

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

Running Title: Tree seedling phenological escape

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Data Availability Statement: Code and data used in this manuscript (i.e., for phenology models) is available on the Zenodo data repository (Lee & Ibáñez, 2021)

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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

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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 *Q. rubra* canopy trees as opposed to *A. 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*, *Quercus rubra*, carbon assimilation, respiration, phenological mismatch, survival, growth, recruitment

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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 & 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)

32 compared to canopy trees which are more responsive to changes in air temperature and
33 photoperiod (Polgar & Primack, 2011; Richardson et al., 2006). Furthermore, a study by Vitasse
34 (2013) demonstrated that tree seedling phenology is cued by the same drivers as adult trees, just
35 with different sensitivities. Together, these findings suggest that climate change responses in
36 phenological escape for tree seedlings may substantially differ from those observed for
37 herbaceous species, however no study we are aware of has yet investigated phenological escape
38 dynamics in woody plants. There is a consequent gap in our knowledge of how climate change
39 will affect access to spring light for woody understory plants such as temperate tree seedlings,
40 and of the implications for demographic performance and recruitment success.

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

57 Determining how climate change will affect phenological escape of deciduous tree
58 seedlings is important because previous work has shown that carbon assimilated during this
59 period is directly linked to plant performance (Lee & Ibáñez, 2021b). Shifts in phenology could
60 therefore have strong effects on tree recruitment and, consequently, forest structure and
61 composition. Tree seedling recruitment is a strong bottleneck that filters which individuals
62 eventually recruit into the canopy (Grubb, 1977; Harper, 1977), and it is also the stage at which

63 trees are most likely to experience nonrandom, directional mortality (Green et al., 2014; Umaña
64 et al., 2016), so studies of tree recruitment can offer unique insight into the composition and
65 structure of future forests. Many studies that investigate the effects of climate change on tree
66 seedling recruitment, however, rely on correlations between demographic performance and
67 environmental conditions (e.g., Batllori et al., 2009; Gamache & Payette, 2005), but this
68 approach can be problematic if these relationships are nonlinear (Ibáñez et al., 2017; Vandvik et
69 al., 2020) or if plants experience novel climates for which there is no modern analogue (Jackson
70 & Williams, 2004). There is thus a need for a more mechanistic approach to assess tree
71 recruitment dynamics and link environmental conditions to demographic success in a more
72 robust way.

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

90 Any change in access to light will affect the net amount of carbon that seedlings
91 assimilate over the course of the growing season (solid grey bars in Fig. 1b). This is important
92 because climate change in many temperate regions is expected to result in hotter and drier
93 summers (Handler et al., 2014; IPCC, 2014), conditions which will increase respiration costs

94 more than they benefit assimilation (Elliott et al., 2015; McDowell et al., 2008), resulting in
95 higher annual carbon demand (hashed bars in Fig. 1b). Thus, reductions in access to light (i)
96 could exacerbate the carbon deficit created by higher respiration costs and lead to a situation
97 where net carbon assimilation and plant performance are greatly reduced. Alternatively, if
98 seedlings gain carbon from improved phenological escape (iii), they might instead offset the
99 higher respiration costs from summer and maintain positive carbon balances nearer to where they
100 are currently. Although these outcomes are both plausible, the information needed to predict
101 which is most likely, and for what species, is currently lacking.

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

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

124 Answering these questions will provide novel insight for how climate change could impact the
125 performance, and thus recruitment, of temperate tree species.

126

127 **Methods**

128 To address our research questions, we first developed models of seedling foliar phenology (leaf
129 expansion in spring and leaf color change and senescence in fall) and timing of understory light
130 availability (as a proxy for canopy close phenology in spring and canopy opening in fall).

131 Previous work has found that fall carbon assimilation is negligible relative to carbon assimilated
132 in spring and summer due to changes in photosynthetic capacity that occur over the duration of
133 the growing season (Lee & Ibáñez, 2021b), so we focus here on the impact of changing spring
134 phenological escape. We still incorporate changes in fall dynamics in our modeling approach and
135 a complete summary of these dynamics is reported in the supporting information (Appendix S1).
136 We developed three growing season environmental simulations representing 1) current
137 conditions in our study region (consistent with the five years of environmental data we collected)
138 and two climate change simulations based on 2) conservative and 3) extreme climate change
139 scenarios commonly used by the Intergovernmental Panel on Climate Change (IPCC; Handler et
140 al., 2014), and used them to predict changes in phenological escape. Lastly, we used species-
141 specific models of seedling photosynthesis and performance developed by Lee & Ibáñez (2021)
142 to estimate how changes in phenological escape will interact with direct effects of environmental
143 drivers on seedling photosynthesis to shape net annual carbon assimilation, growth, and survival.

144

145 **Experimental Design**

146 **Study Locations**

147 Our study took place at three locations in southeastern Michigan, USA: Saginaw Forest
148 (42.270977 N, 83.806022 W), Radrick Forest (42.287083 N, 83.658056 W), and the E. S.
149 George Reserve (42.457104 N, 84.020226 W). All three locations have similar climates,
150 averaging 22 °C in summer (June-August) and -6 °C in winter (December-February); annual
151 precipitation is 925 mm and is evenly distributed throughout the year. Radrick Forest and E. S.
152 George Reserve are mesic temperate hardwood forests dominated by *Acer*, *Prunus*, and *Quercus*
153 species whereas plots at Saginaw Forest are former monocultures of *Acer saccharum* and
154 *Quercus rubra* planted in the early 1900's.

155

156 Study Species

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

168

169 Field experimental set up

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

181

182 **Data collection**

183 Parameterization of seedling photosynthesis and performance models, as well as the data used to
184 fit them, was published by Lee & Ibáñez (2021). Here we describe the methodology and analysis
185 directly relating to seedling and canopy phenology models and to the climate change forecasting

186 methods used to project changes in phenological escape, annual carbon assimilation, and
187 demographic performance. Methods and results described here primarily focus on spring
188 phenological escape, with information pertaining to fall dynamics located in the supporting
189 information (Appendix S1).

