

PRIMARY RESEARCH ARTICLE

Improved phenological escape can help temperate tree seedlings maintain demographic performance under climate change conditions

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Abstract

Phenological escape, a strategy that deciduous understory plants use to access direct light in spring by leafing out before the canopy closes, plays an important role in shaping the recruitment of temperate tree seedlings. Previous studies have investigated how climate change will alter these dynamics for herbaceous species, but there is a knowledge gap related to how woody species such as tree seedlings will be affected. Here, we modeled temperate tree seedling leaf-out phenology and canopy close phenology in response to environmental drivers and used climate change projections to forecast changes to the duration of spring phenological escape. We then used these predictions to estimate changes in annual carbon assimilation while accounting for reduced carbon assimilation rates associated with hotter and drier summers. Lastly, we applied these estimates to previously published models of seedling growth and survival to investigate the net effect on seedling demographic performance. Our models predict that temperate tree seedlings will experience improved phenological escape and, therefore, increased spring carbon assimilation under climate change conditions. However, increased summer respiration costs will offset the gains in spring under extreme climate change leading to a net loss in annual carbon assimilation and demographic performance. Furthermore, we found that annual carbon assimilation predictions depend strongly on the species of nearby canopy tree that seedlings were planted near, with all seedlings projected to assimilate less carbon (and therefore experience worse demographic performance) when planted near *Quercus rubra* canopy trees as opposed to *Acer saccharum* canopy trees. We conclude that changes to spring phenological escape will have important effects on how tree seedling recruitment is affected by climate change, with the magnitude of these effects dependent upon climate change severity and biological interactions with neighboring adults. Thus, future studies of temperate forest recruitment should account for phenological escape dynamics in their models.

KEYWORDS

Acer saccharum, carbon assimilation, growth, phenological mismatch, *Quercus rubra*, recruitment, respiration, survival

1 | INTRODUCTION

With the onset of global warming, plant species are undergoing a variety of physiological changes triggered by their new environment. Plants in temperate forests are experiencing longer growing seasons due to warmer springs and falls (Chuine, 2010; Chuine & Beaubien, 2001; Fu et al., 2014; Menzel & Fabian, 1999; Piao et al., 2019), but also reduced photosynthetic performance due to hotter and drier summers (Elliott et al., 2015; McDowell et al., 2008). These changes will continue to have important implications for their capacity to assimilate positive carbon budgets, and could subsequently affect their demographic performance (Hartmann, 2011; Lee & Ibáñez, 2021b; Mooney, 1972; Wertin et al., 2011). Understory plants may also be affected by changes in seasonal light availability (commonly referred to as phenological escape dynamics; Jacques et al., 2015). Plants ranging from wildflowers to tree seedlings have been shown to rely on this strategy of expanding leaves days or weeks ahead of canopy closure to assimilate positive annual carbon balances (Heberling, Cassidy, et al., 2019; Kwit et al., 2010), with strong implications for their overall growth and survival (Augspurger, 2008; Lee & Ibáñez, 2021b).

Recent projections suggest that herbaceous understory plants will experience reduced phenological escape success in the future as a result of lower phenological sensitivity to environmental conditions compared to surrounding canopy trees (Heberling, McDonough MacKenzie, et al., 2019). However, phenological sensitivity of woody plant species has been shown to differ from that of herbaceous species (Rich et al., 2008; Schleip et al., 2009; Zheng et al., 2016), and they may therefore experience different changes in phenological escape duration in response to climate change. These findings are consistent with evidence reviewed by Neufeld and Young (2014) showing that herbaceous understory plants are more responsive to changes in soil temperature and snow melt phenology (Kudo et al., 2008; Muller, 1978; Yoshie, 2008) compared to canopy trees which are more responsive to changes in air temperature and photoperiod (Polgar & Primack, 2011; Richardson et al., 2006). Furthermore, a

study by Vitasse (2013) demonstrated that tree seedling phenology is cued by the same drivers as adult trees, just with different sensitivities. Together, these findings suggest that climate change responses in phenological escape for tree seedlings may substantially differ from those observed for herbaceous species, however, no study we are aware of has yet investigated phenological escape dynamics in woody plants. There is a consequent gap in our knowledge of how climate change will affect access to spring light for woody understory plants such as temperate tree seedlings, and of the implications for demographic performance and recruitment success.

This strategy, known as phenological escape (Jacques et al., 2015), allows understory plants to assimilate between 50% and 80% of their annual carbon budget in the first few weeks of the growing season prior to canopy closure (Heberling, Cassidy, et al., 2019; Kwit et al., 2010). Although this dynamic in herbaceous plants is partially caused by differences in the environmental cues that they and adult trees respond to (Augspurger & Salk, 2017; Routhier & Lapointe, 2002), there is evidence that phenological escape of tree seedlings (Augspurger & Bartlett, 2003; Kwit et al., 2010) is largely driven by ontogenetic differences in response to shared cues (Vitasse, 2013). In either case, changes in environmental conditions, such as those projected to occur under climate change, have the potential to differently affect the phenology of understory plants and canopy trees such that the duration of phenological escape also changes (Figure 1a). Wildflower species, for example, are projected to lose access to spring light under climate change conditions because they are less sensitive to warming than canopy trees (Heberling, McDonough MacKenzie, et al., 2019). Herbaceous and woody plant phenology can have different sensitivities to environmental drivers (Rich et al., 2008; Schleip et al., 2009; Zheng et al., 2016), however, and so changes in phenological escape associated with climate change may significantly differ between these groups.

Determining how climate change will affect phenological escape of deciduous tree seedlings is important because previous work has shown that carbon assimilated during this period is directly linked to plant performance (Lee & Ibáñez, 2021b). Shifts in phenology

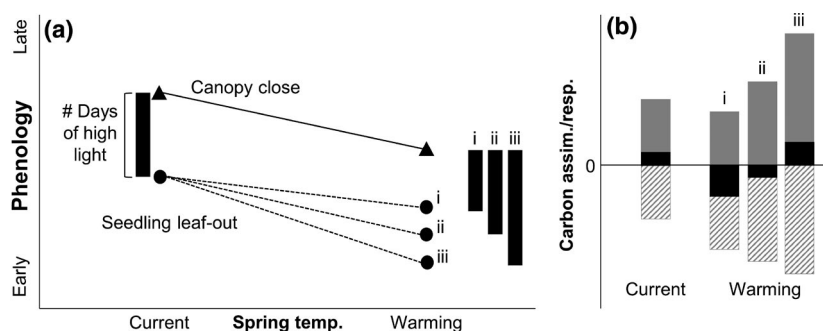


FIGURE 1 (a) As spring temperatures in temperate forests increase with climate change, leaf expansion phenology of canopy trees (triangles, solid lines) is expected to shift earlier. However, it is unclear if leaf expansion of tree seedlings (circles, dashed lines) will shift at a rate that is (i) slower than, (ii) equal to, or (iii) faster than the rate of canopy phenology shifts. This will affect the duration of tree seedlings' access to light (height of bars). (b) Net carbon assimilation (black bars) is the sum of photosynthetic assimilation (solid grey bars) and respiration (hatched bars). Under current climate conditions, tree seedlings maintain positive net carbon assimilation due to gross assimilation being greater than respiration. However, assimilation and respiration rates in future climate conditions will depend on whether seedlings experience decreased (i), maintained (ii), or increased (iii) access to spring light

could therefore have strong effects on tree recruitment and, consequently, forest structure and composition. Tree seedling recruitment is a strong bottleneck that filters which individuals eventually recruit into the canopy (Grubb, 1977; Harper, 1977), and it is also the stage at which trees are most likely to experience nonrandom, directional mortality (Green et al., 2014; Umaña et al., 2016), so studies of tree recruitment can offer unique insight into the composition and structure of future forests. Many studies that investigate the effects of climate change on tree seedling recruitment, however, rely on correlations between demographic performance and environmental conditions (e.g., Batllori et al., 2009; Gamache & Payette, 2005), but this approach can be problematic if these relationships are nonlinear (Ibáñez et al., 2017; Vandvik et al., 2020) or if plants experience novel climates for which there is no modern analogue (Jackson & Williams, 2004). There is thus a need for a more mechanistic approach to assess tree recruitment dynamics and link environmental conditions to demographic success in a more robust way.

