvaticum* abundance depending on the developmental stage in question. Seedling emergence was influenced by the amount of herb cover present, but not by the amount of other grasses, although as discussed above, this may be an artifact of other grass and deciduous canopy collinearity. Adult *B. sylvaticum* density was inversely correlated with the cover of other grasses but not herb cover. Perhaps *B. sylvaticum* seedlings respond differently to plant competition than adults do. It is possible that *B. sylvaticum* seedlings have some tolerance to the presence of adult grasses, while adult *B. sylvaticum* competes more intensely with other grasses. This could be one way in which *B. sylvaticum* could gradually replace other grasses over time. Places where there is a dense herb layer could have a stronger

resistance against *B. sylvaticum* seedlings which they are able to over-top, while abundant herb cover may be inconsequential to large established adult plants. This reveals how ecosystem resistance is subtly dependent upon the timing of arrival of both native and introduced species. The significant site and plot effect in each study reflects the patchiness of the forest vegetation at Milo McIver State Park, and probably also reflects variation in the amount of time since each site was colonized by *B. sylvaticum*.

The role of propagule pressure

As expected, the number of reproductive culms bearing seeds that surrounded a subplot exerted a large influence on the *B. sylvaticum* seedling density in that subplot. The overall size of each population also had an effect on seedling density, but this effect leveled-off beyond a certain patch size. This suggests that propagule pressure is a primary driver of *B. sylvaticum* seedling density up to some maximum threshold, beyond which no more seedlings can possibly fit in a given space. *B. sylvaticum* seedling density can be very high in some sites, demonstrating that propagule pressure is promoting increased density and potentially dominance of *B. sylvaticum* in forest habitats like those at Milo McIver State Park. Although higher propagule pressure will enable the potential for increased density and spread of *B. sylvaticum*, soil structure and plant competition may still limit *B. sylvaticum* densities through their effect on seedling survival (Schramm and Ehrenfeld 2010).

The relative roles that disturbance and propagule pressure play in the invasion process have historically been debated, and are currently topics of interest in invasion

ecology (Colautti et al. 2006, Lockwood et al. 2009). Current research is revealing that the interaction between disturbance and propagule pressure will be unique for each species and ecosystem in question. For instance, Eschtruth and Battles (2009) found that within eastern hemlock forests, an invasive shrub *Berberis thunbergii* was more dependent on canopy disturbance for its invasion, while an invasive grass *Microstegium vimineum* could invade equally well with either high propagule pressure or high disturbance. Despite this context-dependence, the emerging theme is that interactions between propagule pressure and disturbance determine the invasibility of many ecosystems and the success of establishment and spread for many invasive species (Britton-Simmons and Abbott 2008, Clark and Johnston 2009, Eschtruth and Battles 2009, Minton and Mack 2010). It is clear that many variables are influencing the invasion of *B. sylvaticum*, however, it appears that propagule pressure, vegetation disturbance and plant community dynamics are having a much stronger influence than soil disturbance in this case. This study primarily addressed local dispersal and the resulting diffusion of *B. sylvaticum* within colonized sites. It has been rare for studies to focus on this population growth stage of invasion, but Jongejans et al. (2007) recently published a similar study also showing that propagule pressure and vegetation disturbance interacted to facilitate the spread of established invasive thistles in an old field. This study confirms this to be the case in a well-established forest ecosystem as well.

CONCLUSION

The combination of *B. sylvaticum*'s shade tolerance, germination and survival success in coniferous forests, and its high competitive ability under shade and high nitrogen conditions (Holmes et al. 2010), make it a formidable invader in the Pacific Northwest bio-region where coniferous forests predominate the landscape. Especially once it has established, its high fecundity (Roy et al. in review) may insure that heavy propagule pressure will further drive the population growth and spread of this invasive species. Although native perennial vegetation and deeper litter layers may afford forests with some amount of resistance to invasion by *B. sylvaticum*, disturbances of these ecosystem components may provide *B. sylvaticum* an opportunity to further expand its populations. Thus impacts on native vegetation should be minimized, accumulation of deciduous litter encouraged, and reduction of *B. sylvaticum* reproduction implemented in order to effectively prevent increased dominance and spread of this invasive grass.

TABLES

Table 1 Ecological characterization of invasive *Brachypodium sylvaticum* (false brome) habitat. Effects of ecological parameters on the abundance of adult false brome tiller number, culm number and percent cover/ m². Predictor variables shown are those included in the minimal adequate mixed model for the given false brome response variable. The sign of each t-value indicates a positive (+) or negative (-) correlation between the given predictor variable and the log-transformed false brome response variable.