190

191 Environmental Data

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

201

202 Phenology

203 Canopy phenology was approximated as the change in light availability in the understory
204 measured by site-level PAR sensors. Day of canopy closure in spring was defined as the day on
205 which the average daytime PAR (between 1000-1800 local time) dropped below $100 \mu\text{mol m}^{-2} \text{s}^{-1}$
206 ¹ and then did not increase above that threshold for one week (in order to rule out the possibility
207 of low light from cloudy days). Day of canopy opening in fall was defined as when average
208 daytime PAR increased above $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ without then decreasing below that value for more
209 than a week. This value is lower than the threshold used to estimate canopy closure in spring
210 because there is significantly less solar radiation in fall even under similar canopy openness (Fig.
211 S2).

212 Seedling leaf expansion was measured on a weekly basis beginning the year following
213 transplantation (e.g., 2015 for the first cohort planted in 2014). We recorded three fall
214 phenophases for each seedling (sensu Denny et al., 2014), also on a weekly basis: onset of leaf
215 color change, date when leaf color change exceeded 50%, and date of leaf senescence. We used
216 these events to bin seedling photosynthesis into four seasonal bins (described by Lee & Ibáñez,

217 2021) to account for seasonal plasticity in photosynthetic capacity (Bauerle et al., 2012; Peltier &
218 Ibáñez, 2015): Spring (leaf expansion to day of canopy closure), Summer (day of canopy closure
219 to onset of leaf color change), Fall1 (onset to >50% of leaf color change), and Fall2 (>50% leaf
220 color change to leaf senescence).

221

222 **Analyses**

223 Projecting the effects that climate change will have on seedling phenology and carbon
224 assimilation involves great uncertainty. This includes both the uncertainty surrounding what
225 future climates will look like as well as the uncertainty entailed in making long-term predictions
226 using data collected across random variability of climate drivers. The climate change scenarios
227 we use here to project the possible changes in phenology and carbon assimilation of temperate
228 tree seedlings represent the best- and worst-case climate scenarios developed by the IPCC
229 (2014). Therefore, although it is unlikely that either of the two scenarios accurately portrays
230 environmental conditions in 2100 in their entirety (Hausfather et al., 2020), they can still serve to
231 bound our expectations for what seedling performance could look like at the end of the century.

232 A second source of uncertainty, associated with using random variability to make long-
233 term predictions, arises from two main sources. First, climate change is projected to result in
234 combinations of environmental conditions that have no modern analog (Jackson & Williams,
235 2004; J. W. Williams & Jackson, 2007) that are not represented in field experiments without
236 direct manipulation (e.g., Sendall et al., 2015). Climate change relationships are also often
237 nonlinear, and it can be difficult to predict the effects of climate change past the limits of
238 observed variability (Ibáñez et al., 2017; Vandvik et al., 2020). However, capitalizing on natural
239 variability to infer potential future performance, although imperfect, is still currently one of the
240 best tools we have to forecast ecological change (Ibáñez et al., 2013), and is therefore the
241 approach we use in this study.

242

243 Phenology models

244 Spring foliar phenology is tightly linked to climate cues such as temperature forcing (Ibáñez et
245 al., 2010; Richardson et al., 2006), winter chilling (i.e., vernalization; Ettinger et al., 2020;
246 Roberts et al., 2015), and frost occurrence (Vitasse et al., 2014) as well as to photoperiod (Diez
247 et al., 2014; Ettinger et al., 2020; Way & Montgomery, 2015), which varies latitudinally rather

248 than temporally. We tested effects of monthly and seasonal average, minimum, and maximum
249 temperatures and frost occurrence events (i.e., number of days per month or week with average
250 daytime temperature $< 0\text{ }^{\circ}\text{C}$) on day of canopy closure and seedling leaf expansion, and chose
251 the models with the best fit to use in this analysis based on the Deviance Information Criterion
252 (DIC; Spiegelhalter et al., 2002). We analyzed day of canopy closure for each site s , and year y ,
253 using a normal likelihood distribution:

$$CanopyClosure_{s,y} \sim N(\mu_{s,y}, \sigma^2)$$

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

$$\mu_{s,y} = \alpha_s + \beta_n \times ClimateFactor_{n,y}$$

$$\alpha_{site} \sim N(\rho_\alpha, \sigma^2_\alpha)$$

256 Seedling spring foliar phenology was modeled similarly, but, in this case, models included
257 individual random effects (since we collected individual level phenology data across years).
258 Additional analysis did not reveal a significant effect of canopy species, seed source, or planting
259 cohort on seedling phenology, so they were not included in the final models. For all three
260 analyses (canopy closure and seedling phenology for two species), we used non-informative
261 prior distributions in our estimation of parameters, $\beta_n \sim N(0, 1000)$, $\rho_\alpha \sim \text{logN}(1, 1000)$, and
262 $1/\sigma^2_\alpha \sim \text{Gamma}(0.001, 0.001)$. As with spring phenology, we evaluated the relationship between
263 fall phenology and canopy reopening and several climate variables including monthly and
264 seasonal average, minimum, and maximum temperature; monthly and seasonal average,
265 minimum, and maximum soil moisture; and monthly and weekly frost occurrence. We included
266 individual random effects in the seedling models and site random effects in the canopy reopening
267 models.

268 Day of canopy closure and reopening data were included for as far back as we had been
269 taking these measurements (2011 for E. S. George Reserve, 2012 for Radrick Forest, and 2015
270 for Saginaw Forest; $n = 20$ because of occasional missing data). Seedling phenology models
271 included data for all seedlings that successfully established and survived for at least one year.
272 Because of mortality that occurred during the growing season, sample size was higher in spring
273 ($n = 43, 24, 47$, and 23 for *A. saccharum* in 2015, 2016, 2017, and 2018, respectively, and $n =$
274 $23, 17, 95$, and 46 for *Q. rubra*) than in fall ($n = 25, 15, 30$, and 18 for *A. saccharum* and $n = 15,$
275 $11, 59$, and 36 for *Q. rubra*). Models were run for 50,000 iterations using OpenBUGS 3.2.3

276 (Lunn et al., 2009), and posterior densities were calculated following a 10,000-iteration burn-in
277 period. Model code and associated data are publicly available (see Data Availability Statement,
278 Lee & Ibáñez, 2021a). Convergence for parameters was assessed visually and by using the
279 Brooks-Gelman-Rubin statistic from three independent chains (Gelman & Rubin, 1992). Model
280 fit of models with iterative combinations of drivers was assessed using DIC (Spiegelhalter et al.,
281 2002). Parameter values (means, variances, and covariances) were estimated from their posterior
282 distributions. Climate effects (β) were considered significant if the 95% confidence intervals of
283 their posterior distributions did not overlap zero.

