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Geographic variation in growth and reproduction trade-offs: Implications for future tree performance

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Abstract

Forests play a crucial role providing ecosystem services to humans, yet many aspects of forest dynamics remain unknown. One key area is how climate change might impact reproduction of tree species. While most studies have focused on predicting tree growth, understanding how reproduction may change will be vital to forecasting future forest communities. Of particular interest is the relationship between annual growth and reproductive output, which has often been hypothesized as a trade-off between allocating resources to growth or to reproduction. Two proposed pathways of this trade-off, resource accumulation, that is, storage of resources over time, and resource allocation, that is, same year allocation of resources to reproduction, have been widely explored in relation to masting events. It has also been proposed that there is no internal trade-off between the two functions, but rather there exists one or more climate variables that are intrinsically linked to both, that is, the weather hypothesis. In this study, we use 15 years of dendrochronological data and seed rain collections from forest stands at two latitudes to determine whether one or more of these strategies are taking place in two commonly occurring tree species: red maple, *Acer rubrum*; and sugar maple, *Acer saccharum*. We found evidence of a trade-off in both species. We also found a combination of strategies was the norm, and there appeared to be evidence to also support the weather hypothesis. However, in both species, the strategy which dictated the trade-off switched between the northern and southern regions, indicating a degree of plasticity that could be beneficial under changing environmental conditions. By identifying the ways in which growth and reproduction are connected and how these connections vary between different populations, we can gain insights into how trees allocate resources in response to changing conditions.

KEYWORDS
Acer rubrum, *Acer saccharum*, resource accumulation, resource allocation, seed production, tree cores, weather hypothesis

INTRODUCTION

As temperatures increase and growing seasons change, anthropogenically driven global change is impacting plant species across all ecosystems (Clark et al., 2016; Classen et al., 2010). In cold and temperate regions, seasons are expected to lengthen, as springs are beginning earlier while winter is being delayed (Way & Montgomery, 2015). This shift has increased plant productivity (Nussbaumer et al., 2016), and in some instances, it has also resulted in higher reproductive effort (Caignard et al., 2017). However, warming temperatures and associated longer growing seasons have also led to depressed seed output (Redmond et al., 2012). Thus, it is not clear whether the longer growing season and its associated higher plant growth will result in increases (synergies) or decreases (trade-offs) in reproductive output. Still, this information is critical to forecast forest dynamics under global warming.

Both tree growth and reproduction vary year to year as a function of environmental conditions (Buechling et al., 2016; Ibáñez et al., 2017; Speer & Hardy, 2001; Wang & Ibáñez, 2022), but we know little about how those variations might be related or not, that is, whether they affect each other positively or negatively, or whether they are driven by the same or different external variables. Built on masting studies, there are three main competing hypotheses for strategies underlying the growth–reproduction relationship: resource accumulation, resource allocation, and the weather hypotheses (Speer & Hardy, 2001; Żywiec & Zielonka, 2013). The first two identify a link between growth and reproduction that is causal, with growth affecting resources allocated to reproduction (Speer & Hardy, 2001). The third one links growth and reproduction via their independent responses to weather conditions (Knops et al., 2007).

According to the resource accumulation hypothesis, trees store resources over time, allocating them toward a masting event that takes place at multiyear intervals (Figure 1; Speer & Hardy, 2001). Sork et al. (1993) proposed negative correlations in crop sizes in the years prior to a masting event in white oaks, indicating resource accumulation. The concept was also modeled by Isagi et al. (1997) using a resource budget model for an individual plant to explain the usage and accumulation of photosynthate. However, links with actual growth were not made in either case; thus, we do not know whether growth was also impacted. Furthermore, evidence supporting this hypothesis has been inconsistent due to variation in species' masting cycles and the climatic conditions driving them. The warming temperatures seen in the 20th century have benefited tree growth in some areas (Bunn et al., 2005; D'Arrigo et al., 2008; McKenzie et al., 2001), and recent increases in masting events have been attributed to increased levels of carbon dioxide (Övergaard et al., 2007), but there is still little information about how these two processes are interacting (although see Clark et al., 2021). An increase in resources due to climate change could impact trees utilizing resource accumulation, leading to the storage of greater amounts of resources over the years and consequentially to larger and/or more frequent reproductive events (Journé et al., 2022).

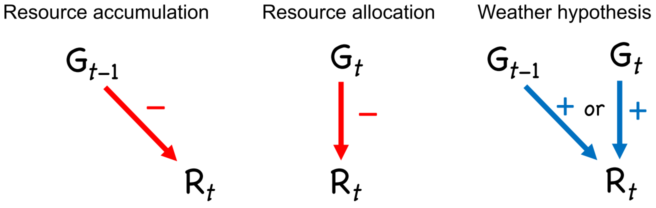

FIGURE 1 Framework for the strategies connecting growth (G) and reproduction (R). In resource accumulation, there is a trade-off between growth in previous years and reproduction (negative sign). In resource allocation, there is a trade-off between growth and reproduction in the same year. Expectations for weather are more variable, as growth and reproduction could respond to different environmental factors. However, there is an expectation that environmental conditions which provide sufficient resources for one function will do the same for the other (positive sign).

