

## ARTICLE

# Seedbed not rescue effect buffer the role of extreme precipitation on temperate forest regeneration

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**Abstract**

Alterations in global climate via extreme precipitation will have broadscale implications on ecosystem functioning. The increased frequency of drought, coupled with heavy, episodic rainfall are likely to generate impacts on biotic and abiotic processes across aquatic and terrestrial ecosystems. Despite the demonstrated shifts in global precipitation, less is known how extreme precipitation interacts with biophysical factors to control future demographic processes, especially those sensitive to climate extremes such as organismal recruitment and survival. We utilized a field-based precipitation manipulation experiment in 0.1 ha forest canopy openings to test future climate scenarios characterized by extreme precipitation on temperate tree seedling survival. The effects of planting seedbeds (undisturbed leaf litter/organic material vs. scarified, exposed mineral soils), seedling ontogeny, species, and functional traits were examined against four statistically defined precipitation scenarios. Results indicated that seedlings grown within precipitation treatments characterized by heavy, episodic rainfall preceded by prolonged drying responded similarly to drought treatments lacking episodic inputs. Moreover, among all treatment conditions tested, scarified seedbeds most strongly affected seedling survivorship (odds ratio 6.9). Compared with any precipitation treatment, the effect size (predicted probabilities) of the seedbed was more than twice as important in controlling seedling survivorship. However, the interaction between precipitation and seedbed resulted in a 27.9% improvement in survivorship for moisture-sensitive species. Seedling sensitivity to moisture was variable among species, and most closely linked with functional traits such as seed mass. For instance, under dry moisture regimes, survivorship increased linearly with seed mass (log transformed; adjusted  $R^2 = 0.72$ ,  $p < 0.001$ ), yet no relationship was apparent under wet moisture regimes. Although precipitation influenced survival, extreme rainfall events were not enough to offset moisture deficits nor provide a rescue effect under drought conditions. The relationships reported here highlight the importance of plant seedbeds and species (e.g., functional traits) as edaphic and biotic controls that modify the

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influence of extreme future precipitation on seedling survival in temperate forests. Finally, we demonstrated the biophysical factors that were most influential to early forest development and that may override the negative effects of increasingly variable precipitation. This work contributes to refinements of species distribution models and can inform reforestation strategies intended to maintain biodiversity and ecosystem function under increasing climate extremes.

#### KEYWORDS

drought, episodic rainfall, functional traits, ontogeny, precipitation manipulation, scarification, seed mass, seedlings

## INTRODUCTION

Anthropogenic climate change is expected to alter ecological processes throughout global ecosystems. Of principal concern are changes in precipitation regimes, which have been documented worldwide as the impacts of global change have become more apparent (IPCC, 2014). Increases in precipitation extremes (i.e., severe droughts, intense flooding) have already been observed (Alexander et al., 2006) and are projected to increase over the 21st century (Sun et al., 2007). These shifts in precipitation volume and frequency are expected to generate impacts on a wide range of human-built and natural environments, modifying ecosystem responses to the effects of global change (Knapp et al., 2008; Veronesi et al., 2014; Woolway et al., 2020). Quantifying the effect of extreme precipitation events on ecosystem functioning is critical for understanding and anticipating changes in community structure, composition, and dynamics.

Many ecosystems are constrained by intermittent, pulsed resources and the timing of these resources can strongly shape the development and dynamics of ecological communities (Roxburgh & Noble, 2001). Likewise, precipitation extremes can cause short-term (i.e., hourly, diurnal) and long-term (i.e., seasonal, annual) alterations in the timing of rainfall, duration between events, or the total accumulation outside the historic range of variability. The increased propensity for episodic, high-intensity rainfall has gained considerable attention given that these extreme precipitation events may alter the hydrological cycle and dynamics of ecological communities (Allan & Soden, 2008; Heisler-White et al., 2008). As such, there is a high likelihood of shifts in ecosystem function if the timing and magnitude of these events change. For example, episodic, extreme precipitation has led to documented changes in grassland net primary production (Felton et al., 2019), aquatic food webs and biogeochemical cycles (Woolway et al., 2020), and wildlife species fecundity (Fisher et al., 2015). Additionally,

interactions among biotic factors and climate have been observed among many ecosystems and organisms (Aubin et al., 2016; Gleason et al., 2017). Nevertheless, there is less experimental evidence documenting how more frequent, episodic extreme precipitation may affect key ecosystems such as temperate forests and especially the future demography of the species contained therein (Asbjornsen et al., 2018).

Plant demographic processes, such as establishment, migration, and survival, have been linked to climate sensitivity (Ogaya & Peñuelas, 2007). Concurrently, plant recruitment is a critical demographic stage controlled by many factors, of which climate (namely temperature and precipitation) is central to germination and seedling performance (Walck et al., 2011). The role of climate on plant recruitment has long been investigated and the effects of shifting future precipitation regimes have been demonstrated across multiple systems (Canham & Murphy, 2016; Lloret et al., 2004; Walck et al., 2011). Still, given the spatiotemporal variability in climate extremes and plant responses, the ways in which seedling establishment will be filtered by global change agents such as extreme precipitation is not fully understood. For long-lived perennial plants such as trees, the response to shifting precipitation is likely to be moderated by ontogeny, because the seedling stage is more sensitive to climate extremes relative to mature individuals due to shallower root systems and less access to water reserves stored in soils (Niinemets, 2010). Moreover, some researchers have postulated that extreme precipitation events may generate a drought rescue effect, recharging soil moisture after extreme drying, and thereby mitigating water stress on plants (Yaseef et al., 2010). As such, episodic pulses from extreme precipitation may govern recruitment patterns and control the successional dynamics of forests for decades or centuries (Brown & Wu, 2005). Additionally, differences in response within a given ontogenetic stage may explain why some researchers have observed a migration failure for many tree species to

recent climate change (Sittaro et al., 2017). Under climate change, shifts in precipitation regimes toward increased episodic extreme precipitation may fundamentally alter tree regeneration patterns with short- and long-term consequences on key forest functions such as carbon storage (Liang et al., 2017), as well as future species distributions (Dyderski et al., 2018).

In addition to climate, the seedling establishment bottleneck is controlled by other factors such as environmental and edaphic conditions, biotic interactions, and plant functional traits (George & Bazzaz, 1999; Shibata et al., 2010), all of which may interact with future precipitation regimes. For many species, microsite conditions such as seedbed can be an important environmental sieve for survival (De Frenne et al., 2021; Flemming & Mossa, 1994). Access to a stable moisture supply in the rooting zone is critical to seedling establishment in which mixed mineral soils can be a key substrate facilitating the establishment of many species, particularly those with smaller massed seeds that would otherwise fail to penetrate forest litter layers. Although exposed soils benefit from improved moisture penetration, these soils may desiccate quicker under drying conditions, increasing the risk of mortality. Furthermore, initial survivorship is generally inversely proportional to the depth of the soil organic layer (Bonan & Shugart, 1989) but, for some species, the protective cooling effect and nutrients afforded by litter layers may facilitate establishment (Marx & Walters, 2008). The role of seedbed conditions on soil moisture retention and stability is clearly an important environmental filter for seedling survival, however the interaction of seedbed and future precipitation scenarios is poorly understood (Fischelli et al., 2014).

Globally, field-based precipitation manipulation experiments have been used to manipulate water inputs to ecosystems to test conditions representative of future climate scenarios (Beier et al., 2012). These experiments have primarily been established in moisture-limited, low-stature ecosystems such as grasslands, with considerably fewer in forests (12%) and rarely in mesic temperate systems (Asbjornsen et al., 2018), or examined in the context of canopy gap disturbance (e.g., natural disturbance, timber harvest operations). Furthermore, the principal foci of forested precipitation manipulation experiments have been on the ecosystem, whole tree, or leaf-scale responses, with less emphasis on forest regeneration and the role of canopy throughfall. Although many studies have examined the critical relationship of seasonal water limitation on vegetation dynamics and biogeochemical cycles, few have included 1st and 99th percentile precipitation extremes in forests (Asbjornsen et al., 2018; Knapp et al., 2017), despite projected increases in extreme precipitation events in humid regions globally (IPCC, 2014).

As such, key information gaps exist regarding the effects of extreme precipitation on the developmental dynamics of temperate forests.

