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Evidence of adaptation of Little Bluestem to the local environment of central Kansas

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Little bluestem is a North American grass species found in native prairie remnants which is used for range, pasture, CRP, and restoration planting. In this study we asked whether the distance between planting site and seed source influenced the growth and survival of little bluestem. In a collaborative project with high school teachers and students, we planted seed at 2 sites in central Kansas, from 7 sources ranging from 6.9 to 814 km distant from the planting sites. We found that our measures of fitness (survival and tiller number) together declined significantly with the distance of the seed source from the site. Our results suggest that local adaptation is important to little bluestem survival and productivity and therefore recommend that land managers seek local sources of seed for range or prairie plantings.

Keywords: Local adaptation, Schizachyrium scoparium*, seed sourcing*

Introduction

In North America, less than 4% of original native prairie ecosystems remain (Samson and Knopf 1994), and thus prairie restoration efforts have become increasingly common. The success of restorations depends in large part on restoration design and implementation (Rowe 2010, Grman et al. 2013, Meissen et al. 2019). One critical aspect of the former is choosing which seed goes into the seed mix. A recommendation that has emerged from decades of restoration practice and research is the use of locally sourced seed (Mijnsbrugge et al. 2010, Leger et al. 2020, Yoko et al. 2020). This approach is consistent with the concept of local adaptation, where plant ecotypes have higher survival, growth, or reproduction when grown at locations close to their seed origin as opposed to more distant locations (Smith et al. 2012, Galliart et al. 2019).

There may be many reasons for local adaptation. Plants may have evolved to have higher fitness in local environments because of abiotic conditions such as water and nutrient availability or temperature (Hargreaves and Eckert 2019, VanWallendael et al. 2019, VanNuland et al. 2019). Plants also may be locally adapted to biotic factors, including pathogens, symbionts, and herbivores (Maron et al. 2019, Richards et al. 2019, Rekret and Maherali 2019). Some recent meta-analyses (Rúa et al. 2016, Briscoe et al. 2020) suggest that biotic and abiotic environmental factors interact to influence local adaptation of plants. For instance, Yang et al. (2018) found interactions between abiotic stress (elevation) and arbuscular mycorrhizal (AM) fungi (a common root-associated obligate symbiont) in local adaptation. AM fungi are often beneficial to plants and are of particular importance to restoration because many native prairie plants are dependent on the symbiont to some degree (Koziol et al. 2020).

Our study focuses on *Schizachyrium scoparium* (little bluestem), a long-lived perennial C4 grass that is both common across North American grasslands and a mainstay of restoration seed mixes. The wide geographic range and mid-to-late successional status (Cheeke et al. 2019) of little bluestem have made it a good candidate for studies of adaptive variation. There is evidence for high genetic variation (Huff et al. 1998), as well as local adaptation (Anderson et al. 1993, Cornelius 1947) in little bluestem populations. One persistent question in local adaptation research is the scale (geographical or ecological) at which local adaptation is important (McKay et al. 2005). While genetic variation of little bluestem is well-studied, there are few field studies which test local adaptation of little bluestem. Most of the local adaptation studies focused on little bluestem are undertaken at broader spatial scales, or strongly contrasting environmental conditions (Anderson et al. 1999, Gustafson et al. 2018). Largely lacking are studies where the seed planted into a particular site come from a wide range of distances and include quite short distances, under 50 km. Further, local adaptation of little bluestem, and prairie plants in general, has not been well-studied in the context of inoculation with native AM fungi. This is an important issue to address, given that little bluestem is positively responsive to AM fungi infection (Cheeke et al. 2019), and that inoculation with native AM fungi is recommended for prairie restoration (Koziol et al. 2018; Koziol et al. 2020).

Keeping these issues in mind, we designed a study using little bluestem seed collected from four central Kansas prairie remnants within a 150 km radius of each other, as well as seed purchased from native prairie seed companies in Missouri, Indiana, and Minnesota. Seedlings derived from seed of all origins were inoculated with a mix of native prairie AM fungi (collected both from prairies in Kansas and in eastern North America) and then planted at two sites near to both the prairie remnants and to each other. We posed the following questions:

1) Is there evidence for local adaptation in little bluestem between the two sites where seeds were reciprocally planted (and are only 68 km apart)? We predicted that seeds will perform better at their “home” site.
2) Do regional differences in seed source affect plant survival and size? We predicted that seeds from Kansas sites would have higher performance than seeds from distant sites.
3) Does site distance from seed source correlate with plant survival and size? We predicted that seed performance will decrease with source distance from study sites.