<i>False brome variable</i>		<i>Tillers</i>			<i>Culms</i>			<i>% Cover</i>		
<i>Random Effects</i>	<i>df</i>	<i>Variance</i>	<i>St Dev</i>	<i>Variance</i>	<i>St Dev</i>	<i>Variance</i>	<i>St Dev</i>	<i>Variance</i>	<i>St Dev</i>	
Site	10	1.274	1.129	0.007	0.085	0.012	0.110			
Residuals	144	2.624	1.620	0.018	0.133	0.031	0.176			
<i>Fixed Effects</i>	<i>df</i>	<i>S. E.</i>	<i>t value</i>	<i>S. E.</i>	<i>t value</i>	<i>S. E.</i>	<i>t value</i>			
Ferns	1	0.005	-4.825	0.000	-3.747	0.001	-4.339			
Other Grass	1	0.010	-4.801	0.001	-3.548	0.001	-3.592			
Litter depth	1	0.045	-3.150	0.004	-4.165	0.005	-4.945			
Shrubs	1	0.007	-3.795	0.001	-2.649	0.001	-3.359			
Canopy Cover	1	0.040	2.708	0.003	2.716	0.004	3.483			
Woody Debris	1	0.036	-3.000							

Table 2 Comparative study of forests with and without invasive *Brachypodium sylvaticum* (false brome). Variables showing significant differences between forests with and without false brome (in bold) are significant to the Bonferroni-adjusted α' level ($P \leq 0.0038$).

	<i>False brome present</i>		<i>False brome absent</i>		<i>False brome effect</i>		<i>Site effect</i>	
	Mean	n	Mean	n	F	P	F	P
Understory height	57.5	45	86.9	45	26.32	< .0001	16.59	< .0001
Soil Compaction	1.07	45	0.42	45	26.32	< .0001	4.01	0.0006
% Canopy cover	92.4	45	86.2	44	25.38	< .0001	30.94	< .0001
% Moss cover	19.5	45	18.0	45	0.14	0.7140	11.10	< .0001
% Coniferous litter	43.9	45	43.8	45	0.00	0.9856	7.48	< .0001
% Deciduous litter	40.5	45	45.4	45	0.45	0.5034	2.49	0.0192
% Grass litter	15.0	45	10.1	45	1.23	0.2717	4.28	0.0003
Litter depth	2.30	45	5.63	45	37.78	< .0001	5.91	< .0001
Litter density	14.0	37	8.0	39	10.13	0.0024	1.36	0.2407
% Soil organic	3.7	24	10.0	32	0.99	0.3260	1.41	0.2324
% Soil sand	16.0	24	14.1	32	0.18	0.6733	8.36	< .0001
% Soil silt	24.1	24	24.1	32	0.07	0.7893	7.09	< .0001
% Soil clay	56.2	24	51.8	32	1.67	0.2030	0.78	0.5916

Table 3 Disturbance experiment. Effects of soil disturbance, propagule pressure (neighboring culms) and other covariates on the propagation of invasive *Brachypodium sylvaticum* seedlings at each month in the growing season, overall and through time.

	May			June			July			August			September			Between Subjects			Time Interaction			
	df	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	
Model	51	15.11	***	14.69	***	12.85	***	13.69	***	11.49	***											
Site (Forest Type)	13	1.78	ns	2.97	**	2.88	**	2.71	*	3.50	**	9.05	***	3.61	***							
Plot (Site*Forest Type)	25	3.95	***	3.29	***	2.89	***	3.44	***	2.96	***	3.66	***	1.56	**							
Soil Disturbance Treatment	3	1.34	ns	0.66	ns	1.39	ns	1.90	ns	2.93	*	1.86	ns	0.86	ns							
Forest Type	1	13.83	**	5.90	*	6.25	*	4.58	*	3.78	ns	39.56	***	4.53	**							
Treatment * Forest Type	3	2.75	*	1.62	ns	1.90	ns	1.32	ns	1.68	ns	2.04	ns	1.00	ns							
Neighboring Culms	1	5.88	*	11.80	***	10.90	**	10.53	**	14.52	***	12.92	***	1.62	ns							
% Other Grasses	1	1.00	ns	0.53	ns	0.04	ns	0.71	ns	0.35	ns	0.09	ns	2.36	ns							
% Herbs	1	0.20	ns	4.73	*	11.13	**	14.07	***	7.09	**	7.57	**	7.41	***							
% Ferns	1	7.28	**	17.70	***	17.01	***	30.85	***	15.41	***	20.48	***	4.18	**							
% Shrubs	1	5.78	*	1.98	ns	2.14	ns	4.84	*	4.68	*	4.52	*	0.91	ns							
% Canopy Cover	1	0.34	ns	0.00	ns	0.04	ns	0.02	ns	0.14	ns	0.00	ns	0.59	ns							
Error	108																					

