First report of enhanced root growth potential achieved by drought preconditioning of western larch (*Larix occidentalis*) seedlings reveals insights into improving drought preconditioning studies

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Abstract

Fine-tuning drought preconditioning regimes for enhanced drought hardiness is an increasingly pressing matter in plant science as the demand for drought hardy seedlings rises alongside global temperatures. First-year western larch (*Larix occidentalis* Nutt.) seedlings were drought-preconditioned under three soil moisture contents for six months and subjected to 21-days of aeroponic growth to assess whether a history of water limitation can be used to increase the ratio of root versus foliar tissue during a subsequent growth period. Drought preconditioning severity related positively with new root biomass, negatively with new foliar biomass, and positively with the length and number of new roots ($P < 0.001$). The mass of lateral root production following drought preconditioning, but prior to aeroponic growth, correlated weakly to the mass, count, and length of new roots produced during aeroponic growth. Drought preconditioning thus appears to have promoted changes in seedling physiology that led to greater root production. However, investigations of plant responses to stress during only one developmental stage may fail to capture effects of ontogeny on plant acclimation processes, and may thereby hinder progress in abiotic stress preconditioning research. We present the perspective that the timing and duration of drought preconditioning treatments represents an important research frontier with the capacity to facilitate climate-ready food systems and forests.

Introduction

Aridity in western North America threatens the survival of planted and natural tree seedlings (Vilagrosa et al., 2003; Minott and Kolb, 2020). Controlled exposure to water limitation in tree nurseries prior to outplanting (i.e. drought preconditioning) may increase seedling survival through altered seedling morphology and physiology while reducing water consumption (Close et al., 2005; Grossnickle, 2012; Sloan et al., 2020). However, drought preconditioning does not always enhance seedling drought tolerance, and there is thus a need to optimize preconditioning protocols to improve seedling drought tolerance without impairing seedling physiology (Villar-Salvador et al., 2013;

Dumroese et al., 2015). In addition to presenting results on root growth following drought preconditioning of western larch (*Larix occidentalis* Nutt.) seedlings, we advocate in this perspective paper for greater investigation into the effect of the timing of exposure to water limitation on seedling responses, which, compared to the severity of water limitation, has received scant attention to date.

Short-term drought preconditioning treatments are easier to conduct and more common than longer-term treatments, but evidence suggests that long-term treatments may be more effective at facilitating plant acclimation to drought (Duguy et al., 2013). For example, a study of three *Eucalyptus* spp. from xeric and riparian habitats showed that photosynthetic and hydraulic acclimation to drought conditions occurred after four months of drought exposure but not after only two months of drought exposure (Zhou et al., 2016). This compares with studies that examined the effects of drought preconditioning on root growth potential (RGP; a measure of plant physiological vigor that evaluates new root production after a short period of growth under optimal growth conditions in a controlled environment; Folk and Grossnickle, 1997), which have typically used a limited-duration period of water limitation. Villar-Salvador et al. (1999) subjected seedlings of *Pinus halapensis* Mill. to two months of water limitation and concluded that drought significantly reduced RGP. Using a rapid dry-down technique consisting of 20 minutes versus two hours of root desiccation via exposure to air, Tinus (1996) found that RGP of Douglas-fir (*Pseudotsuga menziesii* var. glauca) seedlings decreased as the duration of root desiccation increased. In a study of three conifer species exposed to a treatment of varying water limitation intensities lasting 2.5 months, the RGP of white spruce (*Picea glauca* (Moench) Voss) increased with water limitation, but RGP of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and lodgepole pine (*Pinus contorta* Dougl.) was not affected (Driessche, 1992). And in a study of *Pinus pinea* L. exposed to three months of water limitation using three watering levels, Villar-Salvador et al. (2013) found that RGP decreased with the intensity of water limitation. While evidence suggests that drought preconditioning does not always enhance RGP, for most species it remains unknown how long-term drought preconditioning affects RGP and drought acclimation.

