RESEARCH ARTICLE

Key Points:
- We modeled the effects of plant functional groups on drought in semiarid temperate grasslands in current and future climates
- Drought was generally increased beneath shrubs and under high biomass and decreased beneath annual grasses
- Plant functional groups had similar rankings in present and future climates, suggesting that current effects may be consistent in future climates

Correspondence to:
S. D. Wilson,
scott.wilson@uregina.ca

Functional Group, Biomass, and Climate Change Effects on Ecological Drought in Semiarid Grasslands

S. D. Wilson[1,2] , D. R. Schlaepfer[3,4], J. B. Bradford[5], W. K. Lauenroth[6] , M. C. Duniway[5] , S. A. Hall[7,8], K. Jamiyansharav[9] , G. Jia[10] , A. Lkhagva[11], S. M. Munson[5] , D. A. Pyke[12] , and B. Tietjen[13,14]

[1]Department of Biology, University of Regina, Regina, Saskatchewan, Canada, [2]Climate Impacts Research Centre, Department of Ecology and Environmental Science, Umeå University, Abisko, Sweden, [3]Department of Botany, University of Wyoming, Laramie, WY, USA, [4]Yale School of Forestry and Environmental Studies, New Haven, CT, USA, [5]Southwest Biological Science Center, U.S. Geological Survey, Flagstaff, AZ, USA, [6]Yale School of Forestry and Environmental Studies, New Haven, CT, USA, [7]Center for Sustaining Agriculture and Natural Resources, Washington State University, Wenatchee, WA, USA, [8]SAH Ecologia LLC, Wenatchee, WA, USA, [9]Rangeland and Watershed Stewardship Department, Colorado State University, Fort Collins, CO, USA, [10]Institute of Atmospheric Physics, Chinese Academy of Sciences, Beijing, China, [11]Department of Biology, National University of Mongolia, Ulaanbaatar, Mongolia, [12]Forest and Rangeland Ecosystem Science Center, U.S. Geological Survey, Corvallis, OR, USA, [13]Institute of Biology, Biodiversity/Theoretical Ecology, Freie Universität Berlin, Berlin, Germany, [14]Berlin-Brandenburg Institute of Advanced Biodiversity Research, Berlin, Germany

Abstract Water relations in plant communities are influenced both by contrasting functional groups (grasses and shrubs) and by climate change via complex effects on interception, uptake, and transpiration. We modeled the effects of functional group replacement and biomass increase, both of which can be outcomes of invasion and vegetation management, and climate change on ecological drought (soil water potential below which photosynthesis stops) in 340 semiarid grassland sites over 30 year periods. Relative to control vegetation (climate and site-determined mixes of functional groups), the frequency and duration of drought were increased by shrubs and decreased by annual grasses. The rankings of shrubs, control vegetation, and annual grasses in terms of drought effects were generally consistent in current and future climates, suggesting that current differences among functional groups on drought effects predict future differences. Climate change accompanied by experimentally increased biomass (i.e., the effects of invasions that increase community biomass or management that increases productivity through fertilization or respite from grazing) increased drought frequency and duration and advanced drought onset. Our results suggest that the replacement of perennial temperate semiarid grasslands by shrubs, or increased biomass, can increase ecological drought in both current and future climates.

1. Introduction

Drought related to climate change is expected to increase in frequency and severity (Bernacchi & VanLoocke, 2015; Dai, 2013; Zhao & Running, 2010), and ecosystems such as semiarid grasslands may experience desertification and soil loss as a result (Cayan et al., 2010; Prudhomme et al., 2014; Vicente-Serrano et al., 2013). Grassland hydrology can also be profoundly affected by the dominant plant functional group (Pysek et al., 2012; Wilcox et al., 2012). Whether changes in plant functional groups exacerbate or mitigate climate-related drought has received little attention (Cavaleri & Sack, 2010; Prevéy & Seastedt, 2014), even though the role of plant communities in modulating ecosystem responses to global change has recently received increased attention (Suding et al., 2008; Tietjen et al., 2017).

Contrasting functional groups have contrasting effects on soil water availability due to differences in phenology, total biomass, biomass allocation, and rooting depth (Pysek et al., 2012). Monodominant stands of invasive perennial C_3 "cool season" grasses such as *Bromus inermis* (Foster et al., 2009), *Agropyron cristatum* (Balogianni et al., 2015), and *Poa pratensis* (Miles & Knops, 2009) influence soil water availability by transpiring water in the spring when water is available from snowmelt (Blumenthal et al., 2008), reducing water availability for the remainder of the year. Perennial C_4 "warm season" grasses, such as *Andropogon bladhii* (Reed et al., 2005) or *Eragrostis lehmanniana* (Moran et al., 2009) have relatively high water use efficiency (Taylor et al., 2010) and may lower water availability later in the growing season. Annual grasses with a relatively short growing season cause less drying than perennial grasses with roots permanently present (Enloe et al.,

2009; Germino et al., 2016). Relative to mixed grasslands, shrubs such as *Artemisia tridentata* increase evapotranspiration (Wilcox et al., 2012), interception (Bradford, Schlaepfer, & Lauenroth, 2014a), and vegetation access to deeper soil water (Jackson et al., 2005; Knapp et al., 2008), all of which should increase drought conditions. The impact of woody plant invasion on grassland ecohydrology has received considerable attention (Huxman et al., 2005; Wilcox & Huang, 2010; Zhang et al., 2001), but much less attention has been given to herbaceous species (Enloe et al., 2009), and there are few direct comparisons of several functional groups (Cavaleri & Sack, 2010; Ryel et al., 2010).

In addition to being influenced by different functional groups, grassland biomass is often increased by management to maximize forage, biofuel production, and soil carbon (C) sequestration (Balogianni et al., 2015; Driscoll et al., 2014; Foster et al., 2009). Biological invasion also typically increases aboveground biomass even in cases where native species are replaced by exotic species within the same functional group (Eldridge et al., 2011; Henderson & Naeth, 2005; Maron & Marler, 2008; Potts et al., 2008; Vila et al., 2011; Wilsey & Polley, 2006). Further, a recent model suggests that grassland biomass will increase in future climates due to longer growing seasons (Hufkens et al., 2016). Increased biomass generally decreases grassland soil water, regardless of whether the increase accompanies invasion by perennial grasses (English et al., 2005; Fink & Wilson, 2011), annual grasses (Booth et al., 2003), or woody species (Huxman et al., 2004; Jackson et al., 2005). Hydrological modeling suggests that transpiration is strongly influenced by biomass and its seasonality (Lauenroth & Bradford, 2006; Schlaepfer et al., 2012b), but functional group effects have not been examined.

