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ARTICLE
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Seedling passage times in gaps and closed canopies reveal decades of understory persistence in a New England forest

Isabella Stone[1] | **Jeffrey Mintz**[2] | **Claudia J. Garnica-Díaz**[3] | **Chia-Hao Chang-Yang**[4] | **David A. Orwig**[5] | **Audrey A. Barker Plotkin**[5] | **April Zee**[6] | **Raelene M. Crandall**[6] | **Daniel J. Johnson**[6] | **Lukas J. Magee**[6]

[1]Department of Environmental Science, Willamette University, Salem, Oregon, USA

[2]School of Natural Resources and Environment, University of Florida, Gainesville, Florida, USA

[3]Department of Biology, University of Florida, Gainesville, Florida, USA

[4]Department of Biological Sciences, National Sun Yat-Sen University, Kaohsiung, Taiwan

[5]Harvard Forest, Harvard University, Petersham, Massachusetts, USA

[6]School of Forest, Fisheries and Geomatics Sciences, University of Florida, Gainesville, Florida, USA

Correspondence
Lukas J. Magee
Email: mageel@ufl.edu

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Abstract

The duration of tree seedling persistence in the understory varies greatly between forests and across environmental conditions within a forest ecosystem. To examine species-level variation in understory persistence and passage to the sapling life stage, we followed 5236 seedlings in single-tree canopy gaps and closed canopy conditions over three years and simulated seedling passage times and the number of seedlings required to produce one 1.5-m tall sapling of five common tree species in a hemlock–hardwood forest of Massachusetts, USA. Averaged across species, it took 26 years in gaps and 31 years under closed canopies to go from a first-year seedling to a 1.5-m sapling. Across species, the average number of seedlings needed for one sapling was 294 in gaps and 2674 in closed canopy environments. We observed high interspecific variation in passage times and number required for one sapling. *Betula* congeners and *Pinus strobus* took less time and significantly fewer individuals than *Acer rubrum* and *Tsuga canadensis*, which are generally regarded as more tolerant of understory conditions. The largest intraspecific difference in gaps versus closed canopy environments was for *Quercus rubra*, where we estimated the number of seedlings required to produce one sapling in closed canopies to be 172 times higher than in gaps. Stem breakage also increased the number of seedlings needed per sapling, especially in closed canopy environments. We evaluated our estimates in the lab by aging cross-sections obtained from seedlings in gap and closed canopy conditions. Compared to our empirical age-to-height relationships, most simulations tended to underpredict seedling age for a given height, suggesting that passage times may be even longer than our simulations indicated. Our study shows that trees can persist for decades in the seedling life stage, highlighting a need for better-parameterized recruitment processes in demographic forecasting.

KEYWORDS
canopy gaps, Harvard Forest, hemlock–hardwood forest, individual-based model, seedling passage time, stem breakage

INTRODUCTION

Gaps in forest canopies initiate important successional processes that promote regeneration and can enhance species diversity (Brokaw & Busing, 2000; Denslow, 1987; Hubbell et al., 1999). Despite the ecological significance of canopy gaps, most tree seedlings never get the opportunity to thrive within them. Instead, seedlings endure challenging understory conditions typical of closed canopy forests, including light limitation, resource competition, and natural enemies (e.g., pathogens or herbivores). Mortality can be high and growth slow for seedlings in understory conditions (Canham, 1988), and there remains considerable uncertainty about the duration of seedling persistence, which limits our abilities to forecast natural forest dynamics (Ellison et al., 2005).

In the absence of significant disturbances, canopy gaps are infrequent and typically arise from the mortality of a single tree or a group of trees. For example, in some closed canopy eastern US forests, gaps occur in 1%–5% of forested areas (Asner et al., 2013; Gorgens et al., 2023). Forests that experience frequent disturbances (Atkins et al., 2018; Johnson et al., 2021) and those at early successional stages (Swanson et al., 2011) often exhibit higher canopy openness, potentially enhancing tree regeneration through increased light availability. Many tree species require high-light environments to transition from the seedling to sapling life stage (Delissio et al., 2002), meaning only a very small portion of the population grows under optimal conditions.

Due to the rarity of canopy gaps, most species are relegated to persist in closed canopy environments for decades. For example, in British Columbia, individuals in the seedling bank can persist for 50 years without exceeding 1.3 m in height (Antos et al., 2005). In a frequently disturbed Taiwanese forest, the median age of saplings reaching 2 m in height was estimated at 47 years (Chang-Yang et al., 2021). Estimates of seedling persistence, however, remain scarce due to a few factors. First, temporal variability, including climatic variability and episodic events (e.g., masting), can significantly impact seedling dynamics (Schnurr et al., 2002; Xu et al., 2022). Another prominent limitation is that the random nature of many sampling inventories typically fails to capture seedling dynamics in uncommon conditions, such as canopy gaps, while extensive plot inventories (e.g., USDA Forest Inventory and Analysis) may capture rare conditions but typically do not tag and track small individuals through time. Furthermore, because of the complex and nonlinear relationship between age and size, plant size is a problematic tool for estimating the age of seedlings and conditions that enable seedlings to persist for decades (Delissio et al., 2002). Given the demographic importance of juvenile growth and survival to future forest structure and composition and the potential increase in canopy gaps resulting from elevated tree mortality, better estimates of seedling persistence under variable conditions are needed (McDowell et al., 2020).

Species exhibit considerable variation in their canopy gap affinities. The diversity in species' gap affinities, or tolerance to understory conditions, has long been recognized as a driver of forest succession; whereby early-successional, light-demanding species are gradually replaced by shade-tolerant species as canopy gaps close and light diminishes (Hibbs, 1983). Partially underlying these differences are species' abilities to survive low-light conditions and grow in high-light conditions (Canham, 1989; Kobe et al., 1995; Liu et al., 2016). Species more tolerant of understory conditions tend to exhibit slower growth rates but higher survival, while the inverse is true for gap-demanding species (Antos et al., 2005). Canopy gaps not only result in more light availability but also alter soil biota, nutrient pools, and aboveground herbivory (Kushwaha et al., 2021). Quantifying the impact of gaps on the forest community, therefore, requires an integrated approach that considers multiple vital rates (Frederiksen et al., 2014) and relative comparisons with dynamics under closed canopy conditions, both within and between species.

In addition to light limitations and resource competition, seedlings must be able to survive physical damage. Damages include herbivory (Clark & Clark, 1989), litterfall from live and dead trees (Moles & Westoby, 2004), and trampling by scientists in heavily quantified research sites (discussed by Comita et al., 2009). Another cause of stem breakage in temperate and boreal forests is frost heaving

(Goulet, 1995; Schramm, 1958). Studies have shown that seedlings with stronger stems, that is, high stem fracture toughness and high stem tissue density, are better equipped to survive understory conditions (Alvarez-Clare & Kitajima, 2007; Clark & Clark, 1989). For instance, Alvarez-Clare and Kitajima (2009) found a negative correlation between stem breakage and stem strength. Species that are more resistant or resilient to physical damage typically have a higher wood fiber density and mass per unit stem volume (Alvarez-Clare & Kitajima, 2007). Thus, these traits help protect seedlings from damage during long periods of understory persistence.

Plant demographic models can estimate persistence (e.g., seedlings' understory residence time) under different environmental conditions (Canham et al., 1994; Kobe et al., 1995; Pacala et al., 1996; Shugart, 1984). Individual-based forest demographic models, which have been used to understand forest successional change, can incorporate canopy gaps explicitly through direct estimation of light environments (Pacala et al., 1996) or implicitly by projecting separately a proportion of the populations under favorable conditions that represent canopy gaps (Chang-Yang et al., 2021; Johnson et al., 2018; Needham et al., 2018). A benefit of individual-based approaches over cohort-based models is that individuals' properties, contributions, and interactions are included explicitly (e.g., stem breakage), allowing for feedback between individuals and between individuals and the environment.