Our study was unusual in that it explicitly combined research questions with educational objectives; this study was a collaboration between high schools (both teachers and students) and research university scientists. Thus, the methodology and value of this project from a secondary education perspective is presented in the supplemental materials (S1).

Methods

Study Sites: The study sites were located in Pratt, KS, USA (37° 38’ 22.49”, -98° 47’ 3.43”), and Goddard, KS (37° 38’ 49.2”, -97° 34’ 7.18”), USA. Both sites were adjacent to local high schools (Skyline Schools and Goddard High School respectively). The soil type at both sites was silt loam (Natural Resources Conservation Service). Total precipitation for Pratt County (Pratt site) in 2019 was 72.39 cm, total precipitation for Sedgwick County (Goddard site) in 2019 was 114.3 cm (Institute for Policy and Social Research, University of Kansas), while Sedgwick county receives approximately 15 cm a year more in annual rainfall than Pratt (Climate.K-State). Both sites were previously disturbed sites which had been planted with non-native grasses. At both sites, plot areas were covered with plastic tarps for several weeks to kill vegetation before planting.

Table 1. Site coordinates and precipitation averages (20 years) and evapotranspiration averages (50 years).

Site	latitude	longitude	ma_evap	cm average rainfall
Pratt, KS Study Site	37.64	-98.7839	691	1755.14
Goddard, KS Study Site	37.64	-98.7839	691	1755.14
Pratt, KS collection site	37.632	-98.6924	691	1755.14
Medicine Lodge, KS collection site	37.306	-98.5749	691	1755.14
Hutchinson, KS collection site	38.163	-97.9441	744	1889.76
Pawnee Prairie Park, KS collection site	37.655	-97.4532	835	2120.9
Hamilton Native Seed, MO	37.215	-91.946	934	2372.36
Prairie Moon Nursery, MN	43.903	-91.637	663	1684.02
Spence Nursery, IN	40.153	-85.3602	682	1732.28

Seed Source Sites: In October 2018, native prairie-sourced little bluestem (*Schizachyrium scoparium*) seeds were collected from unplowed prairies near participating high schools in Barber, Pratt, Sedgwick, and Reno counties in Kansas (TBL). Seeds from Missouri (Hamilton Native Outpost), Minnesota (Prairie Moon Nursery), and Indiana (Spence Nursery) were used as well. This purchased seed was cultivated from seed collected in native prairies within the same region as the location where they were cultivated. These companies sell native prairie seed rather than cultivated varieties. See Table 1 for approximate site coordinates and average precipitation and evapotranspiration.

Initial growth and AM Fungal Inoculation: Germination of seeds began with a cold moist stratification at 5.5^{o} Celsius for two months. All seeds were germinated in sterile (autoclaved) soil at a Kansas Biological Survey greenhouse in Lawrence, Kansas. The greenhouse temperature was maintained at 20° Celsius, seedlings were grown in natural light and ambient humidity, and watered daily. 280 (10 of each population for each study site) Seedlings were then transplanted into small narrow pots with a volume of 100 cm^3, containing a bottom layer of~ 70 cm^3 sterile field soil, a middle layer of 15 cm^3 of a native prairie mycorrhizal inoculum mix, and covered with 20 cm^3 of sterile soil. The mycorrhizal inoculum consisted of spores of 10 AM fungal species sourced from Kansas, Indiana, and Missouri prairie remnants (Table S1) The plants were then allowed to grow in the inoculum for 12 weeks before transplanting to the field sites. Inoculation of seedlings with prairie AM fungi has been shown to increase establishment of later successional prairie plant species by giving

Table S1. Genus or species level identification and native prairie origin of arbuscular mycorrhizal fungi inoculum mix used in study.

Source	Genus/species
Central KS	*Glomus mortonii*
Central KS	*Septoglomus constrictum*
Central KS	*Paraglomus sp.*
Eastern KS	*Gigaspora giganteae*
Eastern KS	*Funneliformis mosseae*
Indiana	*Racocetra fulgida*
Indiana	*Acaulospora spinosa*
Indiana	*Entrophospora infrequens*
Indiana	*Cetraspora pellucida*
Missouri	*Cetraspora pellucida*
Missouri	*Rhizophagus clarus*
Missouri	*Scutellospora species*

them a competitive edge over other less desirable plant species (Koziol and Bever, 2017; Lubin et al. 2020; House and Bever 2020).

