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## Original Research

Seedling Defoliation and Drought Stress: Variation in Intensity and Frequency Affect Performance and Survival<sup>☆</sup>Elsie M. Denton<sup>a,\*</sup>, Brenda S. Smith<sup>b</sup>, Erik P. Hamerlynck<sup>c</sup>, Roger L. Sheley<sup>c</sup><sup>a</sup> Range Technician, US Department of Agriculture (USDA) –Agricultural Research Service (ARS), Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA<sup>b</sup> Executive Director, High Desert Partnership, Burns, OR 97720, USA.<sup>c</sup> Research Ecologist, US Department of Agriculture (USDA) –Agricultural Research Service (ARS), Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA

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## ABSTRACT

Our ability to restore rangelands is limited, and it is unknown if seedling herbivory on its own, or in interaction with other stressors, is a major contributor to restoration failure. To address this, we conducted two experiments: a No Defoliation (ND) experiment ( $n = 48$ ), in which seedlings from three perennial grasses (crested wheatgrass [*Agropyron cristatum* {(L.) Gaertn.}], bluebunch wheatgrass [*Psuedoroegneria spicata* {Pursh} Á. Love], Sandberg bluegrass [*Poa secunda* J Presl]) were subjected to wet and dry water regimes for 4 mo, and a concurrent Defoliation (D) experiment ( $n = 95$ ), in which seedlings were factorially assigned to two defoliation treatments—frequency (LOW, HIGH) and intensity (30% vegetation removal, 70% vegetation removal). Indicators of seedling performance were aboveground and belowground biomass (AGB and BGB), root:shoot ratio, tillering, and mortality. The effect size statistic, Hedge's  $g$ , allowed for comparisons between performance measures. Water stress induced reductions in most performance measures: BGB ( $g = \text{ND}: -1.3; \text{D}: -1.6$ ), root:shoot ratio ( $g = \text{ND}: \text{n.s.}; \text{D}: -0.2$ ), and tillering ( $g = \text{ND}: -1.7; \text{D}: -1.2$ ), though not significantly for all species. For AGB, water stress interacted with defoliation, reducing performance less at an intensity of 70% ( $g = -2.0$ ) as opposed to 30% ( $g = -3.0$ ), but not always significantly in the former. Water stress also caused less reduction in AGB when no defoliation occurred ( $\text{ND}: -0.8; g = \text{D}: -2.5$ ). Intensity and frequency of defoliation interacted; seedlings were generally resistant to reductions in performance except at high frequency, 70% defoliation. *Agropyron cristatum* and *P. spicata* displayed similar sensitivity to treatments, mostly in terms of changes in AGB and BGB, while *P. secunda* also experienced increased mortality and reduced tillering. If these differences in sensitivity result in differential survival, herbivory could impact species postrestoration population demographics.

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## Introduction

Rangelands are extensive and diverse ecosystems covering around 40% of the world's land area (White et al., 2000). Like many ecosystems on earth, rangelands are threatened. Upper estimates indicate that 20% of these regions are already degraded (Adeel et al., 2005). While net zero land degradation is one of the Millennium Development Goals, unsuccessful restoration projects are common. Most projects result in no change from prevailing conditions whether they are large-scale revegetation after disturbance, such as fire (Dalzell, 2004; Arkle et al., 2014), mine restorations (Herrick et al., 2006), or smaller-scale tests of concept (Bleak et al., 1965; Wilson et al., 2004). Identifying the

mechanisms that cause restoration projects to fail may allow us to develop more successful methods.

A key goal of successful restoration is the formation of self-sustaining and recruiting populations (Hardegree et al., 2016). However, this means that individuals must survive from seed, to seedling, to adult plant. Various ecological conditions, processes, and mechanisms control the ability of a seed to produce a mature adult (James et al., 2013). First, a seed must germinate successfully, which requires breaking potential seed dormancy (Monsen and Stevens, 2004), avoiding seed predation (Barberá et al., 2006), and appropriate light and moisture levels (Isselstein et al., 2002; Barberá et al., 2006; Bailey et al., 2012; Fehmi et al., 2014). A germinated seed must then emerge (Larson et al., 2015) after enduring freeze/thaw cycles, avoiding fungal infection and penetrating soil crusts (James et al., 2011). An emerged seedling further must withstand drought (Leishman and Westoby, 1994; Asay et al., 2001; Engelbrecht et al., 2005) and herbivory (Moles and Westoby, 2004) before it can proceed to future stages and finally become a mature adult.

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Herbivory of newly emerged seedlings has been documented, but the extent to which it is a dominant ecological process during seedling establishment is largely unknown for most ecosystems. In a limited literature synthesis focusing on the tropics, Moles and Westoby (2004) found that herbivory was among the top three causes of seedling mortality, accounting for 38% of explainable deaths. The seedling stage is vulnerable because survival relies on limited cotyledon nutrient and energy reserves to produce sufficient leaf area to sustain net carbon gain (Hanley et al. 2004). Additionally, establishing plants are particularly susceptible to herbivory as plant palatability changes with age, with strong consequences to community structure (Hanley et al., 1995; Barton and Hanley, 2013).