In this study, we followed 5236 seedlings from five common tree species in single-tree canopy gaps and closed canopy (understory) environments over three years in a mixed hemlock–hardwood forest in New England, USA. We investigated how gap dynamics impact seedlings through individual-based simulations, which we parameterized using seedling dynamics data collected under gap and closed canopy conditions. We investigated the following questions: (1) How much time is needed for each species to develop one sapling (known as passage time)? (2) How many seedlings are required to produce one sapling that is 1.5 m in height? (3) How do these statistics vary between gap and closed canopy environments? (4) Does stem breakage affect these estimations? We evaluated model predictions with empirically derived age-to-height relationships obtained from stem cross-sections of harvested seedlings.

MATERIALS AND METHODS

Study area

This study was conducted at the Harvard Forest long-term ecological research (LTER) site, which spans more than 1200 ha in north-central Massachusetts, USA. Within the larger research area, our data collection occurred on the Prospect Hill Tract (Foster, 1992), a late secondary mixed hemlock–hardwood forest. Soils were predominantly Histosols, with perennial and ephemeral wetlands scattered throughout the area.

In 2010, a 35-ha forest monitoring plot was established within the southeastern portion of the Prospect Hill Tract (Orwig et al., 2022). By 2014, all stems ≥1 cm dbh (1.3 m) were tagged, mapped, and measured according to standardized Forest Global Earth Observatory Network (ForestGEO) methods (Anderson-Teixeira et al., 2015; Condit, 1998). A follow-up census occurred five years later, between May and September 2019. Tree basal area in 2014 averaged 42.25 m^2 ha^{-1} and was composed mainly of *Tsuga canadensis* Carrière, *Quercus rubra* L., *Acer rubrum* L., and *Pinus strobus* L. (Orwig et al., 2022). Over the past three years, annual stem mortality of trees >10 cm dbh has averaged 3.01% (Magee & Johnson, unpublished data). Elevated mortality has resulted from natural thinning due to succession and an introduced aphid-like insect, the hemlock woolly adelgid (*Adelges tsugae* Annand), and eastern hemlocks in all life stages are now sharply declining (Case et al., 2017; Ellison et al., 2005).

Data collection

Beginning in July 2021, we established seedling plots in canopy gaps and closed canopy areas. We selected 58 dead and 12 living focal canopy trees. Not all dead trees created gaps (gap definition below). Remotely sensed imagery from an airplane aided in tree mortality detection, which we processed with the Deep Forest python package (https://data.neonscience.org/data-products/DP1.30010.001; NEON, 2023; Weinstein et al., 2020), along with annual tree mortality censuses (Magee & Johnson, unpublished data). All dead focal trees in this study had died within the last seven years. All living and dead focal trees were ≥28 cm dbh. The species of the focal canopy trees were *A. rubrum* ($n = 27$), *Q. rubra* ($n = 27$), and *T. canadensis* ($n = 18$).

Around each living and dead focal tree, we established three transects radiating in three directions: 0°, 120°, and 240°, and each transect had two seedling plots (1 × 1 m) at distances of 2 and 6 m from the focal tree (420 total plots). All woody tree seedlings ≤1 cm dbh were identified to species, mapped (within the 1-m^2 plot), tagged, and measured in height to the nearest half centimeter. We staked plot corner locations so all plots could be relocated in subsequent censuses.

Gap conditions for each seedling plot were categorized as (1) canopy gap—where the focal tree had died and resulted in direct overhead light availability (32% of plots)—or (2) closed canopy (non-gap, understory)—areas around living or dead focal trees where the 1 × 1 m plot had no direct overhead light (68% of plots). For detailed gap classification methods and a schematic, see Appendix S1: Figure S1.

Occasionally, seedlings broke or were damaged, resulting in reductions in height compared to the previous year (i.e., negative height growth). The greatest risks of height reduction were herbivory (e.g., white-tailed deer or moose), stem breakage from falling litter, or frost heaving. We identified breakage or damage by excessive negative changes in height and by explicit field notes documenting the breakage (e.g., "terminal leader browsed by deer"). We considered a seedling to have broken if its change in height was $\leq -2 \text{ cm year}^{-1}$, which was four times our smallest unit of measurement (0.5 cm).

We estimated the probability and magnitude of breakage by species based on the observed breakage rates and magnitudes of seedlings that broke over two one-year monitoring intervals (Table 1). We did not find evidence that the probability of breakage changed with height for any of the species, though the amount of stem breakage did increase linearly with height for two species: *A. rubrum* and *Q. rubra*.

Seedling demographic model

We projected seedling dynamics using a stochastic, spatially implicit simulation model (DeAngelis & Mooij, 2005; Grimm et al., 2006). Our methods were based on the modeling framework described by Chang Yang et al. (2021) and Needham et al. (2018). Our model forecasted individual seedling growth and survival as a function of seedling height. We evaluated the conditions for size-dependent growth and survival under different canopy conditions that we modeled implicitly through separate parameterizations of seedlings in gaps and closed canopy conditions. Mortality and growth were not explicitly correlated in our simulations but rather linked through seedling height, our primary population state variable. We also incorporated stem breakage into the model because ~3% of seedlings broke annually, though did not necessarily die.

We selected five species for our simulations that were common across the Harvard Forest. Four of the study species were red maple (*A. rubrum*), eastern hemlock (*T. canadensis*), northern red oak (*Q. rubra*), and eastern white pine (*P. strobus*). We also modeled birch congeners (*Betula* spp.) as a fifth "species" because black birch seedlings (*Betula lenta* L.) are nearly impossible to distinguish from yellow birch (*Betula alleghaniensis* Britton) seedlings (Carlton & Bazzaz, 1998).

Seedling survival module

We modeled the probability of seedling survival separately for each combination of species i and canopy condition j (canopy gap or closed canopy) with a generalized linear model (Equation 1). Seedling survival was a Bernoulli random variable (1 = survival, 0 = mortality), the odds of which increased linearly with seedling height, h, but did not exceed a maximum survival rate in each canopy condition, s^*_{ij}:

$$P\left(\text{survival}_{ij}\right) = \min\left(\frac{\exp\left(B_{0ij} + \beta_{1ij} \times h\right)}{1 + \exp\left(B_{0ij} + \beta_{1ij} \times h\right)}, s^*_{ij}\right) \quad (1)$$

We adjusted the maximum survival for each species (s^*_{ij}) because we had limited sample sizes for the tallest seedlings of several species, and the high survival

TABLE 1 Sample sizes, survival probability, growth rates, and breakage rates for five seedling species at the Harvard Forest.

Rate	*Acer rubrum*	*Betula* spp.	*Pinus strobus*	*Quercus rubra*	*Tsuga canadensis*
Individual seedlings	3624	375	376	472	379
Survival (annual rate)	0.782 [0.771, 0.793]	0.791 [0.758, 0.821]	0.865 [0.827, 0.896]	0.708 [0.668, 0.746]	0.727 [0.690, 0.762]
Breakage (annual rate)	0.015 (0.0022)	0.043 (0.011)	0.024 (0.016)	0.10 (0.017)	0.056 (0.013)
Average growth, no break (cm year^{-1})	1.39 (1.94)	5.72 (8.23)	1.73 (2.16)	1.93 (2.81)	2.07 (2.06)
Average break (cm)	5.2 (3.20)	8.9 (5.34)	6.1 (1.22)	6.8 (5.43)	8.8 (9.56)

Note: Sample size is the number of unique individual seedlings in the three-year study, and rates are averages across the three-year study. SEs in breakage and growth rates and 95% CI for survival across two sampling intervals are included parenthetically.

