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Legacy Effects of Extreme Drought on the Belowground Bud Bank of Bunchgrass and Rhizomatous Steppe Communities in Inner Mongolia

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Abstract

Belowground bud banks play a crucial role in plant population regeneration, community dynamics and ecosystem functions in response to environmental change and disturbance. In mesic grasslands, belowground bud banks are largely resistant to short-term drought. The sensitivity of belowground bud banks to long-term extreme drought in semiarid steppes is less understood. Here, we investigated the legacy effects of a 4-year experimental drought (i.e., 66% reduction in growing season precipitation) on belowground bud density, aboveground shoot density and their relationship (represented by the meristem limitation index-MLI) in two temperate semiarid steppes with different dominated plant growth forms (i.e., bunchgrass vs. rhizomatous grass). Measurements were made during the first recovery year following drought; thus, we reported the legacy effects of drought on belowground bud bank. Results showed that at community level the densities of both belowground buds and aboveground shoots decreased while there was no change in MLI. However, drought had no significant influences on belowground buds, aboveground shoots and MLI of the dominant plant growth form. The legacy effects of drought were largely dependent on plant community type and growth form. Specifically, due to their cluster/phalanx clonal growth, bunchgrasses and communities they dominated were characterized by greater meristem limitation compared with rhizomatous grasses. Our study implies that integrating belowground bud bank demography into the predictive model of community dynamics and ecosystem functions in response to climate change should be considered to understand the differing responses among community type and dominant plant groups.

Introduction

Climate change is expected to increase rainfall variability as well as the frequency of extreme drought (Min et al. 2011; Smith 2011; IPCC 2013; Hoover et al. 2016), with some regions already experiencing such changes (Williams et al. 2020). In grasslands, drought can alter community composition and structure, decrease aboveground net primary productivity (ANPP), and shift biomass allocation patterns (Frank 2007; Evans et al. 2011; Hoover et al. 2014; Meng et al. 2019; Zhang et al. 2019; Zhao et al. 2020); however, grasslands are also highly resilient ecosystems. Previous studies suggested that ANPP can completely recover to pre-drought levels within one year after drought (Hoover et al. 2014; Wilcox et al. 2020). While legacy effects of drought are often negative (Sala et al. 2012), some grasslands are more productive than expected one year after drought (Griffin-Nolan et al. 2018). Furthermore, a recent meta-analysis suggested that resilience, rather than resistance, maintained grassland ecosystem productivity following extreme drought (Stuart-Haëntjens et al. 2018). Population regeneration is critical for the resistance and/or resilience of grassland vegetation to climate extremes (Stampfli and Zeiter 2004), and is likely linked to belowground bud bank dynamics (VanderWeide et al. 2014).

Plants can regenerate sexually through the production of seeds, or asexually via growth from belowground meristems (Harper 1977; Ott et al. 2019). Belowground bud banks plays a key role in regulating population regeneration, community dynamics and ecosystem functioning in perennial grasslands following disturbances (e.g., fire and grazing), environmental changes (e.g., variations in precipitation) and changes in nutrient availability (Benson et al. 2004; Benson and Hartnett 2006; Dalgleish and Hartnett 2006; Dalgleish and Hartnett 2009; VanderWeide et al. 2014; Qian et al. 2017a, 2017b; Ma et al. 2019; Ott et al. 2019). This suggests that belowground buds, as the primary source of tiller/ramet production in many grassland communities, could contribute to rapid recovery following drought (VanderWeide et al. 2014; Ott et al. 2019). Past studies have shown that belowground bud bank density increases along a precipitation gradient (Dalgleish and Hartnett 2006; Qian et al. 2017a) and is insensitive to short-term (2-year) drought in mesic C_4 grasslands (VanderWeide et al. 2014). Less is known about how long-term extreme drought influence bud bank dynamics of more arid grassland communities.

