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The Challenges of Early Life for Coniferous Trees of the Pacific Northwest

(Peer Reviewed)

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Abstract

Climate change may alter germination of Washington's dominant trees through changes in plant-relevant climatic factors such as soil moisture and snowpack. Responses may be species-specific, altering relative abundances of co-occurring species and changing forest structure. We examined this possibility for conifers in Washington State by: 1) quantifying mortality at early life history stages; 2) identifying environmental variables that influence germination and 3) assessing community composition across adult, seed, and seedling stages. We found high mortality rates from seed to second-year seedling stages for all focal species (*Pseudotsuga menziesii*, *Thuja plicata*, and *Tsuga heterophylla*). Climatic factors likely to be altered by climate change affected the germination of all focal species in ways that could further benefit the successful *Tsuga*. However, understory cover consistently influenced germination, suggesting responses to climate change will be complicated by factors like competition. Community composition differed between adult, seed, and germinant stages, with *Tsuga* dominating at all stages. In all, our results imply responses of early life stages to climate change could affect forest communities in the Pacific Northwest (PNW).

Key Words: Coniferous forests, recruitment, climate change, Wind River Forest Dynamics Plot

Introduction

All trees must begin their lives as seeds. These seeds, and the seedlings they germinate into, experience high mortality because they are sensitive to many factors, including climate (Kroiss and HilleRisLambers 2015). Indeed, the differential effects of climate on tree seedling species may influence the composition of current as well as future forests in a changing climate (Kroiss and HilleRisLambers 2015, Ettinger and HilleRisLambers 2017, Das et al. 2018, Zolbrod and Peterson 1999).

Previous work demonstrates that climate change will influence adult trees (Ettinger et al. 2011, Legendre-Fixx et al. 2018); however, less is known about climate impacts on seeds and seedlings (but see Kroiss & HilleRisLambers 2015, Ettinger & HilleRisLambers 2017). To address this, we examined germination of dominant conifers in a low elevation old-growth forest in Washington State. We first quantified mortality across early life stages (from seeds to germinants to second-year seedlings). We then determined how environmental factors, including those likely to be altered by climate change (Salathé et al. 2010), affect germination. These factors were both climatic and biotic, and their role in recruitment has been the subject of previous studies (Mallik and Prescott 2001, Christy and Mack 1984, Harmon and Franklin 1989). Finally, we quantified diversity across three life stages: adult, seed, and germinant, to assess changes in community composition between stages.

Methods

Study Site

The 27.2 ha Wind River Forest Dynamics Plot (WFDP) is located in southern Washington (45.8197° N, 121.9558° W) at a mean elevation of 370 m (Lutz et al. 2013). The WFDP is old-growth forest (~525 years) dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Western red cedar (*Thuja plicata*), silver fir (*Abies amabilis*), and Pacific yew (*Taxus brevifolia*) occur at lower abundances (Lutz et al. 2013). Understory indicator species include vine maple (*Acer circinatum*), sword fern (*Polystichum munitum*), Oregon-grape (*Mahonia nervosa*), salal (*Gaultheria shallon*), vanilla leaf (*Achlys triphylla*), and foamflower (*Tiarella trifoliata*) (Lutz et al. 2013). Plant nomenclature follows Hitchcock and Cronquist (2018).

Sampling

In summers from 2014 to 2017, we surveyed 40 subplots within the WFDP (32 in 2017), each consisting of a 0.127 m² seed trap and a 1 m² quadrat (Figs. 1 and 2). Seed trap contents were sorted annually to quantify species-specific seed abundances (Kroiss and HilleRisLambers 2015). Seedling
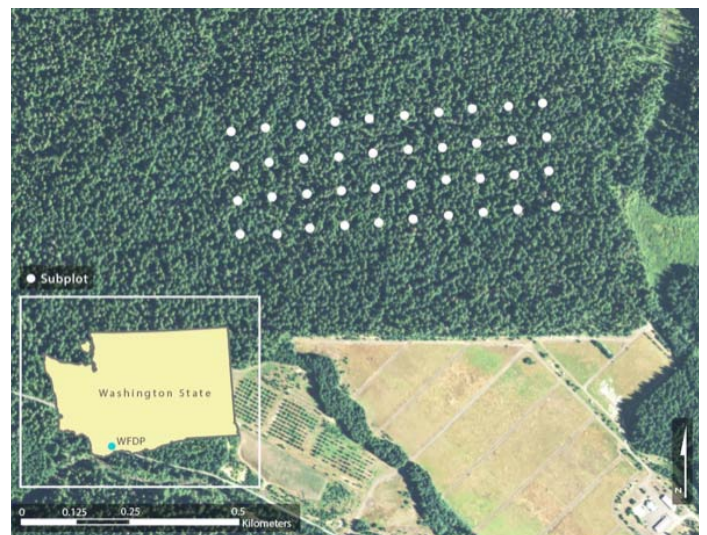