Any changes in annual assimilation, such as those associated with changes in the duration of phenological escape (Heberling, McDonough MacKenzie, et al., 2019; Kwit et al., 2010), could therefore have important effects on demographic success. Three broad possibilities exist for how tree seedling phenological escape and consequent performance could be affected by climate change (Figure 1a). If seedling phenology is (i) less sensitive to climate compared to canopy phenology, as has been found for spring wildflowers (Heberling, McDonough MacKenzie, et al., 2019), access to spring light would decrease. Similarly, (ii) equal sensitivity would result in no change in phenological escape dynamics, and (iii) higher seedling sensitivity would result in an increase in access to spring light. Seedlings of different species may also exhibit different responses associated with observed variation in phenology (e.g., Augspurger & Bartlett, 2003), so it is possible that some species gain access to spring light while others lose access, even if their phenology is relatively similar under current environmental conditions. Phenological escape dynamics at the end of the growing season (i.e., seedlings maintaining leaves later in fall compared to nearby canopy trees) could also be affected by climate change and thus also should be addressed in climate change studies (although there is also contradictory evidence suggesting that this period plays a minor role in overall carbon assimilation and performance; Gill et al., 1998; Lee & Ibáñez, 2021b).

Any change in access to light will affect the net amount of carbon that seedlings assimilate over the course of the growing season (solid grey bars in Figure 1b). This is important because climate change in many temperate regions is expected to result in hotter and drier summers (Handler et al., 2014; IPCC, 2014), conditions which will increase respiration costs more than they benefit assimilation (Elliott et al., 2015; McDowell et al., 2008), resulting in higher annual carbon demand (hashed bars in Figure 1b). Thus, reductions in access to light (i) could exacerbate the carbon deficit created by higher respiration costs and lead to a situation where net carbon assimilation and plant performance are greatly reduced. Alternatively, if seedlings gain carbon from improved phenological escape (iii), they might instead

offset the higher respiration costs from summer and maintain positive carbon balances nearer to where they are currently. Although these outcomes are both plausible, the information needed to predict which is most likely, and for what species, is currently lacking.

Developing projections for how seedling carbon assimilation and performance will be affected by climate change requires several pieces of information (sensu Heberling, McDonough MacKenzie, et al., 2019). First, seedling and canopy foliar phenology must each be linked to environmental conditions so that climate change forecasts can be used to predict changes in phenological escape dynamics. Next, detailed information is required regarding seedling photosynthetic capacity and activity and how they are affected by environmental conditions. These include effects of light, temperature, soil moisture, and CO₂ concentrations, all of which impact carbon assimilation (Lee & Ibáñez, 2021b; Patrick et al., 2009; Peltier & Ibáñez, 2015) and are likely to be affected by climate change. Carbon assimilation must then be estimated under different growing season simulations that represent current and future environmental conditions and then combined with seedling demographic models that link demographic performance to annual assimilation (Lee & Ibáñez, 2021b).

Research has been published for parts of this framework for two species of temperate tree seedlings that commonly co-occur throughout much of eastern North America (*Acer saccharum* and *Quercus rubra*; Lee & Ibáñez, 2021b) provides the necessary photosynthetic parameterization and seedling performance models needed for the latter parts of the analysis. In this study, we focus on how phenological escape dynamics will be affected by climate change and what that could mean for future seedling performance. Specifically, we address the following questions: (1) Will warming temperatures lead to tree seedlings increasing, maintaining, or losing access to seasonal light? (2) How will changes in phenological escape interact with changes in photosynthetic activity to affect net annual carbon assimilation? and (3) How will projected changes in carbon assimilation affect seedling growth and survival? Answering these questions will provide novel insight for how climate change could impact the performance, and thus recruitment, of temperate tree species.

2 | METHODS

To address our research questions, we first developed models of seedling foliar phenology (leaf expansion in spring and leaf color change and senescence in fall) and timing of understory light availability (as a proxy for canopy close phenology in spring and canopy opening in fall). Previous work has found that fall carbon assimilation is negligible relative to carbon assimilated in spring and summer due to changes in photosynthetic capacity that occur over the duration of the growing season (Lee & Ibáñez, 2021b), so we focus here on the impact of changing spring phenological escape. We still incorporate changes in fall dynamics in our modeling approach and a complete summary of these dynamics is reported in Appendix S1.

We developed three growing season environmental simulations representing (1) current conditions in our study region (consistent with the 5 years of environmental data we collected) and two climate change simulations based on (2) conservative and (3) extreme climate change scenarios commonly used by the Intergovernmental Panel on Climate Change (IPCC; Handler et al., 2014), and used them to predict changes in phenological escape. Lastly, we used species-specific models of seedling photosynthesis and performance developed by Lee and Ibáñez (2021a, 2021b) to estimate how changes in phenological escape will interact with direct effects of environmental drivers on seedling photosynthesis to shape net annual carbon assimilation, growth, and survival.

2.1 | Experimental design

2.1.1 | Study locations

Our study took place at three locations in southeastern Michigan, USA: Saginaw Forest (42.270977N, 83.806022W), Radrick Forest (42.287083N, 83.658056W), and the E. S. George Reserve (42.457104N, 84.020226W). All three locations have similar climates, averaging 22°C in summer (June–August) and -6°C in winter (December–February); annual precipitation is 925 mm and is evenly distributed throughout the year. Radrick Forest and E. S. George Reserve are mesic temperate hardwood forests dominated by *Acer*, *Prunus*, and *Quercus* species whereas plots at Saginaw Forest are former monocultures of *A. saccharum* and *Q. rubra* planted in the early 1900s.

2.1.2 | Study species

We measured seedlings of two species of temperate deciduous trees that commonly co-occur throughout eastern North America. The first species, *A. saccharum* (Marsh.), is late-successional, expands leaves early in spring, senesces leaves early in fall, and is relatively intolerant of drought (Augsburger & Bartlett, 2003; Peltier & Ibáñez, 2015; Roman et al., 2015). In comparison, *Q. rubra* (L.) is mid-successional, relatively late-leafing and -senescing, and moderately drought-tolerant (Augsburger & Bartlett, 2003; Peltier & Ibáñez, 2015; Roman et al., 2015). Seedlings of these species differ in their photosynthetic capacities and exhibit different photosynthetic plasticity throughout the growing season (Lee & Ibáñez, 2021b; Peltier & Ibáñez, 2015). Both are predicted to decrease in importance value across eastern North America under climate change (Iverson et al., 2008), with *A. saccharum* expected to experience a relatively stronger decline in the Great Lakes region.