Here, we studied the legacy effects of an experimental extreme drought (66% reduction in growing season precipitation) on belowground bud density, aboveground shoot density and meristem limitation index (MLI) in two semiarid steppes. These two sites share relatively similar climate, but one is dominated by a rhizomatous grass (*Leymus chinensis*) while the other is dominated by a bunchgrass (*Stipa grandis*) (Bai et al. 2004). Previous study has showed a negative effect of extreme drought on ecosystem functioning (Luo et al. 2021), and the present work is assessing the recovery of aboveground shoot density following a long-term drought and its relationships with belowground bud density. We hypothesized that both belowground bud density and aboveground shoot density would recover quickly during the first recovery year following the long-term extreme drought (VanderWeide et al. 2014; Ott et al. 2019). We also hypothesized that the legacy effects of experimental drought on bud and shoot densities as well as their relationships would vary with community types (*L. chinensis* vs. *S. grandis* dominated community) due to their difference in the traits of the dominant grass species.

Materials And Methods

Study sites

This study was conducted at two sites within the Inner Mongolia Grassland Ecosystem Research Station (116°33'E, 43°32'N) in Northern China. The two sites are characterized as temperate semi-arid steppe and share similar climatic conditions. The long-term (1982-2018) mean annual temperature and mean annual precipitation (MAP) are 1.9°C and 333 mm, respectively. About 72% of MAP (i.e., 242 mm) falls during the growing season (May through August). The major soil types of this region are calcic chestnuts and calcic chernozems (Luo et al. 2018).

The two sites differ in species composition with one being dominated by a rhizomatous grass (*Leymus chinensis*) and the other by a bunchgrass (*Stipa grandis*). Importantly, each of these species also occur in the community where they are not dominant, but at lower abundance. The rhizomatous grass and bunchgrass communities have been fenced to exclude large ungulate herbivores since 1999 and 1979, respectively (Bai et al. 2004). Both communities reach peak productivity (ANPP of about 193 g m^{-2} for the *L. chinensis* dominated community, and 217 g m^{-2} for the *S. grandis* dominated community) in mid-August (Kang et al. 2007).

Drought experiment

These sites are part of the Extreme Drought in Grassland Experiment (EDGE) in China (http://edge.biology.colostate.edu/). Beginning in 2015, we imposed drought treatments using rainfall exclusion shelters that blocked 66% of growing season precipitation (GSP). A randomized complete block design with six plots (6 m × 6 m) each for control (i.e., ambient) and drought treatments at each site. We oriented plots such that each plot was separated from neighboring plots by at least 2 m. Rainfall exclusion shelters were installed in May of 2015 and removed them at the end of August each year for four consecutive years (2015-2018). Plots were hydrologically isolated from the surrounding soil matrix using aluminum flashing buried to a depth of 1 m. To minimize edge effects associated with the rainout shelter, a 1 m external buffer zone was established under each shelter. To allow for rapid runoff of intercepted precipitation, the shelters were designed with a slight slope towards a subtle topographic gradient. To reduce greenhouse effects and allow for surface air flow, the roofs were raised so that the lowest section of each shelter was 2 m aboveground. Previous measurements indicated that these shelters allowed >90% penetration of photosynthetically active radiation (Luo et al. 2019, 2021; Muraina et al. 2021).

The average annual precipitation and GSP during the four-year experimental period were 312±25 mm and 199±31 mm, respectively. Based on the estimated long-term (1972-2018) normal distribution of precipitation for the two sites, we effectively imposed an extreme drought during this 4-year period (i.e., precipitation below the 5th percentile of the historical record). For more details on drought treatment infrastructure and effectiveness, see Luo et al., 2021. The precipitation in the months was near normal during the recovery period (2019).