ns P > .05 * P ≤ 0.05 ** P ≤ 0.01 *** P ≤ 0.001

FIGURES

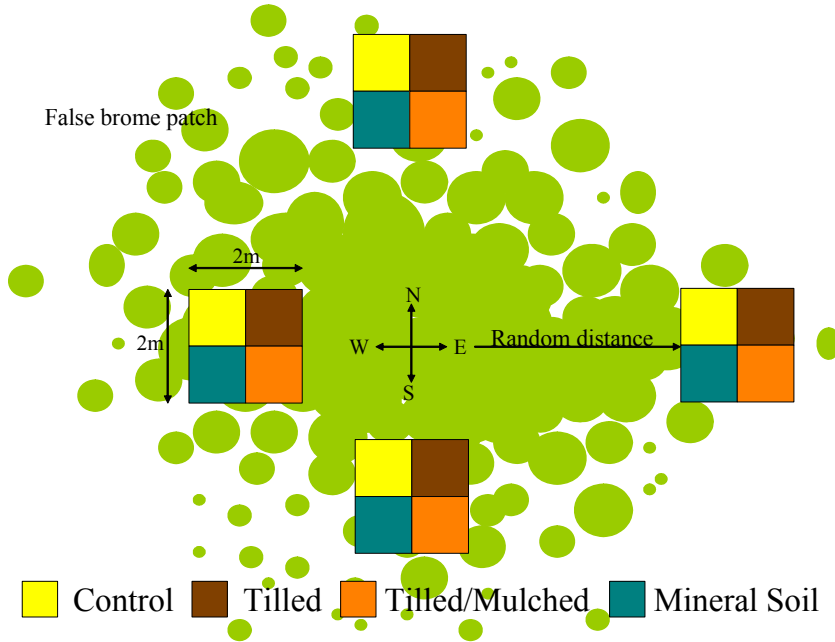
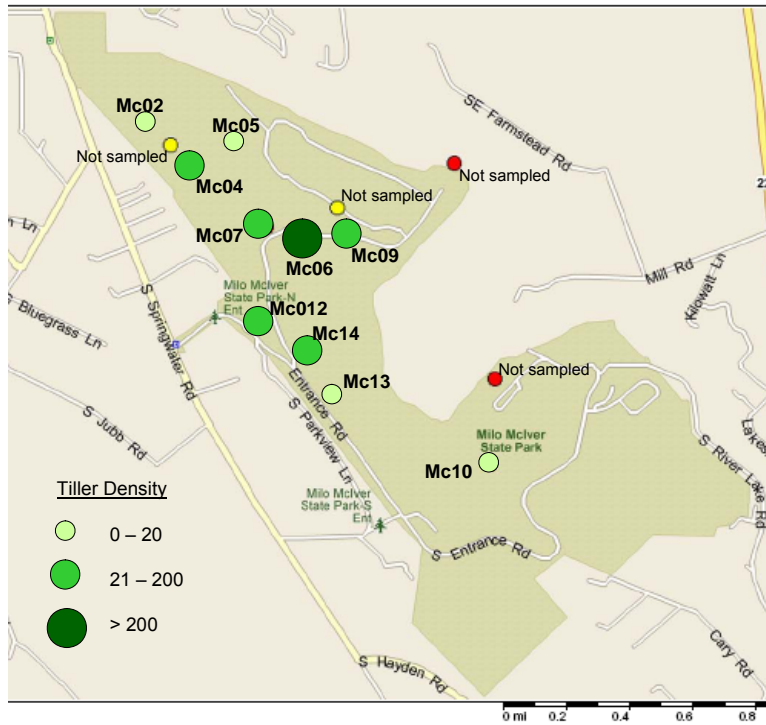


Figure 1 Study sites at Milo McIver State Park. Site markers become larger and darker green with increasing mean tiller density (top). Soil disturbance experiment study design showing one site (bottom).

