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Original Research

Browsing Promotes Drought Resistance of Wyoming Big Sagebrush in a Working Rangeland

Ashley Tribitt[1,*], Lauren M. Porensky[2], Sally E. Koerner[3], Kimberly J. Komatsu[3], Kurt Reinhart[4], Kevin Wilcox[1,3]

[1] Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY 82071, USA
[2] USDA ARS Rangeland Resources and Systems Research Unit, Fort Collins, CO 80526, USA
[3] Department of Biology, University of North Carolina at Greensboro, Greensboro, NC 27412, USA
[4] USDA Miles City, MT 59301, USA

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ABSTRACT

Droughts are projected to become more extreme and more frequent throughout the remainder of the 21st century. Our ability to sustain rangeland functioning relies on understanding the interactive effects of extreme drought and herbivory on vegetation. Here, we report on an experiment in northeast Wyoming, USA that simulated five levels of drought intercepting 0%, 25%, 50%, 75%, or 99% of ambient rainfall for two years. These treatments were crossed with two grazing intensity (50%, 70% utilization) and two browsing intensity (background, +50% leader removal) treatments. We measured canopy volume changes, leader growth, and leaf water potential on a dominant shrub, *Artemisia tridentata* ssp. *wyomingensis* (Beetle & Young), to test three major predictions: (1) canopy volume and leader growth decline with greater drought magnitude, (2) heavy grazing reduces the effects of drought magnitude, and (3) heavy browsing amplifies effects of drought magnitude. Under ambient browsing intensity, extreme drought caused Wyoming big sagebrush (Beetle & Young) canopies to shrink. Interestingly, this effect went away in our heavy browsing treatment, despite overall negative effects of heavy browsing on shrub canopies and leader survival. We show that this drought-buffering effect may be driven by reduced leaf-level water stress in droughted, heavily browsed shrubs compared with droughted, ambiently browsed shrubs; this may have resulted from lower early-season leaf area leading to lower transpiration-related water loss. This potential mechanism for drought resistance in sagebrush steppe highlights the importance of maintaining intact food webs, despite perceived deleterious effects of herbivores for plant abundance and growth. To promote sustainability of sagebrush and other shrub-dominated ecosystems in face of extreme precipitation change, it may be necessary for land managers and policy makers to prioritize conservation of native herbivores within ecosystems.

Introduction

Altered hydrological regimes are likely to increase the severity and frequency of droughts worldwide (Easterling et al., 2017; Kossin, 2017; U.S. Global Change Research Program et al., 2017; Wehner et al. 2017), which will have substantial effects on ecological processes and ecosystem services (Zhang et al. 2013; Moran et al., 2014; Knapp et al., 2015). Additionally, droughts have been shown to cause simultaneous intensification of disturbance regimes such as herbivory (Teague et al., 2004), and these disturbances will have their own effects on ecosystem function (Brodie et al., 2012). Understanding how drought and disturbance intensification interact to impact ecological processes is critical for predicting future states and functioning of ecosystems (Villnäs et al., 2013).

Semi-arid ecosystems may be particularly susceptible to extreme drought and intensified disturbance events because (1) their sensitivity to water limitation may be stronger than more mesic ecosystems due to well established relationships between aridity and precipitation sensitivity (Huxman et al., 2004; Sala et al.,

* Correspondence: Ashley Tribitt, Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY 82071, USA.
E-mail address: ashleymdupuis7@gmail.com (A. Tribitt).

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2012), and (2) their greater abundance and diversity of herbivores compared with more arid ecosystems (Olff et al., 2002) allow for the possibility of heavy herbivory events. Sagebrush-dominated semi-arid ecosystems make up a substantial proportion of the western United States (Still and Richardson 2015) and provide many important ecosystem services, such as wildlife habitat (Beck et al., 2012), forage for cattle (Mack and Thompson, 1982), and belowground carbon sequestration (Heyden and Stock, 1996). *Artemisia tridentata* ssp. *wyomingensis* (Beetle and Young) (hereafter "sagebrush" and/or "shrub") is a foundational species across vast swaths of the western US that maintains biodiversity (Welch, 2005), provides wildlife habitat (Beck et al., 2012), suppresses invasive species (Lysne, 2005), and limits wind and water erosion (Goff et al., 1993). Effects of drought and disturbance on populations of sagebrush will thus have strong effects on many aspects of these important ecosystems.

One characteristic that makes sagebrush an important species is its resistance – that is, the ability to grow or persist during environmental stress (Pimm, 1984) – to moderate drought (Kolb and Sperry, 1999a). Multiple mechanisms lead to drought resistance of sagebrush including having a two-component root system to prevent xylem cavitation (Kolb and Sperry, 1999b; Lysne, 2005), deeper rooting profiles (Tabler, 1964; Wan et al., 1994), mycorrhizal association (Stahl et al., 1998), and water storage in the taproot and stem (Link et al., 1995). Yet, when drought becomes extreme, many of these drought resistance mechanisms may become less effective due to deeper soil layers drying out (Sperry and Love, 2015), embolisms reducing hydraulic conductance (Kolb and Sperry, 1999b), and depletion of water storage reserves within plant tissues. As such, extreme water limitation events may cause declines in sagebrush growth and production despite its resistance to less severe drought (Loik and Harte, 1997; Kwon et al. 2008).

Herbivory by large and small animals is an important disturbance in sagebrush shrublands, and the impact of herbivory on sagebrush itself depends on the intensity and type of herbivory (i.e., grazing versus browsing). Sagebrush evergreen leaves are nutritious (> crude protein) and contain secondary chemicals (e.g. monoterpenoids, sesquiterpenoids) that may either deter or attract consumers (Welch, 2005). Browsers and mixed-feeding herbivores like pronghorn (*Antilocapra americana* Ord, 1815) and mule deer (*Odocoileus hemionus* Rafinesque, 1817) consume large amounts of sagebrush throughout the year (Welch 2005). Although browsing results in direct removal of photosynthetic biomass, which can lead to reductions in growth rates (Rittenhouse and Sneva, 1977) and a depletion of shrub carbohydrate reserves (Heyden and Stock, 1996), moderate browsing can be beneficial to shrubs by removing dead plant tissue enabling new shoots to establish (Billbrough and Richards, 1993). Sagebrush has developed various adaptations that allow it to survive in conjunction with moderate browsing, including maintenance of carbohydrate reserves in its plant tissues to facilitate regrowth after biomass removal (Sturges and Trlica, 1978). These browsing resistance characteristics likely explain its persistence in areas where browsing is very common (Ngugi et al., 1992). However, when browsing pressure becomes too great, this may lead to plant damage or death. For example, Wambolt (1996) found that when too much new growth is consumed by browsers during the winter, this can result in substantial damage or mortality of sagebrush individuals. In addition to browsers, grazers are common in these landscapes, and may also have important effects on sagebrush persistence.

