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For the Special Issue: Evolutionary Insights into Geographic Variation

Geographic patterns of seed mass are associated with climate factors, but relationships vary between species[1]

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PREMISE OF THE STUDY: Seed size is a critical life history attribute with fitness effects that cascade throughout the lifespan of plants. Interspecific studies repeatedly report a negative correlation between seed mass and latitude. Yet, despite its importance, little is known about geographic variation in seed size within species' ranges.

METHODS: To improve our understanding of intraspecific geographic variation in seed size, we collected and weighed seeds by maternal line from 8 to 17 populations of seven herbaceous plant species spanning large geographic areas, and measured a dispersal trait, awn length, for two grass species. We examined the overall relationship between seed mass and latitude, then divided the data into species-specific subsets to compare the fit of three models to explain seed mass and awn length: (1) latitude and longitude, (2) long-term climate, and (3) collection-year weather.

KEY RESULTS: Like previous work, we found a negative relationship between interspecific seed mass and latitude. However, the best-fit models explaining seed size and awn length differed between individual species and often included significant interaction terms. For all species, the best model was either long-term or collection-year climate data instead of latitude and longitude.

CONCLUSIONS: Intraspecific geographic patterns for seed traits were remarkably inconsistent, covarying both negatively and positively with temperature and precipitation. The only apparent generalization is that annual species' seed mass corresponded more with collection-year weather while perennial species covaried more with long-term climate. Overall, this study suggests that the scale of climate variation that molds seed traits is highly species-specific.

KEY WORDS awn length; climate; geographic patterns; interspecific; intraspecific; latitude; longitude; precipitation; seed size; temperature

Seed size varies tremendously, up to 10^{10}-fold between plant species (Westoby et al., 1992) and 6-fold even within single fruits (Stanton, 1984). This enormous diversity in propagule size is especially interesting because seed mass has been shown to strongly influence other important life history and fitness traits including dormancy (Foster, 1986; Baskin and Baskin, 1998), dispersal (Ehrlén and Eriksson, 2000; Graae et al., 2004), germination (Waller, 1985; Baskin and Baskin, 1998), establishment (Foster, 1986; Ehrlén and Eriksson, 2000; Moles and Westoby, 2002), survival (Shipley and Parent, 1991) and reproduction (Stanton, 1984; Shipley and Parent, 1991) as well as biotic interactions (Foster, 1986; Armstrong and Westoby, 1993; Harms and Dalling, 1997; Green and Juniper, 2004; Espelta et al., 2009; Lázaro and Traveset, 2009). Given the importance of this early life history trait, it is surprising how little is known about how seed size varies across species' ranges.

Researchers have long been interested in how organism size varies across latitude. For example, Bergmann's Rule suggests that warm-blooded vertebrates increase in size at higher latitudes (Meiri and Dayan, 2003). Several studies have examined interspecific patterns of seed size and found the opposite trend: plant species with larger seeds are increasingly common toward the equator (Moles et al., 2007). For example, a survey of climbing plants found that more species with larger seeds grew at lower latitudes than species with smaller seeds (Gallagher and Leishman, 2012). Other studies that separated species by functional group or growth form also found that large-seeded species were more common closer to the equator (Moles and Westoby, 2003; Moles et al., 2007). Even when comparing

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congeners, species from tropical low-latitude habitats tend to have larger seeds than their temperate sister taxa (Lord et al., 1997). Given this repeated finding of interspecific latitudinal variation in seed size, it is reasonable to hypothesize that a similar negative relationship between latitude in seed size within species' ranges should exist.

Despite this prediction, studies investigating the relationship between seed size and latitude within species' ranges have found it to be more complex than expected. Previous intraspecific studies have reported latitudinal trends in seed size that both parallel and contrast with the consistently negative interspecific relationship. For example, a meta-analysis showed that latitude was the best predictor of intraspecific seed size, even proving to be better than temperature and precipitation, and that seed size negatively covaried with latitude (De Frenne et al., 2013). Likewise, a study of 34 *Glycine* spp. in Australia found both inter- and intraspecific patterns of increasing seed size at lower latitudes, most often related to temperature and solar radiation (Murray et al., 2004). In contrast, a study of two *Acer* spp. reported increased seed size at higher latitudes, contrary to expectation based on interspecific patterns (Carón et al., 2014). Similarly, within the ranges of a suite of forest herb species, seed size positively covaried with latitude (Graae et al., 2009). Other studies have shown that the relationship between latitude and seed size differs between species (Moles and Westoby, 2003). To build a stronger consensus on relationships between latitude and longitude and seed size within species, more studies that look for underlying causes of the variability in those relationships are required. Here, we investigate both climate variables and life history traits in relation to seed size across latitude and longitude to add to the current knowledge on the topic.

In addition to seed mass, some species can have accessory tissues that can have a large impact on disseminule mass and can be instrumental in the dispersal, survival, and germination success of seeds. For example, in many grass species awns (stiff bristle-like appendages that extend from the accessory tissues associated with seeds in many grass species) are especially important. Long awns can help orient seeds properly for germination (Peart, 1981). Some awns have stiff hairs or thorns on their surface that help provide unidirectional "ratcheting" movement for seeds (Elbaum et al., 2007; Kulic et al., 2009). In some cases, awns react with water to increase seed burying depth through spiraling or "drilling" motions (Garnier and Dajoz, 2001; Elbaum et al., 2007; Johnson and Baruch, 2014; Liu et al., 2014). In many cases, this increased burial depth can lead to increased survival after fire (Garnier and Dajoz, 2001; Johnson and Baruch, 2014). Additionally, some awns can cling to animal fur or feathers to increase zoonotic dispersal (Liu et al., 2014). Many awns have dense numbers of stomata, leading to high rates of transpiration and, in some species, photosynthesis, which can increase seed mass (Grundbacher, 1963). There has also been some suggestion that long awns might be disadvantageous in humid or rainy habitats by retaining water and thereby increasing disease prevalence (Grundbacher, 1963), and plants with shorter awns can be less susceptible to drought (Villegas et al., 2007; Ahmadizadeh et al., 2011; but see Abdolshahi et al., 2015). Thus far, the only geographic studies of awn length have examined origin sites for different landraces of crop species and were more focused on how artificial selection and agricultural practices affect awn traits (e.g., durum wheat; Spagnoletti Zeuli and Qualset, 1987). However, since awns are important traits for successful reproduction (e.g., Peart, 1981), often have high heritability (e.g., Garnier and Dajoz, 2001; Ahmadizadeh et al., 2011), and can be related to local climatic variables (e.g., humidity, wind, temperature via transpiration), it may be particularly useful to understand patterns of awn length across latitude and longitude and how they compare to the same patterns in seed mass.

A fundamental motivation for seeking trends in seed size or other plant traits across latitudes stems from the fact that climate variables, especially temperature, covary strongly with latitude, making latitude a useful proxy for climate (Fig. 1A). However, this correlation may be confounded by other environmental factors that also covary with latitude such as insolation, nutrient availability, soil characteristics, and human influence (De Frenne et al., 2013). Moreover, seed size may respond more closely to annual variation in climate variables such as cumulative growing degree hours (De Frenne et al., 2010) rather than long-term average temperature. Seed size may also be influenced by local factors that are not related to climate such as soil pH (Tautenhahn et al., 2008), and solar irradiance (e.g., Foster and Janson, 1985; De Frenne et al., 2011). In addition, seed size may be jointly influenced by climate variables that covary with longitude, such as precipitation (Fig. 1B). Precipitation can have mixed effects on seed mass that are sometimes positive (e.g., Gallagher and Leishman, 2012) and sometimes negative (e.g., Tautenhahn et al., 2008). It is also likely that temperature and precipitation interact in their influence on seed size, although this possibility is modeled less frequently. Generally, temperature and precipitation are the best-studied abiotic factors across latitude and longitude, are both known to vary geographically, and can both have strong effects on seeds. Thus, we focus our work on these two aspects of climate when looking at abiotic effects on seed mass across latitude and longitude.