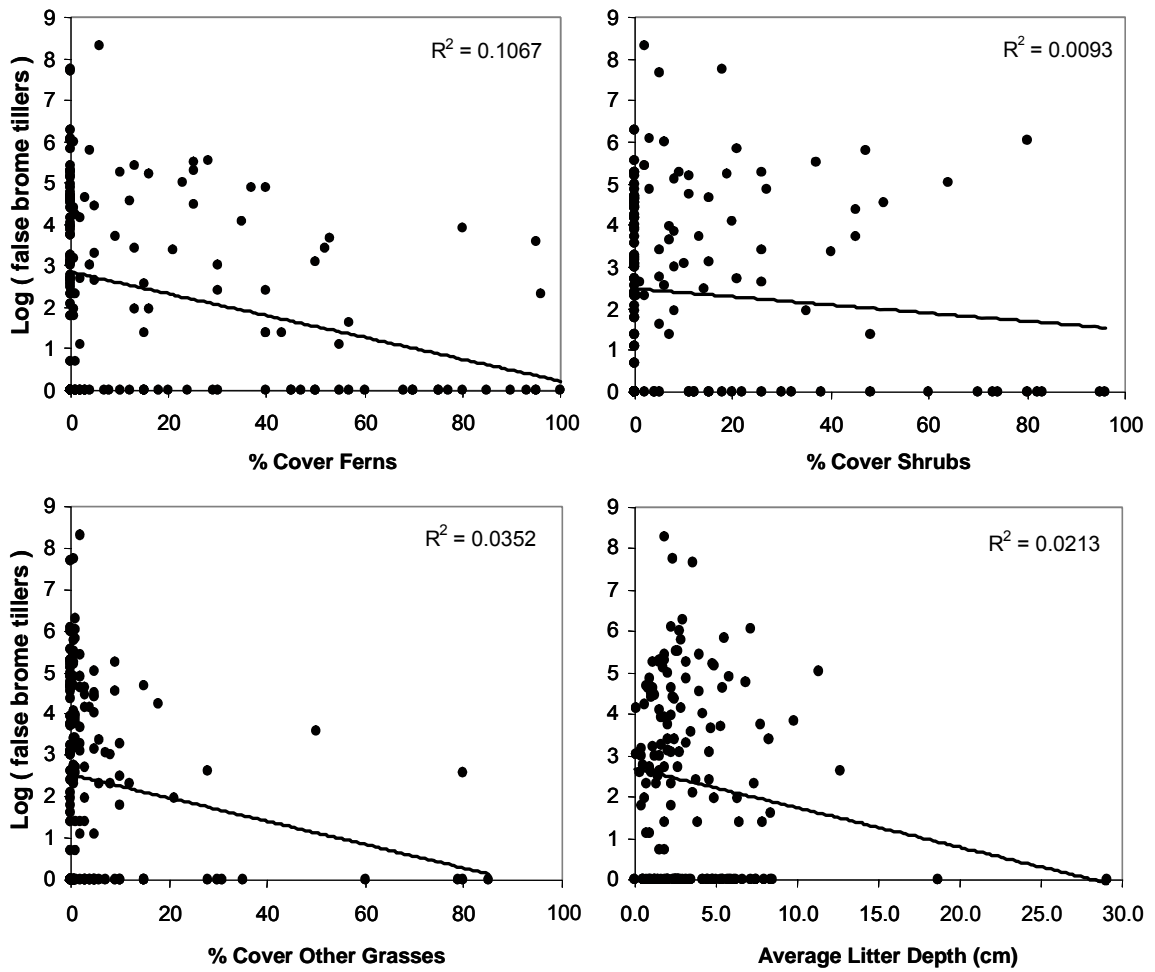


Figure 2 Ecological characterization of invasive *Brachypodium sylvaticum* habitat. Correlation between invasive *Brachypodium sylvaticum* tiller density (tillers/ m^2) and percent cover of ferns, shrubs, other grasses and litter depth.

