

PLANTS TRAITS – A TOOL FOR RESTORATION?

ABSTRACT

Question: Most results of restoration efforts are species-specific and/or site-specific and therefore are not general enough to be easily applied to other species and other sites. Our research addresses the issue of species-specific results by investigating the feasibility of using plant traits instead of taxonomic species to characterize species responses to restoration treatments. Specifically, we test the explanatory power of plant traits, one necessary prerequisite for the development of predictive and general plant trait models.

Location: Ten remnant bunchgrass prairie sites in the Pacific Northwest of North America (Oregon and Washington, USA; British Columbia, Canada).

Methods: We developed two types of quantitative models for each of 10 prairie restoration sites: 1) plant trait models, which related plant traits to species field responses following restoration management treatments, and 2) species identity models, which related species taxonomic identity to species field responses following restoration management treatments. Species identity models determined the maximum amount of variability of field responses that can be explained by differences in individual species' responses to management treatments. Plant trait models determined what proportion of this explanatory power can be attributed to plant traits. This approach contrasts with approaches often used in other plant trait studies that describe how traits vary with environmental conditions.

Specifically, we used these two models to address the following questions: 1) How much of the variability in field responses of plants to restoration management treatments is explained by plant traits? 2) How well do plant traits explain the variability of field responses following restoration management treatments compared to models relating field

responses to species identity? Our approach was to measure two aspects of explanatory power: R^2 (variability explained) and AIC (a measure of model fit that accounts for parsimony, i.e., how well a model fits the data with relatively few explanatory variables).

Results: 1) The plant trait models (relating plant traits with plant field responses) explained much of the variability within each of the ten restoration sites, with R^2 values ranging between 31% and 69%. 2) The species identity models (relating species taxonomic identity with plant field responses) explained between 47% and 74% of variability in field performance (R^2). Thus, the plant trait models explained nearly as much variability as the species identity models.

In seven out of nine sites, the plant trait models were superior to the species identity models as measured by AIC; that is, the trait models did well at explaining variability with less model complexity (i.e., fewer explanatory variables).

Conclusion: Development of general and predictive plant trait models is a multi-step process. Strong explanatory power by plant trait models, both on an absolute scale and as compared to species identity models, supports the feasibility of using plant traits instead of species taxonomic identity as a common language to characterize plant field responses to restoration treatments. Such high explanatory power is one necessary pre-requisite for the development of predictive and general plant trait models.

Our results also indicate that the plant trait models are site-specific even though all sites were upland bunchgrass remnant prairies. We discuss the next steps in the development of more general and predictive models: incorporating environmental factors into the plant trait models to address the issue of site-specificity and testing the power of these models to predict vegetation responses.

INTRODUCTION

Restoration of native habitats is a critical strategy for biological conservation. Progress in the successful restoration of native habitats is slowed, however, by our inability to generalize and predict species responses to restoration management treatments. The scientific literature contains numerous studies describing the effects of restoration management treatments on vegetation, but the studies are often species-specific and site-specific. General patterns, which are necessary to develop predictions of the effects of management, are therefore difficult to identify.

One promising approach to address the issue of species-specific results is the use of plant traits as a common language to characterize plant responses rather than using taxonomic identity. Functional plant traits are well-defined characteristics (McGill et al. 2006) that relate to plant species' patterns of establishment, growth, and resource allocation and that evolved in response to abiotic environmental conditions and interactions with other species (Reich et al. 2003). Thus, functional plant traits are those that strongly influence a plant's performance (McGill et al. 2006).

Traits are universal (that is, all plants have traits), whereas plant species differ according to geographic location. As a result, focusing on species taxonomic identity hinders our ability to make ecological generalizations beyond sites with similar species composition. For example, restoration studies generally describe the responses of particular species to management treatments. It is difficult to generalize or compare these results to other results with different species. Overcoming this limitation requires simplification of species taxonomic identities to a more general level such as plant traits (e.g., Diaz et al. 2001).

