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Influence of Weather on Production Dynamics in Wyoming Big Sagebrush Steppe Across Plant Associations ☆,☆☆

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ABSTRACT

High interannual variability in production occurs in many semiarid rangelands, including the perennial-dominated sagebrush steppe, in response to variable weather conditions. Describing the effects of weather on the dynamics of sagebrush steppe has implications for a broad set of management objectives including forage and wildlife habitat. Here, we investigated the effects of seasonal weather and plant associations, related to abiotic characteristics, on herbaceous production dynamics across 44 intact, representative sagebrush steppe sites across eastern Oregon from 2003 to 2012. We tested for the effects of sampling year, lagged precipitation, and potential evapotranspiration predictors, as well as prior year biomass and plant association on production of major herbaceous functional groups. We also tested for synchrony across functional groups and plant associations. We found that spring precipitation was the most consistent predictor of production. However, several other variables including prior year weather significantly affected production. Production sensitivity to weather was combined with high synchrony across functional groups and associations, suggesting low potential for production stability associated with these factors in sagebrush steppe in the northern Great Basin.

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Introduction

Interannual dynamics in plant community production are strongly influenced by weather, such as precipitation amounts and timing during the growing season, particularly in semiarid systems (Knapp and Smith 2001; Hsu et al. 2012). However, production responses to weather are also moderated by static environmental variables like elevation (Munson et al. 2019), topographic position and aspect (Briggs and Knapp 1995), and soil properties (Fernandez-Going et al. 2012). Production variability in plant communities may be dampened by asynchronous dynamics across species or functional groups (Valencia et al. 2020) due to competition (Silvertown et al. 1994) and tradeoffs between growth rate and density dependence (Hallett et al. 2018).

Sagebrush (*Artemisia* L.) steppe in the intermountain United States is a semiarid system with cold winters and hot dry summers, as well as high production variability associated with annual and seasonal fluctuations in temperature and precipitation (Sneva 1982; Anderson and Inouye 2001). Weather-driven plant community dynamics in sagebrush steppe impact wildlife, notably imperiled greater sage grouse *(Centrocercus urophasianus)* populations (Coates et al. 2018; Donnelly et al. 2018) and carbon fluxes and other ecosystem properties (Svejcar et al. 2008). Temporal dynamics and trends in herbaceous production also impact forage management, invasive species control, and wildfire risk (Pilliod et al. 2017). Herbaceous production patterns in the region are shifting with climate change trends, such as increasing spring growing season temperatures (Tang and Arnone III 2013) and increasing precipitation extremes (Xue et al. 2017). Efforts to predict vegetation productivity and fuel loads with remotely sensed phenology indicators (Jones et al. 2018; Reeves et al. 2020) and climate change forecasts (Adler et al. 2020; Elmendorf et al. 2015) could be informed by greater understanding of the links between weather and production across diverse sites.

Seasonal and interannual weather, both precipitation and temperature, are highly variable in sagebrush steppe, and their effects on interannual production are difficult to identify across gradients of community composition and site factors such as long-term

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Table 1
Association names, acronym code used in manuscript, and number of sites sampled from 2003/04–2012, dominant perennial bunchgrass species and authority, and key characteristics and abiotic variables related to the association designation (Davies et al. 2006; Davies et al. 2007; Bates and Davies 2019).

Association name	Code	No. sites	Dominant species	Distinguishing characteristics
Bluebunch wheatgrass	PS	15	*Pseudoroegneria spicata* (Pursh) Á. Löve	Mainly hillslopes. Silt or clay loams soils.
Thurber's needlegrass	AT	11	*Achnatherum thurberianum* (Piper) Barkworth	Flat slopes and fine texture soils.
Bluebunch-Thurber's	PS-AT	4	*P. spicata*, *A. thurberianum*	
Idaho fescue	FI	5	*Festuca idahoensis* Elmer	High fertility soils. High large bunchgrass and total herbaceous cover.
High desert mix	HD	5	*F. idahoensis*, *P. spicata*, *A. thurberianum*	Sandy-loam A horizons and indurated duripan at 50-90 cm.
Needle and thread	HC	4	*Hesperostipa comata* (Trin. & Rupr.) Barkworth	Sandy soils. Low *Poa secunda*, perennial forb, and total herbaceous cover and high *Bromus tectorum* cover.

climate, topography, and soil characteristics (Passey et al. 1982). While one study suggested fall through spring precipitation is tied to perennial production (Sneva and Britton 1983), another study showed more complex relationships between seasonal and multiyear weather and production in areas dominated by the early-season, short-stature perennial Sandberg bluegrass (Pilliod et al. 2017). Weak relationships between production and recent weather conditions for perennial species may by partially due to the effects of multiyear weather patterns on perennial growth and recruitment. For example, perennial bunchgrasses, which represent a large proportion of herbaceous productivity in intact sagebrush steppe, often respond to multiyear precipitation patterns (Dalgleish et al. 2011). In contrast, annual species production is much more clearly linked to short-term weather variables, though longer-term weather patterns can drive abundance patterns (Poa secunda, J. Presl, Pilliod et al. 2017), perhaps due to accumulation or depletion of seed banks (Smith et al. 2008).