probabilities of those individuals led to upper survival asymptotes of 1.0. Therefore, to obtain biologically reasonable estimates of maximum survival rates by species (i.e., maximum survival probabilities below 1.0), we relied on the survival of sapling stems (defined here as stems 1–3 cm dbh) from 2014 to 2019 across the 35-ha ForestGEO plot (Orwig et al., 2022). We estimated average sapling survival rates for each species (s_i) using the formula proposed by Sheil et al. (1995; equation 6), which annualizes the survival rate over the measurement period (average five years for the ForestGEO plot). Here $N_{t,i}$ is the number of saplings of species i alive at time t, $N_{t+1,i}$ is the number alive at time $t+1$, and dt is the time between surveys:

$$\text{Sapling survival (Average)}, \ s_i = \left(\frac{N_{t+1,i}}{N_{t,i}}\right)^{1/dt} \tag{2}$$

To map the average sapling survival rates of each species (s_i) to sapling survival in each canopy condition (maximum seedling survival, s_{ij}), we considered canopy conditions to affect the odds of survival similarly for seedlings and saplings. For example, if the odds of seedling survival were 5% higher for seedlings under gap conditions than under closed canopy, the odds of survival would also be 5% higher for saplings under gap conditions than under closed canopy conditions.

$$\frac{\text{Odds of sapling survival}\left(\text{Canopy}, s_{ij}\right)}{\text{Odds of sapling survival}\left(\text{Average}, s_i\right)} = \frac{\text{Odds of seedling survival (Canopy)}}{\text{Odds of seedling survival (Average)}} \tag{3}$$

Based on our seedling survival data, we calculated the odds of seedling survival for each species overall, and under gap and closed canopy conditions, independent of height. This calculation and the sapling survival values (s_i; described above) allowed us to algebraically solve for the odds of sapling survival for each species under canopy gap and closed canopy conditions, s_{ij}^* (the maximum seedling survival rate for each species in each canopy condition; Appendix S1: Tables S2–S4).

We adjusted the maximum survival probability (s^*) for *T. canadensis* by −0.05 year^{-1} because the survival of stems ≥10 cm dbh decreased by approximately 5% pre- to post-hemlock woolly adelgid (Magee & Johnson, unpublished data). The adjustment was necessary because the survival of eastern hemlock has declined across size classes in recent years due to hemlock woolly adelgid. We reasoned that seedlings and saplings would experience similar declines in survival.

Seedling growth module

We quantified individual seedling growth as the height difference measured over consecutive years. We modeled the mean annual growth (in centimeters per year) as a logistic function of height, with three parameters A, B, and C, which depend on species and canopy condition (Equation 4). Coefficient A_{ij} represents the long-term mean growth rate of species i in canopy condition j. The height at which growth is increasing most rapidly is given by B_{ij}, and coefficient C_{ij} is a scaling factor that controls the maximum change in growth rate at height B_{ij}.

$$\mu_{ij}(h) = \frac{A_{ij}}{1 + \exp\left(\left(B_{ij} - h\right)/C_{ij}\right)} \tag{4}$$

We fit growth curves for each species by canopy condition combination (Appendix S1: Figures S3 and S4, Table S1) using self-starting nonlinear regression in base R (version 4.4.1). We obtained maximum likelihood estimates and confidence intervals for logistic curve parameters through parametric bootstrapping using library boot, with 1000 bootstrap samples of size 50 (Canty & Ripley, 2024). Competing asymptotic growth functions were also considered (Gompertz, Ricker) but the logistic function was selected due to fit quality and interpretability (Appendix S1: Figure S4).

Variation in individual seedling growth

Logistic curves were used to represent the overall height-dependent growth behavior for each species and gap condition combination. Individual seedlings, however, may grow slower or faster than the expected value for each species in each canopy condition. We allowed the growth behavior of individuals to vary by resampling their growth curves from the collection of all growth curves fit during bootstrapping. For each seedling k in a species by canopy condition cohort, we sampled (with replacement) a mean growth curve μ_{ijk} to represent the seedling's expected growth behavior over the simulation (Appendix S1: Figure S5). The individuals then grew according to their selected curve, subject to their initial height and any stochastic breakage events, described in the next section.

Population projections and demographic assessment

We simulated the behavior of seedling cohorts using an individual-based model to assess how individuals and populations change over time. Each cohort featured 250,000 one-year-old seedlings representing a species and canopy condition combination. Model stochasticity arose from four processes: (1) seedlings varied in their initial heights, (2) individual seedling mean growth was resampled from the collection of curves fit for the corresponding species and canopy condition, (3) seedling survival for each species was modeled as a height-dependent Bernoulli random variable, and (4) seedling breakage was treated as a height-independent Bernoulli random variable.

To determine initial seedling heights for each individual in our simulations, we used empirically derived height distributions from newly recruited woody (one-year-old, post-cotyledon stage) seedlings in the 1×1 m plots. Species' initial height distributions are shown in Appendix S1: Figure S7 and matched well the following distributions:

$$\textit{Acer rubrum}: \mathrm{Ht}_0 \sim \mathrm{Uniform}(\min = 3.5\,\mathrm{cm}, \max = 5.5\,\mathrm{cm})$$

$$\textit{Betula}\ \mathrm{spp.}: \mathrm{Ht}_0 \sim \mathrm{Normal}(\mu = 2.7\,\mathrm{cm}, \sigma = 0.56\,\mathrm{cm})$$

$$\textit{Pinus strobus}: \mathrm{Ht}_0 \sim \mathrm{Normal}(\mu = 5.38\,\mathrm{cm}, \sigma = 0.87\,\mathrm{cm})$$

$$\textit{Quercus rubra}: \mathrm{Ht}_0 \sim \mathrm{Uniform}(\min = 10\,\mathrm{cm}, \max = 13\,\mathrm{cm})$$

$$\textit{Tsuga canadensis}: \mathrm{Ht}_0 \sim \mathrm{Normal}(\mu = 3.5\,\mathrm{cm}, \sigma = 0.54\,\mathrm{cm})$$

Given the initial height of a seedling at the start of the year, we applied Bernoulli trials for survival using the height-dependent survival probability from the survival model fit for the corresponding height and gap condition (Equation 1). Maximum seedling survival rates were the estimated sapling survival rates for each species in each gap condition, s_{ij}^* (Table 1).

Surviving seedlings increased in height according to their height-dependent logistic growth curve, $\mu_{ijk}(h)$ sampled from the collection of all curves fit for each species and gap condition (Equation 2). Figures showing variation in growth curves fit by species and condition can be found in Appendix S1: Figure S6, as well as descriptive statistics reflecting for the range of growth parameters in Appendix S1: Table S1.

In each year of the simulation, after each surviving seedling grew, it had a chance to break. We determined each species' breakage probabilities and breakage amounts by averaging the observed breakage rates and breakage amounts over the three-year study (Table 1).

Height estimates at the start of the subsequent year for seedling k of species i from canopy condition j $(h_{ijk,t+1})$ combined the current height $(h_{ijk,t})$, the expected value of growth evaluated at the seedling's current height $(\mu_{ij}(h_{ijk,t}))$, which depended on each individual's growth curve, and breakage $(b_{ijk,t})$.

$$y_{ijk,t+1} = y_{ijk,t} + \mu_{ij}\left(h_{ijk,t}\right) + b_{ijk,t} \tag{5}$$

Model evaluation

We simulated 100 trials for each species in each canopy condition, with initial cohorts of 250,000 seedlings. Initial simulations consisted of fewer trials and individuals (e.g., 25 trials and 100,000 seedlings), but we increased both values to thresholds where further increases did not alter simulation results. We assessed simulation results by taking the median of three summary statistics across all trials. The median and minimum passage times represent the median age and youngest age of individuals within a cohort reaching the 1.5-m sapling height threshold. The median number of seedlings required to produce one sapling represents the total number cohort size divided by the number that achieved sapling height during the simulation. We ran additional simulations without seedling breakage and compared results to our model with breakage to evaluate how stem breakage influences passage times and the number of seedlings needed to produce one sapling.