The use of plant traits in ecological studies is not new (e.g., Raunkiaer 1934, Grime

1979, Nobel and Slatyer 1980). However, the recent focus of effects of global climate change on vegetation has renewed interest in simplifying long plant species lists into shorter lists of plant functional groups or plant traits, which also retain crucial ecological information. Renewed interest in use of plant traits is also demonstrated in the shift from the species identity approach to a plant trait approach in the classification and description of plant communities (e.g., Suding et al. 2003, Herault and Honnay 2007). However, much of the current research in the use of plant traits is aimed at developing links between plant traits and environmental change, such as responses to disturbance, climate change, succession, and grazing (e.g., Diaz et al. 1998, Lavorel et al. 1999, Diaz et al. 1999, Diaz et al. 2001, Garnier et al. 2004, Kahmen and Poschlod 2004, Nygaard and Ejrnaes 2004, Pakeman 2004, de Bello et al. 2005) or to specific ecosystem processes (e.g. Wardle et al. 1998, Lavorel and Garnier 2002, Quested et al. 2007, Quetier et al. 2007, Gross et al. 2008). These approaches are based on the hypothesis that plants with similar ecologically relevant traits respond similarly to environmental changes.

Relatively few studies have investigated the use of plant traits in the management and restoration of native habitats (Goodridge 2002, Gondard et al. 2003, Pywell et al. 2003, Roberts et al. 2010). A plant trait approach would allow us to develop models that show relationships between plant traits and plant species responses to restoration treatments, thus allowing the results of vegetation responses to management treatment to be reported or modeled as plant traits rather than by species names. Moreover, these trait-response relationships can also provide insight into the actual causes of vegetation change to restoration treatments.

Because a common list of plant traits facilitates recognition of patterns of species responses to management treatments and other disturbances among sites, ecologists have proposed a set of core plant traits, which were selected based on common challenges faced by plants: regeneration (dispersal and establishment), growth, and persistence (Weiher et al. 1999, Cornelisson et al. 2003). However, the final choice of traits to use in the development of a particular plant trait model should vary by which management treatment or other disturbance is to be predicted because plant traits reflect, either directly or indirectly, mechanisms responsible for plant responses. In addition, standardization in the measurement of plant traits will facilitate comparisons of trait responses between different vegetation types with respect to restoration management treatments (Hendry and Grime 1993; McIntyre et al. 1999, Weiher et al. 1999, Diaz et al. 2001, Cornelissen et al. 2003, Garnier et al. 2007). One result of the standardization of plant traits is the increasing number of easily available and accessible plant traits databases all over the world (Klimesova and Klimes 2007, Lui et al. 2008, Kleyer et al. 2008).

Research Goal and Objectives

Our research addressed the issue of species-specific results by investigating the feasibility of using plant traits as a common language instead of taxonomic species to characterize species responses, thus allowing results to be applied more generally, i.e., results are not limited to individual species. Our approach was to develop two types of quantitative models for each of 10 bunchgrass prairie restoration sites: 1) plant trait models, which related plant traits to species field responses following restoration management treatments, and 2) species identity models, which related species taxonomic identity to species field responses following restoration management treatments. Plant trait models were designed to determine

the amount of variability in field responses that is explained by plant traits. Species identity models were designed to determine the maximum amount of variability in plant field responses that is explained due to differences in species.

Species identity models would be expected to fit observed data well, but could not be used to compare results between sites that do not share similar species. Plant trait models could potentially be used to compare results between sites that do not share similar species. If the plant trait models and the species identity models have similar explanatory power and the plant trait model is more parsimonious (i.e., fewer explanatory variables), then plant trait models would be the preferred model, i.e., an entire species list can be reduced to a subset of key functional plant traits.

Specifically, we used the two models to answer the following questions:

- 1) How much of the variability in field responses of plants following restoration management treatments is explained by plant traits?
- 2) How well do plant traits explain the variability of field responses of plants to restoration management treatments compared to models relating field responses to species identity?

This approach contrasts with approaches often used in other plant trait studies that describe how traits vary under different environmental conditions (e.g., Diaz et al. 1999, Pakeman 2004, and de Bello et al. 2005). Our study seeks to investigate the explanatory power of plant traits under different environmental conditions (i.e., restoration treatments).

METHODS

Study sites, restoration treatments, and measurement of plant field responses

In 2005, we began a long-term study to develop and evaluate strategies for restoring bunchgrass prairies invaded by non-native weeds (particularly non-native perennial grasses),

and that can be applied effectively throughout the Pacific Northwest (Stanley et al. 2008). The study was designed to test five combinations of restoration treatments (Appendix A).

