Tradeoffs between Growth and Reproduction in *Acer rubrum* and *A. saccharum*

by

Chantalle Vincent

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
(Environment and Sustainability)
at the University of Michigan
2021

Thesis Committee:

Dr. Ines Ibanez, Chair
Dr. Stella Cousins, Reader

Table of Contents

Abstract

Though forests are vital ecosystems to humans many aspects of forest dynamics remain unknown, including how reproduction of tree species may shift under climate change. Most studies have focused on predicting tree growth, i.e., plant productivity, under novel environmental conditions, but understanding how reproduction may also be affected will be especially 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 tradeoff between allocating resources to growth or to reproduction. Two proposed pathways of this tradeoff, resource accumulation, i.e., storage of resources over time, and resource allocation, i.e., 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 tradeoff between the two functions, but rather there exists one or more climate variables that are intrinsically linked to both, referred to as the "weather hypothesis." In this study, we use dendrochronological data and seed rain collections from forest stands at two latitudes to determine if 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 tradeoff 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 tradeoff switched between the northern and southern regions. Identifying the combination of pathways that link growth and reproduction and how these change between populations can assist in understanding and forecasting plant allocation of resources as growing conditions vary.

Introduction

As temperatures increase and growing seasons change (Way and Montgomery 2015), anthropogenically driven global change is impacting plant species across all ecosystems (Caignard et al, 2017). In cold and temperate regions seasons are expected to lengthen, as springs are beginning earlier while winter is arriving later (Way and Montgomery 2015). This shift has increased plant productivity (Nussbaumer 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 if the longer growing season and its associated higher plant growth will result in increases (synergies) or decreases (tradeoffs) in reproductive output. Still, this information is critical to forecast forest dynamics under global warming. In this study, we address this knowledge gap by investigating the relationship between annual growth and reproductive effort of two tree species.

Both tree growth and reproduction vary year to year as a function of environmental conditions (Speer 2001; Buechling et al, 2016, Ibanez et al. 2017, Wang and Ibanez 2022), but we know little about how those variations might be related or not, i.e., if they affect each other positively or negatively, or if they are driven by the same or different external variables. There are three main competing hypotheses for strategies underlying the growth-reproduction relationship built on previous masting studies: resource accumulation, resource allocation, and weather hypotheses (Speer 2001, Zyweic and Zielonka 2013). The first two identify a link between growth and reproduction that is causal, with growth affecting resources allocated to reproduction (Speer 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, effectively putting them towards a masting event that takes place at multiyear intervals (Fig. 1; Speer 2001). Evidence supporting this hypothesis has been inconsistent due to variation in species' masting cycles and the climatic conditions impacting them. 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 if growth was also impacted. Still, understanding this association is relevant because resource accumulation will likely be impacted by increasing atmospheric carbon dioxide and climatic shifts determining growing season length as well as water availability. The warming temperatures seen in the 20th century have benefited tree growth in some areas (D'Arrigo et al, 2008, McKenzie et al, 2001, Bunn et al, 2005), and recent increases in masting events have been attributed to increased levels of carbon dioxide (Overgaard et al 2007), but we do not know yet to what extent these two processes are interacting. 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 leading up to large reproductive

events and increasing crop size or reducing the number of years in which accumulation occurs.

Alternatively, resource allocation predicts all resources are taken from growth in the year of masting, leading to a significant reduction in growth that year (Fig. 1; Speer 2001). The earliest studies in this topic supported resource allocation (Holmsgaard 1958; Eis et al, 1965), and some more recent work has partially supported this hypothesis too (Speer 2001, Koenig and Knops, 1998). For example, Martin 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, e.g., 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 (Fig. 1; Knops et al, 2007). Zyweic 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 tradeoff. Nussbaumer et al (2021) noted 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. Given these previous findings, it is likely that climatic conditions which would benefit one function would benefit the other, and vice versa (Fig. 1). In the case of the weather hypothesis, climate change would likely modify both reproductive effort and growth (Way and Oren 2010, Nussbaumer et al, 2020).

