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NOTE

Soil moisture strongly limits Douglas-fir seedling establishment near its upper elevational limit in the southern Rocky Mountains

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Abstract: Climate change is causing significant shifts in tree species distributions to higher elevations and latitudes. Seed germination and seedling establishment are particularly important steps in tree range expansion under warmer conditions, yet seedling establishment is influenced by a range of factors beyond temperature, including herbivory, microenvironment, and the timing and amount of precipitation. We conducted an experiment to assess how augmented precipitation regimes, wildlife herbivory, and microclimate influence germination and first-season survival of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) near the upper elevational limit of its range in the southern Rocky Mountains. Germination was strongly influenced by moisture, with over three times higher germination in watered treatments. Seedling survival was similar across watered treatments but was negatively associated with microenvironments with higher maximum temperatures. These results indicate that soil moisture effects on germination and the negative impact of hot growing-season temperatures on seedling survival limit initial seedling establishment in Douglas-fir, even at the cooler and wetter end of its range, suggesting that the planting of this species will be most successful in cooler and wetter microsites. Taken together, this study suggests that continued warming and projected increases in droughts may strongly limit Douglas-fir regeneration and thus its ability to shift upwards with climate change.

Key words: seedling establishment, microclimate, species distribution, soil moisture, Douglas-fir, climate change.

Résumé : Le changement climatique provoque des modifications importantes dans l'aire de répartition des espèces arborescentes aux latitudes et altitudes élevées. La germination des graines et l'établissement des semis sont des étapes particulièrement importantes dans l'expansion de l'aire de répartition des arbres sous des conditions plus chaudes. Par contre l'établissement des semis est influencé par une foule de facteurs au-delà de la température, incluant le broutage, le microenvironnement ainsi que le moment et la quantité de précipitation. Nous avons réalisé une expérience pour évaluer de quelle façon la pluviosité accrue, le broutage de la faune et le microclimat influencent la germination et la survie lors de la première saison de croissance du douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) près de la limite altitudinale supérieure de son aire de répartition dans la partie sud des Montagnes Rocheuses. La germination était fortement influencée par l'humidité et plus de trois fois plus élevée dans les traitements irrigués. La survie des semis était semblable parmi les traitements irrigués, mais elle était négativement associée aux microenvironnements avec des températures maximales plus élevées. Ces résultats indiquent que les effets de l'humidité du sol sur la germination et l'impact negatif des températures chaudes durant la saison de croissance sur la survie des semis limitent l'établissement initial des semis de douglas de Menzies, même aux limites plus fraîches et plus humides de son aire de répartition, indiquant qu'on aura davantage de succès en plantant cette espèce sur des microsites plus frais et plus humides. Cette étude indique qu'ensemble, un réchauffement progressif et l'augmentation prévue des sécheresses pourrait fortement réduire la régénération du douglas de Menzies et par conséquent sa capacité à migrer vers le haut en altitude pour s'adapter au changement climatique. [Traduit par la Rédaction]

Mots-clés : établissement des semis, microclimat, répartition des espèces, humidité du sol, douglas de Menzies, changement climatique.

Introduction

Changing climatic conditions have begun to exceed thresholds for tree species regeneration across significant portions of their ranges, causing spatial shifts in the regenerative niche (Kelly and Goulden 2008; Lenoir et al. 2008; Davis et al. 2019*a*). As the climatic suitability of habitat changes, species are generally predicted to migrate toward cooler and wetter edges of their ranges (Kelly and Goulden 2008; Bell et al. 2014; but see Rabasa et al. 2013) while high rates of mortality from drought, insects, and disease raise questions of species long-term persistence in the hotter and drier portions of their ranges (Linares et al. 2009; Worrall et al. 2010). Together, these processes make juvenile recruitment dynamics central to the persistence and migration of many species (Conlisk et al. 2017; Andrus et al. 2018).

