Traits, neighbors, and species performance in prairie restoration

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Abstract

Questions: Are traits related to the performance of plant species in restoration? Are the relationships between traits and performance consistent across the functional groups of annual forbs, perennial forbs, and grasses? Do the relationships between traits and performance depend on neighboring functional groups?

Location: A former agricultural field, being restored to native upland prairie, in the Willamette Valley of western Oregon USA.

Methods: Twenty-eight native species, representing three functional groups, were sown in seven different combinations. The following summer the performance of each species was measured. Eleven functional traits were measured from plants in the laboratory and in the field. Correlations between individual traits and performance variables were measured and stepwise regression techniques were used to determine which sets of traits were most strongly related to performance.

Results: Sets of traits explained up to 56% of variation in cover, and up to 48% of variation in establishment frequency. The relationships between traits and performance were influenced by functional group identity, and the functional group identity of neighboring species also influenced species' cover and the relationships between traits and cover. Species' establishment rate in monoculture was the trait most strongly correlated to both establishment and cover in mixtures. In multi-trait models, annual forb functional group identity was strongly related to establishment in mixtures, and height, leaf weight ratio at 7 days, and seed mass were strongly related to cover.

Conclusions: Based on the strength of the statistical models, multiple-trait models should be a useful way of predicting the performance of species prior to sowing in restoration. The functional group identity

of each species as well as the other species being sown may need to be taken into account when making predictions.

Keywords: functional ecology; seed mixtures; seedling establishment; leaf weight ratio; seed mass; unit leaf rate

Nomenclature source: USDA & NRCS (2009).

Abbreviations: FG = functional group; LA = leaf area; SLA = specific leaf area; LWR = leaf weight ratio; RGR = relative growth rate; ULR = unit leaf rate

Introduction

When restoring native species to degraded sites, it is often necessary to add seeds of the desired species, because native seeds may be infrequent (Seabloom et al. 2003; Turnbull et al. 2000). Species sown for restoration show a range of establishment abilities (Howell & Kline 1994; Pakeman et al. 2002). A comparative analysis that examines differences in plant traits is one way to investigate this variation in performance (Keddy 1992; Weiher et al. 1999). Simply, a plant trait is “any attribute that has potentially significant influence on establishment, survival, and fitness” (Reich et al. 2003b). Traits are characteristics that relate to species’ patterns of establishment, growth, and allocation, and that evolved in response to abiotic environmental conditions and interactions with other species (Reich et al. 2003b). When the same traits are measured among many species grown under standardized conditions, they can be a particularly useful tool for comparing these species (Cornelissen et al. 1996; Grime & Hunt 1975; Hunt 1982).

Interest is increasing in the use of plant traits for predicting the performance of species. Traits such as seed size, plant height, biomass, and relative growth rate have been correlated with the success of seedlings in greenhouse competition experiments, although the results often depend on the identity of neighbor plants (Goldberg & Landa 1991; Leishman 1999). Traits have been correlated with plant strategies such as ruderality and capacity for vegetative reproduction (Carlyle & Fraser 2006; Craine et al. 2001; Pywell et al. 2003), and traits associated with competitive success have predicted performance in mixtures (Freckleton & Watkinson 2001; Moles & Westoby 2002). Traits can determine species responses to particular environmental conditions such as shade and drought (Suding et al. 2003) and disturbance (Craine et al. 2001; Landsberg et al. 1999; Lavorel et al. 1999). Relationships between dominant traits and environmental variables across different sites have also been identified (Díaz et al. 1999; Weiher et al. 1999).

A sometimes overlooked aspect of recruitment success is the functional identity of plants comprising the seedling’s neighborhood. Niche theory suggests that functional similarity between the sown species and the species in its neighborhood will increase competitive pressure and decrease establishment success. Studies of field invasion have found mixed support for this theory (Emery 2007; Fargione et al. 2003; Leishman 1999). Seedling success in greenhouse competition experiments often depends on the identity and functional role of neighbor plants (Goldberg & Landa 1991; Leishman 1999). Few studies have examined the influence of functional similarity between target species and neighbors in restoration settings.

This study sought to determine whether traits, measured from both laboratory seedlings and field-grown plants, could be related to the performance of species in a restoration setting. Twenty-eight species native to upland prairies in the Willamette Valley of western Oregon USA were sown in experimental field plots. Species were separated into three functional groups: annual forbs, perennial forbs, and grasses. These *a priori* functional groups constituted a way to determine whether functional group identity is related to performance and whether the relationship between traits and performance depends on these broad life history groups (Carlyle & Fraser 2006). Species were sown into seven different mixtures representing all combinations of functional groups to test whether different neighbors influence what traits are associated with performance.