While seed size is notoriously plastic in response to the environment (Fenner and Thompson, 2005), there are many ways that the environment can have a multigenerational effect on seed size. Covariation between seed size and abiotic conditions may arise as a function of environmental effects, such as maternal effects (Platenkamp and Shaw, 1993) or, over the longer-term, by natural selection (Galloway et al., 2009; Lázaro and Traveset, 2009), which may elicit evolutionary responses if phenotypic variation is genetically based (Byers et al., 1997; Thiede, 1998) and may be adaptive in the wild (Galloway and Etterson, 2007). Given that the environment affects seed size through numerous pathways, it is likely this trait will also be impacted by climate change either within or between generations, or both. Some empirical evidence supports this hypothesis. For example, experimental warming of *Anemone nemorosa* plants sampled from across a range of latitudes elicited a plastic response of increased seed mass but decreased seed numbers for all populations across the range (De Frenne et al., 2011). Larger but fewer seeds were also produced in *Campanulastrum americana* as a correlated response to artificial selection for early flowering (Burgess et al., 2007), a phenology which is anticipated to be favored by natural selection with climate change (Anderson et al., 2012). If climate warming is associated with changes in seed size and possibly also accessory structures, such as awns, then dispersal ability, germination success, interactions with competitors or seed predators, and other traits may be directly impacted (Wulff, 1986; Espelta et al., 2009; Walck et al., 2011; Liu et al., 2013). Seed dispersal and establishment are both influenced by seed size and may become especially important under climate change as current habitats begin to change (Westoby et al., 1992; Walck et al., 2011).

To increase our understanding of geographic patterns of seed size, we examined seed mass at several levels: between seven plant

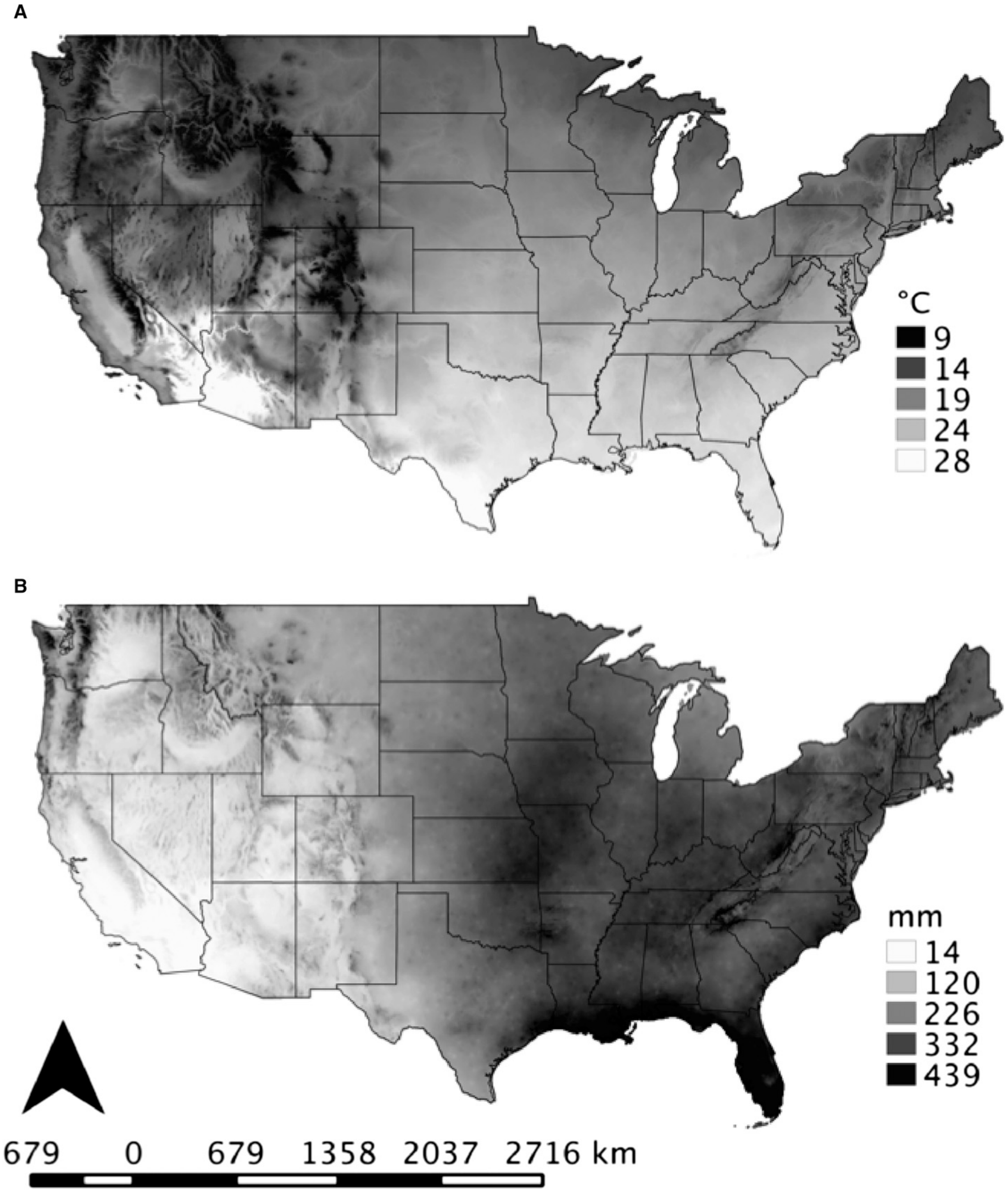


FIGURE 1 Average annual 30-yr climate normals (1981–2010) for May, June, and July for (A) average temperature and (B) total cumulative annual precipitation across the contiguous United States (PRISM Climate Group, 2015).

species, between populations sampled across latitude and longitude within these species' ranges, and between maternal lines within populations. We addressed the following questions: (1) Does seed size across all species in our study covary with latitude, as seen in other studies? (2) Within species' ranges, does seed size or awn length covary with latitude and longitude and/or climate variables? (3) Do species differ with respect to geographic patterns of seed size or awn length, and if so, are there life history characteristics associated with these differences? Together, these data help provide insight into contemporary geographic patterns in seed size and serve as baseline information for future studies of evolutionary response to selection related to natural and anthropogenic factors.

MATERIALS AND METHODS

Data collection—Seeds for this experiment were collected in 2013 and 2014 as part of the Project Baseline seed banking initiative (Project Baseline, 2015; Etterson et al., 2016 in this special issue; Appendix S1 [see Supplemental Data with the online version of this article] contains accession numbers) and are stored at the USDA National Center for Genetic Resources Preservation as a resource for future resurrection studies to dissect the mechanisms of evolutionary change over time and space. Our study included seven species: *Amorpha canescens* Pursh, *Asclepias syriaca* L. *Echinacea pallida* Nutt. (Nutt.), *Helianthus annuus* L., *Impatiens capensis* Meerb., *Schizachyrium scoparium* Michx. (Nash), and *Sorghastrum nutans* (L.) Nash. These species are all native to the central and eastern United States, have large geographic ranges, grow in relatively large populations, and set seeds in late summer and into early fall. However, they vary widely in growth form, life history, and ecology (Table 1).