The distribution of resources 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. Regardless of the internal pathway by which resources are distributed, reproduction is costly for individuals, potentially inhibiting other functions necessary for defense, resource acquisition, and growth (Miyazaki 2013). Understanding how these resources are distributed would increase our understanding of how reproduction and growth are integrated into the life strategies of a species. This in turn could inform forest performance in vegetation models aimed at predicting future dynamics under climate change (Fisher et al. 2018), potentially increasing the biological accuracy of mechanistic steps in particular.

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 data set 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 to an almost 40 yearlong data set of

acorn production, yet did not find any significant pattern between growth and reproduction, except that both were correlated with rainfall. Similarly, Zyweic and Zielonka (2013) were unable to identify a tradeoff 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 *A. saccharum* Marsh.. We focused on radial growth and reproductive effort over a 15-year period at two different latitudes. The questions we aimed to answer are: 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, i.e., understanding the allocation of resources and potential tradeoffs, will assist in our understanding of future forest communities under climate change.

Materials and Methods

Study Areas

Field work was conducted at six forest stands (Table 1) at two latitudes in the Michigan lower peninsula, USA (Fig. 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 ℃, the average July maximum temperature is 26.5 ℃, and average annual precipitation is 739.9 mm (NOAA 2023). At the southern latitude, the three stands are in the area of Ann Arbor, Michigan, where the average January minimum temperature is -9.6 ℃, the average July maximum temperature is 28.2 ℃, 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 (Plantico et al, 2005). At each forest stand (one ha) all trees reaching 2 m in height have been mapped, identified and diameter measured at breast height (dbh, 1.35 m).

Studied Species

The two studied species, *Acer rubrum,* red maple*,* and *A. saccarhum*, sugar maple, are common trees in the eastern North American Biome (Fig. 2). Both species best thrive in well-drained, moist soils, but *A. rubrum* is present in sites from very dry or wet (Walters and Yawney 1990), while *A. saccarhum* is drought intolerant, with lower growth during low precipitation years (Payette et al, 1996). Both species flower between March and May (Walters and Yawney, 1990, Godman et al, 1990). *Acer 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 approximately once every two years (Walters and Yawney 1990). Crop size varies more in *A. saccharum*, which can have a masting event every three to seven years (Houle 2001).

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 meter 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. Seeds are identified and counted at the species level. 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 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. Cores were only collected from trees with a dbh greater than 15 cm to ensure sampling reproductive individuals. 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,1983).

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

Following cross-dating, the 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).

$$BAI_{i,t} = \frac{\pi(dbh_{i,t}^2 - dbh_{i,t-1}^2)}{4}$$

$$BAIS_{i,t} = \frac{BAI_{i,t} - \overline{BAI}_{trees(i)}}{sdBAI_{trees(i)}}$$

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). All data was part of a divisional time series which collected climate data from 1895 to 2023 using a 5 km gridded approach. For this project, data from 1999 to 2022 was used, including total monthly precipitation and monthly average, minimum, and maximum temperatures for May through September in both regions. Data for the southern sites was obtained from Michigan Climate Division 10, which encompasses the southeastern corner of the state. For the north, data was taken from Michigan Climate Division 4, which covers the northeastern portion of the lower peninsula.