In this study we addressed three main questions: 1) Are traits related to the performance of plant species in restoration? 2) Are the relationships between traits and performance consistent across the functional groups annual forbs, perennial forbs, and grasses? 3) Do the relationships between traits and performance depend on neighboring functional groups?

Methods

Field procedures

The study took place at the William H. Finley National Wildlife Refuge (hereafter, Finley NWR) (44°24' N, 123°20' W), approximately 15 kilometers south of Corvallis in the Willamette Valley of Oregon, USA. The Willamette Valley has a semi-Mediterranean climate, characterized by cool, wet winters and warm, dry summers (Oregon Climate Service 2008). The study site was previously used to grow forage for wildlife, but the current goal is to restore upland prairie habitat. Native grasses were sown in 2002 and non-native grasses and forbs were also present. The soil type was mapped as Santiam silt loam with 2-8% slopes (Soil Survey Staff 2008).

Three functional groups were defined *a priori*, based on differences in life history, structure, and potentially competitive ability (Craine et al. 2001; Crawley 1997; Goldberg & Landa 1991; Grime & Hunt 1975; Kindscher & Fraser 2000): grasses, annual forbs, and perennial forbs. Nine species were sown in both the annual forb and grass functional groups, and ten in the perennial forb functional group, for a total of 28 species sown in this study (Table A.1). These species are recommended for Willamette Valley prairie restoration (Native Seed Network 2008; Wilson 1998). Seed was obtained from local native seed vendors. Two species either failed to germinate in the field or in the lab, so were removed from the analyses.

The three functional groups were combined in seven different seed mixes (also called "treatments"): single functional group mixtures (annual forbs, perennial forbs, or grasses), pair-wise combinations (annual forbs + perennial forbs; annual forbs + grasses; or perennial forbs + grasses), and all three functional groups together (annual forbs + perennial forbs + grasses). In each seed mix nine species per replicate were sown together, and the species representing each functional group were chosen randomly. The two-functional-group treatments contained four and five species per functional group (the number per functional group chosen randomly). In the three-functional-group treatment there were three species sown per functional group. A control treatment was also established with no seeds sown, to determine levels of naturally occurring native species.

The field experiment followed a complete randomized design. Each treatment was replicated eight times for a total of 64 quadrats. Seed mixtures were sown within 1-m^2 quadrats, with 1-m buffers. A pilot study in 2004-2005 determined field establishment rates for each species. To achieve approximately equal numbers of germinants per species, each species was sown in inverse relation to its 2005 field establishment rate. The treatment area was tilled and raked prior to seed addition in early November 2005.

A replacement series design was chosen for this study. This design keeps density and number of species constant while the species and functional group composition changes. Constant density ensures that any differences in the abundance of the target species can be attributed to the change in composition rather than a change in overall density. Keeping the number of species constant while increasing the number of functional groups eliminates the possibility that productivity will increase with an increase in species diversity (Spehn et al. 2000). A sowing rate of approximately 1200 seeds·m^{-2} was used in this study, which is within the range suggested in the restoration literature for Willamette Valley prairies (Boyer 2009; Ridgeline Resource Planning 1999).

At the same time the seed mixture quadrats were sown, single-species (monoculture) quadrats were also sown to monitor the performance of each species grown in the absence of interspecific competition and to measure field-based traits. These quadrats were situated in rows interspersed with the functional group treatments in a completely randomized design with four replicates per species. One hundred seeds of each species were sown in 0.25-m^2 quadrats with 1-m buffers. At this sowing density intraspecific competition was assumed to be negligible.

In July of 2006, at the peak of the growing season, each quadrat was subsampled with a 0.5-m^2 square quadrat placed in the center. Performance was defined by both establishment (1/0) and species cover (when present). Establishment frequency was calculated as the percentage of plots where a species sown did successfully establish. The cover (%) of each sown species and each functional group was visually estimated with the aid of calibrated cover templates. Final cover for each species in each quadrat was calculated as the estimated cover minus the average cover in the control plots. The control was not otherwise used for analysis.

Plant trait measurements

Seedlings of each species were grown in a growth chamber to determine standardized plant traits of specific leaf area, leaf area, leaf weight ratio, aboveground biomass, belowground biomass, root-shoot ratio, relative growth rate, and unit leaf rate (Table 1). Seed mass was also measured. These traits influence establishment and the occupation of space (Weiher et al. 1999).