Eight to 17 populations of each species were sampled across gradients of latitude and longitude (Table 1). Seeds were stored by maternal plant in a desiccating environment at ~4°C until they were weighed. Five seeds from each of five maternal lines were weighed to the nearest 0.001 mg for every species-site combination (except for *I. capensis*, where more seeds were weighed as a component of a different experiment; 4–8 seeds per maternal line for 20 maternal lines per site). Seeds of two graminoid species, *S. scoparium* and *S. nutans*, were separated from all accessory tissues (e.g., awns, lemmas) before weighing, with awns further separated for scanning and measuring using ImageJ (v1.48, National Institutes of Health, Bethesda, Maryland, USA).

Climate data were collected at two temporal scales: long term (1981–2010) and year of collection (either 2013 or 2014, depending on collection date). In both cases, we collected data from the nearest weather station from the National Climatic Data Center (2015) network, which allowed a fairly direct comparison between the two data sets. Weather stations were generally very near collection sites, averaging 21 km away (range: 1 to 161 km; median: 14 km), and were always located in the same EPA Level II Ecoregion. Previous studies have suggested that growing season temperatures and/or coldest January temperatures are the best predictors of plant growth traits, such as flowering time (Miller-Rushing and Primack, 2008). We initially modeled average temperature and precipitation for both the growing season (May, June, and July) and for January, but the January analyses were not significant. Therefore, we only present models using average temperature and precipitation for May, June, and July here. Pearson correlation coefficients, r, and their significance were calculated for the relationship between each combination of geographic and climate variables at our sites.

Interspecific seed size and latitude—To examine whether there was a significant interspecific pattern in seed size with latitude for the seven species in this study, we ran a linear mixed effects model using average seed mass per species per site (a total of 88 seed mass by latitude points) as the response and latitude as the explanatory variable, with species identity included as a random effect (REML, JMP 11.0.0, SAS Institute, Cary, North Carolina, USA). This analysis allows us to test for a relationship between seed size and latitude while controlling for species identity and is similar to how previous studies have investigated interspecific patterns in seed size (e.g., Moles et al., 2007). We similarly analyzed the relationship between interspecific pattern in seed size and long-term and collection-year temperature. Seed mass was log-transformed to improve normality of residuals.

Intraspecific patterns in seed size and awn length—Seed mass and awn length data were analyzed using a linear mixed effects model with species and collection year as fixed effects, latitude and longitude as continuous covariates, and maternal line nested within population as a random effect (REML, JMP 11.0.0, SAS Institute). Given that preliminary analyses showed significant two- and three-way interactions between species and the continuous covariates (e.g., species × latitude, species × latitude × longitude; online Appendix S2), we analyzed each species' data separately to ascertain species-specific patterns according to geographical position and climate.

Differences in seed size and awn length between species—For each species, we compared three explanatory models for variation in

TABLE 1. Focal species of this study including family, life history attributes, number of populations collected in 2013 and 2014, and the latitudinal and longitudinal extent of the range of seed collections as expressed by geographical degrees, distance (km), and estimated percentage of the full range.

					Latitude			Longitude		
Species	Family	Life history	Habit	No. of pops. 2013, 2014	Degrees	Km	% Total range	Degrees	Km	% Total range
Amorpha canescens	Fabaceae	Perennial	Shrub/ subshrub	4, 4	9.03	1004	47	4.23	470	32
Asclepias syriaca	Asclepiadaceae	Perennial	Forb/herb	6, 4	6.71	746	40	11.52	1281	47
Echinacea pallida	Asteraceae	Perennial	Forb/herb	13, 3	13.74	1528	68	11.06	1230	39
Helianthus annuus	Asteraceae	Annual	Forb/herb	7, 1	9.67	1075	41	6.65	739	19
Impatiens capensis	Balsaminaceae	Annual	Forb/herb	7, 8	10.67	1187	54	23.52	2615	63
Schizachyrium scoparium	Poaceae	Perennial	Graminoid	13, 0	12.44	1383	51	26.19	2912	55
Sorghastrum nutans	Poaceae	Perennial	Graminoid	17, 0	8.70	967	56	21.99	2445	50

seed size and awn length using a corrected version of Akaike's information criterion, AICc, a model selection approach based on information theory that evaluates goodness of fit vs. model complexity and is especially appropriate for small data sets (Burnham and Anderson, 2004). Our three models were Model 1, latitude and longitude of collected populations; Model 2, long-term climate data; and Model 3, the average weather during the year the seeds were collected. Data for *A. canescens*, *E. pallida*, and *I. capensis* were log-transformed and square-root-transformed for *H. annuus* and *S. scoparium* to improve normality of the residuals. All models were run in JMP (v. 11.0.0, SAS Institute).

RESULTS

Seed mass ranged from 0.016 mg to 18.757 mg, a 1172-fold difference. *Impatiens capensis* produced the heaviest seeds, and *S. scoparium* had the lightest, with a 7.5-fold difference between their respective mean seed masses (online Appendix S3). There was also a lot of variation within species; the standard deviation of seed mass varied from 0.37 for *S. scoparium* to 3.05 for *I. capensis*, with seed mass averaging 1.5 standard deviations within species (see also Appendix S3). The two grass species differed with respect to seed size but not awn length; *S. nutans* seeds were 1.9 times larger than those of *S. scoparium*. For both *S. nutans* and *S. scoparium*, awn length was significantly correlated with seed mass, but the correlation coefficient was small ($r = 0.20$ and $r = 0.26$, respectively; $P < 0.0001$ for each).

For the sites in this study area, geographic and climate variables were strongly associated with one another. Latitude was highly correlated with long-term climate data (temperature $r = -0.91$; precipitation $r = -0.54$) and year-of-collection weather data (temperature $r = -0.90$; precipitation $r = -0.33$) for all sites ($P < 0.0001$ for all). Weaker but significant correlations were observed between longitude and long-term temperature ($r = 0.06$, $P = 0.0008$) and precipitation ($r = 0.20$, $P < 0.0001$), and year-of-collection weather (temperature $r = 0.30$; precipitation $r = 0.45$; $P < 0.0001$ for both).

Interspecific seed size and latitude—We found a significant relationship between seed mass and latitude, with larger seeds found more at lower latitudes ($F_{1,\ 82.5} = 18.9$, $P < 0.0001$), which matches our expectations based on previous studies (Lord et al., 1997; Moles and Westoby, 2003; Moles et al., 2007; Gallagher and Leishman, 2012) that consistently reported a negative relationship between interspecific seed size and latitude. Additionally, both long-term temperature ($F_{1,\ 79.4} = 25.3$, $P < 0.0001$) and year-of-collection temperature ($F_{1,\ 79.5} = 19.3$, $P < 0.0001$) had a positive relationship with seed mass across all species. While latitude and climate variables were highly significant, species identity by itself explained more than 80% of the variation in seed size in all three analyses.

Intraspecific patterns in seed size and awn length—Both seed mass and awn length differed significantly among species, collection years, and geographical position in a model that included the full data set (Appendix S2). Significant two- and three-way interaction terms indicated that the relationship between seed traits and latitude and/or longitude differed by species; therefore, we investigated patterns in seed mass and awn length for each species separately.

Differences in seed size and awn length by species—Interestingly, when seed size and awn length were modeled separately by species, the geographic model that included latitude and longitude (Model 1) was never the best-fit model for any of the species considered herein, although the AICc for the geographic model was sometimes very close (within ~2) compared with the climate model with the lowest AICc (Table 2). Instead, the models with the lowest AICc for our seven species included either long-term average temperature and precipitation (Model 2, 3 species for seed mass and 1 for awn length) or the temperature and precipitation in the year the seeds were collected (Model 3, 4 species for seed mass and 1 for awn length).