Here, we report the 1-year seedling survival results from a precipitation manipulation experiment conducted in situ in a northern hardwood transition forest in north-eastern North America. Our aim was to understand the interaction of novel precipitation regimes on temperate tree seedling establishment. The objectives for this work were to (a) determine the role of various future precipitation scenarios characterized by extreme precipitation (e.g., drought, drought  $\times$  episodic heavy rainfall, frequent heavy rainfall) on tree seedling survival, and (b) examine the influence of biotic (e.g., species, functional traits, ontogenetic development) and edaphic (e.g., seedbed) factors in affecting seedling response to these precipitation regimes. Within this research, we hypothesize that:

**Hypothesis 1.** (1) *Extreme drying periods (droughts) will result in increased mortality, but heavy magnitude extreme precipitation events may offset the negative effects of drought.* (2) *Conversely, under more mesic conditions, heavy magnitude extreme precipitation events will lead to increased mortality in species sensitive to waterlogging.*

**Hypothesis 2.** *The effect of precipitation will be modified by seedling seedbed, such that survival will be higher for seedlings grown in scarified (bioturbated) mineral soils given access to more stable soil moisture supplies.*

**Hypothesis 3.** *Species functional traits associated with early fitness, such as seed mass, will be most strongly linked to seedling sensitivity to precipitation treatments.*

## METHODS

### Site characteristics

The experiment was conducted in the University of Vermont Jericho Research Forest (44.445,  $-73.003$ ), a 192 ha experimental forest located 50 km west of Montpelier, Vermont, USA in the Champlain Hills Biophysical Ecoregion (Thompson et al., 2019). Typical to this region, the site consists of second-growth northern hardwood forests naturally regenerated following agricultural abandonment in the early 20th century. Forest composition in the areas used for this study (percentage, based on species importance values from overstory trees  $>4$  cm at

1.37 m height) was composed of *Acer* spp. L. (maple 25.3%), *Betula* spp. L. (birch 15.1%), *Fagus grandifolia* Ehrh. (American beech 15.0%), *Pinus strobus* L. (eastern white pine 12.0%), *Quercus rubra* L. (northern red oak 11.6%), *Tsuga canadensis* (L.) Carrière (eastern hemlock 10.0%), and other deciduous (7.4%) and coniferous species (3.5%). The soils were sandy glaciofluvial deposits classified as somewhat excessively drained (USDA-NRCS, 2020), which were ideal for a precipitation manipulation experiment that aimed to limit subsurface water inputs. Study sites were identified through field reconnaissance and selected based on stand uniformity in forest conditions and even terrain to maintain relatively uniform soil hydrology and drainage (Asbjornsen et al., 2018; Beier et al., 2012). From 1981 to 2010, mean normal temperatures were  $-8.2$  and  $20.4^{\circ}\text{C}$  in January and July, respectively, in the study area, whereas mean annual precipitation was  $1039.9\text{ mm}\cdot\text{year}^{-1}$  (PRISM Climate Group, 2017).

The experiment was located in three newly harvested 0.1 ha canopy gaps to capture post-disturbance conditions for seedling regeneration. Gap sizes are representative of those associated with mesoscale disturbances and are commonly created by silvicultural systems practiced in the region (Seymour et al., 2002). Harvest operations were conducted during the winter of 2017–2018 under frozen, snow-covered conditions to limit incidental disturbance to soils and organic litter layers.

## Experimental design

Within each canopy gap, a single  $27\text{ m}^2$  precipitation manipulation shelter was positioned at the plot center and oriented east to west ( $N = 3$  shelter replicates; Appendix S1: Figures S1 and S2). Clear 6 mm greenhouse film excluded naturally occurring precipitation while allowing 91% light transmission. Shelter canopies were concaved at 2.5 m and positioned  $\geq 1.5$  m above ground level to maximize airflow and limit any outside environmental influence on the experiment's microclimate (Asbjornsen et al., 2018). Temperature and relative humidity were monitored inside experimental shelters and compared with ambient conditions outside shelters using iButton dataloggers and a psychro-dyne, respectively.

The experiment was active during the growing season months (late May–September) in 2018 and 2019. Ambient rainfall was collected from shelter canopies using a series of gutters and stored in reservoirs. Collected rainfall was redistributed manually using an electric pump and hand-held sprinkler head in a series of irrigation events that varied in daily frequency and volume based on the following precipitation treatments. The flow rate for all treatments was set at  $\sim 3\text{ L}/\text{min}$ , a rate within one standard deviation of the

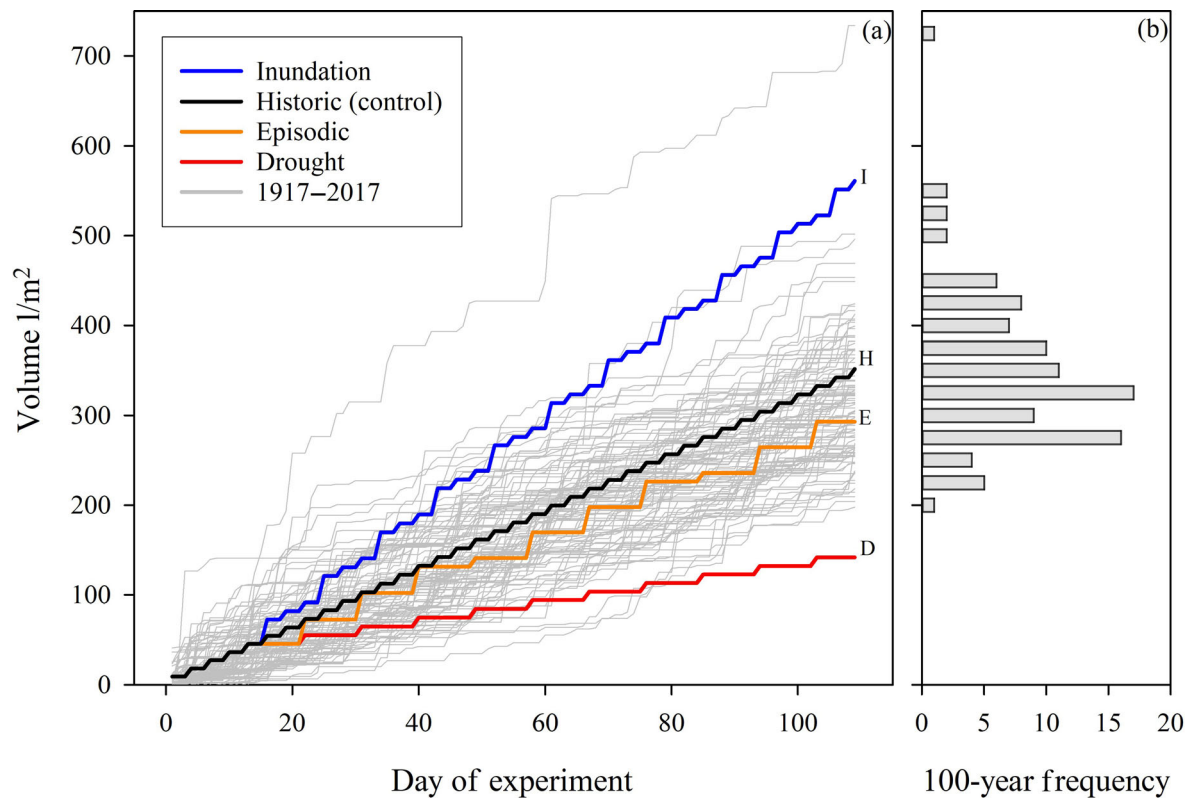
median rainfall duration obtained from 15 min records of nearby land-based meteorological weather station data (NCDC, 2020).

Precipitation treatments were defined statistically using a 100-year historic (1917–2017) daily meteorological record obtained from the nearest land-based weather station (NCDC, 2020) in combination with regional model projections based on the Intergovernmental Panel on Climate Change Greenhouse Gas Representative Concentration Pathway (RCP) 8.5 (IPCC, 2014; Ning et al., 2015). Given the high degree of complexity of simulating natural precipitation regimes (e.g., the potential for variability in volume, frequency, timing, duration, magnitude, spatiotemporal variability, and/or periodicity between extreme events relative to the central tendency), we elected to focus our examination by varying simulated precipitation based on (a) volume of event and (b) frequency between events. These primary facets of precipitation were forecasted to change throughout much of the eastern USA (Ning et al., 2015) and are recognized for strongly affecting biota in other systems (Felton et al., 2019). Like other precipitation manipulation experiments that artificially simulated precipitation regimes (see Felton et al., 2019; Fisichelli et al., 2014), by focusing our examination, we are able to better control for and differentiate the relative contribution of these aspects of precipitation, which were expected to broadly contribute to the vulnerability and adaptive capacity of forested ecosystems in this region (Janowiak et al., 2018; Swanston et al., 2018).

