Plant Ecol (2018) 219:369–379
https://doi.org/10.1007/s11258-018-0801-y

Functional trait heritability and local climatic adaptation among grasses: a meta-analysis

Carla M. Roybal · Bradley J. Butterfield

Received: 25 September 2017 / Accepted: 16 January 2018 / Published online: 30 January 2018

Abstract Variation in climate has been demonstrated to be a powerful driver of selection and local adaptation among plant populations. Variation in functional traits among populations can also be indicative of the drivers of local adaptation. However, it is not clear to what extent species exhibit consistent patterns of local adaptation as revealed by common, heritable trait–environment relationships among populations. To address this, we conducted a meta-analysis of common garden studies of grass populations to quantify the degree of heritability of several commonly measured functional traits, and whether demonstrated heritability was driven by climate. We found that leaf size, specific leaf area (SLA) and total biomass all displayed strong broad-sense of heritability. Both leaf area and SLA decreased significantly with increasing temperature seasonality among populations within species, while total biomass increased with increasing annual and dry season precipitation, and decreased with increasing precipitation seasonality. These results indicate similar, consistent drivers of local adaptation among species of grasses. Further information on trait–environment relationships within species could greatly improve our ability to predict broad scale patterns in functional diversity across multiple levels of ecological organization. Expanding the range of traits and regions incorporated in common garden research, in the present case by incorporating root traits and Southern Hemisphere taxa, will provide even greater benefits to the fields of restoration, conservation, and global change ecology.

Keywords Functional trait · Poaceae · Intraspecific variability · Common garden · Trait–climate relationships

Communicated by Sandor Bartha.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11258-018-0801-y) contains supplementary material, which is available to authorized users.

C. M. Roybal (✉) · B. J. Butterfield
Merriam-Powell Center for Environmental Research and Department of Biological Sciences, Northern Arizona University, Box 5640, Flagstaff, AZ 86011, USA
e-mail: cr344@nau.edu

Introduction

Variation in climate has been demonstrated to be a powerful driver of selection, evolution, and trait differentiation among populations of plants (McMillan 1957; Rehfeldt et al. 1999). There is strong evidence for adaptation to local climate and environment at a number of spatial scales and levels of organization (Joshi et al. 2001; Leimu and Fischer 2008). The degree to which plants are adapted to local environmental conditions has wide-ranging

implications for both basic and applied biology (Joshi et al. 2001; Kawecki and Ebert 2004).

In a parallel approach to the study of inter-population variability, functional ecologists have been increasingly focused on relationships between trait values of populations and their local environment (Violle et al. 2012). Intraspecific variation in functional traits—organismal characteristics that mediate performance in a specific environmental context—accounts for on average between a quarter and a third of total trait variation within communities (Albert et al. 2010a; Siefert et al. 2015). Identifying consistent and strong trait–environment relationships within species can also help identify the strength and nature of local adaptation within populations of plants inhabiting extensive or topographically complex ranges. Thus, determining the degree to which intraspecific trait–environment relationships are consistent and predictable is critical for our ability to scale patterns and consequences of functional diversity (de Bello et al. 2010; Albert et al. 2011), as well as predict responses of communities to environmental change (Albert et al. 2010b; Jung et al. 2014). Establishing scalable and consistent trait–environment relationships within species has practical application for establishing seed transfer zones (Bower et al. 2014), and to better inform assisted migration under changing climate.

At broad spatial scales, plant functional traits respond to climate based on consistent physiological tradeoffs between sets of correlated traits (Grime et al. 1997; Pillar et al. 2010). For example, specific leaf area (SLA), or the area per unit dry mass of a leaf, reliably decreases with nutrient availability in grasses and decreases with temperature across all vegetation types, illustrating a tradeoff between growth rate and tissue quality in response to external factors (Wright et al. 2004; da Silveira et al. 2015). While such broad patterns in trait–environment relationships have been studied extensively, whether or not they hold within species across the range of their realized climate niches requires further examination. For example, Bussotti et al. (2014) reviewed functional trait variation and associated adaptive capacity to climate change broadly in European trees and found that interactions between climate and phenotypic expression—specifically with respect to drought response—seem to be species-specific. However, these diverse responses of disparate tree lineages may mask consistent patterns within more phylogenetically constrained groups. It is possible that consistent, heritable trait–environment relationships exist within more narrowly defined clades.

To that end, we conducted a meta-analysis of broad-sense trait heritability (population-level phenotypic variance) and trait–environment relationships from common garden studies of grasses. Grass (Poaceae) is one of the most speciose plant families (Gibson 2009) and represents a recently evolved, monophyletic group with a relatively simple growth form that creates a high potential for consistent, heritable trait–environment relationships. By standardizing environmental features, common gardens can help to distinguish between purely genetic and plastic responses to environmental variation (Kawecki and Ebert 2004). Through this meta-analysis, we address the questions: (1) for which traits consistently express significant broad-sense heritability (as demonstrated by a significant amount of trait variance explained by population)? and (2) are relationships between source climate and intraspecific trait expression consistent among species? Based on previous meta-analysis, we hypothesize that aspects of temperature will be more strongly correlated with plant functional traits than precipitation (Moles et al. 2014).

