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<https://escholarship.org/uc/item/21805982>

Journal

Plant Ecology, 218(5)

ISSN

1385-0237

Authors

Karban, R
Pezzola, E

Publication Date

2017-05-01

DOI

10.1007/s11258-017-0710-5

Peer reviewed

Effects of a multi-year drought on a drought-adapted shrub, *Artemisia tridentata*

Richard Karban · Enrico Pezzola

Received: 4 November 2016 / Accepted: 3 February 2017 / Published online: 9 February 2017
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Abstract Models of climate change predict more variable precipitation for much of western North America, including more severe multi-year droughts. Droughts are known to increase mortality to trees although less is known about effects on shrubs from arid environments and about effects on reproduction. In this study, we followed a cohort of young sagebrush plants from 2010 to 2016, a period that included a severe drought from 2012 to 2015. Plants experienced little mortality preceding and during the drought. However, in the year following the drought, 14% of individuals died and 33% of branches on living plants died. There was little flowering in the years preceding the drought and flowering increased in each successive year from 2014 to 2016. Plants that produced more flowers in 2015 had more dead branches in 2016. Larger plants had fewer branches that died. Contrary to expectations, afternoon shade was not associated with greater survival or flowering, perhaps because shaded plants were in proximity to large trees which

likely competed for water. Plants of the two common chemotypes had similar rates of survival and flowering. Experimental watering during the summer of 2015 did not affect survival and may have increased flowering in 2016. If multi-year droughts become more common in the future, even drought-adapted shrubs may be expected to suffer high rates of mortality.

Keywords Chemotype · Climate change · Competition · Mortality · Reproduction · Sagebrush · Shade · Water stress

Introduction

Models of future global climates predict that wet areas will get wetter and dry areas drier in coming decades (IPCC 2014). California is predicted to become warmer and to experience more variable precipitation, including longer and more severe droughts (Berg and Hall 2015; Swain et al. 2016). California recently experienced a drought that lasted from December 2012 until December 2015 (longer in some places, although see Fig. 1a for our field site). The severity and duration of this drought were unprecedented over the past 150 years for which weather records have been kept. Analyses of tree rings revealed that this recent drought produced conditions that were likely more extreme than any that trees have faced over the past 1200 years (Griffin and Anchukaitis 2014).

Communicated by William E. Rogers.

R. Karban (✉)
Department of Entomology and Nematology, University
of California, Davis, CA 95616, USA
e-mail: rkarban@ucdavis.edu

E. Pezzola
Department of Agri-Food and Environmental Science,
University of Florence, Viale delle Idee, 30,
I-50019 Sesto Fiorentino, FI, Italy

Fig. 1 **a** Precipitation accumulation for each season at our study site from 2009 to 2016. The horizontal line indicates the mean annual accumulation from 1953 to 2007. The $se = 47$ mm with a range from 378 to 1682 mm over this time span. **b** The cumulative survival of marked sagebrush plants during summer surveys. **c** Production of new inflorescences from 2013 to 2016. Bars indicate means ± 1 se number of inflorescences per plant. Few inflorescences were produced during 2010–2012 although they were not counted

The effects of drought on tree mortality have been noted for decades and are relatively well studied (Hursh and Haasis 1931; Condit et al. 1995; McDowell et al. 2008; Allen et al. 2010). Trees undergoing drought conditions die because of hydraulic failure or because they shut down to avoid hydraulic failure and, as a result, fail to produce sufficient photosynthate and energy (McDowell et al. 2008). These factors weaken the ability of trees to resist pathogens and insects,

which are often the proximate causes of death. We know less about the consequences of drought on shrubs from arid environments than we do about trees although there are some suggestions that shrubs and other plants adapted to desert conditions can also suffer high rates of mortality associated with drought (Condit et al. 1995; Hunt 2010; Esque et al. 2015). We know far less about effects of drought on plant reproduction than on mortality (Orsenigo et al. 2014; Schlaepfer et al. 2014).

In this study, we followed a cohort of sagebrush individuals (*Artemisia tridentata* ssp. *vaseyana* [Rydb.] Beetle [Asteraceae]) from 2010 through 2016. *Artemisia tridentata* is the most common, and the defining, species of the Great Basin biome in western North America. It comprises over 90% of the plant biomass at some sites, particularly those grazed by livestock (Pickford 1932; Young et al. 1988). Sagebrush is a foundational species that provides habitat and food for many associated plants, arthropods, and vertebrates, some of which are of conservation concern (Rowland et al. 2006; Sanford and Huntly 2010). Sagebrush is well adapted to dry conditions. For example, sagebrush roots continue to take up nutrients after the upper layers have dried out, perhaps because of “hydraulic lift” from soil, many meters below the surface (Richards and Caldwell 1987; Matzner and Richards 1996).

