



STUDIES

Seedling defoliation may enhance survival of dominant wheatgrasses but not *Poa secunda* seeded for restoration in the sagebrush steppe of the Northern Great Basin

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Agroecology & Environment. Chief Editor: Amelie Gaudin

Associate Editor: Matthew Germino

Abstract

Restoration of dryland ecosystems is often limited by low seedling establishment and survival. Defoliation caused by insects and small mammals could be an overlooked cause of seedling mortality. In the sagebrush steppe, we examined the effect of seedling defoliation on the survival of perennial grasses commonly used as restoration materials. Under field conditions, seedlings of three perennial bunchgrass species (non-native *Agropyron cristatum*, and native grasses *Poa secunda* and *Pseudoroegneria spicata*) were defoliated at two intensities (30 % and 70 % leaf length removal) and frequencies (one or two clippings) and compared to a non-defoliated control. Following emergence the first year, clippings occurred at the two-leaf stage; a second clipping occurred 1 month later for repeated defoliation treatments. We monitored seedling survival and tillering for 2 years. We expected higher defoliation intensity and frequency to reduce survival for all species, but only a few treatments reduced *Po. secunda* survival. Conversely, larger-statured Triticeae (wheatgrasses) benefited from some defoliation treatments. In both years, *A. cristatum* survival increased with repeated defoliation at both intensities. Defoliation did not affect *Ps. spicata* survival in the first year, but a single defoliation in the second year resulted in increased survival. In both *A. cristatum* and *Ps. spicata*, higher-intensity defoliation reduced the boost to survival resulting from defoliation frequency. Seedlings with more tillers had greater survival probabilities, but tiller number was unaffected by defoliation. Further research may elucidate mechanisms seedlings use to compensate for or benefit from defoliation. In the meantime, managers should aim to select defoliation-tolerant species if they anticipate herbivory will be problematic for restoration sites.

Keywords: Defoliation; plant–herbivore interactions; rangeland restoration; seedling ecology; seedling herbivory.

Introduction

Herbivory has shaped the establishment of vegetation globally, influencing the evolution of plant traits and the assembly of dryland plant communities (Adler *et al.* 2004; Diaz *et al.* 2007). Plant–herbivore interactions and defoliation tolerance

involving mature rangeland vegetation have been extensively studied (Briske 1996), but how herbivores affect seedlings and establishing dryland plant communities during restoration is still poorly understood. Herbivory by insects and small

Received: 4 January 2021; Editorial decision: 10 June 2021; Accepted: 9 August 2021

Published by Oxford University Press on behalf of the Annals of Botany Company 2021.

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mammals may be an overlooked cause of seedling mortality, though some authors have begun to address the topic (Barton and Hanley 2013; Sharp Bowman et al. 2017; Denton et al. 2018). Herbivory during the vulnerable seedling stage may have substantial consequences on the resulting plant community structure because of potential influences on recruitment, productivity and resulting reproductive output (Zhang et al. 2011; Barton and Hanley 2013). Despite decades of research in the Great Basin, seedling establishment remains a significant barrier to restoration (Svejcar et al. 2017). Understanding the influence herbivory has on establishment of important species could offer insight into factors limiting seedling survival and improve restoration outcomes.

Seedling herbivory is expected when restoring propagules to depleted landscapes. Cotyledons and initial leaves are palatable, nutrient-rich and vulnerable to physiological or mechanical disturbances that damage or remove meristems or deplete tissue reserves (i.e. carbohydrates, nitrogen, water) (Fenner et al. 1999; Skinner et al. 1999; Barton and Hanley 2013). Further, seedlings have limited nutrient and energy reserves for initial growth and have lower leaf area available for photosynthesis, making it difficult for them to recover from tissue damage (Hanley et al. 2004). A literature synthesis for tropical environments found herbivory accounted for 38 % of seedling mortality (Moles and Westoby 2004), and Sharp Bowman et al. (2017) found that rodent herbivory reduced grass seedling survival in the Great Basin ranging from 36 % to 57 % depending on species. Even when seedlings are not killed outright, reduced fitness caused by defoliation may impair the ability of native seedlings to compete with invading annuals such as cheatgrass (*Bromus tectorum*) (Pyke 1986). Seedling herbivory resulting in complete leaf removal may be particularly damaging to fitness, and subsequent tissue loss due to wind may be mistaken for emergence failure during restoration (Strauss et al. 2009).

Some evidence indicates perennial grass seedlings can be surprisingly resilient to defoliation (Barton and Hanley 2013), perhaps because perennial grasses have coevolved with herbivores. In the sagebrush steppe, many herbivores may prey upon perennial grass seedlings, including an array of insects, molluscs, nematodes, birds and small mammals (Pyke 1986, 1987; Hulme 1994). Seedlings can have anti-herbivory mechanisms such as delayed greening, unpalatable secondary metabolites or structural defenses [e.g. leaf toughness or pubescence that develops with leaf maturity (Kitajima et al. 2013)] that could reduce herbivory (Barton and Hanley 2013). Development of belowground organs like roots and buds that initiate tillers may be crucial to seedling resiliency (Barton and Hanley 2013; Denton et al. 2018). Additionally, the environment can interact with defoliation to affect seedling responses through temperature extremes and drought. Considering the variability of the climate in the Great Basin, understanding these interactions is crucial for predicting restoration success (Knutson et al. 2014; Shriver et al. 2018). For instance, rabbit grazing under dry conditions was found to promote survival for crested wheatgrass seedlings (Roundy et al. 1985), while Denton et al. (2018) found that defoliation under drought conditions increased mortality in Sandberg bluegrass seedlings. Overall, grass seedling defoliation responses seem species-specific (Denton et al. 2018), likely dependent on grass functional traits that allow seedlings to tolerate or compensate for herbivory.

The paucity of information regarding the impacts and management of seedling herbivory may limit our ability to restore degraded rangeland. However, frameworks developed from large mammal grazing on adult plants (Briske 1991; Ferraro

and Oesterheld 2002) provide a scientific basis for developing hypotheses regarding seedling responses to herbivory. Complete coleoptile and cotyledon loss will likely cause the death of most seedlings; however, as seedlings gain numerous leaves and leaf area, their ability to survive defoliation may improve. In mature grasses, the ability to survive defoliation depends upon how much plant material is removed (intensity) and the number of times it is removed (frequency). Preliminary work indicates that this may also be the case with seedlings (Roundy et al. 1985; Hanley and May 2006; Denton et al. 2018), with more intense and frequent defoliations increasing mortality. Additionally, seedling fitness may depend on whether or not the plants can compensate for defoliation by increasing their photosynthetic rate (Briske 1991; Hamerlynck et al. 2016) and whether they have meristematic tissue available for regrowth (i.e. intercalary, apical or basal meristems) (Wise and Abrahamson 2008). Ultimately, differences in defoliation amount and frequency (e.g. low frequency-high intensity or high frequency-low intensity) could influence establishment and survival of seedlings and affect restoration outcomes (Pyke 1986, 1987; Cumberland et al. 2017).