In the western United States (U.S.), there is growing evidence that climate change is affecting seed germination and initial seedling survival (Liu and El-Kassaby 2015; Conlisk et al. 2017), highlighting the sensitivity of the regeneration niche to ongoing environmental change. Longer growing seasons occurring in the Rocky Mountains as the climate changes may increase overall growth and productivity of established seedlings (Carroll et al. 2017), but longer seasons also lead to greater rates of transpiration, evaporation, and soil drying (Bassman et al. 2003), which

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may disproportionately impact seed germination and first-year survival. Indeed, soil moisture is especially important for seedling recruitment in dry forests of the western U.S. and is often the limiting factor in early regenerative stages (Moyes et al. 2015; Andrus et al. 2018). Precipitation in the western U.S. is predicted to shift toward less frequent and higher intensity events (Intergovernmental Panel on Climate Change (IPCC) 2018), suggesting that soil moisture deficits may become increasingly limiting on tree seedling establishment over the next century, even among species with drought adaptations (Kolb and Robberecht 1996; Hu et al. 2010). As the timing and regularity of precipitation changes, it will play an increasingly important role in regeneration dynamics, with higher rates of germination and seedling survival likely to occur during periods of more consistent moisture (League and Veblen 2006; Kroiss and HilleRisLambers 2015). Changes in moisture patterns will also make syncing germination with environmental conditions increasingly important: too soon and germinants risk early damage by late-spring frost, too late and they are not sufficiently established to withstand the drier periods of the summer (Petrie et al. 2017).

Although regional changes in climate are predicted to affect broadscale species persistence, individual populations of a species may be able to regenerate during selectively favorable climatic periods or in certain microenvironments (Andrus et al. 2018; Redmond et al. 2018). Indeed, climatic microrefugia — areas on the landscape that support the persistence of populations within a regionally unsuitable climate — can allow for successful seedling establishment under increasingly arid conditions (Serra-Diaz et al. 2015; McLaughlin et al. 2017; Davis et al. 2019*b*). Fine-scale heterogeneity at the forest floor in light, moisture, and temperature creates substantial variation in microenvironments and strongly impacts tree recruitment (Moyes et al. 2015; McLaughlin et al. 2017). This variation in microenvironment can mitigate or even override the effect of warmer temperatures, thus altering the speed or extent of species range shifts (Munier et al. 2010; Serra-Diaz et al. 2015; McLaughlin et al. 2017).

Nonclimatic factors can also impact regeneration success. Seed predation, germinant herbivory, and trampling are little studied yet important limitations on conifer recruitment. Seed predation can substantially reduce seed abundance (Johnson and Fryer 1996; Pesendorfer et al. 2016), clipping of germinant cotyledons by birds and small mammals can strongly reduce survival (Noble and Alexander 1977; Pesendorfer et al. 2016), and trampling limits establishment because of the vulnerable size of seedlings (Noble and Alexander 1977; Bingham and Simard 2012).

This study examines seed germination and first-season seedling survival of a widespread conifer, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), under changing environmental conditions. Douglas-fir is a drought-tolerant species of the montane zone of the Rocky Mountains and has had varying recruitment success following recent disturbances (Restaino et al. 2016; Davis et al. 2019*a*; Hankin et al. 2019), with available moisture serving as the primary limitation to seedling regeneration (Rother et al. 2015). Bioclimate models predict that Douglas-fir will be favored in future climate scenarios, particularly at the montane–subalpine ecotone at its current upper range limit (Rehfeldt et al. 2006), yet Douglas-fir recruitment in this zone has not been studied and such models do not account for the influences of climate-induced stress, wildlife, and microenvironment on early seedling establishment. We assessed the in situ effects of augmented precipitation regimes, wildlife predation, and microclimate on germination and early seedling establishment of Douglas-fir at the montane–subalpine ecotone in the southern Rocky Mountains. We hypothesized that (*i*) Douglas-fir would have higher rates of germination and survival in watered treatments and in cooler and wetter microenvironments and (*ii*) wildlife would strongly limit seed germination and seedling survival.