Identical experimental blocks were established within prairie habitats at ten sites in the Pacific Northwest – 3 in Oregon (USA), 6 in Washington (USA), and 1 in British Columbia (Canada). The management treatments (Appendix A), which were developed collaboratively by scientists and land managers from The Nature Conservancy, Institute for Applied Ecology and several partner organizations, included combinations of application of sethoxydim, a grass-specific herbicide (2% solution with surfactant) to reduce dominant exotic grasses; spring or fall mowing to reduce thatch, weed seed production, and stored reserves of exotic grasses; prescribed burning, to reduce thatch and moss and prepare seedbeds for germination; and post-burn application of glyphosate, a broad-spectrum herbicide (1.5% solution, 2 to 4 wk post-burn) to reduce broadleaf non-native weeds that typically resprout quickly after fire compared to native species. These treatments were applied in various combinations over 4 years, along with a no-treatment control, to 5m × 5m plots, which were replicated 4 times at each site (total: 20 plots at each site).

To determine plant responses to the management treatments, cover of each plant species was measured before any restoration treatments in spring 2005 in four 1m × 1m sampling quadrats in each of the 5m × 5m plots. Cover measurements were repeated in spring of 2007 after two years of annual management treatments. Cover was assessed visually, using calibrated templates, to the nearest 1% in each sampling quadrat.

Plant traits measurements and database

Plant traits were measured on the species in the vegetation plots from the restoration project sites described above. Criteria for final inclusion as a target species for plant trait

measurements included abundance at project sites, seed availability, and whether the species could be grown from seed in the growth chamber. Of the 142 species encountered in the plots at the ten research sites, the 42 species (Appendix B) included in the analysis accounted for an average of about 2/3 of the total cover (Table 1).

Using plant traits lists by Weiher et al. (1999) and Cornelissen et al. (2003) as guidelines, we selected 27 plant traits that in our judgment best reflected the mechanisms of the plant responses to our restoration treatments (Table 2). Plant trait data came from several sources. We made the following plant measurements under controlled conditions (growth chamber) using the protocols of the Integrated Screening Programme (Hendry and Grime 1993), which consist of a range of standardized laboratory-based procedures: specific leaf area, leaf area ratio, leaf mass ratio, aboveground biomass, belowground biomass, root-shoot ratio, relative growth rate, and unit leaf rate (Table 2). In addition to these growth chamber measurements, average seed mass for each species was calculated from measurements made on 10 replicates per species (each replicate consisted of 10 seeds). For the other plant traits, we used values readily available in the published literature, including local floras, reference books, and databases. Missing data were infrequent, about 2% of the data. These plant trait data were all included in our database, The Willamette Valley Prairie Plant Trait Database, which includes species from the entire Pacific Northwest region (Wilson 2006).

For a trait to be useful in explaining plant performance, the trait must vary widely between different species. Among the quantitative traits, phenological traits tended to have some of the lowest variation (coefficients of variation [CV] of 0.12 – 0.50), reflecting how most species are synchronized to the seasons of water availability and warm growing conditions. Traits of size under standardized growing conditions tended to show some of the

highest variation: aboveground biomass (CV = 1.2), root biomass (CV = 1.1), and leaf area (CV = 2.9). Growth rates and ratios, such as relative growth rate and specific leaf area, tended to have intermediate levels of variation. A measure of the useful variation within categorical traits is Hill's Index ($I_1 = e^{H'}$), where e is the base of natural logarithms and H' is the Shannon-Weiner diversity index (Hill 1973). Variation was high within many categorical traits, such as growth form ($I_1 = 3.6$), clonality ($I_1 = 4.3$), and dormancy breaking mechanism ($I_1 = 4.8$). Overall, for both quantitative and categorical traits, the study species showed more than ample variation in traits.

Methods of analysis

Variable selection, variable reduction

Three traits were excluded before further variable selection. Nitrogen fixing was discarded because nearly all plants were not. Mass of roots at 21 days was combined with aboveground biomass to create a new variable total biomass at 21 days. A third trait, root-shoot allometric coefficient, was excluded because of too many missing values.

Several of the remaining plant trait variables contained overlapping information. The inclusion of such redundant (collinear) variables causes statistical problems, such as inflated standard errors, reduced power, and arbitrary model structure (Harrell 2001). To avoid such problems, we performed a hierarchical cluster analysis (*varclus* procedure of S-Plus; Harrell 2001) based on the nonparametric similarity of the remaining trait variables. Similarity was measured as Spearman's rank correlation (r_s). Clusters were defined as having a joint correlation of $r_s > 0.6$. Hierarchical cluster analysis identified six clusters of variables and ten individual variables, each showing no strong correlation with all other traits. A single trait was chosen to represent each cluster based on two criteria: The trait had to 1) have data

for all species in the database, and 2) have previously demonstrated usefulness in the literature. In addition, flowering peak month was augmented with its square to allow for non-linear effects in this phenological variable. Thus, the final list of variables for statistical analysis consists of 17 plant trait variables (Table 3). Note that the response variable (the field performance of plants) played no role in variable selection.