Here, we ask how seasonal weather, including the year before sampling, affects herbaceous production across functional groups in intact, low-disturbance Wyoming big sagebrush steppe sites. We also ask whether fine-scale differences in herbaceous community composition linked to soil and topographic microclimates within Wyoming big sagebrush communities drive production variation, in addition to weather. Finally, we tested for the possibility that production variability at larger spatial scales might be buffered by asynchronous patterns across functional groups or plant associations within Wyoming big sagebrush steppe, due to varying responses of groups or communities to weather.

Methods

Sampling and data compilation

Sites were selected across southeastern Oregon representing intact Wyoming big sagebrush steppe (*A. tridentata* ssp. *wyomingensis* Beetle & Young) communities without major known disturbances, such as recent fire or intense grazing (Fig. 1, Davies et al. 2006; Davies et al. 2007). The sites were previously classified into plant associations (The Nature Conservancy 1994) within Wyoming big sagebrush steppe on the basis of dominant perennial bunchgrass species (Davies et al. 2006) and generally linked to soil texture and topographic variables (44 sites, Table 1, Davies et al. 2006; Davies et al. 2007). An additional association, "high desert mix" was defined during resurveys of the sites (see Table 1, Bates and Davies 2019). All associations include all major functional groups used in the analysis, with only subtle variations in relative or total cover. Big sagebrush, the dominant shrub, ranges in cover from 10% to 17%, while total herbaceous cover ranges from 14% to 29% and is primarily perennial bunchgrasses (12–25%), and invasive annual cover is low (generally < 1%, Davies et al. 2006). Herbaceous production in the current year was sampled annually from 2003 to 2012, except for two sites sampled from 2004 to 2012 (see Table 1). Standing crop biomass was collected by randomly selecting and clipping twenty 1-m^2 frames per site in late May to mid-June (date variable by site and year), avoiding quadrants clipped in prior years, within a 50×80 m area. Biomass was collected for the following functional groups associated with life-forms: Sandberg bluegrass (native, *Poa secunda* J. Presl); large perennial bunchgrasses (LPBG, native, e.g., Idaho fescue, bluebunch wheatgrass); annual grasses (AG, mainly invasive *Bromus tectorum,* cheatgrass); perennial forbs (PF, native); and annual forbs (AF, mix of native and non-native). *P. secunda* was collected separately because it is a small-stature perennial bunchgrass with earlier phenology and shallower roots than other common bunchgrasses (Passey et al. 1982). Perennial bunchgrasses were clipped to 2.5-cm stubble height. Other life-forms were clipped to near ground level ($\leq$ 0.5 cm). Harvested standing crop was dried at 60°C for 72 h before weighing. Production of perennial grasses and *P. secunda* was determined by sorting a 5- to 15-g subsample of current year's growth from the past year's (residual) growth and multiplying the percentage of current year's growth by the standing crop weight to estimate the current year's production (Culley et al. 1933). Production for perennial forbs, annual forbs, and annual grasses was equivalent to their standing crop values and required no sorting. Mat-forming perennial forbs (suffruticose forbs) are vulnerable to mortality from excessive clipping due to exposed growth points, so their production was estimated by collecting half the plant and then doubling the weight after drying.

Early spring growth is influenced by cold season precipitation, if preserved as snowpack, and temperature (Blaisdell 1958). In contrast, late spring precipitation is more likely to promote active and continuing growth of herbaceous vegetation (Blaisdell 1958). High spring potential evapotranspiration (PET, atmospheric demand for water associated with temperature and insolation) is likely to contribute to drought stress and limited growth for herbaceous species during the active growth period, when soil water potential is relatively high in sagebrush steppe (Schlaepfer et al. 2012). Lower summer-fall PET, such as a mild summer, could prolong the spring growing season for many species and potentially allow for fall growth (after summer dormancy) for perennial grasses. Previous year's weather can also strongly affect both perennial (Dalgleish et al. 2011) and annual production (Pilliod et al. 2017) in this system, although the relative influence of previous year versus current year weather conditions is likely to vary across weather variables and functional groups.

To address the potential for these weather variables to affect production, we extracted daily precipitation and PET data for all sites for the study years (2003–2012) and a 30-yr long-term climate period including the study yr (1983–2012) from a 4-km gridded weather dataset (28 unique grid points, as some sites were within the same grid cell, GridMET, Abatzoglou 2013) with Google Earth Engine (Gorelick et al. 2017). We compiled four precipitation variables for each site and sampling year. Daily precipitation was summed for the year of sampling and the year prior for each of two seasonal periods: cold season, fall through early spring (Oct.-Mar.), and late spring (Apr.-May), which tends to be a critical period for perennial herbaceous growth in this system. To represent atmospheric demand for water based on temperature and hu-