Sampling and investigation

To assess drought impacts on bud bank dynamics, the belowground bud bank and its corresponding aboveground vegetation were investigated in late July 2019 (the first recovery year following 4- year experimental drought). As most buds in this steppe are located in shallow soil profiles (0-30 cm), all belowground parts were excavated to a depth of 30 cm within a 30 cm × 30 cm quadrat placed in each experimental plot (Qian et al. 2017a, 2017b). The connection between belowground- and aboveground plant parts was kept intact to accurately identify the buds of different species. Samples were stored in plastic bags, taken back to lab and processed them within one week. Following the procedures of Qian et al. (2017a, 2021), the sampled belowground buds were categorized into four bud types: (1) tiller buds (axillary buds at the shoot base of caespitose and rhizomatous grasses), (2) rhizome buds (axillary buds and apical buds on hypogeogenous rhizomes *sensu* Klimešová and Klimeš (2008), (3) bulb buds (meristems wrapped in the swollen leaf base or scale leaf of bulb species) and (4) dicot buds (buds on belowground parts of dicotyledonous herbs). Given that different bud types differ in their morphological characteristics, the shoot and bulb bases need to be dissected to count tiller buds and bulb buds while rhizome- and dicot buds were counted without dissection. Plant species were sorted into grasses (with tiller buds and rhizome buds) and forbs (with bulb buds and dicot buds). To effectively compare the recovery of the two dominant grasses (bunch grass vs rhizomatous grass) following the extreme drought, the number of aboveground shoots (tillers or ramet) were counted within each quadrat which buds were sampled and then classified into two plant groups.

Metrics and statistical analysis

Given that grasses accounted for the 90.75% of the total bud density and 95.77% of total shoot density in the two grassland communities, we mainly focused on grass responses (i.e., bunchgrass vs rhizomatous grass). The number of buds and shoots recorded in each quadrat was regarded as the measures of belowground bud and aboveground shoot densities (per square meter), respectively. The meristem limitation index (MLI), a measure of the degree of limitation that belowground buds imposed on aboveground population recruitment/regeneration in perennial grasslands, was calculated as the ratio of belowground bud density to aboveground shoot density (Benson et al. 2004).

We assessed the legacy effect of extreme drought on total belowground bud density, total aboveground shoot density, and total MLI as well as on those of dominant growth forms (bunchgrass vs rhizomatous grass) across the two steppes and whether the drought legacy effects vary with community type by conducting a mixed-model analysis of variance (ANOVA) with drought treatment and community as fixed factors and block as random factor. When interactive effects of drought treatment and community were marginally significant ($P<0.1$), the mixed model analysis of variance was separately applied for each community with drought treatment as fixed factor and block as random factor.

Before statistical analysis, we used Shapiro-Wilk and Levene's tests confirm all data were normally distributed and had equal variance. Original data were used in our statistical analyses without transformation. All statistical analyses were carried out using the *nlme* package in R (R i386 3.1.1).

Table 1 Results of mixed-effects ANOVA for the effects of drought legacy and community type on the belowground bud density, aboveground shoot density, and meristem limitation index of the whole plant community and two dominant growth forms (bunchgrass and rhizomatous grass).

		Drought legacy (D)	Community type (C)	D×C
Total	Bud density	**0.077**	**<0.001**	0.501
	Shoot density	**0.076**	0.227	**0.069**
	Limitation index	0.205	**<0.001**	0.126
Bunchgrass	Bud density	0.418	**0.004**	0.78
	Shoot density	0.222	0.789	**0.069**
	Limitation index	0.295	**<0.001**	0.241
Rhizomatous grass	Bud density	0.136	**<0.001**	0.1162
	Shoot density	0.194	**0.004**	0.619
	Limitation index	0.866	0.197	0.525

Results

The total bud density and MLI in the *L. chinensis* community were significantly higher than those in the *S. grandis* community both under the control (ambient precipitation) and drought treatment, while there were no significant differences in the total shoot density between the two plant communities (Table 1 and Fig. 1). The legacy of the 4-year drought marginally reduced total belowground bud and shoot densities in each grassland communities (P<0.1), but did not alter total MLI (Fig. 1 and Table 1). The drought treatment × community type interaction was marginally significant for the aboveground shoot density (P<0.1), indicating that the recovery of total shoot density following extreme drought differed between the two community types (Table 1). Specifically, the total shoot density of the *S. grandis* dominated community was lower in drought plots compared to ambient plots (P<0.05) but was unchanged in the *L. chinensis* dominated community (Fig. 1).

When separated by growth form, the extreme drought treatment had no significant legacy effect on bud densities or MLI of either bunchgrass or rhizomatous grasses across the two grassland communities (Table 1). The drought treatment significantly reduced shoot density of bunchgrasses in the *S. grandis* dominated community (Fig. 2).

