

Manuscript title: Spring phenological escape is critical for the survival of temperate tree seedlings

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Author contributions: BRL and II conceived the ideas, designed the methodology, and collected and analyzed the data. BRL led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data Availability Statement

Code and data used in this manuscript (i.e., for photosynthesis, survival, and growth models) are available in the Zenodo digital repository: <http://doi.org/10.5061/dryad.1c59zw3tk> (Lee & Ibáñez, 2021)

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Abstract

1. Understory plants in deciduous forests often rely on access to ephemeral light availability before the canopy closes in spring and after the canopy reopens in fall, a strategy commonly referred to as phenological escape. Although there is evidence for a relationship between understory plant phenology and demographic performance, a mechanistic link is still missing.
2. In this study, we bridged this gap by estimating annual carbon assimilation as a function of foliar phenology and photosynthetic capacity for seedlings of two temperate tree species that commonly co-occur across eastern North America. We then modeled the relationship between estimated carbon assimilation and observed seedling survival and growth.
3. Our results indicate that seedlings of both species strongly depend on spring phenological escape to assimilate the majority of their annual carbon budget and that this mechanism significantly affects their likelihood of survival (but not growth). Foliar desiccation also played a strong role in driving patterns of seedling survival, suggesting that water availability will also help shape seedling recruitment dynamics. We found only weak associations between seedling senescence in fall and annual carbon assimilation, suggesting that phenological escape in fall plays a relatively minor role in seedling demographic performance.

30 4. Our results indicate that spring phenological escape is critical for survival of these
31 temperate tree species, and thus any changes to this dynamic associated with climate
32 change could strongly impact these species' recruitment.

33
34 **Keywords:** Acer saccharum; Carbon assimilation; desiccation; foliar phenology; growth; C3
35 photosynthesis; Quercus rubra

36 **Introduction**

37 For understory plants growing in temperate forests, photosynthetic carbon assimilation is
38 strongly tied to the seasonality of light availability (Heberling, Cassidy, Fridley, & Kalisz, 2019;
39 Heberling, McDonough MacKenzie, Fridley, Kalisz, & Primack, 2019). Although plants are
40 limited by access to light by overstory trees for most of the growing season, many understory
41 species (including tree seedlings) have adapted to expand their leaves before the canopy closes in
42 spring and/or maintain their leaves after the canopy has reopened in fall to gain access to direct
43 light. This behavior, called phenological escape (Jacques et al., 2015), has been shown to allow
44 understory species to accumulate more than half of their annual net carbon assimilation earlier in
45 the spring before canopy closure (Heberling, Cassidy, et al., 2019; Kwit, Rigg, & Goldblum,
46 2010). Under current climate change, quantifying phenological escape becomes critical; with
47 warmer springs, the rate of phenological change between the canopy and the understory, as well
48 as among co-occurring species, could differ and consequentially impact photosynthetic
49 performance of understory plants. Although this dynamic has received recent attention in the
50 scientific literature (Heberling, Cassidy, et al., 2019; Heberling, McDonough MacKenzie, et al.,
51 2019; Kwit et al., 2010), there is relatively little work investigating the potential effects that
52 climate-driven changes to phenological escape will have on plant performance.

53 Previous research has found correlations between leaf out phenology and various
54 performance metrics such as growth, survival, and fruiting (Augspurger, 2008; Routhier &
55 Lapointe, 2002; Seiwa, 1998), but correlative studies such as these may be inaccurate if
56 relationships are nonlinear. For example, although earlier leaf out may provide tree seedlings
57 with increased access to light, potentially improving performance, it also places them at higher
58 risk of death from early spring frost events (Vitasse, Lenz, Hoch, & Körner, 2014). Furthermore,
59 correlative studies may be of little use if climate change results in non-analogue climate
60 conditions outside of the range of variation the studies (Jackson & Williams, 2004). Therefore, a

61 more mechanistic understanding of the physiological mechanisms that underlie these patterns
62 might help to develop more accurate predictions of future plant performance.

63 In forests, linking phenological escape of tree seedlings to demographic performance will
64 be particularly important because of the implications for tree recruitment dynamics. Tree
65 recruitment is a strong bottleneck that filters which individuals eventually recruit into the canopy
66 (Grubb, 1977; Harper, 1977), and it is also the stage at which trees are most likely to experience
67 nonrandom, directional mortality (Green, Harms, & Connell, 2014; Umaña et al., 2016). One
68 possible approach would be to quantify performance by estimating phenological escape success
69 via carbon status, which has been shown to be a good predictor of plant demographic success
70 (Hlásny et al., 2011; Hoch, Siegwolf, Keel, Körner, & Han, 2013; Korol, Running, Milner, &
71 Hunt, Jr., 1991; Lusk & Del Pozo, 2002; Piper, Reyes-Díaz, Corcuera, & Lusk, 2009). If
72 phenological escape determines seasonal carbon assimilation (e.g., if seedlings with earlier leaf-
73 out relative to the canopy experience greater net carbon assimilation), it will thus likely also
74 affect tree seedling performance and consequent recruitment.

75 When carbon status decreases to the point where plants are no longer able to meet
76 metabolic demand, they can succumb to death via carbon starvation (McDowell & Sevanto,
77 2010; Sala, Woodruff, & Meinzer, 2012). Accessing spring light via phenological escape allows
78 understory plants rise above this threshold, but they must then avoid moving back below the
79 threshold for the remainder of the growing season. In shady closed-canopy conditions, this often
80 requires plants to adjust their photosynthetic capacity to minimize respiration costs.
81 Photosynthetic capacity also acclimates to photoperiod (Bauerle et al., 2012), light availability
82 (Peltier & Ibáñez, 2015), and temperature (Larigauderie & Körner, 1995) over the course of the
83 growing season, and there is variability among species regarding the plasticity they exhibit
84 (Patrick, Ogle, & Tissue, 2009). Furthermore, species differ in their photosynthetic capacity
85 (often summarized as shade tolerance; Niinemets 2010), causing differences in carbon
86 assimilation rates even when exposed to the same microenvironment (Walters & Reich, 1996).
87 Warmer summer temperatures can cause disproportionately greater increases in plant respiration
88 rates compared to increases in photosynthetic assimilation rates (Caemmerer, 2000), although
89 there is evidence that suggests that respiration eventually reacclimates (Larigauderie & Körner,
90 1995; Smith & Dukes, 2013). Additionally, increases in vapor pressure deficit (VPD) associated
91 with increased temperature may simultaneously limit photosynthetic activity by reducing

92 stomatal conductance (Grossiord et al., 2020). Greater respiration costs associated with
93 temperature and reduced photosynthetic assimilation caused by reduced light and increased VPD
94 are therefore likely to combine to result in carbon assimilation dynamics where net change in
95 carbon status over summer is overwhelmingly negative (Slot & Kitajima, 2015). This could
96 potentially compromise a plant's ability to maintain a positive carbon status throughout the
97 growing season and lead to subsequent carbon starvation (Dickman, McDowell, Sevanto, Pangle,
98 & Pockman, 2015).

99 Photosynthetic activity, and thus plant carbon status, can also be affected by biotic
100 factors. Natural enemies, such as pathogens and herbivores, can directly limit plant carbon
101 assimilation by reducing the amount of photosynthetically active tissue (Nabity, Zavala, &
102 DeLucia, 2009). Carbon assimilation of understory plants may also be affected by surrounding
103 canopy trees both directly, via variation in canopy openness, and indirectly via soil-mediated
104 mechanisms. The latter include plant-soil feedback effects (McCarthy-Neumann & Ibáñez,
105 2012), allelopathic effects (Gómez-Aparicio & Canham, 2008; Pellissier & Souto, 1999; Ruan et
106 al., 2016), and soil nutrient availability (Classen et al., 2015; Phillips & Fahey, 2006), all of
107 which have been shown to differ according to the identity of neighboring canopy trees.
108 Therefore, a robust estimation of tree seedling carbon status will require accounting for
109 neighborhood effects from surrounding canopy trees.