Western larch is a deciduous conifer species that occurs across the Inland and Pacific Northwest of North America, provides valuable timber and ecosystem services (Schmidt and Shearer, 1995), and is threatened by climate change (Rehfeldt and Jaquish, 2010). Drought preconditioning may improve establishment of planted western larch seedlings under dry conditions, but the effect of drought preconditioning of any duration on drought hardening in western larch remains unknown. The following two research questions were addressed to determine whether long-term drought preconditioning promotes morphological traits associated with drought hardiness without impairing physiological vigor in western larch.

1) Does long-term drought preconditioning increase the ratio of new root tissue mass fraction to new foliar tissue mass fraction?

2) Does long-term drought preconditioning negatively affect seedling physiological vigor as expressed by shorter or fewer new roots?

Methods

Seeds from six provenances across southeastern British Columbia, Canada and two half-sib improved families from a seed orchard in British Columbia representing seed sources in northwestern Montana, USA were used in this study. Western larch seedlings were grown in a greenhouse in 415C

Styroblock® containers (Beaver Plastics, Alberta, Canada) with cavity volumes of 130 ml. Seeds were sown by hand in Styroblock® container cavities filled with Berger© BM8 growing media (Saint-Modeste, QC, Canada) amended with 7.9 g slow-release Osmocote® fertilizer (N = 15%, P = 9%, K = 12%) per liter soil media. Cavities were topped with TARGET® Forestry Sand (no. 9992002; Burnaby, BC, Canada) and thinned to one seedling per cavity as seedlings emerged. Beginning 6.5 weeks after sowing, planted seedlings were subjected to 26 weeks of drought preconditioning treatments (from June 1st – November 30, 2020) by holding plants at the following three gravimetric soil moisture contents: Low (50%-65% saturated container weight), Medium (60%-75% saturated container weight), and High (75%-100% saturated container weight). To establish saturated container weights, tray weights were measured after watering planted Styroblock® containers with a boom irrigation system until tray weight did not increase after further watering, and after gravitational water drained from trays for one hour (following MacDonald et al., 2012). New saturated container weights were calculated monthly to adjust for increases in seedling mass. Targeted percentages of saturated container weights were maintained by weighing containers daily and irrigating trays when tray weights reached the lowest weight permitted for a given soil moisture content treatment (e.g. 50% saturated container weight for the Low treatment). Each pass of the boom irrigation system increased tray weights by 5% of saturated container weight, which facilitated application of the volume of water needed to restore tray gravimetric moisture contents to the maximum content permitted for each treatment. Container weights were based on the average weight across five trays per soil moisture treatment. Bud set was hastened using a 12-day reduced day-length treatment (10.5 hrs light, 13.5 hrs dark) applied 9.5 weeks after initiating drought preconditioning. Average temperature in the greenhouse from the start of the experiment until the end of the short-day treatment was 21.7 °C and average relative humidity was 66%. Eight months after seed sowing, seedlings were removed from containers following standard practices used at the University of Idaho Franklin H. Pitkin Forest Nursery, i.e. trays were secured in-place and seedlings were gently pulled from cavities by the base of seedling stems. Seedlings were then stored at -2.2 °C for one month prior to the RGP trial.

Twenty seedlings from each provenance × watering regime combination (n = 480) were slowly thawed in a refrigerator at 2 °C for two days before gently washing roots free of soil media with tapwater. Rubber gaskets set into a plastic hanger were secured around seedling root collars to suspend roots atop misting chambers as described in Nelson (2019). Full spectrum LED light panels were suspended above chambers to a height at which seedlings were evenly illuminated with a photosynthetic photon flux density of 250 µmol m^{-2} s^{-1} under a photoperiod of 14-hour days and 10-hour nights. Seedlings were grown in mist chambers for 21 days before recording the following measurements: seedling height from root collar to the distal end of the terminal bud (cm), root collar diameter (mm) at the location where hypocotyl and root tissue differentiate visually, the number of new white root tips ≥ 1 cm in length, and the length of the longest new root (cm), following Nelson (2019). New white lateral root tissue was separated from old (dark-toned) lateral root tissue with a razor and placed in coin envelopes to dry. Old lateral root tissue was separated from taproot tissue, and each tissue type was placed in coin envelopes to dry. All tissues were dried in a force-draft oven for a minimum of 72 hours at 65 °C. Weights of each root tissue type and aboveground growth produced during the RGP trial, as well as weights of roots and woody stem and foliage prior to the RGP trial, were recorded to the nearest 10^{-4} gram using a Veritas® M214I balance (H & C Weighing Systems ™).