Mechanisms that underlie vegetation effects on ecohydrology are several, but transpiration is considered to be the most important driver (Bernacchi & VanLoocke, 2015; Huxman et al., 2004). Future transpiration may increase if enhanced atmospheric CO_2 increases biomass more than it reduces transpiration (Morgan et al., 2011) assuming that water use efficiency remains constant (Keenan et al., 2013). On the other hand, interception also increases with biomass and is relatively important in grasslands with fine leaves that capture a large proportion of precipitation (Dunkerley, 2000; Lauenroth & Bradford, 2012; McLaren et al., 2004). Clearly, both transpiration and interception can be expected to vary with climate change, and here we explore how they are also influenced by functional group and biomass.

We modeled ecological drought (soil water potential below which photosynthesis stops) using a soil water simulation model (Bradford et al., 2014b). Because current level of aridity affects dryland responses to climate change (Huxman et al., 2005; Knapp et al., 2008; Wilcox & Huang, 2010) and invasion (Eldridge et al., 2011), we used a gradient approach, examining 340 globally distributed grassland ecosystems with a wide range of current aridity. We examined drought by setting the vegetation to one of five functional groups (pure stands of perennial C_3 grasses, perennial C_4 grasses, annual grasses, shrubs, or control vegetation—climatically determined mixes of functional groups derived from field measurements). Functional groups were modeled by varying values of biomass, phenology, and root depth, using field data derived from the literature. We examined the effect of functional groups on ecological drought in three scenarios: (1) "current" (1980–2010) climate and biomass, (2) future (2069–2099) climate and climate-driven future biomass, and (3) future climate and experimentally increased future biomass that mimics the biomass increases that can accompany invasion by exotics with the same growth form as the invaded vegetation or that can be caused by management for enhanced production. Comparing model outputs from these scenarios allowed us to examine what aspects of vegetation, such as functional group dominance or increased biomass, exacerbated climate change-driven drought.

2. Methods

2.1. Study Sites

The study sites were temperate semiarid grasslands, defined using a combination of Trewartha's climatic classification (group D, temperate) and a ratio of precipitation: potential evapotranspiration (P/PET, the United Nations (UN) aridity index) of 0.2–0.5 (Le Houérou, 1996). We began with a global geographic raster of 0.3125° square (3,864 km²) cells (Saha et al., 2010). Our analyses comprised the 340 cells that met both the temperate and P/PET criteria under both current and future climate (representative concentration pathway (RCP) 8.5) (Moss et al., 2010) and had grass cover >66% (see below). Included cells were dominated by

sites in Mongolia and China (N = 291) but included sites in the western United States, western Asia, South America, and South Africa (N = 36, 7, 5, and 1, respectively).

2.2. Soil Water Model

We modeled ecological drought in each cell using SOILWAT, a daily time step, multiple soil layer, process-based simulation model of ecosystem water balance (Lauenroth & Bradford, 2006; Parton, 1978; Schlaepfer et al., 2012a). SOILWAT has been validated in dryland ecosystems including temperate grasslands (Lauenroth et al., 1994; Parton, 1978), sagebrush stands (Schlaepfer et al., 2012a), and dry forests (Bradford et al., 2014a). Inputs to SOILWAT include daily weather (mean daily maximum and minimum temperature and daily precipitation), mean monthly climate (mean monthly relative humidity, wind speed, and cloud cover), latitude, elevation, vegetation (mean monthly live and litter biomass and active root depth profile), and soil properties (texture of each soil layer). SOILWAT estimates hydrological processes including partitioning of precipitation into snowfall and rain, snow accumulation, melt and loss, infiltration into the soil profile, percolation for each soil layer, bare soil evaporation, and deep drainage (Lauenroth & Bradford, 2006; Schlaepfer et al., 2012a). SOILWAT also estimates ecohydrological processes for each functional plant group including interception by vegetation and litter, evaporation of intercepted water, transpiration, and hydraulic redistribution from each soil layer. SOILWAT was run on the Yellowstone computer at the National Center for Atmospheric Research-Wyoming Supercomputing Center at the University of Wyoming.

Current climate data (1979–2010) were obtained from National Centers for Environmental Prediction/Climate Forecast System Reanalysis (NCEP/CFSR) products (Saha et al., 2010) on the T382 Gaussian grid. We extracted daily maximum and minimum temperature (2 m above ground) and precipitation from the 6-hourly T382 products (USNCEP, 2010a, 2010c). We also extracted relative humidity (2 m above ground), u and v wind speed components (10 m above ground), and total cloud cover converted to sky cover via sunshine percent (Doorenbos & Pruitt, 1975) from the monthly T382 products (USNCEP, 2010b) and calculated mean monthly values.

Future climate scenarios were run for the center of each cell. We accounted for uncertainty in future emissions by using two emission scenarios, RCP 4.5 and RCP 8.5 (Meinshausen et al., 2011; Moss et al., 2010), and for uncertainty in climate modeling by using 16 global circulation models (GCMs) for each RCP scenario. Thus, we extracted 32 climate conditions as monthly time series for 2069–2099 from 0.5° downscaled and bias-corrected products of the fifth phase of the Climate Model Intercomparison Project (Taylor et al., 2012), from the Downscaled CMIP3 and CMIP5 Climate and Hydrology Projections archive (Maurer et al., 2007). We combined historical daily data (NCEP/NFSR) with monthly GCM predictions of historical and future conditions with hybrid-delta downscaling to obtain future daily forcing (Hamlet et al., 2010; Tohver et al., 2014). We chose 16 GCMs, from those that participated in CMIP5, focusing on those that represented the most independent and best performing subset of GCMs (Knutti et al., 2013).

Soil texture data were obtained from the International Soil Reference and Information Centre - World Inventory of Soil Emission Potentials (ISRIC/WISE) global soil data set (Batjes, 2012) at 5 arc min spatial resolution and 20 cm depth intervals up to 1 m. We divided the 0–20 cm layer into two 10 cm layers to improve the representation of shallow soil processes and to account for cells with soils only 10 cm deep (lithosols). We calculated sand and clay content for each layer and cell as area-weighted averages of soil map units and soil types. We based soil depth on the ISRIC-WISE data set unless the soil was deeper than 1 m, in which case we estimated depth as 95% of the maximum root depth (Schenk & Jackson, 2002). We assumed that soil texture below 1 m was the same as the deepest ISRIC-WISE layer. We calculated elevation for each cell as the area-weighted median using a 30 arc sec global data set (FAO/IIASA/ISRIC/ISS-CAS/JR, 2008).