To determine if defoliation of seedlings limits the restoration outcomes, we monitored how three perennial grasses frequently used for restoration in the Northern Great Basin responded to defoliation at the seedling stage. We followed up on work from a short-term pot study (Denton et al. 2018) to determine if our findings held up under field conditions during the initial establishment years. For the previous pot study, defoliation intensity (30 % and 70 % of leaf length) and frequency (one or two clippings) were examined with and without moisture stress and compared to non-defoliated controls. Seedling mortality was monitored, and plants were harvested 4 months after planting to measure the effects of defoliation on seedling biomass and tillering. If the pot study served as a viable proxy for field conditions, we expected similar outcomes. In the pot study, defoliation intensity and frequency had interacting effects on seedling performance, with reductions in biomass and sometimes survival at combined high-frequency and high-intensity defoliation. (i) Therefore, in the current field study, we expect lower survival resulting from high-intensity and high-frequency defoliation. (ii) Similarly, the species of a given seedling will likely influence response to defoliation. In the pot study, the wheatgrasses were relatively less sensitive to defoliation and Sandberg bluegrass was relatively more sensitive. Analogous responses were expected for plants growing in field conditions. (iii) Changes in survival may be caused indirectly through reduced tillering, as high-frequency, high-intensity defoliation caused a reduction in Sandberg bluegrass tillering in the pot study, and a higher number of tillers is known to be tied to overwinter survival. Ultimately, this research could help determine if seedling defoliation limits the restoration success of bunchgrasses seeded in the Northern Great Basin.

Materials and Methods

Location

This study was conducted at the Northern Great Basin Experimental Range (NGBER), 17 km SW of Riley Oregon (43°29'21"N, 119°42'38"W), at 1416 m on the Malheur High Plateau. Mean annual precipitation at NGBER over the last 70 years is 227 ± 76 mm (mean ± SD). Mean soil volumetric water content at 5 cm depth throughout the experiment was 8.7 %, and soil temp was 11.8 °C (unpublished data). Total annual

precipitation as recorded by the nearest NOAA weather station (GHCND:USC00358029) was below average during the years of observation (2016: 202 mm, 2017: 175 mm and 2018: 120 mm), meaning seedling establishment and treatments occurred during unusually dry conditions. The vegetation is characterized as sagebrush steppe, with an overstory of *Artemisia tridentata*. Common understory species include perennial bunchgrasses such as *Pseudoroegneria spicata*, *Festuca idahoensis*, *Poa secunda* and *Achnatherum thurberianum* and perennial forbs such as *Lupinus arbustus*, *Phlox longifolia* and *Crepis acuminata*. The invasive annual grass *B. tectorum* is present but not dominant. Soils are primarily Argiduridic Argixerolls with a sandy-loam texture.

Design

The seedbed was burned, and then rototilled in September 2016 to remove standing dead and kill surface seeds. The disturbed soil was watered daily for a month to encourage the emergence of remaining cheatgrass. Cheatgrass seedlings were treated with 2 % glyphosate, 2 weeks prior to seeding at a rate of 0.1 L/m² and then again on the day of seeding (8 November 2016) to reduce competition.

The seeded species were bluebunch wheatgrass [*Ps. spicata* (variety Columbia, a large, deep-rooted native perennial)], Sandberg bluegrass [*Po. secunda* (variety Vale, a short-statured, shallow-rooted native perennial)] and crested wheatgrass [*Agropyron cristatum* (variety Highcrest II, a large, introduced perennial frequently used to revegetate degraded drylands)]. Plots of each grass species were factorially assigned to one of five defoliation treatments [no defoliation (0 %), light defoliation (30 % of leaf length × 1 clipping), repeated light defoliation (30 % × 2), high defoliation (70 % × 1) and repeated high defoliation (70 % × 2)]. These treatments were randomly assigned to 0.5- × 2-m plots in four blocks (60 plots = 3 species × 5 treatments × 4 blocks). Seeding was done at a rate of 1000 pure live seeds m⁻². Seeds were broadcast over recently tilled soil, and then lightly cultipacked to improve soil–seed contact; seeds were left to germinate with ambient precipitation. Seeded plots were located within exclosures that excluded livestock and meso-herbivores like lagomorphs (excluded with partially buried chicken-wire); however, plots potentially received herbivory from small mammals and insects. In the spring of 2017, seedling emergence was monitored until the majority of seedlings had reached the two-leaf stage (mid-April). The original design called for 10 randomly chosen seedlings per plot to be individually marked with plastic toothpicks and treated, however, due to extremely low emergence (<1 % overall), all seedlings (*n* = 423) with two or more true leaves were marked with a toothpick, treated and then monitored. Seedlings per treatment for bluebunch wheatgrass ranged from 18 to 23, for Sandberg bluegrass, 24 to 52, and for crested wheatgrass 19 to 60. No emergence occurred in 18 plots and these plots were not assessed further. The remaining plots had between 1 and 29 seedlings to which treatments were applied, with an average of 10 seedlings per plot. At the time of tagging, for all seedlings assigned to receive defoliation, each leaf was measured with a ruler and scissors were used to clip off 30 % or 70 % of leaf length. One month later, seedlings assigned repeated treatments were defoliated a second time at the same level. Survival was assessed at the beginning of July. When seedling status was uncertain due to partial desiccation and seedling senescence or dormancy was possible, seedlings were marked as alive. The number of tillers per individual seedling was also counted at this time. In July of 2018, second-year survival was assessed on all plants that survived the first year, the number of tillers were counted and

all aboveground biomass was collected by clipping each plant at ground level. Plants were dried in a 55 °C oven for 48 h, and then weighed individually.

Statistical analysis

Because there was no survival for one treatment in the second year (Sandberg bluegrass repeated 30 % defoliation), a Bayesian hierarchical Bernoulli model with informative priors drawn from James et al. (2011, 2019) was used to model the probability of survival separately for each species. Mean average probability of survival from emergence to establishment for our perennial grass from James et al. (2011, 2019) were used update our priors, Sandberg bluegrass was only included in the second paper. The model was built using the *rethinking* Package in R (R Core Team 2019; McElreath 2020).

The model had the following hierarchical form:

$$y_{\text{survival}} \sim \text{Bernoulli}(1, P_i)$$

$$\text{logit}(P_i) \sim \alpha + \alpha_{\text{block}} [\text{block}] + \beta_{30 \times 1} \times \text{TRT30} \times 1_i + \beta_{30 \times 2} \times \text{TRT30} \times 2_i + \beta_{70 \times 1} \times \text{TRT70} \times 1_i + \beta_{70 \times 2} \times \text{TRT70} \times 2_i$$

$$\alpha \sim \text{Normal}(\text{logit}(P_{\text{prior}}), \sigma_1)$$

$$\alpha_{\text{block}} \sim \text{Normal}(0, \sigma_2)$$

$$\beta_{30 \times 1}, \beta_{30 \times 2}, \beta_{70 \times 1}, \beta_{70 \times 2} \sim \text{Normal}(0, 2)$$

$$\sigma_1, \sigma_2 \sim \text{half-Cauchy}(0, 1),$$

where y_{survival} is the data, P_i is the survival probability for each individual, α is the intercept term for survival, α_{block} is the coefficient to account for spatial variability in survival, $\beta_{30 \times 1}$, $\beta_{30 \times 2}$, $\beta_{70 \times 1}$, and $\beta_{70 \times 2}$ are the coefficients for how each treatment affects survival. P_{prior} is the mean probability for survival for each species from James et al. (2011, 2019). An uninformative half-Cauchy prior was used for σ_1 and σ_2 .

For each species and year (first-year survival, final establishment), a model was fit in R (version 3.6.1) using Hamiltonian Monte Carlo (HMC) methods using a Metropolis-Hastings algorithm with four chains. Code and data are available on Zenodo [<http://doi.org/10.5281/zenodo.5098296> (Denton 2021)]. The HMC algorithm was run for 20 000 iterations with 2000 discarded as burnin. Chains were fit to test convergence. Results are presented as their posterior density functions, probability of change in survival at a biologically significant level (defined as 10 % change, calculated using the *edcf* function), means and 95 % credible intervals (CIs) [see Supporting Information—Table S1]. Probabilities of 0.50–0.67 can be considered weak evidence for a difference, 0.68–0.84 moderate evidence for a difference and >0.85 strong evidence for a difference.

