Hierarchical responses to drought and drought recovery in two sagebrush steppe plant communities

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INTRODUCTION

- The hierarchical-response framework suggests that ecological changes caused by chronic resource alterations begin at an individual level, leading to species reorganization within the community, ending in species loss or immigration (1).
- Responses to drought will vary depending on plant community, even when exposed to similar drought conditions.
- Functional group of dominant species within an ecosystem will also determine rate of response to drought within different hierarchical levels (2).
- It remains difficult to predict how plant communities will respond to prolonged drought, especially in shrub dominated drylands, where precipitation is low and variable (3).

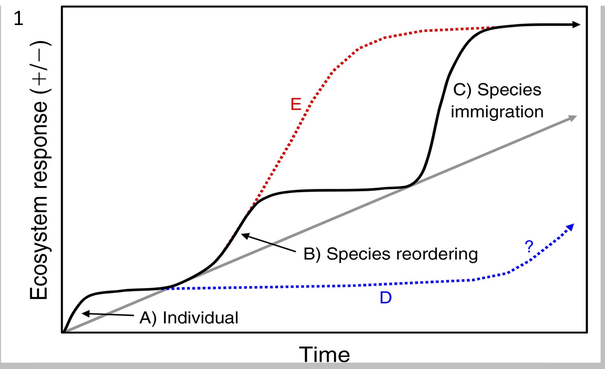


Figure 1. The hierarchical-response framework conceptualized by Smith et al. (1). The framework suggests that ecosystem responses are typically driven by (A) rapid changes on the individual level (physiological/metabolic/mortality), with larger shifts translating to (B) species reordering with traits that favor the altered conditions. This culminates with the largest ecosystem response change with (C) new species that are better adapted to the new resources immigrating into the system. (D) In ecosystems where long living species are dominant, responses aren't likely to occur until a large disturbance/community mortality occurs. (E) Ecosystems that are vulnerable to invasion (exotic species) or widespread mortality are likely to have species reorganization and immigration occur within a short period of time.

RESEARCH OBJECTIVES

Our study aimed to address how two plant community components – aboveground and seed bank species composition – respond to extended drought and drought recovery within the sagebrush steppe. Specifically, we asked:

- How does aboveground species composition change during the first year of drought recovery (**R1**) compared to the third and fourth year of drought (**D3** & **D4**)?
- Does seed bank species composition change during the third year of drought (**D3**) and the first year of recovery (**R1**)?
- Does similarity of aboveground and seed bank species composition increase between and among control and drought plots during the first year of recovery (**R1**) when compared to the third year of drought (**D3**)?

METHODS

- We had two study sites in Southern Oregon, east of the Gerber Reservoir, with different dominant sagebrush species per site.
- **Drought (D):** July 2016 – Oct 2020. Rainfall shelters (n=5) passively excluded ~41% of ambient precipitation.
- **Drought Recovery (R):** Oct 2020 – Oct 2022. Rainfalls shelters removed, all plots receiving ambient precipitation.

Data Collection

- **Aboveground species composition:** We collected data using ocular estimation of plant cover each July from 2016 – 2022.
- **Seed bank species composition:** We collected soil seed bank cores from beneath sagebrush individuals and in the interspace during the third year of drought (2019, **D3**) and first year of recovery (2021, **R1**).

Data Analysis

- We assessed changes in aboveground and seed bank species composition by using nonmetric multidimensional analyses and used PERMANOVAs with distance matrices to find significant pairwise differences in between treatments and years.
- We used the Bray-Curtis similarity index to determine similarity between and among drought and control plots and then ran Wilcoxon rank sum tests to test for significant changes.

Fig. 2. Study site in southern Oregon (yellow star; Fig. 2a), and layout of control (blue circles) and drought (red circles) plots across both sites (Fig. 2b). The *Artemisia arbuscula* (AA) site (Fig. 2c) is characterized by bare ground and rock within the interspace, and the *Artemisia cana* (AC) site (Fig. 2d). Drought shelters were 3.0 m x 3.0 m over 4 m^2 sampling plots and passively excluded ~41% of precipitation**.** Soil seed bank cores spread over soil during comparative germination study (Fig. 2e) and plants that emerged (Fig. 2f).