Seeds were germinated according to each species' light, temperature, stratification and scarification requirements (based on data from published literature and previous research). As soon as possible after germinating, seedlings were transplanted into washed sand in individual cells (27.7 mL) of plug sheets (Landmark™ 98PSP vented) placed in plastic trays. Seedlings were then grown in a growth chamber under standardized conditions (Hendry & Grime 1993) and were fertilized 3 times a week with 5 mL of Hoagland's solution (Hoagland & Arnon 1950). Additional water was added to the trays as necessary to prevent the sand from drying out. Light irradiance was 125 ± 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ producing about 29 $W \cdot m^{-2}$.

Replicate seedlings of each species were grown for either 7 or 21 days and then harvested. The number of replicate seedlings measured per species and growing time averaged 11.6. After harvesting, leaves were separated from the stem, placed flat on a transparency and scanned at a resolution of 600 dpi. Leaf area was measured using Assess image analysis software (Lamari 2002). Leaf, stem, and root biomass were separated and dried at 80° C for at least 48 hours prior to weighing.

The two field measurements of plant traits were carried out on plants in the monoculture plots. Height in the 1st year was measured in July 2006 at the peak of the growing season. Establishment rate in monoculture plots was calculated as the total number of plants present in April 2006 per number of seeds sown.

Data structure and analysis

S-Plus 7.0 (Anon. 2005) was used for all analyses. The data format used for analysis was similar to the abundance-environment-attribute list of Nygaard and Ejrnæs (2004), with rows for species in quadrats and columns for response variables, treatments, and traits.

Explanatory and response variables were log-transformed as necessary to reduce skewness. Correlation between explanatory variables varied greatly (Pearson's r=0.02-0.94). Collinearity between the explanatory variables was reduced by using only the values for 7-day-old seedlings for specific leaf area, leaf area, aboveground biomass, and belowground biomass which were highly correlated with the corresponding 21-day-old values (Pearson's r=0.66-0.81).

Associations between each trait and both establishment frequency and cover (when established) were measured as Pearson product-moment correlations (r). To determine which sets of traits most strongly related to species establishment, traits were used as predictor variables in stepwise logistic regression analyses, with establishment of each species as the response variable. Functional group membership and treatments were included as covariates. The stepAIC procedure in the MASS library was used to create logistic regression models that related the strongest combination of predictor traits to the response variable of establishment. In this procedure, a full model is specified which includes all candidate explanatory variables. Schwarz's Bayesian Information Criterion (BIC) was used to determine which variables were included in the final model. BIC balances explanatory power and model complexity. The stepwise procedure moved both backward and forward. The final model was then fit using the Design and Hmisc libraries, and the goodness of fit of the model was assessed using the le Cessie-van Houwelingen-Copas-Hosmer unweighted sum of squares test. To further test the strength of the model, Wald's tests were used to test the significance of each parameter in the final model and Nagelkerke's R^2 index was used to approximate the strength of the logistic regression model.

Linear regression was used to determine which sets of traits were most strongly related to cover, again using stepAIC with BIC as the selection criterion and using the forward and backward stepwise procedure. The strength of the models was assessed with standard R^2 and p-values.

Results and Discussion

Species traits and responses

The trait values measured in this study were largely comparable to estimates found in previous studies (Grime & Hunt 1975; Hunt & Cornelissen 1997) (Table A2). Variation within groups for many traits (e.g., seed mass and leaf area) was high, with coefficients of variation > 0.5. This high variation between species within *a priori* functional groups has also been seen in previous studies (Reich et al. 2003a). Other traits (e.g., unit leaf rate) varied much less within functional groups. Still others (e.g., relative growth rate) were fairly consistent within and between functional groups.

Variation in establishment rate and cover was also high (Table 2), with standard deviations exceeding means for observed cover of each functional group. Annual forbs tended to have higher cover than perennial forbs and grasses, although they established less frequently (Table 2). This pattern is consistent with annual forbs in general, which are often ruderal species, producing many seeds and having rapid above-ground growth as seedlings in competition for light (Crawley 1997; Grime 1977; Grime & Hunt 1975). Previous research at Finley NWR has shown annual forbs to have much greater cover in the first year than other functional groups (Clark & Wilson 2005).

Question 1: Are traits related to the performance of species in restoration?