Planting and Data Collection: Seventy little bluestem seedlings were planted on April 17th and 18th of 2019 in five 1m × 1m plots at Goddard High School and Skyline Schools. Newly established plants were watered five times per week (for 5 weeks) to ensure initial survival. Measurements of survivorship and tiller number were collected in the first week of June 2020. Only plants which had visible above-ground foliage were counted as "surviving". Tiller number was counted by hand, see Bell (1991) for defining characteristics of a tiller.

Experimental Design: Seedlings from all 7 sources (four from Kansas, three from out of state) were inoculated with the same AM fungal mixture and planted at both Kansas high school sites. At each school, there were five replicate plots. Each plot had 14 plants (two plants from each of the seven sources). Within a plot, seed source was randomized and plants were separated by 10 cm.

Statistical Methods: We used two approaches to testing local adaptation of little bluestem. First, consider Goddard and Pratt source populations (n=40 seedlings). These plants were grown at their home site (where seed was collected) and at a more distant location. We use a full factorial test that includes the two source populations, the two test locations (where plants were grown) and their interaction as fixed effects. In this model, the main effect of test location accounts for differences between sites, the main effect of population source accounts for differences in growth of individual populations, and the interaction term tests whether growth depends upon being grown near to the site of collection. That is, the interaction term tests for local adaptation (Thrall et al. 2002). This analysis of variance was performed with Proc GLM in SAS.

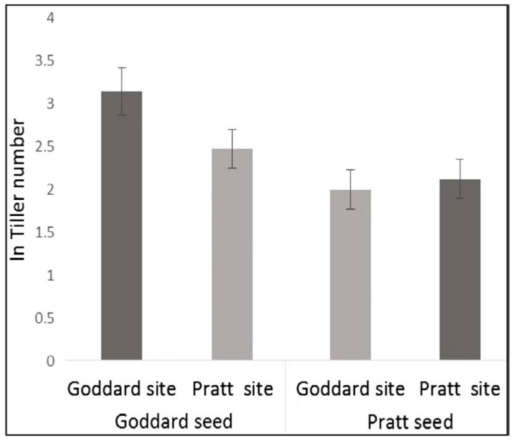

Figure 1. Ln of tiller number of *Schizachyrium scoparium* reciprocally planted between Goddard and Pratt study sites. Darker bars are matched site and seed. Error bars are +/- SE.

The second approach used all of the data (n= 7 populations and 140 seedlings) and tested for declining performance of little bluestem with increasing distance from where the seeds originated. Distance was first treated categorically as very locally sourced from near the high school sites, Kansas sourced, or sourced from out of state. Secondly distance was analyzed as a continuous variable. Distance between the site of origin of the seeds and the location of the plots at Goddard and Skyline high schools were calculated using Google maps. We test for the influence of distance from seed source on the survival and tiller number of little bluestem using mixed models. These mixed models account for the non-independence of replicate plants from different origins within plots, by identifying individual seed collections as random effects. By identifying these random effects, we are testing for consistency across the independent populations that we have collected (n=7). Survival was analyzed using Proc Glimmix in SAS, using a binomial distribution with a logit link. Tiller number of the plants that survived was analyzed using Proc Mixed in SAS (version 9.4).

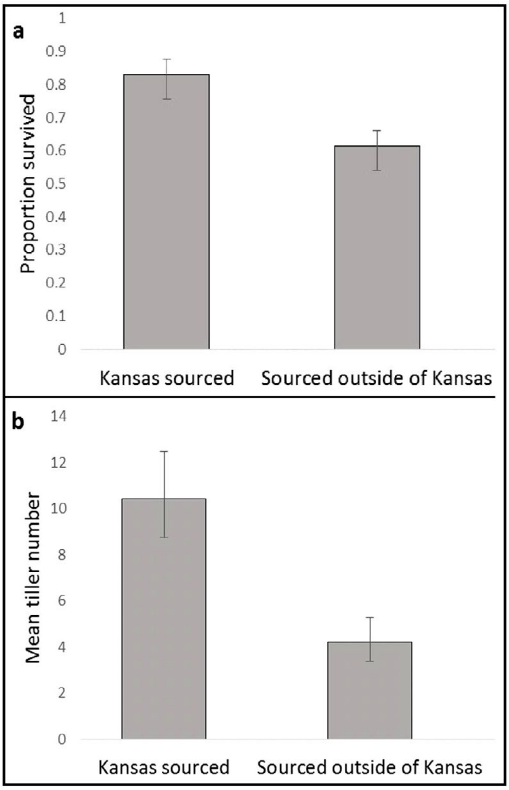

Figure 2(a). Survival of *Schizachyrium scoparium* by regional level seed-sourcing. (b) Tiller number of *Schizachyrium scoparium* by regional level seed-sourcing. (c) Tiller number of *Schizachyrium scoparium* by regional level and within Kansas seed-sourcing. Error bars are +/- SE.