Transformations

Analysis of Box-Cox transformations (Venables & Ripley 1999, Kutner et al. 2005) showed that the square-root transformation was the best transformation at fitting the assumptions of the statistical models. Therefore we used as our measure of field performance

$$(\text{Cover in 2007})^{1/2} - (\text{Cover in 2005})^{1/2}$$

We calculated this measure for every species within each quadrat. Only one explanatory variable (seed mass) was transformed to meet standard statistical assumptions. Residuals were acceptably homoscedastic and approximately normally distributed in all cases.

Statistical analyses

We tested the power of a series of linear models to explain field performance of species identity and plant traits. Our models testing the explanatory power of species identity were of the form of analyses of variance:

$$(\text{Cover in 2007}_i)^{1/2} - (\text{Cover in 2005}_i)^{1/2} = b_0 + b_1 \text{Identity}_i + b_2 \text{Treatment} + b_3 \text{Identity}_i \times \text{Treatment},$$

where i refers to each species included together in the analysis. Our models testing the power of plant traits required a stepwise approach. For each site analysis, all 17 plant-trait variables and their interaction with the treatment variable were examined, using the forward stepwise procedure in S-Plus, which includes variables based on their ability to decrease the

AIC value. AIC measures the fit of a model, penalized by model complexity. AIC value could not be calculated for one of the sites (Scatter Creek) because of an unbalanced analysis matrix. Incomplete distribution of categories of traits across the ten sites prevented a single analysis using site as a categorical variable. We analyzed instead each site individually.

Phylogenetic correction

The 42 species in this analysis are unevenly distributed across 14 families, with the Poaceae (14 species) and the Asteraceae (nine species) most common. Disproportionate representation by some families could result in phylogenetic relationships influencing the search for links between plant traits and field performance (Felsenstein 1985, Harvey and Pagel 1991). We chose not to include phylogenetic correction in our analysis for three reasons. First, many difficulties imposed by phylogenetic relatedness – such as bias in parameter estimation and overestimation of statistical significance – are of less concern because our prime objective is to examine whether traits can be related to field performance under experimental and replicated conditions, rather than to generalize the relationships. Also, controversy remains about the philosophy behind the correction (Westoby et al. 1995) and the methodology of implementation (Felsenstein 1985, Freckleton et al. 2002, Desdvises et al. 2003, Sol et al. 2008). Finally, a recent survey found that phylogenetic correction was necessary in only 10% of the cases involving plants (Cavalho et al. 2006).

RESULTS and DISCUSSION

Most results of restoration efforts are species-specific and site-specific and therefore not general enough to be easily applied to other species and/or other sites. Our research addressed the issue of species-specific results by investigating the feasibility of using plant traits instead of taxonomic species, which allows results to be applied more generally, i.e., results are not limited to only the species included in the study.

We used two models (a species identity model and a plant trait model) for each of 10 bunchgrass prairie restoration sites to address the following two questions:

1) How much of the variability (R^2) in field responses of plants to restoration management treatments is explained by plant traits? The plant trait models (relating plant traits with plant field responses) for each of the ten restoration sites explained a relatively large amount of variability compared to most ecological studies, with R^2 values ranging between 31% and 69% (Table 4). The explanatory powers of these traits models are as large as or larger than those reported by Peek et al. (2003) in their review of a broad range of ecological studies. Traits contributed between three-fourths to nearly all of the variability explained by these models (Table 4). Therefore, the performance of the trait models does reflect the ability of traits to capture changes in plant cover.

2) How well do plant traits explain the variability of field responses to restoration management treatments compared to models relating field responses to species identity? We measured two aspects of explanatory power: R^2 and AIC. Because the species identity models let each taxonomic species vary independently, they explain, for this experimental design, the maximum amount of variability due to differences in species responses to the management treatments. The R^2 values of these species identity models were high, ranging between 47% and 74% (Table 4). The plant trait models explained nearly as much variability *proportionally* (between 0.60-0.93) as the species identity models (Table 4).

In seven out of nine sites (Table 4), the plant trait models were more superior to the species identity models, as measured by AIC, a value that balances explanatory power and model complexity. Smaller values of AIC indicate better performance, that is, greater explanatory power after accounting for number of explanatory variables.