Alternatively, resource allocation predicts most of the year's resources are allocated to reproduction, leading to a significant reduction in growth that year (Figure 1; Speer & Hardy, 2001). Earliest studies in this topic supported resource allocation (Eis et al., 1965; Holmsgaard, 1958), and some more recent work has partially backed this hypothesis (Koenig & Knops, 1998; Speer & Hardy, 2001). For example, Martín et al. (2015) found a negative correlation in acorn production and annual stem growth in holm oak, but only at one of their two study sites, the one with smaller trees in denser conditions. They speculated that this trade-off is more apparent in areas with greater stress. Thus, if climate change increases the incidence of stress conditions, for example, drought events, this trade-off may become more common.

The weather hypothesis, by contrast, states that the relationship between growth and reproductive output, while present, is purely correlational and is caused by unknown environmental variables (Figure 1; Knops et al., 2007). Żywiec and Zielonka (2013) found no evidence of a trade-off between growth and reproduction in subalpine trees in either the year of a masting event or the previous year, in fact noting trees with large crops in masting years had greater growth in the year before than trees with smaller crops. Even in instances where a negative correlation may appear, it may not be a true trade-off, Nussbaumer et al. (2021) found a decrease in stem growth in years when weather conditions promoted fruit production and though a trade-off may have acted to some degree, it appears the effects of climatic conditions were intermixed. In the case of the weather hypothesis, climate change would likely modify both reproductive effort and growth (Nussbaumer et al., 2020; Way & Oren, 2010).

The link between reproduction and tree growth has been frequently assessed using dendrochronological records of tree radial growth (from tree cores or trunk diameter measurements) and long-term reproductive data sets (seed or cone production). Knops et al. (2007) initially proposed the weather hypothesis based on a 13-year dataset of acorn production and growth measured using dendrometers, concluding a negative correlation between growth and reproduction was related to inverse responses to rainfall. Koenig et al. (2020) collected tree cores and compared them with an almost 40-year-long dataset of acorn production yet did not find any significant pattern between growth and reproduction, except that both were correlated with rainfall. Similarly, Żywiec and Zielonka (2013) were unable to identify a trade-off based on a 12-year study involving two datasets from vastly different climates. However, Eis et al. (1965) found evidence of a trade-off using a 28-year cone count record on three conifer species and their tree cores, noting a reduction in growth in the year the cones were present on the trees.

Despite its relevance in predicting tree population dynamics (Miyazaki, 2013), the reproduction–growth relationship is rarely quantified, nor its strategies identified. The objectives of this study were to identify and quantify this relationship in two widely distributed species in Eastern North America, *Acer rubrum* L. and *Acer saccharum* Marsh. We focused on radial growth and reproductive effort over a 15-year period at two different latitudes. We aimed to answer the questions: What strategies best explain the apparent distribution of resources between growth and reproduction? Is there evidence of a trade-off between radial growth and reproductive effort in these species? Answering these questions, that is, understanding the allocation of resources and potential trade-offs, will assist in our understanding of future forest communities under climate change.

MATERIALS AND METHODS

Study areas

Fieldwork was conducted at six forest stands (Table 1) at two latitudes in the Michigan lower peninsula, USA (Figure 2). The three stands located at the northern latitude were on the property of the University of Michigan Biological Station. There, the average January minimum temperature is −12.9°C, the average July maximum temperature is 26.5°C, and average annual precipitation is 739.9 mm (NOAA, 2023). At the southern latitude, the three stands are near Ann Arbor, Michigan, where the average January minimum temperature is −9.6°C, the average July maximum temperature is 28.2°C, and average annual precipitation is 775.5 mm (NOAA, 2023). The two latitudes differ in the length of the growing season, with around 120 days in the northern latitude and around 150 days in the south (NOAA, 2023). At each forest stand (1 ha), all trees reaching 2 m in height have been mapped, identified, and measured for their dbh (1.35 m).

Studied species

The two studied species, *A. rubrum*, red maple, and *A. saccarhum*, sugar maple, are common trees in the eastern North American Biome (Figure 2). Both species best thrive in well-drained, moist soils, but *A. rubrum* is present in sites ranging from very dry or wet (Walters & Yawney, 1990), while *A. saccarhum* is drought intolerant, with lower growth during low precipitation years (Ibáñez et al., 2018; Payette et al., 1996). Both species flower between March and May (Godman et al., 1990; Walters & Yawney, 1990). *A. rubrum* seeds mature and are dispersed at the end of spring, while *A. saccharum* mature during the summer and are dispersed in the fall. Both species produce lightweight, wind-borne seeds, with potential crop size increasing with age. Annual seed production is more consistent in *A. rubrum*, which has a larger crop once every 2 years (Walters & Yawney, 1990). Crop size varies more in *A. saccharum*, which can have a masting event every 3–7 years (Houle, 1999).