At our study site, most precipitation comes during the winter as snow and patchily as rain during summer monsoons. As such, water is most available to plants at snowmelt in late spring. Snowmelt is associated with production of new leaves and most shoot growth. However, flowering and seed formation occur late in the summer, typically after many months of relatively dry conditions.

Local precipitation accumulations that preceded the growing seasons of 2012, 2013, 2014, and 2015 were considerably lower than the mean annual accumulations from 1953 to 2007 (Fig. 1a). However, the precipitation accumulation was close to normal preceding the 2016 growing season. The low precipitation accumulations during this drought were exacerbated by record high temperatures which placed additional stress on plants (Diffenbaugh et al. 2015; Mann and Gleick 2015).

Sagebrush plants emit relatively large quantities of volatile terpenes, and these emissions increase following mechanical damage or herbivory (Kessler et al.

2006). Sagebrush individuals at this study site, and elsewhere, group into one of two common ‘chemotypes’ that produce distinct volatile profiles (Karban et al. 2014). Some plants produce large quantities of thujone and others produce large quantities of camphor. The chemotypes are morphologically indistinguishable, and the ecological significance of this variation is unknown (Karban et al. 2016). We hypothesized that plants of the two chemotypes might have different responses to drought.

In this study, we documented the mortality to sagebrush individuals and to branches on those individuals, as well as the production of inflorescences. We hypothesized that plant and branch mortality were related to unusually hot and dry conditions. Neighboring trees were expected to ameliorate harsh conditions but larger and closer trees were also predicted to compete more strongly with any focal sagebrush plant. We determined the chemotype of each individual and characterized its competitive environment to evaluate whether either of these factors was correlated with our measures of mortality and reproduction. Finally, we provided some of the plants with additional water during the summer of 2015 and compared their performance with unwatered controls.

Methods

Plant and branch demography

Our study site was located in Taylor Meadow at the UC Sagehen Reserve north of Truckee, CA, USA (39° 26.7N, 120°14.7W). During the summer of 2010, we selected and marked 100 young sagebrush plants. We were unable to determine plant age although plants were relatively similar in size (mean height $\pm$ 1, s.e. = 37.3 ± 0.8 cm). All plants were actively growing at the start of our study and had no or few dead branches and no inflorescences. During August of each year (2010–2016), we recorded whether each plant was alive. We counted the number of inflorescences that each plant produced during the summers of 2014, 2015, and 2016. During the summer of 2016, we observed for the first time that many branches had died; we quantified this phenomenon by counting the number of living branches and the total number of living plus dead branches. We compared the

relationships between flowering in 2015 and 2016 and branch survival using least squares regression models in JMP Pro 12.0 (SAS Institute, Cary, NC, USA).

Factors correlated to mortality

Temperature and precipitation were recorded within 1 km of our field site (Sagehen Creek, www.wrcc.dri.edu). Theory predicts that under extreme abiotic stress, neighboring heterospecific plants can ameliorate the effects of those conditions (Bertness and Callaway 1994; He et al. 2013). Some of our marked plants received afternoon shade from pine trees (*Pinus jeffreyi* and *P. contorta*) at the edge of the meadow. Specifically, we hypothesized that individuals that were shaded during the hot afternoon hours would experience less water stress and would be more likely to survive the drought compared to individuals that were growing out in the open and received no afternoon shade. We quantified shading by recording whether plants were in full sun at 15:00 and 17:00 during late July. Plants that were shaded at both of these times received a shading score of two, those shaded at one time received a score of one, and those in full sun at both times a score of 0. This index of shading was used as the independent variable in a least squares linear model (JMP 12.0) of the proportion of branches that survived to 2016.

We estimated a competitive index by identifying the closest heterospecific woody plant for each of our marked sagebrush individuals (following the logic in Pielou 1962). Our index of competition for each sagebrush was the diameter at breast height (dbh) of the nearest tree/distance to that tree. When a sagebrush individual had more than one close neighbor, we recorded the maximum value of neighbor dbh/distance.

We determined the chemotype of each individual by collecting headspace volatiles from each plant and analyzing those volatiles by GC–MS. The details of this method are described elsewhere (Karban et al. 2016).

Our ability to analyze mortality of individual sagebrush plants (compared to branches) was more limited both by a small sample size of plants that died ($n = 15$) and by the binary response variable. We compared survival of individuals with sun exposure and with an index of competition using non-

parametric Wilcoxon tests. We compared the survival of individuals of the two common chemotypes using Chi-square contingency analysis.