Using plant traits provides a basis for more general models of plant response by allowing application of results to species not included in a study. Our results demonstrate that plant traits explain the variability almost as well as do taxonomic species, thus allowing the results of vegetation responses to management treatments to be reported or modeled as plant traits rather than by species names. This relatively high explanatory power of the plant trait models, as shown by the relatively high R^2 values over ten different sites, is a prerequisite for their usefulness in predicting plant responses to restoration treatments.

The relatively high R^2 values also demonstrate that the traits selected for the models were highly relevant to field performance. Plant traits studies frequently focus on the role of single traits. However, it is unrealistic to expect that a single trait would reflect a complex field response to restoration management treatments. Multiple trait analyses, such as done in this study, are likely to have greater explanatory power and generality (Kuster et al. 2008, Roberts et al. 2010).

Even though these plant trait models showed relatively high explanatory power, they are descriptive models and thus, no causation between plant traits and field responses can be inferred. Note that the coefficients cannot be used to interpret direction of effect because of statistical constraints with multivariate analyses. However, these models provide a clear description of the relationship between plant traits and the field plant responses, which can be a starting point for testing hypotheses about mechanisms.

Different traits were included in each of the ten site models, resulting in a total of 17 different plant traits (Table 5). As a result, any given trait variable was used in one to six of the site models, and site models included between two and six trait variables (Table 5). The most common trait found in all ten models was clonality (six of ten sites) (Table 5). The next

most common traits (four of ten sites) were dormancy breaking mechanism, seed germination rate, and seed mass. Seven traits interacted with the restoration treatments; clonality was the most common, interacting with the restoration treatments in 4 out of 6 sites where it was included in the model (Table 5). All traits had adequate variability to serve as powerful explanatory variables.

Comparisons of plant traits found in plant trait models between sites need to be carefully done. The absence of a particular trait in a model is not necessarily due to its lack of biological importance, but from statistical procedures that reward parsimony. Thus, the presence of a trait in multiple models does indicate a pattern, but absence of a trait does not necessarily indicate a pattern.

Although statistical constraints prevented a direct test of the consistency of trait models across sites, our results show that the models differed at each site, even though all sites were upland bunchgrass prairie sites. Because we screened traits so that they were orthogonal, i.e., mutually independent, model differences across sites are likely due to differing underlying biological relationships among traits, treatments, and environmental conditions. One approach to address this issue of site-specificity is to incorporate environmental factors, thus potentially allowing application of the plant trait model to more than one site. Moreover, much of the remaining unexplained variability is likely to be caused by within-site variation in abiotic conditions and biotic interactions. Thus, incorporating environmental factors explicitly within a plant trait model could significantly increase its explanatory power.

Several issues need to be considered when incorporating environmental factors. We indirectly accounted for post-treatment environmental factors in the plant trait models of this study by incorporating management treatments (different regimes of mowing, herbicide

application, and prescribed fire) as explanatory variables. Treatment categories served as composite surrogates for measurement of individual environmental factors.

Another approach for incorporating initial abiotic environmental conditions in plant trait models is to use a core list of abiotic environmental "traits," as has been done for plants. Standardization of measurements of these abiotic environmental "traits" will facilitate comparisons of plant responses to management treatments at different sites and different times, leading to the generalization of plant responses patterns. It is also critical that the measurements are either readily available or easily and quickly measured, particularly because the measurements might need to be made repeatedly to detect changes over time. The list of standardized measurements for core abiotic factors suggested by Garnier et al. (2007) is a notable step in this direction. Most suggestions for standardized abiotic measurements have focused on changes between sites along broad environmental gradients. The core list of abiotic factors for plant trait models used by restoration managers should also account for the subtle but crucial changes in abiotic factors over time at a single site during the restoration process.

Due to their complexity, biotic interactions, such as plant-plant interactions and interactions between plants and predators, herbivores, pathogens, and mutualists, are more difficult to quantify and to incorporate into plant trait models. However, strong quantitative relationships between plant traits and biotic interactions, e.g., plant-herbivore and plant-plant have been demonstrated (Wardle et al. 1998). In particular, Gross et al. (2009) used a trait based framework to successfully demonstrate that the outcomes of plant-plant interactions (competition and facilitation) at an individual level are linked to specific plants traits, which are linked to plant community structure (defined as the distribution of trait values at the

community-level). McGill (2006) has suggested modeling biotic interactions as a "milieu", defined operationally as a frequency distribution of traits that are important for a given type of interaction, e.g., the frequency distribution of heights of plant individuals could estimate plant-plant competition for light at a given site. Biotic associates could be described by species, or preferably by traits, weighted by abundance (e.g., Moretti and Legg 2009).