2.1.3 | Field experimental set up

Seeds of each species were cold-stratified, germinated in a greenhouse in large tubs containing potting soil (Sun Gro Horticulture;

Agawam, MA), and, approximately 4 weeks after germination, gently removed from the soil and transplanted bare root in the field. We transplanted seedlings at all sites in three cohorts (2014–2016). Because seedling survival and growth may be modified by biotic interactions associated with neighboring adult trees via soil mechanisms such as plant–soil feedbacks (McCarthy-Neumann & Ibáñez, 2012), allelopathy (Gómez-Aparicio & Canham, 2008; Pellissier & Souto, 1999), and nutrient availability (Classen et al., 2015; Juice et al., 2006; Phillips & Fahey, 2006), seedlings at each site were planted under both *A. saccharum* and *Q. rubra* trees. There were 5–10 seedlings per target species per cohort planted near three replicate canopy trees per species and site, depending on seed availability (Lee & Ibáñez, 2021b), for a total of 290 *A. saccharum* and 320 *Q. rubra* seedlings.

2.2 | Data collection

Parameterization of seedling photosynthesis and performance models, as well as the data used to fit them, was published by Lee and Ibáñez (2021a, 2021b). Here we describe the methodology and analysis directly relating to seedling and canopy phenology models and to the climate change forecasting methods used to project changes in phenological escape, annual carbon assimilation, and demographic performance. Methods and results described here primarily focus on spring phenological escape, with information pertaining to fall dynamics located in Appendix S1.

2.2.1 | Environmental data

We collected hourly site-level measurements of soil moisture as well as of temperature, photosynthetic active radiation (PAR), and relative humidity at 1 m above the forest floor using HOBO U23 Pro v2 data loggers and HOBO Smart Sensors and Micro Stations (Onset Computer Corp.). Vapor pressure deficit (VPD) was calculated from temperature and relative humidity data according to the Arrhenius equation. We constructed a “current climate” growing season scenario to represent the average environmental conditions across all three sites and all 5 years of this study (2014–2018; Figure S1). Climate change scenarios were then developed by applying forecasts made by Handler et al. (2014) for our study region (see Section 2.2.2 below).

2.2.2 | Phenology

Canopy phenology was approximated as the change in light availability in the understory measured by site-level PAR sensors. Day of canopy closure in spring was defined as the day on which the average daytime PAR (between 1000 and 1800 local time) dropped below 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and then did not increase above that threshold for one week (in order to rule out the possibility of low light from cloudy days). Day

of canopy opening in fall was defined as when average daytime PAR increased above $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ without then decreasing below that value for more than a week. This value is lower than the threshold used to estimate canopy closure in spring because there is significantly less solar radiation in fall even under similar canopy openness (Figure S2).

Seedling leaf expansion was measured on a weekly basis beginning the year following transplantation (e.g., 2015 for the first cohort planted in 2014). We recorded three fall phenophases for each seedling (*sensu* Denny et al., 2014), also on a weekly basis: onset of leaf color change, date when leaf color change exceeded 50%, and date of leaf senescence. We used these events to bin seedling photosynthesis into four seasonal bins (described by Lee & Ibáñez, 2021b) to account for seasonal plasticity in photosynthetic capacity (Bauerle et al., 2012; Peltier & Ibáñez, 2015): Spring (leaf expansion to day of canopy closure), Summer (day of canopy closure to onset of leaf color change), Fall1 (onset to >50% of leaf color change), and Fall2 (>50% leaf color change to leaf senescence).

2.3 | Analyses

Projecting the effects that climate change will have on seedling phenology and carbon assimilation involves great uncertainty. This includes both the uncertainty surrounding what future climates will look like as well as the uncertainty entailed in making long-term predictions using data collected across random variability of climate drivers. The climate change scenarios we use here to project the possible changes in phenology and carbon assimilation of temperate tree seedlings represent the best- and worst-case climate scenarios developed by the IPCC (2014). Therefore, although it is unlikely that either of the two scenarios accurately portrays environmental conditions in 2100 in their entirety (Hausfather et al., 2020), they can still serve to bound our expectations for what seedling performance could look like at the end of the century.

A second source of uncertainty, associated with using random variability to make long-term predictions, arises from two main sources. First, climate change is projected to result in combinations of environmental conditions that have no modern analog (Jackson & Williams, 2004; Williams & Jackson, 2007) that are not represented in field experiments without direct manipulation (e.g., Sendall et al., 2015). Climate change relationships are also often nonlinear, and it can be difficult to predict the effects of climate change past the limits of observed variability (Ibáñez et al., 2017; Vandvik et al., 2020). However, capitalizing on natural variability to infer potential future performance, although imperfect, is still currently one of the best tools we have to forecast ecological change (Ibáñez et al., 2013), and is therefore the approach we use in this study.

2.3.1 | Phenology models

Spring foliar phenology is tightly linked to climate cues such as temperature forcing (Ibáñez et al., 2010; Richardson et al., 2006), winter

chilling (i.e., vernalization; Ettinger et al., 2020; Roberts et al., 2015), and frost occurrence (Vitasse et al., 2014) as well as to photoperiod (Diez et al., 2014; Ettinger et al., 2020; Way & Montgomery, 2015), which varies latitudinally rather than temporally. We tested effects of monthly and seasonal average, minimum, and maximum temperatures and frost occurrence events (i.e., number of days per month or week with average daytime temperature $<0^\circ\text{C}$) on day of canopy closure and seedling leaf expansion, and chose the models with the best fit to use in this analysis based on the Deviance Information Criterion (DIC; Spiegelhalter et al., 2002). We analyzed day of canopy closure for each site s , and year y , using a normal likelihood distribution:

$$\text{Canopy Closure}_{s,y} \sim N(\mu_{s,y}, \sigma^2)$$

The mean, μ , is modeled with linear relationships to different climatic factors (n) and site random effects (α):

$$\mu_{s,y} = \alpha_s + \beta_n \times \text{climate factor}_{n,y}$$

$$\alpha_{\text{site}} \sim N(\rho_\alpha, \sigma_\alpha^2)$$

Seedling spring foliar phenology was modeled similarly, but, in this case, models included individual random effects (since we collected individual level phenology data across years). Additional analysis did not reveal a significant effect of canopy species, seed source, or planting cohort on seedling phenology, so they were not included in the final models. For all three analyses (canopy closure and seedling phenology for two species), we used non-informative prior distributions in our estimation of parameters, $\beta_n \sim N(0, 1000)$, $\rho_\alpha \sim \log N(1, 1000)$, and $1/\sigma_\alpha^2 \sim \text{Gamma}(0.001, 0.001)$. As with spring phenology, we evaluated the relationship between fall phenology and canopy reopening and several climate variables including monthly and seasonal average, minimum, and maximum temperature; monthly and seasonal average, minimum, and maximum soil moisture; and monthly and weekly frost occurrence. We included individual random effects in the seedling models and site random effects in the canopy reopening models.