Treatment differences in final biomass for each plant were tested using a linear mixed model with Block as a random factor and Treatment as fixed factors (from the *nlme* package) (Pinheiro et al. 2019). Biomass was square root-transformed to improve the normality of residuals. Models were fit separately for each species.

To determine if increased tillering at the end of the first growing season influenced final survival, we used Bayesian structural equation modeling (BESM, *blavaan* R project; Merkle and Rosseel 2018). This allowed us to determine if any survival benefit from increased tillering was an indirect effect of defoliation treatment or if tillering and defoliation independently influenced survival. Bayesian methods were used because count data (number of tillers) are not well supported by frequentist structural equation

model methods. BSEMs were fit separately for each species using three chains to ensure convergence. Survival was modeled as a binary outcome variable using a probit link function. See Fig. 1 for the initial hypothesized model used to evaluate factors affecting second-year survival of grass seedlings. A total of 13 parameters are estimated by this model. Posterior predictive probability (PPP) values were used to determine model fit, and posterior density intervals (0.025–0.975) that did not include zero were used to determine significance. Both standardized and unstandardized path coefficients are presented. Recommended ‘srs’ (simple random sampling) priors were used for covariance parameters of regression coefficients (Merkle and Rosseel 2018), and Gelman and Rubin statistics were used to check convergence between chains.

Results

First-year survival

Non-defoliated controls. Crested wheatgrass had the highest overall survival, with 58 % of non-defoliated seedlings surviving (CI 30–86 %) until the end of the first growing season. Bluebunch wheatgrass seedlings had the second highest survival; 56 % of non-defoliated seedlings survived through year 1 (CI 28–94 %). Sandberg bluegrass had the lowest survival at the end of the first growing season. Only 25 % of non-defoliated seedlings survived (CI 10–62 %).

Defoliation frequency. In the first year, crested wheatgrass seedlings that had received repeated defoliation at either intensity had a biologically significant (change in survival of 10 % or more) probability (P) of higher survival than controls ($P = 0.70$), with the average increase in survival of 17 %. This was not true for either bluebunch wheatgrass seedlings or Sandberg bluegrass seedlings, though survival in these species was not reduced by repeated defoliation (Table 1). In crested wheatgrass, this effect is mainly driven by seedlings defoliated at the 30 % level ($P = 0.79$) as opposed to the 70 % level ($P = 0.42$), where the increase in survival does not meet the criteria for weak evidence on its own (Table 2)

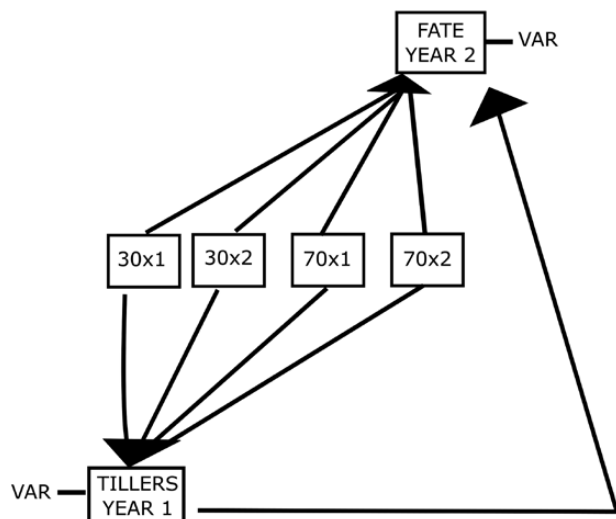


Figure 1. Initial hypothesized structural equation model used to evaluate factors affecting perennial grass survival into the second year. Additionally, two factors estimated are the intercepts for Tillers Year 1 and Fate Year 2 (survival) representing the control treatment. Direct effects are represented by arrows from seedling defoliation treatments (30 × 1, 30 × 2, 70 × 1, 70 × 2) to Tillers Year 1 or Fate Year 2, while the pathway between Tillers and Fate is an indirect effect.

(average increase in survival 26 % and 7 %, respectively). There was no evidence of any treatment differences in survival for Sandberg bluegrass or bluebunch wheatgrass after the first year of observation, and no evidence that a single defoliation in any species resulted in a biologically significant change in survival from the controls (Tables 1 and 2; Fig. 2).

Defoliation intensity. Defoliation intensity seemed to influence survival less than frequency. Only in crested wheatgrass is there any evidence of a biologically significant increase in survival with weak evidence ($P = 0.51$) that seedlings defoliated at the 30 % level had higher survival than the controls in the first year (Table 1), with the average increase in survival of 9 %. There was no indication in either bluebunch wheatgrass or Sandberg bluegrass that defoliation intensity influenced first-year survival.

Second-year survival

Non-defoliated controls. There was a substantial die-off of crested wheatgrass (31 % [CI 11–51 %]) and bluebunch wheatgrass (20 % [CI 2–48 %]) survival between year 1 and year 2. With already low survival in year 1, there was not much difference in Sandberg bluegrass survival by year 2 (survival 14 % [CI 7–30 %]).

Defoliation frequency. The biologically significant increase in survival with repeated defoliation seen in crested wheatgrass in the first growing season seemed to persist into the second year ($P = 0.64$) (Table 1), with an average increase in survival of 18 %. Frequent defoliation at the 30 % level resulted in a moderate probability of higher survival into year 2 than the control ($P = 0.80$), while frequent defoliation at the 70 % level did not have enough evidence of increased survival ($P = 0.49$) (Table 2), with an average increase in survival of 27 % and 10 %, respectively.

Surprisingly, defoliation frequency resulted in biologically significant increases in bluebunch wheatgrass survival in year 2 that were not apparent in year 1. There is weak evidence that plants defoliated once ($P = 0.64$) had higher survival than non-defoliated controls (Table 1), with an average increase in survival of 20 %. This increase in survival was seen at both defoliation intensities (30 × 1: $P = 0.64$ and 70 × 1: $P = 0.64$) and was quite similar in magnitude (20 % and 21 % increase in survival, respectively) (Table 2; Fig. 2).

In aggregate, there is no evidence that any frequency of defoliation changed survival from the control in Sandberg bluegrass. Though there is weak evidence that plants that received repeated defoliation at the 30 % level had reduced survival compared to the control ($P = 0.50$) (Table 2), an average reduction of 12 % in probability of survival was observed.

Defoliation intensity. There is weak evidence that both 30 % and 70 % defoliation regardless of frequency increased second-year survival over that of the control in crested wheatgrass ($P = 0.53$ and 0.51, respectively), with an average increase in survival of 13 % and 12 %, respectively. However, there is no evidence that survival in the two defoliation intensities differ from each other (Table 1). There is no indication that defoliation level mattered in either of the other species in year 2 (Table 1).

Survival–defoliation intensity and frequency interaction for both years

In two of three cases where defoliation frequency seems to increase survival over the control, there is evidence of an interaction between the intensity of defoliation and frequency.

Table 1. Bayesian inference of the probability of biologically significant differences in mean survival between posterior contrasts of interest (combinations of intensity, frequency and intensity × frequency) over 2 years for crested wheatgrass (AGCR), bluebunch wheatgrass (PSSP) and Sandberg bluegrass (POSE). Biological significance was defined as at least a 10 % increase or decrease in survival; the remaining unlisted probability is evidence for no change in survival. When more than half of the weight of probability indicates a biologically significant difference, that number has been bolded. Probabilities of 0.50–0.67 can be considered weak evidence for a difference, 0.68–0.84 moderate evidence for a difference and >0.85 strong evidence for a difference. Read as contrast on the left as compared to contrast on the right to understand the directionality of the change. For instance, for AGCR in 2017, there is a probability of 51 % that seedlings in any of the 30 % defoliation treatments are more likely to survive than seedlings in the control treatment at a biologically significant level. AGCR, *Agropyron cristatum*; POSE, *Poa secunda*; PSSP, *Pseudoroegneria spicata*.