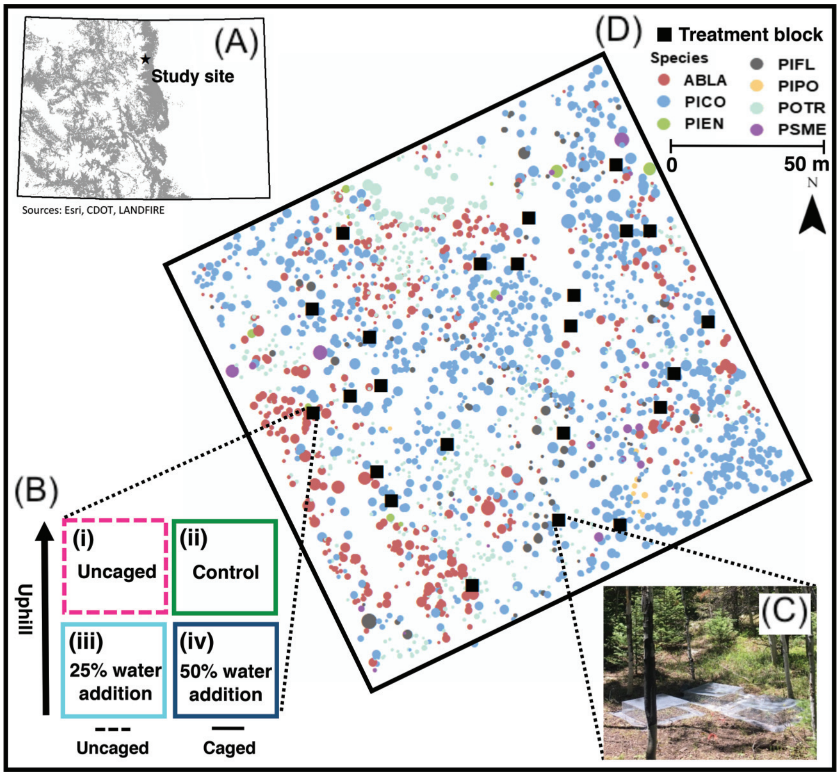
Materials and methods

The experiment was conducted at a permanent study site at an elevation of 2700 m on the Colorado Front Range near Peaceful Valley, Colorado, United States. The site is in a mixed-conifer forest at the interface of upper montane and subalpine forest types. Mean annual precipitation is 618 mm, primarily in the form of snow, with snowmelt occurring in May–June (PRISM Climate Group 2019). Mean growing-season temperature ranges from a mean daily minimum of 5.2 °C to a mean daily maximum of 19.4 °C. Soils are derived primarily from Leighcan family till substratum with glacial till and alluvium parent material derived from igneous and metamorphic rock (Soil Survey Staff 2019). The site is a closed canopy forest with low light levels, and when present, understory vegetation is dominated by ericaceous species. It is free of recent disturbance with no evidence of major blowdown, fire, harvest, or widespread insect outbreaks. The slope is flat overall, but there are widespread small-scale changes in elevation (±10 m), creating rolling topography and significant variation in microtopography. All live and dead adult stems (diameter at breast height (DBH; breast height = 1.30 m) ≥ 10 cm) were measured and tagged in 2016 and 2017. The study area is dominated by lodgepole pine (*Pinus contorta* Douglas ex Loudon) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), with scattered clusters of trembling aspen (*Populus tremuloides* Michx.), limber pine (*Pinus flexilis* E. James), ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and Douglas-fir.

Experimental treatments were installed in 2018 throughout the study area using a randomized blocked design with 24 blocks of four treatments stratified along a gradient of light availability (Fig. 1). Block locations spanned the range of available light (gap light index (GLI) in percentage) observed in the study area and were chosen for low presence of competing plants and a sufficiently large area with the same seedbed, slope, and aspect throughout. Each block (5 m^2) was composed of four treatments (each 0.25 m^2): uncaged (predator allowance, not watered), control (caged, not watered), and two caged water additions. The control served as the control for both the predator allowance and watering treatments. Caged treatments were covered with a square wire mesh cage with a flange on all sides to prevent burrowing by small mammals. The two water treatments were additions of 25% (2.2 L) or 50% (4.5 L) of mean weekly rainfall from mid-May to mid-September and were applied twice weekly during the first month following seed sowing and once weekly thereafter. Mean weekly precipitation quantities were based on recent (2014–2017) precipitation rates derived from a snow telemetry (SNOTEL) station approximately 7 km southwest of the study site (Natural Resources Conservation Service (NRCS) SNOTEL Data Network 2019) and were designed to mimic changes in growing-season soil moisture rather than snowpack specifically. Treatments were positioned within the site so that the watering treatments were always downslope of the other treatments to prevent water from flowing in.