Large ungulate grazers, such as horse and cattle typically consume sagebrush in only trace amounts (Krysl et al., 1984), although elk will consume sagebrush in fall/winter (Hobbs et al. 1996). Instead, the primary effect of grazers on sagebrush ecosystems during summer months is through consumption of grasses and forbs (Beck and Peek, 2005) and/or trampling effects (Davies et al., 2018). Consumption of grasses and forbs by large ungulate grazers during the growing season may benefit shrubs by removing competition for shallow soil water (Meyer, 1994; Williams et al., 2002; Shaw et al., 2005; Riginos, 2009) as well as creating favorable conditions for future seedling establishment (Davies et al., 2020). Yet although grazing may reduce leaf area of perennial grasses and reduce transpiration losses of water (Bremer et al., 2001), it may also increase evaporative losses due to removal of vegetative cover (Veldhuis et al., 2014). Grazing may also alter water balance through changes in species composition and has been shown to increase abundances of warm season grasses over longer time scales (Augustine et al., 2017; Porensky et al., 2017). Given that effects of herbivory on shrubs depend strongly on factors such as herbivore type and consumption pressure, it is reasonable to expect that interactions with drought may also differ depending on the type and intensity of herbivory.

During severe drought, less forage is produced and performance of herbivores is likely to suffer (Craine et al. 2010; White et al., 2014; Gibson et al., 2017; Bondaruk et al., 2022). With less available forage, grazing and browsing pressure will increase. Direct effects of these co-occurring perturbations (extreme drought + heavy herbivory) may be compounding and lead to greater mortality risk (Souther et al., 2020) as drought depletes carbohydrate reserves, ultimately limiting the ability of shrubs to regrow photosynthetic tissue after herbivory (Wandera et al., 1992). However, co-occurring drought and herbivory effects may also ameliorate one another. For example, heavy grazing during drought may increase drought resistance by reducing grass abundance and thus increasing available water for shrubs (Meyer, 1994; Williams et al., 2002, Shaw et al., 2005). Browsing during drought may also reduce transpiration water losses, which could help shrubs cope with water stress. Better information about how herbivory and drought interact will allow us to predict how these ecosystems will respond to ongoing global change.

Here, we report on a fully factorial field experiment in a sagebrush grassland ecosystem simulating five levels of drought, two levels of grazing, and two levels of browsing to address the overarching question: How will co-occurring perturbations interact to impact the growth and persistence of a dominant shrub? To this end, we tested the following hypotheses:

1. Shrub leader growth and canopy volume will be reduced with greater drought magnitude due to increasing water stress (i.e. more negative leaf water potentials).
2. Heavy browsing will amplify the effect of drought on leader growth and canopy volume due to a lack of regrowth of leaders after browsing events.
3. Heavy grazing will ameliorate the effect of drought treatments on shrub leader growth and canopy volume. We predict this will be due to removal of herbaceous vegetation, which will lead to greater soil moisture in heavily grazed areas.

Methods

Site Description

Our study was conducted on private land near the Thunder Basin National Grassland, 15 miles northeast of Bill, Wyoming. This site is an ecotonal sagebrush steppe-grassland ecosystem classified as the northern rolling high plains, southern part, or Major Land Resource Area 058B through the USDA-NRCS, 2022. The experiment was located across a bench and adjacent slope, with slopes ranging from 6% to 15%. Soils were dominated by the Cushman-Worf complex (Soil Survey Staff, Natural Resources Conservation Service, USDA, 2024). Block 1 had relatively homogenous and sandy surface soils (0–10 cm depth increment; percentage

sand:clay ranged from 53:17 to 80:3). Block 2's soils were mixed with areas of sandy (e.g., 65:14) and loamy soils (e.g., 30:39). Block 3's soils were also mixed but ranged from loamy (e.g., 39:42) to clayey (e.g., 13:61). This region has a mean annual precipitation ranging from 250 to 350 mm per year and elevation ranging from 1,097 to 1,585 m (3,599–5,200 ft). The mean monthly temperature ranges from −5 °C in December to 22 °C in July (Porensky et al., 2018). During 2020, the experimental site received 128 mm annual precipitation. The dominant plant species at the site were *A. tridentata* ssp. *Wyomingensis* Beetle & Young; C_3 perennial graminoids such as *Pascopyrum smithii* (Rydb.) Á. Löve, *Koeleria macrantha* (Ledeb.) Schult., *Carex filifolia* and *Hesperostipa comata* (Trin. & Rupr.) Barkworth; C_4 perennial grasses such as *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths and *Aristida purpurea;* C3 annual grasses such as *Bromus tectorum* and *Bromus arvensis*; the cactus *Opuntia polyacantha* Haw.; and the subshrub *Artemisia frigida* Willd. (Frost et al., 2023). The site has been moderately grazed by cattle (*Bos taurus* Linnaeus, 1758) and sheep (*Ovis aries* Linnaeus, 1758) since 1934. Dominant wild mammal species at the site are pronghorn (*Antilocapra americana* Ord, 1815), mule deer (*Odocoileus hemionus* Rafinesque, 1817), pygmy rabbits (*Brachylagus idahoensis* Merriam, 1891), and elk (*Cervus elaphus* Linnaeus, 1758).

Experimental design

We manipulated grazing, drought, and browsing in a full factorial split-split plot experimental design (2 grazing × 5 drought × 2 browsing treatments), although replication within drought and grazing treatments was unbalanced (see below). There were three experimental blocks in which all experimental treatments were nested. Each block was a 81 m × 61 m area fenced to exclude bovine livestock, but fences did not exclude wildlife.

Each block was split into four quadrants, three of these 'paddocks' were randomly assigned a grazing treatment, and the fourth used to hold water for livestock (this fourth quadrant contained no plots). The sagebrush results reported in this manuscript are part of a 5-year study that simulates three different grazing strategies that change through time during and after drought (Frost et al., 2023). At the time of our sagebrush measurements reported here, two of the paddocks per block had received moderate grazing intensity, and one paddock per block had received heavy grazing intensity, resulting in an unbalanced design for grazing treatments. Areas were grazed by two or three angus heifers kept within experimental paddocks until target treatment residual biomass was achieved, 50% (moderate) and 70% (heavy) utilization based on visual obstruction (robel pole; Robel et al., 1970) measurements taken before and throughout the grazing period. The grazing period extended from June 26 to July 18 in 2019, and these treatment designations were applied to sagebrush measurements taken in 2020. Additional grazing treatments were applied in early July of 2020, but these occurred after we collected most of our measurements during the active sagebrush growing period (McArthur and Welch, 1982). Experimental drought infrastructure was removed during grazing events to ensure livestock had full access to experimental plots.