For *A. canescens*, *H. annuus*, and *I. capensis*, the seed mass model with the lowest AICc included long-term average temperature and precipitation during May, June, and July (Table 2). For *A. canescens*, all three models provided an almost equally good fit, but contrary to our results in the interspecific analysis, larger seeds were sampled from populations at higher latitudes with cooler temperatures (Fig. 2A and B). In contrast, for *H. annuus*, there was a negligible difference in AICc for the models that included long-term climate data (Model 2) and latitude and longitude (Model 1). For this species, there was a significant interaction between temperature and precipitation in Model 2 and latitude and longitude in Model 1 (Table 2). *Helianthus annuus* seeds were largest in climates that were hot and wet (southeast) and smallest in climates that were hot and dry (southwest; Fig. 2C and D). Long-term climate data unequivocally provided the best model fit for *I. capensis* seed size. Seeds sampled from populations that occurred in warmer, wetter climates had greater mass (Fig. 2E and F).

Sorghastrum nutans awn length was best explained by the long-term climate model as well (Model 2), although the AICc value for the latitude and longitude model (Model 1) was very similar (+1.77; Table 3). Interestingly, while the long-term climate model provided the best fit according to AICc values, none of the individual long-term climate components (temperature, precipitation, or their interaction) were significant (Table 2). Instead, maternal line accounted for 62% of the variation in awn length. By contrast, Model 1 showed significant effects of latitude, longitude, and their interaction in addition to maternal line (Table 2). *Sorghastrum nutans* awns were shortest in the southeast, with relatively equal lengths throughout the rest of the collections (Fig. 3C).

For the remaining four species (*A. syriaca*, *E. pallida*, *S. scoparium*, and *S. nutans*), growing-season temperature and precipitation during May, June, and July of the collection year provided the best-fit model for seed mass (Table 2). The AICc was similar for *A. syriaca* models that included long-term and collection-year climate data, but collection-year climate data clearly produced the best-fit model for the other three species. While *A. syriaca* produced large seeds in a wide range of climate conditions, their seeds were particularly small in cold, wet climates (Fig. 2G and H). *Sorghastrum nutans* seed size, in contrast, responded primarily to collection-year temperature and not precipitation (Table 2), with larger seeds associated with warmer temperatures (Fig. 2M and N). Models describing *E. pallida* and *S. scoparium* seed size included a significant interaction between current-year temperature and precipitation. For both of these species, plants originating in sites with either cold/wet or warm/dry growing seasons produced larger seeds (Fig. 2I–L).

Collection-year climate data had the greatest explanatory power for *S. scoparium* awn length, similar to seed mass for this species

(Table 3). Both temperature and precipitation during the growing season of the collection year influenced *S. scoparium* awn length, but there was no interaction between these climate variables, suggesting that they acted independently rather than in concert, as was seen in seed mass. Awns increased in length with increasing temperature and decreasing precipitation. Overall, awns of seeds collected in warm/dry sites were long, and awns collected in any other climate were relatively short (Fig. 2A). Awns increased in length with increasing temperature and decreasing precipitation (Fig. 2B). Maternal line explained 35% of the variance in this trait.

The year of collection (2013 vs. 2014) had inconsistent effects on the seed size of different species. Of the five species that were collected over 2 years, four showed a significant effect of year on seed size (Table 2). *Asclepias syriaca* and *E. pallida* had larger seeds in 2013, while *A. canescens* and *H. annuus* had larger seeds in 2014.

Maternal line within population was highly significant for every species in every model (Table 2). The percentage of variation accounted for by this factor varied widely and ranged from 26.57 to 72.40%. Similarly, maternal line was consistently significant in both awn length models (Table 3); *S. nutans*, in particular, was dominated by variance between maternal lines (35–62%). This result suggests that seed size and awn length may have a genetic component, although our experimental design cannot distinguish genetic variance from maternal environmental variance, which is known to strongly affect seed size.

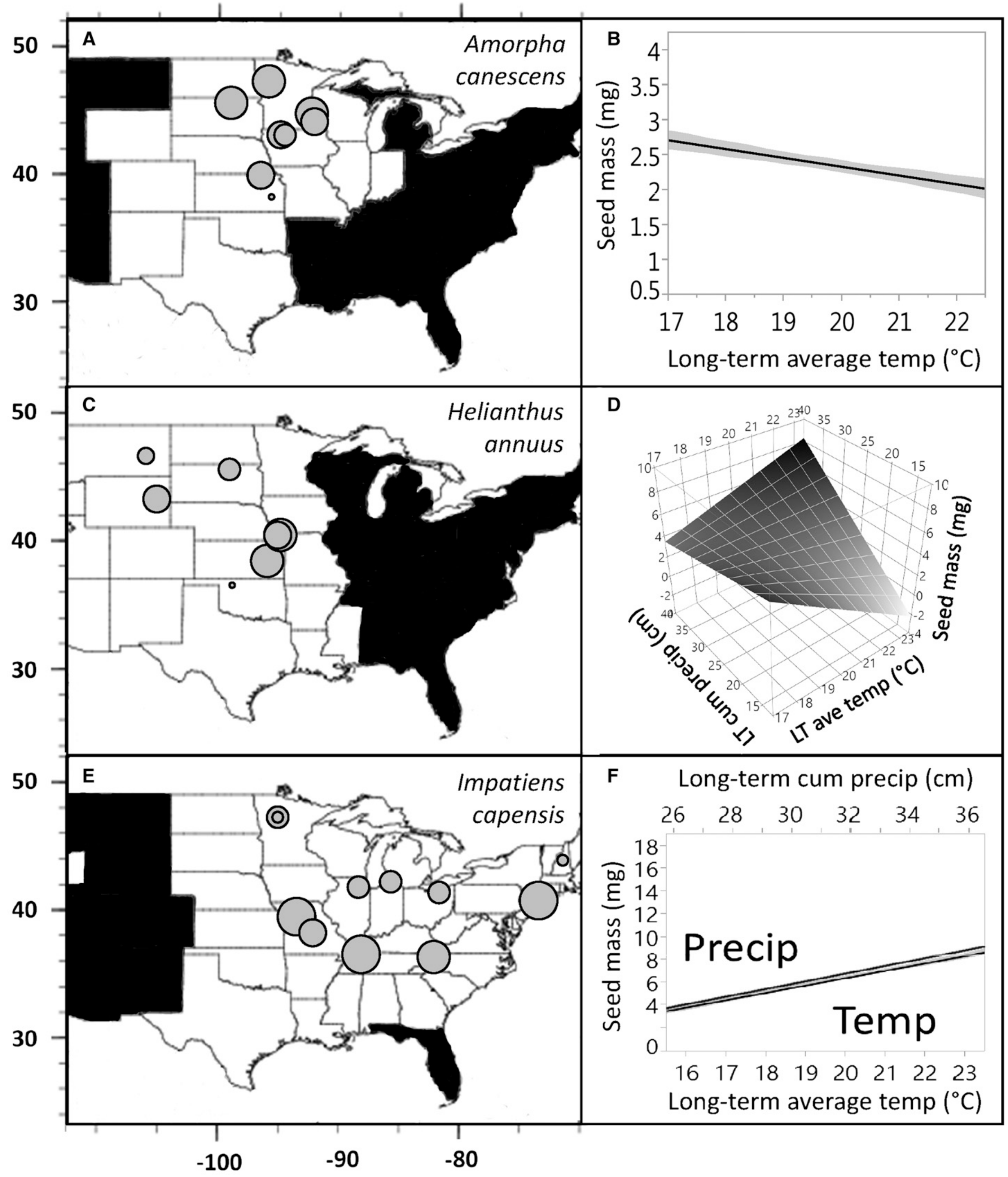
DISCUSSION

As with previous studies, we found that seed mass was greater at lower latitudes when analyzing all species combined. However, analysis of interspecific seed size revealed that patterns in seed size were remarkably inconsistent between species and always best explained by some form of climate data. Further, results for some species were contrary to expectations built on the interspecific comparison. For example, seed mass of *A. canescens* and *H. annuus* increased with decreasing temperature and increasing latitude, whereas seed size decreased in relation to these variables for all of the other species. This pattern suggests that the variables that influence seed size can differ between individual species, leading to a