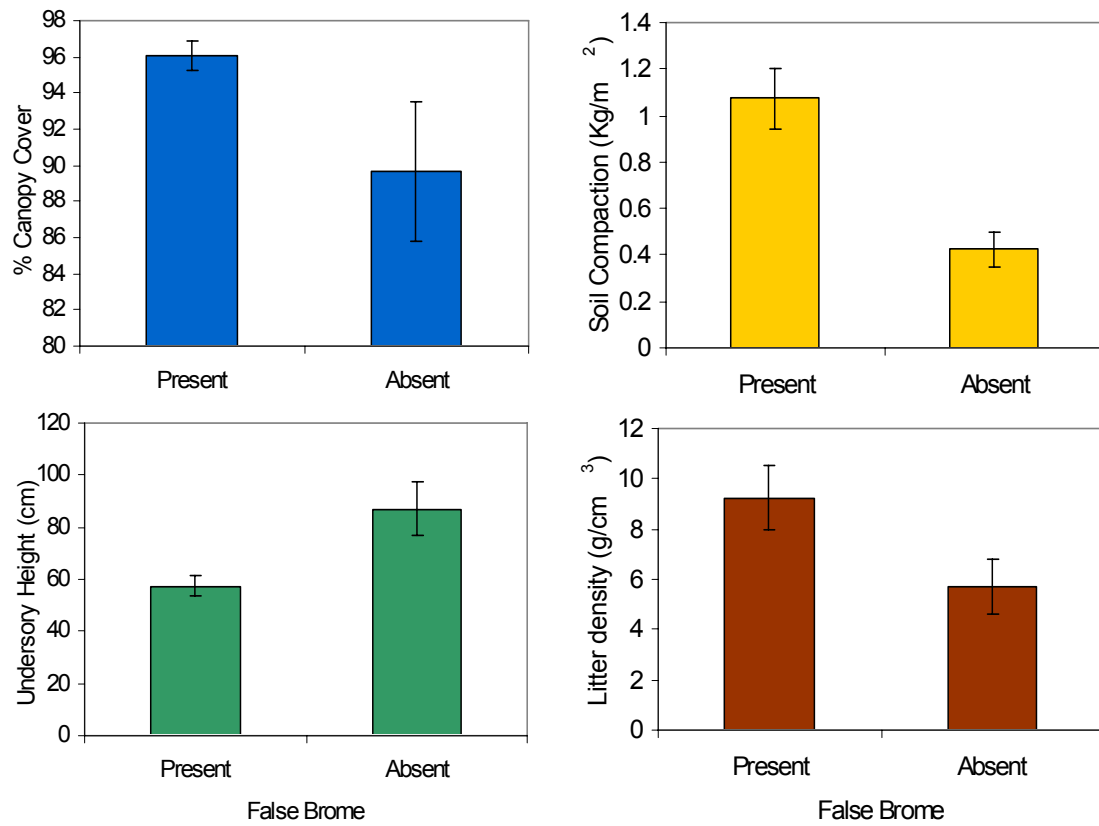


Figure 3 Means \pm one S. E. for canopy cover (top left), understory vegetation height (bottom left), soil compaction (top right) and litter density (bottom right) in forests where invasive *Brachypodium sylvaticum* was present or absent.

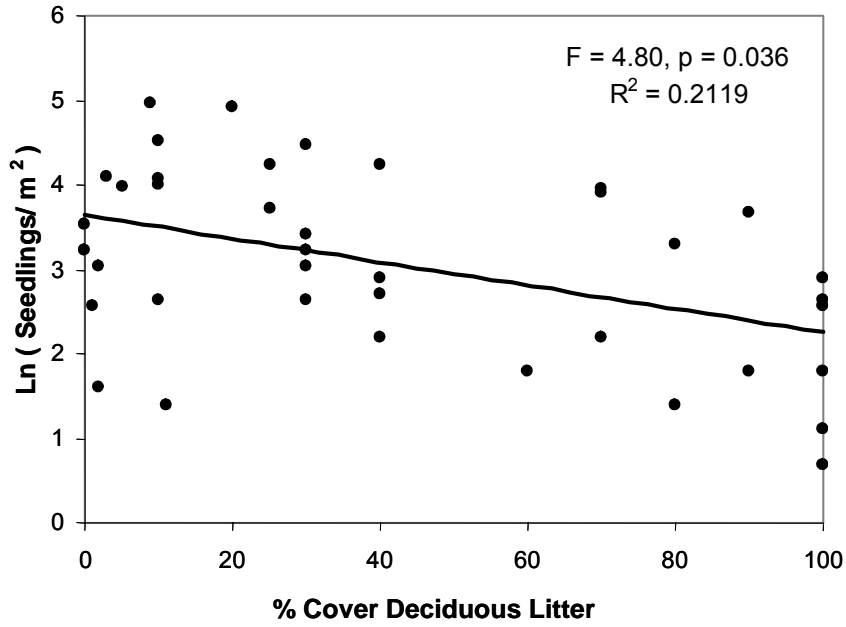


Figure 4 Negative correlation between invasive *Brachypodium sylvaticum* seedling density and the amount of deciduous litter covering the ground.