284

285 Climate Change Forecasts

286 Annual carbon assimilation was estimated for each seedling species X canopy species
287 combination using three growing season environmental simulations: a current scenario
288 (described above) and two climate change scenarios corresponding to the PCM B1 (Washington
289 et al., 2000) and A1F1 (Delworth et al., 2006) scenarios used by the IPCC to bookend climate
290 change projections (Hausfather et al., 2020; IPCC, 2014). These projections were specific to our
291 study region (Handler et al., 2014). The PCM B1 simulation was developed to represent future
292 climate conditions if we achieve significant conservation goals and reduction of global CO₂
293 emissions, whereas the A1F1 simulation represents a ‘business-as-usual’ climate change
294 projection where current emission trends are assumed to continue into the future. They thus
295 represent conservative and extreme estimates, respectively, of climate conditions for the end of
296 the 21st century. A full description of the construction of the current simulation and how we used
297 the IPCC scenarios to modify it is described in Appendix S2.

298 We used these simulations to forecast shifts in seedling and canopy foliar phenology to
299 investigate how climate change might affect phenological escape dynamics. We then used
300 posterior estimates from the phenology models to adjust simulated light levels in our
301 environmental simulations (Appendix S2). Next, we used the simulated light, temperature, soil
302 moisture, and relative humidity values to estimate hourly foliar carbon assimilation rates by
303 applying the photosynthetic parameter posterior estimates published by Lee & Ibáñez (2021),
304 with associated variance included in the forecasts. Importantly, these rates have units of μmol
305 $\text{CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and account only for assimilation and respiration of leaf tissue, imposing some
306 limitations on the predictive power of our models (see Discussion section below). We added up

307 these hourly rates over the course of the growing season to estimate net annual carbon
308 assimilation on a per leaf area per year basis. We then used average values of seedling leaf area
309 for each species (as calculated in Lee & Ibáñez (2021); 103.46 cm² and 88.01 cm² for *A.*
310 *saccharum* and *Q. rubra* seedlings, respectfully) to standardize our predictions by area.

311

312 **Results**

313 Canopy and Seedling Phenology

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

324 Modeled canopy closure shifted 1.6 and 5.4 days earlier in the PCM B1 and A1F1
325 climate change scenarios, respectively, relative to current climate conditions (Fig. 2c). *Acer*
326 *saccharum* seedling leaf-out shifted 2.4 and 9 days earlier in the two climate change scenarios,
327 leading to increased differences between seedling leaf-out and canopy close from 18.4 days in
328 current conditions to 19.2 days in the PCM B1 scenario and 21.5 days in the A1F1 scenario.
329 *Quercus rubra* seedlings shifted leaf-out 2.3 and 8 days earlier in the two climate change
330 scenarios, leading to increased difference between leaf-out and canopy close from 12.2 days in
331 current conditions to 12.9 days in PCM B1 and 14.3 days in A1F1.

332 The best seedling and canopy fall phenology models included only average August
333 temperature as a predictor based on DIC values. Leaf senescence model fit (R^2 of predicted vs.
334 observed values) was 0.87 and 0.37 for *A. saccharum* and *Q. rubra* seedlings, respectively, and
335 0.64 for the canopy closure model. August temperature was positively associated with all three,
336 but the correlation was only significant for canopy opening and *Q. rubra* senescence (Fig. S3b).
337 Canopy opening was more sensitive to temperature than seedling phenology for both species

338 (Fig. S3a), resulting in lower access to light for *Q. rubra* seedlings (Fig. S3c; -2.3 and -11.9 days
339 in the PCM B1 and A1F1 simulations, respectively). *Acer saccharum* senescence was predicted
340 to occur prior to canopy opening in all three simulations, and so light access for this species was
341 not projected to be affected by climate change. More detailed analysis for end of season
342 dynamics, including results for the color change phenophases, can be found in Appendix S1 in
343 the supporting information.

344 The variation in average spring, February, and August temperatures over the course of
345 our experiment was of the same order of magnitude as the projected changes in seasonal
346 temperature (Table S1) made by Handler et al. (2014) for our study region. Average observed
347 February temperature ranged from -11.1 to 1.3 °C (expected change in PCM B1 is +1.4 °C from
348 a baseline temperature of -6.4 °C and is +4.1 °C in A1F1), average March-April temperature
349 ranged from 2.5 to 6.5 °C (projected change +0.9 and +3.3 °C from a baseline temperature of 5.1
350 °C in PCM B1 and A1F1, respectively), and average August temperature ranged from 18.7 to
351 22.4 °C (projected change +1.2 and +6.2 °C from a baseline temperature of 18.3 °C in PCM B1
352 and A1F1, respectively).

353

354 Carbon accumulation simulation

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

366 The climate change simulations forecast strong increases in spring carbon assimilation
367 for both species, but either little change (for the PCM B1 climate change simulations) or
368 substantial decreases (for the A1F1 simulations) in net annual carbon assimilation (Fig. 4).

369 Spring carbon assimilation was predicted to increase by 35.1 to 48.1% in the PCM B1 simulation
370 and by 75.7 to 169.3% in the A1F1 simulation relative to the current climate simulation. In
371 contrast, changes in net annual carbon assimilation relative to the current scenario ranged from -
372 96.9 to 16.4% in the PCM B1 simulation and from -1233.9 to -51.1% in the A1F1 simulation,
373 consistent with strong declines in summer assimilation (Fig. 4). All seedling species X canopy
374 species combinations are projected to experience reductions in annual carbon assimilation in the
375 more extreme A1F1 climate change scenario, with only *A. saccharum* seedlings planted near
376 conspecific canopy trees projected to maintain positive carbon assimilation through to the end of
377 the growing season (Fig. 3a). Forecasted annual carbon assimilation values under the more
378 moderate PCM B1 climate change simulation were very similar to the estimates for carbon
379 assimilation under current environmental conditions for all seedling/canopy combinations (Fig.
380 3), differing by 0.051 mol CO₂ yr⁻¹ or less (Table S2).