In this study we aimed to determine if defoliation, as a proxy for herbivory, occurring at the seedling stage in perennial grasses could be an important contributing factor to restoration failure. We were particularly interested in determining if the intensity and frequency of defoliation influence seedling success. Previous work with grass seedlings indicates frequency of defoliation may influence survival but has not addressed intensity (Roundy et al., 1985; Pyke, 1987). Adult grasses have been found to respond negatively to frequent grazing but are more insensitive to the intensity of that grazing (Ferraro and Oesterheld, 2002; Brewer et al., 2007); however, seedlings, that are still reliant on their coleoptile energy and nutrient reserves may be more sensitive to intensity of defoliation (Hanley and Fegan, 2007). Additionally, stressors rarely occur in isolation in natural environment; water stress may interact with defoliation frequency and intensity to influence seedling growth and survival. Seedlings may display greater sensitivity to defoliation, reduced sensitivity to defoliation, or no change in sensitivity to defoliation under water stress depending on what resources are limiting plant growth (Wise and Abrahamson, 2007). Wise and Abrahamson (2007) indicated that increased tolerance to herbivory under water stress might be most likely; however, Hawkes and Sullivan (2001) found that mature monocots frequently were better able to withstand herbivory at high resource levels, and the same may be true of monocot seedlings.

Also of concern when investigating how seedlings respond to defoliation are potential differences between native and introduced species. Native plants are desirable in restoration projects (Monsen and Stevens, 2004; US Department of Interior, 2004), but since the goal of restoration is often to improve or restore ecosystem services, desirable exotics are often used instead because they establish more reliably and are less expensive (Monsen and Stevens, 2004), particularly at drier sites (Asay et al., 2001). In studies of adult plants, introduced species have been found to be more resistant to defoliation than natives (Kimball and Schiffman, 2003; Ralphs, 2009). It is not yet known if the same holds true for seedlings as the few studies that have investigated this issue have found conflicting results (Huber-sannwald and Pyke, 2005; James et al., 2011).

We hypothesized that the intensity and frequency of defoliation would interact to determine the performance and survivorship of seedlings, with repeated, higher-intensity defoliation leading to the lowest performance in terms of tillering, biomass, and survival. We proposed two competing hypotheses for how defoliation will interact with water stress. Either seedlings would be better able to recover from leaf removal when water is abundant, as has been found in monocots previously, or seedlings would be more resistant to defoliation when drought stressed, as has been found across a range of plant functional types. Since the non-native species we selected has evolved under intense grazing pressure, we hypothesized that the non-native species would be more capable of tolerating intense and frequent defoliation.

## Methods

### Model System

The sagebrush steppe is one of the most extensive ecosystems in North America, but it is under threat from conifer encroachment,

invasive species, and human development (Noss et al., 1995; Salvo, 2008; Davies et al., 2011). Sagebrush steppe vegetation once covered >62 million ha, but only around 30–40 million ha of this ecosystem remain (Knick et al., 2003; Miller et al., 2011). Even under current best management practices, models suggest that, if left unchecked, altered fire cycles and invasive annual grasses will destroy >100 000 hectares of sagebrush steppe each year (Hemstrom et al., 2002). As this rangeland system is both under threat and frequently targeted for restoration (Dalzell, 2004; Pyke, 2011; Pyke et al., 2015), it provided a good model system in which to test drivers of restoration success.

Additionally, a variety of herbivores have been documented in the sagebrush steppe, including invertebrates, birds, and small mammals such as rodents, rabbits, and hares (Larrison and Johnson, 1973; McAdoo et al., 2006). Further, rodents may play an important role in limiting seedling establishment on sagebrush steppe (Pyke, 1986, 1987). Native, large herbivores, such as deer and antelope, can be found in the sagebrush system (Verts and Carraway, 1998), and the ecosystem is extensively grazed by the cattle industry (Young and Sparks, 2002).

### Experimental Design

This study consisted of two concurrent experiments. The first was a randomized block design with four treatments, three species × two watering regimes × two defoliation intensities × two defoliation frequencies, all factorially arranged in four blocks ( $n = 96$ ). This will be referred to as the Defoliation experiment hereafter. Additionally, a control experiment that was not defoliated was conducted simultaneously; it had two treatments, three species × two watering regimes, with two replicates of each treatment combination within each of four blocks ( $n = 48$ ). This will be referred to as the No Defoliation experiment hereafter. The same watering treatments were applied to both the Defoliation and No Defoliation experiments. Watering regimes consisted of a well-watered treatment (water = WET) and dry treatment (water = DRY). Both experiments were conducted in the same place and time, with pots intermixed; however, due to the differing number of treatments that were applied (species and water regime, in the No Defoliation Experiment; species, watering regime, defoliation intensity, and defoliation frequency in the Defoliation Experiment), the data from these experiments could not be analyzed together.

In the Defoliation experiment, defoliation treatments were applied once plants reached the two-leaf stage when individuals are no longer dependent on their cotyledons (Hanley and Fegan, 2007) but have not yet become established or begun to develop their mature root systems (Ries and Svejcar, 1991; Defossé et al., 1997; Moser and Smart, 1997). Either 30% of the leaf blade length (intensity = 30) or 70% of the leaf blade length (intensity = 70) was removed by clipping. Of those plants originally defoliated, half were defoliated a second time 4 wk after the initial defoliation at the same intensity (frequency = HIGH). The other half was not defoliated a second time (frequency = LOW).

### Study

This study was conducted from 20 March to 31 July, 2014 at the Eastern Oregon Agricultural Research Center near Burns, Oregon (43°31'06.7"N, 119°01'18.3"W) in a minimally temperature-controlled hoop house structure. The hoop house allowed ventilation from both sides and one end wall; when temperatures reach 32°C, a fan engages to promote further ventilation. Temperatures in the hoop house mirrored ambient outside temperature over the course of the study.

Two widespread, native, perennial grasses of the Wyoming big sagebrush steppe ecosystem were chosen to serve as model species: bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Love, var *Anatone*) and Sandberg bluegrass (*Poa secunda* J Presl). In addition, we chose an exotic, perennial grass used frequently for rangeland

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