Field sampling and aging of tree seedlings

We harvested seedlings from each of the five study species (*T. canadensis*, *Q. rubra*, *A. rubrum*, *P. strobus*, and *Betula* spp.) from gap ($n = 37$ seedlings) and closed canopy ($n = 41$ seedlings) conditions to examine the relationship between seeding height and age. Samples were collected on the Prospect Hill Tract outside the 35-ha forest plot. At each sampling location ($n = 5$; two gaps, three closed canopy areas), we walked a predetermined random number of steps in a predetermined random direction and selected the first seedling we encountered of the target species. In total, across three canopy gaps, we collected 10 *A. rubrum*, 6 *Betula* spp., 11 *P. strobus*, and 10 *Q. rubra* seedlings. We did not collect *T. canadensis* seedlings in gap conditions, as we could not find enough individuals in the sampling areas to justify destructive collection. We collected nine *A. rubrum*, six *Betula* spp., nine *P. strobus*, eight *Q. rubra*, and nine *T. canadensis* seedlings under closed canopies. When we collected seedlings, we dug up as much of the root system as possible, took aboveground and belowground heights, and measured the basal diameter at ground level with analog calipers. We cut the samples in 2.5-cm intervals above and below the root collar to ensure that processed samples had shoot tissue (Hankin et al., 2018). We removed the cork cambium before slicing cross-sections.

We used a GSL1-microtome—a base sledge microtome (Gärtner et al., 2014) with A-type (A 0.38) blades—to cut 10- to 15-μm cross-sections from each seedling sample. We followed the manufacturer's instructions and best practices for sampling wood anatomy (Gärtner et al., 2015; Von Arx et al., 2016). Blades were sharp with entire edges, and we did not use non-Newtonian fluid preparation (sensu Schneider & Gärtner, 2013) because we were less interested in quantitative wood anatomy (e.g., ring widths), but rather total ring counts. We took multiple 10- to 15-μm cross-sections from each sample, bleached them in 1% bleach (in deionized [DI] water) for 60 s, and rinsed twice with DI water. We then stained cross-section samples with Safranin O (1% Safranin O and 20% EtOH) for 15–30 s, rinsed twice with EtOH 30%, and stained with Astra Blue (1% Astra Blue and 50% EtOH) for 15–30 s. Finally, we returned the samples to the DI water solution, using successive, reverse ethanol dilution series (100%, 90%, 70%, 50%) in 30-s intervals, followed by the DI water solution (Gärtner et al., 2015). We prepared a slide using DI water for each sample to visualize and quantify rings under a compound light microscope.

We counted annual rings to obtain the minimum seedling age (Figure 1). Even though some species can exhibit "missing" rings (Leland et al., 2016; Wilmking et al., 2012), we reasoned that knowing the approximate minimum age in comparison to height would help us better understand the complicated size–age relationship in forest tree seedlings. We plotted the empirical (aged seedlings) age–height relationships over the simulated values to evaluate the estimates from our simulations.

RESULTS

Seedling passage time

Across all species and canopy conditions, the median time for a one-year-old seedling to reach 1.5 m in height was 32 years (Figure 2a), and the average fastest time for a single seedling to reach the sapling stage (minimum passage time) was 17 years (Figure 2a; *Betula* spp.). Averaged across species, the median seedling passage time was shorter in gap (median = 29; minimum = 13) than closed canopy conditions (median = 34; minimum = 21) but with high interspecific variation in this discrepancy. For example, *P. strobus* took 26 years to reach 1.5-m height under gap conditions (minimum 12 years), but seven years longer on average in closed canopy conditions (median = 33 years, minimum passage time = 19 years). In contrast to *P. strobus*, *T. canadensis* required approximately 48 years on average to obtain 1.5 m in height

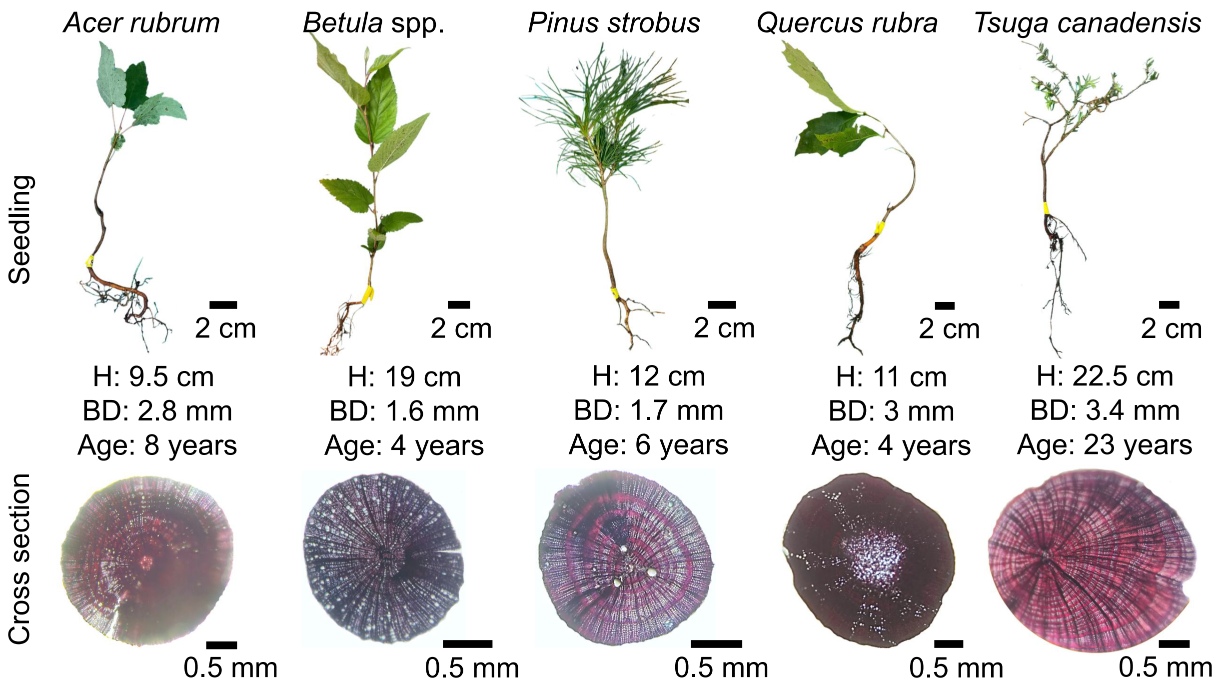

FIGURE 1 Examples of seedlings and stained wood cross-sections. Cross-sections were used to determine annual ring counts for five target species. The associated height (H), basal diameter (BD), and age are listed below each sample. The top scale bar represents 2 cm for seedling heights, while the bottom scale bar represents 0.5 mm on the cross-section. Photo credits: I. Stone, C. Garnica-Diaz.