381

382 Seedling Performance

383 Survival

384 Probability of survival was affected by a combination of seedling species, species of nearby
385 canopy tree, and climate change scenario. *Acer saccharum* seedlings were predicted to have
386 higher probability of survival compared to *Q. rubra* seedlings when planted near *A. saccharum*
387 adults (Table 1), but the opposite was true when seedlings were planted near *Q. rubra* canopy
388 trees, where *A. saccharum* probability of survival declined by > 60% across all three scenarios
389 and *Q. rubra* probability of survival only dropped by ~20%. Probability of survival in the PCM
390 B1 climate change scenario was consistently within 3% of the probability of survival under
391 current environmental conditions for all seedling species X canopy species combinations (Table
392 1). However, probability of survival substantially declined in the A1F1 climate change scenario
393 across the board (survival probability was 16.5-40.1% lower than the current environmental
394 conditions simulation). *Acer saccharum* seedlings were predicted to have > 50% probability of
395 survival when planted near conspecific canopy trees regardless of environmental scenario
396 whereas *Q. rubra* seedlings were only predicted to have > 50% probability of survival in the
397 current and PCM B1 simulations when planted near *A. saccharum* adults. Probability of survival
398 was consistently < 50% for both species when planted near *Q. rubra* canopy trees, regardless of
399 climate simulation.

400

401 Growth

402 Projected changes in growth across the climate change simulations mirrored the projected
403 patterns of probability of survival (Table 1). Growth estimates tended to increase slightly in the
404 PCM B1 climate change scenario relative to the current environmental simulation with the only
405 decrease (-3.59 mm yr^{-1}) occurring for *A. saccharum* seedlings planted near *Q. rubra* adults. The
406 increases in the other seedling X canopy species combinations in the PCM B1 scenario were all
407 $< 2.5 \text{ mm yr}^{-1}$ (Table 1). Growth estimates decreased across the board in the A1F1 scenario
408 relative to the current environmental conditions simulation, with decreases ranging from -7.36 to
409 -6.22 mm yr^{-1} (with the exception of *A. saccharum* seedlings planted under *Q. rubra* canopy
410 trees, which were projected to have negative annual growth resulting in a net change of -46.38
411 mm yr^{-1}). As with survival, projected growth was higher for both species when seedlings were
412 planted near *A. saccharum* canopy trees than when planted near *Q. rubra* canopy trees. Similarly,
413 *A. saccharum* growth projections were greater than *Q. rubra* growth projections when seedlings
414 were planted near *A. saccharum* canopy trees, with the relationship reversed when seedlings
415 were planted near *Q. rubra* canopy trees.

416

417 **Discussion**

418 Climate change is projected to simultaneously affect growing season length (Piao et al., 2019)
419 and summer growing conditions (Choat et al., 2012; IPCC, 2014) for many plant species.
420 However, few studies account for how these processes interact to affect understory plant
421 performance and specifically tree seedling performance and tree recruitment dynamics. In this
422 study, we investigated the potential for climate change to affect tree seedling phenological
423 escape, carbon assimilation, and demographic performance of two deciduous species that
424 broadly co-occur across eastern North America. We found that, for both species, seedling leaf-
425 out is more sensitive to warming compared to canopy closure in spring, leading to projected
426 increases in access to spring light and, consequently, projected gains in spring carbon
427 assimilation under simulated climate change. However, we found that this gain in spring
428 assimilation will be largely offset by higher summer respiration costs that result from warmer,
429 drier environmental conditions. Under a moderate climate change scenario (PCM B1), this
430 increase in respiration cost will approximately equal in magnitude the increase in spring carbon

431 assimilation, resulting in little change to net annual carbon assimilation or seedling demographic
432 performance. However, under the more extreme A1F1 climate change scenario, summer
433 respiration costs will greatly outweigh increases in spring carbon assimilation and lead to net
434 negative annual carbon assimilation in three out of the four seedling species/canopy species
435 combinations (Fig. 3).

436 Furthermore, our models project that changes in fall carbon assimilation will be minimal,
437 suggesting that fall phenological escape does not and will not play a significant role in seedling
438 recruitment dynamics. In contrast, seedling carbon assimilation was strongly affected by the
439 identity of nearby canopy tree species across all seasons, with plants assimilating more carbon
440 per year when planted near *A. saccharum* canopy trees compared to when planted near *Q. rubra*,
441 thus suggesting that biotic interactions will partially shape the future recruitment success of these
442 species. Together, our results suggest that extreme climate change in eastern North America will
443 negatively affect seedling performance of temperate deciduous trees and could consequently play
444 a major role in limiting recruitment success. Still, our models predict that some seedlings (i.e., *A.*
445 *saccharum* seedlings planted near conspecific canopy trees) will be able to increase spring
446 assimilation enough to maintain > 50% probability of survival (Table 1), even in the most
447 extreme climate change scenario. This, in combination with little change in predicted
448 performance under a more conservative climate change forecast, suggests that phenological
449 escape dynamics may allow temperate tree species to maintain recruitment success into the
450 future under certain circumstances, contrasting other studies that predict widespread declines in
451 abundance of these species in response to increased warming and drought (e.g., Iverson et al.,
452 2008).

453 Climate change will enhance spring phenological escape

454 Light availability is often a limiting factor for understory plants growing in temperate forests
455 (Canham et al., 1999; Kobe et al., 1995), in which nutrients and water are often abundant relative
456 to light. Therefore, shade is the factor that generally limits understory plant carbon assimilation
457 (Heberling, Cassidy, et al., 2019; Kwit et al., 2010) and consequent performance (Lee & Ibáñez,
458 2021b). Deciduous tree seedlings utilize phenological escape to optimize access to spring light
459 (Augspurger, 2008; Kwit et al., 2010) while minimizing risk to damage from late spring frosts
460 (Vitasse et al., 2014). However, canopy closure is shifting earlier (Piao et al., 2019), and it was
461

462 previously uncertain if tree seedling phenology is shifting at the same rate. Furthermore, while
463 previous research has investigated how shifts in phenological escape dynamics affect annual
464 carbon assimilation for some understory plant species (Heberling, Cassidy, et al., 2019; Kwit et
465 al., 2010), our study is novel in that it is the first that we are aware of to use these dynamics to
466 forecast changes in demographic and recruitment performance under climate change.