Model application

Once such models are developed that show high explanatory value then the next, critical step in the development of plant trait models as tools for habitat restoration is testing the ability of such models to predict plant responses to management treatment at different times and places, with different species (Webb et al. 2010). For example, these plant trait models can be applied as a restoration tool by helping a land manager choose the best management treatment for promoting the abundance of native species within a plant community, while simultaneously inhibiting the abundance of the non-native species. In straightforward approach response values are calculated by the model after incorporation of the required plant trait values for each of several species of interest. This procedure is repeated for each management treatment under consideration. The results form a matrix of response values by species and management treatment. The sum of the response variables of the native species less the sum of the response variables of the non-native species indicates the efficacy of a treatment to meet the management goal of promoting native species over non-native species. Field measurements of the relative changes in cover can be compared to the predicted responses from the plant trait models to test the validity or power of the model.

Conclusion

Development of general and predictive plant trait models is a multi-step process. Using plant traits allows application of results to species not included in the study. Our results demonstrate that plant traits have strong explanatory power of field responses, explaining the variability almost as well as do species taxonomic identity, thus allowing the results of vegetation responses to management treatments to be reported or modeled as plant traits rather than by species names. Although there was some similarity in the traits between the different site models, each site model included a different suite of plant traits. This pattern suggests that differences in initial environmental factors affected the vegetation response to management treatments. Thus, the next step in development of more general models to predict vegetation responses to restoration treatments is to incorporate environmental factors, allowing application of the plant trait model to more than one site. Once such models are developed that show high explanatory value, then the power to predict vegetation responses needs to be tested (Webb et al. 2010).

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Table 1. Average cover (%) of study species combined for each restoration treatment at each of the 10 study sites in 2005 (before restoration treatments) and the proportion of average combined cover of study species to average total plant cover of research plots at each of the 10 study sites. (See Appendix A for description of treatments.)

Site	Treatments					Average cover of study species for all treatments	Proportion of cover of study species to cover of all measured species
	1	2	3	4	5		
Bellfountain	65.1	48.2	35.1	63.3	43.2	51.0	55.9%
Cowichan	55.4	58.8	56.3	50.6	65.5	57.3	58.8%
Glacial	35.3	30.1	34.9	37.7	26.9	33.0	62.3%
Hoskins	43.9	44.3	52.1	61.5	53.9	51.1	64.9%
Mima	36.6	46.8	40.1	50.6	38.5	42.5	90.3%
Morgan	17.9	19.6	17.5	23.0	20.6	19.7	52.6%
Pigeon	58.7	47.8	39.5	38.9	44.9	46.0	69.1%
Scatter	43.4	37.2	35.6	40.4	37.9	38.9	79.1%
Triangle	32.2	38.0	32.9	42.6	27.4	34.6	75.2%
Weir	9.2	10.4	8.3	15.9	16.6	12.1	30.7%

Table 2. Description of plant traits and categories used in the final analysis. The abbreviations used are: A = area, M = dry mass, L = leaf, R = root, S = shoot (leaf + stem), T=total plant; subscripts 1 and 2 indicate initial time (7 days) and time 2 (21 days) of measurement, respectively. Data type: C=categorical, Q=quantitative.

Trait	Data type	Choices for categorical data	Notes for quantitative data
Clonality	C	clonal aboveground, clonal belowgr. short, clonal other, clonal bulbs or corms, clonal rhizomes, clonal abovegr. short, clonal belowgr. long, clonal abovegr. long, clonal tubers, non-clonal, unknown	
Diaspore feature	C	mucilage, minute, pappus or h=air, balloon, Wing, elaiosome, hook or barb, fleshy, fruit, none awn	
dispersal peak month	Q		Month (Jan = 1) that has the most dispersal
dormancy breaking mechanism	C	not fire, light, after-ripening, fire, not dormant, not stratification, stratification, not light, scarification not scarification, not after-ripening	
flowering peak month	Q		Month (Jan = 1) that has the most flowering
germination peak month	Q		Month (Jan = 1) that has the most germination
germination rate	Q		
growth form (C)	C	climber or scrambler, cushion, erect leafy, long basal, other, palmoid, prostrate, semi-basal, short basal, short succulent, tall succulent, tussock (Cornelissen et al. 1996)	
growth form (standard)	C	dicot forb, fern, graminoid, monocot forb, shrub, suffrutescent, tree, vine	
habitat	C	riparian, upland prairie, wetland prairie, wetland, woodland	
maximum height	Q		
leaf area of 21 day seedling	Q		L _A (measured under standardized conditions (Hendry and Grime 1993))