110 In this experiment, our goal was to evaluate the extent to which foliar carbon assimilation
111 is associated with the performance of seedlings of two co-occurring temperate tree species (*Acer*
112 *saccharum* and *Quercus rubra*) that differ in their foliar phenology, photosynthetic
113 characteristics, shade tolerance, and response to drought. Specifically, we addressed the
114 following questions: 1) What proportion of annual foliar carbon assimilation is accumulated
115 during spring and fall phenological escape, and is there a difference in importance between the
116 two seasons? 2) How does net annual carbon assimilation relate to seedling demographic
117 performance (i.e., growth and survival)? Answers to these questions will provide a more
118 mechanistic link between phenological escape and tree seedling performance, knowledge that
119 will help to predict how tree recruitment will be impacted by climate change.

120

121 **Methods**

122 To address our research questions, we conducted a field experiment where we transplanted
123 seedlings of two widely co-occurring temperate tree species near conspecific and heterospecific
124 adults and observed their foliar phenology, photosynthetic gas exchange, survival, and growth.
125 We estimated net carbon assimilation by combining the phenology observations with
126 photosynthetic rates derived from the gas exchange measurements and with hourly
127 measurements of temperature, light, soil moisture, and vapor pressure deficit. We then used
128 generalized mixed effects models in a Cox survival model to explore how carbon assimilation
129 affects seedling survival and growth, respectively.

130

131 **Experimental Design**

132 Study locations - This study took place at three sites in southeastern Michigan, USA: Saginaw
133 Forest (42.270977 N, 83.806022 W), Radrick Forest (42.287083 N, 83.658056 W), and the E. S.
134 George Reserve (42.457104 N, 84.020226 W). Forests in all three locations were established in
135 the early 1900's following forest clearing and are currently dominated by mid- and late-
136 successional canopy genera, such as *Acer*, *Carya*, *Prunus*, and *Quercus*. Radrick Forest and the
137 E. S. George Reserve have relatively diverse canopies while plots in Saginaw Forest were
138 established in former monocultures of *Acer saccharum* and *Quercus rubra*. Climate across all
139 sites is similar, with average June-August temperatures of 22 °C, average December-February
140 temperatures of -6 °C, and average annual precipitation of 925 mm distributed evenly throughout
141 the year. Average canopy openness (Global Site Factor, GSF) at plots across sites was $12.6 \pm$
142 3.5% standard deviation, values characteristic of relatively closed canopies and shady summer
143 conditions. GSF was similar across sites and between canopy species treatments (Fig. S1).

144

145 Study species - We planted seedlings of two species native to and commonly co-occurring across
146 eastern North America: late-successional sugar maple (*Acer saccharum*, Marsh.) and mid-
147 successional northern red oak (*Quercus rubra*, L.). These two species were chosen because they
148 differ in their shade tolerance (Crow, 1988; Lei & Lechowicz, 1990; Walters & Reich, 1996),
149 phenological escape (Augsburger & Bartlett, 2003), and photosynthetic characteristics (Kaelke et
150 al., 2001; Peltier & Ibáñez, 2015). *Acer saccharum* seedlings are highly shade-tolerant and are
151 typically one of the first species in these forests to leaf out in spring whereas *Q. rubra* seedlings
152 are only moderately shade-tolerant and leaf out later in spring, sometimes at the same time as

153 canopy closure. *Quercus* seedlings typically have higher maximum photosynthetic rates than
154 *Acer* seedlings (Kaelke et al., 2001; Peltier & Ibáñez, 2015) and are also considered to be more
155 drought tolerant (Abrams, 1990; Bahari, Pallardy, & Parker, 1985; Loewenstein & Pallardy,
156 1998). Adults of these species have been shown to differ in stomatal regulation (Cavender-Bares
157 & Bazzaz, 2000; Loewenstein & Pallardy, 1998) and wood anatomy characteristics (diffuse- vs.
158 ring-porous xylem, respectively; Roman et al. 2015), although most of these traits have not been
159 directly measured in seedlings and may not be consistent across ontogeny (Cavender-Bares &
160 Bazzaz, 2000). *Quercus rubra* acorns are substantially larger than *A. saccharum* seeds (Barnes &
161 Wagner, Jr., 2004) and therefore likely confer greater initial carbon sources to first year tree
162 seedlings.

163
164 Field experimental set-up – For three consecutive years, 2014-2016, seeds from each species
165 sourced from multiple populations (see Table S1 in Supporting Information for seed source
166 information) were cold-stratified and sown in a greenhouse in large tubs of potting soil (Sun Gro
167 Horticulture; Agawam, MA, USA). Following germination and development of their first true
168 leaves, seedlings were bare root transplanted to the field. At each site, seedlings were planted in
169 plots established under the canopy of six adult trees, three *A. saccharum* and three *Q. rubra*; this
170 would expose seedlings to conspecific and heterospecific soil communities. Depending on
171 seedling availability in each year, 5-10 seedlings per target species were transplanted in separate
172 rows extending from the base of each adult canopy tree (Table S1). In total we planted 290 *A.*
173 *saccharum* seedlings and 320 *Q. rubra*.

174

175 **Data Collection**

176 Environmental data - One data recording station was established at each site to collect
177 environmental data under the forest canopy. Each station was equipped to measure hourly
178 temperature (°C) and relative humidity (%) using HOBO U23 Pro v2 data loggers (Onset
179 Computer Corp., Bourne, MA, USA) and hourly soil moisture (%) and photosynthetically active
180 radiation (PAR; $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) using HOBO Smart Sensors in combination with HOBO
181 Micro Stations (Onset Computer Corp.). Additionally, plot-level variation in soil moisture was
182 regularly measured using a Fieldscout TDR300 soil moisture meter (Spectrum Technologies;
183 Aurora, IL, USA) at multiple times throughout the growing season. Plot-level variation in

184 midseason light availability was measured by taking hemispherical canopy photos at a height of
185 1 m above seedling level with a Sigma SD14 camera equipped with a Sigma 4.5 mm circular
186 fisheye lens (Sigma Corporation, Japan) each year after the canopy at each plot had completely
187 closed. For each photo we calculated the Global Site Factor (GSF) using Hemiview software
188 (Delta-T Devices, Cambridge, UK), ranging from zero (fully closed canopy) to one (fully open).

189

190 Foliar phenology - We observed leaf-level dates of leaf expansion for seedlings in spring and
191 dates of onset of seedling leaf color change, 50% leaf color change (< 50% of leaf area remains
192 green), and leaf senescence in fall (complete abscission from the plant) beginning the year after
193 planting and going through the end of the 2018 growing season. Seedling phenology was
194 observed weekly in spring and fall, ending in spring when all seedlings had expanded their
195 leaves or been declared dead and ending in fall when all seedlings had fully senesced their
196 leaves.

197

198 Damage – Since leaf damage can affect seedling demographic performance directly by reducing
199 photosynthetic tissue (Gerhardt, 1998; Seiwa, 1998) and indirectly through reductions in
200 photosynthetic capacity, we observed leaf damage for all seedlings coinciding with the weekly
201 phenology observations in spring and fall and then approximately monthly over the rest of the
202 summer. Annual leaf damage was assessed by approximating the total percent area per leaf
203 removed by herbivory or infected by a foliar pathogen to the nearest 5%. Herbivory damage was
204 classified as either mammal or invertebrate herbivory. Plant infection was identified as
205 discoloration of leaf tissue not attributable to resorption of nutrients. Plants were also monitored
206 for foliar desiccation, which entailed having green leaves that were crisp to the touch and not
207 photosynthetically active (determined initially via gas exchange measurements for a subset of
208 seedlings and then visually thereafter). Importantly, we use the term “desiccation” to signify that
209 these observations only reflect leaf-level observations, which may or may not be representative
210 of whole plant water status.