Seed data

At each of the sites, 15 seed traps were set up in summer 2008. Each trap covers approximately 0.16 m^2 and is composed of mesh suspended 1 m off the ground by metal rebar. The traps are organized in three 20 m apart rows of five traps with 10 m between each. Traps are emptied twice a year, summer and fall; following major seed release seasons, each collection is assigned to their corresponding crop year. Viable seeds are identified and counted at the species level. To ensure accurate representation of the seed rain, only seed traps with an average of 5 seeds/year were included in the analysis. Seed data were standardized for each trap during the collection

TABLE 1 Location and characteristics of the six study sites where tree growth and reproduction data were collected.

Site name, latitude, and longitude	Soil texture and drainage	N content (ppm)	Ca content (ppm)	Dominant species	Basal area (cm^2/ha)
North					
Aspen 45.552586928751296 N 84.71387879153637 W	Coarse-textured, well-drained	1.62	13.355	*Acer saccharum* Marshall, *Acer rubrum* L., *Fagus grandifolia* Ehrh.	48.45
Northern Hardwood 45.56555620379388 N 84.69067819038465 W	Coarse-textured, well-drained	1.706	13.425	*Acer saccharum* Marshall, *Fagus grandifolia* Ehrh., *Populus grandidentata* Michx.	32.25
Balsam fir 45.54593653478121 N 84.6672131390859 W	Peat, poorly drained	2.126	210.57	*Abies balsamea* (L.) Mill., *Acer rubrum* L., *Thuja occidentalis* L., *Tsuga canadensis*	52.67
South					
ES George Reserve 42.45867944382887 N 84.02382893461801 W	Coarse-textured, well-drained	7.132	115.71	*Acer saccharum* Marshall, *Hamamelis virginiana* L., *Prunus serotina* Ehrh.	34.35
Stinchfield 42.4009145525115 N 83.9259536671926 W	Coarse-textured, well-drained	6.446	74.44	*Quercus alba* L., *Quercus velutina* L'Her. ex A.DC., *Acer saccharum* Marshall, *Acer rubrum* L.	35.30
Radrick 42.29056101310145 N 83.65857233678238 W	Fine-textured, well-drained	5.628	92.45	*Quercus rubra* L., *Quercus alba* L., *Acer nigrum* Michx. F., *Acer saccharum* Marshall	36.34

Note: Tree densities, measured as basal area per hectare, were calculated based on a census conducted at the sites in the summer of 2022. Soil nitrogen content (N) and calcium (Ca) are based on the average of two samples taking by deploying resin capsules during the growing season (summer 2019). *Acer saccharum* was present in all sites expect for Balsam fir. *Acer rubrum* was present at all sites but was not sampled at Northern Hardwood as there were no trees with a dbh of at least 15 cm.