Together, the bud densities of grasses (bunchgrass vs rhizomatous grass) in the *L. chinensis* dominated community was significantly higher than that in the in the *S. grandis* dominated community (P<0.01) while there was no significant difference in shoot densities between the two plant communities. As such, the MLI in the *L. chinensis* dominated community (MLI=0.74-1.03 under ambient precipitation and MLI=0.81-0.91 under drought treatment) was significantly higher than that in the in the *S. grandis* dominated community (MLI=0.08-0.45 under ambient precipitation and MLI=0.09-0.31 under drought treatment) (P<0.01) (Table 1, Fig. 2). Furthermore, there were no significant differences in the bud density between bunchgrass and rhizomatous grass while the shoot density of bunchgrass was significantly higher (P<0.01) than that of rhizomatous grass, which led to a higher MLI of rhizomatous grasses compared with bunchgrasses (P<0.01) (Table 1, Fig. 2).

Discussion

The potential for vegetation to recover from extreme drought is an important driver of grassland ecosystem dynamics (Stampfli and Zeiter 2004) and is likely limited by the resistance/resilience of belowground bud banks (VanderWeide et al. 2014). We investigated the density of belowground buds and aboveground shoots in two semi-arid steppes one year after a long-term (4-yr) extreme drought (66% reduction in ambient precipitation). At both sites, we observed reduced belowground bud density in plots that had previously experienced drought. The observed negative legacy effect contradicts previous work in more mesic grasslands where bud density was unchanged following a 2-year drought of similar intensity (VanderWeide et al. 2014). A negative drought legacy effect was also observed aboveground (i.e., shoot density), but only at the site dominated by the bunchgrass, *S. grandis.* However, we did not detect a legacy effect of extreme drought on MLI (i.e., buds per shoot) at either site. This suggests that while extreme drought reduced bud and shoot density, the response potential of these communities to further changes in precipitation was unaltered (Knapp and Smith 2001; Dalgleish and Hartnett 2006).

Belowground bud density tends to decline with increasing aridity, a trend observed in both North America and northern China (Dalgleish and Hartnett 2006; Qian et al. 2017a). While plants in semi-arid communities are often drought tolerant, they also operate near their limit of water stress. Accordingly, ANPP of xeric grasslands is often more sensitive to drought than that of mesic grasslands (Knapp et al. 2015). This may explain why our observed sensitivity of belowground bud density was higher than that reported for more mesic sites (MAP of 333 vs. 880 mm; VanderWeide and Hartnett 2014). Grasses in more mesic areas may allocate more resources to belowground tissue during drought which ensures population regeneration when normal precipitation conditions return, whereas in semiarid environments, short-term extreme drought substantially reduces productivity and subsequent resource allocation belowground.

We also noted significant differences between the two plant communities in belowground bud dynamics. Specifically, the belowground bud density and MLI in the *L. chinensis* dominated community were significantly higher than those in the *S. grandis* dominated community under both ambient precipitation and drought treatment, which suggests bunchgrass communities may face greater meristem limitation. Thus, the belowground bud bank constrains its response ability to resource pulses and restrict its resistance/resilience to climatic perturbation (Benson et al. 2004; Dalgleish and Hartnett 2006; Qian et al. 2021). This might be attributed to the differences in root systems as *L. chinensis* dominated community has a relatively shallower root system than the *S. grandis* dominated community (Xiao et al. 1995; Wang et al. 2016). Thus, drought could negatively affect belowground buds via higher reductions in soil moisture in surface soil than in deeper soil profile (Schwinning et al. 2005; Hoover et al. 2017).

Our results also showed that the bud banks of bunchgrass and rhizomatous grass recovered differently after an extreme drought. Bunchgrasses face a greater meristem limitation than rhizomatous grasses due to their clustered. Wang et al. (2019) found that short-term summer drought decreased the bud bank density and shoot production of *L. chinensis*, and consequently constrained both its current and future productivity, but increased the proportion of buds which developed into rhizomes. In combination with our results, this suggests we must consider belowground bud bank demography in predictive models of how drought may alter community dynamics and ecosystem functions.