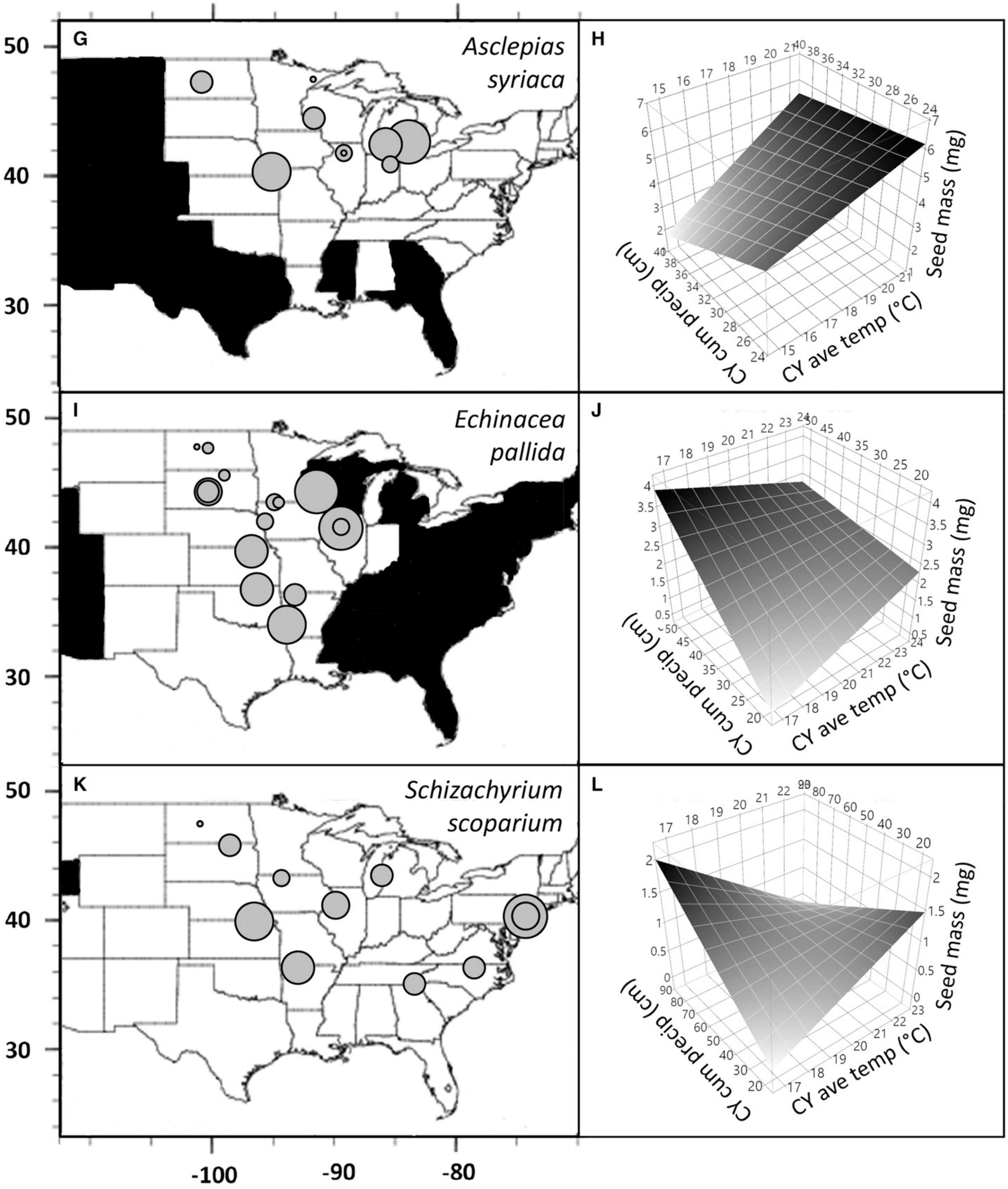
TABLE 2. Mixed model ANCOVA test statistics for analyses of seed mass conducted separately for each of seven species sampled broadly across their ranges. Three sets of explanatory variables were tested: Model 1, latitude and longitude; Model 2, 30-year average May–July temperature and precipitation; Model 3, May–July temperature and precipitation in the year seeds were collected. Likelihood ratio tests were used to test the significance of maternal line nested within population. Significant test statistics are shown in boldface. The best-fit model(s) based on AICc are shaded gray. If AICc values are within ±2.13 of one another, they were considered to be tied.