Results

When just analyzing the Goddard and Pratt populations, the Goddard population grew more tillers than the Pratt population ($F_{1, 29}$= 9.64, p= 0.004, Fig. 1). While not a significant effect, both tended to grow best in the plots most closely located near their origin ($F_{1, 29}$=2.71, p= 0.11, Fig. 1). While the Goddard population survived best in the plots near to its origin, there was not enough variation in survival across the two sites by population combinations to allow meaningful statistical analysis.

When testing across all populations, little bluestem survival tended to be higher if collected from the state of Kansas than from out of state ($F_{1, 6}$ = 5.35, p = 0.06, Fig. 2a), but there was not a significant difference due to being very locally collected (i.e., from the same county; $F_{1, 6}$ = 0.45, p = 0.5). When analyzing the tiller number of the plants that survived, we find that little bluestem from Kansas grew significantly more tillers on average than little bluestem from out of state ($F_{1, 6}$ = 10.51, p = 0.02, Fig. 2b). While tiller number tended to be larger when seed was sourced very locally, there were not significant differences in comparisons among three source categories (local Kansas, other Kansas, and out-of-state) ($F_{1, 6}$ = 2.12, p = 0.19, Fig. 2c).

When analyzing the distance as a continuous variable, survival of little bluestem tended to decline with distance from their origin ($F_{1, 11}$ = 2.90, p=0.12, Fig. 3a). Of the little bluestem seedlings that survived, tiller number of little bluestem declined markedly with distance from the population origin ($F_{1, 11}$ =18.85, p=0.001, Fig. 3b). Combining the probability of survival with the productivity as assessed by tiller number of the plants that survived, we confirm that distance from the origin has a strong effect on expected fitness of little bluestem ($F_{1, 11}$ =8.10, p=0.014, Fig. 3c)

Discussion

Locally collected seed is often recommended for restoration practice, but the question posed by McKay et al. (2005) “How local is local?” has not been answered for little bluestem. Briscoe et al. (2020) noted that most studies of local adaptation focus on extreme or rare environments. Such studies are important to understanding the mechanisms and drivers of plant local adaptation, but have limited practical application. In our study we compared seed sources that are relevant to restoration, and tested local adaptation between two populations with relatively subtle differences in abiotic environments. Overall, we found that seed source affected establishment and growth of little bluestem; generally, seed that was more locally sourced had greater survival and growth. Tiller number seemed to be particularly sensitive to source distance in analyses of all seven seed collections.

Kansas populations in general fared better than any of the purchased seed from varying distances north and east of Kansas. Some of the difference could be attributed to differences between wild-collected versus purchased seed, however studies such as Baer et al. (2014) and Stover et al., (2017) found little difference in productivity between cultivars and wild-collected prairie grasses without respect to geographic origin. All of the out-of-state seed obtained for this study was sourced from native seed companies that propagate wild-collected seed in field conditions, rather than named cultivars or cultivars that are propagated vegetatively. Moreover, the fitness measures of both wild-collected and