Contrasts	AGCR				PSSP				POSE			
	2017		2018		2017		2018		2017		2018	
	<	>	<	>	<	>	<	>	<	>	<	>
30 vs control	0.25	0.51	0.16	0.53	0.23	0.49	0.23	0.42	0.34	0.15	0.49	0.01
70 vs control	0.232	0.44	0.12	0.51	0.42	0.29	0.24	0.41	0.26	0.27	0.15	0.33
30 vs 70	0.31	0.43	0.32	0.39	0.18	0.56	0.30	0.31	0.37	0.18	0.50	0.00
×1 vs ×2	0.61	0.16	0.54	0.20	0.42	0.28	0.07	0.72	0.17	0.39	0.02	0.09
1× vs control	0.35	0.32	0.21	0.40	0.36	0.36	0.10	0.64	0.24	0.27	0.23	0.04
2× vs control	0.12	0.62	0.08	0.64	0.29	0.42	0.37	0.18	0.36	0.15	0.41	0.01
Defoliation vs control	0.23	0.48	0.14	0.52	0.33	0.39	0.23	0.41	0.30	0.21	0.32	0.03

Table 2. Bayesian inference of the probability of a biologically significant difference in mean survival between seedling defoliation treatment (intensity × frequency) and non-defoliated controls over 2 years for crested wheatgrass (AGCR), bluebunch wheatgrass (PSSP) and Sandberg bluegrass (POSE). We have defined a biologically significant difference as a change in survival of 10 % or more as compared to the control treatment. The probability of either an increase or a decrease in survival of that magnitude is shown for each treatment; the remaining unlisted probability is evidence for no change in survival. When more than half of the weight of probability indicates a biologically significant difference, that number has been bolded. Values of 0.50–0.67 can be considered weak evidence for a difference, 0.68–0.84 moderate evidence for a difference and >0.85 strong evidence for a difference. AGCR, *Agropyron cristatum*; POSE, *Poa secunda*; PSSP, *Pseudoroegneria spicata*.

Year	Treatment	AGCR		PSSP		POSE	
		<	>	<	>	<	>
2017	30 × 1	0.46	0.22	0.25	0.30	0.35	0.15
	30 × 2	0.03	0.80	0.20	0.37	0.33	0.15
	70 × 1	0.25	0.43	0.47	0.16	0.15	0.39
2018	70 × 2	0.20	0.46	0.38	0.20	0.38	0.15
	30 × 1	0.29	0.26	0.10	0.64	0.40	0.01
	30 × 2	0.03	0.80	0.36	0.19	0.58	0.00
	70 × 1	0.13	0.53	0.11	0.64	0.06	0.33
	70 × 2	0.12	0.49	0.38	0.18	0.23	0.06

In crested wheatgrass, the contrast of both repeated treatments versus the control shows increased survival in both year 1 and year 2 (Table 1). However, while the probability of increased survival over the controls in the repeated treatments at 30 % defoliation has moderate evidence ($P = 0.80$ year 1 and 0.80 year 2; average increases in survival of 26 % and 27 % respectively), outside of the contrast, the evidence threshold for a biologically significant difference is not met in either year at

the 70 % defoliation level ($P = 0.46$ year 1 and 0.49 year 2; average increases in survival of 7 % and 10 % respectively) (Table 2). This seems to indicate that high-intensity defoliation can mute the positive effect that frequent defoliation seems to have on crested wheatgrass seedling survival.

In year 2, when a single defoliation treatment increased bluebunch wheatgrass survival over the control, it seemed to do so at a similar amount between the 30 % and 70 % defoliation level ($P = 0.64$ and 0.64, and average increase in survival of 20 % and 21 %, respectively) (Table 2). This indicates that there is no interaction between defoliation intensity and frequency in bluebunch wheatgrass (Fig. 2).

Second-year biomass

There were no treatment differences in final biomass for any species. Final mean biomass for crested wheatgrass plants was 2.4 g (95 % confidence interval 1.34 - 3.54 g), there were no treatment differences in biomass ($p = 0.88$, $F_{1,4} = 0.30$). Bluebunch wheatgrass had a final biomass of 0.57 g (confidence interval 0.12 - 0.95 g), there were no treatment differences in biomass ($p = 0.31$, $F_{1,4} = 1.22$). Sandberg bluegrass had a final biomass of 0.030 g (confidence interval 0.000 - 0.060 g), and also had no effect of treatment on biomass ($p = 0.26$, $F_{1,4} = 1.32$).

Structural equation models

For all species, first-year tiller number (range of tillers per seedling by species: crested wheatgrass 0–21, bluebunch wheatgrass 0–22 and Sandberg bluegrass 0–12) and defoliation treatments directly affected second-year survival (Fig. 3; Table 3), but there was no evidence of any indirect effect of treatment moderated through tiller production. Models fit the data well: PPP = 0.51, 0.49 and 0.50 for crested wheatgrass, bluebunch wheatgrass and Sandberg bluegrass, respectively. Overall, defoliation treatments did not significantly affect tillering. Therefore, any changes in survival probabilities are due to direct effects of the treatment on survival rather than treatments that influence survival via altered tillering. For each species, at least one treatment either directly