In conclusion, the density of both belowground buds and aboveground shoots were reduced one year following drought but meristem limitation was unaltered in this temperate semiarid steppe. The legacy effects of extreme drought on belowground bud bank and its relationship with aboveground vegetation depended on plant community type and plant growth forms. Due to the cluster form/phalanx clonal growth, bunchgrass communities face a greater meristem limitation than rhizomatous grass communities. Belowground bud bank dynamics may constrain community responses to climate change and human disturbances, and consequently has important implications on ecosystem function and services.

Declarations

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Figures

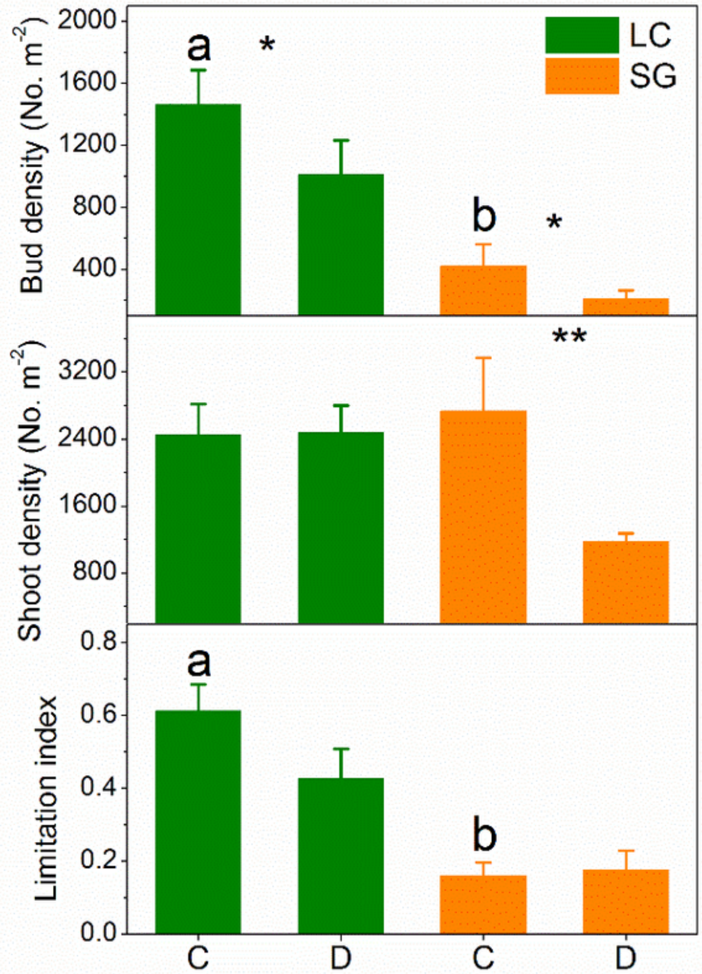

Figure 1

Effects of drought legacy and community type on total belowground bud density, total aboveground shoot density and the meristem limitation index (MLI) in two plant communities with different dominant species (LC, L. chinensis dominated community; SG, S. grandis dominated community). Each point represents the means with error bars indicating standard errors calculated from replicate plots for each treatment. Different letters indicate significant differences between the L. chinensis and S. grandis dominated at P<0.05. Statistical significance of drought legacy effect is depicted *P<0.1 and **P<0.05. C, control (i.e., the ambient precipitation); D, recovery following the drought treatment (i.e., 4-year reduction of 66% growing season precipitation).