Seedling root length and the ratio of new root mass fraction to new foliage mass fraction in response to drought following the first growth season were assessed using linear mixed-effect models (lme4 package in the *R* statistical environment, version 3.6.2). Count of new root tips was treated as an integer and analyzed specifying a Poisson distribution and log-link function in a generalized linear mixed-effects model (glmmTMB package in *R*). A Gaussian distribution was specified for models of all other response variables. For all models, provenance was included as a random effect and normality of model residuals was assessed using quantile-quantile plots. Tukey HSD was used to calculate post-hoc contrasts. Estimated marginal means and corresponding confidence intervals of new root count were back-transformed from log values derived from models following Strimbu et al. (2018). To investigate whether initial lateral root mass (i.e. following drought preconditioning but before aeroponic growth) influenced the production of roots during aeroponic growth, Pearson product-moment correlations were calculated for initial lateral root mass as a function of: (1) new lateral root mass, (2) new root tip count, and (3) length of the longest new root.

Results

The first research question was supported in that water limitation during long-term drought preconditioning increased the ratio of new root tissue to new foliar tissue mass (χ^2 = 184.13, $P = 2.2e^{-16}$, Table 1A, Fig. 1A). The largest proportional difference in new biomass attributed to new roots versus new foliage occurred between the Medium and Low watering treatments (Table 1A). Water limitation during drought preconditioning correlated positively with new root mass and negatively with new foliage mass (Table 1B), though when corrected for initial total mass it is evident that root production responded more than foliage production to water limitation (Fig. 1B & Fig. 1C). For each gram of initial lateral root biomass, seedlings in the Low, Medium, and High watering treatments produced a mean of 0.11 g, 0.07 g, and 0.04 g of new root biomass, respectively. Meanwhile, lateral root masses at the end of the drought preconditioning period and prior to the RGP study were 0.77, 0.89, and 0.76 for seedlings subjected to the Low, Medium, and High watering treatments, respectively. A low but statistically significant correlation was found between initial lateral root mass and the mass of new roots produced during the RGP trial (r = 0.13, t = 2.5, P = 0.012)

The second research question was not supported, i.e. water limitation corresponded to a greater abundance of new roots (χ^2 = 1208.9, P < 0.0001, Table 1A) and longer new roots (χ^2 = 97.2, P < 0.0001, Table 1A). The largest increase in root number and root length across levels of water limitation occurred between the High and Medium treatments (Table 1A), and water limitation correlated positively with both the number of new root tips and the length of the longest new roots (Figures 1C and 1D, Table 1B). Low but statistically significant correlations were found between initial lateral root mass and root tip count (r = 0.26, t = 5.8, P = 1.212e-08), and between initial lateral root mass and the length of the longest new root (r = 0.13, t = 2.9, P = 0.003).

Discussion

Long-term drought preconditioning of western larch seedlings promoted an increase in the production of new roots relative to new foliar tissue. Altered partitioning of carbon between root and shoot tissues linked to water limitation may be due to responses of plant hormones, such as auxin, abscisic acid, gibberellin, and cytokinin, to water limitation (McAdam et al., 2016; Omena-Garcia et al., 2019; Ramachandran et al., 2020; Sinclair and Friml, 2019). Morphological shifts to more root versus foliar tissue are expected to correspond to reduced seedling transplant shock and greater seedling outplanting survival due to greater root abundance facilitating enhanced uptake of soil water coupled with decreased foliar tissue and associated reductions in leaf-level evaporative demand (Close et al., 2004; Grossnickle, 2005). Furthermore, long-term drought preconditioning appears to have enhanced the physiological vigor of western larch seedlings, as water limitation increased the mass, count, and length of new roots produced during aeroponic growth (none of which were strongly correlated with initial lateral root mass). These results agreed with those of Pritzkow et al. (2021), who subjected seedlings of *Eucalyptus obliqua* to long-term drought preconditioning and found that preconditioning induced drought-adaptive reductions in foliar biomass. Pritzkow et al. (2021) reported that drought preconditioning did not influence plant water-relations or anatomy, but the smaller aboveground mass of preconditioned seedlings was associated with reduced water use and increased seedling survival under dry outplanting conditions. While it is unknown how seedlings might respond to short-term drought preconditioning, this study establishes that long-term preconditioning of western larch promotes seedling responses considered desirable for outplanting into dry conditions. Future studies should be conducted to establish whether a less technically demanding short-term preconditioning treatment achieves similar results.