Ten seeds of Douglas-fir were sown into a randomly generated grid of cells in each treatment replicate, resulting in a total of 960 seeds sown or 240 seeds per treatment. All seeds were sown at least 8 cm apart to avoid competition among germinants. Seeds were obtained from the U.S. Forest Service Bessey Nursery from seeds collected within similar proximity (within 10 km) and elevation (2560 m) as the study site and stratified prior to sowing in the field following guidelines from the U.S. Forest Service Woody Plant Seed Manual (Schopmeyer 1974). We also stratified and sowed seeds of ponderosa pine, lodgepole pine, subalpine fir, and Engelmann spruce, but these species did not germinate in sufficient numbers for study. During periods of high germination (18 June – 30 July 2018), germinants were checked twice weekly to more accurately measure time of germination.

Fig. 1. Study site and plot design. (A) Study site in relation to the distribution of Douglas-fir in Colorado. (B) Four treatments: (*i*) uncaged, not watered; (*ii*) control: caged, not watered; (*iii*) caged, 25% water addition; (*iv*) caged, 50% water addition. (C) Photograph of one treatment block. (D) Stem map of site with treatment block locations (black squares). ABLA, subalpine fir; PICO, lodgepole pine; PIEN, Engelmann spruce; PIFL, limber pine; PIPO, ponderosa pine; POTR, trembling aspen; PSME, Douglas-fir. Panels A and D were created using ArcMap version 10.7.1 (Esri, Redlands, Calif., USA), with vegetation type layers from LANDFIRE (2012). The base map in panel A is from the Colorado Department of Transportation (CDOT). [Color online.]



Microenvironment was quantified with available light (in percentage) and soil surface temperatures (in degrees Celsius). Available light of each block was measured with digital hemispherical photographs used to compute the block's GLI (the combined incident diffuse and direct beam radiation over a growing season expressed as a percentage of full sun) with Gap Light Analyzer (GLA) version 2.0 (Frazer et al. 1999; Martin and Canham 2010). Soil temperature data were recorded every 2 h from 6 June to 8 October 2018 in all 24 blocks using iButton Thermochron sensors (Maxim Integrated, San Jose, Calif., USA) placed on the soil surface beneath the litter layer. Growing-season temperatures were calculated as the mean of all daily minimum temperatures and the mean of all daily maximum temperatures from 6 June to 8 October 2018. Because we were unable to measure soil temperature and moisture levels in each treatment block, we are unable to disentangle the effects of watering on reduced soil temperatures compared with increases in soil moisture.

We analyzed germination and survival rates of Douglas-fir. We used a repeated-measures approach in a generalized linear mixed-effects model (GLMM) with a Poisson distribution to examine whether watering treatments and precipitation affected the timing of germination. The model included an interaction of watering treatment and observation date, fixed effects of total biweekly ambient precipitation (from PRISM data: PRISM Climate Group 2019), watering treatments, observation date, a random effect of treatment block, and a response variable of total biweekly germination. We included observation date as a second-order polynomial term to allow for the unimodal distribution of germination across time. Significance was tested in a type III analysis of variance (ANOVA).