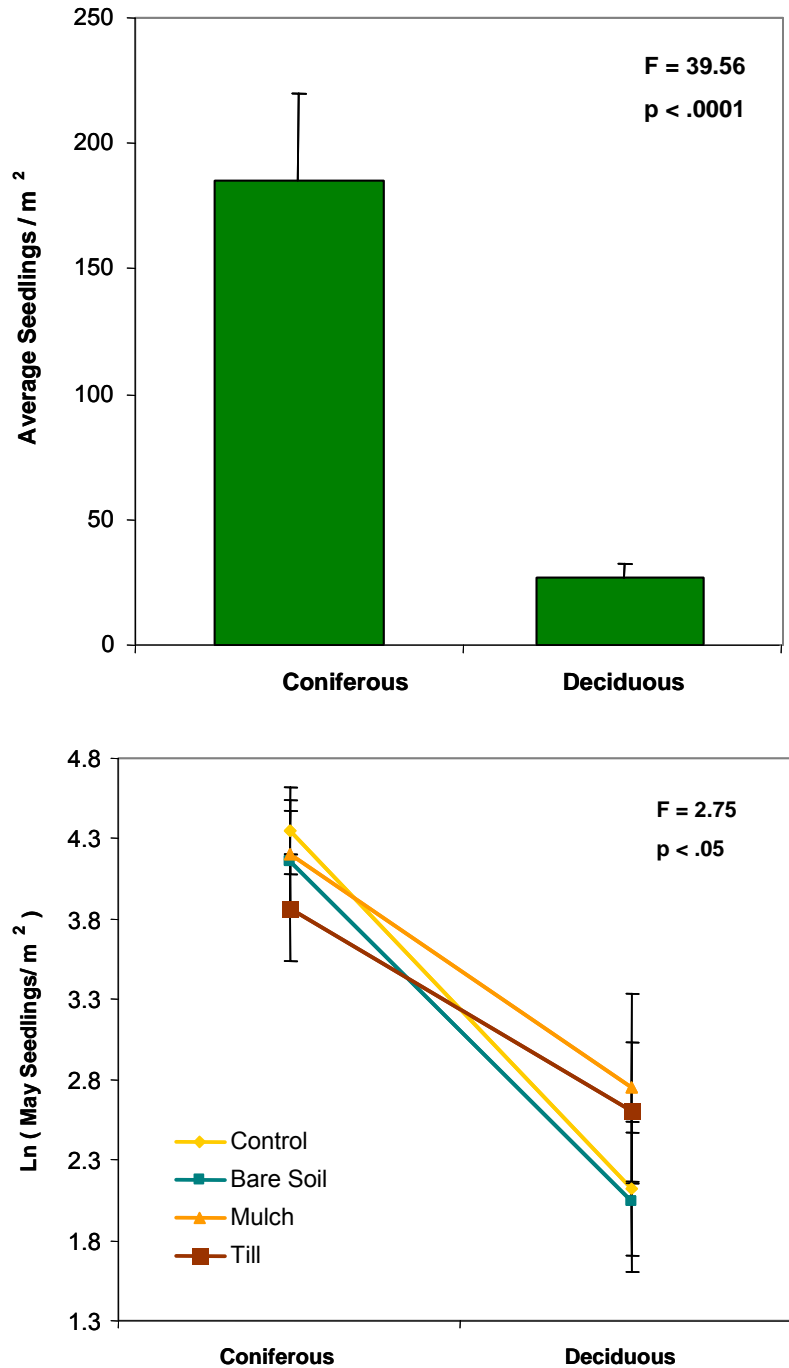


Figure 5 Effects of coniferous versus deciduous forest type on average invasive *Brachypodium sylvaticum* seedling density in experimental disturbance plots (top). Interaction between forest type and soil disturbance treatment in May (bottom). Error bars represent \pm one Standard Error.