leaf area ratio	Q		L_A / T_M (measured under standardized conditions (Hendry and Grime 1993))
leaf mass ratio	Q		L_M / T_M (measured under standardized conditions (Hendry and Grime 1993))
leaf shape	C		
life form	C	phanerophyte, chamaephyte, hemicryptophyte, geophyte, therophyte	
shoot mass of 21 day seedling	Q		S_M (measured under standardized conditions (Hendry and Grime 1993))
root + shoot mass of 21 day old seedling	Q		$R_M + S_M$ (measured under standardized conditions (Hendry and Grime 1993))
perenniality	C	annual, annual/biennial, biennial, facultative perennial, perennial	
reproductive schedule	C	monocarpy, polycarpy	
relative growth rate	Q		$(\log_e T_{M2} - \log_e T_{M1}) / (t_2 - t_1)$ (measured under standardized conditions (Hendry and Grime 1993))
root system	C	fibrous, tap	
seed mass	Q		
specific leaf area	Q		L_A / L_M (measured under standardized conditions (Hendry and Grime 1993))
stem arrangement	C	single upright, multiple upright, creeping	
unit leaf rate	Q		$(T_{M2} - T_{M1} / t_2 - t_1) \times$ $(\log_e L_{A2} - \log_e L_{A1} / L_{A2} - L_{A1})$ (measured under standardized conditions (Hendry and Grime 1993))
where native	C	Willamette Valley, other North America, South America, Europe, Asia, Eurasia, Africa, cosmopolitan	

Table 3. Results of hierarchical cluster analysis, which was conducted to identify clusters of closely related trait variables, and to select the trait variable that best represents the underlying biological trait associated with cluster. Each of the six clusters was represented by a single trait variable; in addition, flowering peak month was supplemented with its 2-degree polynomial. The final list of variables for statistical analysis consists of 17 plant trait variables. (See Table 2 for complete description of the traits.)

Cluster name	Representative variable	Other variables in cluster
Size	root + shoot mass of 21 day old seedling	shoot mass of 21 day seedling, leaf area of 21 day seedling
RGR	relative growth rate	leaf mass ratio
SLA	specific leaf area	leaf area ratio
Phenology	flowering peak month, flowering peak month ²	dispersal peak month, germination peak month
Growth form	growth form (C)	diaspore feature, growth form (standard), root system
Perenniality	perenniality	reproductive schedule (i.e., monocarpy or polycarpy), life form
Height	maximum height	
Germ.	germination rate	
Seed mass	seed mass	
Dormancy	dormancy breaking mechanism	
ULR	unit leaf rate	
Habitat	habitat	
Stems	stem arrangement	
Clonality	Clonality	
Nativity	where native	
Leaf shape	leaf shape	

Table 4. Comparison of species identity models and plant trait models for each of ten remnant native bunchgrass prairie sites in the Pacific Northwest. Species identity models relate species taxonomic identity to plant responses following restoration management treatments. Plant trait models relate plant traits to plant responses following restoration management treatments. Treatment R^2 is the proportion of variability explained by treatments for each of the species identity models and for each of the plant traits models. R^2 is the overall proportion of variability explained by the model. The difference between treatment R^2 and overall R^2 is the amount of variability explained by species in the species identity models and explained by traits in the plant trait model. AIC is a statistical test that balances explanatory power and model complexity. Smaller values of AIC indicate greater explanatory power after accounting for parsimony (i.e., number of explanatory variables). *The better model is based on greater explanatory power and parsimony. **AIC value could not be calculated for the Scatter site because of an unbalanced analysis matrix.