Within the grazing treatments, five levels of drought were imposed using rain-out shelters with clear polycarbonate strips suspended over the plot from mid-April to mid-October each year, covering 0%, 25%, 50%, 75%, and 99% of the plot area (2 × 2 m). Rain-out shelters were 3.2 × 4.0 m and 1 m tall at the highest point with a double angled roof to prevent rain blow-in during storms with a minimum of a 0.5-m buffer zone around the sampling plot to limit horizontal transfer of water to vegetation within the sampling plot (Yahdjian and Sala, 2002). This design has been shown to have minimal impacts on air temperature and humidity under drought shelters (Yahdjian and Sala, 2002), although there may be up to 10% lower photosynthetically active radiation transmittance under drought shelters (Hoover et al., 2014). One extra set of plots were assigned to the ambient (0%) precipitation plots such that each paddock had 6 plots with one plot randomly assigned to each of the 25%, 50%, 75%, and 99% treatments and two plots randomly assigned to the 0% treatment, resulting in an unbalanced precipitation treatment design.

Finally, within each rain-out shelter or control plot, two established sagebrush individuals were selected and randomly assigned one of two browsing treatment subplots: ambient browsing or heavy browsing. The ambient browsing treatment was exposed to ambient herbivory by native browsers including mule deer, pygmy rabbits, and pronghorn. Personal observations of herbivory by rabbits were made before and during the study. For the heavy browsing treatment, we clipped all new growth from half of the leaders (i.e., stems having new growth) in April 2020. This browsing intensity removal method was chosen to reflect a heavy browsing removal event typical of wildlife in the region (Bilbrough and Richards, 1993; Singer and Renkin, 1995).

This resulted in a total of 108 potentially sampled shrubs, coming from 3 experimental *blocks* * 3 grazing *paddocks* per block (2 moderate, 1 heavy) * 6 precipitation *plots* per paddock (one each of each drought magnitude and two ambient precipitation) * 2 *shrubs* per plot (one ambient, one heavy browsing). However, three plots did not have live sagebrush individuals in them, which removed six total shrubs from the final analysis, resulting in a final N = 102.

Sampling methods

In October 2019, we took one 0–10 cm soil core per plot, and determined soil texture using the hydrometer method (Bouyoucos 1962). Volumetric soil moisture integrated from 0 to 7.6 cm was measured in two random locations in each drought plot twice per month from April-October 2020 using a Field Scout TDR-100 soil moisture probe (Spectrum Technologies, Inc 2009).

To estimate leader growth of sagebrush individuals, in April 2020 we fitted each sagebrush with six different colored zip-ties randomly assigned to 5–10 cm long leaders that were not exposed to experimental browsing. Then in April and October 2020, we measured from the top of the zip-tie to the end of the furthest live leaf, to the nearest millimeter. Leader growth was calculated as the difference between October and April length measurements (Connell et al., 2018). Leaders that died were analyzed separately. We note that our estimates of leader growth do not capture growth occurring before natural herbivory of leaders. Leader mortality was also estimated for each shrub as the proportion of the six tagged leaders that died between April and October.

We used measurements of canopy height, width, and length to estimate the canopy volume of each shrub in April and June in 2020. Height was the measurement from the ground to the topmost live leaf. Canopy length and width of each shrub was measured by orienting north to south and west to east of the plot, respectively, and assessing the distance between the furthest tips of left-most and right-most live leaves. Canopy volume (V) was calculated as the elliptical area multiplied by canopy height following Rittenhouse and Sneva (1977) and Mack (1977): $V = (\frac{\pi \cdot L \cdot W}{4})H$, where L, W, and H are canopy length, width, and height measurements, respectively. Canopy volume differences were calculated by subtracting June from April canopy volume measurements for each shrub.

To assess water availability at the root-soil interface and plant water stress during the drought, we measured predawn and midday leaf water potential for sagebrush individuals in June for a subset of the plots (N = 30). We chose this time point because this was at peak growth (McArthur and Welch, 1982) and the drought treatments were in full effect. All sagebrush individuals

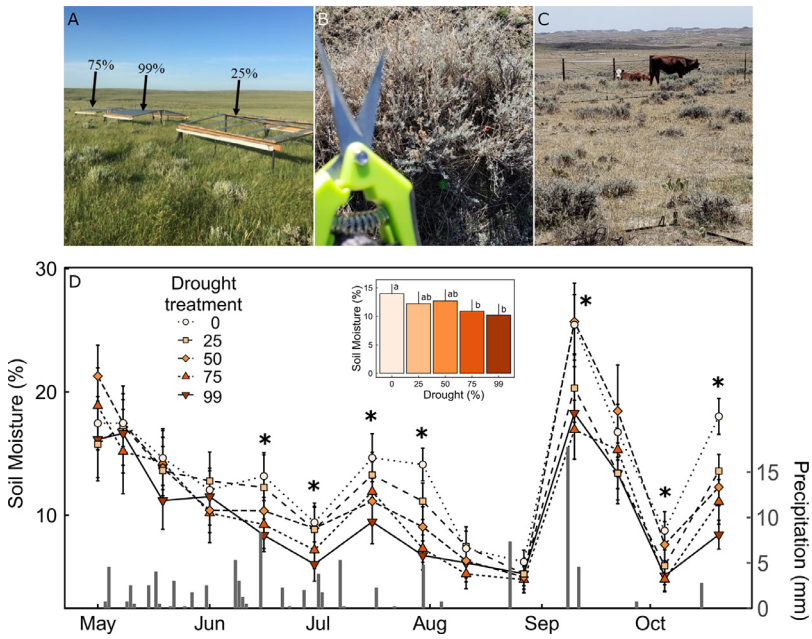

Figure 1. Photos of (A) drought, (B) browsing, and (C) grazing simulation approaches. (D) Daily precipitation and biweekly volumetric soil moisture measurements integrated from 0 to 10 cm in the soil within drought treatments throughout the growing season of 2020. Asterisks represent significant drought effects at specific time points. Inset: Average soil moisture across the growing season. Different letters represent significant differences based on Tukey-adjusted comparisons.

were sampled within one block. The exceptions to this were (1) one of the 99% drought plots within the chosen block was missing a sagebrush individual so one sagebrush individual in a corresponding 99% drought plot in the second block was measured, and (2) we randomly selected one of the two ambient precipitation plots per paddock to include in these measurements. The water status measurements of each of these sagebrush individuals were taken at the same time (2:00–4:00 predawn and 12:00–14:00 midday) to ensure similar environmental conditions across all individuals.