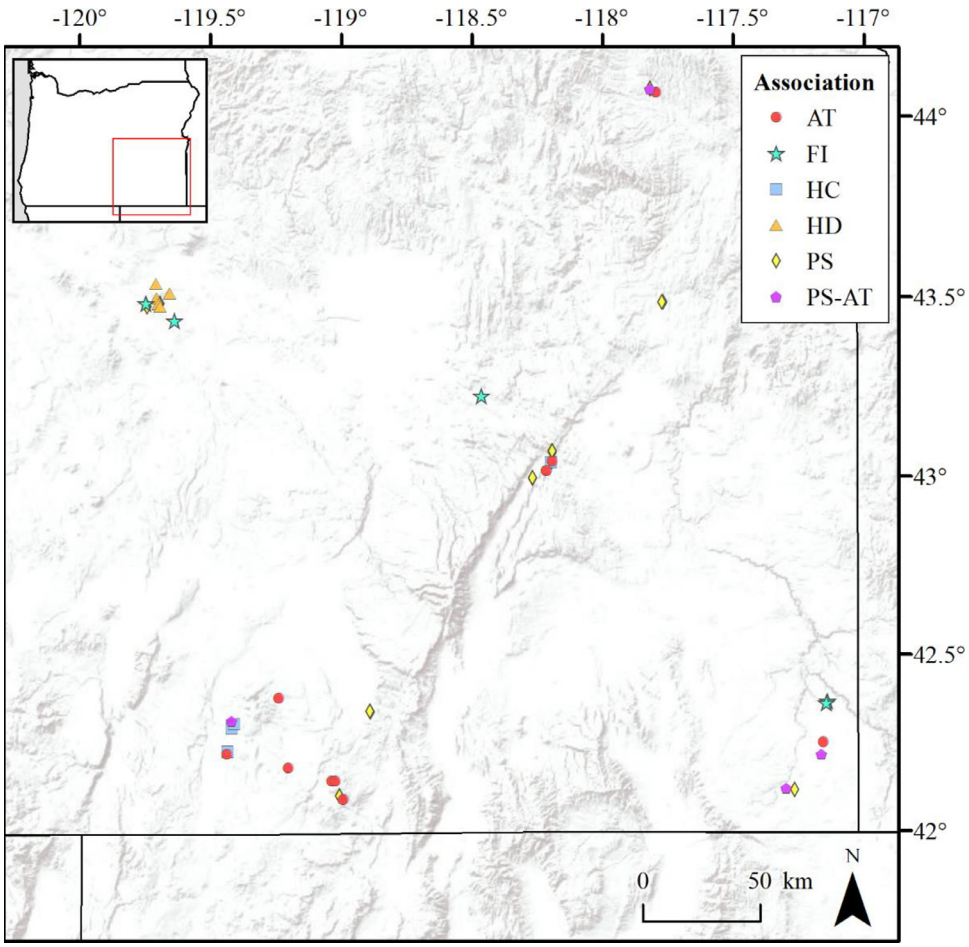

Figure 1. Map of sites by plant association. AT indicates *Achnatherum thurberianum;* FI, *Festuca idahoensis;* HC, *Hesperostipa comata;* HD, high desert mix; PS, *Pseudoroegneria spicata;* PS-AT, *Pseudoroegneria spicata-Achnatherum thurberianum.* Details in Table 1. Terrain basemap, sources: Environmental Systems Research Institute, US Geological Survey, National Oceanic and Atmospheric Administration. Study area in southeastern Oregon, USA is shown with the red rectangle in the inset map.

midity, we used a measure of reference PET for a uniform vegetated surface (grass for this study) with the Penman-Monteith method, which relies on minimum and maximum temperatures, wind speed, and vapor pressure deficit (Allen et al. 1998; ASCE-EWRI 2005; Abatzoglou 2013). We compiled four evapotranspiration variables per site and sampling year: the sum of daily evapotranspiration for the hot and dry season, summer-early fall (Jun.-Sep.), for 2 yr and 1 yr before the sampling year. We also summed daily evapotranspiration for the spring (Mar.-May) in the year of sampling and year prior. While these evapotranspiration and precipitation variables represent distinct weather elements affecting production, they are also correlated (Table S1, available online at doi:10.1016/j.rama.2022.09.002).

We calculated standardized weather anomalies (difference divided by the standard deviation) for each variable, time period, and site to estimate the effect of difference from mean conditions. In contrast to raw precipitation or evapotranspiration values, anomalies are not highly correlated with mean precipitation or evapotranspiration among sites and therefore approximate the effects of weather variation as opposed to the long-term mean climate of a site. The standardized anomalies were calculated for each seasonal and yearly weather variable in each sample-year and site combination with the following equation where "year" refers to the seasonal variable in a given year and "long-term mean" refers to the 30-yr mean (1983–2012) for that same seasonal weather variable:

$$(\text{Year}_{\text{weather var}} - \text{Longterm Mean}_{\text{weather var}}) / \text{Standard Deviation}_{\text{weather var}}$$

Negative or positive anomaly values indicate if the weather variable is lower or higher than the respective mean, whereas the magnitude indicates whether the anomaly value is relatively extreme (> 1 or < -1 anomaly values are > 1 standard deviation from the mean).