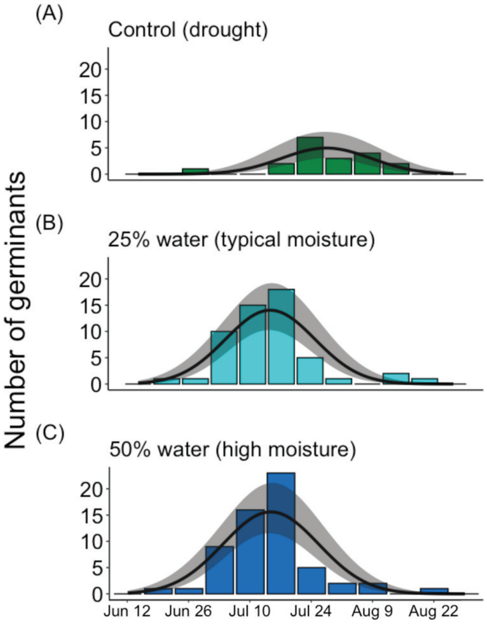
To model germination and survival rates, we used GLMMs with a binomial distribution and a logit link function. Each model included a random effect of block with fixed effects of treatment (control, 25% water, or 50% water) and mean minimum and mean maximum growing-season soil surface temperatures for each block. Germination and survival were run separately. Light availability and mean maximum soil surface temperature were highly correlated (Pearson's $r > 0.8$); thus, only mean maximum temperature was included in the model, as we hypothesized that soil temperature was more important for early seedling establishment. Variance inflation factors for each predictor were all <2. Significant effects of treatment and differences between treatments were tested using a type III ANOVA and Dunnett-adjusted pairwise comparisons of means using the emmeans package (Lenth 2014) in R (R Core Team 2018).

The effect of wildlife exclusion was tested using a similar approach by fitting GLMMs and performing model selection for separate models of germination and survival. Both models had a fixed effect of treatment (caged or uncaged) and a random effect of block, with a binomial response of germination or survival. GLMMs were fit using the glmer function in the lme4 package (Bates et al. 2015); analyses were done in R version 3.5.1 "Feather Spray" (R Core Team 2018).

Results

During the year of the study (2018), the site experienced its hottest growing season (15 May – 1 October) in the past 70 years (for both mean minimum and mean maximum temperatures) and received only half of its typical precipitation (PRISM Climate

Fig. 2. Timing of Douglas-fir seed germination by treatment: (A) control, (B) 25% water addition, and (C) 50% water addition. Model-predicted germination (black line) with a 95% confidence interval (gray shading) over the growing season is shown while holding all other predictors constant. Because of the unusually hot and dry growing season, the control provided drought conditions, whereas the 25% and 50% water additions provided typical and high-moisture conditions, respectively. [Color online.]



Group 2019). Ambient precipitation was sufficiently low that only the water addition treatments had typical growing-season moisture levels: the 25% addition had a seasonal total of 195 mm (86% of mean), and the 50% addition had a seasonal total of 274 mm (121% of mean). The control was, in effect, a drought treatment (51% of mean).

The germination rate across all treatments for Douglas-fir was 17.6%, and survivorship of germinants was 82.8%, with 140 surviving individuals. Repeated-measures tests that found watering treatments were significantly correlated with the timing of germination ($p = 0.01$); nonwatered treatments germinated later than those that received supplemental water (Fig. 2). However, the biweekly ambient precipitation inputs were not associated with the timing of germination.

Mean germination rates were significantly higher in the watered treatments, with germination 1.8 and 2.2 times higher in the 25% and 50% treatments, respectively, than in the control (drought) treatment (Fig. 3A). Once germinated, however, survival was high (>80%) across the caged control and both watering treatments (Fig. 3B). There were no significant effects of wildlife exclusion on germination or survival, though the mean rate of survival was substantially higher in the caged (81%) than in the uncaged control (59%) (Figs. 3A and 3B). Mean daily maximum temperature at the soil surface had a strong negative association with survival (Fig. 3C). Neither temperature variable was associated with germination rates (Supplementary Table S1[1]).

Discussion

This study provides evidence that Douglas-fir regeneration success is limited by moisture and heat stress, even at the cooler and wetter edge of its range. The timing and amount of germination were significantly increased with watering during an unusually dry and hot growing season. Whereas the warmer temperatures across microsites did not affect germination rates, survivorship was markedly reduced in microsites with higher mean daily maximum temperatures. Together, the combined effects of drought (reduced germination) and warmer temperatures (reduced survivorship) strongly limited early recruitment. These microsite and drought treatment effects were likely more pronounced because of the hotter growing-season temperatures (1.7 °C higher than the mean), although these climatic conditions are consistent with future climate projections (Lukas et al. 2018). Whereas complete recruitment failure of Douglas-fir in a hot, dry growing season would be unsurprising in some portions of its range, it is notable that it occurred at the higher elevational (cooler and wetter) end of Douglas-fir's range, precisely where it is predicted to fare well under climate change on the Colorado Front Range (Rehfeldt et al. 2006). If Douglas-fir is unable to recruit under such conditions at its upper elevational limit, the outlook for less drought-tolerant species in such sites is likely to be even poorer.