Methods

We conducted a search using the term "Common garden*" and "*grass*" in mid-September 2015 using Web of Science, which initially yielded 365 studies. References to studies selected for data extraction were also examined. This was reduced to 148 studies with at least one grass species in which some trait was evaluated in a common garden-style experiment. Further inclusion criteria were (1) source population coordinates for the seeds used in the common garden, and/or (2) an *F*-value and degrees of freedom from a trait-by- population ANOVA. If the study was published in the past 10 years, authors were approached to obtain these data. When data were presented in a graphic format, values were determined via Image J plot digitization (Schneider et al. 2012).

We analyzed a total of 26 studies (including studies counted multiple times for reporting on more than one species), though not all 26 offered both information for the trait-population analysis and climatic correlates (Table 1). The majority of studies took place in the

Table 1 Summary of studies, which analyze data was incorporated, study region and species reported

Reference	Heritability analysis	Trait–climate correlations	Study region	Mean annual temperature	Temperature seasonality	Mean Diurnal Range	Mean annual precipitation	Precipitation seasonality	Precipitation of driest quarter	Species
Aspinwall et al. (2013)	x	x	Midwestern United states	12.2	4921	23	529	24	136	*Panicum virgatum*
Beierkuhnlein et al. (2011)	x		Europe	20.5	2178	24	205	16	62	*Arrhenatherum elatius*
Beierkuhnlein et al. (2011)	x		Europe	48	2239	26	480	12	127	*Festuca pratensis*
Beierkuhnlein et al. (2011)	x		Europe	12.4	1219	15	162	6	31	*Holcus lanatus*
Beierkuhnlein et al. (2011)	x		Europe	12.4	1051	12	124	5	32	*Alopecurus pratensis*
Butterfield and Wood (2015)	x	x	Western United States	11.7	2515	52	501	50	68	*Bouteloua gracilis*
Carter and VanderWeide (2014)	x	x	Midwestern United states	5	1944	11	492	31	142	*Sorghastrum nutans*
Cheplick (2011)	x	x	Italy, Morocco, United States	5.9	3191	75	474	45	39	*Lolium perenne*
Flory et al. (2011)	x	x	China, United States	12.7	5015	36	462	83	243	*Microstegium vimineum*
Gibson et al. (2013)	x	x	Midwestern United states	1.5	1375	28	475	36	184	*Andropogon gerardii*
Giuliani et al. (2013)	x	x	Western United States	4.1	2462	2	41	3	3	*Andropogon gerardii*
Giuliani et al. (2013)	x	x	Western United States	7.9	2845	2	79	3	5	*Bouteloua gracilis*
Hartman et al. (2012)	x		Midwestern United states	Double check	3144	12	363	11	5	*Panicum virgatum*
Holmstrom et al. (2010)	x		Midwestern United states	3.5	1426	4	104	23	73	*Ammophila breviligulata*

Table 1 continued

Reference	Heritability analysis	Trait–climate correlations	Study region	Mean annual temperature	Temperature seasonality	Mean Diurnal Range	Mean annual precipitation	Precipitation seasonality	Precipitation of driest quarter	Species
Johnson et al. (2015)	x		Western United States	10.9	4033	63	1171	68	84	*Poa secunda*
Matlaga et al. (2012)	x		United States, Japan	6.5	2191	55	570	37	109	*Miscanthus sinensis*
Mnif et al. (2006)	x	x	Tunisa	2.3	1219	15	70	25	7	*Cenchrus cilaris*
Parsons et al. (2011)	x		Western United States	4.8	2842	38	528	53	30	*Elymus elymoides brevifolius*
Poulin et al. (2007)	x		Western United States	12	6213	83	1509	69	327	*Pennisetum setaceum*
Rapson and Wilson (1992)		x	New Zealand	3.9	2740	47	1809	11	436	*Agrostis capillaris*
Reisch and Poschlod (2003)	x	x	Europe	2.1	815	22	400	15	92	*Sesleria albicans*
Skálová et al. (1997)	x		Czech Republic	–	–	–	–	–	–	*Festuca rubra*
St. Clair et al. (2013)	x		Western United States	9	3505	64	1791	64	113	*Pseudoroegneria spicata*
Talkington (2015)	x	x	Western United States	4.6	2233	17	153	30	41	*Sporobolus airoides*
Zhou et al. (2013)	x		China	7.9	5033	50	1272	40	143	*Oryza rufipogon*