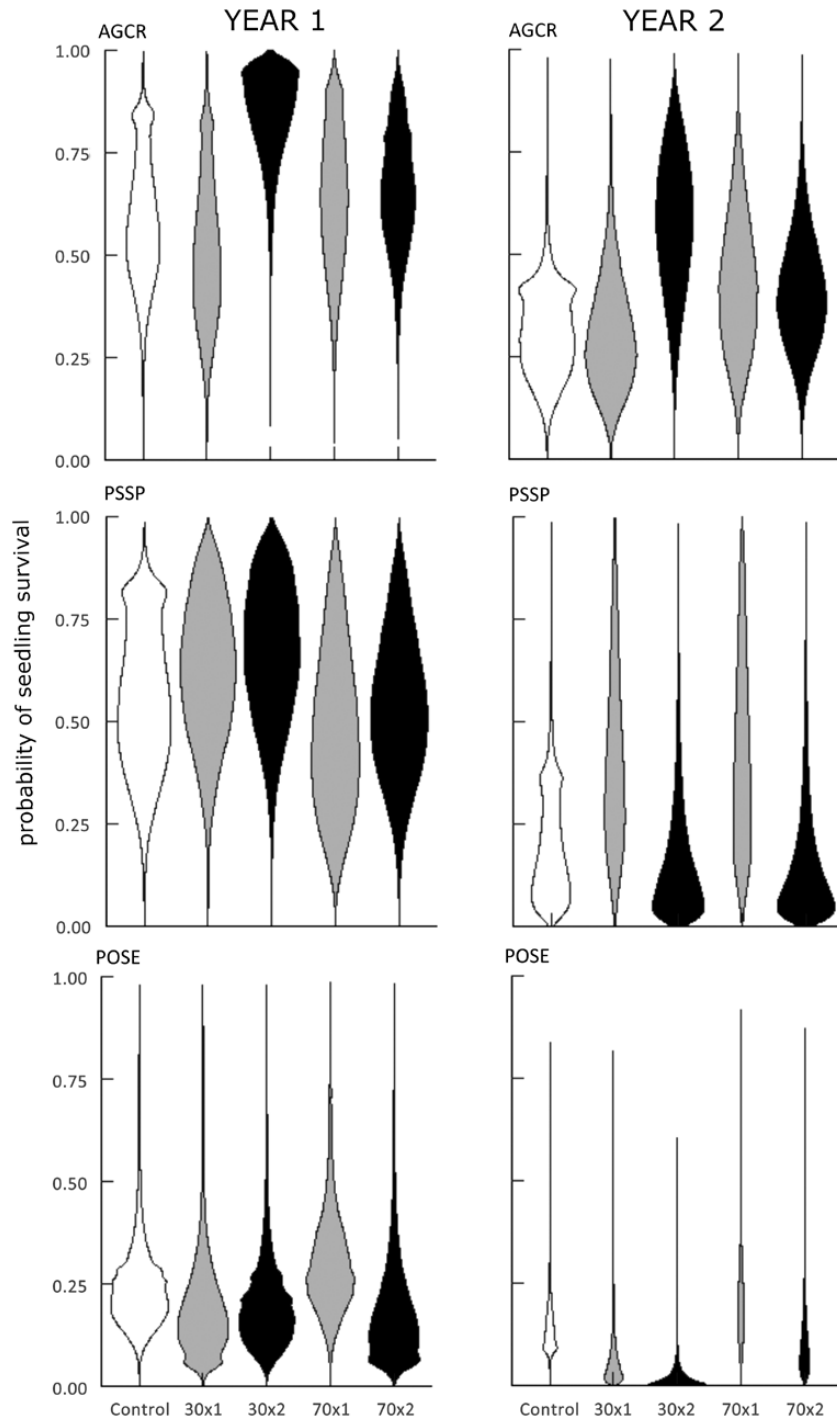


Figure 2. Bayesian posterior predictive distributions of survival probability for bunchgrass species [crested wheatgrass (AGCR), bluebunch wheatgrass (PSSP) and Sandberg bluegrass (POSE)] in Year 1 (2017) and Year 2 (2018) of the study demonstrating response to seedling defoliation treatments (intensity \times frequency). The width of the violin plot indicates the probability distribution of survival, where greater width indicates a higher probability of a survival value and lesser width indicates a lower probability. Mean survival and CIs are provided in [Supporting Information—Table S1](#) to aid in interpretation. AGCR, *Agropyron cristatum*; POSE, *Poa secunda*; PSSP, *Pseudoroegneria spicata*.

increased or decreased survival from the control. Crested wheatgrass demonstrated increased survival under the 30 \times 2 treatment (path coefficient = 0.20), bluebunch wheatgrass demonstrated increased survival under the 30 \times 1 treatment (path coefficient = 0.18) and Sandberg bluegrass demonstrated decreased survival under the 30 \times 2 treatment (path coefficient = -0.12). Standardized path coefficients indicate

that tiller number was always the largest predictor of 2018 survival for each species model, and tiller number positively correlated with increased survival ([Table 3](#)). The impact of each single tiller on survival was greatest for Sandberg bluegrass (path coefficient = 0.13), followed by crested wheatgrass (path coefficient = 0.068) and had the least effect on bluebunch wheatgrass (path coefficient = 0.057). The Sandberg bluegrass

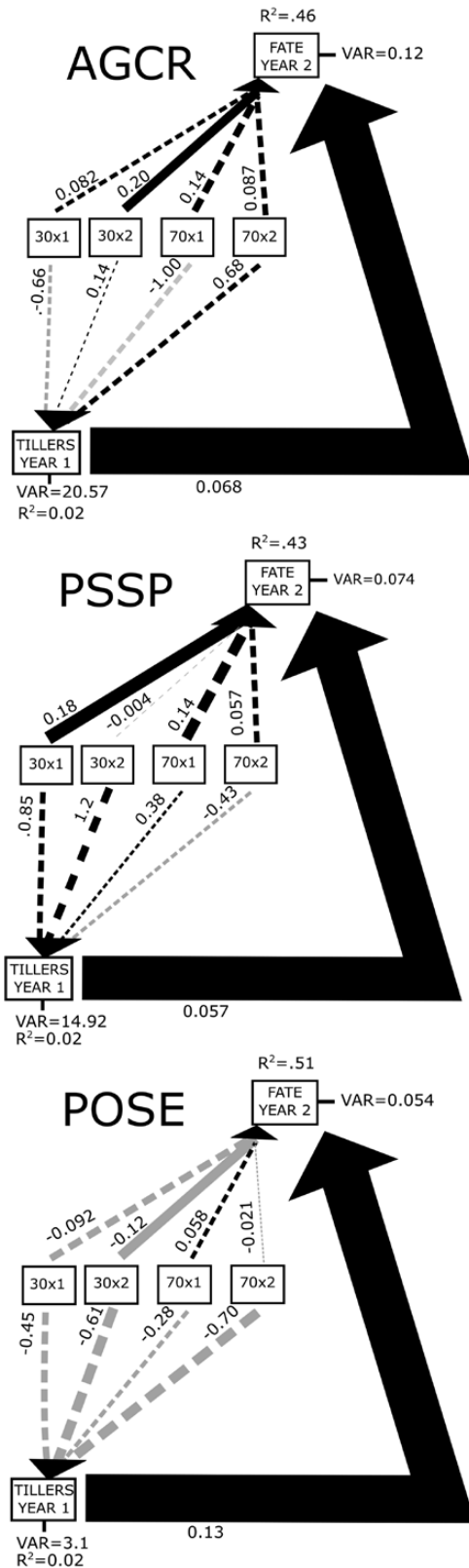


Figure 3. Bayesian structural equation models for crested wheatgrass (AGCR), bluebunch wheatgrass (PSSP) and Sandberg bluegrass (POSE) of factors affecting perennial grass survival into the second year comparing all defoliation treatments (intensity × frequency) as compared to the control. Numbers along paths are unstandardized path coefficients; path widths are proportional to standardized path coefficients. Black paths represent positive values, while grey

model had the most explanatory power to predict survival, followed by the crested wheatgrass model and then the bluebunch wheatgrass model ($R^2 = 0.51, 0.46$ and 0.43 , respectively). Gelman and Rubin statistics for all estimated coefficients were between 0.999 and 1.002, indicating strong convergence between chains [see [Supporting Information—Table S2](#)].

Discussion

This research aimed to test the influence of seedling defoliation on perennial bunchgrass establishment and survival in the sagebrush steppe to a biologically significant extent (a change of at least 10 % in survival probability from the control seedlings) under field conditions, which could improve our understanding of mechanisms driving restoration outcomes of perennial grasses in the Northern Great Basin. We assumed that higher levels of defoliation intensity, frequency and their interaction would ultimately reduce seedling survival relative to non-defoliated controls, as our prior pot study had indicated that such defoliation combinations reduced below and sometimes aboveground biomass (Denton et al. 2018), a prediction supported by other research (Pyke 1987). Surprisingly, seedlings of all species proved largely resilient to defoliation in terms of survival. In the larger perennial bunchgrasses (Triticeae, the wheatgrass tribe), we even found enhanced survival with some of the defoliation treatments. Frequent defoliation improved survival in crested wheatgrass, though less so when the defoliation was also of high intensity. A single defoliation treatment enhanced bluebunch wheatgrass survival at either intensity; however, this benefit did not occur until the second growing season. Sandberg bluegrass survival was not promoted by any seedling defoliation treatment. Additionally, there is weak evidence that defoliation might cause a reduction of Sandberg bluegrass survival in the second year. Species-specific responses to controlled defoliation pressure show that herbivory could impose selection on plant establishment in diverse species mixtures seeded to restore rangeland ecosystems. Surprisingly, survival outcomes within species were not modulated by treatment-driven increases or decreases in tillering, though plants with a greater number of tillers had improved survival.