Statistical analysis

We used linear mixed models, with a random term for site, to test for relationships between weather variation and production across functional groups and associations (R package lme4, version 1.1.26, Bates et al. 2015). Each initial full model included eight weather variables (precipitation and evapotranspiration anomalies for each site for two seasons and 2 yr) and all six plant associations (see Table 1). Because initial conditions in terms of biomass could strongly affect the capacity for subsequent production through growth or recruitment, we also included the previous year's production as a main predictor. For the first year of sampling for each site (2003 or 2004), we used the mean production for that functional group and site across all sampling years as a substitute for the previous year's production value.

$$\begin{aligned}\text{Full model equation}: \ \text{Production biomass} \sim\ & \beta_{\text{intercept}} \\ & + \beta_{\text{Yr0 Precip Late Spring}} + \beta_{\text{Yr0 Precip.Fall-Spring}} \\ & + \beta_{\text{Yr-1 Precip.LateSpring}} + \beta_{\text{Yr-1 PrecipFall-Spring}} + \beta_{\text{Yr0 PETSpring}} \\ & + \beta_{\text{Yr-1 PETSumFall}} + \beta_{\text{Yr-1 PETSpring}} + \beta_{\text{Yr-2 PETSummer-Fall}} \\ & + \beta_{\text{previous production biomass}} + \alpha\beta_{\text{association}}\end{aligned}$$

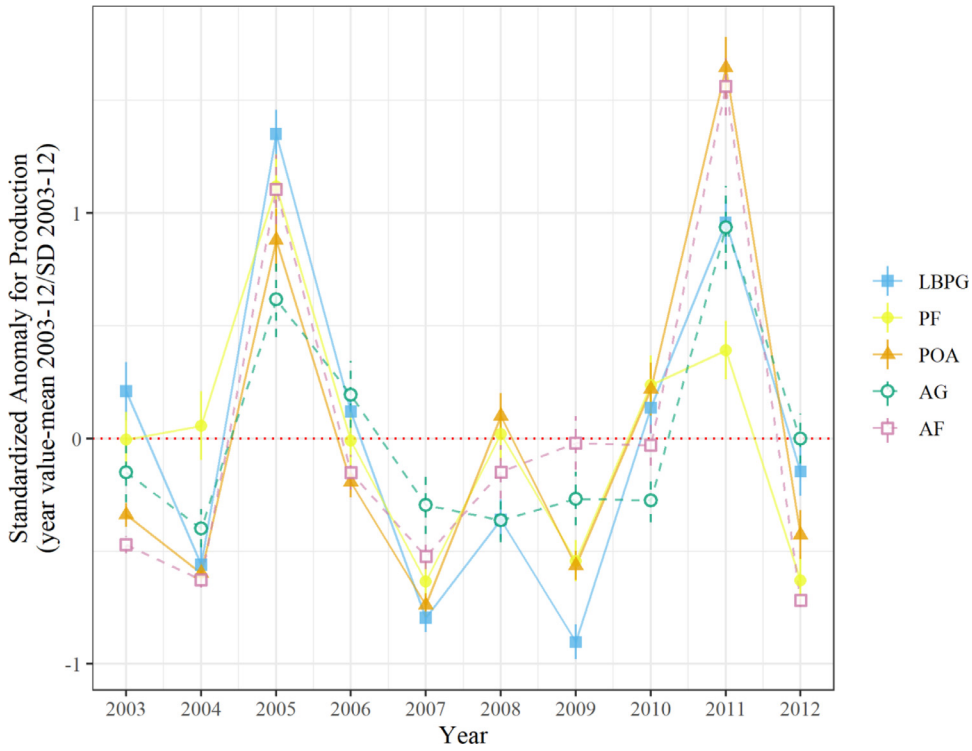

Figure 2. Standardized anomalies for production (mean ± standard error across sites) by year and functional group (perennial groups with *solid lines* and *symbols:* LBPG indicates large perennial bunchgrass; PF, perennial forb; POA, *Poa secunda;* annual groups with *dashed lines* and *open symbols:* AG, annual grass, AF, annual forb).

We created separate models for large perennial bunchgrass, *P. secunda,* perennial forb, annual forb, and annual grass production. We removed sites that had zero biomass in more than three years for *P. secunda* biomass (one HC association site) and annual grass (9 sites, 3 PS, 3 FI, 1 PS-AT, 1 AT) models because sites where the functional group was largely absent did not have the capacity to exhibit interannual production dynamics with weather. Models for annual grass biomass were log-transformed before analysis to meet normality assumptions with zero values for current and previous year's biomass omitted (49 yr samples across 17 sites).