2.3. Ecological Drought

Definitions of drought vary among fields of study (Wilhite & Glantz, 1985) and include reduced river flow (Dai, 2011), the Palmer drought severity index (Sheffield et al., 2012), and climate variation (Vicente-Serrano et al., 2012). Here we focus on ecological drought: levels of soil water potential associated with very low rates of grassland photosynthesis, which may limit productivity, based on field measurements (Zhao & Running, 2010). Grassland photosynthesis is close to zero at < -2 MPa in soils >15 cm deep (Sala et al., 1981), at < -3 MPa in soils 15–30 cm deep (Pockman & Small, 2010), and at < -3 MPa for plant-accessible soil depths expressed as predawn xylem water potential (Hamerlynck et al., 2012; Thomey et al., 2011). We used the closest relevant parameters in SOILWAT, soil water potential ≤ -3 MPa in soil layers >20 cm deep.

Table 1

Aboveground Biomass (g/m^2) Under Various Grazing and Fertilizer Regimes in Noninvaded and Invaded Grasslands

Noninvaded	Invaded	Increase	Location	Source
190	230	1.2	Saskatchewan	Bakker et al. (2003)
200	275	1.3	California	Potts et al. (2008)
425	590	1.4	Saskatchewan	Fink and Wilson (2011)
300	550	1.8	Alberta	Henderson and Naeth (2005)
30	70	2.3	Saskatchewan	Christian and Wilson (1999)
225	800	3.5	Montana	Balogianni et al. (2014)
56	204	3.6	California	Wolkovich et al. (2010)
250	1,675	6.7	Montana	Balogianni et al. (2015)

Note. Results are from field studies and do not include pot experiments or planted trials. We searched the Web of Science for keywords "grass invasion (productivity or mass)" during 1997–2017. For multiyear studies, we report biomass from the final year.

Drought duration associated with climate change is predicted to be longer in deep soils than shallow soils (Schlaepfer et al., 2017).

We examined three aspects of ecological drought: (1) frequency was determined by calculating the proportion of years (over the 30 years examined) in which drought occurred for at least half the year; (2) duration was determined by calculating the mean number of days with drought each year; and (3) onset was defined as the mean first date (over the 30 years examined) of drought that was followed by at least nine consecutive drought days (~10% of the growing season in temperate grasslands). Sites in the Southern Hemisphere were included, with 1 July set as the first day of the year.

2.4. Functional Groups

Functional group effects on ecological drought were examined by running SOILWAT for each of the five functional groups: perennial C_3 grasses, perennial C_4 grasses, annual grasses, shrubs, and control vegetation, that is, site-determined mixes of perennial C_3 and C_4 grasses. We modeled pure stands of each functional group (i.e., total biomass set to 100% of that functional group) because invasions tend to replace diverse communities with low-diversity stands dominated by invaders (Alofs & Fowler, 2013; Knapp et al., 2008; Pysek et al., 2012).

Functional groups differed in combinations of phenology, aboveground biomass, height, and rooting depth derived from field data (Appendix 2 in Bradford et al., 2014b). In brief, annual grasses had production restricted to the first part of the growing season (Figure S2.2, Bradford et al., 2014b). C_3 grasses, annual grasses, and shrubs had most production in early summer. C_4 grasses had most production in late summer. Shrubs also differed by having greater aboveground biomass. Interception for grasses was proportional to biomass, and interception for shrubs increased with both biomass and height. C_3 and C_4 grasses had identical root depth profiles, whereas profiles for annual grasses were shallower, and profiles for shrubs were deeper. Transpiration was proportionate to root abundance in each soil layer (Figure S2.8, Bradford et al., 2014b). For control vegetation, the proportions of C_3 and C_4 grasses varied based on relationships developed from field data (Paruelo & Lauenroth, 1996) according to mean annual precipitation, the ratio of winter precipitation to mean annual precipitation, the ratio of summer precipitation to mean annual precipitation, and mean annual temperature (Appendix 2 in Bradford et al., 2014b).

2.5. Scenarios

We used SOILWAT to calculate the frequency, duration, and onset of ecological drought for each of the four functional groups in three scenarios. First, we examined a scenario for current (1980–2010) climate and climate-driven biomass. Biomass varied daily throughout the 30 years of this scenario, driven by climate, soil, and functional group.

Second, we examined a scenario for future (2069–2099) climate and climate-driven future biomass. As above, biomass varied daily throughout the 30 years of this scenario, driven by future climate, soil, and functional group. Future climate is expected to affect many of the factors that influence soil water (see section 2.2), and these may interact with background variation in soils and imposed variation in functional groups to influence drought. We report results for a future climate near the 50th percentile of the 16 GCMs based on RCP8.5, leading to ~1,370 ppm CO_2 (Van Vuuren et al., 2011). We present results only for RCP8.5 because results for RCP4.5 are qualitatively similar (Tietjen et al., 2017) and because RCP8.5 simulates a plausible scenario of heavy dependence on fossil fuels until at least 2100.

Third, we examined a scenario for future climate combined with experimentally increased future biomass. As above, biomass varied daily throughout the 30 years of this scenario, driven by future climate, soil, and functional group. However, biomass was experimentally increased to represent increased biomass that occurs even in the absence of a change in functional group dominance, such as cases where relatively productive grass species that were introduced to improve forage production or for restoration later invade native grassland, and in cases where grassland is managed through nutrient addition or grazing respite to

increase forage, biofuel production, and soil carbon (C) sequestration (Driscoll et al., 2014). Such invasions or management can increase grassland aboveground biomass several fold (Table 1), and we represented increased biomass by multiplying the daily biomass predictions by 3, near the median of the range in Table 1, and examining the resultant effects on ecological drought.

We examined 30 year average outcomes for five response variables (drought frequency, duration, onset, transpiration, and interception) for three scenarios for five functional groups from 340 sites ($5 \times 3 \times 5 \times 340 = 25,500$ outcomes). We summarized these outcomes by calculating means for each response variable, for each functional group in each scenario. In the case of drought onset (expressed as day of year) we calculated circular means using the package "circular" in R (R Core Team, 2016) because day 1 and day 365 are ecologically more similar to each other than they are to day 180.