Precipitation treatments were designed to replicate daily and seasonal precipitation conditions under various combinations of extreme drought and/or episodic rainfall forecasted for this region. Precipitation treatments were defined and calculated as follows (see Figure 1 and Appendix S1: Figure S3 to aid interpretations):

1. *Historic treatment (control)*: “typical” rainfall, statistically defined as the median daily volume and frequency of nontrace rainfall ( $>1\text{ mm}$  total daily rainfall). Values were calculated for each growing season month and derived from historic meteorological records (1917–2017). This treatment is analogous to an experimental control.
2. *Drought treatment*: a “once-in-a-century” (1st percentile) growing season drought, statistically defined using the 95th percentile of consecutive rainless days ( $<1\text{ mm}$  total daily rainfall) for each growing season month. To control for the amount of water distributed, the total allocated during each irrigation event was also based on the median daily volume, similar to the per-event volume used in the historic treatment.





**FIGURE 1** Outcomes from experimental precipitation regimes relative to observed precipitation trends spanning a 100-year period from 1917 to 2017, obtained from the nearest meteorological station. (a) Growing season rainfall accumulation in terms of daily rainfall volume and frequency among four precipitation treatments shown in bold trendlines (I, inundation [blue]; H, historic [control; black]; E, episodic [orange], and D, drought [red]) overlaid on 100 observed annual precipitation accumulation curves (thin gray trendlines). (b) Frequency of observed precipitation in terms of growing season accumulation, presented on the same y-axis to allow for comparisons between treatments and observed.

3. *Episodic treatment*: characterized as infrequent rainfall with periodic, high volume (95th percentile) extreme precipitation events. Monthly extreme precipitation frequency and interval were derived from regional projections less than RCP 8.5 (Ning et al., 2015), based on the forecasted number of days with precipitation larger than the 95th percentile of daily precipitation amount. To control for frequency, such as drought treatment, the periodicity between irrigation events was statistically determined based on the 95th percentile of consecutive rainless days (<1 mm) per month.
4. *Inundation treatment*: characterized as historic rainfall punctuated by periodic, high volume (95th percentile) extreme precipitation events. Modeled after historic conditions, this treatment is defined by “typical” daily precipitation volume and frequency (see “*Historic treatment*”), interspersed by pulsed extreme precipitation events (see “*Episodic treatment*”).

Two seedbed treatments, (a) scarified and (b) unmodified were established in each experimental precipitation treatment unit to capture substrate conditions commonly

found in forested settings. Scarification is the loosening of upper soils and the complete removal of undecomposed litter and hummus to expose mineral soil. This form of soil bioturbation commonly occurs from disturbances such as trees being uprooted during windstorms in this region (Hellmer et al., 2015) or deliberately created through forest management activities (via disking, mounding, or skidding) that abrade seedbeds to favor the establishment of certain tree species (Löf et al., 2012). Unmodified seedbeds were not disturbed, leaving the naturally occurring litter and hummus layer intact. Leaf litter depth on-site ranged from 3–6 cm and decomposing organic and humus layers were underdeveloped, typically between 2–4 cm thick.

Each experimental precipitation treatment unit was  $\sim 2.5 \times 3$  m and was arranged linearly beneath shelter canopies ( $N = 3$ , or one replicate per precipitation treatment type per shelter). Treatments were positioned under shelter canopies with a  $\geq 0.5$  m buffer between treatments to limit the influence from antecedent water sources such as adjacent treatments or shelter perimeter (Skaggs & Trout, 2010). The locations

of precipitation treatment units were randomized under shelter canopies. Both seedbed treatments were replicated within precipitation treatments ( $N = 3$ , or one replicate per seedbed type per precipitation treatment unit). Each seedbed was  $30 \times 120$  cm separated by a  $\geq 0.5$  m buffer. A 1 m deep trench was excavated around the shelter perimeter to limit subsurface water inputs. Additionally, a  $\geq 50$  cm trench fitted with plastic landscaping edging and backfilled with soil was positioned between plots and all treatments to reduce the lateral influence of experimental precipitation treatments. Experimental units were fenced with 1 cm gridded welded wire to limit the influence of wildlife predation. To measure the effect of precipitation treatments, five 20 cm point-source measures of volumetric soil water content (SMC) were recorded using a Campbell Scientific hydrosense. Measurements were recorded every 3 days just prior to and approximately 1 hr after irrigation events and averaged to obtain a treatment unit level effect. To examine the extent of soil drying, we focused our analysis on the interval between irrigation events.

The species selected for this experiment were selected based on a suite of functional traits and current regional distribution relative to future habitat projections using the USDA Climate Change Tree Atlas (Peters et al., 2020). During the first growing season (2018), 10 tree species were sown from seed ( $n = 28$  seeds per seedbed replicate, or  $N = 648$  total seeds per species; Table 1; Appendix S1: Table S1). Due to a shortage in seed supply for *Castanea dentata* (Marshall) Borkh (American chestnut), this species was only tested in scarified soils ( $n = 14$  seeds per seedbed replicate, or  $N = 168$  total seeds). In the following growing season (2019), six tree species were sown from seed ( $n = 18$  seeds per treatment, or  $N = 216$  total seeds per species) but were only tested in scarified seedbeds. All seeds were cold stratified in a laboratory setting, cut tested, and sown following procedures described in Bonner and Karrfalt (2008). Planting locations were randomized within treatments and occurred as early as possible in the growing season. Although the focus of our work was on seedling survival from sown seed (to simulate natural conditions), we also tested six species planted as

**TABLE 1** Species and associated selected functional traits for seedlings tested. See Appendix S1: Table S1 for a comprehensive list of species traits and application within the experimental design.

Species tested	Select species silvical characteristics <sup>a</sup>				
	Seed mass (g)	Germination type	TolW	TolD	Life stage
<i>Acer saccharum</i> Marshall Sugar maple	0.540	Hypogeal	1.1	2.3	S
<i>Betula alleghaniensis</i> Britton Yellow birch	0.001	Epigeal	2.0	3.0	S
<i>Betula lenta</i> L. Black birch	0.007	Epigeal	2.0	3.0	S,T
<i>Carya cordiformis</i> (Wangenh.) K. Koch Bitternut hickory	2.831	Hypogeal	2.5	4.0	S,T
<i>Castanea dentata</i> (Marshall) Borkh. American chestnut (B3F3 <sup>b</sup> )	4.516	Hypogeal	1.0	3.0	S
<i>Fagus grandifolia</i> Ehrh. American beech	0.394	Hypogeal	1.5	1.5	S
<i>Pinus strobus</i> L. Eastern white pine	0.016	Epigeal	1.0	2.3	S,T
<i>Prunus serotina</i> Ehrh Black cherry	0.082	Hypogeal	1.1	3.0	S,T
<i>Quercus rubra</i> L. Northern red oak	5.665	Hypogeal	1.1	2.9	S,T
<i>Tsuga canadensis</i> (L.) Carrière Eastern hemlock	0.004	Epigeal	1.3	1.0	S,T

<sup>a</sup>Mean seed mass measured from seedlings tested, all other traits compiled from Niinemets and Valladares (2006) and USDA-NRCS (2021). TolD, drought tolerance and TolW, waterlogging tolerance on a 1–5 scale, where 1 = very intolerant and 5 = very tolerant. Life stage tested in the experiment, where S seedlings sown from seed and T, nursery-grown  $3 \pm 1$ -year-old bare-rooted seedling transplants.

<sup>b</sup>A hybrid “B3F3” *Castanea dentata* bred for tolerance to the chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) by the American Chestnut Foundation (Steiner et al., 2017) through controlled pollination between surviving trees and disease-tolerant *C. mollissima* (Blume).

$3 \pm 1$ -year-old nursery-grown bare-root seedling transplants ( $n = 5$  per precipitation treatment, or  $N = 60$  total per species). Species were selected to examine the role of seedling ontogeny. Due to experimental constraints, nursery transplants were only planted within unmodified litter seedbeds.

Sown seedling survival counts were performed at the treatment level and occurred periodically throughout the growing season at time intervals ranging between every 3–11 days. Nursery seedling transplants were only assessed for end-of-season survival. Given the principal focus of our examination was seasonal survival trends, we relied on the end-of-growing-season outcomes for our analysis. Last, we also measured the percentage cover of naturally seeded and ancillary herbaceous and woody competition at the end of the growing season.

## Statistical analysis

All analyses were performed using the statistical package R version 3.6.1 (R Core Team, 2019). Two sets of generalized linear mixed models (Bolker et al., 2009) were used to test the relative importance of treatments and biotic factors in affecting seedling survival with a binomial error distribution using the *glmmTMB* package (Brooks et al., 2017). The first set of models explicitly examined the role of species-level response to treatments, whereas the second examined the functional mechanisms that determined a survival response to treatments. In the first set of models, fixed effects included precipitation treatment, seedbed, and species with precipitation manipulation shelter included as a random effect. The second set of models included the same fixed and random effects except the species covariate was omitted and replaced with combinations of select plant functional traits including seed mass (averaged weight per seed lot, in grams), drought or waterlogging tolerance (1–5 scale, where 1 = very intolerant and 5 = very tolerant; see Niinemets & Valladares, 2006), and germination type (hypogeal, epigeal; USDA-NRCS, 2021). Numeric covariates were standardized to  $z$ -scores to facilitate predictor comparisons. Given that nursery seedling transplants were only replicated within a subset of species and restricted to one seedbed type (unmodified only), this ontogenetic stage was not explicitly tested in models. However, we restricted our examination of ontogeny to post hoc tests (outlined below). In total, we examined 12 species-level and 62 trait-level survival models. Each set of models contained an intercept-only null model and utilized various combinations of predictors representing different a priori hypotheses regarding ecological factors affecting seedling response.