Correlations between individual traits and both establishment frequency and cover indicate that some traits are strongly and significantly related to the performance of species in restoration (Table 3). Eight out of the 11 traits analyzed were significantly correlated with cover at the $p<0.0001$ level (the Bonferroni-corrected critical value for $\alpha=0.05$ is 0.003), evidence that traits were strongly related to cover as a measure of performance. Height and establishment rate in monoculture were the two traits most highly correlated with cover. Fewer individual traits were strongly related to establishment; only two, establishment rate in monoculture and leaf weight ratio at 7 days, were significantly related to establishment.

Sets of traits added significant additional explanatory power over individual traits. In some cases, traits are important in the multivariate model (Table 4, "No interactions" column) but insignificant in univariate tests (Table 3). These results show that sets of traits provide distinct and complementary information about the ability of plants to establish and grow. Establishment was most strongly related to the set of establishment rate in monoculture plots, unit leaf rate, leaf weight ratio (21 days), and the indicator variable for annual forbs (Nagelkerke R^2 = 37.0%, Z=-1.32) (Table 4, "No interactions" column). All these predictor variables were significant below the 0.05 level by their Wald's statistics. Cover was related to the set of height, establishment rate in monoculture plots, leaf weight ratio (7 and 21 days), seed mass, and the indicator variable for perennial forbs ($R^2 = 50.5\%$, $F_{6,365} = 62.1$, $p<0.0001$) (Table 5, "No interactions" column).

The traits most strongly and consistently related to performance give an impression of how traits influence success in the field. Perhaps not surprisingly, field establishment rate in monoculture plots is strongly related to both cover and establishment in mixtures. The more seedlings of a given species establish without competition, the more likely it is to both occur in a plot with other species and species groups, and the greater cover that species will have. This pattern has been found in previous studies (Pywell et al. 2003). Traits linked to greater aboveground biomass are also associated with success. The strong relationship between height and cover may reflect the advantage gained by taller plants from shading their neighbors (Goldberg 1996). Leaf weight ratio is a measure of the "leafiness" of a seedling; in this study, the more a species allocates to its leaves at seven days, the more cover it is likely to have at the time of peak productivity in its first year (Table 5, "no interactions" column).

Greater height, high establishment rate, and large leaf-weight ratios are all associated with an early successional strategy of capturing light and aboveground space (Huston & Smith 1987; Weiher et al. 1999). Aboveground resource capture is favored when resources becomes abundant, such as following disturbance (Grime 1977). The study site was tilled prior to sowing, giving species that thrive on abundant light ideal conditions. Annual forbs are often ruderal species which are common after habitat disturbance (Grime 1977; Weiher et al. 1999). The annual forb indicator variable had a negative coefficient in the analysis of establishment rate (Table 4, "no interactions" column) and was absent in the analysis of cover (Table 5, "no interactions" column). Yet annual forbs had more cover than perennial forbs and grasses. These results suggest that the traits of the constituent species are sufficient to explain the advantages associated with the annual forb functional group.

Question 2: Are the relationships between traits and performance consistent across functional groups?

When functional groups and their interactions with traits were used to explain establishment, the final, parsimonious model included significant interaction terms between annual forbs and the traits unit leaf rate and relative growth rate (Nagelkerke R^2= 48.9%, Z=-1.50) (Table 4, "FG interactions" column). When functional groups and their interactions with traits were used to explain cover, the final, parsimonious model included interaction terms between perennial forbs and leaf weight ratio (7 days) and seed mass (R^2 = 54.2%, $F_{8, 363}$ = 53.6, p<0.0001) (Table 5, "FG interactions" column).

These results demonstrate that the relationships between traits and performance do vary between functional groups. For example, high relative growth rate is associated with increased establishment among perennial forbs and grasses, but has almost zero net effect for annual forbs (Table 4, "FG interactions" column), and all else being equal, the relationship between seed mass and cover was more strongly negative among perennial forbs relative to other functional groups (Table 5, "FG interactions" column). These different patterns point to different strategies among functional groups, with the same trait having different consequences for a species depending on whether it must flower and set seed soon, or whether it must grow roots to survive the dry season (Pywell et al. 2003).

Question 3: Do the relationships between traits and performance depend on neighboring functional groups?