To represent global variation in the results, we presented data from all 340 sites as a function of aridity (the ratio of current precipitation to potential evapotranspiration ratio (P/PET)), since current level of aridity affects dryland responses to climate change (Huxman et al., 2005; Knapp et al., 2008; Wilcox & Huang, 2010) and invasion (Eldridge et al., 2011). These relationships allowed us to examine how future drought may vary with current aridity.

3. Results

The frequency of ecological drought in the current climate was higher for shrubs (mean = 0.27, Figure 1a) than other functional groups (0.20–0.23) but varied little among other functional groups. Similar patterns occurred in the future climate (Figure 1b). In contrast, experimentally increased aboveground biomass combined with the future climate increased drought frequency for all functional groups (Figure 1c). Annual grasses in this scenario had about 25% fewer droughts than other functional groups. In all scenarios, drought frequency was greatest at sites that are currently most arid.

Global variation in ecological drought frequency (shown by the slopes of the relationships between frequency and variation in P/PET) was less in future climates with increased biomass (Figure 1c) than in current climates and biomass (Figure 1a), because increased biomass in future climates increased drought frequency more in wet sites (high P/PET) than in dry ones (low P/PET). Overall variation in drought frequency and other variables, shown by the scatter of points, is related to the background variation in soil and climate among our 340 study sites.

The duration of ecological drought in the current climate, relative to control vegetation, was greater for shrubs and less for annuals (Figure 2). Control vegetation (mixed stands) and pure stands of C_3 and C_4 grasses were very similar. These patterns were consistent in future climates (Figure 2b) and with experimentally increased biomass (Figure 2c). The future climate had longer droughts (means: 105–164 days) than the current climate (means: 95–158 days). In contrast, the future climate with increased biomass had drought duration increased by about 50% (means: 141–231 days). In all scenarios drought duration was greatest at sites that are currently most arid.

The onset of ecological drought in the current climate was delayed in the case of annuals and shrubs (means: day of years 103 and 67, respectively) relative to control vegetation (day 53) in current (Figure 3a) and future climates (Figure 3b). Drought onset for C_4 grasses was delayed, resulting in concentrations of points at the end and start of the year and a low value for the circular mean. Rankings of functional groups were consistent in future climates (Figure 3b) and with experimentally increased biomass (Figure 3c). In the future climate with experimentally increased biomass, drought onset was advanced (Figure 3c). In all scenarios, drought onset was earliest at sites that are currently most arid, as shown by the positive slopes.

Global variation in the onset of ecological drought (shown by the slopes of the relationships between onset and global variation in P/PET) was less in future climates with increased biomass (Figure 3c) than in current climates and biomass (Figure 3a), because increased biomass in future climates advanced onset more in wet sites (high P/PET) than in dry ones (low P/PET).

To understand the mechanisms underlying differences in ecological drought caused by functional groups, climate change, and experimentally increased biomass, we explored the effect of these factors on the
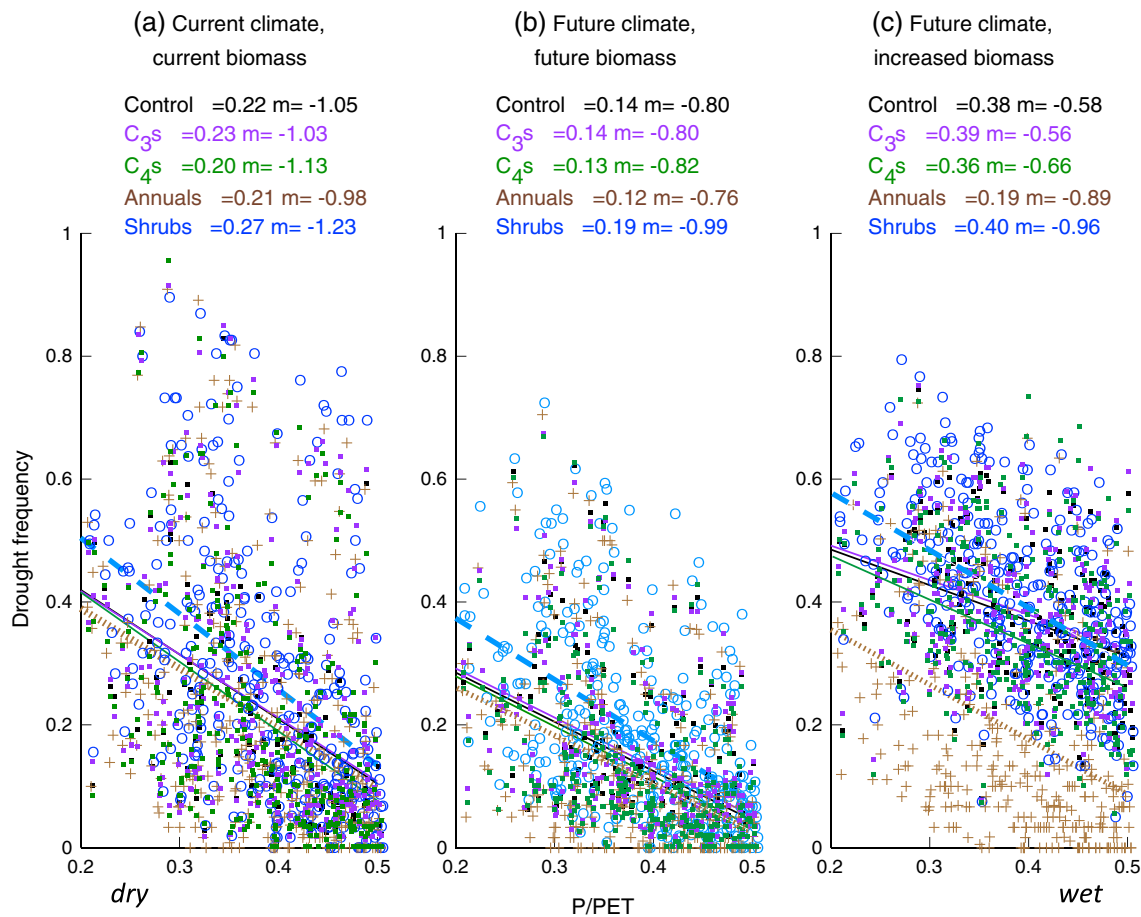
Figure 1. Frequency of ecological drought as a function of current aridity (precipitation/potential evaporation; P/PET) in three scenarios: (a) current climate and climate-driven biomass, (b) future climate and climate-driven biomass, and (c) future climate and experimentally increased biomass. Each point represents a 30 year average for one of 340 study sites. Points and matching line colors represent control vegetation (mixed grassland) and four functional groups (perennial C_3 and C_4 grasses, annual grasses (crosses, fine dashed line), and shrubs (circles, coarse dashed line). μ: overall mean for each functional group; m: slope of regression relationship between drought frequency and P/PET.