Day of canopy closure and reopening data were included for as far back as we had been taking these measurements (2011 for E. S. George Reserve, 2012 for Radrick Forest, and 2015 for Saginaw Forest; $n = 20$ because of occasional missing data). Seedling phenology models included data for all seedlings that successfully established and survived for at least 1 year. Because of mortality that occurred during the growing season, sample size was higher in spring ($n = 43, 24, 47,$ and 23 for *A. saccharum* in 2015, 2016, 2017, and 2018, respectively, and $n = 23, 17, 95,$ and 46 for *Q. rubra*) than in fall ($n = 25, 15, 30,$ and 18 for *A. saccharum* and $n = 15, 11, 59,$ and 36 for *Q. rubra*). Models were run for 50,000 iterations using OpenBUGS 3.2.3 (Lunn et al., 2009), and posterior densities were calculated following a 10,000-iteration burn-in period. Model code and associated data are publicly available (see Data Availability Statement, Lee & Ibáñez, 2021a). Convergence for parameters was assessed visually and by using the Brooks-Gelman-Rubin statistic

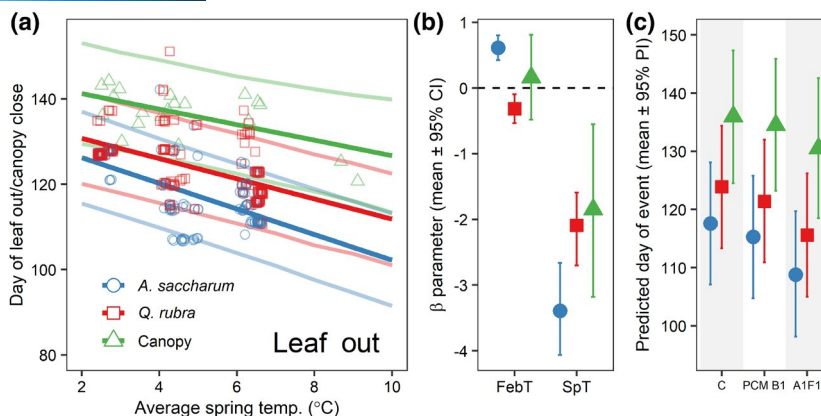


FIGURE 2 (a) Observed (points, jittered slightly so they are distinguishable from one another) day of year of canopy closure ($n = 20$) and seedling leaf out phenology ($n = 137$ and 181 for *Acer saccharum* and *Quercus rubra*, respectively) as a function of average March–April (i.e., ‘spring’) and February temperatures. Lines represent posterior predicted means (bold lines) and 95% predictive intervals (light lines). (b) Posterior estimated mean values (and 95% confidence intervals) of spring phenology model β parameters. Posterior estimates are considered significant if the confidence interval does not overlap 0. (c) Predicted phenology dates (means and 95% predictive intervals) for seedling leaf out and canopy closure in the three climate simulations

from three independent chains (Gelman & Rubin, 1992). Model fit of models with iterative combinations of drivers was assessed using DIC (Spiegelhalter et al., 2002). Parameter values (means, variances, and covariances) were estimated from their posterior distributions. Climate effects (β) were considered significant if the 95% confidence intervals of their posterior distributions did not overlap zero.

2.3.2 | Climate change forecasts

Annual carbon assimilation was estimated for each seedling species \times canopy species combination using three growing season environmental simulations: a current scenario (described above) and two climate change scenarios corresponding to the PCMB1 (Washington et al., 2000) and A1F1 (Delworth et al., 2006) scenarios used by the IPCC to bookend climate change projections (Hausfather et al., 2020; IPCC, 2014). These projections were specific to our study region (Handler et al., 2014). The PCMB1 simulation was developed to represent future climate conditions if we achieve significant conservation goals and reduction of global CO₂ emissions, whereas the A1F1 simulation represents a “business-as-usual” climate change projection where current emission trends are assumed to continue into the future. They thus represent conservative and extreme estimates, respectively, of climate conditions for the end of the 21st century. A full description of the construction of the current simulation and how we used the IPCC scenarios to modify it is described in Appendix S2.

We used these simulations to forecast shifts in seedling and canopy foliar phenology to investigate how climate change might affect phenological escape dynamics. We then used posterior estimates from the phenology models to adjust simulated light levels in our environmental simulations (Appendix S2). Next, we used the simulated light, temperature, soil moisture, and relative humidity values to estimate hourly foliar carbon assimilation rates by applying the

photosynthetic parameter posterior estimates published by Lee and Ibáñez (2021a, 2021b), with associated variance included in the forecasts. Importantly, these rates have units of $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and account only for assimilation and respiration of leaf tissue, imposing some limitations on the predictive power of our models (see Section 4 below). We added up these hourly rates over the course of the growing season to estimate net annual carbon assimilation on a per leaf area per year basis. We then used average values of seedling leaf area for each species (as calculated in Lee & Ibáñez, 2021b); 103.46 and 88.01 cm² for *A. saccharum* and *Q. rubra* seedlings, respectively) to standardize our predictions by area.

3 | RESULTS

3.1 | Canopy and seedling phenology

The best spring phenology model for both canopy and seedlings included average February temperature and average Spring (March–April) temperature (based on deviance information criterion, DIC; Spiegelhalter et al., 2002; Figure 2a). Model fits (R^2 , predicted vs. observed values) for the spring phenology models were 0.55 for *A. saccharum* seedlings, 0.39 for *Q. rubra* seedlings, and 0.38 for canopy closure. Average spring temperature (SpT) was negatively and significantly associated with spring leaf-out (leaf-out took place earlier in years with warmer springs) in all three models (Figure 2b). However, average February temperature (FebT) was positively and significantly associated with *A. saccharum* seedling leaf-out, negatively and significantly associated with *Q. rubra* seedling leaf-out, and positively, but non-significantly, associated with canopy closure (Figure 2b).

Modeled canopy closure shifted 1.6 and 5.4 days earlier in the PCMB1 and A1F1 climate change scenarios, respectively, relative to current climate conditions (Figure 2c). *A. saccharum* seedling leaf-out

shifted 2.4 and 9 days earlier in the two climate change scenarios, leading to increased differences between seedling leaf-out and canopy close from 18.4 days in current conditions to 19.2 days in the PCM B1 scenario and 21.5 days in the A1F1 scenario. *Q. rubra* seedlings shifted leaf-out 2.3 and 8 days earlier in the two climate change scenarios, leading to increased difference between leaf-out and canopy close from 12.2 days in current conditions to 12.9 days in PCM B1 and 14.3 days in A1F1.

The best seedling and canopy fall phenology models included only average August temperature as a predictor based on DIC values. Leaf senescence model fit (R^2 of predicted vs. observed values) was 0.87 and 0.37 for *A. saccharum* and *Q. rubra* seedlings, respectively, and 0.64 for the canopy closure model. August temperature was positively associated with all three, but the correlation was only significant for canopy opening and *Q. rubra* senescence (Figure S3b). Canopy opening was more sensitive to temperature than seedling phenology for both species (Figure S3a), resulting in lower access to light for *Q. rubra* seedlings (Figure S3c; -2.3 and -11.9 days in the PCM B1 and A1F1 simulations, respectively). *A. saccharum* senescence was predicted to occur prior to canopy opening in all three simulations, and so light access for this species was not projected to be affected by climate change. More detailed analysis for end of season dynamics, including results for the color change phenophases, can be found in Appendix S1.