Each model was assessed and diagnosed to pass model assumptions including independence and multicollinearity. Model selection was performed using the Akaike information criterion (AIC; Burnham & Anderson, 2002) to determine the best-approximating model in a given candidate set, using the *AICcmodavg* package (Mazerolle, 2020). Multiple competing models were compared and ranked according to the change in AIC ( $\Delta$ AIC), in which top candidate models were considered to have strong support when  $\Delta$ AIC values were less than 7 (Burnham & Anderson, 2002).

To further analyze the relationship of the covariates on seedling survival not otherwise interpretable from models, we isolated predictors from the best supported models for post hoc tests. To compare associations among focal covariates (e.g., effect of precipitation treatments modified by seedbed), marginal estimates in terms of adjusted predicted probabilities were determined using the *ggeffects* package (Lüdtke, 2018). Based on an observed bifurcated survival response to precipitation across species, a general moisture regime was created and analyzed by grouping precipitation treatments into two categories: dry = drought and episodic treatments, wet = historic and inundation treatments. The influence of treatment and generalized moisture regime on seedling survival as well as differences by ontogenetic stages were tested using analysis of variance (ANOVA; significance threshold  $\alpha = 0.05$ ). The relationship between functional traits (e.g., seed mass) and generalized moisture regimes was examined using linear models. Additional analyses performed on categorical variables (e.g., soil moisture, treatments) included ANOVAs and single-sample  $t$ -tests. Each test was assessed to pass model assumptions of linearity and normality of residuals. Following the inspection of residuals, we determined that a log transformation for seed mass was appropriate for linear models. Given the volatility of seedling survival time series, locally weighted survival regression curves (Loess smoothing) were generated to graphically present seedling germination and survival. Loess smoothing was produced using the “stat\_smooth” function in the *ggplot2* package (Wickham, 2016).

## RESULTS

### Effect of treatments

Total seasonal accumulation for historic experimental precipitation treatments ( $351.7 \text{ L/m}^2$ ) closely matched mean seasonal rainfall accumulation from 100 years of meteorological data ( $362.9 \pm 8.6 \text{ L/m}^2$ ; 1 – standard error; Figure 1). Drought and inundation treatments

(141.7 and 560.8 L/m<sup>2</sup>, respectively) closely matched 1st and 99th percentile seasonal meteorological events (198.0 and 501.7 L/m<sup>2</sup>, respectively). In general, drought treatments were slightly more extreme than the driest growing season observed, whereas inundation treatments were lower than the wettest observed (100th percentile = 733.8 L/m<sup>2</sup>), which occurred in 2016 and 1998, respectively. These modest differences reflected the high degree of variability in actual precipitation regimes. No attempt was made to statistically validate seasonal volumes for episodic treatments, although total accumulation (292.9 L/m<sup>2</sup>) was within one standard deviation (85.3 L/m<sup>2</sup>) of the mean seasonal accumulation from meteorological records. Daily rainfall volumes tested ranged from 9.4 L/m<sup>2</sup> ( $\pm 0.14$ ) for typical rain events to 28.4 L/m<sup>2</sup> ( $\pm 0.4$ ) for extreme precipitation events and occurred over  $\sim 3$ -day and 9-day intervals depending on precipitation treatment.

Prior to irrigation events, soil moisture content varied among precipitation treatments ( $F_{(3,356)} = 80.47$ ,  $p < 0.001$ ), in which mean percentage SMC followed expected trends in moisture accumulation by treatment: SMC drought ( $10.9\% \pm 0.3\%$ ) < SMC episodic ( $12.0\% \pm 0.3\%$ ) < SMC historic ( $14.2\% \pm 0.3\%$ ) < SMC inundation ( $15.5\% \pm 0.3\%$ ; Appendix S1: Figure S4). Mean SMC increased linearly (adjusted  $R^2 = 0.60$ ,  $F_{(1,105)} = 156.74$ ,  $p < 0.001$ ). After irrigation events, SMC in inundation and historic treatments increased by  $16.8\% \pm 4\%$  ( $t_{(1,71)} = 10.13$ ,  $p < 0.001$ ) and  $14.3\% \pm 3.5\%$  ( $t_{(1,71)} = 9.29$ ,  $p < 0.001$ ), respectively. Conversely, SMC post irrigation was only marginally

different in episodic ( $2.4\% \pm 3.2\%$ ;  $t_{(1,71)} = 3.45$ ,  $p = 0.001$ ) or unchanged in drought treatments ( $0\% \pm 1.2\%$ ;  $t_{(1,71)} = 0.59$ ,  $p = 0.554$ ).

The temperatures inside experimental shelters were slightly warmer than ambient conditions outside ( $0.6 \pm 0.0^\circ\text{C}$ ;  $t_{(1,5131)} = 108.85$ ,  $p < 0.001$ ). Relative humidity was not different between experimental shelters and ambient conditions ( $F_{(1,158)} = 0.12$ ,  $p = 0.725$ ).

## Seedling survival response

Among our species-level models, seedling survival was best explained by precipitation treatment, seedbed, and species based on the best-approximating model in our candidate set (AIC weight = 0.85; Table 2; Appendix S1: Tables S2 and S3). Using the best-approximating model, seedbed had the greatest effect on seedlings, such that survival in scarified seedbeds was 6.9-fold more than that in unmodified (reference) substrates (Table 3). Relative to historic precipitation treatments (reference), survivorship increased in inundation treatments but was not significantly different. Conversely, the predicted odds of seedling survival in episodic and drought treatments were weakly, but significantly, reduced by 2.6-fold and 2.9-fold relative to the reference, respectively. The mean predicted odds of survival among historic and inundation treatments (wet precipitation regimes) adjusted for scarified seedbeds was 44% compared with unmodified seedbeds, which was 10.5%

**TABLE 2** Summary of confidence set and intercept-only (null) models for (A) species-level and (B) functional-trait model approaches for end-of-season seedling survival, based on the Akaike information criterion ( $\Delta\text{AIC} \leq 7$ ). For a complete list of models tested and parameter estimates, see Appendix S1: Tables S2 and S3.

Model	K	AIC <sub>c</sub>	$\Delta\text{AIC}_c$	AIC <sub>c</sub> Wt
(A) Top species survival models				
$\sim \beta_0 + \textit{Species} + \textbf{Bed} + \textit{Precip} + \epsilon_{\text{shelter}}$	15	219.34	0	0.85
$\sim \beta_0 + \textit{Species} + \textbf{Bed} + \epsilon_{\text{shelter}}$	12	223.17	3.83	0.12
$\sim \beta_0 + \textit{Species} + \textbf{Bed} + \textit{Precip} + \text{Bed} \times \textit{Precip} + \epsilon_{\text{shelter}}$	18	226.16	6.82	0.03
$\sim \beta_0 + \epsilon_{\text{shelter}}$	2	299.57	80.22	0
(B) Top functional-trait survival models				
$\sim \beta_0 + \textbf{SMass} + \textbf{Bed} + \textit{Precip} + \epsilon_{\text{shelter}}$	7	231.71	0	0.58
$\sim \beta_0 + \textbf{SMass} + \textbf{Bed} + \textit{Precip} + \textbf{SMass} \times \textit{Precip} + \epsilon_{\text{shelter}}$	10	234.04	2.34	0.18
$\sim \beta_0 + \textbf{SMass} + \textbf{Bed} + \epsilon_{\text{shelter}}$	4	234.58	2.87	0.14
$\sim \beta_0 + \textbf{SMass} + \textbf{Bed} + \textbf{SMass} \times \textit{Precip} + \epsilon_{\text{shelter}}$	5	236.45	4.75	0.05
$\sim \beta_0 + \textbf{SMass} + \textbf{Bed} + \textit{Precip} + \text{Bed} \times \textit{Precip} + \epsilon_{\text{shelter}}$	10	238.07	6.37	0.02
$\sim \beta_0 + \epsilon_{\text{shelter}}$	2	299.57	67.86	0

Note: Parameter significance: *italic* =  $p \leq 0.05$ , **bold** =  $p \leq 0.01$ , and **bold-italic** =  $p \leq 0.001$ . Parameter codes: Precip, precipitation treatment (reference = historic); Bed, seedbed (reference = unmodified); SMass, seed mass (z-scores); shelter, independent experimental unit used for random effects.