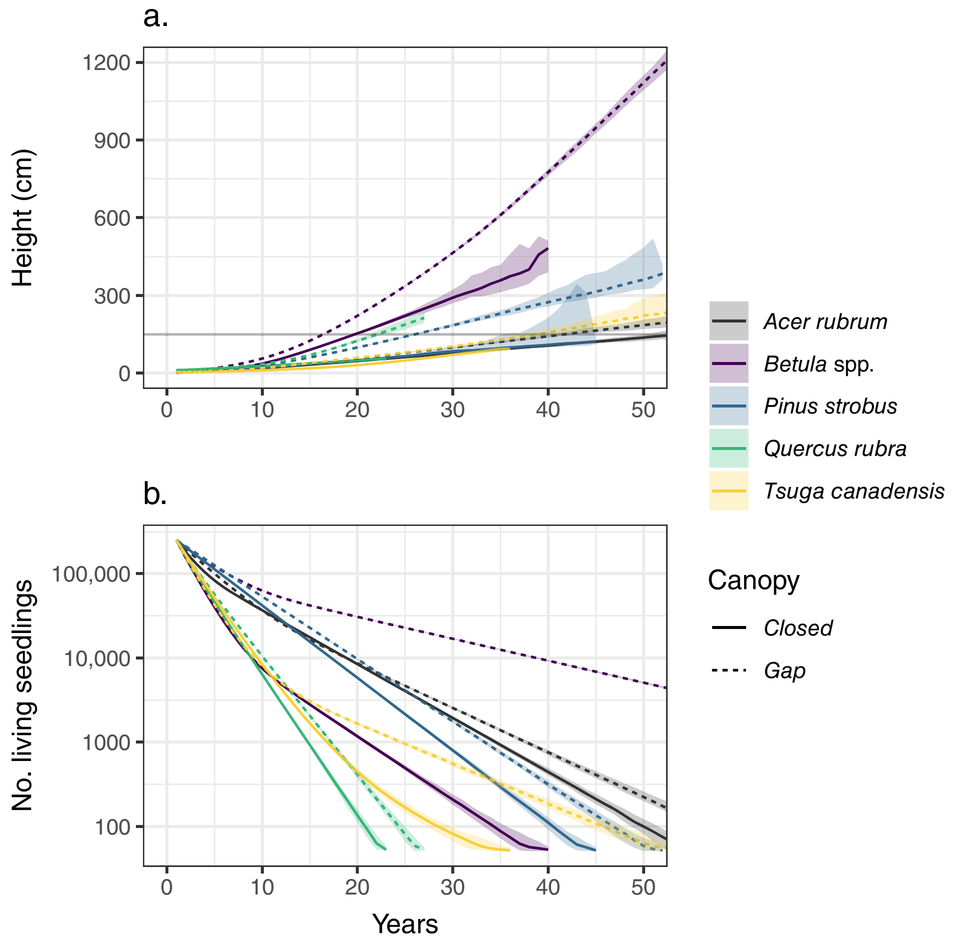

FIGURE 2 (a) Mean height and (b) number of seedlings remaining through simulated years. Individual-based simulations are for five species across two canopy conditions (gaps and closed canopies). Values are averaged across 100 simulations to account for model stochasticity, and confidence envelopes represent the 2.5 and 97.5 quantiles across the simulations. Medians shown here do not necessarily reach 150 cm (solid gray line in panel a), but all species had individuals within the cohorts reach the sapling threshold (Figure 3, Table 2).

under closed canopy conditions (minimum = 30 years) but with proportionally less reduction in passage time (median = 42 years, minimum = 20) under closed canopy conditions. The other three species fell between these two extremes; unexpectedly, we found that the median passage times were longer in canopy gaps for both *Betula* spp. (29 years in gaps, 22 years in closed canopy) and *A. rubrum* (37 years in gaps, 36 years in closed canopies). The minimum passage times for these two species reflected the expected behavior in gaps: the average minimum passage time for *A. rubrum* was 17 years in gap conditions and 21 years in closed canopies, and the minimum times for *Betula* spp. were 10 and 12 years for gaps and closed canopies, respectively. *Q. rubra* took 25.5 years on average (minimum 24 years) to go from a one-year-old seedling to a 1.5-m tall sapling in closed canopy conditions. Under canopy gaps, the median passage time for *Q. rubra* decreased to 21 years (13 minimum).

Number of seedlings required to produce one sapling

Across all species, the median number of one-year-old seedlings required to produce a single 1.5-m tall sapling was 896 (Figure 3). Fewer individuals were required in gaps (median 294) than in closed canopy conditions (median 2674), but there was a large interspecific variation in this discrepancy. For *Betula* spp. and *P. strobus*, the median number of seedlings required to produce one sapling under gap conditions was 7 and 63, respectively. The number required for those two species was more than an order of magnitude greater under closed canopy conditions, 229 for *Betula* spp. and 2674 for *P. strobus*, proportionally 32× and 63× greater, respectively. *A. rubrum* and *T. canadensis* had smaller proportional discrepancies in the number of seedlings required in gap versus closed canopy conditions. For *A. rubrum*, it took an average of 294 seedlings in gaps and 871 seedlings in

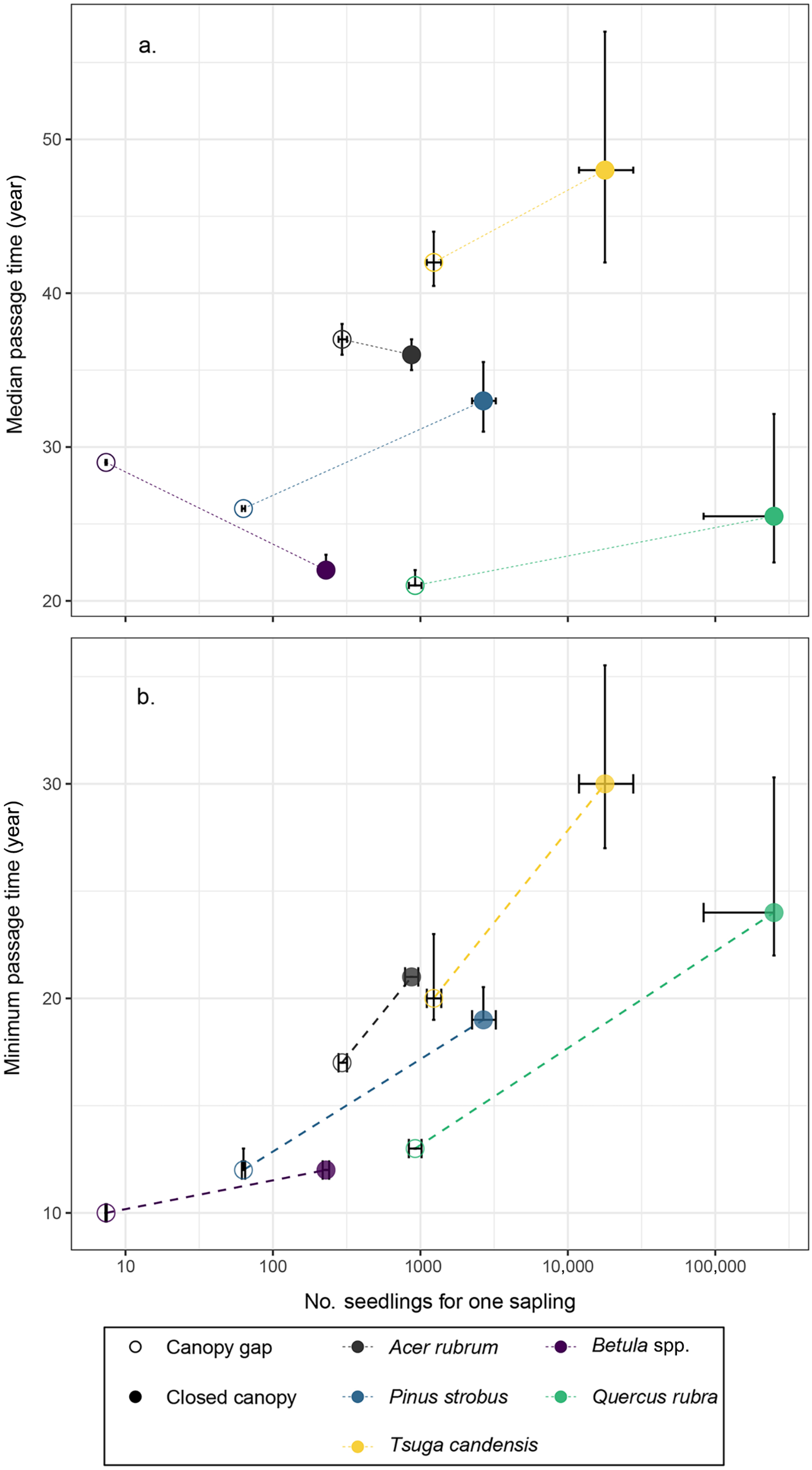

FIGURE 3 (a) Median and (b) minimum passage times to 1.5 m and the number of seedlings required to produce one sapling for five species in canopy gaps and in the non-gap closed canopy areas at the Harvard Forest. Error bars delineate the 2.5 and 97.5 quantiles from 100 simulations in each canopy condition. Note log scale on x-axis.

closed canopy conditions (3×). *T. canadensis* needed 1232 seedlings to produce a sapling in gap conditions and 17,857 seedlings (14.5×) in closed canopy conditions. *Q. rubra* required 271× more seedlings to produce one sapling in closed canopy conditions (250,000) versus canopy gaps (920).