467 Our models predict that seedling access to light will increase in spring as a result of
468 seedling leaf-out phenology being more sensitive to warming compared to that of nearby canopy
469 trees (Fig. 2). This contrasts a previous study focusing on herbaceous species where reductions in
470 phenological escape duration under climate change were predicted for understory wildflowers
471 (Heberling, McDonough MacKenzie, et al., 2019). This discrepancy is consistent with evidence
472 that woody plant phenology is more sensitive to environmental conditions compared to
473 phenology of herbaceous species (Schleip et al., 2009; Zheng et al., 2016), and suggests that
474 woody plants may be more able to maintain phenological escape under climate change
475 conditions. This disparity in phenological sensitivity likely stems from a combination of
476 phylogenetic constraints (Davies et al., 2013), ontogenetic variation (Vitasse, 2013), and
477 differences in the environmental factors to which plants respond. An example of the latter is the
478 difference between tree leaf-out phenology, which is driven by changes in air temperature (e.g.,
479 growing/chilling degree days) and photoperiod (Ettinger et al., 2020), and the emergence of
480 herbaceous wildflowers which respond more strongly to soil temperature and snowmelt
481 (Routhier & Lapointe, 2002). However, changes in phenological escape in response to climate
482 change have yet only been estimated for a limited number of species and more research is needed
483 to determine if the discrepancies between herbaceous and woody plant species are broadly
484 generalizable. Still, our results suggest that there are at least some tree species for which
485 seedlings will be able to extend the duration of phenological escape in spring under climate
486 change conditions.

487
488 Increased summer respiration costs will largely offset increased spring carbon assimilation

489 Warmer and drier summers associated with climate change are projected to reduce plant
490 performance (A. P. Williams et al., 2013; Zhao & Running, 2010) and survival (Allen et al.,
491 2015; McDowell et al., 2008). Previous research has shown that photosynthetic capacity is
492 directly limited by soil water availability and VPD via stomatal regulation for temperate plants in

493 general (Grossiord et al., 2020; Niinemets, 2010; Oren et al., 1999), and specifically for
494 temperate tree seedlings (Lee & Ibáñez, 2021b; Peltier & Ibáñez, 2015). We therefore used
495 photosynthetic models from a previous study (Lee & Ibáñez, 2021b) to estimate foliar carbon
496 assimilation rates across simulated growing season conditions to quantify how climate change
497 will affect tree seedling photosynthetic activity.

498 We found that reduced water availability and warmer temperatures could lead to sharp
499 increases in summer respiration costs for temperate tree seedlings, particularly under extreme
500 climate change scenarios. The resulting summer carbon deficit was approximately equal in
501 magnitude to the increases in spring carbon assimilation in the moderate (PCM B1) climate
502 change scenario (Fig. 3), leading to little change in annual carbon assimilation (Fig. 4, Table 1).
503 However, increases in summer respiration costs in the extreme A1F1 climate change scenario
504 vastly outweighed the increases in spring carbon assimilation, resulting in reduced annual
505 assimilation for all seedlings (Fig. 4). This suggests that increased phenological escape duration
506 in spring may be insufficient to offset increasing summer respiration costs if climate change is
507 severe. For example, *A. saccharum* seedlings planted under conspecific canopy trees were
508 projected to increase spring carbon assimilation by 47.5% and 167.7% in the PCM B1 and A1F1
509 climate change scenarios, respectively, whereas net annual assimilation was only projected to
510 increase by 16.2% in the PCM B1 scenario and was projected to decrease by 51.3% in the A1F1
511 scenario. Therefore, it is not change in spring or summer assimilation alone, but rather the
512 combination of both, that will determine the net changes in annual assimilation and,
513 consequently, changes in demographic performance and recruitment success.

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

524 in this experiment (ES George Reserve and Radrick Forest) found significantly higher
525 concentrations of inorganic nitrogen in soils associated with *A. saccharum* compared to those
526 associated with *Q. rubra* (McCarthy-Neumann & Ibáñez, 2012).

527 In addition to positive effects associated with *A. saccharum* soil, seedlings may also
528 simultaneously experience negative effects from *Q. rubra* soil mediated through pathogens or
529 other nutrients (Classen et al., 2015; McCarthy-Neumann & Ibáñez, 2012, 2013; McCarthy-
530 Neumann & Kobe, 2010). *Acer saccharum* seedlings are highly sensitive to biotic effects
531 associated with different canopy soils and, even though they are negatively affected by
532 conspecific soil biotic effects, negative impacts are stronger when planted in heterospecific soils
533 (McCarthy-Neumann & Ibáñez, 2013), and the reduced performance in this study when planted
534 under *Q. rubra* is consistent with these results. Soils cultured by *Q. rubra* in our study region
535 were found to be generally negative for the performance of many tree seedling species
536 (McCarthy-Neumann & Ibáñez, 2012), including for conspecific seedlings which were
537 negatively affected by soil biotic effects relative to various “away” soils. Our results are thus
538 consistent with evidence of positive plant-soil feedbacks for *A. saccharum* seedlings and
539 negative plant-soil feedbacks for *Q. rubra* seedlings, both of which would result in reduced
540 performance when planted near *Q. rubra* adults. Alternatively, McCarthy-Neumann and Ibáñez
541 (2012) also found that soil calcium concentrations in *Q. rubra* soils were lower than six out of
542 the other seven soils measured, including being significantly lower than calcium concentrations
543 in *A. saccharum* soils. *Acer saccharum* performance is tied to soil calcium status in eastern North
544 American forests (Juice et al., 2006), so reduced survival in this study could also be tied to
545 calcium limitations in *Q. rubra* soils.