To construct final models for each dependent variable, we sequentially removed predictor variables with $P > 0.05$ significance, starting with the highest P values and comparing models fit with maximum likelihood with likelihood ratio tests (Zuur et al. 2009). We also combined plant association categories included in the full model if they were not significantly different from one another based on multiple comparisons with Tukey contrasts (R multcomp package, version 1.4-15, Hothorn et al. 2008). The significance of final model terms is reported based on F-tests with type II sum of squares (R car package, version 3.0.10, Fox and Weisberg 2011) with Kenward-Roger degrees of freedom (Halekoh and Højsgaard 2014; Kenward and Roger 1997). The proportion of variance associated with both random and fixed effects (conditional) and fixed effects only (marginal) was calculated with pseudo-R^2 for final models (R package piecewiseSEM, version 2.1.2, Nakagawa and Schielzeth 2013; Lefcheck 2016).

For each site, we calculated a metric of community synchrony (Loreau and de Mazancourt 2008) with all five functional groups (large perennial bunchgrasses, *P. secunda,* perennial forbs, annual forbs, and annual grasses) and for the three perennial groups only for each site across all years with a randomization procedure in R package synchrony (version 0.3.8, community.sync function, $N = 999$, Gouhier and Guichard 2014). We also tested whether or not synchrony across plant associations occurred across the 10 years of the analysis for mean functional group and total production. All analyses were conducted in R (version 4.0.3, R Core Team 2020).

Results

Weather variability

Long-term (1983–2012) averages for predictor variables across all sites in the analysis were 171.9 ± 55.4 (mm, mean and standard deviation) for fall-early spring (Oct.-Mar.) and 68.8 ± 29.8 for late spring (Apr.-May) precipitation and 303.1 ± 28.8 for spring (Mar.-May) and 675.4 ± 30.2 for summer-fall (Jun.-Sep.) PET. Sampling yr (2003–2012) values were comparable with long-term variability with precipitation 168.3 ± 53.3 in fall-early spring and 74.7 ± 32.5 in late spring and PET 301.3 ± 33.4 in spring and 687.3 ± 31.8 in summer-fall (Fig. S1, available online at doi:10.1016/j.rama.2022.09.002), as well as within multivariate space associated with previous year weather variables used in prediction (Fig. S2, available online at doi:10.1016/j.rama.2022.09.002).

Weather response by functional group

Production was highly variable across the 10-yr study period for all groups (Fig. 2). Weather variability was also high with several years of higher and lower values for seasonal variables included in production models (Fig. 3).

Both precipitation and evapotranspiration significantly affected large perennial bunchgrass (LPBG) production (Table 2). Higher LPBG production was associated with wetter springs (increased late spring precipitation) the year of sampling and with decreased prior year precipitation in either spring or cold season (fall-spring), as well as increased spring PET the year prior and decreased summer-fall evapotranspiration in the two years before sampling (see Table 2). Associations with Thurber's needlegrass as a dominant or codominant (see Table 1, AT, AT-PS, HD) had lower biomass