components of actual evapotranspiration (AET) most influenced by plants: transpiration and interception. Relative transpiration (% of AET) differed little among functional groups in both current and future climates (Figures 4a and 4b). At the most arid sites (lowest P/PET), shrubs had slightly greater transpiration than perennial grasses, and annual grasses had slightly lower transpiration. Transpiration increased with increasing water availability (P/PET). In contrast, relative transpiration behaved quite differently in the future climate with experimentally increased biomass (Figure 4c). Annual grasses had greater transpiration (mean: 41%) than perennials (means: 29–34%). Further, transpiration associated with annual grasses varied little with P/PET (slope: −6.2) compared with transpiration associated with perennials (slopes: −15 to −32). In scenarios with experimentally increased biomass, transpiration decreased with P/PET for all functional groups (Figure 4c: negative slopes), in contrast to the cases without experimentally increased biomass (Figures 4a and 4b: positive slopes).

Interception (evaporation from precipitation intercepted by vegetation) was consistently lowest for annual grasses (Figure 5). Interception was greatest for shrubs in most scenarios. One exception was that shrubs had interception values lower than those of perennial grasses at wet sites (high P/PET) in future climate with experimentally increased biomass (Figure 5c), because experimentally increased biomass removed differences in interception among these perennial functional groups. Interception by shrubs was also marked by being the least responsive to current aridity, with the lowest slopes in all scenarios. Interception was not affected by the future climate but increased twofold to threefold in future climate accompanied by experimentally increased biomass.
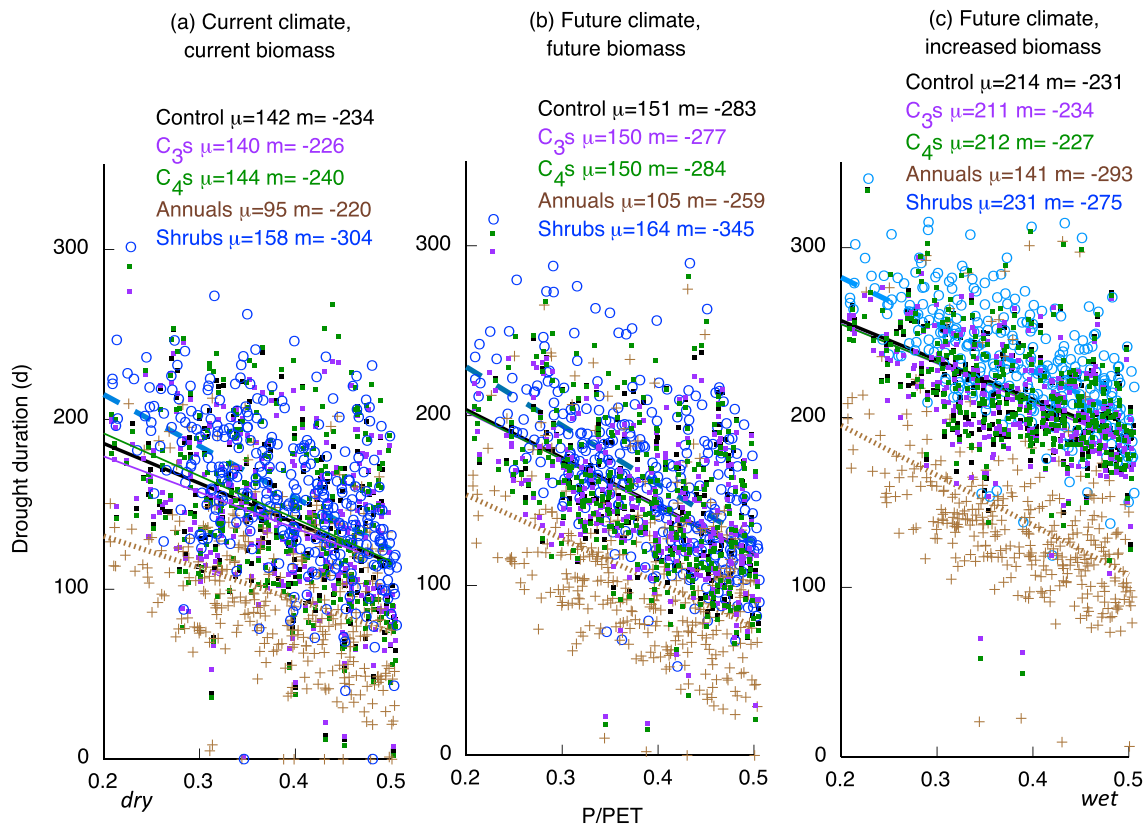
Figure 2. Duration of ecological drought (days) as a function of current aridity (precipitation/potential evaporation; P/PET) in three scenarios: (a) current climate and climate-driven biomass, (b) future climate and climate-driven biomass, and (c) future climate and experimentally increased biomass. Each point represents a 30 year average for one of 340 study sites. Points and matching line colors represent control vegetation (mixed grassland) and four functional groups (perennial C_3 and C_4 grasses, annual grasses (crosses, fine dashed line), and shrubs (circles, coarse dashed line)). μ: overall mean for each functional group; m: slope of regression relationship between drought frequency and P/PET.

4. Discussion

Relative to control vegetation (mixed grassland), the frequency and duration of ecological drought were increased by shrubs and decreased by annual grasses. Further, the rankings of shrubs, perennial grasses, and annual grasses were generally consistent in spite of variation in climate and experimentally increased biomass, suggesting that current differences among functional groups predict differences among them in future climates. Contrasting functional groups both exacerbated and mitigated drought, whereas changes caused by experimentally increased biomass consistently exacerbated drought.

Annuals had the largest effects on drought in terms of departures from control vegetation. Effects particular to annuals were magnified at experimentally increased biomass, where annuals decreased drought frequency (Figure 1c) and duration (Figure 2c) to a much greater extent than all other functional groups. Magnification of effects at experimentally increased biomass was presumably related to relatively low interception by annuals at experimentally increased biomass (Figure 5c) due to their relatively short growing season. Field studies suggest that invasive annual grasses use less water and are thus associated with more soil moisture than invaded perennial grasses (Cline et al., 1977; Gasch et al., 2013), as did a global meta-analysis (Pysek et al., 2012).