To result in a positive or neutral response, as observed with the wheatgrasses, defoliation must have elicited a compensatory response that improved or maintained seedling fitness. Similar studies have found neutral or positive responses to seedling herbivory (Roundy et al. 1985; Hanley and May 2006), indicating defoliated seedlings are often resilient. Mechanisms regulating resistance and recovery from seedling defoliation remain unclear (Barton and Hanley 2013), but there may be plant traits that compensate for defoliation stress, such as increased photosynthetic rate or water use efficiency after defoliation events (Hamerlynck et al. 2016). Seedlings may also compensate for defoliation stress with an increased growth rate and improved reallocation of carbohydrates and other substrates for regrowth (Ryle and Powell 1975; Detling et al. 1979), and even modification of root architecture and growth (Arredondo and Johnson 1999). Another potential mechanism driving enhanced survival might be increased tiller recruitment in response to defoliation, a compensation mechanism employed

paths represent negative values. Solid lines represent estimates that do not include zero in their 95 % posterior density interval. AGCR, *Agropyron cristatum*; POSE, *Poa secunda*; PSSP, *Pseudoroegneria spicata*.

Table 3. Bayesian structural equation model coefficient estimates for crested wheatgrass (AGCR), bluebunch wheatgrass (PSSP) and Sandberg bluegrass (POSE). Estimate is the unstandardized path coefficient followed by 95 % CIs and the standardized path coefficient. CIs that include do not include zero are considered significant and are bolded. AGCR, *Agropyron cristatum*; POSE, *Poa secunda*; PSSP, *Pseudoroegneria spicata*.

AGCR	AGCR	PSSP		POSE		Standardized
	Estimate (CI)	Standardized	Estimate (CI)	Standardized	Estimate (CI)	
Fate 2018~						
30 × 1	0.08 (−0.08, 0.24)	0.06	0.18 (0.01, 0.36)	0.19	−0.09 (−0.21, 0.02)	−0.10
30 × 2	0.20 (0.02, 0.38)	0.13	0.00 (−0.18, 0.17)	0.00	−0.12 (−0.22, −0.01)	−0.14
70 × 1	0.14 (−0.03, 0.32)	0.10	0.14 (−0.02, 0.32)	0.15	0.06 (−0.06, 0.17)	0.07
70 × 2	0.09 (−0.05, 0.23)	0.08	0.07 (−0.09, 0.23)	0.08	−0.02 (−0.14, 0.09)	−0.03
Tillers 2017	0.07 (0.06, 0.08)	0.67	0.06 (0.04, 0.07)	0.62	0.13 (0.10, 0.15)	0.68
Tillers 2017~						
30 × 1	−0.66 (−2.73, 1.38)	−0.05	0.85 (−1.64, 3.36)	0.08	−0.48 (−1.30, 0.38)	−0.10
30 × 2	0.14 (−2.12, 2.43)	0.01	1.19 (−1.12, 3.62)	0.12	−0.62 (−1.40, 0.13)	−0.14
70 × 1	−1.07 (−3.40, 1.08)	−0.08	0.38 (−2.05, 2.84)	0.04	−0.30 (−1.12, 0.48)	−0.06
70 × 2	0.68 (−1.15, 2.51)	0.06	−0.43 (−2.64, 1.81)	−0.05	−0.70 (−1.55, 0.15)	−0.14
Intercepts						
Fate 2018	−0.02 (−0.12, 0.08)	−0.04	−0.09 (−0.21, 0.03)	−0.24	0.05 (−0.01, 0.12)	0.16
Tillers 2017	3.74 (2.64, 4.90)	0.82	2.31 (0.69, 3.93)	0.59	1.12 (0.64, 1.60)	0.63
Variances						
Fate 2018	0.12 (0.10, 0.15)	0.54	0.07 (0.06, 0.10)	0.57	0.05 (0.04, 0.07)	0.49
Tillers 2017	20.57 (16.45, 25.54)	0.99	14.92 (11.23, 19.76)	0.98	3.11 (2.49, 3.94)	0.98

by mature perennial grasses (Caldwell *et al.* 1981; Zhang and Romo 1995; Ferraro and Oesterheld 2002; Ott *et al.* 2019) and has been observed in seedlings of similar species of perennial grasses (Denton *et al.* 2018). In establishing grasses, a higher tiller number is linked to increased overwinter survival (Chester and Shaver 1982) and survival from weevil herbivory (Hume and Chapman 1993). However, it should be reiterated that a treatment-driven increase in tiller number was definitively not found in the present study.

Caldwell *et al.* (1981) described mechanisms for the physiological recovery of mature crested and bluebunch wheatgrass following severe defoliation, including greater tiller recruitment and photosynthetic rate. Physiological responses and flexibility of resource allocation (carbohydrates, nitrogen) were greater for crested wheatgrass, including greater allocation of resources to shoot growth relative to roots. Compensatory physiological responses of crested wheatgrass following defoliation could explain the enhanced survival with low-intensity, high-frequency defoliation (30 × 2 treatment). Bluebunch wheatgrass is capable of recovering from severe defoliation but is less likely to overcompensate.

Sandberg bluegrass seedlings (Poeae tribe) were resilient with most defoliation treatments, only displaying reduced survival in a single defoliation treatment in the second year. Unlike the wheatgrasses, Sandberg bluegrass never had a positive survival response to defoliation. In established plant communities, Sandberg bluegrass has a suite of grazing avoidant traits, including small stature, often concealed among taller vegetation, and early phenology that offsets its growth from most perennial grasses. This reduces the access and total amount of time herbivores could graze on its vegetation

(Howard 1997). It is possible that the grazing avoidant traits of mature plants could translate into fewer mechanisms to tolerate herbivory at earlier developmental stages. Alternatively, Sandberg bluegrass seedlings at the time of treatment (two- to three-leaf stage) would have been much smaller than the Triticeae seedlings and remained so even through the end of the growing season with a total height of ~2 cm or less, compared to ~15–17 cm for Triticeae. Total carbohydrate and water reserves in non-defoliated tissue at this stage could explain divergent responses of Poeae and Triticeae, as larger seedlings are generally more defoliation tolerant (Armstrong and Westoby 1993). Despite Sandberg bluegrass' relative defoliation sensitivity, it is abundant through the intermountain west and can dominate disturbed sites. Perhaps, Sandberg bluegrass seedlings, as well as mature plants, successfully employ grazing avoidance strategies. Sandberg bluegrass seedlings are so small that they may not present attractive feeding opportunities for major consumers like lagomorphs and grasshoppers. Indeed, some research has indicated that rodent herbivores prefer larger seedlings (Hulme 1994).

In this experiment, increased tillering observed in the first year was associated with improved second-year survival; however, tillering was not influenced by seedling defoliation treatments. This means individual seedlings that produced a greater pool of available meristems (i.e. a bud bank, including apical and axillary meristems) during the establishment year had a higher probability of survival, likely because they had greater meristematic availability and tissue reserves to survive late summer drought and winter cold. Carter and VanderWeide (2014) similarly found seed sources that resulted in greater bud and tiller density resulting in the improved establishment of *Sorghastrum nutans*. In

contrast, in our previous experiment (Denton et al. 2018), tillering was influenced by simulated defoliation intensity and frequency. Crested wheatgrass increased tillering with repeated defoliation, while Sandberg bluegrass had decreased tillering under combined high-frequency and high-intensity defoliation (Denton et al. 2018). Tiller recruitment and bud dormancy are regulated by complex external and internal factors, which are regulated by the microclimate, resource availability, disturbance and plant interactions (Ott et al. 2019). Differences in growing conditions between the two experiments could explain this difference. For example, in a study conducted by Denton et al. (2018), three seedlings were grown to a pot, allowing for competition between seedlings, while low emergence in the current study resulted in low seedling density with no near neighbours. Perhaps the added stress of competition for water, light and soil nutrients may have promoted tiller recruitment in response to the defoliation treatments. Alternatively, lack of response to treatment by tillering could be attributed to differing plant cultivars (Carter and VanderWeide 2014; Santos and Diola 2015). While Hycrest II was the crested wheatgrass variety used in both studies, different cultivars were used for both bluebunch wheatgrass (Anatone vs Columbia) and Sandberg bluegrass ('not specified' vs Vale).