211

212 Seedling growth and survival - Individual mortality was recorded during the phenology and
213 damage censuses when mortality was obvious (e.g., for fully uprooted plants) or during spring of
214 the following year if the individual did not produce new leaves. Mortality events that were

215 clearly unrelated to carbon assimilation dynamics (e.g., death directly resulting from squirrel or
216 deer herbivory/uprooting) were not included in the survival analyses. Seedling height (distance
217 from soil to apical meristem) was recorded prior to planting to account for maternal effects,
218 which have previously been demonstrated to affect tree seedling growth and survival (Castro,
219 1999; González-Rodríguez, Villar, & Navarro-Cerrillo, 2011; Ibáñez, Katz, & Lee, 2017).
220 Height growth was then measured annually thereafter at the end of each growing season.
221 Although radial stem growth has also been strongly linked to survivorship (Martin, Canham, &
222 Kobe, 2010), particularly for shade-tolerant seedlings such as *A. saccharum* which can persist for
223 decades in the understory with relatively little vertical growth (Marks & Gardescu, 1998), we
224 chose to measure height growth as it is more commonly used to categorize recruitment stages
225 (Green et al., 2014) and is strongly correlated with light availability (Montgomery, 2004;
226 Wagner, Madsen, & Ammer, 2009).

227

228 Carbon assimilation – We used a LI-6400 Portable Photosynthesis System equipped with a CO₂
229 mixer assembly and LI-02B LED red/blue light source (Li-COR Biosciences, Lincoln, NE,
230 USA) to measure in situ gas exchange for a subset of transplants following spring leaf expansion
231 and continuing through the growing season. Gas exchange measurements were taken once every
232 two weeks in spring and fall and approximately monthly during the summer for the 2015-2017
233 growing seasons. We constructed A-Ci (at 400, 300, 200, 100, 50, 400, 400, 600, 800, 1000,
234 1250, and 1500 ppm CO₂) and A-Q curves (at 1500, 1000, 750, 500, 250, 125, 60, 30, 20, 10, and
235 0 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$) for each seedling, maintaining ambient humidity and temperature. Leaves
236 smaller than the cuvette were traced in the field and leaf area was measured using ImageJ
237 software (Schneider, Rasband, & Eliceiri, 2012). Soil moisture was measured at the individual
238 seedling level during each measurement using the Fieldscout TDR300 Soil Moisture Meter.

239

240 **Analyses**

241 Photosynthesis

242 We analyzed our gas exchange data using a Bayesian adaptation of the Farquhar et al. (1980)
243 model of C3 photosynthesis originally developed by Patrick et al. (2009) and then further
244 modified by Peltier and Ibáñez (2015). In short, this modeling approach allowed us to estimate
245 seasonal photosynthetic capacity at the species level that incorporates the effect of environmental

246 variables (i.e., light, temperature, and water availability) in the estimation of net photosynthetic
247 activity. A detailed description of the model (along with supplemental analysis) can be found in
248 the Supporting Information along with tables of associated parameter definitions (Table S2) and
249 parameter posterior estimates (Table S3).

250 Because photosynthetic rates have been shown to vary over the course of the growing
251 season (Bauerle et al., 2012; Peltier & Ibáñez, 2015), we estimated photosynthesis model
252 parameters for each of the following phenophases : 1) spring period between leaf-out and the day
253 of canopy closure; 2) summer, defined as the time between canopy closure and the beginning of
254 seedling leaf coloration; 3) Fall 1, the time between the onset of coloration and when a specific
255 leaf had surpassed 50% of coloration; and 4) Fall 2, measurement taken between 50% coloration
256 and leaf senescence. Day of canopy closure in the spring was defined as the day on which the
257 average daytime PAR (between 1000-1700 hours) dropped below $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ and then did
258 not increase above that threshold for one week (Fig. S2, in order to rule out the possibility of low
259 light resulting from cloudy days). Preliminary analysis did not indicate differences in
260 photosynthetic rates based on seed source, seedling cohort, or seedling age, so these variables
261 were not included in the analysis.

262 Carbon assimilation estimates

263 We used hourly climate data (temperature, VPD, soil moisture, and light [photosynthetic active
264 radiation; PAR]) collected from our site-level environmental stations and simulated at the plot
265 level (see Appendix S3 in Supporting Information for details on data simulation) into the fitted
266 photosynthesis model and estimated hourly rates of foliar carbon assimilation for each seedling.
267 Parameter estimates depended on the seedling species, seedling phenophase, and canopy tree
268 species they were planted under. We then adjusted calculations according to individual leaf area,
269 which varied over time to reflect observed reductions in leaf area caused by herbivory for
270 individual plants. Hourly estimates of carbon assimilation were then summed over the duration
271 of the growing season, resulting in estimations of net annual foliar carbon assimilation (Fig. 1)
272 representing the net amount of CO_2 assimilated by seedling leaf tissue over the course of the
273 growing season ($\text{mol CO}_2 \text{yr}^{-1}$) for each individual (full description of this process is included in
274 Appendix S4 in the Supporting Information). Importantly, we did not measure soil respiration or
275 stem photosynthesis, and so this value does not reflect total seedling carbon status. However,

277 carbon assimilated by the stem is proportionally negligible compared to foliar assimilation
278 (Pfan­z & Aschan, 2001), so net annual foliar assimilation is representative of gross annual
279 carbon accumulation before accounting for belowground respiration. We then modeled the
280 relationship between seedling foliar phenology (day of leaf out in spring or day of leaf
281 senescence in fall) and estimated annual foliar assimilation using linear models in the lm package
282 in R (v3.5.3) with day of event as a fixed effect.

283

284 Survival

285 We analyzed seedling survival using a Bayesian Bernoulli model where the probability of
286 survival (p) for each seedling (i) to the end of the growing season in year (t), dead $Survival_{i,t} = 0$
287 or alive $Survival_{i,t} = 1$, is estimated with likelihood: $Survival_{i,t} \sim Bernoulli(p_{i,t})$, and process
288 model: $logit(p_{i,t}) = \log\left(\frac{p_{i,t}}{1-p_{i,t}}\right) = \bar{\beta}X_{i,t}$. We systematically evaluated models for best fit using
289 different combinations of eight covariates and seven categorical variables (Table S4), the latter
290 included as random effects. Models started with an intercept (β_0) and a foliar carbon assimilation
291 term (β_C):

$$logit(p_{i,t}) = \beta_0 + \beta_C * C_{Annual_{i,t}}$$

292 Where C_{Annual} is each seedling's estimated net annual foliar carbon assimilation in a given year.
293 Values of all continuous covariates, including C_{Annual} , were standardized around their respective
294 means. Covariates and random effects (Table S4) were then added one at a time with models
295 being iteratively chosen based on best fit according to the area under the receiving operator
296 characteristic curve (AUROC; Metz 1978, Murtaugh 1996). A description of the AUROC
297 criterion is available in the Supporting Information (Appendix S5) and posterior estimates of
298 intercepts, covariates, and random effects are available in Table S5. To avoid
299 overparameterization of the models, either plot or site random effects, but not both, were allowed
300 in each best-fit model. Each species was analyzed independently. The relationship between
301 carbon assimilation and survival was estimated and plotted by using the average values of all
302 continuous covariates (besides assimilation) and assuming that all binary covariates equal zero
303 (see Appendix S4 in Supporting Information for further detail).

304

305 Growth

306 Growth measurements, standardized for each seedling i and year t were analyzed with a
307 normal likelihood: $Growth_{i,t} \sim N(\rho_{i,t}, \sigma^2)$, limited to positive values, and process model: $\rho_{i,t} =$
308 $\beta_0 + \bar{\beta}X_{i,t}$. We evaluated models for best fit using combinations of C_{Annual} and the same
309 covariates described in the survival analysis, with the addition of a seedling random effect. Only
310 seedlings with non-negative growth values were included in this analysis. Negative growth
311 values were generally associated with stem die-back or deer herbivory and did not represent the
312 realized growth of each seedling. Model selection for growth models was done based on
313 comparisons of the Deviance Information Criterion (DIC; Spiegelhalter et al. 2002) and on
314 goodness of fit (R^2 , predicted vs. observed), fully described in Appendix S5 in the Supporting
315 Information. Posterior estimates of all growth model parameters are available in Table S6.
316 Species were analyzed individually.