Shrubs were associated with more frequent and longer ecological droughts in sites that are currently arid (low P/PET; Figures 1 and 2). Shrubs increased drought frequency and duration probably due to higher levels of interception for shrubs (26%) than perennial grasses (15%; Figure 5a). Shrubs differed from all other functional groups because interception for shrubs generally increased very slightly with increasing water availability (P/PET) relative to other functional groups (Figure 5). Interception varies with leaf area index (LAI), and high LAI values for shrubs (~10 times greater than perennial grasses (Frank & Karn, 2005)) may allow
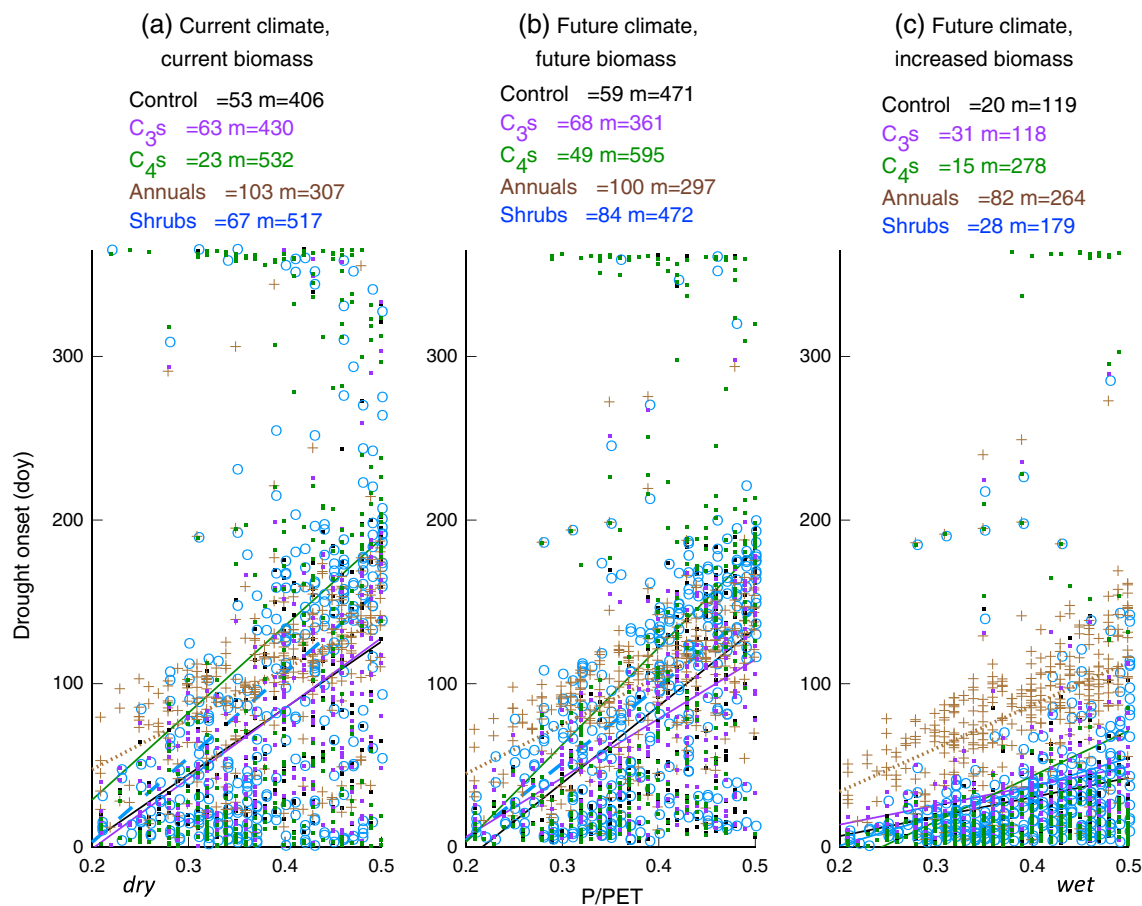
Figure 3. Onset of ecological drought (day of year) as a function of current aridity (precipitation/potential evaporation; P/PET) in three scenarios: (a) current climate and climate-driven biomass, (b) future climate and climate-driven biomass, and (c) future climate and experimentally increased biomass. Each point represents a 30 year average for one of 340 study sites. Points and matching line colors represent control vegetation (mixed grassland) and four functional groups (perennial C_3 and C_4 grasses, annual grasses (crosses, fine dashed line), and shrubs (circles, coarse dashed line)). μ: circular mean for each functional group; m: slope of regression relationship between drought frequency and P/PET.

little variation in interception. Further, shrubs had a greater proportion of actual evapotranspiration accounted for by transpiration than did grasses, in agreement with a different dryland water simulation model (Wilcox et al., 2012). Field measures showed no differences between sagebrush and bunchgrass early in the spring but greater evapotranspiration beneath shrubs in midsummer (Prater & DeLucia, 2006). Increased drought has been attributed to tree plantations (Jackson et al., 2005), but our results show that replacement of grasses by shrubs may have a similar effect, even though the increase in biomass associated with shrubs is only about twofold (Bradford et al., 2014b). Trees enhance drought by increasing transpiration (Jackson et al., 2005), but in our model shrubs enhanced drought by both increased transpiration and interception (Figures 4 and 5).