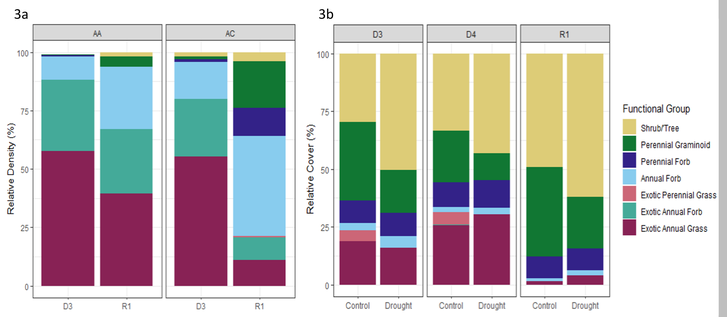
RESULTS

- Exotic annual grass decreased in relative seed density and relative plant cover during **R1** at the AC site (Fig. 3a & 3b).
- Seed bank species composition shifted away from exotic annual forbs and grasses towards native forbs and graminoids during **R1** at AC site (Fig. 4).
- Similarity in seedling emergence between and control and drought plots decreased from **D3** to **R1** at both sites (Fig. 5).
- Density of total germinated seeds decreased by ~%70 from **D3** to **R1** at both sites, with the AA site going from 341 to 83 and the AC site from 501 to 154 individual seedlings.

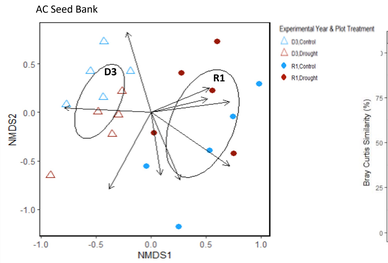
Table 1. Aboveground and seed bank community component responses during Drought (**D3** & **D4**) and Drought Recovery (**R1**) at both sites. ↓/↑ represent significant directional responses while Δ represents significant nondirectional response. (!) Significance found through Hedge's G effect size and boot strapped confidence intervals that did not overlap with zero (4). (***) = p-value <0.001, (**) = p-value <0.01, (*) = p-value<0.05. — represents no significance.

Drought Response	Species Diversity	Species Richness	Species Composition
AA Aboveground	—	—	—
AA Seed bank	↓ (!)	—	Δ (*)
AC Aboveground	—	—	—
AC Seed bank	—	—	—

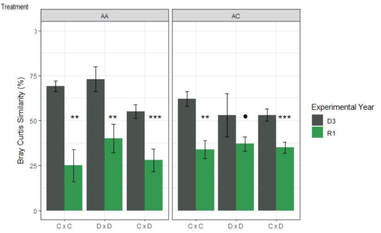
Drought Recovery Response	Species Diversity	Species Richness	Species Composition	Bray-Curtis Similarity
AA Aboveground	—	—	—	—
AA Seed bank	—	—	—	↓ Control x Control (**) ↓ Drought x Drought (**) ↓ Control x Drought (***)
AC Aboveground	—	—	Δ**R1** to **D3** (*) Δ**R1** to **D4** (**)	—
AC Seed bank	—	—	Δ**R1** to **D3** (*)	↓ Control x Control (**) ↓ Control x Drought (***)



(Fig. 3a) Relative seed density within the seed bank during **D3** compared to **R1** at both sites. (Fig. 3b) Relative cover of aboveground plant cover at the AC site during **D3**, **D4**, and **R1**. Functional groups are stacked in the same order for in each bar for both panels.



(Fig. 4). NMDS ordination plot (95% confidence ellipses) of seed bank species composition differences between **D3** (left ellipses) and **R1** (right ellipses) at the AC site. The arrows point in direction of taxa creating significant year differences in seed bank species composition (p<0.05).



(Fig. 5) Mean similarity within the seed bank during **D3** (grey bars) and **R1** (green bars) at each site. C x C (control by control), D x D (drought by drought) represents mean similarity among plots, while C x D (control by drought) represents average similarity between treatments. Asterisks above **R1** denote significant differences in similarity when compared **D3** (*** = p-value <0.001, ** = p-value <0.01). Closed circle represents a p-value of <0.06.

DISCUSSION

- Changes in species composition during drought and recovery occurred within non-dominant plant functional groups, thus not creating changes in fundamental community structure, as explained by the hierarchical response framework (1,5).
- Likewise, the large reduction in seed density also points towards a physiological change occurring on an individual scale. However, it's likely that drought would have to persist for an extended period before community level changes occur within the sagebrush steppe (Fig. 1).
- The sagebrush steppe is adapted to be resistant to drought, but the impacts of climate change often impact more than one resource in an ecosystem. Further alterations of other resources within this system may induce changes that travel up the hierarchical levels (6).

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References