317 In both analyses, covariate parameters were estimated from non-informative normal
318 distributions $\beta_* \sim N(0, 1000)$. Random effect parameters associated with the categorical
319 variables were estimated from hierarchical normal distributions $\alpha_* \sim N(0, \sigma^2_{\alpha_*})$. Precision
320 parameters (1/variance) were estimated from non-informative gamma prior distributions
321 $1/\sigma^2_{\alpha_*} \sim Gamma(0.001, 0.001)$. All models were run using OpenBUGS software v3.2.3
322 (Lunn, Spiegelhalter, Thomas, & Best, 2009). We tracked 40,000 iterations for three Monte
323 Carlo chains following a 30,000-iteration burn-in period. Convergence of parameters was
324 assessed visually and by using the Brooks-Gelman-Rubin statistic (Gelman & Rubin, 1992), and
325 models were iterated until convergence was reached. Parameter values (means, variances, and
326 covariances) were estimated from their posterior distributions. Data and model code for all
327 analyses are available (see Data Availability Statement).

328

329 **Results**

330 Seedling mortality rates were high for both species. Out of the 70 *A. saccharum* and 115 *Q.*
331 *rubra* seedlings that survived at least one year, 27 and 94 survived to the end of the study,
332 respectively. Data were recorded every year that a seedling was alive, however, so seedling
333 survival models had $n = 116$ and 167 and growth models had $n = 72$ and 86 , for *A. saccharum*
334 and *Q. rubra*, respectively. Sample sizes in the growth models were lower because growth was
335 not measured the year a seedling died. *Quercus rubra* seedlings (146.2 ± 34.9 mm) were taller on
336 average than *A. saccharum* seedlings (76.7 ± 14.4 mm) at the time of planting but had slightly

337 lower annual growth rates thereafter ($19.7 \pm 14.9 \text{ mm y}^{-1}$ and $23.7 \pm 16.1 \text{ mm y}^{-1}$, respectively).
338 The photosynthesis models were fit using a total of 254 and 259 paired A-Q and A-Ci curves for
339 A. saccharum and Q. rubra seedlings, respectively.

340

341 Photosynthetic capacity

342 Model fits for the seedling gas exchange models (R^2 , predicted vs. observed) were 0.72
343 for A. saccharum seedlings and 0.76 for Q. rubra seedlings. Photosynthetic parameter posterior
344 estimates (Fig. S3) were similar to values published elsewhere for these two species (Peltier &
345 Ibáñez, 2015). A full list of parameter posterior estimates can be found in Table S3.

346 We found significant differences in $V_{\text{cmax}25}$ between the two seedling species, but the
347 differences that were observed depended on the species of neighboring tree (Fig. S3c-d).
348 Quercus rubra $V_{\text{cmax}25}$ was consistently greater compared to that of A. saccharum seedlings,
349 with significant differences in Spring and Summer when planted near mature A. saccharum trees
350 and in Spring and Fall 1 when planted near mature Q. rubra. Quercus rubra $V_{\text{cmax}25}$ did not
351 significantly differ according to phenophase or neighbor identity. However, A. saccharum
352 $V_{\text{cmax}25}$ was significantly higher in Summer when planted near mature Q. rubra. Phenophase
353 also affected A. saccharum seedlings when planted near mature Q. rubra, with significantly
354 higher $V_{\text{cmax}25}$ in Summer compared to Spring and Fall 1.

355 RuBP regeneration-limited carbon assimilation rate ($J_{\text{max}25}$) experienced a relatively
356 higher degree of variation compared to $V_{\text{cmax}25}$ (Fig. S3a-b). Acer saccharum seedlings planted
357 near conspecific adults had significantly higher Spring $J_{\text{max}25}$ and significantly lower Summer
358 and Fall 1 $J_{\text{max}25}$ compared to when planted near mature Q. rubra. Quercus rubra seedling
359 $J_{\text{max}25}$ was only significantly affected by neighbor identity in Fall 1, when $J_{\text{max}25}$ was
360 significantly greater when planted near mature conspecifics. Both species showed strong
361 variation in $J_{\text{max}25}$ associated with phenophase, but patterns tended to differ between the two
362 canopy treatments. Rates were more consistent across phenophase when planted near adult A.
363 saccharum whereas both species had significantly lower Spring $J_{\text{max}25}$ compared to the other
364 phenophase bins when planted near mature Q. rubra. In general, Q. rubra seedlings had higher
365 $J_{\text{max}25}$ compared to A. saccharum seedlings in Spring, Summer, and Fall 1, regardless of canopy
366 treatment or phenophase.

367 Rates of dark respiration (R_{d25}) did not differ significantly by seedling or canopy species
368 (Fig. S3e-f), but there were some significant differences associated with phenophase. Rates
369 tended to be highest in Fall 1 and Fall 2 for both species, with the lowest respiration rates
370 occurring in Spring and Summer. Stomatal conductance (g_{m25}) similarly did not differ
371 significantly by seedling or canopy species (Fig. S3g-h). It only significantly differed by
372 phenophase for *A. saccharum* seedlings planted near *Q. rubra* canopy trees, with rates in
373 Summer that were significantly lower compared to those in Fall 1 and Fall 2.

374

375 Water Availability and VPD Effects

376 Soil moisture had a significant positive association (i.e., confidence intervals did not
377 overlap 0) with J_{max25} in Spring and Summer for both species and this association was
378 significantly negative in Fall 1 (Fig. S4). There were significant differences between species in
379 Spring, Summer, and Fall 1 where *A. saccharum* seedling J_{max25} consistently had stronger
380 correlations with soil moisture. VPD had significantly positive correlations with J_{max25} in Spring
381 and Summer, but the effects in Fall 1 and Fall 2 differed between species. VPD was positively
382 associated with J_{max25} for *Q. rubra* seedlings (significantly so in Fall 2) but negatively
383 associated with J_{max25} for *A. saccharum* seedlings (significant in Fall 1). The effect of VPD only
384 significantly differed by species in Fall 1 and 2.

385 Soil water availability had relatively weaker correlations with V_{cmax25} for both species
386 (Fig. S5). The associations with soil moisture were significantly positive for both species in
387 Summer and significantly negative for *A. saccharum* seedlings in Fall 1. Fall 1 was also the only
388 season where associations with soil moisture differed between the two species. The only
389 significant association V_{cmax25} had with VPD was for *A. saccharum* seedlings in Fall 1, which
390 was significantly negative. There was no phenophase where the magnitude of the association
391 differed significantly between species.

392

393 Net Annual Assimilation

394 Annual foliar CO_2 assimilation estimated at the individual level ranged from -0.014 to 0.364 mol
395 $CO_2 yr^{-1}$ and 0.001 to 0.453 mol $CO_2 yr^{-1}$ for *A. saccharum* and *Q. rubra* seedlings, respectively.
396 For *A. saccharum* seedlings, an average of 84.3% of foliar carbon was assimilated in spring,
397 15.9% was assimilated in summer and -0.2% was lost in fall (i.e., respiration in fall was greater

398 than photosynthetic assimilation for this species; Fig. 1). In contrast, an average of 52.5% of Q.
399 rubra seedling annual carbon was assimilated in spring, 43.5% was assimilated in summer, and
400 4.0% was assimilated in fall (Fig. 1).

401 The correlations between estimated annual CO₂ assimilation and seedling leaf out
402 phenology were stronger than the correlations with leaf senescence phenology for both species
403 (Fig. 2). Day of leaf out in spring (Fig. 2a) was significantly negatively correlated with estimated
404 annual CO₂ assimilation for *A. saccharum* (adj. R² = 0.406, p < 0.05) and *Q. rubra* seedlings
405 (adj. R² = 0.16, p < 0.05). Day of leaf senescence in fall (Fig. 2b) negatively correlated with
406 estimated annual CO₂ assimilation for *A. saccharum* seedlings (p = 0.33) and positively
407 correlated with estimated *Q. rubra* assimilation (p = 0.30), but neither relationship was
408 statistically significant.