546 Regardless of the mechanism underlying these differences, both species were predicted to
547 have > 50% survival only when planted near *A. saccharum* canopy trees under the current
548 environmental simulation. This was consistent with greater observed survival rates for seedlings
549 planted near *A. saccharum* adults (Fig. S6), with the range of predicted probability of survival in
550 the current simulation (26-91%, Table 1) generally consistent with the range of observed survival
551 rates (38-84%). Together, these results suggest that the identity of nearby canopy species will
552 play an important role in affecting seedling recruitment of these two species, mediated via
553 differences in photosynthetic carbon assimilation.

554

555 Climate change will reduce seedling performance

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

567 The changes in demographic performance were more drastic under the extreme A1F1
568 climate change scenario, with probability of survival decreasing by 16.5-40.1% compared to
569 under current conditions. Growth was also predicted to decrease proportionally more in the
570 extreme climate change scenario, but the predictions must be interpreted within the context of
571 the predicted changes in survival. For example, annual carbon assimilation was predicted to be
572 negative in about half of our simulations (Table 1), which is biologically feasible only if plants
573 are able to mobilize latent carbohydrates to meet metabolic demands. However, the seedlings in
574 this study were less than 5 years old and were unlikely to have accrued sufficient carbon reserves
575 in the heavily shaded understory where this study took place. Furthermore, our carbon
576 assimilation estimates accounted for only foliar assimilation and respiration (Lee & Ibáñez,
577 2021b), meaning that belowground respiration, which can be of equal or greater magnitude as
578 aboveground respiration (Hopkins et al., 2013), would further exacerbate the energy needed to
579 maintain metabolic rates and make it even more unlikely that plants withstand net negative foliar
580 assimilation. Therefore, growth estimates for any seedling with negative annual carbon
581 assimilation will likely be inaccurate or inconsequential given that they would likely succumb to
582 carbon starvation first.

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

586 under the moderate PCM B1 simulation, suggesting that increasing phenological escape duration
587 could be enough to offset rising summer respiration costs if realized climates are nearer to
588 conservative versus extreme forecasts. *Acer saccharum* seedlings were predicted to maintain >
589 50% probability of survival under extreme climate change conditions, but only when planted
590 near conspecific canopy trees (Table 1), while *A. saccharum* seedlings planted near *Q. rubra*
591 adults and *Q. rubra* seedlings in general were not predicted to survive in this scenario. This
592 suggests that earlier leaf out phenology may allow some temperate tree species to maintain
593 recruitment success even under extreme climate change, contrasting with abundance and
594 occurrence forecasts made for these species using models that do not account for phenological
595 escape (e.g., Iverson et al., 2008).

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

604

605 Fall phenological escape minimally affects annual carbon assimilation

606 Although the contribution of spring phenological escape to net carbon assimilation is more
607 commonly studied, temperate tree seedlings have also been observed to maintain their leaves in
608 fall past when the canopy reopens (e.g., Augspurger & Bartlett, 2003; D. S. Gill et al., 1998).
609 This suggests that this period of light availability may also be important to annual carbon
610 assimilation for understory plants and that similar phenological escape dynamics to those
611 reported in spring might likewise affect seedling performance. However, there is evidence to
612 suggest that carbon assimilated during this period will be far less important due to atmospheric
613 filtering of light that results in lower PAR levels, even under similar canopy openness (Gill et al.,
614 1998; Lee & Ibáñez, 2021b). Our findings agree with this assertion and are consistent with
615 previous findings from Lee & Ibáñez (2021) who found that, on average, fall carbon assimilation
616 makes up a small fraction of total annual assimilation for temperate tree seedlings. Furthermore,

617 our models predict that seedling access to fall light will decrease in the future due to lower
618 phenological sensitivity relative to canopy opening (Fig. S3; Appendix S1), indicating that late-
619 seasonal assimilation is likely to play an even smaller role under future climate change. Thus,
620 although climate change is projected to increase growing season length in both spring and fall for
621 many species (Piao et al., 2019), it will be changes in spring phenology and spring phenological
622 escape that will be most important for the carbon assimilation dynamics of temperate understory
623 plants.

624

625 Limitations and topics for future study

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

646 In contrast, there is also evidence that photosynthetic capacity and foliar respiration rates
647 may acclimate to climate change conditions (e.g., Ainsworth & Rogers, 2007). This could result

648 in less severe respiration costs under future warming and thus greater net carbon assimilation
649 than estimated in our analysis. Furthermore, we did not account for the role of small canopy gaps
650 (i.e., sunflecks), which play an important role in understory plant carbon balance (Canham, 1988;
651 Chazdon & Pearcy, 1991; Hull, 2002). This, too, makes our estimations somewhat conservative
652 and suggests that reductions in assimilation and performance may be less severe, and more
653 variable, than we predicted.

654

655 **Conclusion**

656 Despite these limitations, our study presents compelling evidence that shifts in seedling
657 phenological escape in spring will help offset the negative impacts of reduced summer
658 assimilation associated with warmer temperatures and reductions in water availability. Net
659 changes in seedling performance will depend on the severity of climate change that occurs. Our
660 results also suggest that seedling recruitment will be shaped by biotic interactions with
661 neighboring canopy species, but the potential mechanism underlying these relationships remain
662 unknown and so further investigation is necessary. Projected gains in spring carbon assimilation
663 in the extreme A1F1 climate change scenario were not enough to offset the reductions in carbon
664 assimilation for three of the four seedling species X canopy species combinations, indicating that
665 unmitigated climate change is still likely to have severe negative impacts on seedling
666 recruitment. However, our study demonstrates that phenological escape will help mitigate and
667 offset these negative effects for some species and under certain conditions, meaning that shifts in
668 phenological escape will be important to consider in future models of temperate tree recruitment
669 and demography.