We carried out each water potential measurement by harvesting a single 8–10 cm live leader that was not exposed to experimental browsing. Each cutting was placed in a labeled airtight bag with a damp paper towel. Leaf water potential was assayed with a PMS pressure chamber (PMS Instrument Company, 2019) following routine methods.

Statistical analyses

Main effects of drought, grazing, and browsing treatments, as well as interactive effects drought*grazing and drought*browsing on leader growth, leader mortality, and canopy volume change were assessed using a mixed-effects analysis of covariance (ANCOVA) using Satterthwaite denominator degrees of freedom. Drought was treated as a continuous fixed effect. Grazing and browsing were treated as categorical fixed effects. To account for the experimental design, models included plot nested within paddock nested within block as random factors. When significant interactions between drought and grazing or browsing were found, data were split by the significant interaction term (browsing or grazing) and the drought effect was assessed separately for each level. Three outliers were removed in the canopy volume change dataset (studentized residuals: −6.1, 5.5, −4.1; Bonferroni adjusted p values: all <0.01). One outlier was removed in the leader mortality dataset (studentized residual: 4.1; Bonferroni adjusted P-value<0.01). Results from models run with outliers included were less robust but qualitatively similar to results from models run with outliers excluded.

Effects of drought and grazing on soil moisture throughout the growing season were assessed using repeated measures linear models using a compound symmetry covariance structure. Drought, grazing, and sampling time point were set as main effects. Plot nested within paddock nested within block were set as random effects. We found a significant interaction between time point and drought, so the model was then split by time point to determine time points at which drought effects were significant. To assess differences between season-long drought treatments, Tukey-adjusted multiple comparisons of least squared means were conducted.

To motivate comparisons of shallow versus deeper soil water availability as drivers of changes in shrub canopies, we assessed relationships between average June soil moisture from 0 to 10 cm, predawn leaf water potential, and midday leaf water potential and canopy volume difference (June-April) and leader growth using mixed model regressions. Soil moisture, predawn leaf water potential, and midday leaf water potential were set as continuous predictor variables of canopy volume difference and leader growth in separate models. Plot nested within paddock nested within block were set as random factors within each model.

Drought treatment and browsing effects on predawn leaf water potential and midday leaf water potential within a single block were assessed using mixed-model ANCOVAs with drought set as a continuous predictor variable and browsing treatment as a main categorical fixed effect. Plot nested within paddock nested within block were set as random factors. We also checked for effects of soil texture (% sand, % silt, % clay) on predawn and midday leaf water potentials using linear regression.

Data were checked for the assumptions of homogeneity of variance and normality of residuals. Leader mortality proportions were arcsine transformed for analysis to improve normality. Statistical significance was set at $\alpha=0.05$ for all tests, and marginal significance was assigned to $0.05<\alpha<0.1$. All statistical analyses were conducted in R version 4.2.1 (R Core Team 2021), mixed effects models were run using the *lmer* function in the 'lme4' package (Bates et al., 2015), and type 3 ANCOVAs were run using the *anova* function within the 'lmerTest' package (Kuznetsova et al., 2017).

Results

Soil moisture

Soil moisture was low overall during 2020 and varied through time ($F_{13,649}$=97.1, $P < 0.01$; subscripts after F denote numerator, denominator degrees of freedom) in experimental plots, starting relatively moist in the early season and then becoming drier over the course of the growing season. Soil moisture increased again in September due to large rainfall events that occurred at the field site (Fig. 1D). Drought effects on soil moisture varied across the growing season (drought*time $F_{13,649}$=4.0, $P < 0.01$) such that drought effects were strongest during periods of dry-down and less evident during periods of high soil moisture (Fig. 1d). Differences in season-long average soil moisture across drought magnitude were significant ($F_{1,43}$=26.7, $P < 0.01$) with greater drought magnitude resulting in lower soil moisture. Specifically, soil moisture in 75% and 99% drought magnitude treatments were lower than ambient treatment soil moisture ($t = 3.7$ and $t = 4.5$, respectively, both $P < 0.01$). Please note that drought was necessarily converted to a categorical variable for multiple comparisons of means.

Shrub canopy volume and leader growth

Heavily browsed shrubs had a negative change in crown volume from April to June under ambient precipitation (−0.005 m^3 ± 0.002) while ambiently browsed shrubs increased in crown volume (0.006 m^3 ± 0.005, $F_{1,44}$=5.2, $P = 0.03$; Fig. 2A). The overall main effect of drought magnitude on crown volume change was not significant ($F_{1,41}$=1.6, $P = 0.21$), but the effect of drought varied by browsing treatment ($F_{1,44}$=8.1, $P < 0.01$). When drought effects were split by browsing treatment, we found that with ambient browsing, canopy volume decreased as drought intensity increased (Fig. 3A; $F_{1,42}$=11.2, $P < 0.01$). Under heavy browsing, drought magnitude had no effect on canopy volume (Fig. 3B; $F_{1,47}$=0.31, $P = 0.58$). We found no overall effects of grazing on canopy volume change ($F_{1,41}$=0.14, $P = 0.71$) nor a significant drought-by-grazing interaction term ($F_{1,41}$=2.46, $P = 0.12$).

Heavy browsing significantly increased shrub leader mortality from an average of 5% on ambiently browsed shrubs to 10% leader mortality on shrubs that experienced heavy browsing treatments (Fig. 2B, $F_{1,51}$=7.7, $P < 0.01$). There was a weak negative relationship between leader mortality and drought magnitude ($F_{1,49}$=3.5, $P = 0.07$). There were no significant effects of grazing ($F_{1,49}$=0.0005, $P = 0.98$), drought-by-browsing ($F_{1,51}$=2.2, $P = 0.15$), or drought-by-grazing ($F_{1,49}$=0.01, $P = 0.91$) on leader mortality.