409

410 Seedling survival

411 In addition to C_{Annual}, the best fit survival models for both species included covariates for
412 presence of foliar desiccation and percent foliar damage, with the *A. saccharum* survival model
413 also including a term for signs of deer herbivory. The effect of annual carbon was positive and
414 significant for both species while the effects of desiccation and percent leaf damage were
415 negative and significant (Fig. 3). Deer herbivory had a negative but non-significant effect on *A.*
416 *saccharum* seedling survival (Fig. 3a). Model fit for *A. saccharum* was highest when site random
417 effects were added and the best-fit model for *Q. rubra* survival included plot-level random
418 effects. The models resulted in AUROC values of 0.912 and 0.891 for *A. saccharum* and *Q.*
419 *rubra* seedlings, respectively. All parameter values can be found in Table S5.

420 The negative association with desiccation was of similar magnitude to the positive
421 association with C_{Annual}. Desiccation events were observed for six *A. saccharum* (n = 116) and 20
422 *Q. rubra* seedlings (n = 167) across the four years of this study, and most seedlings (92.3%) died
423 the year foliar desiccation was recorded. Moreover, most of the desiccation events (73.1%) were
424 recorded during the 2017 growing season. Soil moisture in 2017 was largely consistent with the
425 other years in this study throughout most of the summer except for particularly low soil moisture
426 in August and September (Fig. S6).

427 Figure 4 shows the relationship between survival probability and estimated annual foliar
428 CO₂ assimilation (C_{Annual}) for seedlings of both species. *Quercus rubra* seedlings assimilated

429 more CO₂ annually than *A. saccharum* seedlings on average (symbols in Fig. 4) but had lower
430 average probability of survival. *Quercus rubra* seedlings passed below a mean probability of
431 survival equal to 0.5 at 0.106 mol of estimated CO₂ assimilation. This was an order of magnitude
432 greater than the threshold for *A. saccharum* seedlings which occurred at 0.012 mol assimilation.
433

434 Seedling growth

435 The best fit growth models each included C_{Annual} and only one other covariate. *Acer saccharum*
436 seedling growth was best predicted by a model that included GSF (canopy openness) whereas *Q.*
437 *rubra* seedling growth was best predicted by a model that included signs of deer herbivory. All
438 covariates were positively associated with growth for both species, but the only significant
439 relationship was between C_{Annual} and *A. saccharum* seedling growth (Fig. 5a). The best fit *A.*
440 *saccharum* growth model had a goodness of fit $R^2 = 0.504$; goodness of fit for *Q. rubra* growth
441 was 0.456. Models for both species included seedling and plot random effects, with the *A.*
442 *saccharum* model also including a year random effect and the *Q. rubra* model including random
443 effects for seedling age and planting cohort. All parameter values can be found in Table S3.

444 As with probability of survival, predicted growth of *A. saccharum* seedlings with the
445 average value of estimated annual CO₂ assimilation was greater than that of *Q. rubra* seedlings,
446 despite the latter estimated to assimilate more CO₂ per year on average (Fig. 6). *Acer saccharum*
447 seedlings were predicted to grow more than *Q. rubra* seedlings (23.23 ± 5.81 and 13.61 ± 28.56
448 mm yr⁻¹ ± s.d., respectively), but the difference was not statistically significant.

450 Discussion

451 Shifts in plant phenology have been one of the most widely reported responses of organisms to
452 current climate change (Ibáñez et al., 2010; Menzel & Fabian, 1999; Piao et al., 2019), but few
453 studies have addressed how differences in spring phenology affect individual performance (but
454 see Augspurger, 2008) and what the resulting implications will be for populations and
455 communities (Forrest & Miller-Rushing, 2010). Tree seedling phenology, carbon assimilation,
456 and performance will be particularly important to understand with respect to forest ecosystems
457 because survival and recruitment at this stage can act as a bottleneck determining the structure
458 and composition of future forest canopies (Grubb, 1977; Harper, 1977). Recent studies have
459 demonstrated that the annual carbon assimilation of temperate understory plants, including tree

460 seedlings, is strongly affected by spring foliar phenology and access to light before the canopy
461 closes (Heberling, Cassidy, et al., 2019; Heberling, McDonough MacKenzie, et al., 2019; Kwit
462 et al., 2010), i.e., phenological escape (Jacques et al., 2015). However, it is yet unclear how
463 differences in carbon assimilation linked to this mechanism impact the growth and survival of
464 temperate tree seedlings.

465 Here, we modeled the relationship between foliar net annual CO₂ assimilation of
466 individual tree seedlings and their demographic performance (i.e., growth and survival) for two
467 temperate tree species that commonly co-occur across eastern North America, *Acer saccharum*
468 and *Quercus rubra*. Furthermore, we quantified how seedling carbon assimilation is affected by
469 spring and fall phenological escape, allowing us to directly link phenology to plant performance.
470 We found strong relationships between estimated carbon assimilation and seedling survival but
471 relatively weak (and likely biologically irrelevant) relationships between carbon assimilation and
472 aboveground height growth. Seedlings of both species were found to assimilate most of their
473 annual carbon during spring phenological escape with relatively minor contributions in fall,
474 suggesting that capacity for phenological escape early in the growing season will play an
475 important role in shaping future tree recruitment. Furthermore, our results suggest that studies of
476 temperate tree seedling carbon assimilation, performance, and recruitment should concentrate on
477 these early season dynamics and that photosynthetic capacity in midseason plays a much smaller
478 role in influencing overall demography.

479

480 Spring leaf out date drives annual carbon assimilation

481 Understory plants in deciduous forests are generally limited by access to light for most of the
482 growing season while the canopy is closed. Therefore, many species have adapted phenological
483 escape behavior that allows them to access ephemeral periods of high light availability in spring
484 by leafing out earlier than the canopy or in fall by senescing their leaves after the canopy
485 (Jacques et al., 2015). Recent studies have suggested that climate change may affect the amount
486 of carbon assimilated during phenological escape by differently affecting the phenology of
487 understory and canopy species (Heberling, Cassidy, et al., 2019; Heberling, McDonough
488 MacKenzie, et al., 2019), but it is as yet unexplored what effect this would have on the
489 demographic performance of understory plants.

490 We found significant negative correlations between spring leaf out phenology and annual
491 carbon assimilation for seedlings of both species (Fig. 2a), indicating that seedlings assimilated
492 more carbon per annum the earlier they leafed out. This agrees with previous research published
493 by Kwit et al. (2010), which found that *A. saccharum* seedlings could substantially increase their
494 annual carbon gain with earlier leaf out relative to artificial canopy closure treatments. Although
495 this result is intuitive, previous studies which investigated relationships between phenology and
496 performance speculate at or assume this relationship (e.g., Augspurger, 2008; Routhier &
497 Lapointe, 2002; Seiwa, 1998), without quantifying it. Some studies included measurements of
498 species-level photosynthetic characteristics (e.g., Routhier & Lapointe, 2002), but not with
499 enough detail needed to calculate the change in net carbon assimilation as a function of
500 phenology.

501 In contrast, annual foliar CO₂ assimilation was not significantly correlated with leaf
502 senescence date for either species (Fig. 2b), suggesting that fall phenological escape plays a far
503 less important role in driving seedling carbon dynamics. This is further supported by our findings
504 that spring foliar CO₂ assimilation on average accounted for 84.3% and 52.5% of the total annual
505 assimilation for *A. saccharum* and *Q. rubra* seedlings, respectively, whereas fall assimilation
506 only accounted for -0.2% and 4.0%. One possible reason for this is that timing of leaf senescence
507 could just reflect timing of spring phenology (Fig. S7), echoing results from other research which
508 found similar correlations (Keenan & Richardson, 2015). Alternatively, it has been recently
509 hypothesized that leaf senescence could be driven by sink limitations (Zani, Crowther, Mo,
510 Renner, & Zohner, 2020), where senescence occurs earlier when early- and midseason carbon
511 assimilation is higher, but this hypothesis remains controversial because it contradicts substantial
512 evidence from Free-Air CO₂ enrichment (FACE) experiments (Norby, 2021). Regardless of the
513 underlying mechanism, our results suggest that phenological escape late in the growing season
514 will have negligible effects on net CO₂ assimilation.