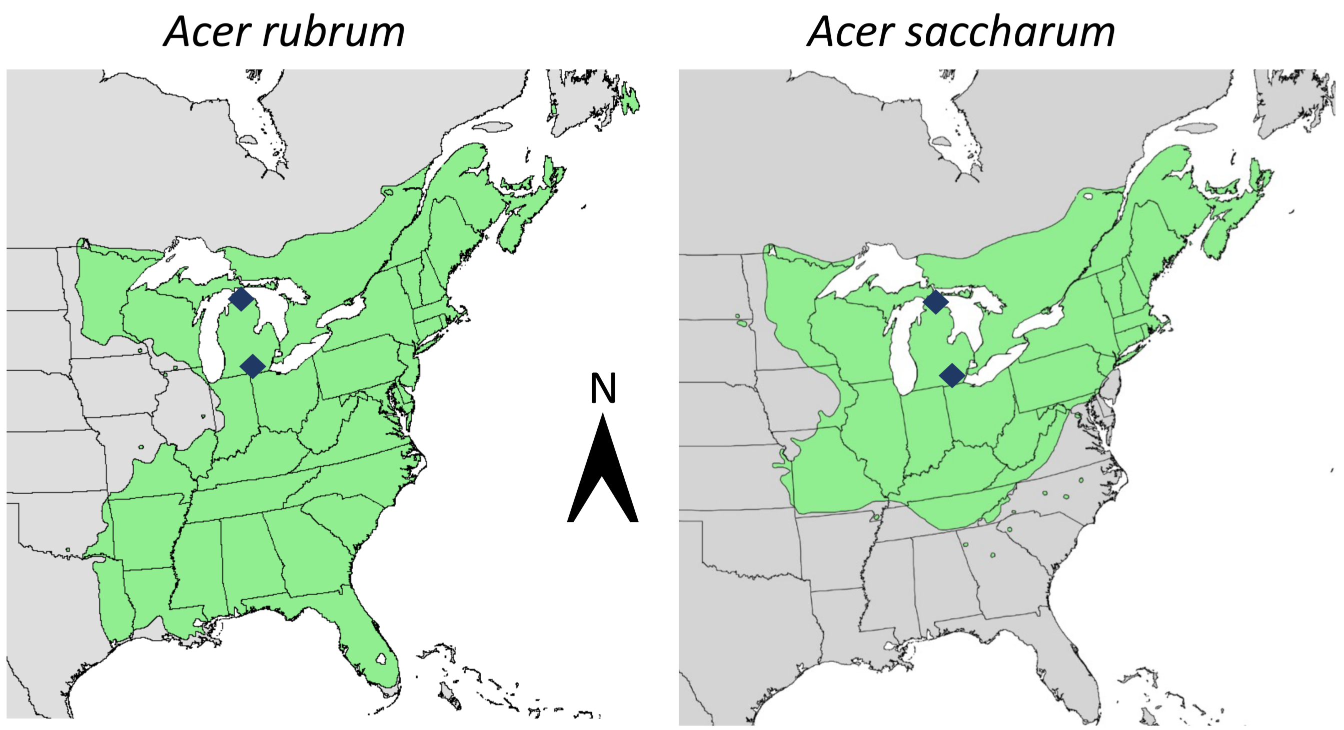

FIGURE 2 Native distribution of study species (green) and location of study sites (diamonds) in eastern North America (Little, 1971). Digital representation of "Atlas of United States Trees," United States Geological Survey.

period, 2009–2022 for *A. rubrum*, and 2008–2021 for *A. saccharum*.

Tree core collection and processing

At each site, we identified 25 trees per species. To ensure sampling reproductive individuals, cores were only collected from trees with a dbh greater than 15 cm *A. rubrum* (Walters & Yawney, 1990) and 20 cm *A. saccharum* (Godman et al., 1990). We collected two cores from each tree on the east and west sides. Cores were extracted at dbh. We used 5-mm diameter increment borers. Each core was placed in a paper straw until processing. Cores were left to air-dry and then mounted on wooden frames and sanded using a belt sander with increasingly fine sandpaper, beginning with 240 to 320 to 400 grit. Each core was then further sanded by hand using 400 grit sandpaper. After sanding, each core was scanned with a high-resolution scanner at a resolution of 3200 dpi.

Measurements of the annual growth rings were collected for each core using the program CooRecorder Version 9.4. The cores of the same species at the same site were then cross-dated using the program COFECHA Version 6.02P (Holmes, 1983). The intercorrelation values (r) given by COFECHA and sample sizes (n) were used to calculate the expressed population signal (EPS, Wigley et al., 1984).

$$\mathrm{EPS}=\frac{n\times r}{1+(n-1)\times r} \tag{1}$$

Following cross-dating, cores taken from the same individual tree were averaged to provide a single annual growth value. dbh was back calculated for each tree from 2022 to 1999 based on field measurements of dbh and the average annual growth for each year in this period. For cores that were damaged and did not have sufficient growth measurements in later years, we used previous census, 2017, dbh data to calculate historical dbh values. Based on the dbh, basal area increment (BAI) for tree i in year t was calculated and standardized for each tree (BAIS).

$$\mathrm{BAI}_{i,t}=\frac{\pi\left(\mathrm{dbh}_{i,t}^{2}-\mathrm{dbh}_{i,t-1}^{2}\right)}{4} \tag{2}$$

$$\mathrm{BAIS}_{i,t}=\frac{\mathrm{BAI}_{i,t}-\overline{\mathrm{BAI}}_{\mathrm{trees}(i)}}{\mathrm{sdBAI}_{\mathrm{trees}(i)}} \tag{3}$$

Environmental data

All environmental data for this project were obtained from the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Information (NOAA, 2023; https://www.ncei.noaa.gov/access/monitoring/climate-at-a-glance/divisional/mapping). Data for the southern sites were obtained from Michigan Climate Division 10, which encompasses the southeastern corner of the state. All data were part of a divisional time series which has collected climate data from 1895 to 2023 using a 5-km gridded approach. For this project, data from 1999 to 2022 were used, including total monthly precipitation and monthly average, minimum, and maximum temperatures for May through September in both regions.

Analysis

We analyzed standardized values of seed production (seed) and growth (BAIS) to assess the temporal dynamics taking place at each of the forest stands we worked on. We first developed a model for growth as a function of previous year's growth and year random effects to reflect growth dependencies across years documented for these species (Ibáñez et al., 2018) and growth variability due to environmental conditions across years in each region. Each species was analyzed independently. For tree i and year t, we analyzed standardized growth data using a normal likelihood:

$$\mathrm{BAIS}_{i,t}\sim\mathrm{Normal}\left(G_{i,t},\sigma^{2}\right) \tag{4}$$

And process model:

$$G_{i,t}=\alpha_{\mathrm{region}(i)}\cdot\mathrm{BAIS}_{i,t-1}+\mathrm{YearRandomEffects}_{\mathrm{region}(i),t} \tag{5}$$

Since we were analyzing standardized growth centered at zero, we did not include an intersect. In a second step, we explored whether the year random effects, estimated for each region, were correlated with any climatic variables.