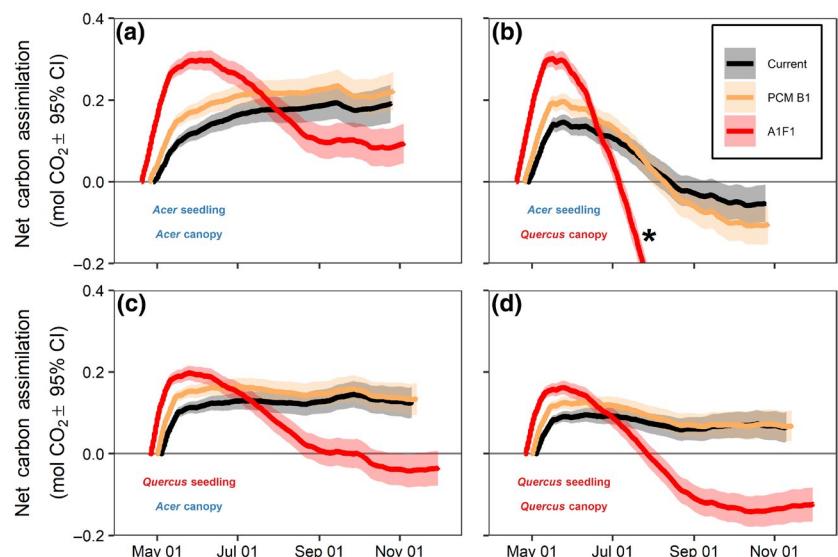
The variation in average spring, February, and August temperatures over the course of our experiment was of the same order of magnitude as the projected changes in seasonal temperature (Table S1) made by Handler et al. (2014) for our study region. Average observed February temperature ranged from -11.1 to 1.3°C (expected change in PCM B1 is $+1.4^\circ\text{C}$ from a baseline temperature of -6.4°C and is $+4.1^\circ\text{C}$ in A1F1), average March–April temperature ranged from 2.5 to 6.5°C (projected change $+0.9$ and $+3.3^\circ\text{C}$ from a baseline temperature of 5.1°C in PCM B1 and A1F1, respectively), and average August temperature ranged from 18.7 to 22.4°C (projected change $+1.2$ and $+6.2^\circ\text{C}$ from a baseline temperature of 18.3°C in PCM B1 and A1F1, respectively).

3.2 | Carbon accumulation simulation

Seedlings of both species were predicted to accumulate net positive carbon assimilation in spring under both canopy treatments and in all three climate simulations (Figure 3). Average daily rates of carbon assimilation, which were used to integrate the curves in Figure 3, are shown in Figure S5. Net summer carbon assimilation ranged from positive (e.g., *A. saccharum* seedlings planted near conspecific canopy trees in the current and PCM B1 climate simulations; Figure 3a), to neutral (e.g., *Q. rubra* seedlings planted under *A. saccharum* in the current and PCM B1 simulations; Figure 3c), to strongly negative (e.g., all seedlings in the A1F1 simulation). Carbon assimilation projections were neutral or slightly negative in fall (Figure 3; Appendix S1), with carbon assimilation not changing much compared to the end of summer. Annual carbon assimilation projections were consistently higher for both species for seedlings planted near *A. saccharum* canopy trees compared to those planted near *Q. rubra* canopy trees.

The climate change simulations forecast strong increases in spring carbon assimilation for both species, but either little change (for the PCM B1 climate change simulations) or substantial decreases (for the A1F1 simulations) in net annual carbon assimilation (Figure 4). Spring carbon assimilation was predicted to increase by 35.1% to 48.1% in the PCM B1 simulation and by 75.7% to 169.3% in the A1F1 simulation relative to the current climate simulation. In contrast, changes in net annual carbon assimilation relative to the current scenario ranged from -96.9% to 16.4% in the PCM B1 simulation and from -1233.9% to -51.1% in the A1F1 simulation, consistent with strong declines in summer assimilation (Figure 4). All seedling species \times canopy species combinations are projected to experience reductions in annual carbon assimilation in the more extreme A1F1 climate change scenario, with only *A. saccharum* seedlings planted near conspecific canopy trees projected to maintain positive carbon assimilation through to the end of the growing season (Figure 3a). Forecasted annual carbon assimilation values under the more moderate PCM B1 climate change simulation were very similar to the estimates for carbon assimilation under current environmental conditions for all seedling/

FIGURE 3 Posterior estimates of simulated running carbon accumulation for *Acer saccharum* (a and b) and *Quercus rubra* seedlings (c and d) planted beneath *A. saccharum* (a and c) and *Q. rubra* canopy trees (b and d). Line color represent predictions in the current climate simulation (black), climate in 2100 under the conservative PCM B1 simulation (orange), and climate in 2100 under the extreme A1F1 simulation (red). Asterisk indicates that values fall outside the range of the figure (full panel shown in Figure S4a)



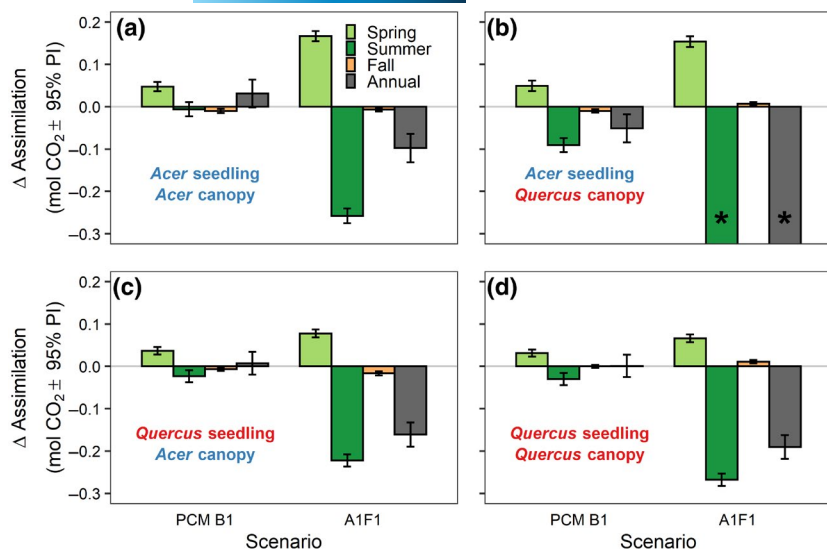


FIGURE 4 Estimated difference (mol CO₂ ± 95% predictive intervals) in spring (light green), summer (dark green), fall (orange), and annual (grey) carbon assimilation in the PCM B1 and A1F1 climate scenarios relative to the estimated carbon assimilation under the current environmental conditions scenario for different seedling species × canopy species combinations. Asterisk indicates differences that were beyond the range of the graph (full panel shown in Figure S4b)