515 516 CO₂ assimilation affects survival more than growth

517 Plants rely on photosynthetic carbon assimilation to survive, grow, reproduce, and defend
518 themselves (Mooney, 1972), and our results reflect that dependency. Survival of both species
519 was significantly associated with net annual foliar CO₂ assimilation (Fig. 3), but the relationship
520 between carbon and growth was only significant for *A. saccharum* seedlings (Fig. 5), and the

521 relationship was weak. *Acer saccharum* seedlings were predicted to have higher overall
522 probability of survival compared to *Q. rubra* seedlings (Fig. 4) and they also maintained > 50%
523 mean predicted probability of survival at lower CO₂ assimilation compared to *Q. rubra*. Thus,
524 even though *Q. rubra* seedlings assimilated more foliar CO₂ on average than *A. saccharum*
525 seedlings (Fig. 1), their predicted probability of survival at the average value was lower (points
526 in Fig. 4).

527 The differences in predicted survival probability between species could be due to a few
528 reasons. First, our study only accounted for foliar carbon dynamics and did not account for stem
529 or belowground carbon dynamics. Root respiration rates in temperate forests can be of similar or
530 greater magnitude compared to foliar respiration rates (Reich, Walters, Tjoelker, Vanderklein, &
531 Buschena, 1998), and thus could cause a dissociation between foliar carbon assimilation and
532 seedling performance. This may be particularly true for *Q. rubra* seedlings which develop deep
533 taproots (Wilson, Vitols, & Park, 2007) and might therefore allocate proportionally more carbon
534 to belowground processes compared to *A. saccharum* seedlings. This is supported by previous
535 research that has shown that 2-year-old *Q. rubra* seedlings allocated more carbon to storage than
536 *A. saccharum*, red maple (*Acer rubrum*), or black cherry (*Prunus serotina*) seedlings on a mass
537 basis (Canham, Kobe, Latty, & Chazdon, 1999). However, we lack the evidence needed to
538 further support this theory in this study because we did not quantify belowground carbohydrate
539 concentrations or mass allocation.

540 Additionally, our results could reflect differences in aboveground growth and respiration
541 costs between these two species. We found consistently higher respiration rates for *Q. rubra*
542 seedlings compared to *A. saccharum* seedlings in the parameterization of our photosynthesis
543 models (Table S5), reflecting higher carbon costs for foliar maintenance. Further, evidence in the
544 literature suggests that *Q. rubra* tend to have thicker leaves (i.e., lower specific leaf area)
545 compared to *A. saccharum* (Abrams & Kubiske, 1990; Lapointe, 2001; Salifu, Apostol, Jacobs,
546 & Islam, 2008) and that they have higher foliar C:N ratios (Midgley, Brzostek, & Phillips, 2015).
547 These qualities provide this species with greater constitutive defense and lower palatability to
548 insect herbivores (Throop & Lerdau, 2004), but make leaves more costly to construct. Thus,
549 greater relative aboveground carbon costs for *Q. rubra* seedlings could make it so that this
550 species requires greater net annual CO₂ assimilation to achieve the same probability of survival.

551 The higher probability of survival of *A. saccharum* seedlings may also be indicative of
552 the higher shade tolerance reported for this species in the literature since seedlings were grown
553 under low light conditions. Moreover, our results suggest that phenological escape may even be a
554 critical component of shade tolerance for some species. In our study, *A. saccharum* seedlings had
555 lower summer photosynthetic capacity, but also lower respiration costs compared to *Q. rubra*
556 seedlings. This behavior allows seedlings to minimize carbon loss when resources are limited in
557 the middle of the growing season (Craine & Reich, 2005). However, our results also show
558 seedlings must accumulate a strong reserve of carbon in the spring to allow them to withstand
559 low assimilation rates throughout the rest of the growing season (e.g., Fig. 1b; Kwit et al., 2010).
560 Future research should investigate this dynamic further and evaluate whether phenological
561 escape dynamics are correlated with shade tolerance in temperate deciduous forests more
562 generally.

563 Annual CO₂ assimilation was only significantly associated with height growth for *A.*
564 *saccharum* (Fig. 5) and our models explained only about 50% of the variation in the data for both
565 species. Furthermore, the predicted changes in growth were relatively small, with seedlings
566 predicted to grow less than 1 cm in height for every additional 0.1 mol CO₂ yr⁻¹ assimilated (Fig.
567 6). This low amount of growth in part reflects the strongly light-limited environments that these
568 seedlings were grown in. For example, *A. saccharum* seedlings have been recorded to grow less
569 than a meter in height over a period of decades under closed-canopy conditions (Marks &
570 Gardescu, 1998). Thus, it is possible that this relationship would have been better quantified
571 using other metrics of growth such as radial stem growth, belowground growth, or total biomass
572 (e.g., Kaelke et al., 2001; Sevillano, Short, Grant, & O'Reilly, 2016). Future studies in this area
573 should thus account for multiple growth metrics and, when possible, investigate the extent to
574 which using different metrics affects analysis and results.

575 Survival models for both species also showed significantly negative associations with
576 desiccation and foliar damage due to pathogens and herbivory. We accounted for the negative
577 effects that reduced water availability can have on photosynthetic performance (i.e., by directly
578 correlating carbon assimilation rates with plot-level VPD and soil moisture, as described in
579 Appendix S2), so this additional effect of desiccation suggests that temperate tree seedlings are
580 additionally vulnerable to dying from hydraulic failure (McDowell et al., 2008), where plants die
581 from catastrophic embolisms resulting from extremely negative water potentials. We did not

582 collect data on xylem conductance or plant water potential as part of this study, however, so we
583 are unable to draw substantive conclusions from these results. Similarly, leaf damage also
584 reduced survival after accounting for reductions in photosynthetic area in our CO₂ assimilation
585 calculations (Appendix S4), suggesting that foliar damage negatively affects performance
586 beyond the effects associated with leaf area. We can only speculate about the mechanism
587 underlying this effect, but one possible explanation is that foliar damage is correlated with
588 systemic damage such as whole-plant infection that could be a contributing factor in mortality
589 (Jain, Sarsaiya, Wu, Lu, & Shi, 2019).

590 Deer herbivory was important for *A. saccharum* survival and *Q. rubra* growth, but with
591 opposite effects. Although the association between *A. saccharum* survival and deer herbivory
592 was negative, deer herbivory had a positive association with *Q. rubra* growth, suggesting that
593 this species grew more in response to deer herbivory events. This result, although potentially
594 counterintuitive, is consistent with previously documented compensatory growth dynamics
595 (McNaughton, 1983), and could reflect a potential trade-off between growth and foliar defense
596 (Coley, 1988). However, we did not quantify nonstructural carbohydrate concentrations in this
597 study and thus more substantive conclusions will require further research.

598

599 Water limitation and neighboring canopy tree effects

600 Our results suggest that spring phenological escape is the dominant driver of seedling carbon
601 assimilation and performance, but they also suggest that water availability plays an important
602 role. Soil moisture and VPD both affected seedling photosynthetic capacity seasonally and
603 between species (Fig. S4-S5), with generally positive associations in Spring and Summer and
604 negative relationships at the end of the growing season. Photosynthetic activity is thus likely to
605 be strongly affected by water availability in summer when soil moisture is lowest. Our results
606 also suggest that drought stress can directly affect seedling performance, as evidenced by the
607 significant association between seedling survival and observed desiccation (Fig. 3). Although
608 only a small proportion of seedlings (< 10% of the total) were observed to desiccate, nearly all
609 the desiccation events took place in 2017 when soil moisture reached the lowest values recorded
610 throughout this experiment (Fig. S6). Although this could implicate hydraulic failure as the cause
611 of mortality for these seedlings, we did not measure plant water potentials or other metrics that
612 would allow us to make more substantive conclusions.