We then used these growth estimates, G, averaged for each stand, in a seed production model that included growth of the current and previous year as predictors, but also seed production the previous year to account for the autoregressive dynamics in seed production and the effects of masting on seed production in consequent years already documented for these species (Ibáñez et al., 2017). We also tried variations that included year random effects and longer lag effects, that is, growth 2 years before current, but did not improve the fit of the model. Reproduction data, as standardized number of seeds in trap i for year t, was also modeled using a normal distribution:

$$\text{reproduction}_{i,t} \sim \text{Normal}\left(R_{i,t}, \sigma^2\right) \quad (6)$$

And process model:

$$R_{i,t} = \beta_{\text{region}(i)} \cdot \text{reproduction}_{i,t-1} + \gamma 1_{\text{region}(i)} \cdot G_{t-1} + \gamma 2_{\text{region}(i)} \cdot G_t \quad (7)$$

All parameters were estimated using a Bayesian approach from non-informative prior distributions, $\alpha, \beta, \gamma \sim \text{Normal}(0, 10)$, $\text{YRE}_{*,*} \sim \text{Normal}\left(0, \sigma^2_{\text{RE}}\right)$, and $1/\sigma^2_* \sim \text{Gamma}(1, 1)$. Analyses were run in JAGS 3.4 (Plummer, 2003) using the rjags package (Plummer, 2021) in R (R Development Core Team, 2018). Three chains with different initial values were run. Parameter values, posterior mean, 95% credible intervals, and SDs were estimated from 50,000 iterations after convergence. To visualize results, we used these parameter estimates, mean, variances, and covariances, to simulate current year growth and reproduction as a function of growth in the previous year.

RESULTS

Our analysis includes 208 trees, 81 in the north and 127 in the south. Of the 81 northern trees, 35 were *A. rubrum* and 46 *A. saccharum*. In the south, 61 trees were *A. rubrum* and 66 *A. saccharum*. Expressed population signal estimates are reported in Appendix S1: Table S1. Seed data included 66 traps between the 6 sites, with 27 for *A. rubrum* and 39 for *A. saccharum*. All parameter values are reported in Appendix S2: Table S1. Goodness of fit of each of the analyses (R^2) were 0.39 and 0.33 in *A. rubrum* for growth and reproduction, respectively, and 0.26 and 0.38 for *A. saccharum* (Appendix S3: Figure S1).

Results of the autoregressive terms, that is, the dependency between growth performance in consecutive years (parameters α) and in seed production from one year to the next (parameters β), show a positive relationship for growth across species and latitudes (Figure 3) and a negative relationship between seed years (although this relationship was not always statistically significant; Figure 3).

For *A. rubrum*, in both regions, there is a negative relationship between growth and reproduction the following year (parameter γ1 Figure 3). The association between growth and reproduction in the same year (parameter γ2) was positive in the south and negative in the north (Figure 3). For *A. saccharum*, there is a positive association between growth in the previous year and reproduction in the south, but this association was negative in the north (Figure 3; γ1). With respect to the association of same year growth and reproduction, the pattern was the opposite, negative in the south and positive in the north (Figure 3; γ2). Integrated results for each species show a different combination of strategies at each region (Figure 4), and simulations using the covariance structure among the model parameters reflect contrasting allocation of resources between species and sites (Figure 5).

Post-analysis exploration of the year random effects in the growth analysis (Appendix S4: Table S1) showed