The values listed under each climate dimension variable are the range within each species in a given study

northern hemisphere and concentrated in the United States and Europe (Table 1, Fig. 2). For the analysis, we grouped all functional traits reported in a given category (Fig. 1) from each study. Sample sizes of studies reporting on a given functional trait were generally small, even when reported functional traits were collapsed into more encompassing categories. For a given trait, sample sizes did not exceed 15 when analyzed for heritability and eight for analysis of climate drivers. Traits were grouped into 21 categories (Fig. 1, see supplemental material document 5 for details on category components), as different measurements were utilized in multiple studies that represent similar types of traits. For example, seed mass, seed number, and number of flowering heads, as well as other measurements, were all categorized as reproductive effort. The six trait categories with the largest sample size based on F value reporting (Fig. 1) were reproductive effort, aboveground biomass, specific leaf area, height, leaf size and total biomass. Both biomass measures reflect average individual biomass, not population biomass. These six categories were included in all further analyses based on their adequate sample size. Analysis included 34 different species and 27 genera. Almost all species included in the study were perennials. Analyses were performed on all species grouped together for the same trait category.

To assess trait heritability, F values from trait-by-population ANOVAs were extracted from the literature and converted to Fisher's Z effect size (Del Re 2013). To quantify effect sizes of trait–environment correlations, climate data were acquired from WorldClim, which provides 30 arc-second ($\sim$ 1 km) resolution raster layers interpolated from weather station data (Hijmans et al. 2005), using population coordinates provided in each study. These data represent 30 year normals from the period $\sim$ 1960–1990. Based on a principal components analysis of 19 standard bioclimatic variables, we identified six approximately orthogonal climate variables: mean annual temperature, mean annual precipitation, precipitation of driest quarter, mean diurnal temperature range, temperature seasonality, and precipitation seasonality. Temperature and precipitation seasonality illustrate the respective range of annual values, and are calculated as 100 $\times$ temperature standard deviation

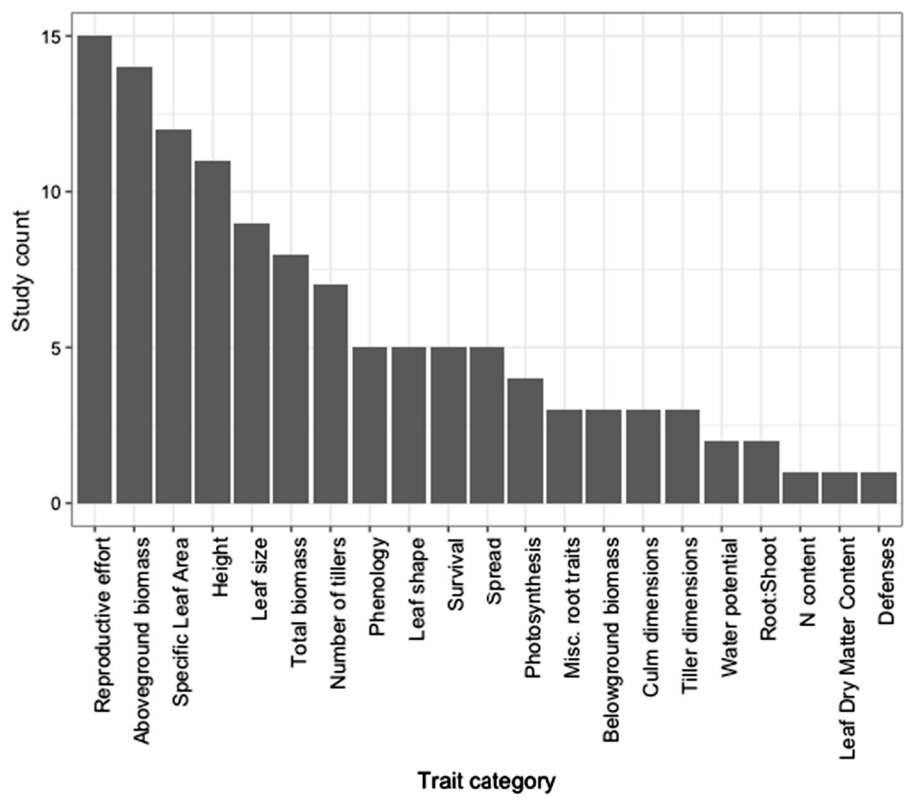

Fig. 1 Histogram of trait categories reporting trait by population outcomes used in heritability analysis throughout published literature. The first six categories were used for analysis. The same six were subsequently used in trait–climate relationship analysis. There were no significant relationships between height and aboveground biomass, and any of the given climate variables. Despite marginal evidence of heritability for reproductive effort, this trait category still has one significant relationship with mean annual temperature

Table 2 Statistical outcomes of trait-heritability analysis

Functional category	Mean Fisher's *Z*	95% CI	*P* value	*n*
Aboveground biomass	0.2	− 0.04, 0.43	0.095	11
Height	0.27	− 0.04, 0.58	0.092	7
Leaf size	**0.21**	**0.03**, **0.4**	**0.023**	9
Reproductive effort	0.17	− 0.02, 0.36	0.077	15
SLA	**0.25**	**0.03**, **0.48**	**0.026**	8
Total biomass	**0.3**	**0.09**, **0.51**	**0.005**	6

Significant outcomes bolded. Significant outcomes indicate population-level differences within the indicated trait category persisted when grown in a standardized climate. *N* indicates the number of studies used in analysis for each trait category, for example, 15 publications reported on some aspect of reproductive effort

and the coefficient of variation of precipitation, respectively. These variables were then used to assess correlations between climate and population-mean trait values within studies. These correlation effect sizes were based on back-transformed Fisher's *Z* values.