Related evidence suggests that the plant developmental period during which abiotic stress exposure occurs may be another important dimension to consider in optimizing drought preconditioning regimes. For example, in a study of the timing of greatest sensitivity to moderate moisture stress, Álvarez et al. (2013) found that geraniums (*Pelargonium* × *hortorum* L.H. Bailey) watered to 75% of container weight at field capacity during flowering were stunted in height and produced less flowers than plants subjected to moisture deficits outside of the flowering period. In a potted study, responses of Aleppo pine (*Pinus halapensis* Mill) exposed to drought stress during the first and second years of growth differed markedly due to the developmental stage at which drought occurred (Alexou, 2013). In a field study of *Pinus tabuliformis* exposed to three drought hardening intensities crossed with three durations of drought in the nursery, Luo et al. (2021) found that seedlings exposed to the medium-duration drought treatment had the highest mortality but greatest growth in the field whereas drought hardening intensity did not affect mortality and had a minor effect on seedling growth. In a study of southwestern white pine (*Pinus strobiformis* Engelm.) seedlings exposed to experimental warming during embryogenesis, seed germination, and early seedling growth, Moler et al. (2021) found that elevated temperatures during germination and early seedling growth, but not during embryogenesis, altered oxidative stress resistance, seedling morphology, and water relations physiology. Meanwhile, seedling survival was influenced by warming applied during all developmental stages. Given the prevalence of short-term rather than long-term abiotic stress preconditioning treatments in the literature and in practice, it remains unknown whether drought preconditioning would result in equally desirable seedling responses if applied when seedlings are rapidly growing as opposed to when seedling meristematic activity and growth slows (i.e., hardening phase). The drought preconditioning treatment used in the present study was initiated during the beginning of the rapid growth phase and was maintained through the hardening phase, which may have been instrumental in producing the drought acclimation that was achieved. Based on this and prior studies, we encourage future investigations into the potential for not only the severity but also the timing of drought preconditioning, including each seedling growth phase separately and a long-term treatment encompassing all phases, to induce desirable drought acclimation responses. Finally, the efficacy of a drought preconditioning regime should always be evaluated using field trials that measure survival through at least the second year of growth under dry conditions, as illustrated by Benigno et al. (2014).

Author Contributions

Both authors designed the study, grew the experimental seedlings, and conducted measurements. ERVM analyzed the data and drafted the manuscript. ASN provided critical reviews and coordinated funding that facilitated this project.

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Data Availability Statement

The dataset analyzed for this study is available through Open Science Framework as: Moler, E. (2021, July 13). Timing is Everything: Long-duration drought preconditioning induces drought-hardy traits in western larch (*Larix occidentalis*) seedlings. Retrieved from osf.io/jer72.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Table 1. (A) Estimated marginal means of treatment contrasts. CL is 95% confidence limit; *t* is the calculated *t* statistic; *P* indicates the probability of observing the value of *t* by chance. (B) Morphological measures by drought preconditioning treatment (±95% confidence interval shown in parentheses).