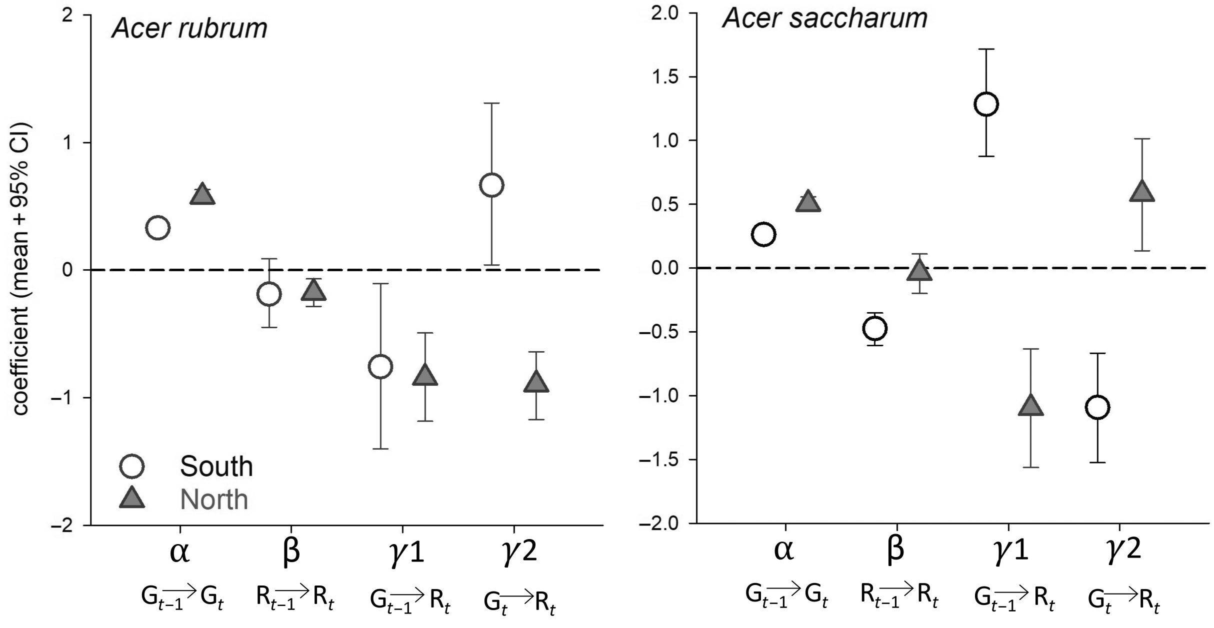

FIGURE 3 Parameter values, means, and 95% CI from the integrated analysis of growth and reproduction data of the two studied species, *A. rubrum* (left) and *A. saccharum* (right), at two latitudes (south and north). G, growth; R, reproduction; *t*, year.

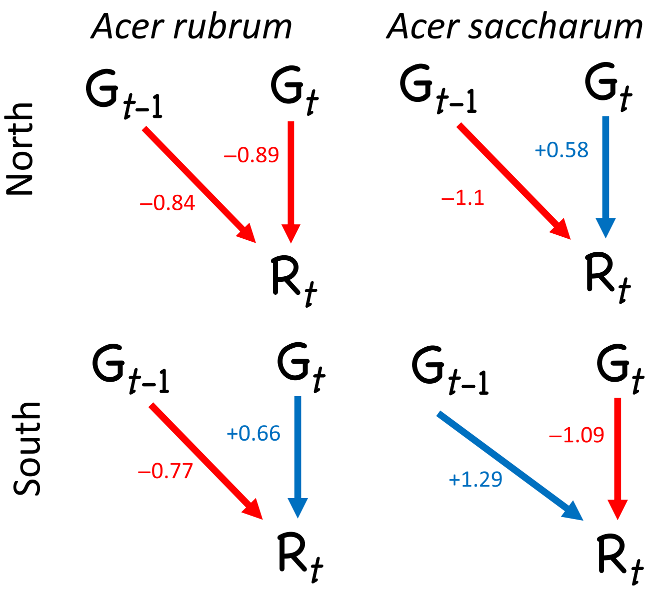

FIGURE 4 Integrated representation of results showing the nature of the relationship (red negative, blue positive; parameters γ1 and γ2) between growth (G) and reproduction (R) across years (*t*) for each species (right and left panels) and regions (top and down panels). Values represent the parameter means. All parameters were statistically significant (95% CI did not include zero). For each species and region, parameters estimated were not statistically different in magnitude (95% CI of absolute values overlapped).

substantial correlations with environmental conditions during the growing season (Appendix S4: Table S2). In the southern locations, *A. rubrum* had a high correlation (Pearson's *r*) with summer temperature (0.56), while *A. saccharum* showed a negative correlation with previous summer temperature (−0.33) and a positive association with spring temperature in the same year (0.59). At the northern locations, *A. rubrum* growth was positively correlated with summer precipitation (0.4) in the same year, and negatively correlated with end of the summer temperature of the previous year (−0.54). In this region, *A. saccharum* growth was positively correlated with spring and late summer temperature (0.22 and 0.31) of the same year and negatively correlated with previous year summer temperature (−0.46).

DISCUSSION

The distribution of resources to reproduction and radial growth in trees, whether a trade-off (resource accumulation or resource allocation) or solely dependent on external conditions (weather), could have ramifications for how tree populations cope with climate change. Reproduction is costly for individuals, potentially inhibiting other functions necessary for defense, resource acquisition, and growth (Miyazaki, 2013). While a trade-off between growth and reproduction has long been hypothesized in woody plants, there has been a lack of consensus on the precise strategy dictating such a relationship. We attempted to answer this question through the analysis of dendrochronological and seed data collected from *A. rubrum* and *A. saccharum* at two latitudes. Outcomes from our work identified and quantified the internal trade-offs and potential associations via climate that determined allocation of resources to growth and reproduction. Our results indicate the existence of a trade-off controlled by a combination of strategies that switched between latitudes (Figure 4). Understanding how these resources are distributed (Figure 5) could increase the biological accuracy of vegetation models aimed at predicting future dynamics under climate change (Fisher et al., 2018).