670

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676

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

3 Ben Lee and Inés Ibáñez

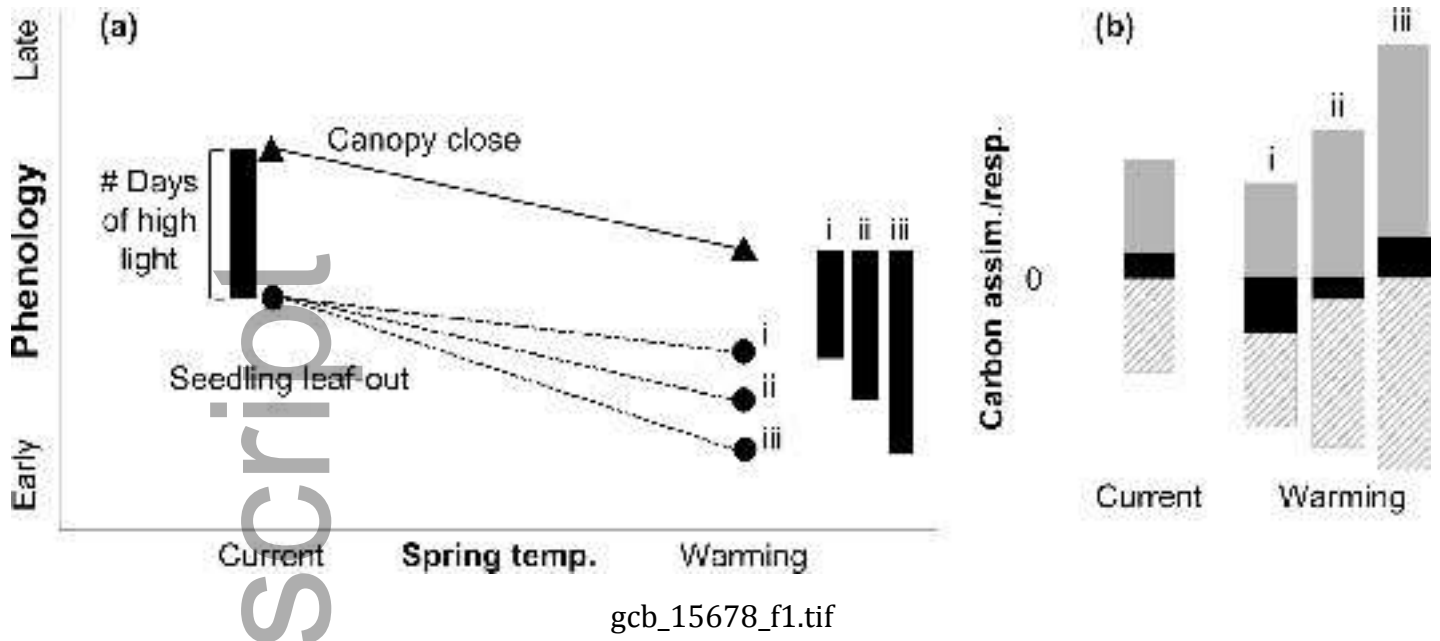
4
 5 **Table 1:** Predicted values of net annual foliar carbon assimilation (\pm 95% confidence intervals),
 6 projected probability of survival (\pm 95% predictive intervals), and projected height growth (\pm
 7 95% predictive intervals) for each seedling species X canopy species X climate scenario
 8 combination.

Seedling Species	Canopy Species	Climate Scenario	Net Annual Carbon Assimilation (mol yr ⁻¹ \pm 95% C.I.)	Probability of Survival (mean % and 95% P.I.)	Projected Growth (mean mm yr ⁻¹ and 95% P.I.)
Acer saccharum	Acer saccharum	Current	0.191 \pm 0.023	0.907 (0.228, 0.998)	28.99 (17.57, 42.37)
		PCM B1	0.222 \pm 0.023	0.932 (0.341, 0.999)	31.23 (19.27, 45.36)
		A1F1	0.093 \pm 0.024	0.742 (0.047, 0.977)	22.04 (10.43, 33.94)
	Quercus rubra	Current	-0.053 \pm 0.023	0.262 (0.003, 0.78)	11.62 (-3.66, 25.24)
		PCM B1	-0.104 \pm 0.024	0.257 (0.001, 0.639)	8.03 (-9.17, 23.3)
		A1F1	-0.703 \pm 0.029	0.002 (6E-11, 0.005)	-34.76 (-81.7, 9.68)
Quercus rubra	Acer saccharum	Current	0.126 \pm 0.019	0.549 (0.364, 0.701)	17.55 (-0.33, 39.97)
		PCM B1	0.133 \pm 0.019	0.571 (0.39, 0.718)	17.83 (-0.04, 40.22)
		A1F1	-0.035 \pm 0.021	0.148 (0.029, 0.366)	11.33 (-7.92, 35.13)

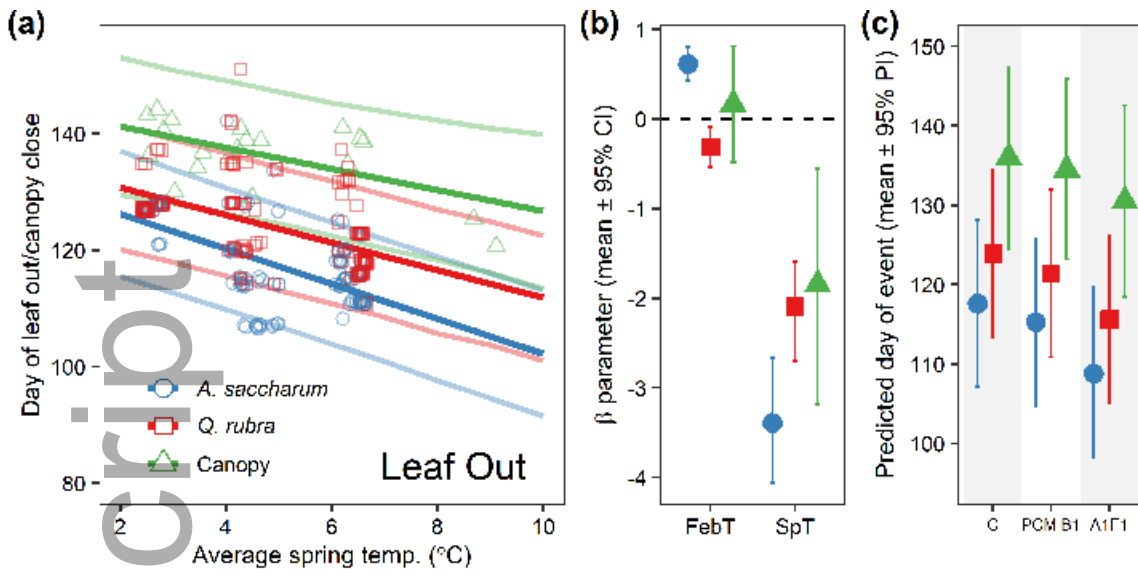
	Quercus rubra	Current	0.067 ± 0.018	0.364 (0.171, 0.562)	15.26 (-2.9, 37.98)
		PCM B1	0.068 ± 0.019	0.367 (0.174, 0.564)	15.3 (-2.86, 38.02)