All meta-analytical calculations were performed using R and the Metafor package (Viechtbauer 2010). When studies presented multiple data points per trait category, the values were averaged and weighted by the inverse of their variance. Effect sizes were fit to general linear random-effects models, which does not make the assumption that effect sizes are the same between studies, and therefore, accounts for variability between studies (Koricheva et al. 2013). When studies reported on more than one species the results were not pooled. That is, if data for multiple species were reported within a single study (see Leva et al. 2013), then each species was treated as a separate data point, and therefore, analyzed separately. These types of results were viewed as independent enough to have been published as two separate studies, had the authors chosen to do so.

Finally, we constructed a funnel plot, an indirect method of assessing publication bias in this field of literature. Funnel plots depict effect size plotted against standard error (Chaplin-Kramer et al. 2011). Symmetrical funnel plots with an equal number of studies plotted on either side of the centerline suggest little publication bias or thoroughly measured heterogeneity amongst the studies. Asymmetry in the funnel plot indicates an unequal number of studies published with significant versus non-significant results, suggesting bias toward publishing significant results. We checked for the potential impact of publication bias on our dataset using the trim and fill method (Duval and Tweedie 2000a, b). Briefly, the trim and fill method re-assesses the overall effect size using the symmetrical portion of the funnel plot to estimate the center of the funnel plot, then using the remaining studies in the symmetric part of the plot and their estimated, symmetric counterpoints to estimate the true mean and variance.

Results

Leaf size, SLA, and total biomass all exhibited a significant mean effect size for heritability (all $P < 0.025$), while mean effect sizes for aboveground biomass, height and reproductive effort were only marginally insignificant (all $0.05 > P < 0.1$; Table 2). As significant heritability is a prerequisite for significant trait–environment relationships among populations, only results for leaf size, SLA and total biomass are further assessed. We note that the sample sizes of studies per functional trait category are small, and that as more research in this field is conducted, we may find that marginally insignificant outcomes may become significant with greater statistical power (Koricheva et al. 2013). We also note that outcomes did not change when studies reporting on annual species were excluded.

All three traits exhibited significant mean effect sizes for at least one dimension of climate (Table 3). Leaf size and SLA both had significant, negative mean effect sizes for temperature seasonality. Total biomass had significant mean effect sizes for mean annual

Table 3 Statistical results of climate-trait correlations

	Climate variable	mean Fisher's Z	95% CI	P value
SLA	MAT	− 0.7	− 0.8, 0.66	0.846
Study N: 6	Diurnal range	− 0.18	− 0.8, 0.44	0.572
	Temperature seasonality	**− 0.44**	**− 0.85, − 0.03**	**0.037**
	MAP	− 0.08	− 0.5, 0.33	0.693
	Precipitation seasonality	0.19	− 0.43, 0.8	0.549
	Precipitation of driest quarter	− 0.01	− 0.59, 0.57	0.968
Leaf size	MAT	0.42	− 0.13, 0.97	0.137
Study N: 3	Diurnal range	0.01	− 0.3, 0.33	0.931
	Temperature seasonality	**− 0.64**	**− 0.88, − 0.39**	**< 0.001**
	MAP	− 0.04	− 0.5, 0.42	0.866
	Precipitation seasonality	0.14	− 0.6, 0.88	0.707
	Precipitation of driest quarter	0	− 0.37, 0.37	0.999
Total biomass	MAT	− 0.15	− 0.55, 0.25	0.458
Study N: 3	Diurnal range	− 0.12	− 0.63, 0.38	0.629
	Temperature seasonality	0.1	− 0.28, 0.48	0.612
	MAP	**0.26**	**0.2, 0.33**	**< 0.001**
	Precipitation seasonality	**− 0.14**	**− 0.21, − 0.08**	**< 0.001**
	Precipitation of driest quarter	**0.18**	**0.12, 0.25**	**< 0.001**

Significant results bolded. Significant outcomes indicates the variable of the home climate is correlated with the trait outcome when grown in a standardized climate, suggesting the given climate variable may be a contributor to broad-sense heritability

precipitation (positive), precipitation seasonality (negative) and precipitation of the driest quarter (positive).

We pooled all outcomes from the heritability assessment (F-tests) to generate the funnel plot, which proved to be markedly asymmetrical (Figure S1). Trim and fill analysis suggests 23 hypothetical studies not significant at the $P < 0.05$ level were not published. With these 23 studies, (df = 78), the mean Fisher's Z value was 2.18, with a P value of 0.029 (95% CI 0.014, 0.278). Despite the suggestion of strong publication bias from the funnel plot analysis, significant heritability still holds when unpublished data are taken into account, indicated by the trim and fill analysis (Fig. 2).