Figure 1: Forty subplots (white dots) were distributed in an 80 m grid throughout the WFDP.

identity, density, and age were surveyed in adjacent quadrats. The WFDP tree demography study provided information on the identity and diameter of all trees ≥1 cm diameter at breast height (DBH) surrounding subplots (Lutz et al. 2013).

We quantified environmental factors at each quadrat (Table 2). We visually estimated the percentage of each quadrat covered by understory vegetation and nurse logs. We quantified canopy openness using a densiometer (Lemmon 1956) and soil moisture using a Decagon Devices ECH20 probe (Decagon Devices, Pullman, Washington, USA). Finally, we calculated snow cover duration (in days) from temperature readings collected using HOBO temperature loggers (Onset Computer;

Figure 2. Lewis and Clark College students survey a seed trap (left) and seedling quadrat (right).

Bourne, Massachusetts, USA; see Kroiss and HilleRisLambers 2015, Raleigh et al. 2013).

Statistics

We calculated the density of seeds, germinants, and second-year seedlings from all subplots and years for three focal species (*Pseudotsuga*, *Thuja*, and *Tsuga*) and used analyses of variance and a post-hoc Tukey test to show how these densities varied between stages. We also estimated average mortality from year-subplot specific transition rates.

We fit generalized mixed effects models with binomial error and a logit link to subplot-year seed and seedling data with non-zero seed or germinant values (288 out of 456 possible combinations), to quantify effects of soil moisture, snow duration, canopy openness, vegetation, and nurse logs on germination of focal species. When seed densities were less than germinant densities (23 out of 288 instances), we assumed seed densities equaled germinant densities. Subplot ID and year were random effects, except for *Pseudotsuga* models with only subplot ID random effects due to model convergence issues.

We standardized explanatory variables to facilitate comparison of coefficients, and did not fit interactions due to a lack of power.

We next determined the relative abundance of all tree species at adult, seed, and germinant stages across subplots. For seeds and germinants, we considered averages across all four years of sampling. For trees, we considered relative abundances of trees >10 cm DBH in 2017 within 20 meters of each seed trap. We used these data to calculate Shannon-Wiener diversity at each subplot, and applied analyses of variance with a post-hoc Tukey test to analyze how diversity changed across stages.

All analyses were conducted using R (version 3.4.4) and RStudio (RStudio Team 2016) and the package lme4 (version 1.1.21) for generalized mixed effects models (Bates et al. 2015).