For the leaders that lived throughout the growing season, we then assessed leader growth. We found that heavy grazing weakly increased leader growth under ambient precipitation ($F_{1,47}$=2.9, $P = 0.097$). We also found a weak interactive effect between drought and browsing treatment ($F_{1,49}$=3.6, $P = 0.07$) so we then assessed the effect of drought on leader growth separately for ambient and heavy browsed shrubs. We found leader growth increased with drought magnitude in the extreme browsing treatment ($F_{1,41}$=4.2, $P = 0.047$; Fig. 4D) but not in the ambient browsing treatment ($F_{1,48}$=0.0001, $P = 0.99$; Fig. 4C).

To assess whether non-linear threshold responses existed along drought magnitude, we compared AIC values between a model that contained a quadratic parameter to allow for a non-linear relationship between drought magnitude and canopy volume change and a model that did not include a quadratic parameter. The AIC of the linear model was lower (AIC: −414.2) than the non-linear model (AIC: −388.5).

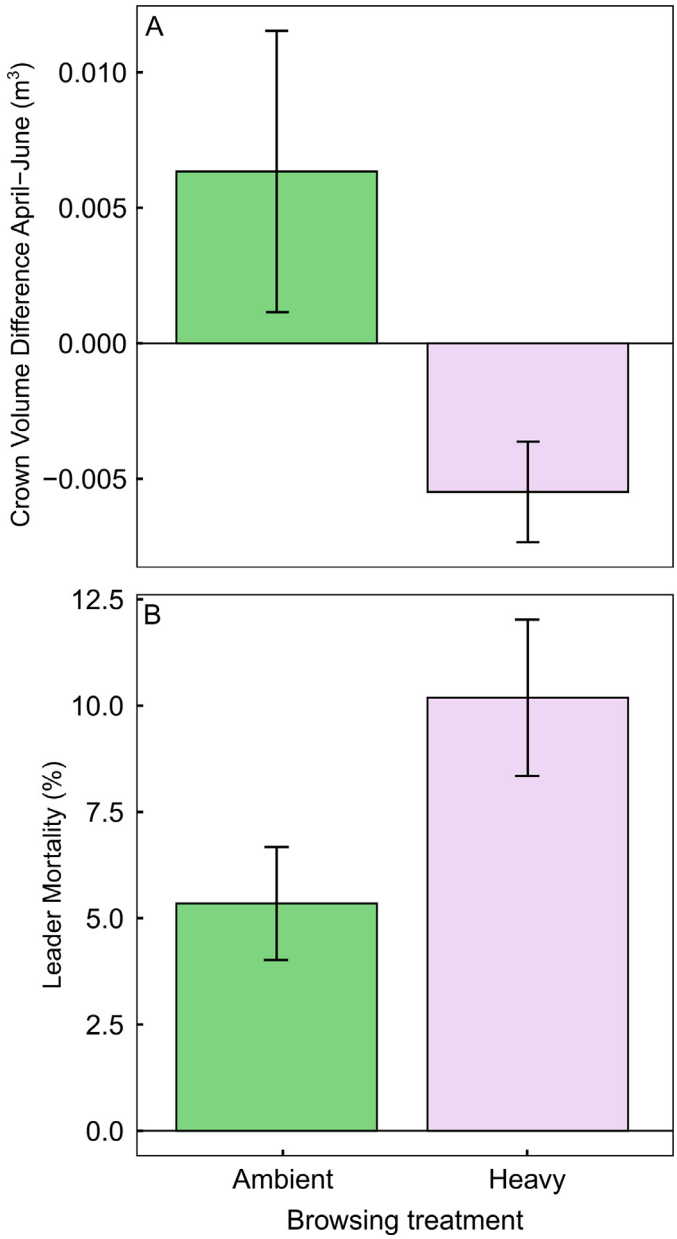

Figure 2. Browsing effects on crown volume change (A) and leader mortality (B). Crown volume change means were calculated from shrubs that did not receive drought due to significant interactions between browsing and drought treatments in the full model. Leader mortality means were calculated from all shrub individuals and represents the percentage of tagged leaders that died throughout the growing season in 2020. Both panels show significant differences between browsing treatments at $\alpha = 0.05$.

Drought and browsing effects on leaf water potential

With ambient precipitation, predawn leaf water potential was more negative under heavy browsing than ambient browsing ($F_{1,13}$=6.1, $P = 0.03$; Fig. 4A). Drought effects on predawn water potential varied slightly across browsing treatments (drought*browsing interaction: $F_{1,13}$=3.7, $P = 0.08$) so models were split by browsing treatment. Predawn water potential under ambient browsing was more negative under greater drought magnitude ($F_{1,13}$=4.2, $P = 0.06$, Fig. 4A), while there was no relationship between predawn water potential and drought magnitude for heavily browsed shrubs ($F_{1,13}$=0.14, $P = 0.72$). Midday leaf water potential measurements were variable both within and