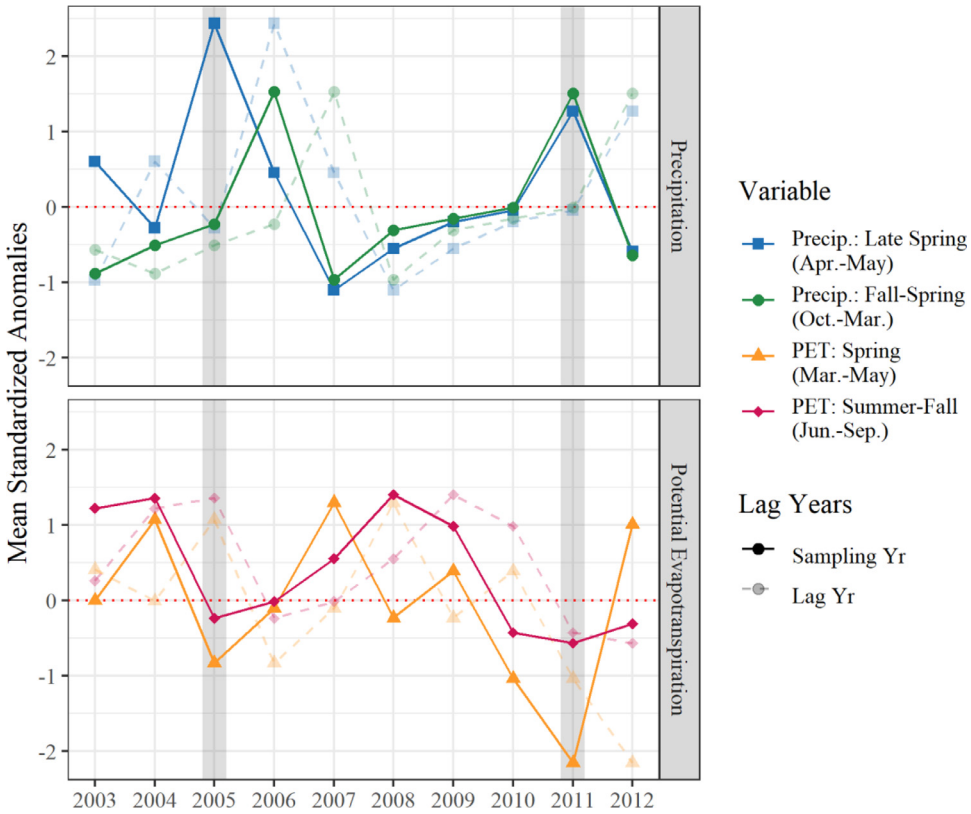

Figure 3. Mean weather anomalies across study yr (2003–2012, $N = 44$ sites, yr value—long-term mean/standard deviation, regional means, precipitation: late spring, *blue squares,* fall-spring, *green circles,* potential evapotranspiration: spring, *orange triangles,* summer-fall, *pink diamonds*). Lag years (years before sampling) are indicated by fading and line type with *darker, solid lines* for year of sampling. Peak production yrs, 2005 and 2011, are indicated by *gray bars.*

Table 2
Final linear mixed models (random intercept term for site) for large perennial bunchgrass (LPBG), perennial forb (PF), *Poa secunda,* annual grass (AG), and annual forb (AF) production (model fit with marginal, main effects only, and conditional, main and random effects, R^2, final predictors, effect direction, F-statistics, Kenward-Roger degrees of freedom, and *P* values). Full models included all plant associations (described in Table 1), previous year's functional group biomass (production), late spring (Apr.-May) and fall-spring (Oct.-Mar.) precipitation in the sampling year (Y_0) and the previous year (Y_{-1}) and potential evapotranspiration (PET) in spring (Mar.-May) of the sampling year and previous year and and summer-fall (Jun.-Oct.) in the previous year and two years prior (Y_{-2}).

Response	Predictor	Yr	Effect	*F*-statistic	df	*P* value
LPBG	Association groups (PS/FI/HC & AT/PS-AT/HD)		NA	21.9	49	< 0.001
$R^2_m = 0.50$	Previous yr biomass		+	38.2	356	< 0.001
$R^2_c = 0.61$	Precip. late spring	Y_0	+	36.0	406	< 0.001
	Precip. late spring	Y_{-1}	−	7.9	399	< 0.001
	Precip. fall-spring	Y_{-1}	−	13.8	412	0.005
	PET spring	Y_{-1}	+	13.7	397	< 0.001
	PET summer-fall	Y_{-1}	−	52.9	414	< 0.001
	PET summer-fall	Y_{-2}	−	10.6	394	0.001
PF	Association groups (HC & non-HC)		NA	7.8	42	0.008
$R^2_m = 0.17$	Precip. late spring	Y_0	+	31.5	393	< 0.001
$R^2_c = 0.66$	PET spring	Y_{-1}	+	16.6	392	< 0.001
	PET summer-fall	Y_{-1}	−	5.8	394	0.016
P. secunda	Association groups (HC & non-HC)		NA	14.3	42	< 0.001
$R^2_m = 0.43$	Precip. late spring	Y_0	+	8.7	391	0.003
$R^2_c = 0.52$	Precip. late spring	Y_{-1}	−	72.2	388	< 0.001
	Precip. fall-spring	Y_0	+	15.1	396	< 0.001
	Precip. fall-spring	Y_{-1}	−	17.1	401	< 0.001
	PET summer-fall	Y_{-1}	−	51.6	401	< 0.001
	PET summer-fall	Y_{-2}	−	17.4	390	< 0.001
AG (log)	Previous yr biomass (log)		+	14.9	284	< 0.001
$R^2_m = 0.13$	Precip. late spring	Y_0	+	36.0	264	< 0.001
$R^2_c = 0.44$	PET summer-fall	Y_{-2}	−	6.3	273	0.012
AF	Precip. late spring	Y_0	+	51.1	392	< 0.001
$R^2_m = 0.29$	Precip. late spring	Y_{-1}	−	38.7	395	< 0.001
$R^2_c = 0.44$	Precip. fall-spring	Y_0	+	97.1	398	< 0.001
	Precip. fall-spring	Y_{-1}	+	28.1	395	< 0.001

than the other three associations (PS, HC, FI) and were grouped in final models (Table S2, available online at doi:10.1016/j.rama.2022.09.002). Previous year LPBG production was positively associated with current-year production (see Table 2). Standardized coefficients indicated that the influence of weather variables, particularly sampling year late spring precipitation and the previous year's summer-fall evapotranspiration, were similar in magnitude to the effects of previous year's biomass and association (see Table S2).

Perennial forb (PF) production was linked to relatively few weather variables and not with previous year's production and, model fit was relatively weak (see Table 2). Higher PF production was strongly associated with higher sampling-year late spring precipitation and spring evapotranspiration the year prior to sampling and weakly with lower PET the summer through fall before sampling (see Tables 2 and S2). PF production in needle-and-thread (HC) association sites was lower compared with other associations, with the effect of association relatively large compared with individual weather variables as indicated by standardized coefficients (see Table S2).