Clearly, there are other controls on tillering beyond the amount of defoliation. Both in the present study and in other research, increased tillering corresponds to increased plant fitness. Perhaps because, once initiated, each tiller acquires its own resources from the environment, these resources can then be shared with the parent plant increasing the probability of overall survival (Pitelka and Ashmun 1985). One candidate for the wide differences in tiller number observed between individuals in the present study might be seed weight, which has been identified as both a strong predictor of grass seedling emergences, but also the number of tillers that seedling eventually produces (Sanderson and Elwinger 2004).

It is important to recognize that our defoliation treatments simulated herbivory, and the treatments may not be entirely reflective of actual herbivory and associated foraging behaviours. Under field conditions, defoliation timing, frequency and utilization can differ from the treatments tested here. Seedlings could differ in their defoliation sensitivity with phenology, the initial clipping occurred when seedlings were at a similar stage, but species likely developed at different rates before the second clipping. Further, we overlooked the effect of a single defoliation at a later time (when the second clipping occurred). That said, the authors feel it is unlikely that the increase in crested wheatgrass survival with multiple defoliations is a positive response to defoliation occurring later in the growing season. In the sagebrush steppe, precipitation diminishes as the growing season progresses, and Denton et al. (2018) found that seedlings were more sensitive to defoliation under drought conditions, though there were no interactions between intensity and frequency of defoliation and drought. Further, our treatments also did not simulate indirect effects of grazing activities for larger herbivores (e.g. rodents or lagomorphs), which could include trampling or pulling seedlings from soil. There may be other indirect effects associated with herbivory like secondary pathogen attack or biochemical cues exchanged between herb and herbivore.

A further caveat when interpreting our results is that much like mature plants, emergent seedlings likely face selective grazing pressure. Seedlings of different species likely differ in palatability, which could influence establishment potential among species, and ultimately shape plant community composition (Fenner et al. 1999; Strauss et al. 2009; Barton and Hanley 2013; Cumberland et al.

2017). For example, Cumberland et al. (2017) found that Sandberg bluegrass survival under grasshopper herbivory was improved in the presence of cheatgrass because grasshoppers preferred the invasive annual as food. There can also be selectivity among different seedling tissues. For example, herbivores may select for the larger cotyledons of emergent forbs (Hanley and May 2006; Zhang et al. 2011), and forb seedlings may be more susceptible to apical meristem damage than graminoid seedlings that conceal their apical meristem below the soil surface until late growing season. Further, not all herbivory occurs above ground, like the treatments imposed. Belowground organs are also susceptible to selective herbivory, with previous studies identifying root consumption in the spring after seeding, which limits second-year survival (Byers et al. 1985). As our experiment applied the same treatments to all species and minimized disturbance of roots and shoots, this selective pressure was not evaluated, but it is likely an important mechanism that interacts with utilization. It is possible that plant communities observable on restored rangelands in the Great Basin are a legacy of seedling–herbivore interactions during community assembly. Further research should observe seedling herbivore selectivity and foraging behaviour (e.g. single complete defoliation vs infrequent grazing) on the fate of plants seeded for dryland restoration.

Control of seedling herbivores can ultimately result in improved plant recruitment (Byers et al. 1985); however, we should be cautious with the idea of treating for seed and seedling predators, which are typically native fauna. This experiment showed that grasses seeded for restoration of sagebrush steppe in the Great Basin are quite tolerant of seedling defoliation and may benefit from the ambient defoliation from native seedling herbivores. If seedling herbivory is a concern on a restoration site, there is potential to select grasses and other restoration plants tolerant of seedling defoliation (Cumberland et al. 2017; Denton et al. 2018).

In summary, our study shows that in the common restoration species tested, seedling defoliation rarely results in any reduction in survival. Some species of Triticeae even had improved survival under simulated seedling herbivory. This is good news for land managers as it indicates damage from insects and small mammal feeding is unlikely to cause restoration failure. Instead, tiller recruitment was the best predictor of seedling survival, independent of the defoliation treatments imposed. Further research is required to identify why some individuals produce higher numbers of tillers than others and therefore display increased survival. If these mechanisms can be elucidated and harnessed, our success at restoring perennial grasses could be greatly improved.

Supporting Information

The following additional information is available in the online version of this article—

Table S1. Means and credible intervals for survival probability for all species and years.

Table S2. Gelman and Rubin statistics.

Sources of Funding

Funding for this project was provided by the Range Current Research Information System grant.

Conflict of Interest

None declared.

Acknowledgements

We thank Emily R. Bishop, Dustin A. Golembiewski, Sarah R. Hurt, Derek M. Hyde, Jennifer R. MacMillan and Mieke R. Vrijmoet for their field assistance. Statistical advisement was provided by Bruce Macky (Agricultural Research Service) and Mevin Hooten (Colorado State University).

Contributions of Authors

R.L.S. developed the research idea and applied for funding. R.L.S. and E.M.D. designed the experiment. E.M.D. led field research and data collection and ran the analyses. R.L.S. and L.A.P. were consulted regarding results. L.A.P. and E.M.D. wrote the manuscript. R.L.S. reviewed the final draft.

Data Availability

All data and R code are available from Zenodo: <http://doi.org/10.5281/zenodo.5098296> (Denton 2021).