In contrast to the large departures from control vegetation for annuals and shrubs, replacement of control vegetation with pure stands of either C_3 or C_4 grasses had little effect on the frequency or duration of ecological drought (Figures 1 and 2). Differences between stands of C_3 and C_4 grasses were also small, presumably because both had leaves present throughout the growing season, and differences in phenology and the timing of transpiration were not sufficient to affect ecological drought. Taken together, the results suggest that differences among functional groups in life-history strategies (i.e., perennial grasses, annual grasses, and shrubs) have much larger effects on ecological drought than do differences in physiologically driven phenology, that is, C_3 and C_4 grasses. On the other hand, other differences between C_3 and C_4 grasses, such as photosynthetic efficiency and physiologically controlled transpiration, are not modeled in SOILWAT, and this may have contributed to minimizing differences between the groups. In addition to drought effects,
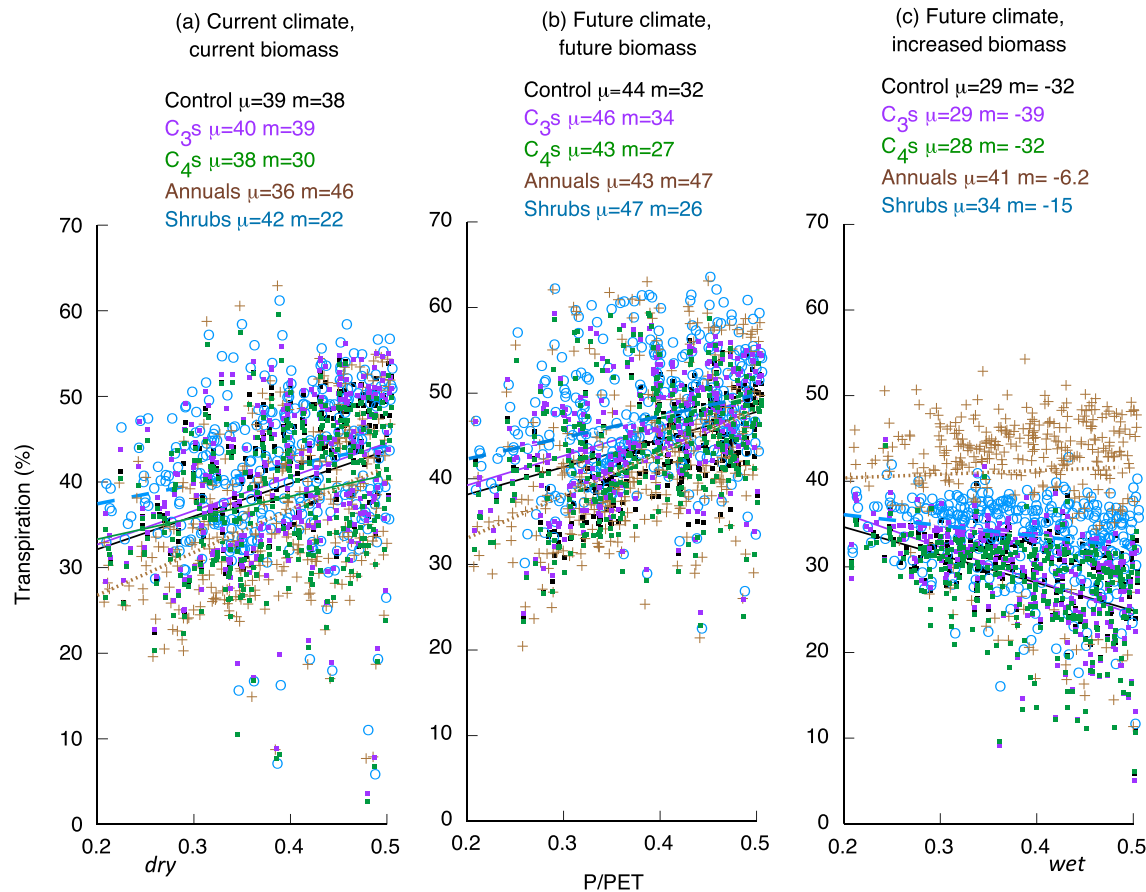
Figure 4. Transpiration as a function of current aridity (precipitation/potential evaporation; P/PET) in three scenarios: (a) current climate and climate-driven biomass, (b) future climate and climate-driven biomass, and (c) future climate and experimentally increased biomass. Each point represents a 30 year average for one of 340 study sites. Points and matching line colors represent control vegetation (mixed grassland) and four functional groups (perennial C_3 and C_4 grasses, annual grasses (crosses, fine dashed line), and shrubs (circles, coarse dashed line)). μ: overall mean for each functional group; m: slope of regression relationship between drought frequency and P/PET.

C_3 and C_4 grasses may differ in other important ecosystem effects such as responses to elevated CO_2 (Morgan et al., 2011), fire frequency (Reed et al., 2005), and nutrient feedbacks (Seastedt & Pyšek, 2011).

Grassland biomass varies widely, even if the dominant functional group does not change (Driscoll et al., 2014; Potts et al., 2008; Pysek et al., 2012; Vila et al., 2011). Although our shrub simulation incorporated a biomass increase, our separate simulations of experimentally increased biomass allowed us to explore its effect even in the absence of a change in functional group dominance. Both transpiration (Morgan et al., 2011) and interception (Dunkerley, 2000) are heavily dependent on biomass, so a large biomass effect is not surprising. In SOILWAT, biomass controls transpiration more strongly than do soil texture or precipitation (Lauenroth & Bradford, 2006). In a field comparison of C_4 grasses, an invasive grass with greater biomass had lower soil moisture (English et al., 2005). Relative to other functional groups, annuals showed small changes in drought frequency and onset when biomass was increased, probably because their relatively short growing season restricted their effects on soil water to a fraction of each year. Overall, our analysis suggests that biomass has greater effects on ecological drought than either functional group or climate change, underscoring the need to recognize vegetation structural changes that emerge from biological invasions or grassland management aimed at increasing productivity.