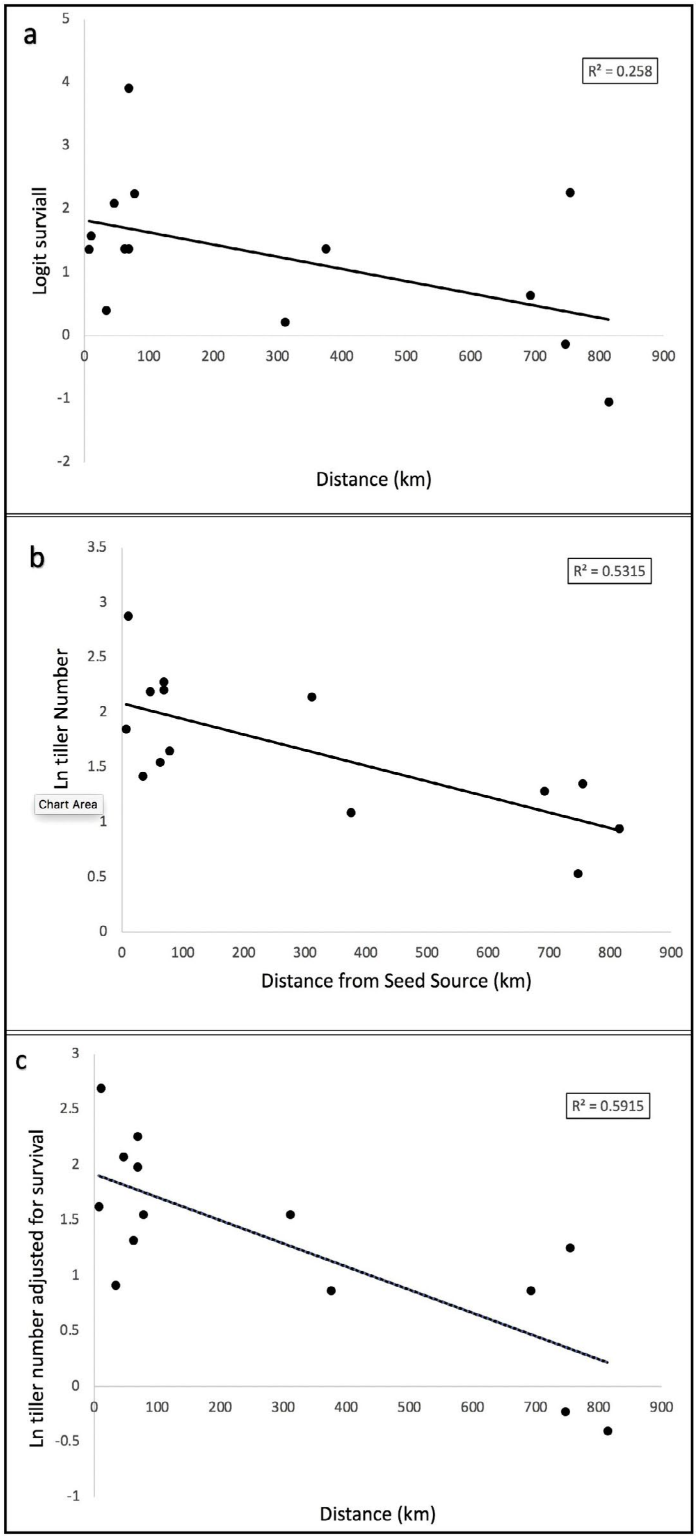

Figure 3. Linear regression showing relationship between distance of seed source from study site and (a) proportion survival (b) tiller number (c) tiller number adjusted for survival. Each plot has 14 values (7 sources planted at Goddard, 7 sources planted at Pratt). Tiller number has been log-transformed and survival logit-transformed for analyses to meet assumptions of normality. The R^2 coefficients are indicated.

purchased seeds generally declined with distance, suggesting that local adaptation is a primary driver of fitness differences.

Whether seed would perform even better it was collected very locally (i.e. from within 10 km instead of 60 kilometers away) cannot be answered definitively with our data. Our test of local adaptation at this small scale (i.e. between the Goddard and Pratt collected plants) was not significant. However, there was a tendency for performance of very local populations (i.e. within the same county) to outperform the more geographically distant Kansas populations. The degree of local adaptation has been found to depend upon interactions between the abiotic and biotic environments (Runquist et. al. 2020), but Briscoe et al. (2020) point out that site is often classed as an abiotic environment, when sites actually vary in both biotic and abiotic conditions. These findings indicate that further study on local adaptation of this species at sites on a fine geographic scale is warranted.

We do not know what abiotic or biotic factors are most important to survival and growth of little bluestem, although Huff et al. (1998) suggest that differences in local ecology can promote genetic differentiation between geographically distinct populations of *Schizachyrium scoparium*. The decline in fitness with distance from planting, however, could be driven by local adaptation to the harsh climate of central Kansas relative to the other sites. Climate variation between sites, and thus differing plant phenology and drought tolerance, likely contribute to these differences (Cornelius 1947; McKay et al. 2005; Galliart et al. 2019). While these results can provide only an inference regarding local adaptation, they do provide a strong recommendation for acquiring little bluestem seed that is proximate as possible for restoration or CRP planting. Given constraints on the availability of local seed (Broadhurst et al. 2008) and budgetary constraints on restoration projects (Henry et al. 2019), there are clear trade-offs for restoration projects when sourcing seed.

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