**TABLE 3** Model estimates (OR, odds ratios, CI, confidence interval) for the top candidate models including (A) species-level and (B) functional-trait approaches for end-of-season seedling survival. For a complete table of models tested and parameter estimates, see Appendix S1: Tables S2 and S3.

Model	Predictors	OR	CI	p
(A) Top species model: Species + Bed + Precip	(Intercept)	1.2	0.38–3.84	0.758
	Precip [Historic] <sup>†</sup>			
	Precip [Inundation]	1.36	0.52–3.56	0.537
	Precip [Episodic]	0.38	0.13–1.06	<b>0.055</b>
	Precip [Drought]	0.34	0.12–0.98	<b>0.045*</b>
	Bed [Unmodified] <sup>†</sup>			
	Bed [Scarified]	6.9	2.35–20.27	<b>&lt;0.001***</b>
	Species [ <i>Quercus rubra</i> ] <sup>†</sup>			
	Species [ <i>Castanea dentata</i> ]	0.37	0.10–1.34	0.129
	Species [ <i>Betula lenta</i> ]	0.15	0.03–0.68	<b>0.014**</b>
	Species [ <i>Fagus americana</i> ]	0.11	0.03–0.41	<b>0.001***</b>
	Species [ <i>Pinus strobus</i> ]	0.09	0.03–0.30	<b>&lt;0.001***</b>
	Species [ <i>Tsuga canadensis</i> ]	0.04	0.01–0.24	<b>&lt;0.001***</b>
	Species [ <i>Acer saccharum</i> ]	0.02	0.01–0.11	<b>&lt;0.001***</b>
	Species [ <i>Prunus serotina</i> ]	0.01	0.00–0.11	<b>&lt;0.001***</b>
	Species [ <i>Carya cordiformis</i> ]	0.01	0.00–0.11	<b>&lt;0.001***</b>
	Species [ <i>Betula alleghaniensis</i> ]	0.01	0.00–0.11	<b>&lt;0.001***</b>
(B) Top trait model: SMass + Bed + Precip	(Intercept)	0.1	0.04–0.27	<b>&lt;0.001***</b>
	Precip [Historic] <sup>†</sup>			
	Precip [Inundation]	1.29	0.53–3.10	0.573
	Precip [Episodic]	0.43	0.16–1.12	0.084
	Precip [Drought]	0.4	0.15–1.04	0.061
	Bed [Unmodified] <sup>†</sup>			
	Bed [Scarified]	6.75	2.75–16.62	<b>&lt;0.001***</b>
	SMass	2.86	2.07–3.94	<b>&lt;0.001***</b>

Note: Parameter codes: Precip, precipitation treatment (<sup>†</sup>reference value = historic); Bed, seedbed (<sup>†</sup>reference value = unmodified); SMass, seed mass (z-scores).

\* $p < 0.05$ .

\*\* $p < 0.01$ .

\*\*\* $p < 0.001$ .

(Table 4). Likewise, the mean predicted odds of survival among episodic and drought treatments (dry precipitation regimes) adjusted for scarified seedbeds was 22% compared with unmodified seedbeds, which was 4%. Species ranked in terms of survival odds relative to the reference (*Q. rubra*) included *C. dentata* (–63%), *Betula lenta* L. (black birch, –85%), *F. grandifolia* (–89%), *P. strobus* (–91%), *T. canadensis* (–96%), *Acer saccharum* Marshall (sugar maple, –98%), *Carya cordiformis* (Wangenh.) K.Koch (bitternut hickory, –99%), *Prunus serotina* Ehrh. (black cherry, –99%), and *Betula alleghaniensis* Britt. (yellow birch, –99%). All species differed relative to the

reference ( $p \leq 0.014$ ), except for *C. dentata*, which did not differ.

Among our models that included functional traits, seedling survival was best explained by precipitation treatment, seedbed, and seed mass based on the best-approximating model in our candidate set (AIC weight = 0.58). The effect of seed mass increased survival by 2.86-fold for every unit increase in mass. Trends among seedbed and treatment effects were very similar to the species-level model.

Seedbed strongly affected end-of-season survivorship. We observed an increase in the mean end-of-season

**TABLE 4** Predicted probabilities of survival for precipitation treatments adjusted for seedbed.

Precipitation treatment	Adjusted for seedbed	Predicted probability	95% CI
Inundation	Scarified	0.47	0.32–0.63
Inundation	Unmodified	0.12	0.05–0.25
Historic (control)	Scarified	0.41	0.26–0.57
Historic (control)	Unmodified	0.09	0.04–0.21
Episodic	Scarified	0.23	0.12–0.38
Episodic	Unmodified	0.04	0.01–0.11
Drought	Scarified	0.21	0.11–0.37
Drought	Unmodified	0.04	0.01–0.11

survivorship for seedlings grown in scarified seedbeds that was greater ( $36.1\% \pm 2.7\%$ ) than those in unmodified forest soils ( $9.3\% \pm 1.7\%$ ;  $F_{(1,4)} = 96.06$ ,  $p < 0.001$ ). This pattern in survivorship was observed across nearly all species tested and had the most pronounced effect on *P. strobus* ( $34.3\% \pm 5.4\%$  vs.  $5.7\% \pm 1.8\%$ ,  $F_{(1,4)} = 5.88$ ,  $p = 0.046$ ), *P. serotina* ( $5.7\% \pm 1.4\%$  vs.  $0.9\% \pm 0.6\%$ ,  $F_{(1,4)} = 16$ ,  $p = 0.016$ ), *A. saccharum* ( $12.5\% \pm 2.6\%$  vs.  $3.0\% \pm 0.9\%$ ,  $F_{(1,4)} = 42.76$ ,  $p = 0.003$ ), *Q. rubra* ( $84.0\% \pm 2.8\%$  vs.  $41.7\% \pm 3.6\%$ ,  $F_{(1,4)} = 24.37$ ,  $p = 0.002$ ), and *B. alleghaniensis* ( $5.4\% \pm 2.1\%$  vs.  $0\% \pm 0\%$ ,  $F_{(1,4)} = 8.31$ ,  $p = 0.0449$ ). Two species showed similar, but weakly insignificant, patterns in survivorship between substrates, *F. grandifolia* ( $34.5\% \pm 4.3\%$  vs.  $12.2\% \pm 2.5\%$ ,  $F_{(1,4)} = 6.43$ ,  $p = 0.064$ ) and *C. cordiformis* ( $4.8\% \pm 1.4\%$  vs.  $1.8\% \pm 0.7\%$ ,  $F_{(1,4)} = 2.94$ ,  $p = 0.161$ ). *T. canadensis* and *B. lenta* were not examined due to inadequate germination and *C. dentata* was not tested in both seedbed treatments.