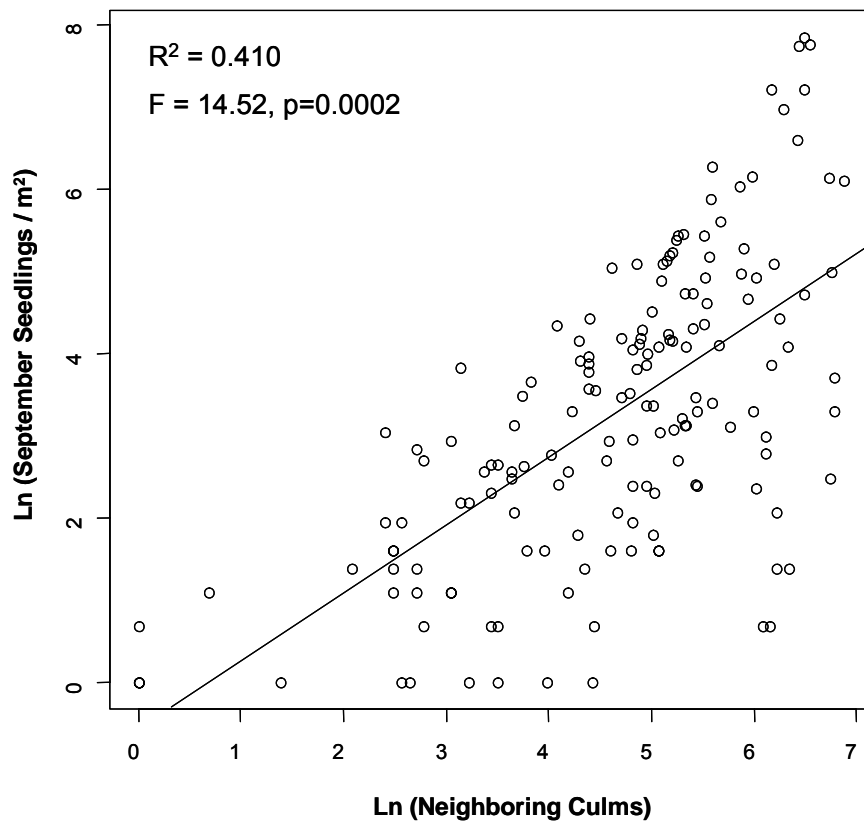


Figure 6 Effects of propagule pressure on invasive *Brachypodium sylvaticum* seedling density in experimentally disturbed plots.

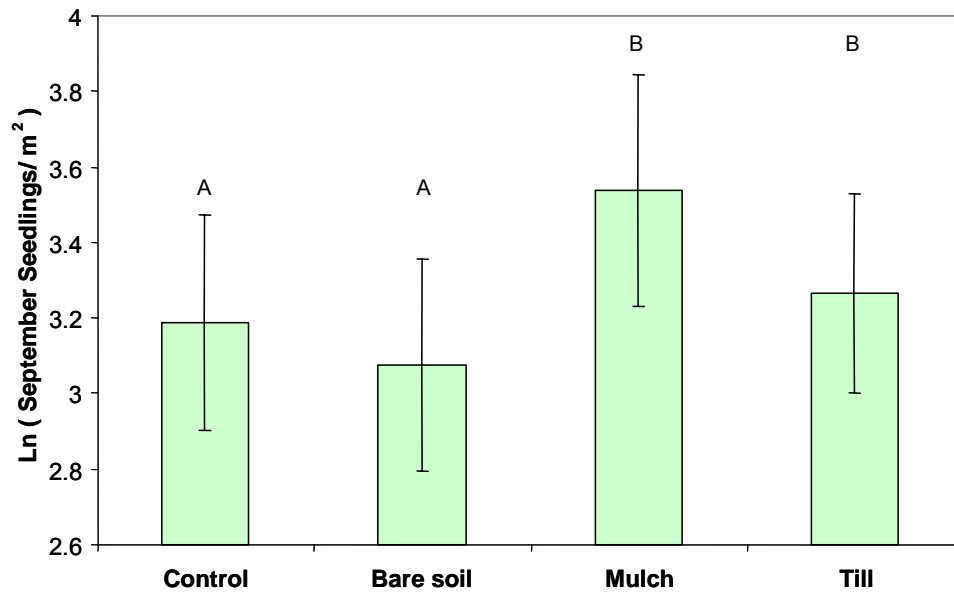


Figure 7 Effects of soil disturbance treatments on invasive *Brachypodium sylvaticum* seedling density in September. Means having the same uppercase letter are not significantly different from each other based on Tukey's multiple range test ($P < 0.05$). Error bars represent \pm one Standard Error.