TABLE 1 Predicted values of net annual foliar carbon assimilation (±95% confidence intervals), projected probability of survival (±95% predictive intervals), and projected height growth (±95% predictive intervals) for each seedling species × canopy species × climate scenario combination

| Seedling species | Canopy species | Climate scenario | Net annual carbon assimilation (mol year ⁻¹ ± 95% CI) | Probability of survival (mean % and 95% PI) | Projected growth (mean mm year ⁻¹ and 95% PI) |
|-----------------------|---------------------|------------------|--|---|--|
| <i>Acer saccharum</i> | <i>A. saccharum</i> | Current | 0.191 ± 0.023 | 0.907 (0.228, 0.998) | 28.99 (17.57, 42.37) |
| | | PCM B1 | 0.222 ± 0.023 | 0.932 (0.341, 0.999) | 31.23 (19.27, 45.36) |
| | | A1F1 | 0.093 ± 0.024 | 0.742 (0.047, 0.977) | 22.04 (10.43, 33.94) |
| | <i>Q. rubra</i> | Current | -0.053 ± 0.023 | 0.262 (0.003, 0.78) | 11.62 (-3.66, 25.24) |
| | | PCM B1 | -0.104 ± 0.024 | 0.257 (0.001, 0.639) | 8.03 (-9.17, 23.3) |
| | | A1F1 | -0.703 ± 0.029 | 0.002 (6E-11, 0.005) | -34.76 (-81.7, 9.68) |
| <i>Quercus rubra</i> | <i>A. saccharum</i> | Current | 0.126 ± 0.019 | 0.549 (0.364, 0.701) | 17.55 (-0.33, 39.97) |
| | | PCM B1 | 0.133 ± 0.019 | 0.571 (0.39, 0.718) | 17.83 (-0.04, 40.22) |
| | | A1F1 | -0.035 ± 0.021 | 0.148 (0.029, 0.366) | 11.33 (-7.92, 35.13) |
| | <i>Q. rubra</i> | Current | 0.067 ± 0.018 | 0.364 (0.171, 0.562) | 15.26 (-2.9, 37.98) |
| | | PCM B1 | 0.068 ± 0.019 | 0.367 (0.174, 0.564) | 15.3 (-2.86, 38.02) |
| | | A1F1 | -0.124 ± 0.021 | 0.064 (0.005, 0.233) | 7.90 (-13.04, 33.0) |

canopy combinations (Figure 3), differing by 0.051 mol CO₂ year⁻¹ or less (Table S2).

3.3 | Seedling performance

3.3.1 | Survival

Probability of survival was affected by a combination of seedling species, species of nearby canopy tree, and climate change scenario. *A. saccharum* seedlings were predicted to have higher probability of survival compared to *Q. rubra* seedlings when planted near *A. saccharum* adults (Table 1), but the opposite was true when seedlings were planted near *Q. rubra* canopy trees, where *A. saccharum* probability of survival declined by >60% across all three scenarios and

Q. rubra probability of survival only dropped by ~20%. Probability of survival in the PCM B1 climate change scenario was consistently within 3% of the probability of survival under current environmental conditions for all seedling species × canopy species combinations (Table 1). However, probability of survival substantially declined in the A1F1 climate change scenario across the board (survival probability was 16.5%–40.1% lower than the current environmental conditions simulation). *A. saccharum* seedlings were predicted to have >50% probability of survival when planted near conspecific canopy trees regardless of environmental scenario whereas *Q. rubra* seedlings were only predicted to have >50% probability of survival in the current and PCM B1 simulations when planted near *A. saccharum* adults. Probability of survival was consistently <50% for both species when planted near *Q. rubra* canopy trees, regardless of climate simulation.

3.3.2 | Growth

Projected changes in growth across the climate change simulations mirrored the projected patterns of probability of survival (Table 1). Growth estimates tended to increase slightly in the PCM B1 climate change scenario relative to the current environmental simulation with the only decrease ($-3.59 \text{ mm year}^{-1}$) occurring for *A. saccharum* seedlings planted near *Q. rubra* adults. The increases in the other seedling \times canopy species combinations in the PCM B1 scenario were all $<2.5 \text{ mm year}^{-1}$ (Table 1). Growth estimates decreased across the board in the A1F1 scenario relative to the current environmental conditions simulation, with decreases ranging from -7.36 to $-6.22 \text{ mm year}^{-1}$ (with the exception of *A. saccharum* seedlings planted under *Q. rubra* canopy trees, which were projected to have negative annual growth resulting in a net change of $-46.38 \text{ mm year}^{-1}$). As with survival, projected growth was higher for both species when seedlings were planted near *A. saccharum* canopy trees than when planted near *Q. rubra* canopy trees. Similarly, *A. saccharum* growth projections were greater than *Q. rubra* growth projections when seedlings were planted near *A. saccharum* canopy trees, with the relationship reversed when seedlings were planted near *Q. rubra* canopy trees.

4 | DISCUSSION

Climate change is projected to simultaneously affect growing season length (Piao et al., 2019) and summer growing conditions (Choat et al., 2012; IPCC, 2014) for many plant species. However, few studies account for how these processes interact to affect understory plant performance and specifically tree seedling performance and tree recruitment dynamics. In this study, we investigated the potential for climate change to affect tree seedling phenological escape, carbon assimilation, and demographic performance of two deciduous species that broadly co-occur across eastern North America. We found that, for both species, seedling leaf-out is more sensitive to warming compared to canopy closure in spring, leading to projected increases in access to spring light and, consequently, projected gains in spring carbon assimilation under simulated climate change. However, we found that this gain in spring assimilation will be largely offset by higher summer respiration costs that result from warmer, drier environmental conditions. Under a moderate climate change scenario (PCM B1), this increase in respiration cost will approximately equal in magnitude the increase in spring carbon assimilation, resulting in little change to net annual carbon assimilation or seedling demographic performance. However, under the more extreme A1F1 climate change scenario, summer respiration costs will greatly outweigh increases in spring carbon assimilation and lead to net negative annual carbon assimilation in three out of the four seedling species/canopy species combinations (Figure 3).

Furthermore, our models project that changes in fall carbon assimilation will be minimal, suggesting that fall phenological escape does not and will not play a significant role in seedling recruitment

dynamics. In contrast, seedling carbon assimilation was strongly affected by the identity of nearby canopy tree species across all seasons, with plants assimilating more carbon per year when planted near *A. saccharum* canopy trees compared to when planted near *Q. rubra*, thus suggesting that biotic interactions will partially shape the future recruitment success of these species. Together, our results suggest that extreme climate change in eastern North America will negatively affect seedling performance of temperate deciduous trees and could consequently play a major role in limiting recruitment success. Still, our models predict that some seedlings (i.e., *A. saccharum* seedlings planted near conspecific canopy trees) will be able to increase spring assimilation enough to maintain $>50\%$ probability of survival (Table 1), even in the most extreme climate change scenario. This, in combination with little change in predicted performance under a more conservative climate change forecast, suggests that phenological escape dynamics may allow temperate tree species to maintain recruitment success into the future under certain circumstances, contrasting other studies that predict widespread declines in abundance of these species in response to increased warming and drought (e.g., Iverson et al., 2008).

4.1 | Climate change will enhance spring phenological escape

Light availability is often a limiting factor for understory plants growing in temperate forests (Canham et al., 1999; Kobe et al., 1995), in which nutrients and water are often abundant relative to light. Therefore, shade is the factor that generally limits understory plant carbon assimilation (Heberling, Cassidy, et al., 2019; Kwit et al., 2010) and consequent performance (Lee & Ibáñez, 2021b). Deciduous tree seedlings utilize phenological escape to optimize access to spring light (Augsburger, 2008; Kwit et al., 2010) while minimizing risk to damage from late spring frosts (Vitasse et al., 2014). However, canopy closure is shifting earlier (Piao et al., 2019), and it was previously uncertain if tree seedling phenology is shifting at the same rate. Furthermore, while previous research has investigated how shifts in phenological escape dynamics affect annual carbon assimilation for some understory plant species (Heberling, Cassidy, et al., 2019; Kwit et al., 2010), our study is novel in that it is the first that we are aware of to use these dynamics to forecast changes in demographic and recruitment performance under climate change.