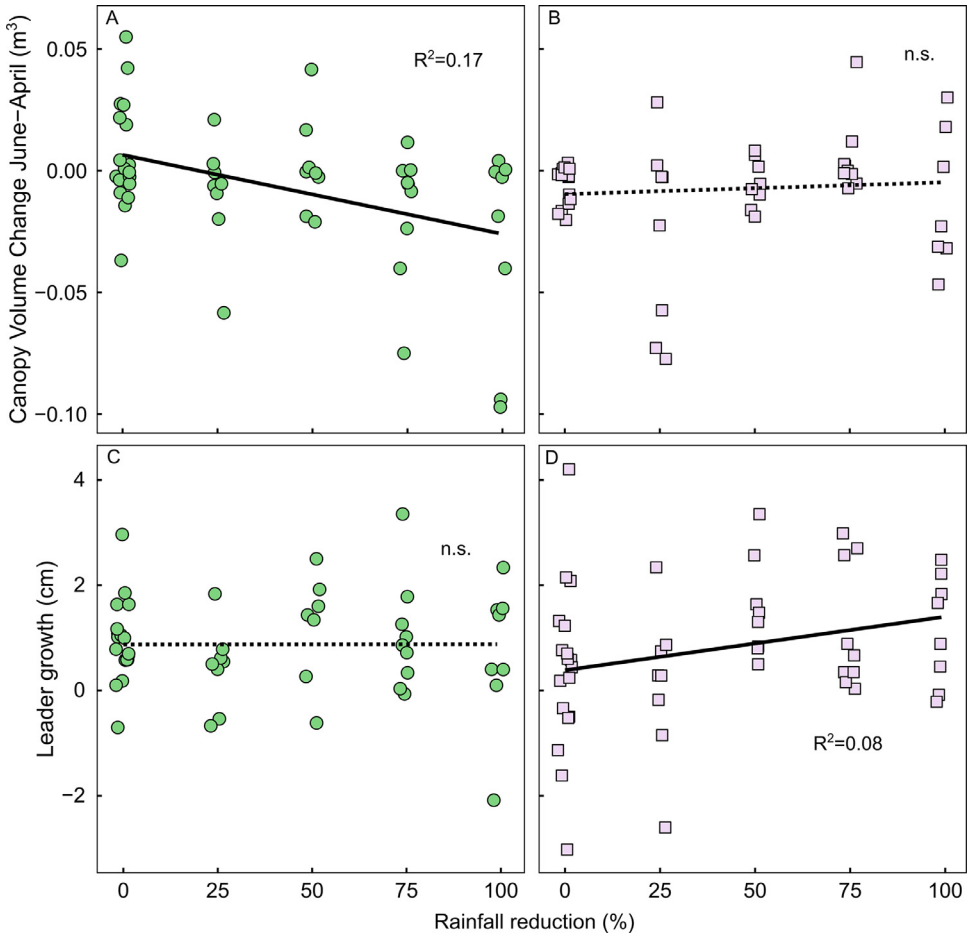

Figure 3. Changes in canopy volumes (A, B) and leader growth (C, D) of *A. tridentata* ssp. *wyomingensis* from April to June in 2020 in response to drought magnitude under ambient (A, C) and heavy browsing (B, D) treatments. Solid trendlines indicate significant regression at $\alpha = 0.05$. Points are jittered on the x-axis for clarity.

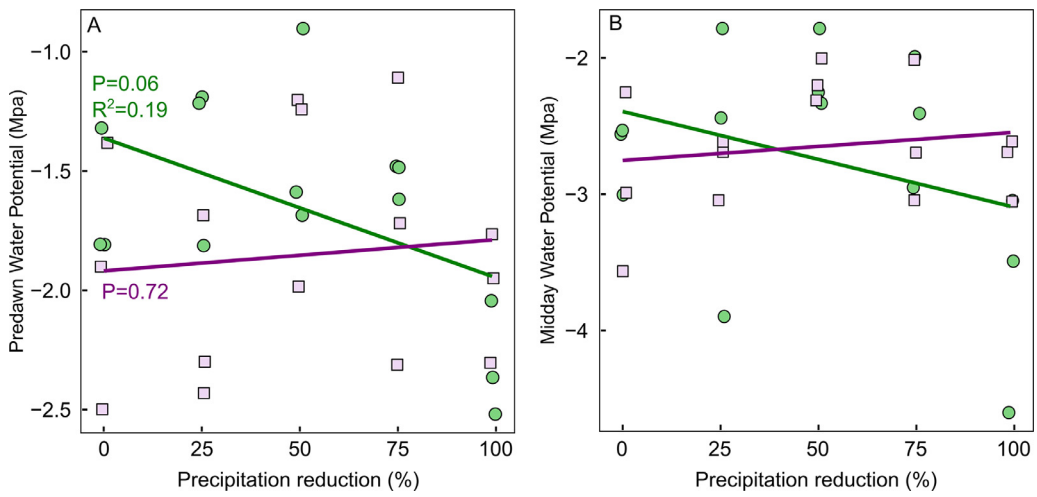

Figure 4. Leaf water potentials pre-dawn (A) and mid-day (B) across different drought magnitudes for ambient browsed (green circles) and heavy browsed (purple squares) shrubs. Points are jittered on the x-axis for clarity.

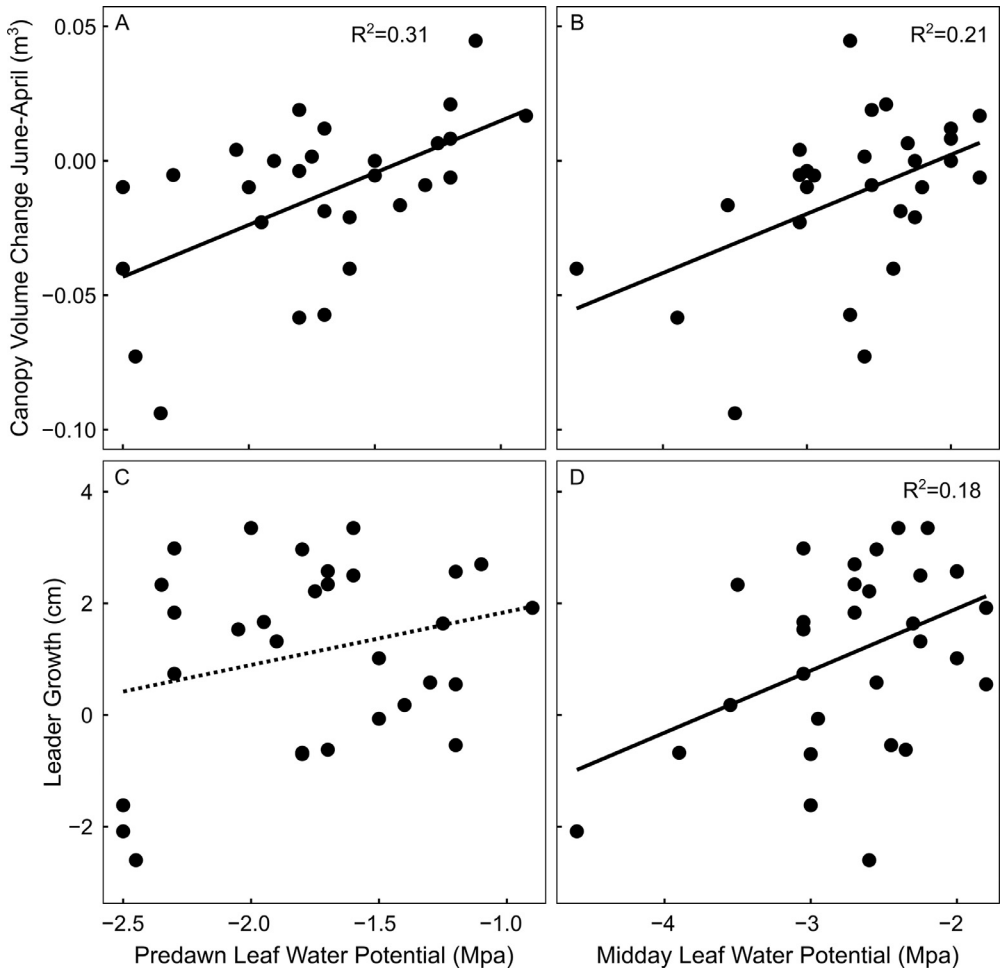

Figure 5. Changes in canopy volumes (A, B) and leader growth (C, D) of *A. tridentata* ssp. *wyomingensis* from April to June in 2020 related with leaf water potential measurements collected before dawn (A, C) or at mid-day (B, D) in June. Solid trend lines indicate significant regression at $\alpha = 0.05$.

across treatments (Fig. 4B), resulting in no significant model effects (Drought: $F_{1,13}=0.41$, $P=0.53$, Browsing: $F_{1,13}=1.3$, $P=0.27$, Drought*Browsing: $F_{1,13}=3.1$, $P=0.10$).