	Model 1: Latitude and longitude				**Model 2: Long-term average temperature and precipitation**				**Model 3: Collection year temperature and precipitation**			
Species	**Factor**	**df**	***F*/ *X*²**	**AICc**	**Factor**	**df**	***F*/ *X*²**	**AICc**	**Factor**	**df**	***F*/ *X*²**	**AICc**
A. canescens	Lat	1, 43	**13.20****	**120.85**	LT Temp	1, 44	**3.67+**	**119.77**	CY Temp	1, 44	**12.15***	**119.91**
	Long	1, 44	2.46		LT Precip	1, 44	0.18		CY Precip	1, 44	0.38	
	Lat × Long	1, 44	0.41		LT T × P	1, 44	1.35		CY T × P	1, 44	2.54	
	Year	1, 44	3.68+		Year	1, 44	**8.16***		Year	1, 44	0.46	
	Line (Pop)	1	**11.58****		Line (Pop)	1	**10.10****		Line (Pop)	1	**11.37****	
H. annuus	Lat	1, 35	**6.52***	**350.32**	LT Temp	1, 35	2.63	**349.44**	CY Temp	1, 35	**6.75***	353.77
	Long	1, 35	14.26		LT Precip	1, 35	**4.31***		CY Precip	1, 35	**4.58***	
	Lat × Long	1, 35	**10.63***		LT T × P	1, 35	**8.48***		CY T × P	1, 35	0.61	
	Year	1, 35	**8.03***		Year	1, 35	1.83		Year	1, 35	0.77	
	Line (Pop)	1	**25.11*****		Line (Pop)	1	**19.11*****		Line (Pop)	1	**70.00*****	
I. capensis	Lat	1, 199	**161.63*****	1513.10	LT Temp	1, 196	**84.68*****	**1480.02**	CY Temp	1, 199	**139.62*****	1525.95
	Long	1, 201	**4.62***		LT Precip	1, 194	**13.48****		CY Precip	1, 199	**5.88***	
	Lat × Long	1, 201	**36.31*****		LT T × P	1, 190	0.003		CY T × P	1, 200	**7.04***	
	Year	1, 205	2.83+		Year	1, 207	1.03		Year	1, 208	3.46+	
	Line (Pop)	1	**107.94*****		Line (Pop)	1	**87.56*****		Line (Pop)	1	**140.43*****	
A. syriaca	Lat	1, 45	**40.10*****	699.12	LT Temp	1, 35	**29.54*****	**592.22**	CY Temp	1, 35	3.18+	**590.75**
	Long	1, 45	1.27		LT Precip	1, 35	**1.35***		CY Precip	1, 35	**13.49****	
	Lat × Long	1, 45	26.81		LT T × P	1, 35	1.21		CY T × P	1, 35	**5.08***	
	Year	1, 45	**38.2*****		Year	1, 35	**7.48***		Year	1, 35	**15.91****	
	Line (Pop)	1	**148.99*****		Line (Pop)	1	**122.42*****		Line (Pop)	1	**114.70*****	
E. pallida	**Lat**	1, 83	**7.59***	276.99	LT Temp	1, 82	**12.89****	278.13	CY Temp	1, 82	**5.15***	**265.41**
	Long	1, 83	0.00		LT Precip	1, 82	0.27		CY Precip	1, 82	**14.06****	
	Lat × Long	1, 83	**10.20***		LT T × P	1, 84	**5.20***		CY T × P	1, 83	**14.69****	
	Year	1, 82	1.02		Year	1, 82	**5.28***		Year	1, 82	**14.61****	
	Line (Pop)	1	**7.32***		Line (Pop)	1	**10.09***		Line (Pop)	1	**4.33***	
S. scoparium	Lat	1, 66	2.35	−244.89	LT Temp	1, 66	0.005	−238.13	CY Temp	1, 66	**4.45***	**-247.02**
	Long	1, 66	3.02+		LT Precip	1, 66	17.62***		CY Precip	1, 66	1.13	
	Lat × Long	1, 66	**35.09*****		LT T × P	1, 66	3.08+		CY T × P	1, 66	**22.3*****	
	Line (Pop)	1	**95.91*****		Line (Pop)	1	**89.16*****		Line (Pop)	1	**55.60*****	
S. nutans	Lat	1, 82	2.21	532.35	LT Temp	1, 82	2.12	531.54	CY Temp	1, 82	**4.60***	**527.50**
	Long	1, 82	3.20+		LT Precip	1, 82	0.03		CY Precip	1, 82	1.93	
	Lat × Long	1, 82	0.03		LT T × P	1, 82	0.15		CY T × P	1, 82	1.41	
	Line (Pop)	1	**167.51*****		Line (Pop)	1	**179.88*****		Line (Pop)	1	**359.70*****	

Notes: + 0.1 > P > 0.05; * 0.05 > P > 0.001; ** 0.001 > P > 0.0001; *** P < 0.0001.


A
Amorpha canescens
B
Seed mass (mg)
4
3.5
3
2.5
2
1.5
1
0.5
17
18
19
20
21
22
Long-term average temp (°C)
C
Helianthus annuus
D
LT cum precip (cm)
LT ave temp (°C)
Seed mass (mg)
E
Impatiens capensis
F
Long-term cum precip (cm)
26
28
30
32
34
36
Seed mass (mg)
18
16
14
12
10
8
6
4
0
Precip
Temp
16
17
18
19
20
21
22
23
Long-term average temp (°C)
50
40
30
-100
-90
-80

(Continued)


G
Asclepias syriaca
H
CY cum precip (cm)
CY ave temp (°C)
Seed mass (mg)
I
Echinacea pallida
J
CY cum precip (cm)
CY ave temp (°C)
Seed mass (mg)
K
Schizachyrium scoparium
L
CY cum precip (cm)
CY ave temp (°C)
Seed mass (mg)
50
40
30
-100
-90
-80

(Continued)

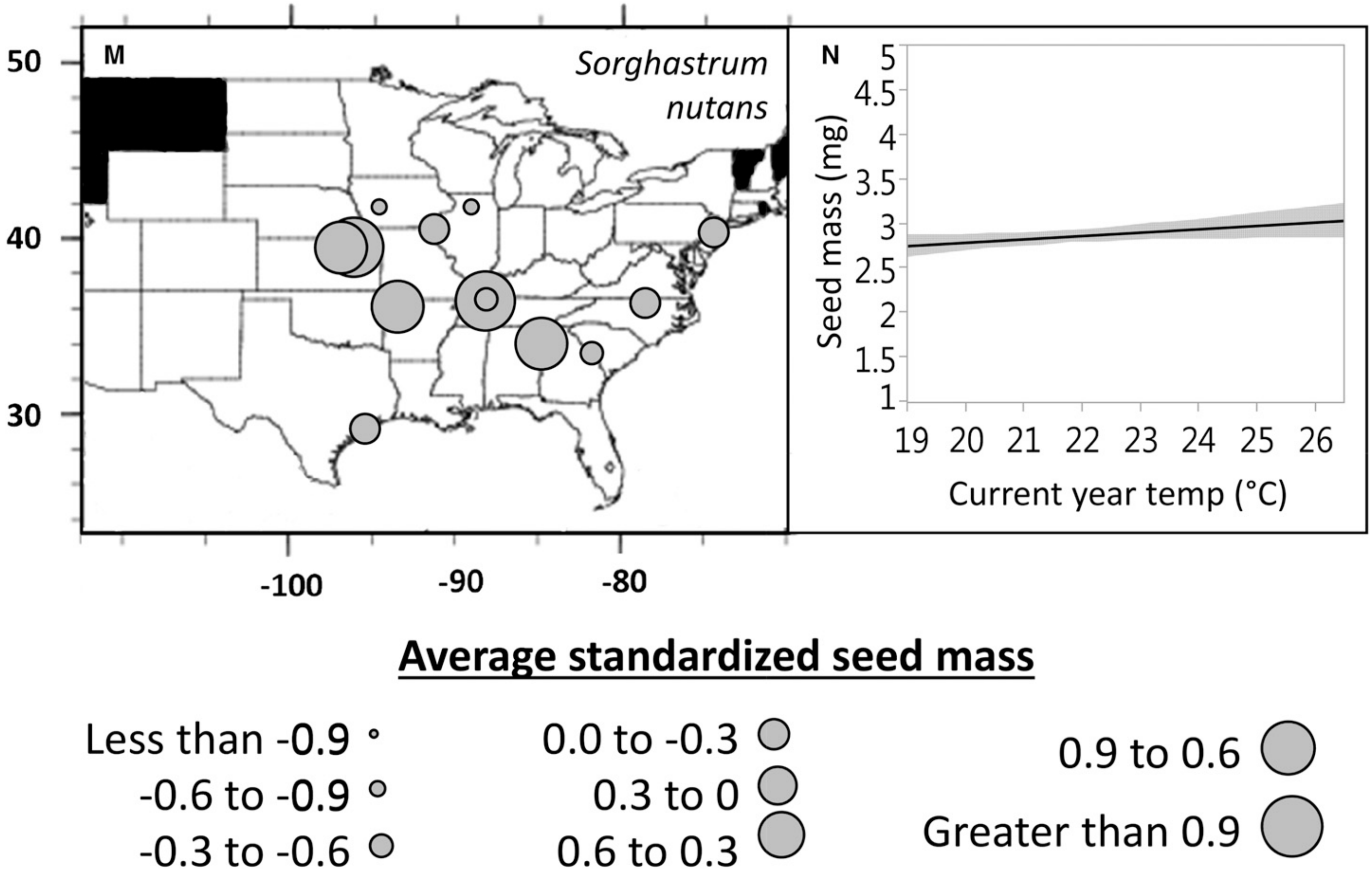


FIGURE 2 Illustration of the relationship between seed mass and climate factors for seven species sampled across their geographic ranges. The first column of panels show the species range (white) and the location of populations (gray circles) sized in proportion to standardized seed mass. The second column of panels show the estimated relationship between seed mass and climate variables that were significant in the best-fit model. A three-dimensional graph indicates that the interaction term was significant, while a two-dimensional graph shows significant one-way interactions when the interaction term was not significant. For two-dimensional graphs, the black line indicates the best-fit trend, and the gray shaded area indicates the 95% confidence interval. (A, B) *Amorpha canescens*, (C, D) *Helianthus annuus*, (E, F) *Impatiens capensis*, (G, H) *Asclepias syriaca*, (I, J) *Echinacea pallida*, (K, L) *Schizachyrium scoparium*, and (M, N) *Sorghastrum nutans*.

mosaic of seed size patterns across suites of species that defy generalization. Our results, in conjunction with those of other studies (e.g., Moles and Westoby, 2003), reinforce the conclusion that geographic patterns in intraspecific seed size do not consistently follow interspecific patterns.