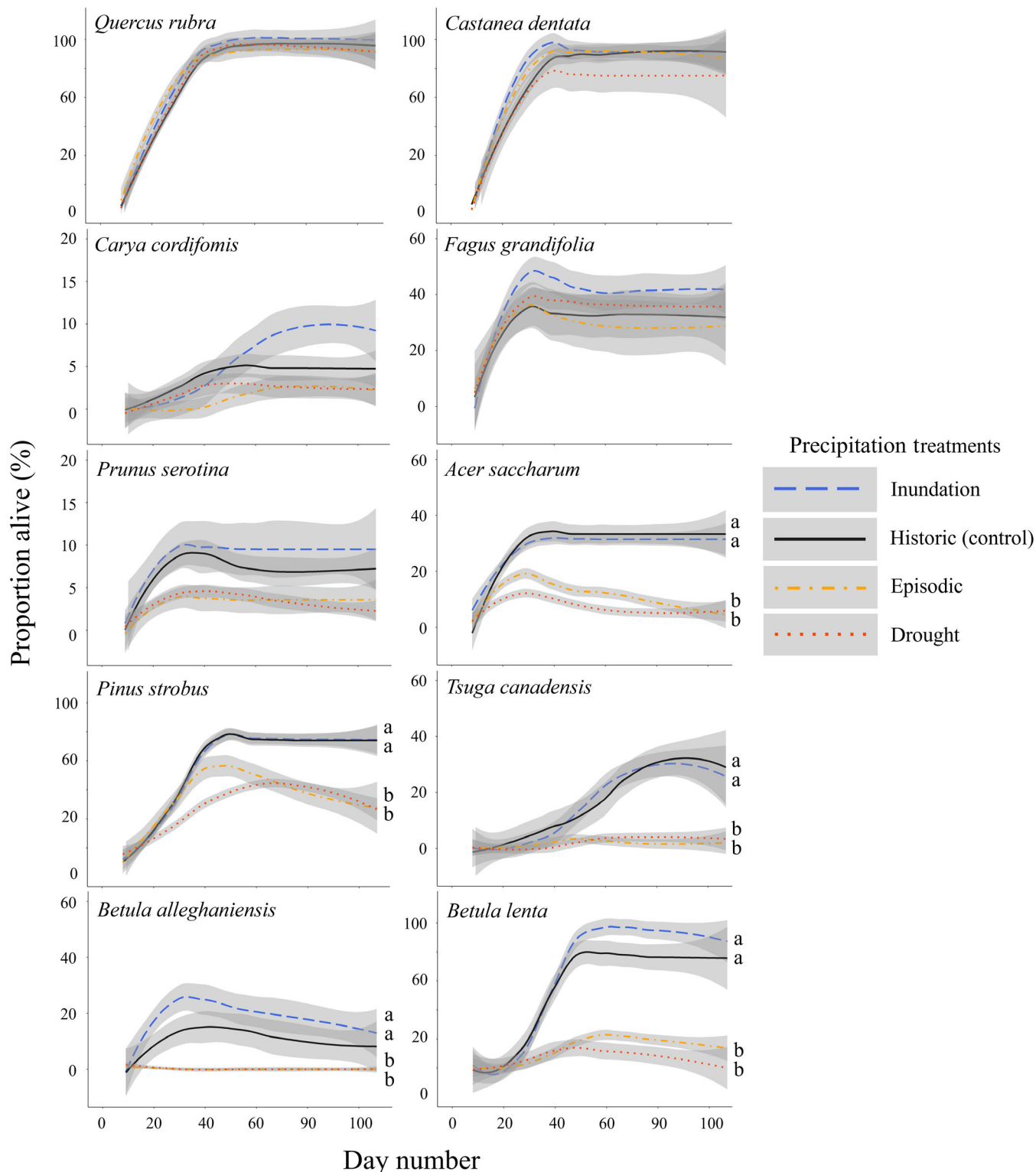
Survivorship response to precipitation treatments varied by seedbed conditions, with higher mean survival and more robust results in the scarified soil group. Given that survival in unmodified litter was consistently low across all species, we focused our post hoc analysis of seedling response to precipitation treatments on those grown in scarified seedbeds to achieve adequate sample sizes. Precipitation treatment had no effect on the end-of-growing-season survivorship for half of the species tested, including *Q. rubra*, *C. dentata*, *C. cordiformis*, *F. grandifolia*, and *P. serotina* (Figure 2). Conversely, *A. saccharum*, *P. strobus*, *T. canadensis*, *B. lenta*, and *B. alleghaniensis* were sensitive to precipitation treatment, as demonstrated by the significant differences in survival between precipitation treatments. For the moisture-sensitive group, pairwise differences in survival were not uniformly distributed between each of the four treatments. However, a bifurcated response

was observed in which seedling survival did not differ among drought and episodic treatments (dry moisture regimes) or among historic and inundation treatments (wet moisture regimes). The difference in mean survivorship for species sensitive to precipitation was  $38.1\% (\pm 3.4\%)$  between moisture regimes in which survivorship in the dry group was consistently lower ( $8.7\% \pm 2.3\%$ ) compared with higher rates of survival in the wet group ( $46.8 \pm 5.6\%$ ,  $F_{(1,4)} = 91.62$ ,  $p < 0.001$ ). Similar to results from scarified seedbeds, three species grown in unmodified seedbeds were affected by precipitation treatments (*F. grandifolia*, *A. saccharum*, and *C. cordiformis*) with slightly higher rates of survival under inundation compared with drought or episodic rainfall treatments (mean  $\Delta = 8.1\% \pm 3.1\%$ ,  $F_{(3,8)} = 6.62$ ,  $p = 0.015$ ).

We examined the maximum survivorship potential within a species (a proxy for optimum germination for each seed lot) between seed mass (log transformed) and generalized moisture regime (wet, dry conditions; Figure 3). Under dry moisture regimes, survival was positively related to seed mass (adjusted  $R^2 = 0.72$ ,  $F_{(1,52)} = 133.80$ ,  $p < 0.001$ ), but we observed no relationship under wet conditions (adjusted  $R^2 = 0.04$ ,  $F_{(1,52)} = 2.53$ ,  $p = 0.117$ ). Functional traits appear to be associated with species sensitivity to precipitation treatments, such that mean seed mass was greater for the insensitive group ( $2.7 \pm 1.1$  g) compared with the sensitive group ( $0.02 \pm 0.01$  g,  $F_{(1,8)} = 5.96$ ,  $p = 0.040$ ). Furthermore, all species classified as moisture sensitive relied on epigeal germination, whereas those insensitive to precipitation treatment relied on hypogeal germination, with the exception of *A. saccharum*.

Seedbed moderated the effect of precipitation treatment such that the percentage change ( $\%\Delta$ ) in mean survivorship between scarified and unmodified seedbeds was lower ( $\%\Delta = 16.6 \pm 0.8$ ) under dry moisture regimes compared with wet regimes ( $\%\Delta = 29.6 \pm 1.4$ ,  $F_{(1,4)} = 64.61$ ,  $p = 0.001$ ). This interacting effect was most pronounced for sensitive seedlings (dry  $\%\Delta = 7.1 \pm 1.7$ , wet  $\%\Delta = 35.0 \pm 1.6$ ,  $F_{(1,4)} = 152$ ,  $p < 0.001$ ), whereas no modifying trends were observed for the insensitive group of seedlings. Nevertheless, one of the most precipitation-insensitive species, *Q. rubra*, exhibited the opposite trend in survival by precipitation treatment in which the difference in survivorship between scarified and unmodified seedbeds under wet conditions was actually lower ( $22.0\% \pm 6.5\%$ ) compared with dry conditions ( $39.9\% \pm 4.2\%$ ,  $F_{(1,4)} = 5.29$ ,  $p = 0.044$ ).

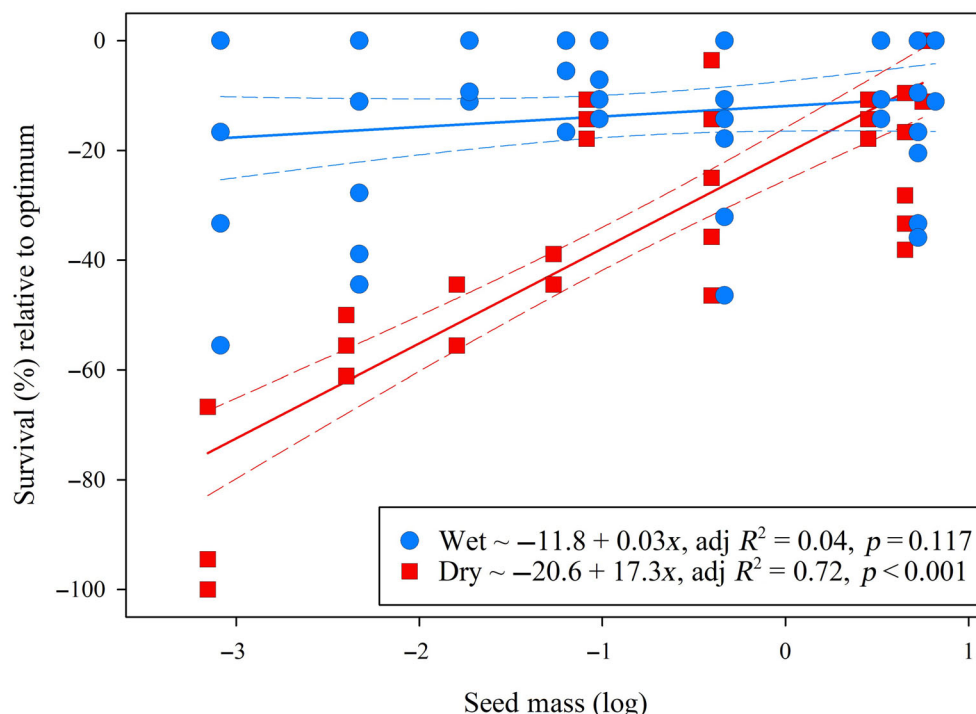
Compared with seedlings sown from seed, survival response to precipitation varied by ontogenetic stage. Precipitation treatment had no effect on growing season survival for nursery-grown seedling transplants. Understandably, rates of survival for the more mature



**FIGURE 2** Locally weighted regression survival curves (loess smoothing) for species tested (sown seeds, in scarified soils only) in response to the four precipitation regimes tested. Gray boundaries are 95% CI. Figures are presented in descending order by seed mass. Letters denote significant differences in end-of-growing-season survivorship between group means, based on Tukey honestly significant differences ( $p \leq 0.05$ ). Note changes in y-axis scales.

seedling transplants were consistently higher compared with those established from sown seed ( $\% \Delta = 33.3 \pm 4.7$ ,  $t_{(1,71)} = -9.1$ ,  $p < 0.001$ ), but these differences were much

more pronounced in small-seeded, moisture-sensitive species ( $43.4 \pm 6.8$ ; *P. strobus*, *B. lenta*, *T. canadensis*) compared with larger massed, moisture-insensitive



**FIGURE 3** Relationship between seed mass (log) and growing season survival relative to potential survivorship optimum (e.g., maximum survivorship potential, based on maximum proportion germinated achieved per species seed lot) presented by two general moisture regimes (dry = episodic and drought precipitation treatments; wet = historic and inundation precipitation treatments). Solid lines are linear regressions and dashed lines are 95% CI.

species ( $17.3 \pm 4.2$ ; *Q. rubra*, *C. cordiformis*, *P. serotina*). Moreover, seedling transplants from sensitive species survived at higher rates under dry moisture regimes relative to those same species sown in the field ( $63.4\% \pm 9.1\%$ ) compared with wet regimes ( $23.4 \pm 7.9$ ;  $F_{(1,34)} = 11.12$ ,  $p = 0.002$ ), whereas there were no differences in rates of survival for insensitive seedling transplants (Figure 4).