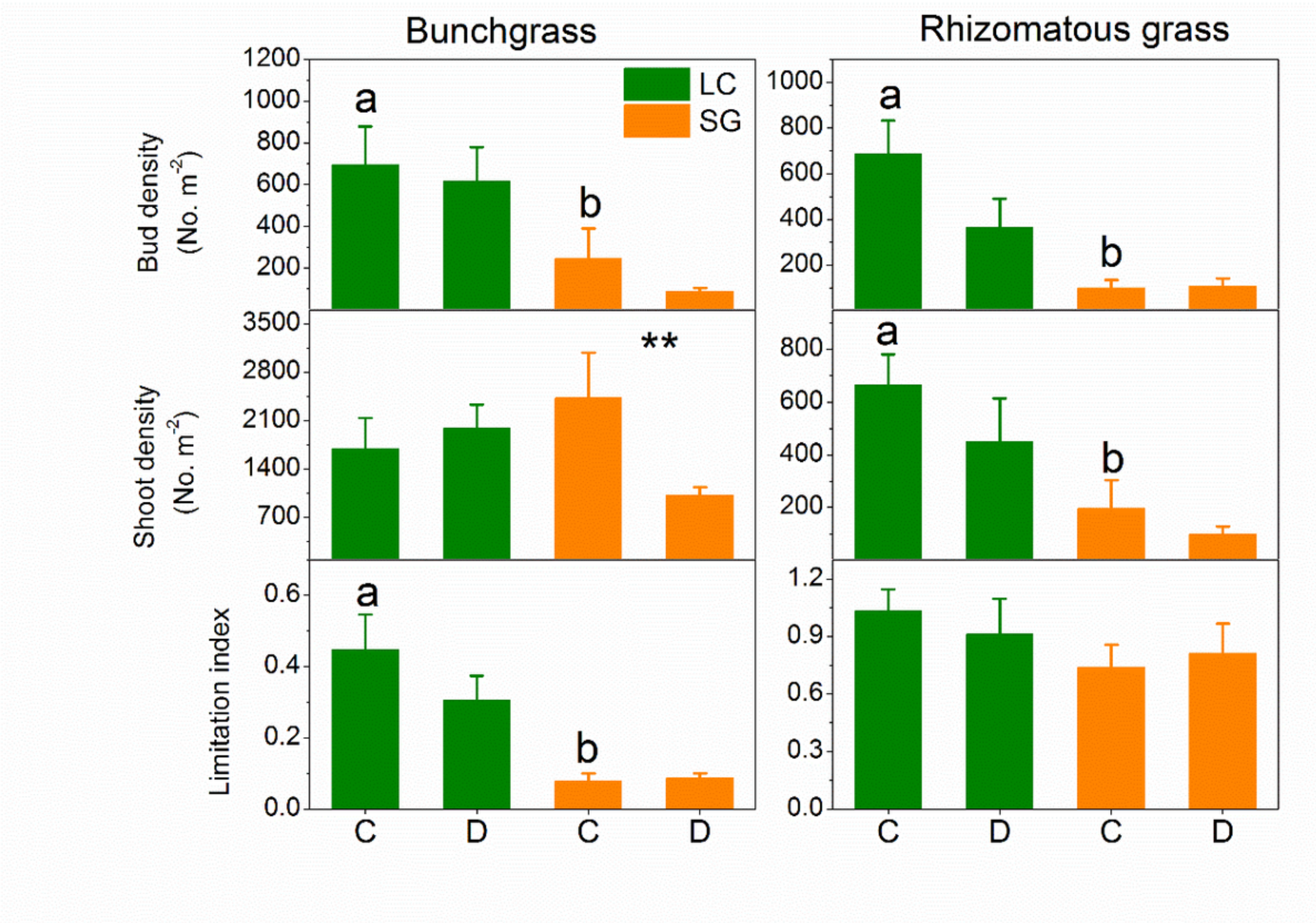

Figure 2

Effects of drought legacy and community type on belowground bud densities, aboveground shoot densities and the meristem limitation index (MLI) of two dominant growth forms (bunchgrass vs. rhizomatous grasses) in two grassland communities with different dominant species (LC, L. chinensis dominated community; SG, S. grandis dominated community). Each point represents the means with error bars indicating standard errors calculated from replicate plots for each treatment. Different letters indicate significant differences between the L. chinensis and S. grandis dominated at P<0.05. Statistical significance of drought legacy effect is depicted *P<0.1 and **P<0.05. C, control (i.e., the ambient precipitation); D, recovery following the drought treatment (i.e., 4-year reduction of 66% growing season precipitation).