In this study, we observed an association between plant life history and the timescale at which climate affected seed size. Seed size was best explained by long-term climate data for three species and by year-of-collection weather for four species (Table 2). For two of the three species best explained by long-term climate (*A. canescens* and *H. annuus*), a model with latitude and longitude fit equally well, perhaps because the long-term climate data was more closely correlated with latitude and longitude for sites in this study. Additionally, two species best explained by long-term climate data (*H. annuus* and *I. capensis*) were annual species, and two (*A. canescens* and *H. annuus*) had significantly larger seeds in 2014 than 2013. In the Midwest, 2013 was a particularly dry year, especially compared with 2014, which was wetter than average (e.g., Des Moines, IA had 8.2 cm of rain in June 2013 and 19.0 cm in 2014 compared with an average 12.5 cm; National Weather Service, 2015). Thus, our results may suggest that species with seed size best explained by long-term climate conditions are more sensitive to variation from average conditions, such as drought. Alternatively, of the four species for which year-of-collection weather data best explained variation in seed size, none had latitude and longitude models that fit well; all were perennial species, and both of the species measured across years (*A. syriaca* and *E. pallida*) had larger seeds in 2013. Altogether, our data suggests that some species (e.g., annuals in our study) may be adapted to long-term climate norms across latitudes, while others (e.g., perennials in our study) had a more plastic response to weather conditions from year to year. Previous work suggests that perennials often express greater plasticity in their seed production traits, while annuals express greater plasticity in growth-related traits (Bradshaw, 1965). Annual species may be able to adapt more easily to local climate conditions due to their short lifecycle, leading to populations locally adapted to conditions along environmental gradients. Alternatively, the ability to elicit a plastic response may be more beneficial for perennials that encounter year-to-year variation within an individual's lifetime. Additional research is needed

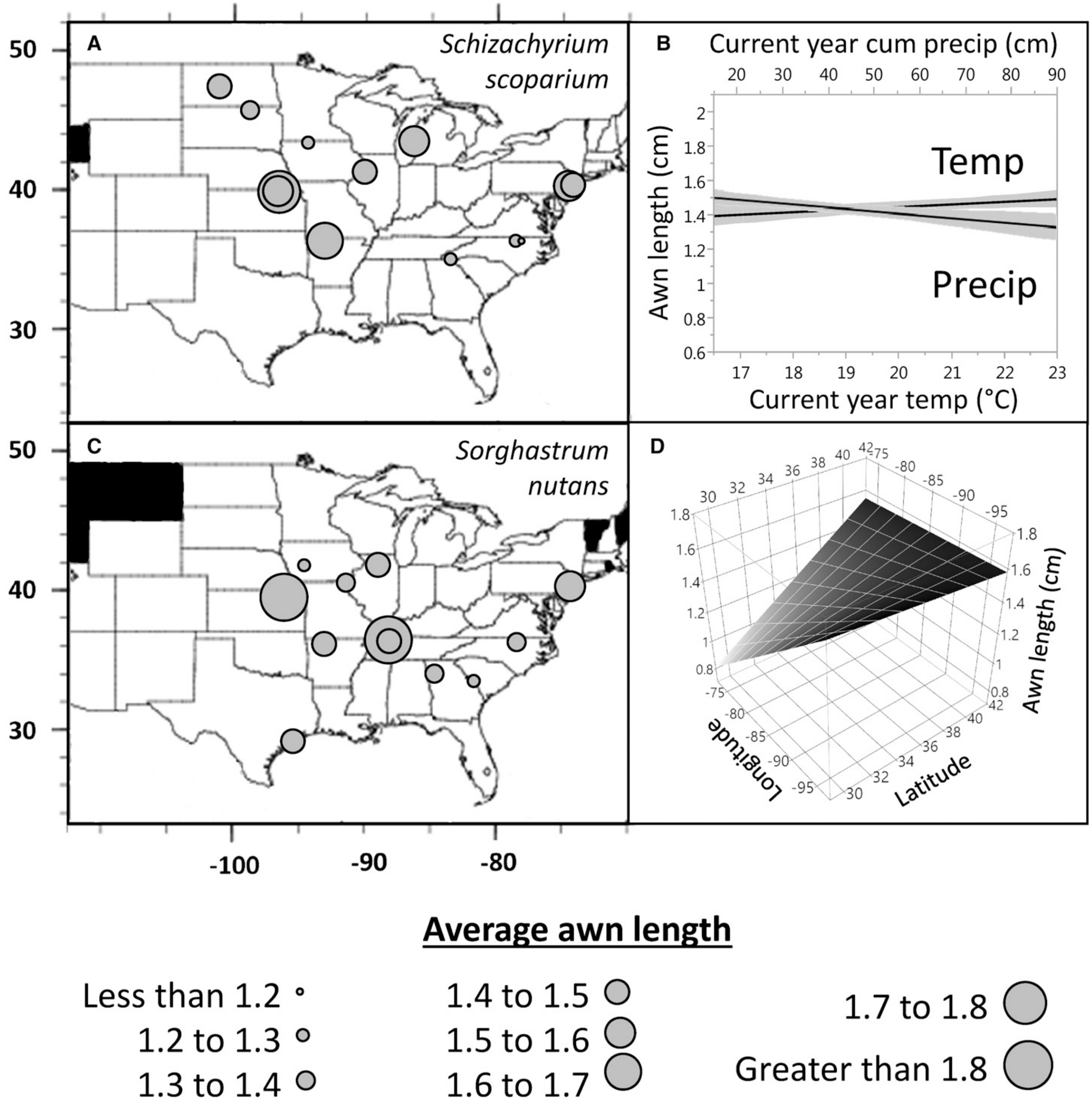


FIGURE 3 Illustration of the relationship between awn length and climate factors for two grass species sampled across their geographic ranges. The first column of panels shows the species range (white) and the location of populations (gray circles) sized in proportion to awn length (not standardized, since they were not significantly different in length between species). The second column of panels shows the estimated relationship between awn length and climate variables from the best-fit model. (A, B) *Schizachyrium scoparium*; the black line indicates the best-fit trend, and the gray shaded area indicates the 95% confidence interval. (C, D) *Sorghastrum nutans*; the best-fit model for this species was long-term climate data, but the only significant term in the model was maternal line. Instead, we graphed the significant interaction term in the second-best model, which included latitude and longitude.

to determine whether this association between life history and scale of climate effects extends across annuals and perennials in general and to investigate possible underlying causes.