Stem breakage versus no breakage

We found that stem breakage increased the median passage time by 0.75 years and the minimum passage time by 0.6 years when averaged across species and canopy conditions (Table 2). Although breakage did not strongly affect passage times, the number of seedlings required to produce one sapling consistently increased when we included breakage in the simulations (Table 2). Breakage increased the number of seedlings per sapling by 70%, averaged across all species. Two species, *Q. rubra* and *T. canadensis*, had higher breakage rates than the other species (10% and 4.5%, respectively; Table 1). These two species also had the largest disparities in the number of seedlings needed to produce one sapling between simulations that included stem breakage versus simulations without breakage (Table 2). The number of seedlings needed for one *T. canadensis* sapling was 2.8× higher when breakage was included in closed canopies and 2× higher in canopy gaps. The number of seedlings for one *Q. rubra* sapling was 2× higher in closed canopies and 1.9× higher in canopy gaps. The other three species, *A. rubrum*, *Betula* spp., and *P. strobus*, were less affected by breakage (Tables 1 and 2), but breakage did tend to influence seedlings more under closed canopy conditions than under canopy gaps.

Seedling age-to-height comparisons and model evaluation

The relationship between seedling height and age varied widely among species for individuals in gaps versus closed canopy conditions (Figure 4). When evaluating simulated height-to-age relationships with aged seedling samples, we found that, for most species, our simulations tended to underestimate age for a given height, especially in closed canopy conditions (Figure 4). The fitted lines describing the closed canopy, empirical (lab samples) height-to-age relationship of *A. rubrum* and *P. strobus* were steeper (0.69 and 0.53 years cm^{-1}) than simulated relationships (0.41 and 0.34 years cm^{-1}; Figure 4). Under gap conditions, simulations predicted older *P. strobus* and *Betula* spp. seedlings for a given height. *Betula* spp. in gap conditions achieved the fastest growth observed, 0.070 years cm^{-1}, or <1 month cm^{-1} of height growth. The empirical age-to-height relationships for *T. canadensis* and *Q. rubra* under closed canopies and *A. rubrum* under canopy gaps were closest to simulated fit lines (Figure 4).

TABLE 2 Simulation results for five species in gap and closed canopy conditions.

		Without breakage				With breakage			
Species	**Canopy condition**	**No. to 1.5 m**	**No. seedlings sapling^{-1}**	**Min. passage (years)**	**Median passage (years)**	**No. to 1.5 m**	**No. seedlings sapling^{-1}**	**Min. passage (years)**	**Median passage (years)**
Acer rubrum	Canopy	316	793	21	36	287	871	21	36
	Gap	951	263	17	37	850	294	17	37
Betula spp.	Canopy	1440	174	12	22	1092	229	12	22
	Gap	37,711	6.6	10	29	33,860	7.4	10	29
Pinus strobus	Canopy	120	2092	19	33	93.5	2674	19	33
	Gap	4432	56	12	26	3961	63	12	26
Quercus rubra	Canopy	2	125,000	23	25	1	250,000	24	25.5
	Gap	528	473	13	21	272	921	13	21
Tsuga canadensis	Canopy	40	6250	28	47.25	14	17,857	30	48
	Gap	403	620	20	41	203	1232	20	42

Note: We provide summary statistics when simulations include stem breakage (right) and without (left). The number of one-year-old seedlings reaching 1.5-m height from an initial cohort of 250,000 seedlings; seedlings per sapling is the transition ratio, and minimum and median passage times are the times needed to reach the 1.5-m height sapling threshold.

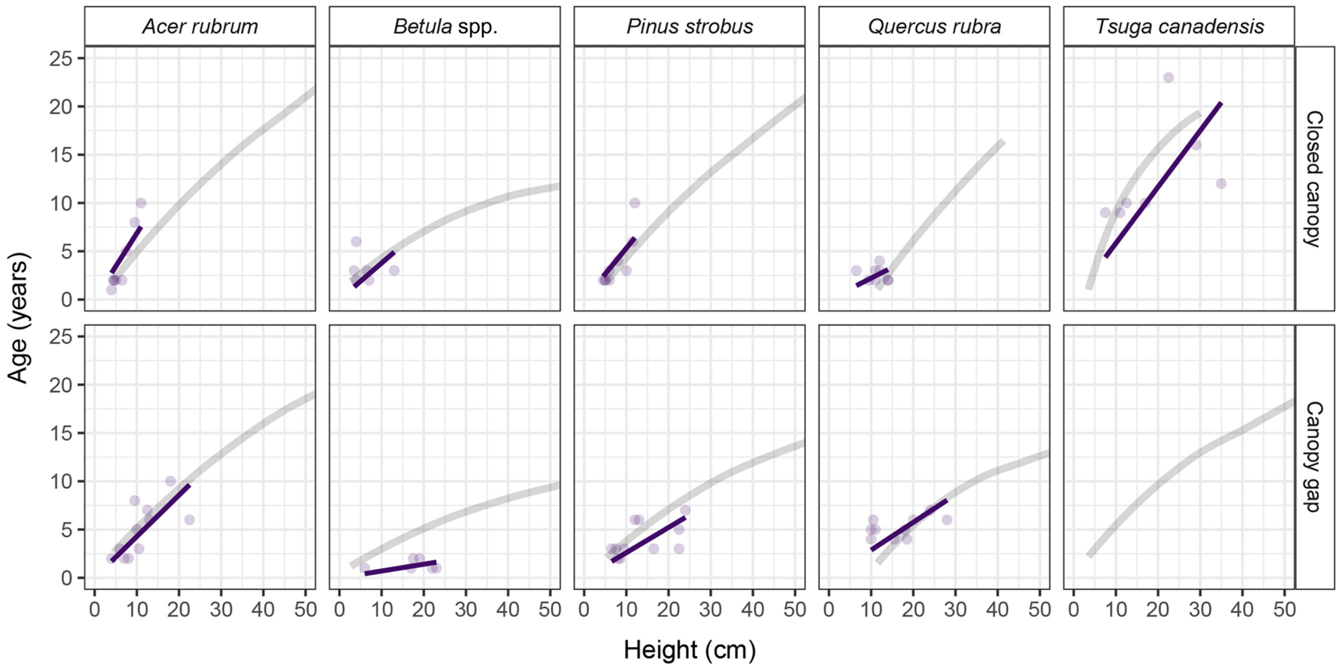

FIGURE 4 Seedling age as a function of height from empirically parameterized simulations (gray) and aged samples (purple). We consider height to predict age because it can be easily measured. The aged lines below simulated lines indicate younger seedlings for a given height (shorter seedlings for a given age) than would be expected from the counted rings on the seedling cross-sections. No samples were collected for *Tsuga canadensis* in canopy gap conditions. A figure with transposed axes is available in Appendix S1: Figure S8.