Literature Cited

- Adler PB, Milchunas DG, Lauenroth WK, Sala OE, Burke IC. 2004. Functional traits of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology* 41:653–663.
- Armstrong DP, Westoby M. 1993. Seedlings from large seeds tolerated defoliation better: a test using phylogenetically independent contrasts. *Ecology* 74:1092–1100.
- Arredondo JT, Johnson DA. 1999. Root architecture and biomass allocation of three range grasses in response to nonuniform supply of nutrients and shoot defoliation. *The New Phytologist* 143:373–385.
- Barton KE, Hanley ME. 2013. Seedling–herbivore interactions: insights into plant defence and regeneration patterns. *Annals of Botany* 112:643–650.
- Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using *lme4*. *Journal of Statistical Software* 67:1–48.
- Belsky AJ. 1986. Does herbivory benefit plants? A review of the evidence. *The American Naturalist* 127:870–892.
- Briske DD. 1991. Developmental morphology and physiology of grasses. In: Heitschmidt RK, Stuth JW, eds. *Grazing management: an ecological perspective*. Portland, OR: Timber Press, Inc.
- Briske DD. 1996. Strategies of plant survival in grazed systems: a functional interpretation. In: Hodgson J, Illius A, eds. *The ecology and management of grazing systems*. Wallingford, UK: CAB International, 37–67.
- Byers RA, Templeton Jr WC, Mangan RL, Bierlein DL, Campbell WF, Donley HJ. 1985. Establishment of legumes in grass swards: effects of pesticides on slugs, insects, legume seedling numbers and forage yield and quality. *Grass and Forage Science* 40:41–48.
- Caldwell MM, Richards JH, Johnson DA, Nowak RS, Dzurec RS. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* 50:14–24.
- Carter DL, VanderWeide BL. 2014. Belowground bud production is linked to population establishment in *Sorghastrum nutans* (Poaceae). *Plant Ecology* 215:977–986.
- Chester AL, Shaver GR. 1982. Seedling dynamics of some cotton grass tussock tundra species during the natural revegetation of small disturbed areas. *Holarctic Ecology* 5:207–211.
- Cumberland C, Jonas JL, Paschke MW. 2017. Impact of grasshoppers and an invasive grass on establishment and initial growth of restoration plant species. *Restoration Ecology* 25: 385–395.
- Denton EM. 2021. Elsie-Denton/SD-IF: Zenodo repository for SD-IF data and code (version v1). Zenodo. doi:10.5281/zenodo.5098296
- Denton EM, Smith BS, Hamerlynck EP, Sheley RL. 2018. Seedling defoliation and drought stress: variation in intensity and frequency affect performance and survival. *Rangeland Ecology & Management* 71:25–34.
- Detling JK, Dyer MI, Winn DT. 1979. Net photosynthesis, root respiration, and regrowth of *Bouteloua gracilis* following simulated grazing. *Oecologia* 41:127–134.
- Diaz S, Lavorel S, McIntyre SUE, Falczuk V, Casanoves F, Milchunas DG, Skarpe C, Rusch G, Sternberg M, Noy-Meir I, Landsberg J. 2007. Plant trait responses to grazing—a global synthesis. *Global Change Biology* 13:313–341.
- Fenner M, Hanley ME, Lawrence R. 1999. Comparison of seedling and adult palatability in annual and perennial plants. *Functional Ecology* 13:546–551.
- Ferraro DO, Oosterheld M. 2002. Effect of defoliation on grass growth. A quantitative review. *Oikos* 98:125–133.
- Hamerlynck EP, Smith BS, Sheley RL, Svejcar TJ. 2016. Compensatory photosynthesis, water-use efficiency, and biomass allocation of defoliated exotic and native bunchgrass seedlings. *Rangeland Ecology & Management* 69:206–214.
- Hanley ME, Fenner M, Whibley H, Darvill B. 2004. Early plant growth: identifying the end point of the seedling phase. *The New Phytologist* 163:61–66.
- Hanley ME, May OC. 2006. Cotyledon damage at the seedling stage affects growth and flowering potential in mature plants. *The New Phytologist* 169:243–250.
- Howard JL. 1997. *Poa secunda*. In: *Fire effects information system*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. <https://www.fs.fed.us/database/feis/plants/graminoid/poasec/all.html> (25 March 2020).
- Hulme PE. 1994. Seedling herbivory in grassland: relative impact of vertebrate and invertebrate herbivores. *Journal of Ecology* 82:873–880.
- Hume DE, Chapman DF. 1993. Oversowing of five grass species and white clover on a Taupo hill country pumice soil. *New Zealand Journal of Agricultural Research* 36:309–322.
- James JJ, Svejcar TJ, Rinella MJ. 2011. Demographic processes limiting seedling recruitment in arid grassland restoration. *Journal of Applied Ecology* 48:961–969.
- James JJ, Sheley RL, Erickson T, Rollins KS, Taylor MH, Dixon KW. 2013. A systems approach to restoring degraded drylands. *Journal of Applied Ecology* 50:730–739.
- James JJ, Sheley RL, Leger EA, Adler PB, Hardegree SP, Gornish ES, Rinella MJ. 2019. Increased soil temperature and decreased precipitation during early life stages constrain grass seedling recruitment in cold desert restoration. *Journal of Applied Ecology* 56:2609–2619.
- Kitajima K, Cordero RA, Wright SJ. 2013. Leaf life span spectrum of tropical woody seedlings: effects of light and ontogeny and consequences for survival. *Annals of Botany* 112:685–699.
- Knutson KC, Pyke DA, Wirth TA, Arkle RS, Pilliod DS, Brooks ML, Chambers JC, Grace JB. 2014. Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. *Journal of Applied Ecology* 51:1414–1424.
- McElreath R. 2020. *rethinking*. R package version 2.00. <https://github.com/mcElreath/rethinking> (November 2020).
- Merkle EC, Rosseel Y. 2018. blavaan: Bayesian structural equation models via parameter expansion. *Journal of Statistical Software* 88:1–30.
- Moles AT, Westoby M. 2004. What do seedlings die from and what are the implications for evolution of seed size? *Oikos* 106:193–199.
- Ott JP, Klimešová J, Hartnett DC. 2019. The ecology and significance of below-ground bud banks in plants. *Annals of Botany* 123:1099–1118.
- Pinheiro J, Bates D, DebRoy S, Sarkar D; R Core Team. 2019. *nlme: linear and nonlinear mixed effects models*. R package version 3.1-142. <https://CRAN.R-project.org/package=nlme> (September 2019).
- Pitelka LF, Ashmun JW. 1985. Physiology and integration of ramets in clonal plants. In: Jackson JBC, Buss LY, Cook RE, eds. *Population biology and evolution of clonal organisms*. New Haven, CT: Yale University Press, 399–435.
- Pyke DA. 1986. Demographic responses of *Bromus tectorum* and seedlings of *Agropyron spicatum* to grazing by small mammals: occurrence and severity of grazing. *Journal of Ecology* 74:739–754.
- Pyke DA. 1987. Demographic responses of *Bromus tectorum* and seedlings of *Agropyron spicatum* to grazing by small mammals: the influence of grazing frequency and plant age. *Journal of Ecology* 75:825–835.
- R Core Team. 2019. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/> (November 2020).
- Roundy BA, Cluff GJ, McAadoo JK, Evans RA. 1985. Effects of jackrabbit grazing, clipping, and drought on crested wheatgrass seedlings. *Journal of Range Management* 38:551–555.
- Ryle GJ, Powell CE. 1975. Defoliation and regrowth in the graminaceous plant: the role of current assimilate. *Annals of Botany* 39:297–310.

- Sanderson MA, Elwinger GF. 2004. Emergence and seedling structure of temperate grasses at different planting depths. *Agronomy Journal* 96:685–691.
- Santos F, Diola V. 2015. Chapter 2: physiology. In: Santos F, Borém A, Caldas C, eds. *Sugarcane: agricultural production, bioenergy, and ethanol*. Academic Press, 13–33.
- Sharp Bowman TR, McMillan BR, St Clair SB. 2017. Rodent herbivory and fire differentially affect plant species recruitment based on variability in life history traits. *Ecosphere* 8:1–10.
- Shriver RK, Andrews CM, Pilliod DS, Arkle RS, Welty JL, Germino MJ, Duniway MC, Pyke DA, Bradford JB. 2018. Adapting management to a changing world: warm temperatures, dry soil, and interannual variability limit restoration success of a dominant woody shrub in temperate drylands. *Global Change Biology* 24:4972–4982.
- Skinner RH, Morgan JA, Hanson JD. 1999. Carbon and nitrogen reserve remobilization following defoliation: nitrogen and elevated CO₂ effects. *Crop Science* 39:1749–1756.
- Strauss SY, Stanton ML, Emery NC, Bradley CA, Carleton A, Dittrich-Reed DR, Ervin OA, Gray LN, Hamilton AM, Rogge JH, Harper SD, Law KC, Pham VQ, Putnam ME, Roth TM, Theil JH, Wells LM, Yoshizuka EM. 2009. Cryptic seedling herbivory by nocturnal introduced generalists impacts survival, performance of native and exotic plants. *Ecology* 90:419–429.
- Svejcar T, Boyd C, Davies K, Hamerlynck E, Svejcar L. 2017. Challenges and limitations to native species restoration in the Great Basin, USA. *Plant Ecology* 218:81–94.
- Wise MJ, Abrahamson WG. 2008. Applying the limiting resource model to plant tolerance of apical meristem damage. *The American Naturalist* 172:635–647.
- Zhang J, Romo JT. 1995. Impacts of defoliation on tiller production and survival in northern wheatgrass. *Journal of Range Management* 48:115–120.
- Zhang S, Zhao C, Lamb EG. 2011. Cotyledon damage affects seed number through final plant size in the annual grassland species *Medicago lupulina*. *Annals of Botany* 107:437–442.