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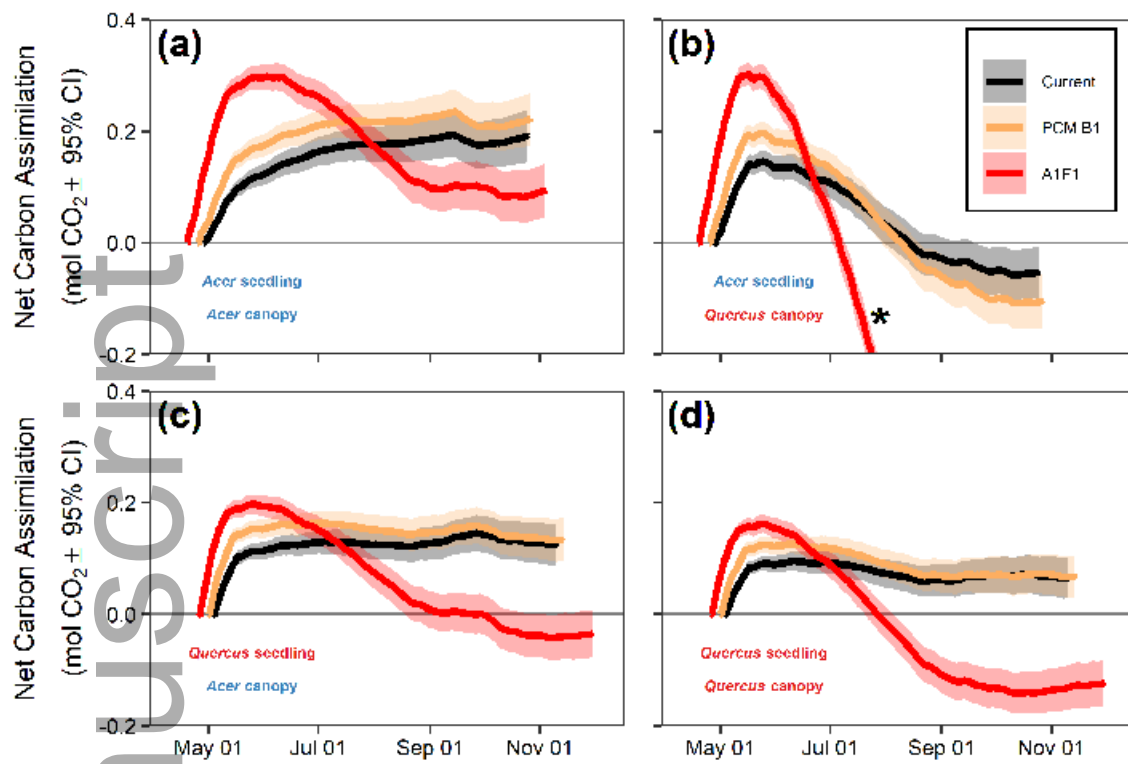
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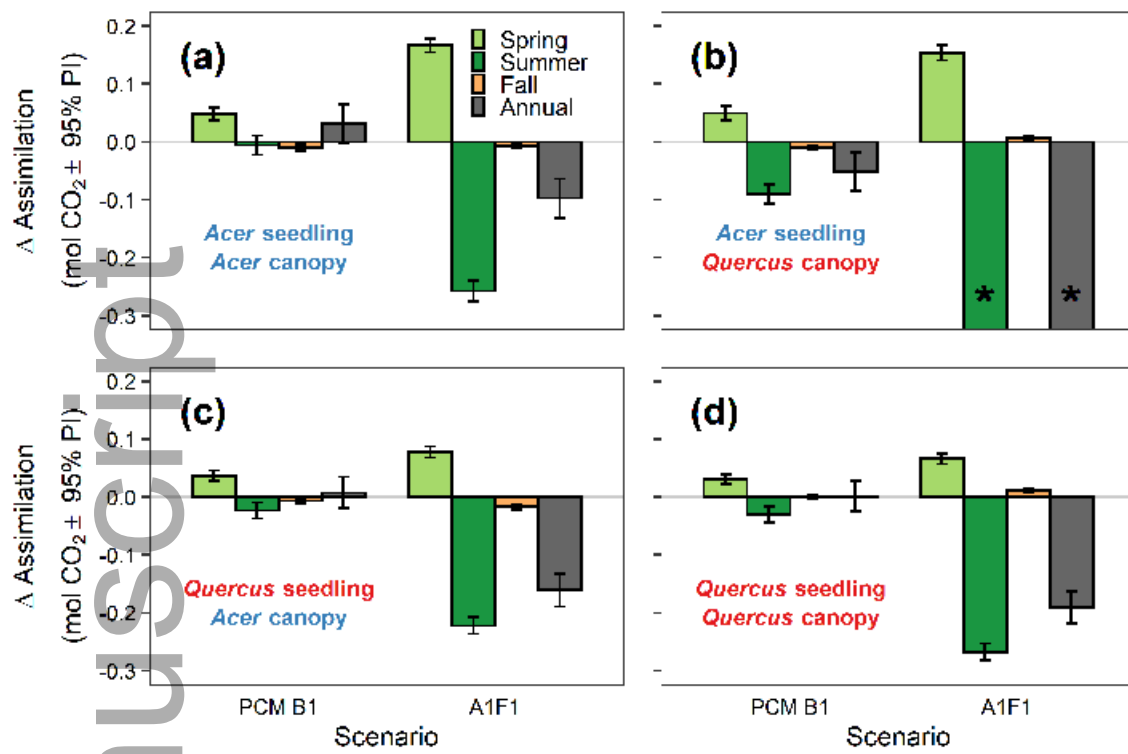
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