Discussion

Through meta-analysis of grass common garden studies, we found several traits exhibited consistent broad-sense heritability across species, and furthermore that these traits exhibited consistent trait–environment relationships. These results indicate consistent patterns of climatic selection via functional traits that may help to develop predictive models of patterns of local adaptation in grasses. These promising results, coupled with potential publication bias and a relative dearth of functional trait data, indicate that additional research in this realm is highly warranted.

Differences in heritability among traits indicates that leaf physiology and overall plant size play important roles in mediating local adaptation to abiotic and biotic selective factors, whereas reproductive effort and aboveground size (biomass and height) may be less critical. The latter may reflect greater plasticity in these traits due to high interannual or microenvironmental variability in conditions necessary for germination and growth (Galloway et al. 2008; Nagashima and Hikosaka 2011), though it is worth noting that reproductive effort was nearly significantly heritable ($P = 0.077$). These results pertain largely to perennial species. Heritability in reproductive effort would be, we predict, stronger in perennials as environmental adaptation may not have the chance to occur in the lifespan of an annual plant. Conversely, the demonstrated relationships of SLA, leaf size and total biomass with climate suggest these traits may represent fundamental tradeoffs in response to consistent selection pressures. Other factors, such as light environment, also play an important role in driving variation in leaf traits and morphology (Poorter et al. 2012), but could not be accounted for due to limited information on source population environments beyond climate.

Fig. 2 Map of grass common garden population sources used in meta-analysis. Polygons indicate the geographic extent of source populations in the given study

Environmental responses of consistently heritable traits indicated independent selective effects of temperature and precipitation. In the case of temperature, leaves with low SLA typically have thicker cell walls and denser tissues, which may serve to buffer the effects of temperature fluctuations and extremes (Pons et al. 2008). Leaf size responds to climate similar to SLA. Especially in areas with high insolation and arid locations, smaller leaf size relates the plant's ability to regulate temperature and transpiration (Butterfield and Wood 2015). The positive relationship between total biomass and measures of precipitation may be associated with interactions between soil characteristics and fertility, water use efficiency the competitive environment (Van Wijk 2011). Coupled with the lack of consistent trend in aboveground biomass, the size-precipitation relationships indicate that belowground biomass may display strong relationships to climate. This finding would be in concordance with research linking belowground traits to soil moisture (Nippert et al. 2012; Pérez-Ramos et al. 2012), however, data were lacking for this meta-analysis.

The relatively small number of studies that were suitable for this analysis, from amongst the many grass common garden studies, underlines an unfortunate gap between quantitative genetics and functional ecology approaches to local adaptation research. Rather than measuring traits associated with reproduction or grass morphology, our results suggest that functional traits (e.g., SLA) are likely to exhibit more consistent patterns of heritability as well as relationships with climate, which are critical links for tying common garden research to applications such as seed transfer zones or conservation (Wang et al. 2010). Furthermore, only a few studies included characterizations of belowground traits, with little consistency in specific traits or methods (Kik et al. 1990; Leva et al. 2013). Given the significance of roots in the percentage of total biomass in grasses and their potentially unique functions (Sandel et al. 2016; Butterfield et al. 2017), root traits should be quantified to complete the functional profile of grasses and other groups. It is also of note that the majority of the research of this field is located within the Northern hemisphere, particularly in the United States and Europe. In conclusion, our meta-analysis reveals that traits relating to leaf and whole-plant size are more heritable than traits relating to the reproductive effort. These results suggest that leaf and size-related traits may be good candidates for identifying predictable variation in functional traits across the distributions of grass species as a function of climate, whereas other, perhaps localized factors such as soils and the biotic environment may be important in driving variation in other functional traits. These findings are encouraging, and given the evidence of publication bias, small

sample sizes of traits and the potential practical applications for this research related to restoration and assisted migration, additional research in this field would be beneficial.

Acknowledgements The authors would like to thank Liza Holeski, Nate Nieto and Troy Wood for their comments and input on this manuscript. The manuscript was greatly improved with input by our reviewers. This research was supported in part by the US Bureau of Land Management Colorado Plateau Native Plants Program, the US Forest Service Great Basin Native Plants Program, and the US Geological Survey Restoration Assessment and Monitoring Program for the Southwest (RAMPS).