Short-stature perennial grass *P. secunda* production was related to several weather variables and was not associated with previous year's biomass (see Table 2). Higher *P. secunda* production was associated with higher sampling-year late spring and fall-spring (cool season) precipitation (see Table 2). Previous year late spring and fall-spring precipitation, as well as the evapotranspiration in the previous two summer-fall periods, were negatively related to *P. secunda* production. Similar to perennial forb models, needle-and-thread (HC) associations had lower *P. secunda* production than other associations (see Table S2). Models suggested strong lag effects of previous year weather, as indicated by the large negative standardized coefficients for summer-fall PET and precipitation the year before the sampling year (see Table S2).

Annual grass (AG) production was associated with few weather variables and positively associated with the previous year's AG production, though model fit was relatively weak (see Table 2). AG production was higher with increased late spring precipitation in the sampling year and lower spring evapotranspiration 2 years prior to sampling (see Table 2). The positive effects of late-spring precipitation were similar in magnitude to the effects of previous years' biomass as measured by standardized coefficients (see Table S2). Association categories were not significantly associated with AG production.

Neither association nor previous year's production were strongly related to annual forb (AF) productivity, but several weather variables including previous year's variables were influential, particularly late-spring and fall-spring precipitation the year before sampling (see Tables 2 and S2). AF production was higher with increased late-spring and fall-spring precipitation in the sampling year, as well as higher precipitation the fall-spring before sampling and negatively associated with the previous year's late-spring precipitation (see Table 2).

Synchrony

The proportion of sites with significant synchrony ($P < 0.05$) across plant functional groups varied by association and by the inclusion of annual functional groups in the analysis (Table 3). Synchronous production was uncommon for needle-and-thread and bluebunch-Thurber's needlegrass associations and relatively more common among bluebunch wheatgrass and Idaho fescue associations. Synchronous production patterns occurred for a majority of sites whether or not annual groups were included (significant proportion of sites, all groups: 75%, perennial groups: 61%). Plant association total and functional group production (mean production across sites) was also highly synchronous across years for all groups (see Table 3). Production means for total and functional group production were also significantly ($P \leq 0.001$) synchronous across the six plant associations (observed synchrony, φ, range: 1/6 [no. of associations]–1, with 1 = high synchrony, total mean production: $\varphi = 0.922$, LPBG: $\varphi = 0.760$, PF: $\varphi = 0.704$, *P. secunda:* $\varphi = 0.840$, AG: $\varphi = 0.829$, AF: $\varphi = 0.819$).

Table 3
Percent sites with significant (1-sided test, $P < 0.05$) synchrony (Loreau and de Mazancourt 2008) by association across all functional groups (large perennial bunchgrasses, *Poa secunda,* perennial forbs, annual forbs, and annual grasses) and perennial functional groups only.

Association (no. of sites)	All groups	Perennial only
Bluebunch wheatgrass (15)	87	80
Thurber's needlegrass (11)	91	55
Bluebunch-Thurber's (4)	50	25
Idaho fescue (5)	80	80
High desert mix (5)	60	60
Needle-and-thread (4)	25	25

Discussion

Our results show that late-spring precipitation is a key weather factor regulating herbaceous production of different functional groups in intact Wyoming big sagebrush vegetation, consistent with previous observations (Sneva 1982; Pilliod et al. 2017). Hot and dry conditions (associated with higher PET) in the summer and fall before the spring sampling period also dampened productivity for all perennial groups. Plant associations with distinct species composition and abiotic features had relatively little effect on dynamics overall, and prior year biomass only influenced large perennial bunchgrass and annual grass production. In addition, contrary to expectations, we observed relatively low potential for production stability associated with asynchronous dynamics in functional groups within sites or across associations in the region.

Relationships between weather variables and productivity were different among some functional groups, despite the general importance of spring precipitation. For example, weather responses of functional groups were different for the two peak production years in this dataset, 2005 and 2011 (see Fig. 2). All groups had relatively high production in 2005. In contrast, in 2011 annual forbs and *P. secunda* reached much higher relative production values than in other years, while perennial forb production was closer to average values (see Fig. 2). Perennial forbs likely benefited from the particularly high late-spring precipitation in 2005, which was muted in 2011, resulting in a prolonged growing season and associated higher yields (see Fig. 3). Annual forbs and *P. secunda* benefited from the combination of lower spring PET and higher cool season (fall-spring) precipitation along with slightly higher late-spring precipitation in 2011 (see Fig. 3). The early phenology of this annual group and common small-statured perennial grass species may have allowed them to benefit from prolonged cooler and wetter spring conditions compared with other groups (Passey et al. 1982). Weather variables before the sampling year influenced production for all functional groups, though the direction and influence of variables differed by functional group. The influence of prior year weather was significant in models even though the previous year's biomass was also included. This supports previous observations that multiyear patterns of favorable conditions can allow perennial species to accumulate reserves leading to higher production, via mechanisms such as increased size by tillering in perennial grasses (Dalgleish et al. 2011). In contrast, annual species will respond to combinations of weather factors related to seed production, seedbank dynamics, and emergence, which can be complex for species capable of germinating in either spring and fall, as is the case with cheatgrass (Smith et al. 2008). However, prior year's weather variables did not have consistent effects across functional groups.