Watering experiment

We provided additional water to 29 plants four times during the summer of 2015 (once every two weeks from 27 June to 12 August). During each of these watering events, we poured 5 l of water at the base of each plant. The remaining 69 control plants received no additional water over this time period. We compared survival of watered and unwatered control individuals using χ^2 contingency analysis. We evaluated the effects of our watering treatment on the survival of branches and number of inflorescences produced in 2016 for each plant using a least squares linear model (JMP 12.0).

Results

Plant and branch demography

The marking tape that identified one of our marked plants was lost almost immediately in 2010, reducing our sample size to 99 individuals. One plant died during the summer of 2013, but otherwise, there was little mortality of branches and no mortality to individual plants through the summer of 2015 (Fig. 1b). Between the summers of 2015 and 2016, 14 marked plants died and most individuals that survived had many dead branches (mean proportion of living branches ± 1 se = 0.67 ± 0.03 , $n = 84$ living plants). In each of the summers between 2010 and 2013, a few plants produced a few inflorescences, and these were not recorded. Flowering increased in the summers 2014–2016 (Fig. 1c).

Plants that produced more flowers in 2015 had lower branch survival by the following summer (Fig. 2a, slope = -0.014 ± 0.003 se, $t = 4.71$, $P < 0.001$). Plants that produced more flowers in 2016 had higher branch survival than those producing fewer flowers that year (Fig. 2b, slope = 0.009 ± 0.002 se, $t = 4.96$, $P < 0.001$). Larger plants that had more branches at the start of the study kept a larger proportion of branches alive through the drought (data not shown, slope = 0.005 ± 0.002 se, $t = 2.34$, $P = 0.02$).

Fig. 2 Relationships between the proportion of branches that were alive in 2016 and the number of inflorescences produced in 2015 (*top*) and 2016 (*bottom*). Regression lines indicate significant best fit models

Factors correlated to mortality

Shade during summer afternoons was not significantly related to survival of branches (the relationship between the index of shade and branch survival was negative but not significant [$F_{1,96} = 1.19$, $P = 0.24$]). The relationship between shade and branch survival was similar for the common chemotypes (data not shown). Shade was not associated with increased flowering (data not shown). Plants that received afternoon shade also experienced a higher index of competition from neighboring woody plants ($F_{1,97} = 3.97$, $P = 0.05$).

Sun exposure was not associated with mortality of sagebrush individuals (Wilcoxon test, $\chi^2 = 0.20$, $df = 1$, $P = 0.66$). Sagebrush individuals that died had a higher index of competition from neighboring woody plants than those that survived (Fig. 3, Wilcoxon test, $\chi^2 = 5.18$, $df = 1$, $P = 0.02$). Rates of

survival were similar for plants of the two common phenotypes (Camphor chemotype: 25/29 survived; Thujone chemotype: 57/65 survived, $\chi^2 = 0.04$, $df = 1$, $P = 0.84$).

Watering experiment

Plants that were watered during the summer of 2015 were no less likely to die by 2016 than unwatered controls (4/29 watered plants died compared to 10/70 controls, $\chi^2 = 0.004$, $df = 1$, $P = 0.95$). Watering had no discernable effect on survival of branches either (Fig. 4a, $F_{1,97} = 1.51$, $P = 0.22$). Plants that received additional water during the summer of 2015 produced 57% more inflorescences in 2016 than controls, a difference that was marginally significant with our sample size (Fig. 4b, $F_{1,97} = 1.84$, $P = 0.07$).

Discussion

Climate change is predicted to cause increasing aridification, particularly in areas that are already dry such as the Great Basin (Diffenbaugh et al. 2015; Swain et al. 2016). It has become critically important to be able to understand how drought affects plants that grow in these areas and to predict the many consequences that droughts are likely to impart. Soil water availability is considered to be a key limiting resource for sagebrush (Schlaepfer et al. 2014) and for many other plants that grow in arid and semi-arid

Fig. 3 The competitive index associated with sagebrush plants that either survived or died in 2016. The competitive index is the dbh (cm) of the nearest woody plant/distance between the focal sagebrush plant and its neighbor (m)

Fig. 4 Performance of sagebrush plants in 2016 that were given additional water during the summer of 2015. Bars indicate means ± 1 se. **a** The proportion of branches that survived. **b** The number of inflorescences produced

environments (Noy-Meir 1973). Soil water is likely to become even less available for sagebrush in the future (Palmquist et al. 2016).