Numerous studies have also found climate-related recruitment limitations to Douglas-fir at other areas of its range (Williams et al. 2013; Rother et al. 2015; Davis et al. 2019*b*; Hankin et al. 2019), but our study is the first in situ experimental study documenting moisture and temperature limitations to Douglas-fir recruitment at its upper elevational limit. Moisture stress strongly limits Douglas-fir photosynthetic rates, root growth, germination rate, and nutrient uptake and allocation (Roberts et al. 2005; Rother et al. 2015), and despite moderate drought tolerance, Douglas-fir growth is strongly limited by vapor pressure deficits and water availability throughout much of its range (Littell et al. 2008; Restaino et al. 2016). Douglas-fir germinants are more resistant to embolism than other western species, but this resistance is at the cost of hydraulic efficiency and may prove less advantageous in all circumstances except severe drought (Miller and Johnson 2017). The moisture limitation that we observed at the upper extent of Douglas-fir's range suggests that recruitment will be limited to exceptionally cool and wet years.

Wildlife herbivory did not appear to affect germination or first-year survival of Douglas-fir in our study, despite evidence of seed predation and wildlife herbivory substantially limiting germinant survival (Noble and Alexander 1977; Maguire 1989; Pesendorfer et al. 2016). However, germination rates in the uncaged and caged control treatments were low (<10%, likely because of limited water availability); thus, we had limited power to detect differences. Furthermore, seeds were sown in late spring, so seed predation could only occur during a limited time period. We hypothesize that water stress in a hot, dry growing season is the primary limitation on recruitment and that wildlife effects may be important during years of typical and above-average moisture. However, future experimental work that spans multiple growing seasons and climatic conditions is necessary to disentangle the relative importance of water stress and herbivory on limiting Douglas-fir establishment. In addition, research that spans multiple years would allow insights on the relative importance of these factors over time as seedlings mature.

Water availability has been shown to strongly limit tree recruitment (Rother et al. 2015; Kueppers et al. 2017*a*), and these moisture limitations have been documented even at the upper elevational limit of tree species ranges (Daniels and Veblen 2004; Sánchez-Gómez et al. 2006; Kueppers et al. 2017*b*). Consistent with these findings in other ecosystems, we document that water availability during the growing season was a fundamental limitation on germination and that germinant survival was higher in cooler microenvironments at the montane–subalpine ecotone of the

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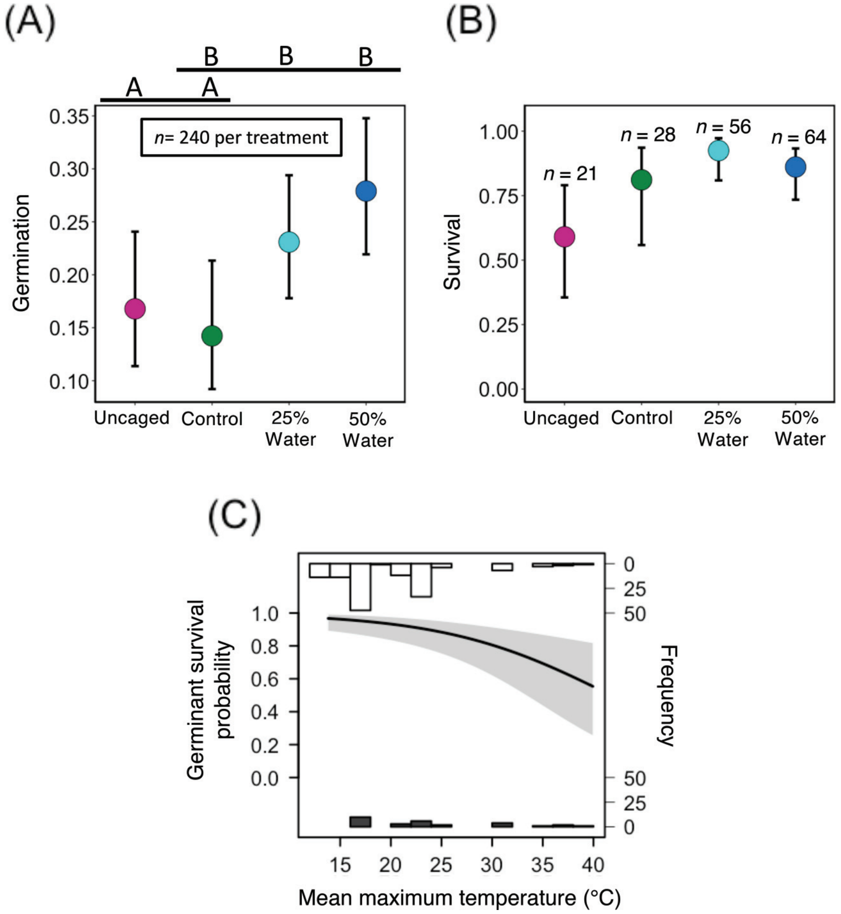
[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2019-0296.