High synchrony across groups indicates limited potential for stabilizing mechanisms associated with functional group responses due to competition or other factors, as observed with the trade-off between years dominated by grasses or forbs in annual California grasslands (Hobbs et al. 2007; Hallett et al. 2019). High synchrony across these sites spanning a large area and with varying composition further supports evidence that regional oscillations in sensitive wildlife species abundance are associated with weather-driven dynamics in herbaceous habitat resources (e.g., greater sage grouse, Coates et al. 2018). Synchrony was generally higher in most sites when annual groups were included, suggesting that increasing perennial biomass does not depress annual groups in these sites or vice versa. However, individual species, particularly in higher-diversity groups like perennial and annual forbs, may have been responding divergently to weather patterns and increasing the stability for those groups across years. Shrub production is also absent from this analysis, and production patterns might differ for big sagebrush given its deeper roots and corresponding capacity to access deep soil-water unavailable to many herbaceous plants in these associations (Germino and Reinhardt 2014).

The plant association groups used in this analysis describe distinct communities based on species occurrence and relative abundance and linked to interacting environmental factors, particularly soil characteristics like texture and depth to restricting layer (Davies et al. 2006; Davies et al. 2007; Bates and Davies 2019). However, our results suggest that only some compositional differences, associated with a limited number of associations, influenced production in models when weather variables were included. Specifically, needle-and-thread (HC) associations, which tend to occur on sandy soils (Davies et al. 2007), were associated with significantly lower perennial forb and *P. secunda* production compared with other associations. It is also possible that some aspects of the community composition in different associations may interact with weather variables in ways that were not captured in our relatively simple models. For example, variable weather responses of the dominant grass species within the associations (Dalgleish et al. 2011) could lead to production differences for the large perennial bunchgrasses functional group that differ across association types.

The analysis presented here is fundamentally exploratory, and therefore specific relationships between weather and biomass lack independent confirmation for generalization beyond this dataset (Tredennick et al. 2021). The relatively low R^2 for some functional group models, indicate that a significant amount of production variability was not associated with weather, previous biomass production, or association composition, suggesting that other factors unexamined here are likely playing a role in production. Weather effects on production in this region are notably difficult to disentangle from site abiotic and biotic factors (Passey et al. 1982), further suggesting that specific relationships identified in our models may not broadly apply spatially (to other sites) or temporally (other years). Correlations between weather variables are also a persistent feature of this (see Table S1) and similar datasets (Sneva 1982; Sneva and Britton 1983) and particularly limit any ability to predict or infer production responses for the multitude of unexamined weather conditions. While similar previous analyses have sometimes concluded that cool season precipitation is more influential than in our analysis (Sneva 1982), methodological differences, such as the timing of biomass collection, could readily underestimate the biomass of early phenology groups particularly responsive to spring precipitation, such as Sandbergs bluegrass and most forbs. The weather variables used in this analysis are also relatively coarse (seasonal), so it is unclear to what extent the exact timing and amount of precipitation pulses could influence production, particularly for annual and/or fast-growing species with the potential to take advantage of short-lived increases in soil moisture. In addition, the sites in this study are distinct from much of the surrounding sagebrush steppe because of their relatively intact herbaceous perennial communities. Dynamics in the large swathes of the region altered by wildfire and/or highly invasive annual cover may diverge significantly from these observed patterns. For example, more pronounced weather-related dynamics in annual grass production are likely in sites where annual grasses dominate the herbaceous community (Pilliod et al. 2017), and competition with perennial species is not a major limiting factor as in this study.

Conclusions and Management Implications

Observational studies of plant community dynamics spanning a relatively large number of sites and years with consistent monitoring efforts are relatively rare in Great Basin sagebrush steppe (Passey et al. 1982; Sneva 1982; Anderson and Inouye 2001; Pilliod et al. 2017), despite concerns regarding ecosystem degradation and variable and declining wildlife populations in the region (Knick et al. 2003; Coates et al. 2018). Our results illustrate a high magnitude of production variability associated with weather, particularly spring precipitation, across several plant associations in relatively intact sagebrush steppe vegetation. This implies that any shifts in spring precipitation, such as with climate change, could significantly impact production. Some plant association differences constrained production of some perennial functional groups, suggesting a need to identify and include plant community (and/or related site factors) in management expectations when linked to longer-term differences in production. Synchronous dynamics for plant associations (across sites) and functional groups (within sites) suggest low potential for functional group or plant association responses to weather have stabilizing influences on production patterns. These weather-related patterns in production could substantially impact the forage base for livestock production, as well as wildlife habitat, including the imperiled greater sage grouse. Though the time frame for management adjustments is relatively short, spring precipitation data can inform management decisions needed to adjust stocking rates to better match potential production, though the expense associated with such adjustments may outweigh gains (Derner et al. 2021). Future research should focus on how plant composition and site characteristics alter the effects of weather on vegetation dynamics in sagebrush steppe in order to more accurately deliver expectations and forecasts for managers in this variable landscape.

Declaration of Competing Interest

None.

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Supplementary materials

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