References

Albert CH, Thuiller W, Yoccoz NG, Douzet R, Aubert S, Lavorel S (2010a) A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. Funct Ecol 24:1192–1201. https://doi.org/10.1111/j.1365-2435.2010.01727.x

Albert CH, Thuiller W, Yoccoz NG, Soudant A, Boucher F, Saccone P, Lavorel S (2010b) Intraspecific functional variability: extent, structure and sources of variation. J Ecol 98:604–613. https://doi.org/10.1111/j.1365-2745.2010.01651.x

Albert CH, de Bello F, Boulangeat I, Pellet G, Lavorel S, Thuiller W (2011) On the importance of intraspecific variability for the quantification of functional diversity. Oikos 121:116–126. https://doi.org/10.1111/j.1600-0706.2011.19672.x

Aspinwall MJ, Lowry DB, Taylor SH, Juenger TE, Hawkes CV, Johnson M-VV, Kiniry JR, Fay PA (2013) Genotypic variation in traits linked to climate and aboveground productivity in a widespread C_4 grass: evidence for a functional trait syndrome. New Phytol 199:966–980. https://doi.org/10.1111/nph.12341

Beierkuhnlein C, Thiel D, Jentsch A, Willner E, Kreyling J (2011) Ecotypes of European grass species respond differently to warming and extreme drought. J Ecol 99:703–713. https://doi.org/10.1111/j.1365-2745.2011.01809.x

Bower AD, St Clair JB, Erickson V (2014) Generalized provisional seed zones for native plants. Ecol Appl 24:913–919. https://doi.org/10.1890/13-0285.1

Bussotti F, Pollastrini M, Holland V, Brüggemann W (2014) Functional traits and adaptive capacity of European forests to climate change. Environ Exp Bot 111:91–113. https://doi.org/10.1016/j.envexpbot.2014.11.006

Butterfield B, Wood T (2015) Local climate and cultivation, but not ploidy, predict functional trait variation in *Bouteloua gracilis* (Poaceae). Plant Ecol 216:1341–1349. https://doi.org/10.1007/s11258-015-0510-8

Butterfield BJ, Bradford JB, Munson SM, Gremer JR (2017) Aridity increases below-ground niche breadth in grass communities. Plant Ecol 218:385–394. https://doi.org/10.1007/s11258-016-0696-4

Carter DL, VanderWeide BL (2014) Belowground bud production is linked to population establishment in *Sorghastrum nutans* (Poaceae). Plant Ecol 215:977–986. https://doi.org/10.1007/s11258-014-0353-8

Chaplin-Kramer R, O'Rourke ME, Blitzer EJ, Kremen C (2011) A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecol Lett 14:922–932. https://doi.org/10.1111/j.1461-0248.2011.01642.x

Cheplick GP (2011) Endosymbiosis and population differentiation in wild and cultivated *Lolium perenne* (Poaceae). Am J Bot 98:829–838. https://doi.org/10.3732/ajb.1000226

da Silveira Pontes L, Maire V, Schellberg J, Louault F (2015) Grass strategies and grassland community responses to environmental drivers: a review. Agron Sustain Dev 35:1297–1318. https://doi.org/10.1007/s13593-015-0314-1

de Bello F, Lavorel S, Albert CH, Thuiller W, Grigulis K, Doležal J, Janecek S, Lepš J (2010) Quantifying the relevance of intraspecific trait variability for functional diversity. Methods Ecol Evol 2:164–174. https://doi.org/10.1111/j.2041-210X.2010.00071.x

Del Re A (2013) compute.es: Compute Effect Sizes

Duval S, Tweedie R (2000a) A nonparametric, "Trim and Fill" method of accounting for publication bias in meta-analysis. J Am Stat Assoc 95:89–98. https://doi.org/10.1080/01621459.2000.10473905

Duval S, Tweedie R (2000b) Trim and fill: a simple funnel-plot-based method of testing and adjusting for publication bias in meta-analysis. Biometrics 56:455–463. https://doi.org/10.1111/j.0006-341X.2000.00455.x

Flory SL, Long F, Clay K (2011) Invasive *Microstegium* populations consistently outperform native range populations across diverse environments. Ecology 92:2248–2257

Galloway JN, Townsend AR, Erisman JW, Bekunda M, Cai Z, Freney JR, Martinelli LA, Seitzinger SP, Sutton MA (2008) Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. Science 320:889–892. https://doi.org/10.1126/science.1136674

Gibson DJ (2009) Grasses and grassland ecology. Oxford University Press, Oxford

Gibson DJ, Sendor G, Donatelli J, Baer SG, Johnson L (2013) Fitness among population sources of a dominant species (*Andropogon gerardii* Vitman) used in prairie restoration 1. J Torrey Bot Soc 140:269–279. https://doi.org/10.3159/TORREY-D-12-00063.1

Giuliani AL, Kelly EF, Knapp AK (2013) Geographic variation in growth and phenology of two dominant central US grasses: consequences for climate change. J Plant Ecol 7:211–221. https://doi.org/10.1093/jpe/rtt036

Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, Rorison IH, Hendry GAF, Ashenden TW, Askew AP, Band SR, Booth RE, Bossard CC, Campbell BD, Cooper JEL, Davison AW, Gupta PL, Hall W, Hand DW, Hannah MA, Hillier SH, Hodkinson DJ, Jalili A, Liu Z, Mackey JML, Matthews N, Mowforth MA, Neal AM, Reader RJ, Reiling K, Ross-Fraser W, Spencer RE, Sutton F, Tasker DE, Thorpe PC, Whitehouse J (1997) Integrated screening validates primary axes of specialisation in plants. Oikos 79:259. https://doi.org/10.2307/3546011