613 We also found that seedling photosynthetic capacity was significantly affected by the
614 identity of canopy tree species that the seedlings were planted near. Canopy tree identity strongly
615 affected RuBP regeneration-limited carbon assimilation rate ($J_{\max 25}$) of *A. saccharum* seedlings
616 (Fig. S3a). Values were significantly higher in spring, but lower in summer and fall for seedlings
617 planted beneath conspecific canopy trees, suggesting that this species benefits more from
618 phenological escape but less from growing season sunflecks compared to when planted near *Q.*
619 *rubra* canopy trees. *Acer saccharum* summer respiration rates were also substantially (though not
620 significantly) higher when planted near *Q. rubra* canopy trees, meaning that net carbon
621 assimilation rates are especially negatively impacted by hot, droughty conditions. Our
622 photosynthesis models accounted for temperature and soil moisture for each gas exchange
623 observation, so it is unlikely that these results are due to differences in microenvironment
624 between the two canopies. The underlying mechanism behind this difference is uncertain, but it
625 is possible that some combination of inorganic nitrogen availability, concentrations of other soil
626 nutrients, and plant-soil feedback effects could be responsible for the observed differences in
627 seedling photosynthetic rates (Classen et al., 2015; Juice et al., 2006; Liang et al., 2020;
628 McCarthy-Neumann & Ibáñez, 2012, 2013; McCarthy-Neumann & Kobe, 2010). However, this
629 is speculative and future research should investigate this relationship and further explore how
630 drought interacts with phenological escape more generally.

631

632 **Conclusion**

633 The results from this study suggest that temperate tree seedling survival is strongly associated
634 with annual foliar CO₂ assimilation, which in turn depends on spring phenological escape.
635 Seedlings assimilated relatively little carbon in fall compared to spring, suggesting that the
636 timing of leaf senescence has little effect on seedling performance. Future studies should thus
637 place an emphasis on measuring photosynthetic capacity and activity at the beginning of the
638 growing season rather than in summer or fall. Water availability plays an important role in
639 seedling carbon assimilation and potentially directly via hydraulic failure, but more research is
640 needed on this topic, particularly in investigating how water availability and phenological escape
641 interact to affect seedling performance.

642 Still, this study mechanistically links tree seedling phenology to survival and growth
643 performance and will therefore allow future research to make accurate demographic projections

644 for these species based on climate change forecasts and estimated changes in annual carbon
645 assimilation. The importance of spring phenological escape to net foliar carbon assimilation
646 suggests that any changes to these dynamics resulting from climate change will have strong
647 effects on overall seedling performance and tree recruitment. Furthermore, warmer temperatures
648 and decreased water availability predicted for our study region (Handler et al., 2014) will make
649 phenological escape dynamics even more important, as seedlings will need to assimilate more
650 carbon in spring to make up for the increasing respiration costs in summer and fall. Determining
651 whether temperate deciduous tree seedlings are capable of improving their phenological escape
652 success is an important topic for future research and will have important implications for
653 predictions of future forest structure and composition.

654

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660

661 **Data Availability Statement**

662 Code and data used in this manuscript (i.e., for photosynthesis, survival, and growth models) are
663 available in the Zenodo digital repository: <http://doi.org/10.5061/dryad.1c59zw3tk> (Lee & Ibáñez,
664 2021)

665

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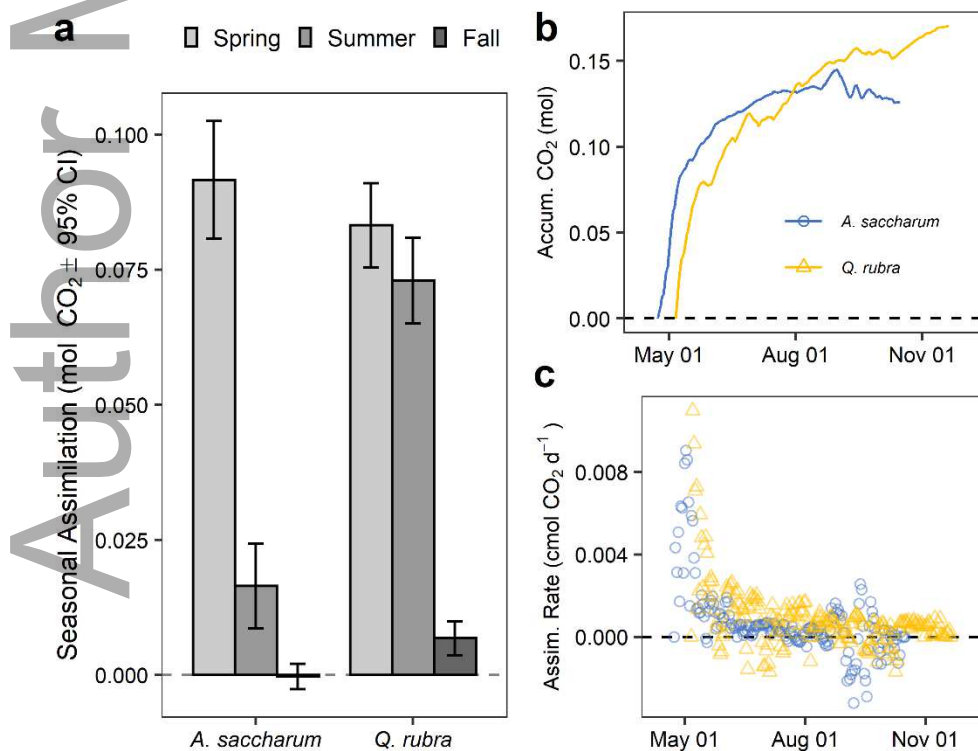
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935 **Figures**

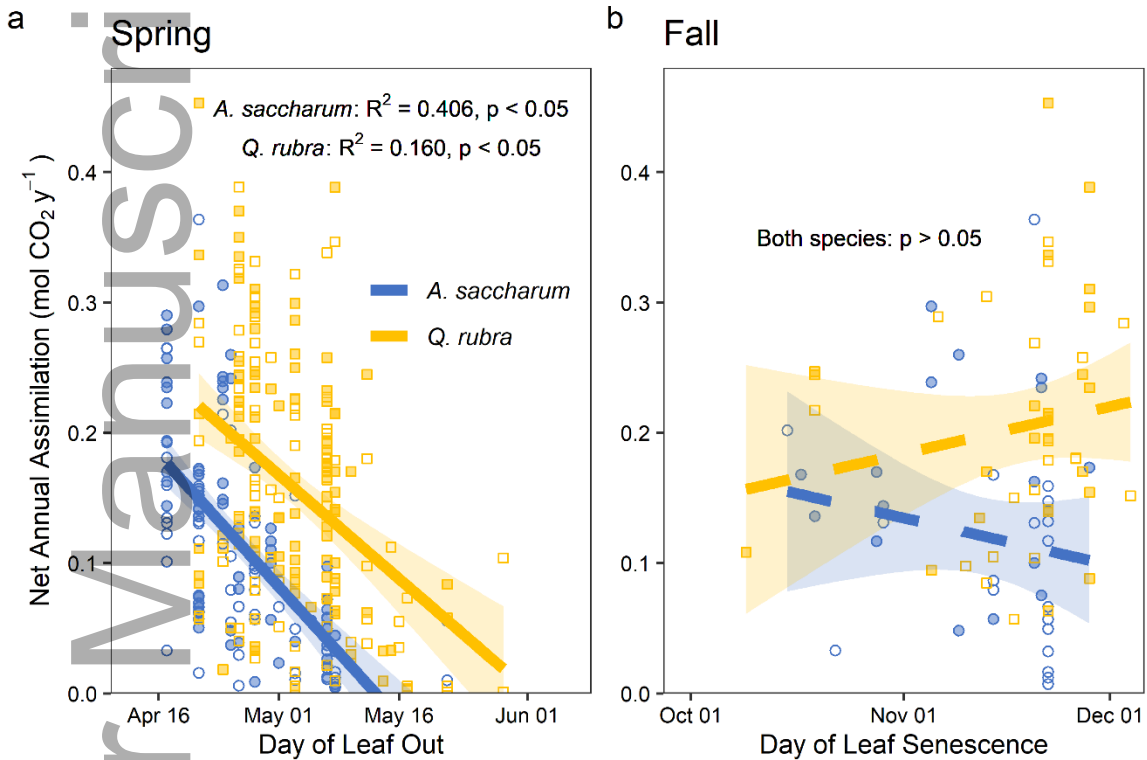
936 **Figure 1:** Average tree seedling net foliar CO₂ assimilation estimates (\pm 95% Confidence
937 Intervals) for spring, summer, and fall. Panels on the right show examples of (b) additive CO₂
938 assimilation and (c) average daily assimilation rates for representative *A. saccharum* (blue,
939 circles) and *Q. rubra* (yellow, triangles) individuals.