Results

All focal species densities declined significantly from seed to germinant stages, while declines from germinant to second-year stages were not significant (Fig. 3). Mortality was high for
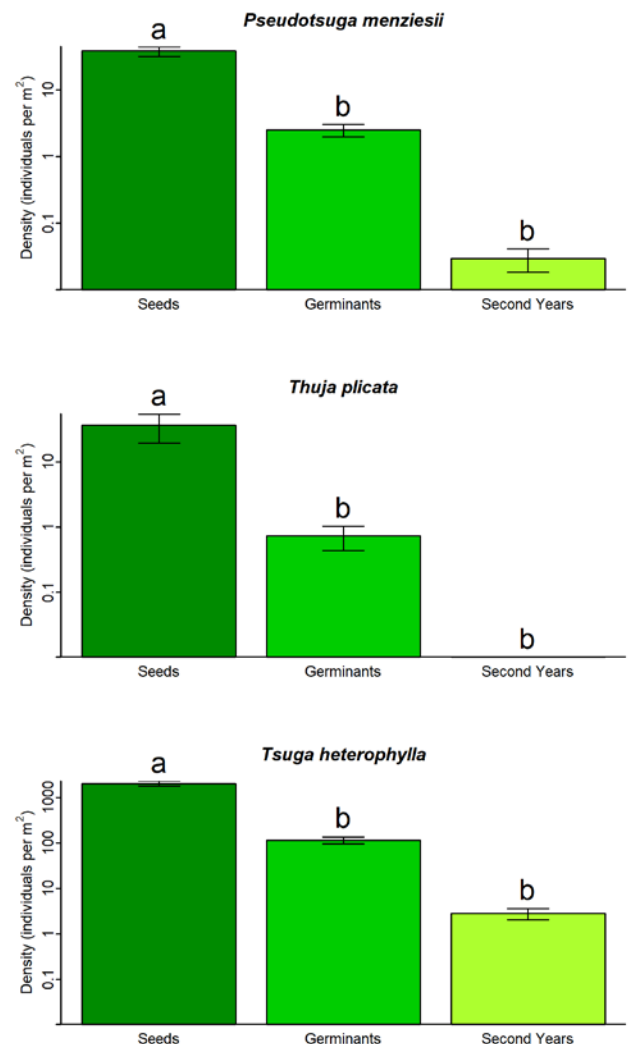

Figure 3. Mean ± SE seed, germinant, and second-year seedling densities (log-transformed, 0.01 set as the baseline) for three focal species. Different letters indicate significant differences between means at α < 0.05.

all species and all transitions (Table 1). Seed density was much higher for *Tsuga* than for *Pseudotsuga* and *Thuja*.

Some effects of the environment on germination were generalizable (Table 2): understory vegetation negatively and nurse logs positively affected germination of all species (although not significantly for all). Other variables had less consistent effects; for example, canopy openness only significantly influenced germination of one species (*Thuja*). Soil moisture positively affected *Thuja*, but negatively affected *Tsuga* germination. Similarly, snow duration positively affected *Pseudotsuga* germination, but negatively affected *Tsuga* germination.

Transition	*Pseudotsuga menziesii*	*Thuja plicata*	*Tsuga heterophylla*
Seed-germinant	88.1	72.6	93.8
Germinant 2nd year	95.2	100	86.5
Seed–2nd year	99.4	100	99.2

Table 1. Mortality (%) observed during early life stages.

Coefficient	*Pseudotsuga menziesii*	*Thuja plicata*	*Tsuga heterophylla*
Canopy Openness	-0.137	2.205*	-0.050
Percent Cover Nurse Log	0.351*	1.181	0.272*
Percent Cover Vegetation	-0.307	-4.819*	-0.383*
Soil Moisture	0.097	3.807*	-0.103*
Snow Duration	0.830*	1.881	-1.125*
* significant at $\alpha < 0.05$			

Table 2. Model coefficients describing environmental effects on germination of three focal species.

Composition varied from tree to seed to seedling, with *Tsuga* dominating at all stages, especially at seed and germinant stages (Fig. 4A). This was driven by extremely high seed production in *Tsuga* (Fig. 4A – note y axis scale). As a consequence, the diversity of seeds and germinant communities are both lower than that of adults (Fig. 4B).

Discussion

Our findings suggest early life history stages may strongly influence forest community composition, with at most 8 in 1000 dispersed seeds surviving as seedlings two years after dispersal (based on *Tsuga* mortality, the lowest rate we observed; Table 1). We also found that environmental factors, including those influenced by climate change, explained some variation in germination success, suggesting that these dynamics could structure future forests. Community composition of adults differed from juvenile stages largely because of the high fecundity of *Tsuga*.

Soil moisture and snow duration, both predicted to decrease with warming climates (Salathé et al. 2010), influenced germination of the region's dominant conifers in our study (Table 2). Positive effects of soil moisture and snow duration may occur if seeds and seedlings are protected from desiccation in moist or snow-covered microsites. Conversely, negative effects of these factors could result if moist soils are associated with fungal pathogens or if longer snow duration shortens the growing season (Ettinger and HilleRisLambers 2017). Our study suggests that declining snow and soil moisture with climate change could benefit *Tsuga* over two other dominant conifers (Table 2), although a similar study found opposite effects of soil moisture on *Tsuga* (Kroiss & HilleRisLambers 2015). Regardless of the direction of effects, our results demonstrate climate change could differentially alter germination success, and thus, forest structure.