When indicator variables for treatment were added as factors explaining establishment, no indicator variables for treatment entered the final model, making it identical to the final model from Question 1 (Nagelkerke R^2 = 37.0%, Z=-1.32) (Table 4, "Treatment interactions" column). Thus, the identity of neighbors provides no significant additional information on the relationships between traits and establishment rate. When indicator variables for treatment were added as factors explaining cover, the final model included terms for the grass functional group treatment, annual forb functional group treatment and an annual forb functional group treatment interaction with leaf weight ratio (7 days) (R^2 = 56.3%, $F_{9, 362}$ = 51.8, p<0.0001) (Table 5, "Treatment interactions" column). Thus, the functional group identity of neighbor species did influence cover, and how one trait relates with cover also depends on the neighbor functional group present. Little research has examined the relationships between traits, performance, and neighbor species (but see Leishman (1999)). Early differences in the ability to capture light, as indicated by leaf weight ratio at 7 days, seemed to play an important role in the success of the rapidly growing annual forbs, but not with the more slowly growing perennial forbs and grasses (Table 2).

Using traits to predict performance

Studies looking at the relationship between traits and performance using simple linear regression models have found the variance in abundance explained by individual traits to vary widely, with R^2 from 0.03 to 0.88 (e. g., Austrheim et al. 2005; Fargione & Tilman 2006; Leishman 1999; Reader 1998). Few studies have tried to find the best combination of traits that relate to performance. In this study, single variables explained no more than 9% of the variance in establishment frequency and 32% of the variance in cover (Table 4), but sets of traits explained 37% to 56% of the variance in establishment and cover; Reader (1998) found three traits together explained 99% of the variance in relative abundance. One of the advantages to examining multiple traits simultaneously is that complex statistical and biological interactions between traits and between traits and plant responses can be incorporated (Küster et al. 2008). Simultaneous analysis of multiple traits allows the testing of specific hypotheses about the relationships of functional traits, functional groups, and performance.

We intend this research as a step towards the creation of robust models that can be used to predict the performance of species in restoration. These relationships between plant traits and performance we report should be tested on an independent data set to determine how well they predict the cover and establishment probabilities of other species and at other sites. Models that have been tested have shown that traits can have strong predictive power (Freckleton & Watkinson 2001; Moles & Westoby 2002). Individually, and in combination, traits were more strongly related to cover as a measure of performance, than to establishment. In this study, establishment rate in monoculture was the trait most consistently related to both establishment and cover in mixtures. Annual forb functional group identity was also strongly related to establishment in mixtures, while height, leaf weight ratio, and seed mass were strongly related to cover. These would be worthwhile traits to investigate in further modeling efforts.

External biotic and abiotic factors not investigated in this study also play a large role in species success in restoration (Bakker et al. 2003). The presence of unsown propagules and existing species can affect native species establishment (Howell & Kline 1994) and may favor different traits (Gross 1984). Conditions such as precipitation, temperature, pH, and nutrient levels can influence what traits are successful (Kahmen & Poschlod 2004), so future models could take into account the interaction of traits with such environmental factors. Once reliable models of species responses are available, data in trait databases can be useful to land managers wishing to apply these models to their own species of interest (Knevel et al. 2003; Poschlod et al. 2003). Such validated trait-based models would be useful to predict, prior to seed sowing, which species are likely to be strong performers, and which combinations may produce the greatest overall native diversity. Such knowledge could save land managers money and effort in designing seed mixes and could identify which species, though desirable, are unlikely to establish from seed and require other methods, such as planting plugs. We encourage other researchers to carry out similar research at other sites so that the relationships between traits and species performance can be better understood.

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Table 1. Traits measured, their relevance to establishment and performance, the sources indicating each trait's relevance, and how traits were measured or calculated. A = area, W = dry weight, 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. *Indicates traits measured for both 7- and 21-day-old seedlings.

Trait	Relevance	Citation	How measured
		Growth chamber measurements	
Seed Mass	Seedling resources	Leishman (2001)	Mean seed or diaspore mass
Specific Leaf Area* (SLA)	Quickly grown, low density tissue	Craine et al. (2001)	$\frac{L_A}{L_W}$
Leaf area* (LA)	Light interception	Cornelissen et al. (2003)	L_A
Leaf Weight Ratio* (LWR)	Biomass allocation to leaves; light capture	Poorter (1989)	$\frac{L_W}{T_W}$
Aboveground biomass*	Light capture	Weiher et al. (1999)	S_W
Belowground biomass*	Nutrient uptake	Boot (1989)	R_W
Root-shoot ratio*	Nutrient uptake	Boot (1989)	$\frac{R_W}{S_W}$
Relative growth rate (RGR)	Rate of resource acquisition	Grace (1990)	$\frac{\log_e T_{W_2} - \log_e T_{W_1}}{t_2 - t_1}$
Unit leaf rate (ULR)	Photosynthetic efficiency	Hunt (1982)	$\frac{T_{W_2} - T_{W_1}}{t_2 - t_1} * \frac{\log_e L_{A_2} - \log_e L_{A_1}}{L_{A_2} - L_{A_1}}$
		Field measurements	
Height in 1st year	Light interception	Weiher et al. (1999)	Measured at time of flowering
Establishment rate in monoculture	Colonization ability	Pywell et al. (2003)	Counted in spring

Table 2. Mean establishment frequency and cover (when present) for annual forb, perennial forb, and grass species in the seed mixture plots (excluding control). Numbers in parentheses indicate standard deviations.