Our results confirmed that transpiration dominated actual evapotranspiration in current and future climates (Asner et al., 2004; Bernacchi & VanLoocke, 2015; Huxman et al., 2004). Transpiration was greatest beneath deep-rooted shrubs and least beneath shallow-rooted annuals (Figure 4a). In the case of experimentally increased biomass, however, interception was also important. In contrast to the positive slopes for the relationships between transpiration (%) and current water availability (P/PET) in current and future climates
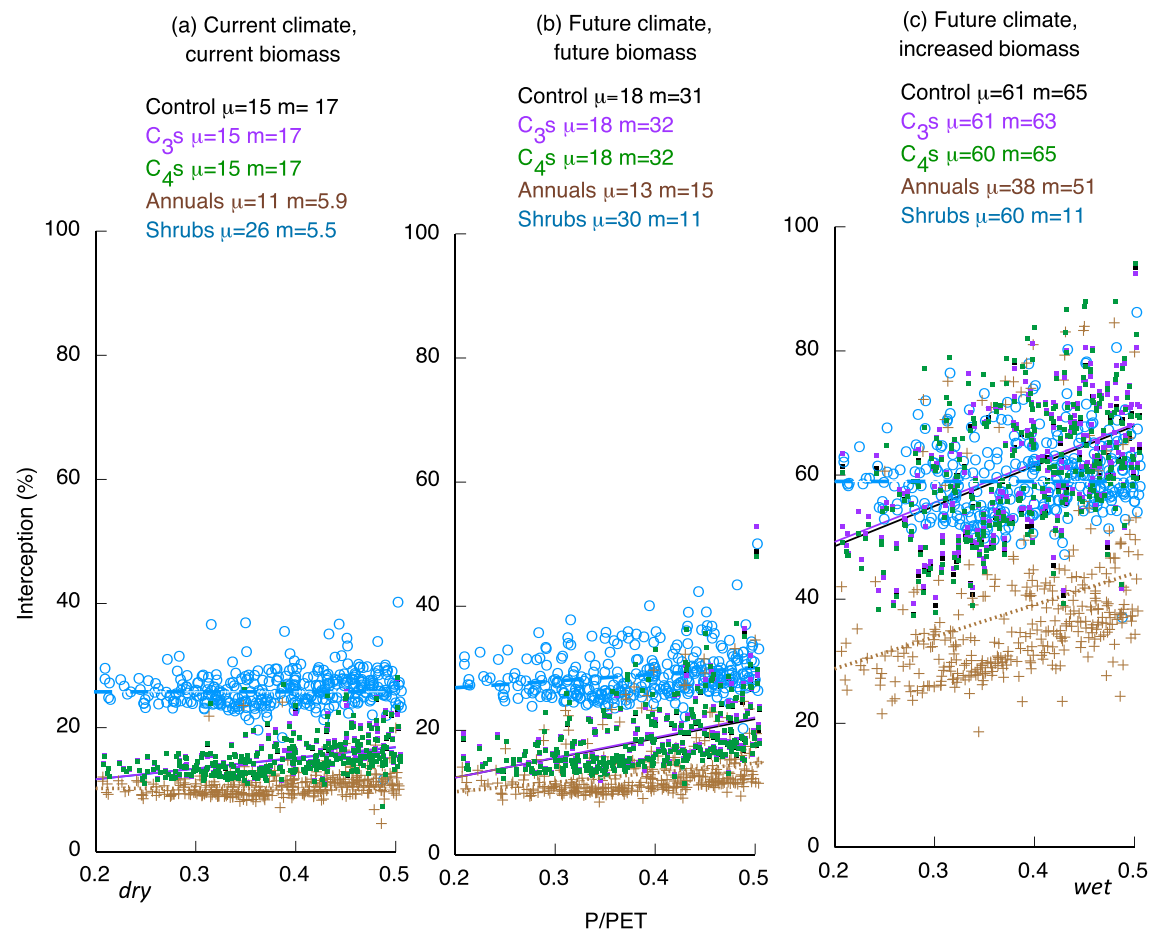
Figure 5. Interception as a function of current aridity (precipitation/potential evaporation; P/PET) in three scenarios: (a) current climate and climate-driven biomass, (b) future climate and climate-driven biomass, and (c) future climate and experimentally increased biomass. Each point represents a 30 year average for one of 340 study sites. Points and matching line colors represent control vegetation (mixed grassland) and four functional groups (perennial C_3 and C_4 grasses, annual grasses (crosses, fine dashed line), and shrubs (circles, coarse dashed line)). μ: overall mean for each functional group; m: slope of regression relationship between drought frequency and P/PET.

(Figures 4a and b), these slopes were mostly negative under experimentally increased biomass (Figure 4c). The negative slopes were likely linked to the increase in interception with increasing precipitation (Figure 5c). Water intercepted by the canopy before it reaches the soil is not available for transpiration, so increased interception in sites with high precipitation and consequently high productivity left little water available for transpiration. The high values of interception predicted by the model are consistent with field measures from grasslands (Brye et al., 2000; Dunkerley, 2000; McLaren et al., 2004). Fine grass leaves intercept much of the water from the small rainfall events typical of semiarid grasslands (Lauenroth et al., 2014). Interception is well recognized as a major component of hydrology in arid systems characterized by precipitation that occurs during the growing season (Dunkerley, 2000), and our results suggest that it will be relatively important in future climates regardless of whether grassland biomass is increased by invasion or by management to enhance production. The trade-off between transpiration and interception may account for the fact that overall evapotranspiration did not vary between invaded and noninvaded vegetation in a review of field measurements (Cavaleri & Sack, 2010).

There are important limitations to the use of simulation models like SOILWAT in studying the effects of plant functional groups on ecological drought. First, our analysis did not incorporate feedback (Turnbull et al., 2012), and vegetation changes that follow climate change further exacerbate drought in SOILWAT (Tietjen et al., 2017). Similarly, biomass increased by factors such as fertilization, grazing respite, or invasion by identical functional groups with greater productivity should all increase ecological drought, but grassland aboveground biomass in turn varies strongly with water availability independently of other drivers (Lauenroth &

Sala, 1992). Thus, biomass increased through management via fertilizers or the introduction of more productive species for the purposes of increasing grazing capacity or C sequestration may enhance ecological drought and lower productivity in the long term. Second, our model does not consider plant plasticity in physiology (e.g., stomatal control) or allocation (e.g., increased allocation to roots). Third, our study did not consider interactions between functional groups, but soil moisture influences competitive outcomes (Goldstein & Suding, 2014), and drought-related facilitation has been reported among contrasting functional groups (de Dios et al., 2014). However, our objective was to explore the effect of monodominant stands on ecological drought, and such stands are typical of invaded communities (Driscoll et al., 2014; Pysek et al., 2012), regardless of the mechanism that has allowed invasion to occur. Fourth, more details could be incorporated into the model. For example, the relative importance of physiology and phenology in partitioning contrasting effects of C_3 and C_4 grasses could be explored. Also, interception in the model currently depends on biomass but could additionally take into account allocation to stems and leaves, or leaf area index. Lastly, contrasting functional groups can exert other ecosystem-level changes such as altering herbivory (Maron et al., 2014), fire (MacDougall et al., 2013), or erosion (Wilcox et al., 2012). Large-scale data reviews and path analyses may be useful for understanding the relative importance of multiple invasion effects (Grace et al., 2016).

5. Conclusions

The effects of plant functional groups on ecological drought were distinguished most strongly in the cases of increased biomass and contrasting life histories (annual grasses, perennial grasses, and shrubs), as opposed to differences in physiology and phenology (C_3 and C_4 perennial grasses). Importantly, the ranks of functional group effects on drought were generally consistent in our three scenarios, suggesting that current differences among functional groups may predict differences in the future.

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