Like seedling survival, the abundance of naturally occurring vegetative followed similar trends relative to precipitation treatments. Percentage cover was lower in drought ( $24.9 \pm 0.3$ ) and episodic ( $36.5 \pm 2.9$ ) compared with historic ( $78.5 \pm 11.6$ ) and inundation ( $74.8 \pm 10.9$ ). When grouped as dry and wet moisture regimes, group means were significantly different ( $F_{(1,10)} = 35.02$ ,  $p < 0.001$ ).

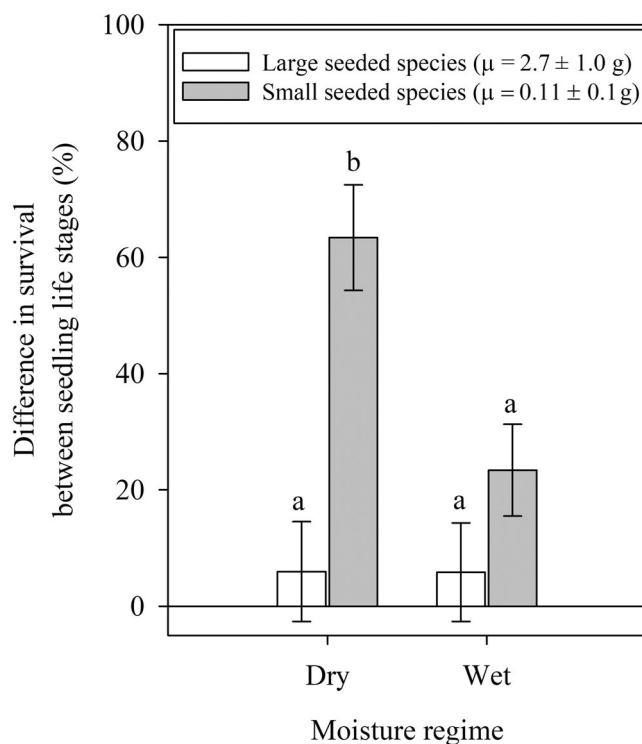
## DISCUSSION

Quantifying the effect of global change agents such as extreme rainfall on ecological functioning is critical for understanding and anticipating changes in key demographic processes, such as plant establishment; however the interactive effects with biotic and edaphic factors are not fully understood. Through the use of a precipitation

manipulation experiment established within disturbed forest canopy gaps, we demonstrate that the first-year survival of tree seedlings in response to changing precipitation regimes was contingent on the relationship between seedbed conditions and variability in precipitation, but not the occurrence of episodic, extreme precipitation events. Moreover, these responses were further modified by species, seed functional traits (e.g., seed mass), and ontogeny.

Our observations of seedling survival relative to precipitation are generally consistent with ecohydrological theory, which links hydrologic dynamics with ecological patterns and processes (Rodríguez-Iturb, 2000); however, the mechanisms underlying this dynamic differed across systems (Matías et al., 2012). Typically, under increased soil water losses, plant physiological adjustments are made to optimize water use and are observed along a continuum (Felton et al., 2019). Although we showed that SMC increased linearly among precipitation treatments prior to irrigation events, post-treatment SMC did not respond linearly. For instance, SMC within drought and episodic treatments responded similarly, despite heavy inputs of water in the latter. Correspondingly, seedling survival (a proxy for plant physiological adjustment) was not linear, however, we reported a bifurcated response in which higher survivorship was observed





**FIGURE 4** Differences in relative survivorship of seedlings by ontogeny (two seedling life stages). Positive values signify higher rates of survival of 3 ± 1-year-old bare-root seedling transplants compared with seedlings sown from seed. Letters denote significant differences in group means ( $p \leq 0.05$ ). Large-seeded species: *Quercus rubra*, *Carya cordiformis*, *Prunus serotina*. Small-seeded species: *Pinus strobus*, *Betula lenta*, *Tsuga canadensis*.

under wet moisture regimes (historic and inundation treatments) compared with lower survival under dry moisture regimes (drought and episodic treatments; Figure 3). Although we could not explicitly isolate different aspects of a given precipitation regimes (e.g., volume, frequency) with our treatment design, the drying effect between simulated rainfall events appeared to be the strongest factor in controlling seedling survival. More importantly, the effect of pulsed extreme precipitation events was not enough to compensate for moisture deficits during dry periods under episodic precipitation scenarios, nor overwhelm soils and waterlog seedlings due to flooding under inundation scenarios. With respect to our first hypothesis, although precipitation regimes containing extreme drying periods resulted in increased mortality, seedling survival in episodic treatments characterized by periodic, extreme precipitation events was comparable with drought treatments not containing these events. Therefore, we surmised that episodic heavy precipitation was not enough to offset the negative effects of drought. Concurrently, under more mesic conditions (historic and inundation treatments), extreme precipitation events did not result in increased mortality.

We therefore were unable to confirm our first hypothesis. It is possible, however, that this response pattern may still exist under soils with greater moisture-holding capacity, warranting further investigation. Nevertheless, these results illustrated the relative contribution (or lack thereof) of precipitation extremes in controlling temperate forest regeneration.

Many efforts to examine tree response to future climate rely on seasonal or yearly climate summaries, such as mean seasonal or annual precipitation (e.g., Peters et al., 2020). Our research illustrates the importance of precipitation timing and frequency, and the lesser importance of extreme precipitation events for restructuring seasonal precipitation volumes. For example, despite the similarity in overall seasonal accumulations between historic and episodic precipitation treatments, seedlings responded to episodic treatments much like a once-in-a-century drought. Although some have theorized that extreme precipitation events may generate a drought rescue effect, recharging soil moisture after extreme drying, and thereby mitigating water stress on plants (Yaseef et al., 2010), our results suggested that the effects of extreme precipitation on tree seedlings were not enough to compensate for water stress during extreme drying periods in mesic temperate systems.

Climate played an important role in seedling survival in our experiment; however, our findings suggested that the effect of seedbed was more than twice as important as any precipitation treatment tested at affecting seedling survival, either positively or negatively. Among biophysical factors tested, survival in scarified seedbeds resulted in a nearly seven-fold increase in survivorship relative to a less than three-fold decrease under dry precipitation regimes. Although survivorship was much greater under wet precipitation regimes, the influence of seedbed strongly and positively adjusted these outcomes. For instance, the probability of survival for seedlings grown in scarified soils under dry precipitation regimes was nearly twice that of those grown in unmodified soils under wet conditions. These findings suggested that seedlings grown in scarified seedbeds may be buffered from some of the negative effects of extreme drought precipitation. With respect to our second hypothesis, we confirmed that the effect of precipitation was modified by seedling seedbed, such that survival was positively affected for seedlings grown in scarified mineral soils compared with those in undisturbed seedbeds.

Seedbed microsite is well recognized to be a key environmental sieve for important seedling physiological processes that control germination and survival (Bonan & Shugart, 1989; Flemming & Mossa, 1994; Marx & Walters, 2008); however, this relationship is poorly understood in the context of shifting future precipitation and episodic

extreme precipitation. Fisichelli et al. (2014) actually showed the opposite survival response to artificial additions of leaf litter in growth chamber trials in which the presence of leaf litter increased survival, even for species and genera that commonly favor or require seedbed conditions absent of organic material, such as *Betula* spp. (Hutnik & Cunningham, 1965) and *Q. rubra* (Sander, 1965). These differences may be attributable to the lack of decomposing organic material and humus layers in the aforementioned growth chamber study, as these soil conditions are found in naturally occurring forest settings and may alter moisture penetration capacity, especially under extremely dry conditions.