Our models predict that seedling access to light will increase in spring as a result of seedling leaf-out phenology being more sensitive to warming compared to that of nearby canopy trees (Figure 2). This contrasts a previous study focusing on herbaceous species where reductions in phenological escape duration under climate change were predicted for understory wildflowers (Heberling, McDonough MacKenzie, et al., 2019). This discrepancy is consistent with evidence that woody plant phenology is more sensitive to environmental conditions compared to phenology of herbaceous species (Schleip et al., 2009; Zheng et al., 2016), and suggests that woody plants may be more able to maintain phenological escape under

climate change conditions. This disparity in phenological sensitivity likely stems from a combination of phylogenetic constraints (Davies et al., 2013), ontogenetic variation (Vitasse, 2013), and differences in the environmental factors to which plants respond. An example of the latter is the difference between tree leaf-out phenology, which is driven by changes in air temperature (e.g., growing/chilling degree days) and photoperiod (Ettinger et al., 2020), and the emergence of herbaceous wildflowers which respond more strongly to soil temperature and snowmelt (Routhier & Lapointe, 2002). However, changes in phenological escape in response to climate change have yet only been estimated for a limited number of species and more research is needed to determine if the discrepancies between herbaceous and woody plant species are broadly generalizable. Still, our results suggest that there are at least some tree species for which seedlings will be able to extend the duration of phenological escape in spring under climate change conditions.

4.2 | Increased summer respiration costs will largely offset increased spring carbon assimilation

Warmer and drier summers associated with climate change are projected to reduce plant performance (Williams et al., 2013; Zhao & Running, 2010) and survival (Allen et al., 2015; McDowell et al., 2008). Previous research has shown that photosynthetic capacity is directly limited by soil water availability and VPD via stomatal regulation for temperate plants in general (Grossiord et al., 2020; Niinemets, 2010; Oren et al., 1999), and specifically for temperate tree seedlings (Lee & Ibáñez, 2021b; Peltier & Ibáñez, 2015). We therefore used photosynthetic models from a previous study (Lee & Ibáñez, 2021b) to estimate foliar carbon assimilation rates across simulated growing season conditions to quantify how climate change will affect tree seedling photosynthetic activity.

We found that reduced water availability and warmer temperatures could lead to sharp increases in summer respiration costs for temperate tree seedlings, particularly under extreme climate change scenarios. The resulting summer carbon deficit was approximately equal in magnitude to the increases in spring carbon assimilation in the moderate (PCM B1) climate change scenario (Figure 3), leading to little change in annual carbon assimilation (Figure 4; Table 1). However, increases in summer respiration costs in the extreme A1F1 climate change scenario vastly outweighed the increases in spring carbon assimilation, resulting in reduced annual assimilation for all seedlings (Figure 4). This suggests that increased phenological escape duration in spring may be insufficient to offset increasing summer respiration costs if climate change is severe. For example, *A. saccharum* seedlings planted under conspecific canopy trees were projected to increase spring carbon assimilation by 47.5% and 167.7% in the PCM B1 and A1F1 climate change scenarios, respectively, whereas net annual assimilation was only projected to increase by 16.2% in the PCM B1 scenario and was projected to decrease by 51.3% in the A1F1 scenario. Therefore, it is not change in spring or summer assimilation alone, but rather the combination of

both, that will determine the net changes in annual assimilation and, consequently, changes in demographic performance and recruitment success.

Importantly, photosynthetic activity was strongly affected by the identity of the canopy tree species that seedlings were planted near. Both species were projected to assimilate more annual carbon when planted near *A. saccharum* canopy trees compared to when planted near *Q. rubra* canopy trees (Figure 3), regardless of climate change scenario. Seedlings of both species experienced increases in photosynthetic rate ($V_{C_{max}}$ and J_{max}) when planted under *A. saccharum* canopy trees, but dark respiration was not affected by canopy tree species identity (Lee & Ibáñez, 2021b). This difference could be partially attributable to facilitative effects of elevated inorganic nitrogen concentrations (e.g., NO_3 and NH_4) in soils associated with *A. saccharum* canopy trees (McCarthy-Neumann & Ibáñez, 2012). Inorganic nitrogen is directly linked to plant photosynthetic rates (Liang et al., 2020), and a previous study conducted at two of the same sites in this experiment (ES George Reserve and Radrick Forest) found significantly higher concentrations of inorganic nitrogen in soils associated with *A. saccharum* compared to those associated with *Q. rubra* (McCarthy-Neumann & Ibáñez, 2012).

In addition to positive effects associated with *A. saccharum* soil, seedlings may also simultaneously experience negative effects from *Q. rubra* soil mediated through pathogens or other nutrients (Classen et al., 2015; McCarthy-Neumann & Ibáñez, 2012, 2013; McCarthy-Neumann & Kobe, 2010). *A. saccharum* seedlings are highly sensitive to biotic effects associated with different canopy soils and, even though they are negatively affected by conspecific soil biotic effects, negative impacts are stronger when planted in heterospecific soils (McCarthy-Neumann & Ibáñez, 2013), and the reduced performance in this study when planted under *Q. rubra* is consistent with these results. Soils cultured by *Q. rubra* in our study region were found to be generally negative for the performance of many tree seedling species (McCarthy-Neumann & Ibáñez, 2012), including for conspecific seedlings which were negatively affected by soil biotic effects relative to various “away” soils. Our results are thus consistent with evidence of positive plant–soil feedbacks for *A. saccharum* seedlings and negative plant–soil feedbacks for *Q. rubra* seedlings, both of which would result in reduced performance when planted near *Q. rubra* adults. Alternatively, McCarthy-Neumann and Ibáñez (2012) also found that soil calcium concentrations in *Q. rubra* soils were lower than six out of the other seven soils measured, including being significantly lower than calcium concentrations in *A. saccharum* soils. *A. saccharum* performance is tied to soil calcium status in eastern North American forests (Juice et al., 2006), so reduced survival in this study could also be tied to calcium limitations in *Q. rubra* soils.

Regardless of the mechanism underlying these differences, both species were predicted to have >50% survival only when planted near *A. saccharum* canopy trees under the current environmental simulation. This was consistent with greater observed survival rates for seedlings planted near *A. saccharum* adults (Figure S6), with the range of predicted probability of survival in the current simulation

(26%–91%, Table 1) generally consistent with the range of observed survival rates (38%–84%). Together, these results suggest that the identity of nearby canopy species will play an important role in affecting seedling recruitment of these two species, mediated via differences in photosynthetic carbon assimilation.

4.3 | Climate change will reduce seedling performance

There is increasing evidence that annual carbon assimilation directly affects plant demographic performance, with carbon status linked to survival, growth, and reproductive success of various species (Augsburger, 2008; Lee & Ibáñez, 2021b; Routhier & Lapointe, 2002; Seiwa, 1998). This makes the quantification and prediction of carbon assimilation a useful tool with which to better predict plant population- and community-level dynamics. Recent work published by Lee and Ibáñez (2021b) directly linked annual carbon assimilation to growth and survival of tree seedlings of the two species in our study, allowing us to forecast changes in these two metrics under simulated climate change scenarios. The relatively small differences in annual carbon assimilation between the current and PCM B1 simulations meant little change to probability of survival or growth under moderate climate change (probability of survival changed by <3% and projected growth changed by <4 mm year⁻¹ for all seedlings; Table 1).