Soil moisture and leaf water potential regressions with canopy volume and leader growth

We found no significant relationship between canopy volume response and June soil moisture ($F_{1,43}=1.33$, $P=0.26$). Conversely, we found that predawn and midday leaf water potential measurements correlated with canopy volume responses (Fig. 5A and B) with more negative water potential values relating to greater declines in sagebrush canopy volumes (predawn: $F_{1,26}=12.2$, $P<0.01$; midday: $F_{1,26}=7.3$, $P=0.01$). Leader growth was not significantly related to soil moisture ($F_{1,49}=0.60$, $P=0.44$) or predawn leaf water potential ($F_{1,28}=1.19$, $P=0.28$; Fig. 5C), but was positively related with midday leaf water potential ($F_{1,28}=6.5$, $P=0.02$; Fig. 5D), such that leaders grew more on shrubs experiencing less water stress.

We also tested whether water potential measurements varied with soil texture and found no significant relationships between percent clay, silt, or sand and predawn water potential (% sand: $F_{1,28}=0.79$, $P=0.38$; % silt: $F_{1,28}=0.01$, $P=0.93$; % clay: $F_{1,28}=1.8$, $P=0.19$). Nor did we find significant relationships between midday water potential values and % sand ($F_{1,28}=2.8$, $P=0.11$ or % silt ($F_{1,28}=0.45$, $P=0.51$). We did find a weak negative relationship between % clay and midday water potential ($F_{1,28}=3.8$, $P=0.06$).

Discussion

Two years of extreme drought caused declines in canopy volume of sagebrush individuals, despite these shrubs having morphological and physiological characteristics that provide drought resistance. These changes in canopy volumes increased with water stress, estimated by leaf water potential measurements. Heavy browsing treatments resulted in greater resistance of sagebrush to extreme drought, possibly due to lesser transpiration water loss and increased leader growth for heavily browsed and droughted shrubs. Ultimately, these results highlight the complex nature of vegetation responses to environmental drivers and the importance of including herbivory, a nearly universal phenomena (The Herbivory Variability Network 2023), in predictions of ecosystem responses to extreme drought.

Sagebrush response to drought

We predicted that shrubs growing in drought treatments would be more water stressed than shrubs in ambient precipitation treatments, and that this would reduce their growth and canopy size. Our findings showed that canopy volumes of sagebrush were negatively affected by drought under ambient browsing, and this effect was linearly related to drought magnitude (Fig. 3). While the negative effect of drought matches our predictions, the linear nature is somewhat surprising based on previous findings of shrub resistance to moderate drought due to plant physiology (Kolb

and Sperry 1999b), mycorrhizal associations (Matzner and Richards 1996; Stahl et al. 1998), and rooting distribution (Tabler 1964; Ryel et al., 2003; Prieto and Ryel, 2014). That is to say, we expected sagebrush responses to mild and moderate drought to be buffered by the above mechanisms, but strong negative responses to emerge as drought magnitude became extreme, thus leading to a non-linear drop off of shrub performance at high drought magnitudes. The linear pattern we observed may be due to the multi-year nature of our experimental drought and the presence of a natural drought in 2020, effectively increasing the severity of our milder drought treatments. By depleting precipitation inputs during the 2019 growing season as well as the 2020 growing season in experimental drought plots, our treatments may have reduced deeper soil moisture into the winter and early spring of 2020, which has been shown to be an important regulator of sagebrush canopy volumes (Germino and Reinhardt, 2014). We only measured soil moisture in the surface soil layer (0-7.5 cm), so we cannot determine whether 2019 treatments had legacy effects on deeper soil moisture. However, more negative leaf water potential measurements under droughted shrubs in June 2020 suggests lower soil water content along the entire rooting profile. In addition to reducing the total amount of precipitation falling in the growing season, our drought simulations also reduced the average size of rainfall events by blocking a proportion of each rainfall event (Knapp et al. 2015), thus aligning with how droughts are likely to occur in the future (Knapp et al. 2015). Smaller event sizes and less precipitation overall reduce the amount of water entering deeper into the soil, which is protected from evaporative loss (Sala et al. 1992; Heisler-White et al. 2008; Porensky et al. 2020). As such, our experimental two-year drought combined with the natural drought in 2020 may have caused these deeper soil layers to dry down, and this process may have caused reductions of sagebrush crown volumes even at lesser precipitation reductions of our drought treatment.

We found that shrub canopy responses were much better predicted by leaf water potential values (Fig. 5) than by shallow soil moisture. We predicted that the leaf water potential of sagebrush will be more negative under greater drought magnitude, resulting in less growth. Two major factors that may alter leaf water potentials are atmospheric water potentials – with more negative atmospheric water potentials causing more rapid water loss from inside the leaf – and water potentials in the soil adjacent to the entire rooting system of the plant. Because atmospheric water potentials should be relatively consistent across individuals in our study, it is likely that soil water potentials surrounding the root network of individual shrubs are responsible for the leaf water potentials we observed in this study. Based on this rationale and the lack of relationship between shrub canopy volume and shallow soil moisture, we suggest that reductions in deeper soil moisture may be more likely to drive sagebrush responses to drought. However, we do note that leaf water potentials were variable and did not always perfectly match our drought gradient (Fig. 4), which alludes to the multifaceted nature of deeper soil moisture with other factors, such as insect and small mammal activity, and competition with shallow rooted species. Small scale differences in soil texture may also be an important determinant of water potential, and we did find a weak negative relationship between soil clay content and midday water potentials.