Fig. 3. Mean probabilities (with 95% confidence intervals) from mixed linear regression of (A) germination and (B) survival of Douglas-fir by treatment. Sample sizes for germination (number seeds sown) and survival (number of total germinants) rates are shown. Significantly different groups within each model are denoted by different uppercase letters above the graph. There were no significant differences in germinant survival between watering or wildlife exclusion treatments. Note the different scales in the *y* axes. (C) Predicted effect of mean maximum temperature on the probability of Douglas-fir germinant survival. Histograms show the observed frequencies (secondary *y* axis) of germinants that survived (white, top) and germinants that died (gray, bottom) across mean maximum temperature. [Color online.]



southern Rocky Mountains. Douglas-fir populations near the upper elevational limit of its range may thus experience recruitment failure with increasing aridity and higher temperatures despite drought adaptations and predictions of expansion (Rehfeldt et al. 2006). This also suggests that future Douglas-fir planting efforts will be most successful in cooler and wetter microclimates (such as beneath overstory tree canopies) (Von Arx et al. 2013; Davis et al. 2019*b*) and during years of above-average precipitation, even in locations near the upper elevational range limit of Douglas-fir. This field-based experiment illustrates the complexity in predicting species expansions and the vulnerability of early seedling establishment to changing heat and water stress.

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SUPPLEMENTAL MATERIAL

Table S1. Generalized linear mixed-effect models of Douglas-fir germination and survival on treatment and microenvironment.

Watering and precipitation on timing of germination		
	Chi square	*P* value
Intercept	45.28	< 0.001
Bout × watering treatment	14.70	< 0.001
Bout^2	58.22	< 0.001
Bout	41.13	< 0.001
Watering treatment	4.31	0.003
Precipitation	0.12	0.72

Watering treatments		
Germination model		
	Chi square	*P* value
Intercept	0.61	0.43
Watering treatment	17.06	< 0.001
Mean maximum temperature	1.25	0.26
Mean minimum temperature	0.06	0.81
Dunnett- adjusted pairwise comparison of means	Odds ratio	*P* value
Control - 25% Water	0.39	0.01
Control - 50% Water	0.26	< 0.001
25% Water - 50% Water	0.67	0.24
Survival model		
	Chi square	*P* value
Intercept	3.37	0.07
Watering treatment	2.02	0.36
Mean maximum temperature	9.35	0.002
Mean minimum temperature	0.51	0.48
Dunnett- adjusted pairwise comparison of means	Odds ratio	*P* value
Control - 25% Water	0.37	0.41
Control - 50% Water	0.77	0.93
25% Water - 50% Water	2.09	0.48

Wildlife exclusion		
Germination model	Chi square	*P* value
Intercept	41.66	< 0.001
Wildlife exclusion treatment	0.64	0.42
Survival model	Chi square	*P* value
Intercept	6.10	0.01
Wildlife exclusion treatment	1.23	0.27