Hartman JC, Nippert JB, Springer CJ (2012) Ecotypic responses of switchgrass to altered precipitation. Funct Plant Biol 39:126. https://doi.org/10.1071/FP11229

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978. https://doi.org/10.1002/joc.1276

Holmstrom RM, Etterson JR, Schimpf DJ (2010) Dune Restoration Introduces Genetically Distinct American Beachgrass, *Ammophila breviligulata*, into a Threatened Local Population. Restor Ecol 18:426–437

Johnson RC, Horning ME, Espeland EK, Vance-Borland K (2015) Relating adaptive genetic traits to climate for Sandberg bluegrass from the intermountain western United States. Evol Appl 8:172–184. https://doi.org/10.1111/eva.12240

Joshi J, Schmid B, Caldeira MC, Dimitrakopoulos PG, Good J, Harris R, Hector A, Huss-Danell K, Jumpponen A, Minns A, Mulder CPH, Pereira JS, Prinz A, Scherer-Lorenzen M, Siamantziouras A-SD, Terry AC, Troumbis AY, Lawton JH (2001) Local adaptation enhances performance of common plant species. Ecol Lett 4:536–544. https://doi.org/10.1046/j.1461-0248.2001.00262.x

Jung V, Albert CH, Violle C, Kunstler G, Loucougaray G, Spiegelberger T (2014) Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. J Ecol 102:45–53. https://doi.org/10.1111/1365-2745.12177

Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. Ecol Lett 7:1225–1241. https://doi.org/10.1111/j.1461-0248.2004.00684.x

Kik C, Van Andel J, Van Delden W, Joenje W, Bijlsma R (1990) Colonization and differentiation in the clonal perennial *Agrostis stolonifera*. J Ecol 78:949–961. https://doi.org/10.2307/2260945

Koricheva J, Gurevitch J, Mengersen K (2013) Handbook of meta-analysis in ecology and evolution. Princeton University Press, New Jersey

Leimu R, Fischer M (2008) A meta-analysis of local adaptation in plants. PLoS ONE 3:e4010. https://doi.org/10.1371/journal.pone.0004010

Leva PE, Aguiar MR, Premoli AC (2013) Latitudinal variation of genecological traits in native grasses of Patagonian rangelands. Aust J Bot 61:475. https://doi.org/10.1071/BT12249

Matlaga DP, Quinn LD, Davis AS, Stewart JR (2012) Light response of native and introduced *Miscanthus sinensis* seedlings. Invasive Plant Sci Manag 5:363–374. https://doi.org/10.1614/IPSM-D-11-00056.1

McMillan C (1957) Nature of the plant community. III. Flowering behavior within two grassland communities under reciprocal transplanting. Am J Bot 44:144. https://doi.org/10.2307/2438305

Mnif L, Belgacem AO, Cortina J, Chaieb M (2006) A comparative analysis of establishment of *Cenchrus ciliaris* provenances in arid zone of Tunisia. Arid L Res Manag 19:341–351. https://doi.org/10.1080/15324980500299565

Moles AT, Perkins SE, Laffan SW, Flores-Moreno H, Awasthy M, Tindall ML, Sack L, Pitman A, Kattge J, Aarssen LW, Anand M, Bahn M, Blonder B, Cavender-Bares J, Cornelissen JHC, Cornwell WK, Díaz S, Dickie JB, Freschet GT, Griffiths JG, Gutierrez AG, Hemmings FA, Hickler T, Hitchcock TD, Keighery M, Kleyer M, Kurokawa H, Leishman MR, Liu K, Niinemets Ü, Onipchenko V, Onoda Y, Penuelas J, Pillar VD, Reich PB, Shiodera S, Siefert A, Sosinski EE, Soudzilovskaia NA, Swaine EK, Swenson NG, van Bodegom PM, Warman L, Weiher E, Wright IJ, Zhang H, Zobel M, Bonser SP (2014) Which is a better predictor of plant traits: temperature or precipitation? J Veg Sci 25:1167–1180. https://doi.org/10.1111/jvs.12190

Nagashima H, Hikosaka K (2011) Plants in a crowded stand regulate their height growth so as to maintain similar heights to neighbours even when they have potential advantages in height growth. Ann Bot 108:207–214. https://doi.org/10.1093/aob/mcr109

Nippert JB, Wieme RA, Ocheltree TW, Craine JM (2012) Root characteristics of C4 grasses limit reliance on deep soil water in tallgrass prairie. Plant Soil 355:385–394. https://doi.org/10.1007/s11104-011-1112-4

Parsons MC, Jones TA, Larson SR, Mott IW, Monaco TA (2011) Ecotypic variation in *Elymus elymoides* subsp. *brevifolius* in the Northern intermountain West. Rangel Ecol Manag 64:649–658. https://doi.org/10.2111/REM-D-09-00143.1