DISCUSSION

Summary

The frequency and time needed for tree recruitment tend to be underestimated by dynamic vegetation models of global forests (Díaz-Yáñez et al., 2024). Large uncertainties in recruitment arise from model disparities in seedling and sapling understory passage times, partially due to variable responses across heterogeneous forest environments, including canopy gaps. Using targeted data collection, we sampled and forecasted seedling dynamics under single-tree canopy gap conditions relative to dynamics under closed canopies to estimate the time and number of seedlings required for sapling recruitment. We found that it took hundreds of seedlings and over two decades for one sapling in most species, but passage times were shorter, and the number of seedlings required to produce one sapling was fewer in gap versus closed canopy conditions.

Interspecific variation in persistence and passage times

We observed high interspecific variation in responses to gap conditions, mostly consistent with previous accounts of the species' ecology and natural history (e.g., Kobe et al., 1995; Orwig & Abrams, 1995). For example, *Betula* spp. and *P. strobus*—generally regarded as intolerant and moderately intolerant to understory conditions, respectively—grew faster in gaps, as indicated by shorter passage times than other species. These two species also needed far fewer seedlings to produce one sapling (i.e., lower seedling-to-sapling transition ratios) than the other species. *T. canadensis* and *A. rubrum* took the longest time to reach 1.5-m sapling height, which aligns well with the shade tolerance classifications for these species, particularly *T. canadensis*, which is considered very tolerant of understory conditions (Burns et al., 1990).

Q. rubra rarely reaches 1 cm dbh in the Harvard Forest ForestGEO plot. In fact, only two new *Q. rubra* seedlings recruited to the 1 cm dbh threshold in the 2019 plot census (0.057 sapling recruits ha^{-1}). Reported seedling densities of *Q. rubra* at the Harvard Forest range from 11,238 seedlings ha^{-1} (four years post-mast; this study) to 47,000 seedlings ha^{-1} (one-year post-mast; Jevon et al., 2022). We found that in closed canopy conditions, *Q. rubra* required upward of 250,000 one-year-old seedlings to produce a single 1.5-m tall sapling. At the Harvard Forest, *Q. rubra* seedlings are also sensitive to soil-borne pathogens, which might partially explain the high mortality rate relative to the other four species (Jevon et al., 2020, 2021). Additionally, many oaks are experiencing widespread recruitment failure across North America attributed to a suite of biotic (see browsing discussion below; Yamazaki et al., 2009) and climatic factors (Abrams, 2003; MacDougall et al., 2010), and the low recruitment of *Q. rubra* at the Harvard Forest provides supporting evidence for this demographic bottleneck. Large, multi-tree canopy gaps, such as those arising from forest-wide disturbance or harvest, are likely required for the successful recruitment of *Q. rubra*. Land use shifts and frequent tree harvest in the early-to-mid 20th century resulted in high oak recruitment and the contemporary abundance of canopy oaks at the Harvard Forest (Foster, 1992; Foster et al., 1998).

The seedling vital rates observed in this study align with reports of seedling dynamics in other New England forests. For example, the low average growth (1–2 cm year^{-1}) and high mortality (20%–30% year^{-1}) of *Q. rubra* match well with another multi-year study in New Hampshire (Cleavitt et al., 2024). The differences in survival in gaps versus closed canopies also reflect those previously found for maples at the Harvard Forest (Sipe & Bazzaz, 1995). Kern et al. (2012) measured growth and survival for four of our study species—*Q. rubra*, *T. canadensis*, *B. alleghaniensis*, and *P. strobus*—and found species-level rates similar to ours for closed canopies and small (<10 m diameter) gaps; however, rates in large gaps (>46 m diameter) far exceeded those we observed for all species. Our study does provide one notable contrast to older reports: the high (~30% year^{-1}) *T. canadensis* mortality rate, which increased in recent years due to hemlock woolly adelgid.

Species characteristics underlying gap affinities

Different characteristics play into species' abilities to survive the understory and to take advantage of available light (Denslow, 1987). Light- or gap-demanding species tend to exhibit higher specific leaf area than understory-tolerant species, allowing these plants to grow faster under high-light conditions relative to species tolerant of understory conditions (Grubb et al., 2013; Poorter, 2007). *Betula* is generally an early successional genus (Archambault et al., 1998; Purves et al., 2008) that can establish rapidly in gaps through high seed production and rapid growth, but typically exhibits higher mortality than other canopy tree species, particularly in closed canopy environments (Lorimer et al., 2001). *P. strobus* seedlings have also been shown to respond well to gaps or partial gaps (Powers et al., 2008), displaying enhanced survival and faster growth under high-light conditions (Boucher et al., 1998; Santala et al., 2019). *P. strobus* and *B. lenta* are the two tree species predicted to benefit most from increased hemlock mortality at the Harvard Forest (Case et al., 2017; Foster et al., 2014). Understory-tolerant species, namely *T. canadensis* and *A. rubrum*, exhibited more consistent growth rates across heterogeneous environments, as demonstrated by the smaller proportional decreases in passage time and number of seedlings required in canopy gaps versus closed canopies. Understory-tolerant species were more resilient to physical damage.

Seedling adaptive response and physiological adjustments to release upon gap formation determine success of advance regeneration (Uhl et al., 1988). Some individuals may respond well, while others lack the plasticity or even experience photoinhibition (Huang et al., 2015). The height-dependent growth and survival patterns observed in this study were likely different for seedlings that established pre- versus post-gap formation. Even though we tracked thousands of seedlings in gap conditions, for most individuals, we were unable to verify seedling recruitment time relative to gap formation. Furthermore, newly recruited seedlings observed over the course of the study were small such that we could not parameterize the full height-dependent growth and survival models. Longer monitoring in gap conditions will permit more accurate forecasting and the ability to evaluate the relative contribution of advance regeneration to tree recruitment.

Stem breakage

Interspecific variation in stem breakage might also influence species' persistence in the understory. Most studies of tree growth and demographic projections omit broken stems and negative growth because they are difficult to model; however, removing negative growth can induce bias (Phillips et al., 2002). Here, we included negative growth mechanistically through stem breakage. In our demographic forecasts, breakage increased the number of seedlings needed to produce a sapling, especially in closed canopy environments. We note here that breakage likely has a larger impact on seedling passage times than we observed because our simulations only consider breakage to influence seedling survival and growth via implicit reductions in seedling height; however, we ignore the perennial impacts breakage has on subsequent growth and survival.

A review of the causes of seedling damage found that herbivory and physical damage accounted for 38% and 4.6% of seedling mortality, respectively (Moles & Westoby, 2004). Ungulates and smaller mammals tend to preferentially browse on *A. rubrum*, *T. canadensis*, and *Q. rubra* in temperate forests (among other species;

Faison et al., 2010). We likewise observed the most browsing and highest stem breakage rate in *Q. rubra* seedlings in our plots. Species least resilient to breakage, as indicated by higher proportional increases in the number of seedlings needed to produce one sapling, also had the largest differences in transition ratios for gap versus closed canopy conditions (Appendix S1: Figure S5). This similarity suggests an interesting tradeoff, whereby species with stronger gap affinities are also more susceptible to breakage (in terms of survival and transition ratios). Our results highlight the complex suite of traits (e.g., stem fracture toughness, and resilience to physical damage) that allow seedlings to survive in forest understories.

Individual variation in growth and minimum passage times

Consistently fast growth is often needed to escape high mortality during the earliest seedling life stages (Chang-Yang et al., 2021). Our study's minimum passage times reflect the positive deviation in growth from the population mean and the best-case scenario for the species. High intraspecific growth variation within canopy conditions suggests that localized habitat conditions besides overhead light (e.g., microsites) might also drive this growth variation (Delucia et al., 1998; Magee et al., 2021). One unexpected result from our study highlights this important heterogeneity: We found shorter median passage times for *Betula* spp. in closed canopies than in gaps, which is inconsistent with the early successional classification of *Betula* (Archambault et al., 1998). This contradictory finding was driven by the observed faster initial height growth under closed canopies than in gaps (Appendix S1: Figure S6). Faster growth of *Betula* spp. under closed canopies was likely due to confounding habitat variables, such as soils or dead woody debris microsites that facilitated *Betula* growth. Another explanation is that intraspecific genetic variation, or perhaps differences between *B. lenta* and *B. alleghaniensis*, confounded the effect of canopy conditions on *Betula* spp. growth (Blumstein, 2024). When we evaluated the minimum passage times for *Betula* spp. in gaps versus closed canopy conditions, however, we found results more consistent with the expectations for a gap-demanding species, suggesting heterogeneous responses to differences in gap characteristics.