Plant performance in a particular year is rarely independent of performance in previous years (Montoro Girona et al., 2017). A few analyses have quantified the autoregressive nature on growth in tree species, with responses varying based largely on climate. In stressful environments, associations tend to be negative (Peltier et al., 2018, 2022), while under optimal growing conditions, like those in our study area, the association can be positive (McCollum & Ibáñez, 2020; Wang & Ibáñez, 2022). With respect to reproduction, the relationship between performance in consecutive years has often been reported to be negative, likely the result of resource exhaustion following a significant production year (Ibáñez et al., 2017; Nussbaumer et al., 2021). Without acknowledging the effects of these associations, it would have been difficult to quantify the potential trade-off between growth and reproduction. In our analysis, we included these relationships, that is, the influence of previous year's growth or reproduction, to better assess the growth-reproduction trade-off. Our analyses confirmed these relationships (Figure 3), with a positive correlation between growth across years in both species, likely reflecting optimal growing conditions in these locations, and a negative association between years of seed production, showing depletion of resources after high seed production years.

After accounting for these inter-year associations, we were able to explore the relationships between growth and reproduction to determine whether there is any evidence of a trade-off. In *A. rubrum*, we found a negative association between growth and seed production in both the northern and southern regions (Figure 4). However, there did not appear to be a sole reliance on either of the three strategies on which we built the framework of our analysis (Figure 1). Instead, all three, resource accumulation, resource allocation and weather, appeared to take place, although the combination of strategies varied between regions (Figure 4). At the northern sites, there