Sagebrush is considered to be well adapted to withstand arid conditions and droughts (Schlaepfer et al. 2014). It develops a dominant tap root and is able to access water at considerable depths (Campbell and Harris 1977). Adult plants have generally been thought to be resilient to most droughts (Schlaepfer et al. 2014). In keeping with this expectation, we observed little mortality of sagebrush individuals during the summers characterized by drought conditions. However, in the year following the drought, when water accumulation returned to normal levels, 14% of plants died (Fig. 1). This delayed mortality by a drought-adapted shrub is not unprecedented in the literature. Hanson et al. (1982) reported extensive foliage die-off in sagebrush following an unusually dry winter. Venturas et al. (2016) found rates of mortality of chaparral shrubs that ranged from 0 to 93% in 2014 at one site in southern California in response to this same severe drought. Generally, larger

plants and those with deeper roots were more likely to survive. Harper (1977:588) observed that mortality of *Plantago* spp. was negligible during midsummer periods of drought but became apparent when growth resumed at the end of the season. Similarly, mortality associated with water stress in trees often occurred in the year following the drought (Allen et al. 2010). At a larger scale, global models of responses of vegetation to variation in precipitation were improved by including time lags (Wu et al. 2015).

We observed little flowering during the years preceding the drought in our study presumably because the plants did not yet have sufficient resources. Flowering increased during the last of the drought years and was even greater in 2016, the first year of above average precipitation (Fig. 1c). Heavy flowering in 2015 was associated with greater branch mortality in 2016 (Fig. 2 top). Those plants that had more branches that died in 2016 had produced more flowers in 2015 than those plants that fared better in terms of surviving branches. The phenomenon of a heavy burst of flowering prior to death has been observed often (e.g., Harper 1977:656, 699; Boot et al. 1986). This relationship between branch mortality and flowering was no longer found during the year following the drought. In 2016, a less stressful year with more available water, the relationship between branch survival and flowering was positive (Fig. 2 bottom).

We found that larger individuals with more branches were able to keep a higher proportion of branches alive during this recent multi-year drought. Smaller individuals have been found to be more vulnerable to mortality in other droughts, presumably because they have smaller, shallower root systems (Campbell and Harris 1977). Individual trees that died in years following droughts grew less before the droughts than individuals that survived (Bigler et al. 2007). Interspecific comparisons of mortality of other species during this and other droughts support the hypothesis that deep-rooted plants are better able to survive dry conditions (West et al. 2012; Venturas et al. 2016).

We expected that plants that received afternoon shade would experience lower rates of mortality caused by the drought and have a lower proportion of dead branches than plants in full sun (Bertness and Callaway 1994; He et al. 2013). We failed to find evidence supporting either of these hypotheses. Most of the shade at our study site was associated with large pine trees, and rather than ameliorating soil–water

relations, these trees may have been more intense competitors for water and other resources. Plants that died in our study were associated with a higher competitive index (Fig. 3). Plants in the sun may have had more resources to allow them to withstand the drought. Sagebrush survives extremely dry periods by closing its stomata and reducing evaporative losses (Evans and Black 1993), although this strategy may result in carbon starvation (McDowell et al. 2008).

We also expected that providing additional water in summer would allow plants to extend the brief season during which vegetative growth occurs (DePuit and Caldwell 1973; Evans and Black 1993) and to experience less branch mortality (Campbell and Harris 1977). However, watering in the summer of 2015 failed to affect survival of individuals or branches (Fig. 4a). Watered plants may have produced more inflorescences in the following year although our results were not statistically significant and therefore ambiguous (Fig. 4b). Other experiments that supplemented water to young sagebrush plants also failed to improve their overall or branch survival (Evans and Black 1993; DiCristina and Germino 2006).

Models of climate change predict that we are likely to experience more variable precipitation in the coming decades, including more multi-year droughts such as the one that California recently underwent (Diffenbaugh et al. 2015; Swain et al. 2016). It is important to understand how these droughts affect the foundational plant species at both physiological and demographic levels. Sagebrush is a relatively drought-adapted species (Evans and Black 1993; Matzner and Richards 1996). Nonetheless, it experienced considerable mortality of branches and individuals, particularly during the first year of normal precipitation.

Acknowledgements This study was conducted at UC Sagehen Field Station in Tahoe National Forest, and we thank Jeff Brown and Faerthan Felix for facilitating our work there. James Blande conducted the volatile analyses that allowed us to characterize the chemotypes, Mikaela Huntzinger helped with fieldwork, and Louie Yang lent us equipment. This paper was improved by William Rogers and two anonymous reviewers. We were supported by USDA regional project NC-7 and a fellowship from the University of Florence.

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