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Drought tolerance in ecotypes of big bluestem (*Andropogon gerardii*) relates to above-ground surface area: Results from a common garden experiment

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ABSTRACT

Big bluestem (*Andropogon gerardii* Vitman) is a dominant tallgrass species that has a wide range in North America with numerous genetically-distinct ecotypes, each adapted to conditions in their native habitat. In an evolutionary context, it was hypothesized that drought adaptation in *A. gerardii* would relate to plant surface area, where drought-adapted ecotypes were expected to be short with narrow leaves, thin stems, and few leaves per tiller. In the context of individual plants acclimating to reduced rainfall, rainout shelters were hypothesized to cause morphological reductions in surface area of individual plants. Morphological measurements were taken from four genetically-distinct ecotypes of *A. gerardii* across a precipitation gradient ranging from 500 to 900 mm rain per year at three common garden sites in Colby, Hays, and Manhattan, Kansas, USA. Evolutionary responses to drier soils in *A. gerardii* resulted in reduction of evaporative surface area from leaves, as drought-adapted plants had fewer and smaller leaves. The most mesic ecotype of *A. gerardii* had the highest maximum leaf width, stem diameter, and leaf count across sites. There were few effects of environment on morphology in *A. gerardii* with reduced rainfall, however, indicating genetics plays a more prominent role than environment to influence morphology. We conclude that increased drought tolerance is related to an evolutionary reduction in evaporative surface area.

1. Introduction

How morphology relates to evolution is a central question in plant ecology (Lowry et al., 2015; Wang et al., 2011). Environmental variables and genetics influence morphology, both within the lifetime of a plant and over evolutionary time. When reproduction among populations is restricted, as when populations are separated geographically (Álvarez et al., 2010; Beierkuhnlein et al., 2011; McMillan, 1959, 1965), genetically-distinct ecotypes can arise within the species (Lowry, 2012). The term "ecotype" was first used by Turesson (1922) to describe groups of populations of the same species with different suites of characters, which often show adaptations for conditions in their native environment (Lowry, 2012). Ecotypes within a number of grass species have been demonstrated to have habitat-specific adaptations (Beierkuhnlein et al., 2011; Chen et al., 2006; Hameed et al., 2012; Liu et al., 2012; McMillan, 1959, 1965; Olsen et al., 2013). How ecotypic variation is related to evolutionary adaptation to environmental conditions (Chen and Wang, 2009; Hartman et al., 2012; White et al., 2014) and perhaps as a stage in speciation (Lowry, 2012; Lowry et al., 2015) is beginning to be understood.

Evolution of drought tolerance in grasses can be studied intraspecifically by investigating ecotypes (Lowry et al., 2015) across climate gradients. Big bluestem (*Andropogon gerardii* Vitman) is a dominant tallgrass species that has a wide range in North America with numerous genetically-distinct ecotypes, each adapted to conditions in their native habitat (Caudle et al., 2014; Gray et al., 2014; Johnson et al., 2015; Maricle et al., 2017; Mendola et al., 2015; Olsen et al., 2013). Ecotypes of *A. gerardii* were first described by McMillan over 50 years ago (1959, 1964, 1965) across a latitudinal gradient, with variation in growing season length, photoperiod, and temperature. A longitudinal gradient across the central grasslands of North America, by contrast, varies primarily in precipitation, with greater precipitation in the east and drier conditions in the west (Lauenroth et al., 1999). We have tested numerous aspects of *A. gerardii* ecotypes across this longitudinal gradient (Caudle et al., 2014; Gibson et al., 2013; Goad, 2012; Gray et al., 2014; Johnson et al., 2015; Maricle et al., 2017; Mendola

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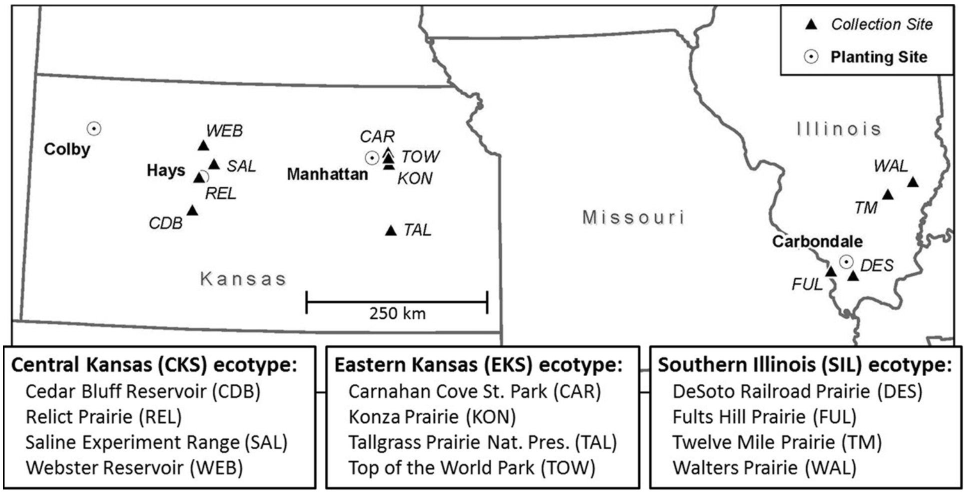

Fig. 1. Map showing collection sites for *Andropogon gerardii* seeds (triangles) and common garden sites (circles) in this study. Each regional ecotype of *A. gerardii* consisted of four collection sites within 230 km of each city; collectively, plants from these four prairies constitute an ecotype. Seeds for the Central Kansas ecotype were collected near Hays, Kansas, USA. Seeds for the Eastern Kansas ecotype were collected near Manhattan, Kansas, USA. Seeds for the Southern Illinois ecotype were collected near Carbondale, Illinois, USA. In this study, morphological characteristics were measured in common gardens in Colby, Hays, and Manhattan, Kansas, USA.

et al., 2015; Olsen et al., 2013), with particular interest in adaptations related to the precipitation gradient (Fig. 1).