Other than the relationship between plant lifespan and climate models, we found few differences in seed size among plants with contrasting life histories or growth forms. Grass species had

TABLE 3. Mixed model ANCOVA test statistics for analyses of awn length conducted separately for each of two grass species sampled broadly across their ranges. Three sets of explanatory variables were tested: Model 1, latitude and longitude; Model 2, 30-year average May–July temperature and precipitation; Model 3, May–July temperature and precipitation in the year seeds were collected. Likelihood ratio tests were used to test the significance of maternal line nested within population. Significant test statistics are shown in boldface. The best-fit model(s) based on AICc are shaded gray. Lowest AICc that are within ±2.13 are shown as ties.

	Model 1				Model 2				Model 3			
	Latitude and longitude				Long-term average temperature and precipitation				Collection year temperature and precipitation			
Species	**Factor**	**df**	**F/X^2**	**AICc**	**Factor**	**df**	**F/X^2**	**AICc**	**Factor**	**df**	**F/X^2**	**AICc**
S. scoparium	Lat	1, 66	0.01	24.25	LT Temp	1, 66	1.35	23.49	CY Temp	1, 66	**4.87***	**15.10**
	Long	1, 66	0.35		LT Precip	1, 66	0.90		CY Precip	1, 66	**4.56***	
	Lat × Long	1, 66	**7.76****		LT T × P	1, 66	3.57+		CY T × P	1, 66	1.34	
	Line (Pop)	1	**90.15*****		Line (Pop)	1	**41.32*****		Line (Pop)	1	**17.60*****	
S. nutans	Lat	1, 81	**4.59***	**69.55**	LT Temp	1, 81	1.06	**67.78**	CY Temp	1, 81	0.02	71.07
	Long	1, 81	**9.04***		LT Precip	1, 81	0.70		CY Precip	1, 81	**9.06***	
	Lat × Long	1, 81	**4.80***		LT T × P	1, 81	1.79		CY T × P	1, 81	1.05	
	Line (Pop)	1	**157.45*****		Line (Pop)	1	**176.65*****		Line (Pop)	1	**160.04*****	

Notes: + 0.1 > *P* > 0.05; * 0.05 > *P* > 0.001; ** 0.001 > *P* > 0.0001; *P* < 0.0001.

significantly smaller seeds than other species, which is not surprising considering that monocots, including the grasses, and dicots have one of the largest evolutionary divergences in seed size, with monocots having significantly smaller seeds (Moles et al., 2005b). In other systems, seed size is frequently correlated with life history or plant growth traits. For example, trees (Foster and Janson, 1985; Moles et al., 2005b; Tautenhahn et al., 2008) and other large species (Foster and Janson, 1985; Moles et al., 2005a; Pérez-Ramos et al., 2010) tend to have large seeds. Data sets that include more diversity and replication of life history and growth forms would be valuable to discover any generalizations about geographic patterns in size as it relates to these functional groups. Additionally, data that allow comparisons in a phylogenetic context could greatly increase our understanding of such patterns.

We are not aware of any previous studies that have investigated geographic patterns in awn length, despite its importance for contributing to disseminule mass, secondary dispersal, and germination (e.g., Peart, 1981). Several other studies have demonstrated awn-length plasticity in response to abiotic conditions (Grundbacher, 1963; Peart, 1981; Villegas et al., 2007; Ahmadizadeh et al., 2011; Abdolshahi et al., 2015). For example, an experimental study with a water manipulation treatment showed that plants exposed to drought grew shorter awns (Ahmadizadeh et al., 2011). Furthermore, durum wheat seeds with shorter awns produced plants that were less susceptible to drought and therefore had greater yield (Villegas et al., 2007). These previous results conflict with our *S. scoparium* data that showed that plants from sites with warmer and drier climates produced seeds with longer awns. One possible explanation is that long awns are disadvantageous in particularly rainy or humid conditions because they serve as a reservoir for surface moisture, leading to higher incidence of disease (Grundbacher, 1963). Since awn length is related to plant reproduction (e.g., Abdolshahi et al., 2015) and germinability (e.g., Peart, 1981), this first step in understanding the factors that drive its phenotype across large geographic areas is important for both agricultural and ecological systems.

Maternal line explained a significant amount of variation in seed size and awn length for all of the species in this study, which may suggest that there is at least some genetic component of these traits. However, it is not possible with our experimental design to determine whether this maternal line effect is due to genetics or environmental maternal effects or how much impact plasticity has on final seed size or awn length. Reciprocal transplant and common garden experiments such as experiments along a latitudinal gradient are needed to tease apart genetic differences in seed characteristics and plastic responses to the environment (Rehfeldt et al., 1999; Etterson and Shaw, 2001; Etterson, 2004a, b; Maes et al., 2014). In addition, at least one prior generation of crossing may be required to remove environmental maternal effects. One unique aspect of the study presented here is that the seeds are stored and available for use in future experiments, such as common gardens or genetic analyses, through the Project Baseline seedbank (Project Baseline, 2015; Etterson et al., 2016 in this special issue; see online Appendix S1 for accession numbers). This resource will allow powerful new approaches to studying the temporal and spatial factors that determine seed size and awn length and the evolution of these traits over time and across species' ranges.

As climate change progresses, warm temperatures are projected to move northward and rainfall is expected to become more erratic (Intergovernmental Panel on Climate Change, 2014). This projected change in environmental conditions associated with latitudes may alter seed size across geographic space. Seed size, quality, and germinability can be significantly affected by experimental increases in both temperature and CO_2 (Hovenden et al., 2008). Additionally, seed bank size, persistence, composition, and germinability may be altered in response to changes in climate (Plue et al., 2013). Previous research suggests that the effects of climate change on seed traits may depend on the phenology or native ranges of the plants in question. For example, increased temperature may have a more profound effect on early-season northerly distributed species (De Frenne et al., 2009). However, despite the species in this study all having mid to late season flowering times and large ranges, we still saw strong significant effects of latitude and climate variables (Tables 2, 3) on seed size and awn length. This finding suggests that changes in temperature or precipitation due to climate change may affect seed size, awn length, and, by extension, seedbank persistence, dispersal, and establishment traits. Such responses in seed traits could ultimately lead to divergent responses in how plant species track climate change spatially, potentially resulting in no-analogue communities in which novel species assemblages form. To better understand these effects and predict future patterns, we need more experiments looking at the relative genetic and phenotypic components of seed size and awn length and how these traits affect dispersal potentials in response to changes in climate.

CONCLUSIONS

Overall, we found that while our interspecific data support a negative relationship with latitude, climate variables were better at predicting seed size and awn length within species than latitude or longitude. The species in our study exhibited diverse responses to climate, with seed mass of some species better predicted by long-term climate and seed mass of others by current-year weather. Some species had larger seeds in warm temperatures and others cool, and some species grew larger seeds in wet and others dry conditions. Awn length was similarly variable, sometimes best explained by current-year temperature and precipitation and sometimes better explained by long-term climate and maternal line. Although we observed few consistent patterns, seed size of annual plants was better explained by long-term climate and seed size of perennials by weather during the year of collection, suggesting that differences in drivers of seed size among species with contrasting life histories may be a fruitful avenue for future study. Taken together, our data suggest that climate is strongly associated with seed size over large geographic areas, but patterns vary by species. Future studies of other abiotic factors (e.g., insolation, soil pH) may provide additional insight into differences in seed size across varying latitudes and longitudes. Results of such studies, in addition to current literature on how such abiotic landscape traits will change in the future, should provide valuable insights into potential effects of climate change on seed characteristics and other important plant traits.

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