	Annual forbs	Perennial forbs	Grasses
Establishment frequency	0.65 (0.48)	0.88 (0.33)	0.86 (0.35)
Cover (%)	6.01 (6.73)	1.84 (2.12)	1.88 (2.62)

Table 3. Pearson product-moment correlation coefficient (r) values between individual traits measured and cover (log transformed) and establishment frequency . *p<0.05, **p<0.01, ***p<0.001, ****p<0.0001

Trait	Establishment frequency n=466	Log (Cover) n=373
Log (Seed mass)	0.01	0.11*
Specific leaf area 7 days	0.04	-0.04
Specific leaf area 21 days	0.09	0.02
Log (Leaf area 7 days)	0.00	0.32****
Log (Leaf area 21 days)	-0.01	0.28****
Leaf weight ratio 7 days	0.10*	0.27****
Leaf weight ratio 21 days	0.08	-0.10*
Log (Aboveground biomass 7 days)	-0.02	0.30****
Log (Aboveground biomass 21 days)	-0.03	0.24****
Log (Belowground biomass 7 days)	0.00	0.28****
Log (Belowground biomass 21 days)	0.02	0.31****
Root-shoot ratio 7 days	0.06	-0.29****
Root-shoot ratio 21 days	-0.06	0.00
Relative growth rate	-0.01	-0.15**
Unit leaf rate	-0.06	-0.26****
Log (Height)	-0.06	0.57****
Log (Establishment rate in monoculture)	0.30****	0.35****

Table 4. Coefficients for the three logistic multiple regression models relating traits with frequency of establishment (n=466.) FG: functional group. ns: variable not present in final model. --- : variable not added to full model. * p<0.01, **p<0.001, ***p<0.0001.

	Coefficient		
Variable	**No interactions (R^2=37.0%)**	**FG interactions (R^2=48.9%)**	**Treatment interactions (R^2=37.0%)**
Intercept	- 5.28*	- 9.81***	- 5.28*
Log (Establishment rate in monoculture)	2.27***	2.63***	2.27***
Annual functional group	- 2.41***	9.76***	- 2.41***
Unit leaf rate	- 3.07**	- 2.74*	- 3.07**
Leaf weight ratio 21 days	8.48**	ns	8.48**
Relative growth rate	ns	36.19***	ns
Leaf weight ratio 7 days	ns	7.16***	ns
Unit leaf rate*Annual forb	---	- 11.07**	ns
Relative growth rate*Annual forb	---	- 31.01*	ns

Table 5. Coefficients for the three linear regression models relating traits with cover (log transformed) (n=373). FG: functional group. ns: variable not present in final model. --- : variable not part of the analysis. LWR = leaf weight ratio. *p<0.05, **p<0.01, ***p<0.001, ****p<0.0001. See Table 2 for trait descriptions.

	Coefficient		
Variable	**No interactions (R^2=50.5%)**	**FG interactions (R^2=54.2%)**	**Treatment interactions (R^2=56.3%)**
Intercept	- 3.68****	- 2.13*	- 2.76****
Log (Height)	0.97****	0.93****	0.91****
Log (Establishment rate in monoculture)	0.44****	0.44****	0.41****
Leaf weight ratio (LWR) 7 days	5.17****	4.66****	4.55****
Log (Seed mass)	- 0.19***	- 0.15**	- 0.17***
Unit leaf rate	ns	ns	- 0.84*
Leaf weight ratio (LWR) 21 days	- 3.15**	- 4.66****	- 2.80**
Perennial forb	0.26***	1.56**	ns
Leaf weight ratio 7 days*Perennial forb	---	- 1.89*	---
Log (Seed mass)*Perennial forb	---	- 0.15**	---
Grass treatment	---	---	- 0.56***
Annual forb treatment	---	---	- 6.60****
LWR 7 days*Annual forb treatment	---	---	8.63****