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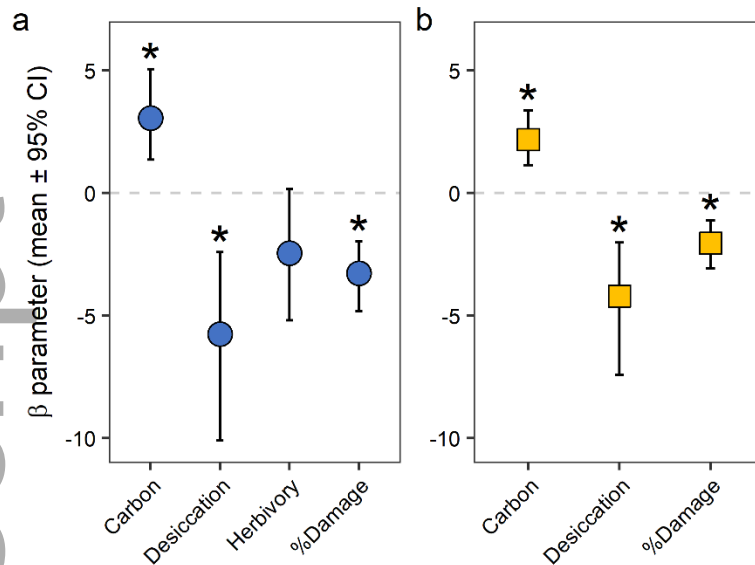
942 **Figure 2:** Relationships between estimated net annual CO₂ assimilation and a) day of leaf out or
943 b) day of leaf senescence. Blue lines and symbols represent the trends for *A. saccharum*
944 seedlings and yellow lines and symbols represent trends for northern *Q. rubra* seedlings. Symbol
945 shading indicates whether seedlings were planted under *A. saccharum* (filled) or *Q. rubra*
946 (empty) canopy trees.



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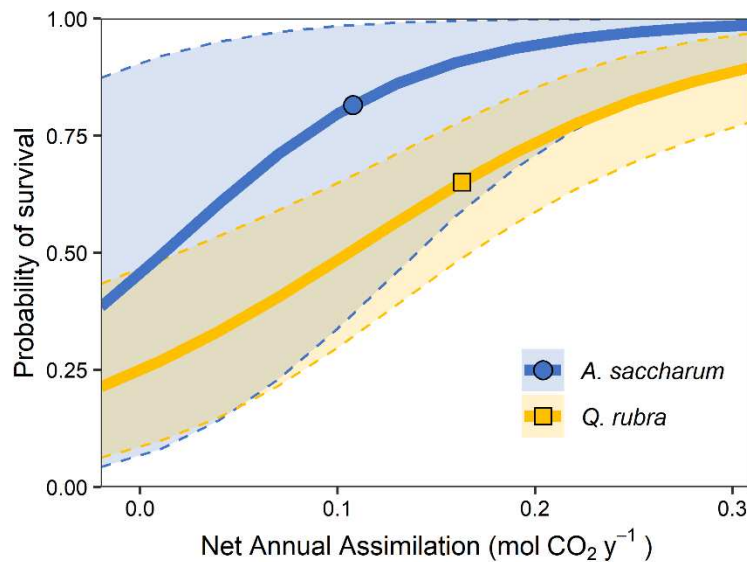
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949 **Figure 3:** Posterior estimated means and 95% credible intervals (CI) for survival model
950 parameters for (a) *A. saccharum* and (b) *Q. rubra* seedlings. Asterisks indicate parameter
951 estimates that are significantly different from zero.



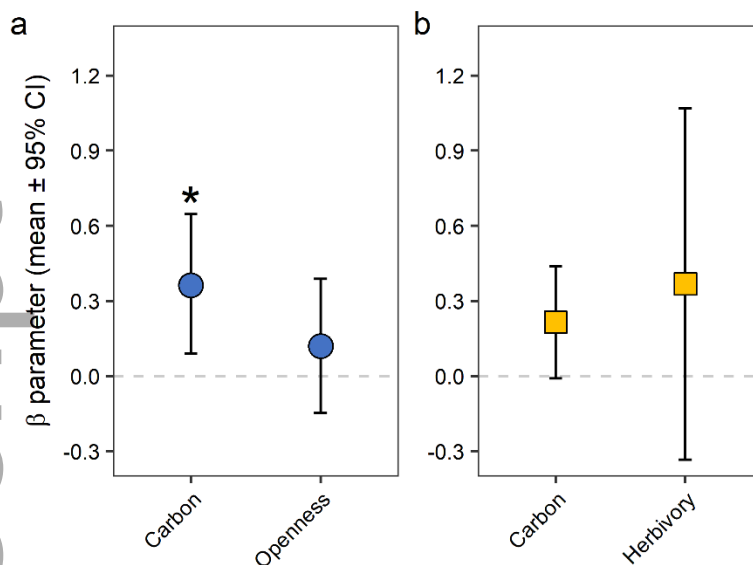
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Figure 4: Predicted probability of survival (lines; mean \pm 95% predictive intervals) as a function of estimated annual foliar CO₂ assimilation for *A. saccharum* (blue) and *Q. rubra* seedlings (yellow). Points represent the probability of survival for seedlings with the average estimated assimilation for each species.



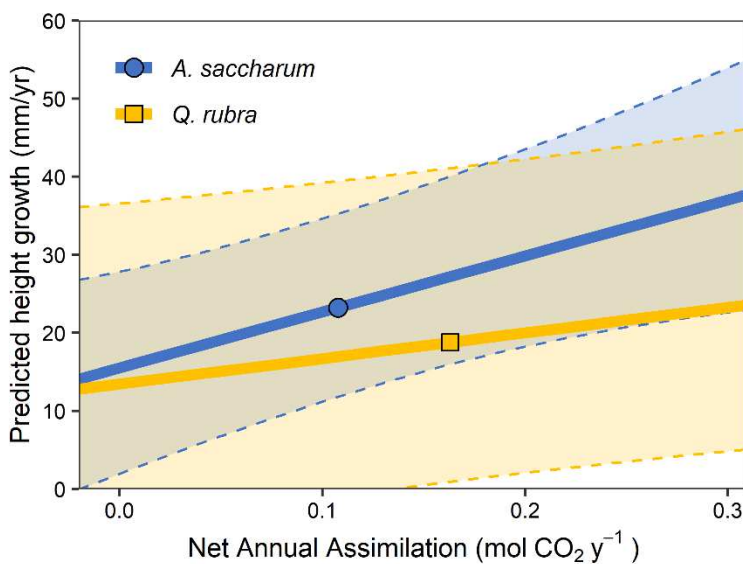
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Figure 5: Posterior estimated means and 95% credible intervals (CI) for growth model parameters for (a) *A. saccharum* and (b) *Q. rubra* seedlings. Asterisks indicate parameter estimates that are significantly different from zero.



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Figure 6: Predicted height growth (lines; mean \pm 95% predictive intervals) as a function of estimated annual foliar CO₂ assimilation for *A. saccharum* (blue) and *Q. rubra* seedlings (yellow). Points represent the predicted growth for seedlings with the average estimated assimilation for each species.



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