Despite negative responses of canopy volume to drought under ambient browsing, we found no significant relationship of leader growth with drought under ambient browsing (Fig. 3C), which begs the question: how do shrub volumes retract without reductions in leader growth? We think the answer lies in the fact that 2020 was a dry year overall. During 2020, the experimental site received 128 mm annual precipitation compared with the average from the site between 2018 and 2022 of 283 mm. The average leader growth across all drought treatments was ca. 1 mm, which is below previously observed rates of leader growth of sagebrush (between 5 and 8 cm per year, McArthur and Welch 1982). It may be that the natural drought constrained leader growth across all drought magnitudes and the reduction of canopy volume with extreme drought was due to a lack of new leaders being produced by shrubs. A similar disconnect between leader growth and shrub canopies was observed at Snow Field Station in central Utah, where sagebrush leader growth was increasing after a two-year drought, but canopy volumes declined (McArthur and Welch, 1982).

Interactions between herbivory and drought

We hypothesized that browsing would cause drought effects on shrub canopy volume and leader growth to become more extreme due to reductions in photosynthetically active plant biomass. Indeed, we found that browsing decreased crown volume and increased mortality of leaders overall (Fig. 2), which coincides with findings for a different subspecies of sagebrush, *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle (Bilbrough and Richards, 1993). Yet despite these overall effects of browsing on crown volume and leader mortality, we found that in the presence of heavy browsing, increasing drought severity did not lead to reduced canopy volumes or reduced growth of the surviving leaders (Fig. 3B,D) as we expected. Instead, drought showed no relationship with crown volume in the heavy browsing treatment. We think that reductions in total leaf area caused by the heavy browsing treatment may have reduced water losses via transpiration and prevented depletion of water in the rooting zone (Herkenrath et al. 2024). We find some evidence for this in that midday water potentials of shrubs in the 99% drought treatment that received heavy browsing were less negative (average of −2.8 Mpa) than those that received ambient browsing (−3.7 MPa, Fig. 4B). As leaf water potentials showed linkages with canopy volume changes and leader growth (Fig. 5), we think this ultimately points to browsing as an important potential mechanism for shrub resistance to drought. Yet, substantial uncertainty in these relationships exists (e.g., Fig. 4) and we feel that this mechanism should be explored further in subsequent studies.

Another factor that may partially explain the lack of drought effects on crown volume for heavily browsed shrubs is the small, positive, and seemingly idiosyncratic relationship between leader growth and drought (Fig. 3D). Under ambient precipitation, it may be that increased mortality of leaders on heavily browsed shrubs (Fig. 2B) stimulated growth of new leaders (Bilbrough and Richards, 1993), and these new leaders grew at the expense of existing leaders that we tracked throughout the season. This pattern is somewhat born out through the reduced leader growth observed under ambient rainfall (left side of Fig. 3D). Conversely, in the 99% rainfall reduction treatment, these shrubs had been exposed to a severe drought the previous year, which may have limited any new leader formation in 2020 (Levine and Paige, 2004). In this case, it is possible that the shrubs simply maintained low levels of growth on the existing leaders, even after the browsing treatments. Furthermore, although the relationship between drought magnitude and leader mortality was not significant, heavily browsed shrubs in the 99% rainfall reduction treatment showed zero leader mortality, the lowest mortality rate of all treatments. Whatever the mechanism, it seems as if the combination of heavy browsing and extreme drought results in persistence of sagebrush more so than would be expected based on the effects of either driver alone.

Finally, we hypothesized that heavy grazing would have positive effects on sagebrush performance in the presence of drought due to reduction in grass abundance limiting competition for soil water (Robertson, 1972). We found minimal evidence supporting this hypothesis in that there were no significant grazing effects or graz-

ing interactive effects with drought on sagebrush leader growth or shrub canopy volume, except for a marginally significant positive effect of heavy grazing on leader growth. The overall lack of response may be because our study focused on adult individuals of sagebrush and in soils that allowed for deeper rooting profiles. Previous effects of grazing on sagebrush were shown in studies with shallow soils (Robertson, 1972) or done with seedlings (Williams et al., 2002). The lack of response under heavy grazing may be indicative of the strong niche partitioning present in this system through multi-layered root abundances (Walter, 1939; Ward et al., 2013). Also, it could be indicative of larger rainfall events and spring thaw events percolating to deeper soil depths to be utilized by deeper rooted species (Noy-Meir, 1973), effectively limiting competition effects from grasses. It also may be that the timing and short duration of grazing treatments limited our ability to detect grazing effects on shrubs – early grazing during the primary growth period of cool season grasses and sagebrush may have stronger impacts, as may grazing patterns that extend for multiple years. It would be particularly interesting for future studies to assess how the timing of grazing and browsing interacts with the timing of extreme drought to control sagebrush performance and persistence.

We feel these results are informative for many sagebrush dominated ecosystems across the western US, yet local practitioners should likely consider a number of contingencies when applying these findings to their system. One such consideration revolves around the subspecies of sagebrush dominating the site. There are seven subspecies of *Artemisia tridentata* (NRCS PLANTS, 2024), each having different characteristics and strategies to deal with herbivory and drought. For example, the subspecies we used in this study, ssp. *wyomingensis*, is more drought tolerant than ssp. *vaseyana* and ssp. *tridentata* (Kolb and Sperry, 1999a), so sagebrush systems that have these subspecies may be even more responsive to drought. Another consideration is the type of herbivores present in the ecosystem. Soil texture and vegetation composition at individual sites may alter the effects of drought and herbivory. For example, herbaceous vegetation at our site was dominated by a mixture of warm and cool season grasses, which means that competition for shallow soil water was stronger throughout the growing season. In systems having only cool season grasses, such as those more northward, soil water competition during later summer months may be less. Sites with sandier soils will likely have greater percolation of rainfall to deeper soil layers (Tsoar, 1990), which may buffer sagebrush from even more severe drought. Ultimately, we suggest that drought and herbivory will impact sagebrush populations across the western US, yet site-level characteristics will likely modulate these responses.

Management Implications and Conclusions

When imposed in isolation, two years of extreme drought and heavy browsing both caused negative effects on sagebrush through reduced canopies and increased leader mortality. Yet when these stressors were combined, drought magnitude had no negative effects on heavily browsed shrub canopy volumes or leader growth. As browsing intensity naturally increases during drought events due to limitation of food for native herbivores, we argue this may be a built-in mechanism for drought resistance of sagebrush with intact food webs, and highlights the importance of maintaining functionality across trophic levels despite perceived deleterious effects of herbivores for plant abundance and growth. To promote sustainability of sagebrush and other shrub-dominated ecosystems in the face of extreme drought events, conservation of native herbivores within ecosystems may be an important priority for land managers and policy makers to consider.

Declaration of Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Ashley Tribitt: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Lauren M. Porensky:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Sally E. Koerner:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Kimberly J. Komatsu:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Kurt Reinhart:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Kevin Wilcox:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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