Although our top candidate models did not carry an interactive term between seedbed and precipitation treatment, the relationship between the two factors clearly modified key aspects of seedling survival. As we outlined above, the predicted probability of survival of these predictors was adjusted and, in some instances, amplified when treated in combination. Still, the absence of an interaction term in our top models can most likely be attributed to the highly variable, occasionally conflicting, species-specific responses. For example, species most sensitive to precipitation regimes (*A. saccharum*, *P. strobus*, *T. canadensis*, *B. lenta*, and *B. alleghaniensis*) survived at much higher rates in scarified, compared with unmodified, litter seedbeds, but this effect was 27.9% greater under wet compared with dry moisture regimes. This relationship was not apparent for species insensitive to precipitation treatments, indicating that, whereas exposed soils probably desiccate quicker, the conditions that permitted greater moisture penetration offset the risk of mortality. Only two species, *F. grandifolia* and *A. saccharum*, showed a modest positive effect from unmodified seedbeds under the wettest treatment (inundation) relative to the dry treatments (episodic or drought), which is likely to reflect the ability of these species to establish under cool, moist microclimates such as leaf litter; a condition that may become less common under global change and associated stressors (e.g., climate warming and drying conditions, invasive earthworms; Eisenhauer et al., 2012). Conversely, the most moisture-insensitive species tested, *Q. rubra*, exhibited the opposite trend with greater differences in survivorship by seedbed under xeric conditions. In other words, whereas the absence of a litter layer positively affected survivorship for all species, this effect was significantly amplified for sensitive species under mesic conditions but was more important for insensitive species under xeric conditions.

Future species will probably respond to climate according to functional traits favored by future climate (Aubin et al., 2016). In this study, species sensitive to precipitation treatment were overwhelmingly small seeded

(mean  $0.11 \pm 0.1$  g) and apparently more prone to desiccation. Large-seeded species ( $2.7 \pm 1.0$  g) were insensitive to the effects of rainfall and demonstrated the ability to persist under a wider moisture envelope. Species sensitivity to precipitation appeared to be predicated on functional traits, namely seed mass, although germination type was likely to have played a role in initial germination and survival (Kozlowski & Gentile, 1959). This relationship also appeared to be strongly related to seedbed microsite, as large-massed and hypogeal species were able to penetrate and persist in the presence of litter compared with smaller massed epigeal species, which largely failed to penetrate organic layers. Irrespective of the mechanism, our results showed that seed functional traits would probably filter the plant community response to future climates, whereby species with smaller seed masses may have reduced performances under novel precipitation scenarios, namely those characterized by extreme precipitation events punctuated by long periods of drying. With respect to our third hypothesis, we illustrate that species functional traits, such as seed mass, are most strongly linked to the seedling's sensitivity to precipitation treatments. As slight differences in growth and establishment may favor species adapted to prevailing climatic conditions compared with others, species more plastic or tolerant to broader variability in precipitation extremes may be better adapted to new and changing conditions.

The young seedling and germination stage is a critical demographic bottleneck in plant recruitment (Walck et al., 2011), however the role of ontogeny in influencing the response to future climate is not fully understood (Day et al., 2014; Schupp, 1995). Relative to older plant stages, seedlings are generally more sensitive, with delicate plant parts, underdeveloped root structures, and limited energy reserves and are more likely to be affected by a narrower range of climatic conditions. Although these results are restricted to 1-year survival, the implications for future demography are important, as early demographic processes are strongly linked to longer term performance. As seedlings mature into larger sized classes, important physiological changes support greater adaptive capacity to adverse conditions (e.g., water stress), such as the development of more robust belowground rooting structures (Canham et al., 1999). Although these differences have been reported in the context of comparisons of ontogenetic differences between seedlings and mature trees (Niinemets, 2010), we showed that important physiological differences were apparent within seedling ontogenetic stages (<5 years) that permitted mature seedlings to persist under adverse precipitation scenarios at greater rates relative to 1-year-old counterparts. Subsequently, this relationship is again modified by seed functional

traits whereby differences in seedling survival are unaffected under mesic moisture regimes, but profoundly reduced for species with smaller seed masses relative to nursery transplants. These results are important when considered in the context of natural recruitment dynamics of forests under climate change relative to recent efforts to plant seedlings to enhance forest carbon stocks (e.g., reforestation, afforestation; Domke et al., 2020) or adapt species to shifting ranges (e.g., assisted migration; Clark et al., 2021; Palik et al., 2022). By testing sown seeds (analogous to natural regeneration), our results showed that future precipitation regimes may filter the germination and survival response for certain species (and traits), although these differences are less apparent for planted nursery stock. These findings may help to inform conservation biologists or natural resource managers who are considering natural versus artificial regeneration techniques to maintain, restore, or adapt forested ecosystems and composition under future climate conditions using a trait-based approach.

The strength of vegetative competition is an important ecological filter for seedlings, whereby the presence of a competitive understory can limit the growth and survival of seedling species (George & Bazzaz, 1999; Royo & Carson, 2006). Although the primary focus of this study was on seedling survival, we report notable differences in ancillary vegetation associated with moisture regimes. Given the short timescale of the experiment, it is unclear how this will affect surviving tree seedlings, although it is possible that precipitation-insensitive species may benefit from increased resource availability due to reduced competition under a drier future climate. As such, these interactive effects of the precipitation regime on future competitive conditions need to be accounted for in subsequent investigations.

How species respond to future precipitation may also be controlled by factors not accounted for in this experiment. As illustrated in Figure 2, species displayed varying survival curves that were linked to germination rates, germination velocities and varying distributions within survivorship (e.g., peaked, sustained, declining). Likewise, the temporal trends associated with rainfall can also be highly variable, further modifying a species' response. For instance, even more pronounced 99th percentile drying periods (up to 30 days), extending longer than the 95th percentile conditions we tested, are expected to occur more frequently in this region. Although we are unable to explicitly test the effect of these extraordinary drying events, their timing in the growing season (e.g., early vs. later) will probably further exacerbate or filter regeneration bottlenecks, particularly for smaller seeded species, which are the most sensitive during germination and emergence stages.

The experimental conditions used here have direct implications for understanding temperate forest developmental dynamics under future climatic conditions characterized by episodic extreme precipitation events. Despite this, some limitations may alter the interpretation of our findings. For example, our experiment tested seedling regeneration responses to canopy disturbance using recently harvested forests to capture ideal germination conditions required for most temperate forest species established from seed. As such, this study design omits throughfall effects from partial or full overstory canopy, which would reduce the overall soil wetting effect under modest rain events, but may permit extreme precipitation to better saturate soils. It is unclear how this would interact with other factors such as reduced transpirational stress on seedlings under various canopy microclimates, although it is likely that the potential cooling effect of partial or full canopy cover may not offset reductions in rainfall (De Frenne et al., 2021). Additionally, our precipitation manipulation structures were modestly warmer than ambient conditions ( $+0.6^{\circ}\text{C}$ ), which could have influenced our results both positively (greenhouse effect) or negatively (transpirational stress). Although not intentionally, this measured increase in temperature falls within the boundaries of forecasted climate for this region ( $+2^{\circ}\text{C}$ ), such that experimental conditions may actually represent future conditions. Last, we elected to establish our precipitation manipulation experiment in well drained soils to isolate the effects of simulated precipitation and limit the outside influence of subsurface moisture inputs. Although, we successfully highlighted important drivers behind seedling survival under these conditions, this pattern may change under finer soils with greater moisture-holding capacity. Nevertheless, the relationships we found highlighted the importance of edaphic and biotic controls such as seedbed, functional traits, and seedling ontogeny in influencing and potentially overriding the effects of extreme precipitation on seedling survival in temperate forests.

## CONCLUSION

Understanding the effect of global change on ecological functioning has been a critical line of inquiry across ecosystems. As the impacts of global change are increasingly realized, the examination of the biophysical factors that interact with climate improves the understanding of the potential vulnerability or adaptability of future ecosystems. Our findings demonstrate that pulsed extreme precipitation events were not enough to compensate for moisture deficits, nor provide a rescue effect for seedlings during prolonged

periods of drought. More importantly, we illustrate that edaphic (e.g., seedbed) and biotic (e.g., functional traits, ontogenetic stage) factors interact with, and in some cases buffer, the negative effects of extreme precipitation on tree seedling recruitment. These findings are congruent with research from other ecosystems and organisms (e.g., grasslands, aquatic systems, wildlife), and support mounting evidence that, although climate remains important, other biophysical factors may interact with or potentially override the effects of climate change, at least in the near term.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Clark & D'Amato, 2022) are available in Figshare at <https://doi.org/10.6084/m9.figshare.20291523>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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