<u>Table 1A</u>

	Treatment Contrast	*P*	Estimate	SE	*t*
New Root : Shoot Mass Fraction	Low - Medium	< 0.0001	0.076	0.009	8.441

	Low - High	< 0.0001	0.121	0.009	13.423
	Medium - High	< 0.0001	0.045	0.009	5.011
	Treatment	**Emmean**	**lower.CL**		**upper.CL**
	Low	0.151	0.138		0.164
	Medium	0.075	0.062		0.088
	High	0.030	0.017		0.043
Count of New Root Tips	**Treatment Contrast**	***P***	**Estimate**	**SE**	***t***
	Low - Medium	< 0.0001	0.169	0.016	10.870
	Low - High	< 0.0001	0.615	0.018	34.712
	Medium - High	< 0.0001	0.446	0.018	24.450
	Treatment	**Emmean**	**lower.CL**		**upper.CL**
	Low	56.990	53.671		59.912
	Medium	48.080	45.280		51.053
	High	30.657	28.872		32.553
Length of Longest New Root	**Treatment Contrast**	***P***	**Estimate**	**SE**	***t***
	Low - Medium	0.0014	1.670	0.477	3.511
	Low - High	< 0.0001	4.640	0.478	9.708
	Medium - High	< 0.0001	2.970	0.477	6.218
	Treatment	**Emmean**	**lower.CL**		**upper.CL**
	Low	11.600	10.780		12.430
	Medium	9.930	9.110		10.750
	High	6.960	6.130		7.790

Table 1B

Treatment	**New Foliage Mass (g)**	**New Root Mass (g)**	**New Root Tip Count**	**Longest New Root Length (cm)**
Low	0.57 (±0.03)	0.08 (±0.01)	56.73 (±4.31)	11.60 (±0.65)
Medium	0.84 (±0.04)	0.06 (±0.01)	48.04 (±4.33)	9.93 (±0.76)

High	1.11 (±0.05)	0.03 (±0.01)	30.74 (±3.43)	6.96 (±0.59)

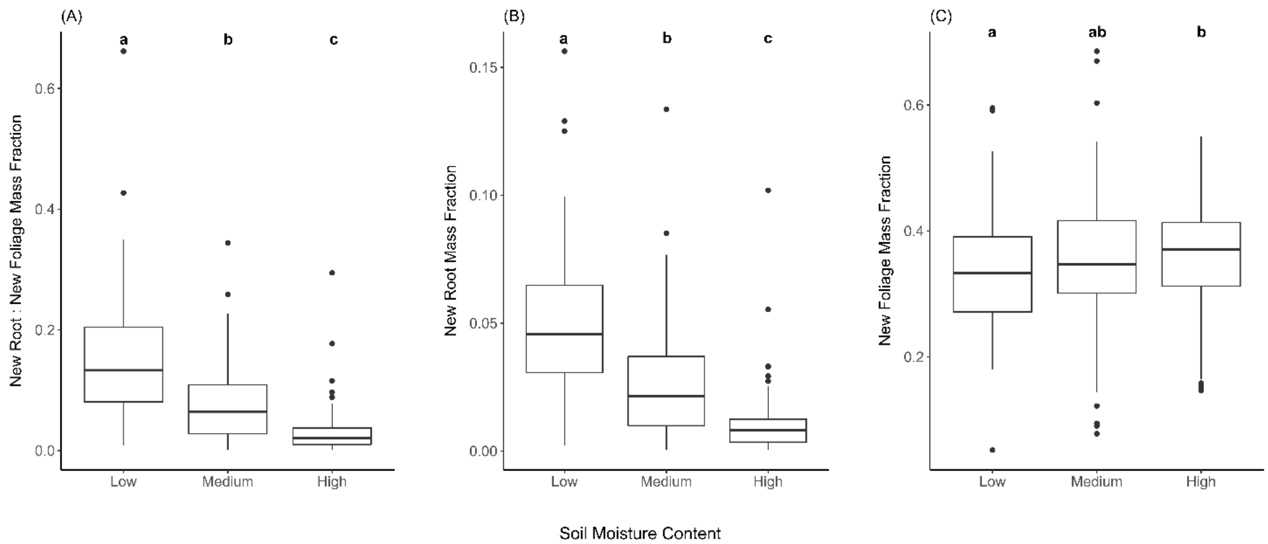

Figure 1. New root and foliage tissue biomass responses to drought preconditioning soil moisture contents. Treatment levels that do not share lower-case letters within a panel are significantly different based on Tukey's HSD pairwise comparisons (*P* < 0.05).