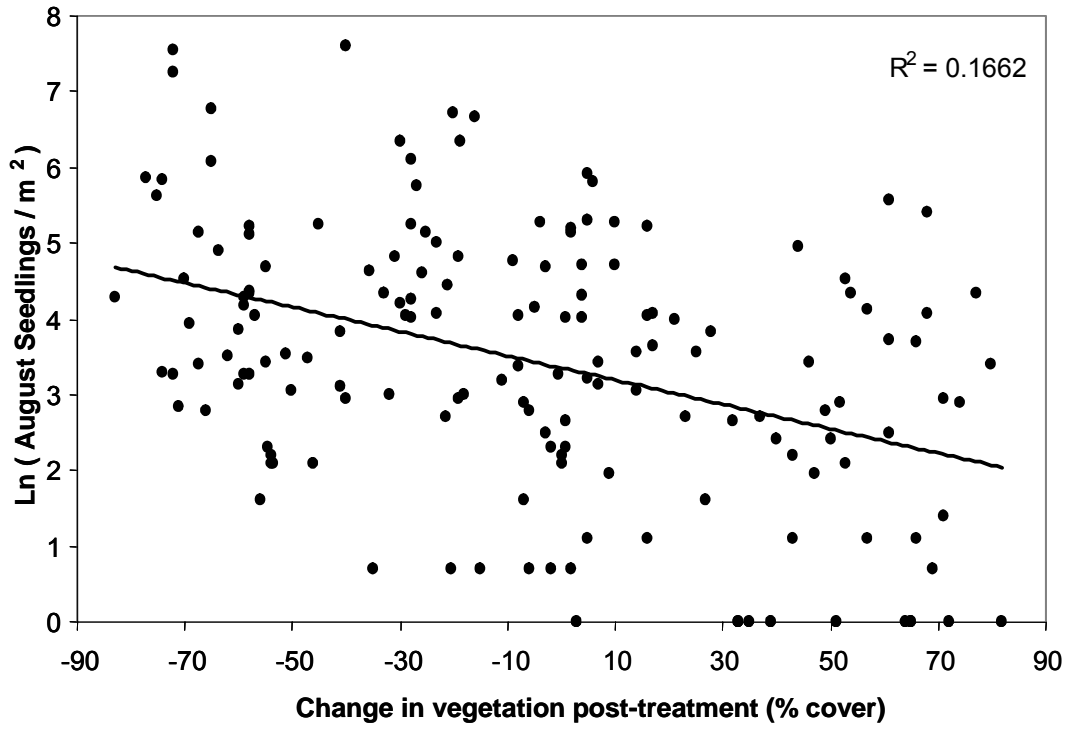


Figure 8 Effects of vegetation disturbance on the propagation of invasive *Brachypodium sylvaticum* seedlings in experimentally disturbed plots.

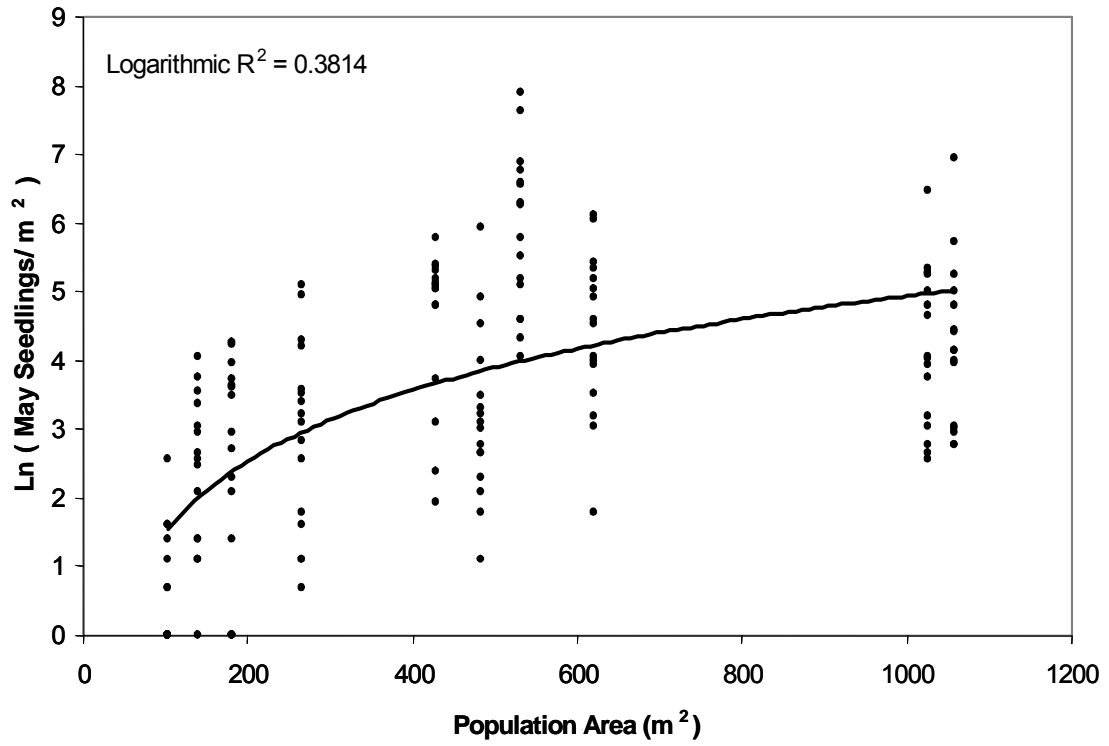


Figure 9 Logarithmic increase in invasive *Brachypodium sylvaticum* seedling density with increasing area occupied by each *B. sylvaticum* population.

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