Pérez-Ramos IM, Roumet C, Cruz P, Blanchard A, Autran P, Garnier E (2012) Evidence for a "plant community economics spectrum" driven by nutrient and water limitations in a Mediterranean rangeland of southern France. J Ecol 100:1315–1327. https://doi.org/10.1111/1365-2745.12000

Pillar VD, Duarte L (2010) A framework for metacommunity analysis of phylogenetic structure. Ecol Lett 13:587–596. https://doi.org/10.1111/j.1461-0248.2010.01456.x

Pons TL, Lambers H, Chapin FS III (2008) Plant physiological ecology, 2nd edn. Springer, New York

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol 193:30–50. https://doi.org/10.1111/j.1469-8137.2011.03952.x

Poulin J, Sakai AK, Weller SG, Nguyen T (2007) Phenotypic plasticity, precipitation, and invasiveness in the fire-promoting grass *Pennisetum setaceum* (Poaceae). Am J Bot 94:533–541. https://doi.org/10.3732/ajb.94.4.533

Rapson G, Wilson J (1992) Genecology of *Agrostis capillaris* L. (Poaceae)–an invader into New Zealand: 2. Responses to light, soil fertility and water availability. New Zeal J Bot 30:1–11

Rehfeldt GE, Ying CC, Spittlehouse DL, Hamilton DA (1999) Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. Ecol Monogr 69:375–407. https://doi.org/10.1890/0012-9615(1999)069[0375:GRTCIP]2.0.CO;2

Reisch C, Poschlod P (2003) Intraspecific variation, land use and habitat quality—a phenologic and morphometric analysis of *Sesleria albicans* (Poaceae). Flora Morphol Distrib Funct Ecol Plants 198:321–328. https://doi.org/10.1078/0367-2530-00103

Sandel B, Monnet A-C, Vorontsova M (2016) Multidimensional structure of grass functional traits among species and assemblages. J Veg Sci 27:1047–1060. https://doi.org/10.1111/jvs.12422

Schneider C, Rasband W, Eliceiri K (2012) NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675

Siefert A, Violle C, Chalmandrier L, Albert CH, Taudiere A, Fajardo A, Aarssen LW, Baraloto C, Carlucci MB, Cianciaruso MV, Dantas V, de Bello F, Duarte LDS, Fonseca CR, Freschet GT, Gaucherand S, Gross N, Hikosaka K, Jackson B, Jung V, Kamiyama C, Katabuchi M, Kembel SW, Kichenin E, Kraft NJB, Lagerström A, Le Bagousse-Pinguet Y, Li Y, Mason N, Messier J, Nakashizuka T, Overton JM, Peltzer DA, Pérez-Ramos IM, Pillar VD, Prentice HC, Richardson S, Sasaki T, Schamp BS, Schöb C, Shipley B, Sundqvist M, Sykes MT, Vandewalle M, Wardle DA (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecol Lett 18:1406–1419. https://doi.org/10.1111/ele.12508

Skálová H, Pecháčková S, Suzuki J, Herben T, Hara T, Hadincová V, Krahulec F (1997) Within population genetic differentiation in traits affecting clonal growth. J Evol Biol 10:383. https://doi.org/10.1007/s000360050031

St. Clair BJ, Kilkenny FF, Johnson RC, Shaw NL, Weaver G (2013) Genetic variation in adaptive traits and seed transfer zones for *Pseudoroegneria spicata* (bluebunch wheatgrass) in the northwestern United States. Evol Appl 6:933–948

Talkington NE (2015) Trait variation between populations of *Sporobolus airoides* (Poaceae): implications for restoring invaded grasslands. Northwestern University and the Chicago Botanic Garden, Evanston

Van Wijk MT (2011) Understanding plant rooting patterns in semi-arid systems: an integrated model analysis of climate, soil type and plant biomass. Glob Ecol Biogeogr 20:331–342. https://doi.org/10.1111/j.1466-8238.2010.00601.x

Viechtbauer W (2010) Conducting meta-analysis in R with the metafor package. J Stat Softw 36:1–48

Violle C, Enquist BJ, Mcgill BJ, Jiang L, Cile C, Albert H, Hulshof C, Jung V, Messier J (2012) The return of the variance: intraspecific variability in community ecology. Trends Ecol Evol 27:245–253. https://doi.org/10.1016/j.tree.2011.11.014

Wang T, O'neill GA, Aitken SN (2010) Integrating environmental and genetic effects to predict responses of tree populations to climate. Ecol Appl 20:153–163

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas M-L, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821–827. https://doi.org/10.1038/nature02403

Zhou W, Wang Z, Davy AJ, Liu G (2013) Geographic variation and local adaptation in *Oryza rufipogon* across its climatic range in China. J Ecol 101:1498–1508. https://doi.org/10.1111/1365-2745.12143