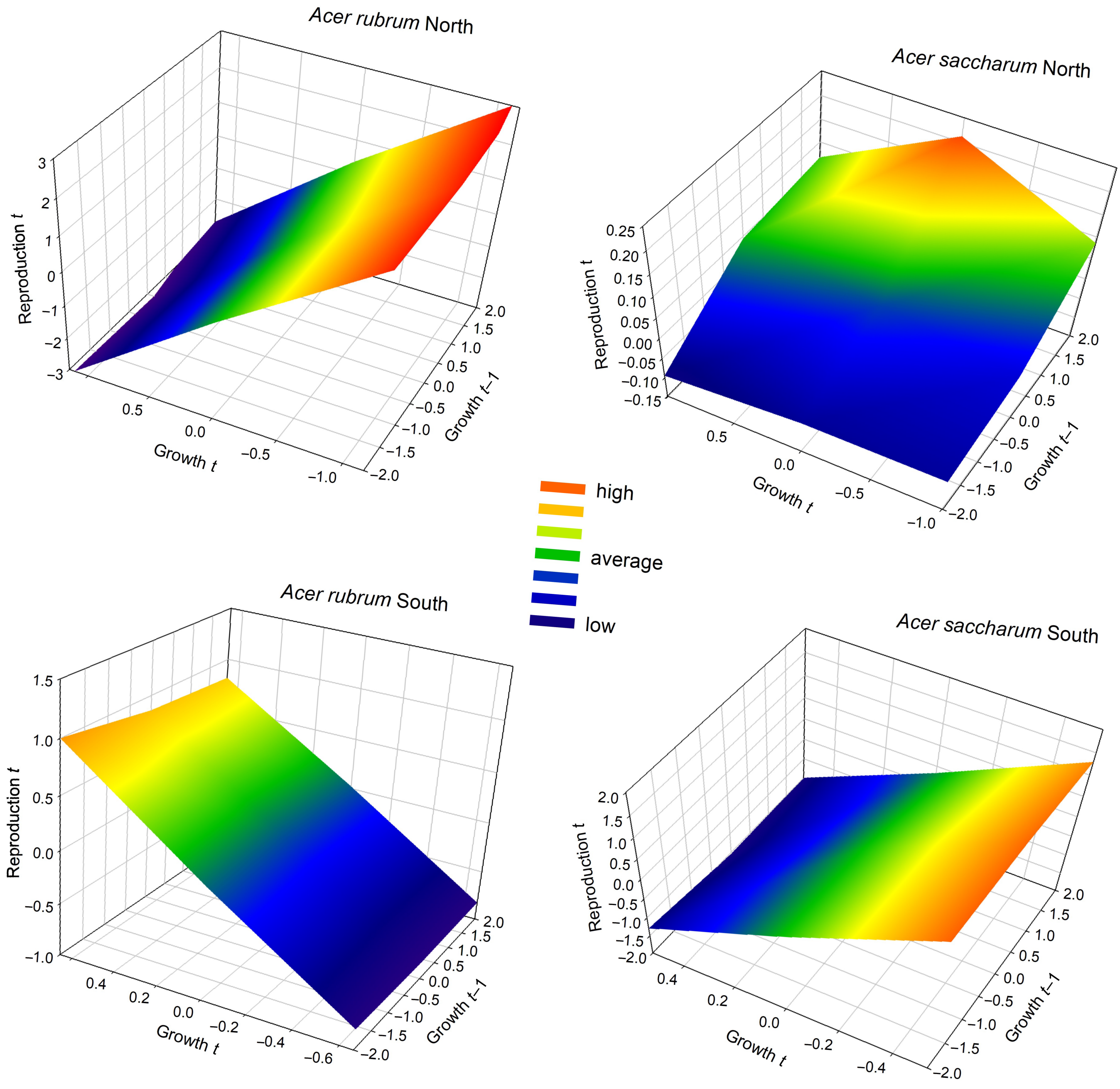

FIGURE 5 Simulated growth and reproduction at time *t* as a function of growth at time $t - 1$ using the covariance structure of the parameters estimated in the analysis. Growth at time $t - 1$ was a gradient between −2 and 2, representing average growth for that species and region and a 2 SD range. All values are standardized; zero represents average performance.

was a trade-off between seed production and both growth the current year and one year prior, while at the southern location the trade-off only took place with growth in the previous year. This likely indicates that while in the north both strategies are taking place with similar strength, in the south resource accumulation prevailed. In the southern sites, where the growing season is longer, resource accumulation may be sufficient, potentially indicating this strategy is best suited to areas with better growing conditions, allowing greater buildup of resources for reproduction over time while still being able to allocate enough to growth the year of a larger seed crop (Isagi et al., 1997). In the northern sites, the switch to reproduction having to rely on both resource accumulation and resource allocation may be in response to the shorter growing season. A greater trade-off between reproduction and growth within a single year in sites with higher stress has been previously noted in oak species (Martín et al., 2015), lending support to the idea that resource allocation is more likely to be found in areas with scarcer resources. The ability for *A. rubrum* to display either resource accumulation or allocation may be a plastic response that could be advantageous under shifting climatic conditions.

In both regions, similar to that seen for *A. rubrum*, *A. saccharum* appears to display a combination of mechanisms dictating the relationship between growth and reproduction (Figure 3). For this species, the strongest association took place between reproduction and growth the year prior (Figure 4). However, this association was positive in the south and negative in the north. The pattern in the south, with drier summers, may be an indication that weather is a major determinant of growth and reproduction while there is still a trade-off between same year growth and reproduction. Conversely, in the north, weather appears to have a lesser effect, more optimal growing seasons. Instead, a trade-off with the previous year's growth might be driving reproduction. The role of one or more climate variables in impacting both growth and reproduction is likely related to the masting cycle of *A. saccharum*, which seems to be contingent on specific environmental cues (Bogdziewicz, 2022).

Both *A. rubrum* and *A. saccharum* appear to have flexible strategies linking growth and reproduction in our study region, indicating the potential for plastic responses to variable growing conditions. Based on the differences in growing season length between regions, both species may have the ability to cope with climate change by switching to a more optimal allocation of resources between growth and reproduction. Along with trade-offs, both species also displayed a positive relationship between growth and reproduction in at least one region, potentially indicating the influence of climatic conditions which benefit both functions. There are clear impacts of climate on both growth and reproduction, including increased growth over the 20th century in accordance with rising temperatures (D'Arrigo et al., 2008). However, changes in climate alone have not been attributed to fluctuations in growth and reproduction, given both tend to vary annually to a greater extent than climate variables (Kelly, 1994). As such, there are likely other factors driving both functions aside from changes in the environment, which may be supported by previous studies which have noted a negative relationship without identifying a trade-off (Nussbaumer et al., 2021). This is supported by our analysis, in which a potential response to weather is combined with either resource allocation or accumulation.

Improved understanding of the internal mechanisms dictating resource distribution in trees can improve the accuracy of vegetative models (Bogdziewicz et al., 2020). The future of a forest community is dictated by reproduction, which in turn is driven by, among other things, the availability of resources (Nussbaumer et al., 2021). Having a greater understanding of the strategies a species displays to allocate those resources offers the opportunity to better predict the reproductive potential of a population (Figure 5). This can be further enhanced with species-specific knowledge on which pathways are taken under different climatic conditions, allowing for predictions of reproduction based on climate change models (Sykes, 2009). More precise accounting of reproductive effort can also be used to understand a population's ability to shift their range in response to climate change.

AUTHOR CONTRIBUTIONS

Chantalle Vincent and Inés Ibáñez worked together developing the idea, carrying out the analysis, and writing the manuscript. Chantalle Vincent collected the tree data and Inés Ibáñez oversaw the seed data collection.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Tree data (Vincent & Ibanez, 2023) are available from the Environmental Data Initiative (EDI) Data Portal: https://doi.org/10.6073/pasta/22ed2505d207b53055b762346dd2a2a3. Climate data are available from NOAA National Centers for Environmental Information: https://www.ncei.noaa.gov/access/monitoring/climate-at-a-glance/divisional/time-series. R scripts (Ibanez, 2023) are available from the Center for Open Science: https://doi.org/10.17605/OSF.IO/UWJV2.

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SUPPORTING INFORMATION

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

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