However, factors other than climate will also influence seed and seedling dynamics. For example, understory cover negatively affected germination, suggesting competitive interactions (Table 2). This is consistent with previous studies documenting negative effects of canopy cover on germination (Kroiss and
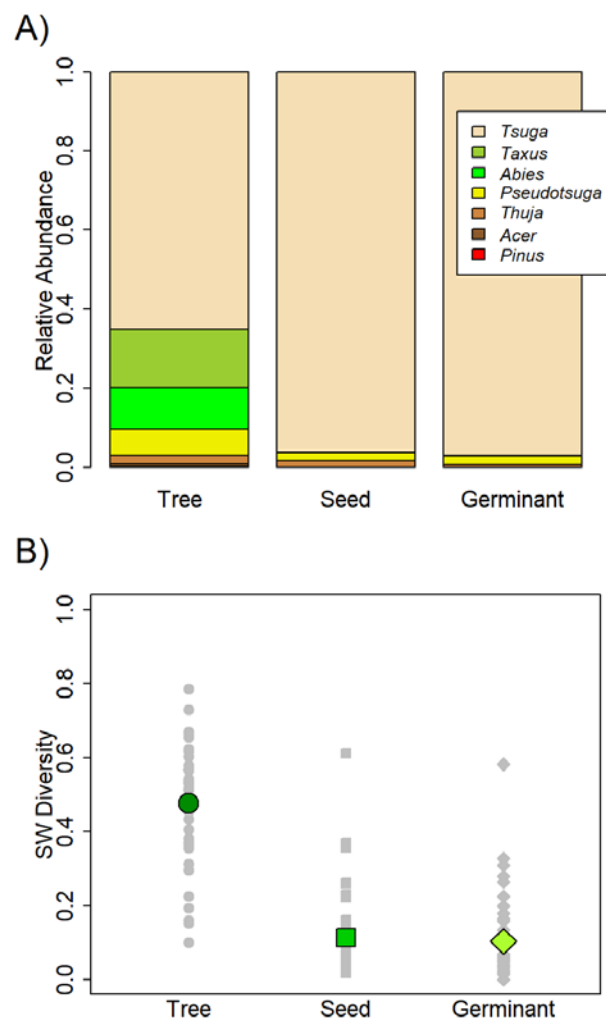

Figure 4. A) Community composition and B) Shannon-Wiener diversity at tree, seed, and germinant stages. Seed and germinant communities were significantly less diverse than trees (p < 0.0001), but similar to each other (p = 0.942).

HilleRisLambers 2015, Mallik and Prescott 2001) and inhibitory effects of large trees on the growth of small trees (Lutz et al. 2014). Positive effects of nurse log cover on two focal species are also consistent with previous studies (Christy and Mack 1984, Harmon and Franklin 1989), and may arise because decaying logs maintain higher moisture in dry summers.

Our study adds to others suggesting climate change will have complex effects on forests, both due to species-specific responses to climate and the effects of non-climatic variables (HilleRisLambers et al. 2015, Table 2). For example, the predicted decrease in snow duration in the PNW (Salathé et al. 2010), which will likely be associated with declines in soil moisture, could negatively affect *Thuja* and *Pseudotsuga* while benefitting *Tsuga* (Table 2). However, the effects of climate change on understory cover and nurse logs, which had more consistent effects on germination (Table 2), are unknown. These non-climatic factors thus complicate our ability to predict impacts of climate change on early life stages.

In conclusion, we believe forest composition can be influenced by dynamics at early life history stages. For example, forest community composition in seed and seedling stages was markedly different than that of adult trees (Fig. 4; Larson et al. 2015), presumably due to the high fecundity and lower mortality of *Tsuga* at seed and seedling stages (Fig. 3). With climate change, the differential effects of plant-relevant climatic factors on fecundity, germination (e.g. Table 2) and seedling stages (e.g. Ettinger & HilleRisLambers 2017) may further change the community composition of seedlings and eventually forests. Because seed and seedling dynamics are understudied in comparison to adult trees, we suggest future studies should explore how climate change effects on early life history stages can influence forest composition.

Acknowledgements

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