The changes in demographic performance were more drastic under the extreme A1F1 climate change scenario, with probability of survival decreasing by 16.5%–40.1% compared to under current conditions. Growth was also predicted to decrease proportionally more in the extreme climate change scenario, but the predictions must be interpreted within the context of the predicted changes in survival. For example, annual carbon assimilation was predicted to be negative in about half of our simulations (Table 1), which is biologically feasible only if plants are able to mobilize latent carbohydrates to meet metabolic demands. However, the seedlings in this study were less than 5 years old and were unlikely to have accrued sufficient carbon reserves in the heavily shaded understory where this study took place. Furthermore, our carbon assimilation estimates accounted for only foliar assimilation and respiration (Lee & Ibáñez, 2021b), meaning that belowground respiration, which can be of equal or greater magnitude as aboveground respiration (Hopkins et al., 2013), would further exacerbate the energy needed to maintain metabolic rates and make it even more unlikely that plants withstand net negative foliar assimilation. Therefore, growth estimates for any seedling with negative annual carbon assimilation will likely be inaccurate or inconsequential given that they would likely succumb to carbon starvation first.

Despite the reduced performance predicted in some of the climate change simulations, seedlings were predicted to continue to have >50% survival probability under certain circumstances. Both species maintained (or even slightly improved) annual carbon assimilation under the moderate PCM B1 simulation, suggesting that

increasing phenological escape duration could be enough to offset rising summer respiration costs if realized climates are nearer to conservative versus extreme forecasts. *A. saccharum* seedlings were predicted to maintain >50% probability of survival under extreme climate change conditions, but only when planted near conspecific canopy trees (Table 1), while *A. saccharum* seedlings planted near *Q. rubra* adults and *Q. rubra* seedlings in general were not predicted to survive in this scenario. This suggests that earlier leaf out phenology may allow some temperate tree species to maintain recruitment success even under extreme climate change, contrasting with abundance and occurrence forecasts made for these species using models that do not account for phenological escape (e.g., Iverson et al., 2008).

It also suggests that *A. saccharum* will recruit better than *Q. rubra* under climate change conditions, further contrasting predictions made on the basis of drought sensitivity alone. Still, seedling survival is not the only component of recruitment success and other processes such as seed production and seedling establishment will also affect the recruitment of these species and they could potentially differ in their response to climate change. For example, evidence from previous research suggests that *A. saccharum* seed initiation and maturation will decline in response to climate change in our study region (Ibáñez et al., 2017), potentially counteracting the increase in seedling performance projected here.

4.4 | Fall phenological escape minimally affects annual carbon assimilation

Although the contribution of spring phenological escape to net carbon assimilation is more commonly studied, temperate tree seedlings have also been observed to maintain their leaves in fall past when the canopy reopens (e.g., Augspurger & Bartlett, 2003; Gill et al., 1998). This suggests that this period of light availability may also be important to annual carbon assimilation for understory plants and that similar phenological escape dynamics to those reported in spring might likewise affect seedling performance. However, there is evidence to suggest that carbon assimilated during this period will be far less important due to atmospheric filtering of light that results in lower PAR levels, even under similar canopy openness (Gill et al., 1998; Lee & Ibáñez, 2021b). Our findings agree with this assertion and are consistent with previous findings from Lee and Ibáñez (2021b) who found that, on average, fall carbon assimilation makes up a small fraction of total annual assimilation for temperate tree seedlings. Furthermore, our models predict that seedling access to fall light will decrease in the future due to lower phenological sensitivity relative to canopy opening (Figure S3; Appendix S1), indicating that late-seasonal assimilation is likely to play an even smaller role under future climate change. Thus, although climate change is projected to increase growing season length in both spring and fall for many species (Piao et al., 2019), it will be changes in spring phenology and spring phenological escape that will be most important for the carbon assimilation dynamics of temperate understory plants.

4.5 | Limitations and topics for future study

The modeling approach we used allowed us to directly link changes in phenology and photosynthetic activity to changes in plant performance via net annual carbon assimilation, but it also introduced certain limitations that deserve further inspection. First, we did not account for belowground respiration in our modeling approach and therefore lack an understanding of how climate-driven changes in root respiration might affect the relationship between foliar carbon assimilation and seedling performance. For example, increased temperature could lead to higher root respiration costs (Hopkins et al., 2013), exacerbating the negative impacts of climate change past what greater spring assimilation can offset and further decoupling seedling performance from foliar carbon assimilation. Canopy closure has also been demonstrated to significantly affect soil temperatures (Redding et al., 2003; Villegas et al., 2010), which then affect root respiration rates (Atkin et al., 2000; Zogg et al., 1996), so changes in canopy closure phenology could further alter root respiration rates. Changes in canopy leaf area index (LAI) predicted to occur with higher CO₂ concentrations (Li et al., 2018) could similarly reduce soil temperatures and increase soil moisture, thus reducing the overall costs of root respiration and altering predicted changes in seedling survival. Our carbon assimilation simulations were also estimated using assumptions of average species-specific initial leaf area and of no loss in leaf area over the course of the growing season. We made the latter assumption because leaf damage, although common (Lee & Ibáñez, 2021b), was highly variable for both species. Making these assumptions means that realized annual carbon assimilation will likely be lower, on average, than indicated in our results.

In contrast, there is also evidence that photosynthetic capacity and foliar respiration rates may acclimate to climate change conditions (e.g., Ainsworth & Rogers, 2007). This could result in less severe respiration costs under future warming and thus greater net carbon assimilation than estimated in our analysis. Furthermore, we did not account for the role of small canopy gaps (i.e., sunflecks), which play an important role in understory plant carbon balance (Canham, 1988; Chazdon & Pearcy, 1991; Hull, 2002). This, too, makes our estimations somewhat conservative and suggests that reductions in assimilation and performance may be less severe, and more variable, than we predicted.

5 | CONCLUSION

Despite these limitations, our study presents compelling evidence that shifts in seedling phenological escape in spring will help offset the negative impacts of reduced summer assimilation associated with warmer temperatures and reductions in water availability. Net changes in seedling performance will depend on the severity of climate change that occurs. Our results also suggest that seedling recruitment will be shaped by biotic interactions with neighboring canopy species, but the potential mechanism underlying these relationships remain unknown and so further investigation is necessary.

Projected gains in spring carbon assimilation in the extreme A1F1 climate change scenario were not enough to offset the reductions in carbon assimilation for three of the four seedling species × canopy species combinations, indicating that unmitigated climate change is still likely to have severe negative impacts on seedling recruitment. However, our study demonstrates that phenological escape will help mitigate and offset these negative effects for some species and under certain conditions, meaning that shifts in phenological escape will be important to consider in future models of temperate tree recruitment and demography.

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DATA AVAILABILITY STATEMENT

Code and data used in this manuscript (i.e., for phenology models) are available on the Zenodo data repository (Lee & Ibáñez, 2021a). *Data and model code for "Improved phenological escape can help temperate tree seedlings maintain demographic performance under climate change conditions."* Zenodo. <https://doi.org/10.5281/zenodo.4737332>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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