Questions of whether populations are adapted for local conditions or if responses are more plastic and can be shaped within the lifetime of a plant can be addressed with common garden experiments (Bresson et al., 2011; Clausen et al., 1948). In this study, environmental and genetic influences on morphology were measured in different ecotypes of *A. gerardii* reciprocally planted in common gardens across a precipitation gradient (Johnson et al., 2015). Seeds of *A. gerardii* were collected from plants across 1150 km of a mean annual precipitation gradient from 500 mm in western Kansas to 1200 mm in southern Illinois (Fig. 1). Furthermore, this precipitation gradient has been present for at least 10,000 years (Axelrod, 1985), providing ample time for selection pressures to result in local adaptation among ecotypes of *A. gerardii* across this gradient. There are conspicuous morphological differences among ecotypes of *A. gerardii* (Johnson et al., 2015; Mendola et al., 2015; Olsen et al., 2013); the present study quantified morphological variation among *A. gerardii* ecotypes in common gardens across Kansas, USA, to determine genetic and environmental effects of decreased precipitation on *A. gerardii*. Such questions are important when considering broader issues of drought tolerance in plants or evolution of drought-tolerant morphological adaptations.

Many grasses can adjust to dry climates, either within the lifetime of the plant through plasticity (Droste et al., 2010) or over evolutionary time, through the development of differentiated drought tolerant-ecotypes (Lowry et al., 2015). Typical morphological responses to decreased precipitation involve a decrease in above-ground surface area of the plant; adaptations include narrow (Redmann, 1985) and thick (Barnes, 1986; Olsen et al., 2013) leaves (but see Hameed et al., 2012). Other drought-adapted traits include shorter plants (McMillan, 1959) and generally small surface areas (Daubenmire, 1974), including individual leaves that are small and few leaves per plant (Hameed et al., 2012). Decreased precipitation has been shown to reduce plant height (Cenzano et al., 2013; Hartman et al., 2012), number of leaves per tiller (Hartman et al., 2012), and total numbers of leaves per plant (Cenzano et al., 2013). In addition, many grasses fold or roll leaves to conserve water during times of drought (Kadioglu et al., 2012). In some cases, morphological characters like leaf length, leaf width, and internode length are adapted to home-site temperature instead of precipitation (Aspinwall et al., 2013). A common garden experiment (Clausen et al., 1948) with manipulation of precipitation (Yahdjian and Sala, 2002) can provide clear evidence of morphological responses to drought in plants, and investigate the evolution of drought tolerance in *A. gerardii*.

Andropogon gerardii has many anatomical features of leaves related to drought, including bulliform cells (Magai et al., 1994) and thicker leaves and lower proportions of vascular tissue in drought-tolerant ecotypes (Olsen et al., 2013). Morphological differences among ecotypes of *A. gerardii* might also relate to drought tolerance. Many aspects of morphological drought adaptation relate to surface area of plants (e.g., Cenzano et al., 2013; Hameed et al., 2012; Hartman et al., 2012; Redmann, 1985), as one strategy of plants is to reduce area for evaporation (Daubenmire, 1974). In addition, *A. gerardii* is known to fold or roll leaves when droughted (Barnes, 1985, 1986), which can reduce the evaporative surface area (Kadioglu et al., 2012) and help prevent the leaf from over-heating (Maricle et al., 2007; Redmann, 1983). The role of vegetative morphology in drought tolerance in a dominant prairie grass like *A. gerardii* has implications for understanding plant trait evolution, plant ecophysiology, and composition and changes in prairie communities, especially as the climate changes.

In this study, we measured several aspects of vegetative morphology among *A. gerardii* ecotypes in common gardens across Kansas, USA, to analyze genetic and environmental effects of decreased precipitation on *A. gerardii*. This study is part of an experimental platform studying genetic and environmental influences among *A. gerardii* ecotypes to assess evolutionary and ecological differences at an intraspecific level (Caudle et al., 2014; Gibson et al., 2013; Goad, 2012; Gray et al., 2014; Johnson et al., 2015; Maricle et al., 2017; Mendola et al., 2015; Olsen et al., 2013). We have documented numerous differences among ecotypes, most of which relate to genetic adaptations correlated with a precipitation gradient across the native range of *A. gerardii*. The most drought-tolerant ecotype is associated with smaller and thicker leaves (Olsen et al., 2013) and higher chlorophyll concentration (Caudle et al., 2014) compared to mesic ecotypes, and it shows higher photosynthetic rates (Johnson et al., 2015; Maricle et al., 2017) and cover (Johnson et al., 2015) when grown in dry settings. Consequently, we are addressing functional aspects of drought tolerance among ecotypes. In the present study we address morphological patterns in *A. gerardii* as they relate to precipitation, both in an evolutionary context and in the context of individual plants acclimating to reduced rainfall. We hypothesized that ecotypes of *A. gerardii* native to drier habitats would be short with narrow leaves, narrow stems, and few leaves to minimize evaporative surface area as a putative drought adaptation. Ecotypes native to mesic environments were hypothesized to be tall, with wide leaves and stems, and more leaves than ecotypes from dry habitats. Furthermore, we hypothesized that decreases in precipitation through experimental rainfall reduction would cause decreases in leaf width, stem diameter, plant height, and leaf number as individual plants responded to drier conditions, but plasticity was expected to amount to smaller differences than evolutionary adaptation.