Site	Treatment R^2	Species Identity Models		Plant Traits Models		Is trait model better? *
		R^2	AIC	R^2	AIC	
Bellfountain	0.02	0.51	1495.1	0.34	1494.5	Yes
Cowichan	0.03	0.74	744.0	0.69	734.3	Yes
Glacial	0.03	0.72	775.2	0.64	768.1	Yes
Hoskins	0.02	0.51	1092.6	0.41	1104.2	No
Mima	0.09	0.48	975.4	0.37	954.3	Yes
Morgan	0.07	0.49	585.0	0.38	565.0	Yes
Pigeon	0.05	0.52	1337.3	0.37	1285.1	Yes
Scatter	0.02	0.55	1001.9	0.45	**	NA
Triangle	0.05	0.51	1122.8	0.31	1124.0	No
Weir	0.04	0.47	669.1	0.39	631.1	Yes

Table 5. Plant traits included in the final models that relate plant traits to plant responses following restoration management treatments for each of ten remnant native bunchgrass prairie sites in the Pacific Northwest. "Forced" indicates that variable is required to be in model. "Main" indicates that the trait was an explanatory variable in the model. "Interaction" indicates treatment-trait interaction. *The variable *seed mass* received a square root transformation.

Site	Treatment	Clonality	Dormancy breaking mechanism	Growth form	Habitat	Leaf shape	Perenniality	Stem arrangement	Where native	Flowering peak month
Bellfountain	forced		Main and interaction							
Cowichan	forced	Main							Main and interaction	
Glacial	forced	Main and interaction		Main	Main					
Hoskins	forced		Main and interaction				Main			
Mima	forced	Main and interaction				Main				
Morgan	forced	Main and interaction								
Pigeon Scatter	forced forced	Main	Main and interaction	Main			Main	Main		
Triangle Weir	forced forced	Main and interaction	Main	Main			Main			Main
Number (of sites)		6	4	3	1	1	3	1	1	1

Site	(Flowering peak month) ²	Germination rate	Maximum height	Seed mass*	Relative growth rate	Specific leaf area	Unit leaf ratio	Shoot +root mass of 21 day seedling	Number (of 17 traits)
Bellfountain		Main		Main and interaction	Main				4
Cowichan		Main				Main			3
Glacial				Main					5
Hoskins		Main		Main					4
Mima			Main						3
Morgan							Main		2
Pigeon				Main				Main and interaction	5
Scatter		Main and interaction							3
Triangle	Main				Main and interaction			Main	6
Weir									2
Number (of sites)	1	4	1	4	2	1	1	2	

Appendix B

The species used for analysis (n = 42).

Symbol Key	Full species name
ACMI2	<i>Achillea millefolium</i>
AGGR	<i>Agoseris grandiflora</i>
AICA	<i>Aira caryophylla</i>
ANMI3	<i>Antennaria microphylla</i>
ANOD	<i>Anthoxanthum odoratum</i>
AREL3	<i>Arrhenatherum elatius</i>
BRCO3	<i>Brodiaea coronaria</i>
BRCA5	<i>Bromus carinatus</i>
BRHO2	<i>Bromus hordeaceus</i>
CAQU2	<i>Camassia quamash</i>
CATU3	<i>Carex tumulicola</i>
CEAR4	<i>Cerastium arvense</i>
CYEC	<i>Cynosurus echinatus</i>
DAGL	<i>Dactylis glomerata</i>
DACA3	<i>Danthonia californica</i>
DASP2	<i>Danthonia spicata</i>
DACA6	<i>Daucus carota</i>
ELGL	<i>Elymus glaucus</i>
ERSP4	<i>Erigeron speciosus</i>
ERLA6	<i>Eriophyllum lanatum</i>
FERO	<i>Festuca roemerii</i>
FRVI	<i>Fragaria virginiana</i>
FRAF2	<i>Fritillaria affinis</i>
GAPA5	<i>Galium parisiense</i>
HOLA	<i>Holcus lanatus</i>
HYPE	<i>Hypericum perforatum</i>
HYRA3	<i>Hypochaeris radicata</i>
LEVU	<i>Leucanthemum vulgare</i>
LOTR2	<i>Lomatium triternatum</i>
LUAL3	<i>Lupinus albicaulis</i>
LUBI	<i>Lupinus bicolor</i>
LULE2	<i>Lupinus lepidus</i>
MAGR3	<i>Madia gracilis</i>
MILA	<i>Microseris laciniata</i>
PAVI3	<i>Parentucellia viscosa</i>
PLLA	<i>Plantago lanceolata</i>
POPR	<i>Poa pratensis</i>
POG R9	<i>Potentilla gracilis</i>
RAOC	<i>Ranunculus occidentalis</i>
RUAC3	<i>Rumex acetosella</i>
VUBR	<i>Vulpia bromoides</i>
ZIVE	<i>Zigadenus venenosus</i>