High intraspecific growth variation in gap conditions could also result from differences in gap attributes. Our grouping of single-tree gaps versus closed canopy environments somewhat limits our inference because gap size is a quantitative variable, and differences in gap attributes (e.g., size, location within gap) can create different microsites and emergent plant dynamics (Gray & Spies, 1996; Sipe & Bazzaz, 1995). Furthermore, large, multi-tree canopy gaps, such as those that arise from large disturbances, are predicted to increase at the Harvard Forest due to the decline of eastern hemlock (Case et al., 2017). Spatially aggregated hemlocks dying from hemlock woolly adelgid also gradually lose leaf area such that increased understory light occurs prior to tree death.

Our modeling approach assumed that gap conditions remained constant for the longevity of the simulation. This simplifying assumption would rarely be true. Canopy gaps can fill rapidly through lateral growth or advance regeneration (Messier et al., 1999; Uhl et al., 1988). Therefore, optimal gap conditions would decline over time, especially for smaller gaps that fill quickly (Bullock et al., 1995; Feldmann et al., 2018). Conversely, tree mortality might also create new gaps such that closed canopy conditions would open. New gaps would be less likely in most forests given the rarity of big tree mortality and gap creation, although elevated hemlock mortality is causing high canopy turnover at the Harvard Forest. Even under these static assumptions, though, our analyses highlight species' fitness differences in gap versus closed canopy conditions. Moreover, by including growth variation for each species within each canopy condition, our simulations implicitly assumed some differences in growth environments not accounted for by our gap classification dichotomy. Thus, incorporating other local conditions should also improve model predictions.

Additional modeling considerations

Our data were temporally limited, and we were not confident in extending our predictions beyond the sapling life stage; forecasting sapling recruitment to the canopy would allow for a better understanding of future forest composition. We also had a limited number of large seedlings in our data and thus relied on sapling-sized stems in the ForestGEO plot data to obtain estimates for maximum seedling survival rates. Incorporating forest inventory data, like ForestGEO censuses, can help inform predictions of transitions to later life stages (e.g., Condit, 2022). Although we were able to calculate parameters for size-dependent survival and growth, we lacked long-term temporal variation, which affects seedling dynamics (Bachelot et al., 2015; Magee et al., 2021). By allowing each seedling to have unique growth characteristics, we induced a degree of temporal autocorrelation in individual growth. However, accurately measuring interannual variation within individuals relies on longer monitoring, and high variation could decrease differences in seedling dynamics across heterogeneous environments (Chang-Yang et al., 2021).

Other considerations for species fitness

Species rates other than seedling growth and survival influence species' gap associations, namely, seed dispersal and seedling recruitment. For example, differences in seed production and dispersal could offset survival and growth (dis)advantages, altering a species' ability to colonize canopy gaps (Levin et al., 2003; Nathan & Muller-Landau, 2000). Because we began our seedling sampling by measuring post-cotyledon (typically one-year-old) woody seedlings, we did not evaluate seed or germination dynamics. Higher germination rates and first-year survival can strongly filter the species pool (Chang-Yang et al., 2013). Interspecific variation in negative conspecific density dependence also filters the species pool at the Harvard Forest (Jevon et al., 2022) and has been shown to correlate negatively with species growth in canopy gaps at other sites (Song et al., 2020). Recent evidence also suggests that negative density dependence persists after neighbor trees die (Esch & Kobe, 2021; Magee et al., 2024), which might explain intraspecific variation in seedling recruitment around different species of dead trees. Masting species at this site, *Q. rubra* and *P. strobus*, rely on large, synchronous seed output for predator satiation (Zwolak et al., 2022), and from such pulse events might emerge differences in density-dependent seed and seedling survival (Norghauer & Newbery, 2016). Including the above processes in demographic forecasting would allow for more comprehensive assessments of species gap affinities.

Aging seedlings

Seedling height often poorly predicts seedling age due to large variability in growth across forest environments (Gutsell & Johnson, 2002). By evaluating simulations with aged seedling cross-sections, we confirmed that individuals persist for decades as seedlings. Intraspecific variation in observed age-to-height relationships revealed differences in growth in gaps versus closed canopy conditions, and interspecific variation in age-to-height relationships validated species growth variation across gap environments and, in some instances, allowed us to confront unexpected simulation statistics. For example, as we mentioned above, the slower initial growth of *Betula* spp. under gap conditions relative to closed canopy conditions was counterintuitive. Aged *Betula* spp. seedlings showed that simulations tended to overpredict age for a given height (underpredict height for a given age), implying faster growth of *Betula* spp. in gaps than observed in our seedling monitoring plots.

It is also important to note that aged samples were assigned minimum ages and could be older. Elucidating why individuals and species exhibit missing rings in the annual transition from early- to late-season wood is a longstanding problem in dendrochronology. Individual features such as slow growth or stem breakage might yield undetectable diameter increases. Certain slow-growing species (e.g., *A. rubrum*) or those at the northern range limits could also be more likely to exhibit missing rings (Leland et al., 2016; Pederson et al., 2017). In the context of this study, the observed minimum seedling age-to-height relationships underscore the slow growth of forest seedlings, and seedling height should be used with great caution as a proxy for age.

CONCLUSIONS

We demonstrated that several decades are required for most seedlings to reach the sapling stage. Furthermore, our targeted sampling of "rare" gap conditions showed that gaps decrease passage times and the number of seedlings needed to produce one sapling. Consistently fast-growing seedlings, even within gaps, are required for quick passage to the sapling stage. Stem breakage contributes to the duration of seedling understory persistence, and increased exposure to potential breakage in closed canopy conditions limits the probability of sapling recruitment. Empirically derived age-to-height relationships from aged seedlings indicated that our simulations tended to overpredict seedling age for a given height, especially in closed canopy conditions. Our results are restricted to the dynamics of this forest successional phase; however, our modeling framework and model assessment highlight the slow growth and high mortality of the seedling life stage and the large variation in interspecific gap affinities across a forest community.

AUTHOR CONTRIBUTIONS

Lukas J. Magee and Daniel J. Johnson conceived the study. Lukas J. Magee, Isabella Stone, April Zee, and Daniel J. Johnson collected the data. Isabella Stone, Lukas J. Magee, and Claudia J. Garnica-Díaz developed the sample collection and cross-sectional methods for the laboratory, and Isabella Stone led the sample processing. Jeffrey Mintz, Lukas J. Magee, and Isabella Stone performed statistical analyses and modeling. Isabella Stone, Lukas J. Magee, and Jeffrey Mintz led the writing of the first draft. All authors provided feedback and approved the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Stone et al., 2025) are available on Zenodo: https://doi.org/10.5281/zenodo.15185916. ForestGEO plot data are available on ForestGEO: https://forestgeo.si.edu/explore-data.

ORCID

Jeffrey Mintz https://orcid.org/0000-0003-4345-366X
Claudia J. Garnica-Díaz https://orcid.org/0000-0003-0065-1172
Chia-Hao Chang-Yang https://orcid.org/0000-0003-3635-4946
David A. Orwig https://orcid.org/0000-0001-7822-3560
Audrey A. Barker Plotkin https://orcid.org/0000-0002-4473-9785
Raelene M. Crandall https://orcid.org/0000-0002-0229-5418
Daniel J. Johnson https://orcid.org/0000-0002-8585-2143
Lukas J. Magee https://orcid.org/0000-0003-3124-2275

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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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