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:

$$BAIS_{i,t} \sim Normal(G_{i,t}, \sigma^2)$$

And process model:

$$G_{i,t} = \alpha_{region(i)} \cdot BAIS_{i,t-1} + YearRandomEffects_{region(i),t}$$

Since we were analyzing standardized growth centered at zero, we did not include an intersect. In a second step we explored if 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 this species (Ibáñez et al. 2017). We also tried variations that included longer lag effects, i.e., growth two 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:

$$reproduction_{i,t} \sim Normal(R_{i,t}, \sigma^2)$$

And process model:

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

All parameters were estimated using a Bayesian approach from non-informative prior distributions, $\alpha, \beta, \gamma \sim Normal(0,10)$, $YRE_{*,*} \sim Normal(0, \sigma_{RE}^2)$, and $\frac{1}{\sigma_*^2} \sim Gamma(1,1)$. Analyses were run in JAGS 3.4 (Plummer 2003) using the rjags package (Plummer et al. 2018) in R (R Development Core Team 2013), model code can be found in Appendix I. Parameter values, posterior mean, 95% credible intervals, and standard deviations were estimated from 50,000 iterations after convergence. We used these parameters estimates, mean, variances and covariance, 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 are *A. rubrum* and 46 are *A. saccharum.* In the south, 61 trees are *A. rubrum* and 66 are *A. saccharum.* Expressed population signal estimates are reported in Appendix II. 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 III. 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 IV).

Results of the autoregressive terms, i.e., 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 (Fig. 3), and negative relationship between seed years (although this relationship was not always statistically significant Fig. 3).

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

Post-analysis exploration of the year random effects in the growth submodel (Appendix V) showed substantial correlations with environmental conditions during the growing season. 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

While a tradeoff 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 tradeoffs and potential associations via climate that determined allocation of resources to growth and reproduction. Our results indicate the existence of a tradeoff controlled by a combination of strategies that switched between latitudes (Fig. 4). This information can now be directly incorporated in vegetation models forecasting future forest communities in this region (Fig. 5).

Plant performance in a particular year is rarely independent of performance in previous years (Girona et al, 2017). A few analyses have quantified the autoregressive nature of growth in tree species, with responses varying based largely on climate. In stressful environments associations tend to be negative (Anderegg et al, 2015), while under optimal growing conditions the association can be positive (Wang and Ibanez 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 (Nussbaumer et al, 2021; Ibanez et al. 2017). In our analysis we included these relationships, i.e., the influence of previous year's growth or reproduction, to better assess the growth-reproduction tradeoff. Our analyses confirmed these relationships (Fig. 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. Without acknowledging the effects of these relationships, it would have been difficult to quantify the potential tradeoff between growth and reproduction.

After accounting for these autoregressive associations, we were able to explore the relationships between growth and reproduction in order to determine if there is any evidence of a tradeoff. In *A. rubrum* we found a negative association between growth and seed production in both the northern and southern regions (Fig. 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. Instead, all three, resource accumulation, resource allocation and weather, appeared to take place. Althouh the combination of strategies varied between regions (Fig. 4). At the northern sites, there 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 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. This may indicate this strategy is best suited to areas with better growing conditions, allowing greater build-up of resources for reproduction over time while still being able to allocate a sufficient amount 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 and fewer resources. A greater trade-off between reproduction and growth within a single year in sites with higher stress has been previously noted in oak species (Martin 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 what was seen for *A. rubrum, A. saccharum* appears to display a combination of mechanisms dictating the relationship between growth and reproduction (Fig. 3). For this species the strongest association took place between reproduction and growth the year prior (Fig. 4). However, this association was positive in the south and negative in the north. The pattern in the south may be an indication that weather is a major determinant of growth and reproduction while there is still a tradeoff between same year growth and reproduction. Conversely, in the north, weather appears to have a lesser effect. Instead, a tradeoff with previous year's growth might be driving reproduction. The role of one or more climate variables in impacting both growth and reproduction may be related to the masting cycle of *A. saccharum,* with reproduction in particular more contingent on specific environmental cues (Bogdziewicz 2022).

Both *A. rubrum* and *A. saccharum* appear to have flexible tradeoffs between growth and reproduction in our study region, indicating the potential for plastic responses to variable environments. 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 tradeoffs, 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 designating a tradeoff (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, 2019). 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 more accurately predict the reproductive potential of a population (Fig. 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. 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 (Sykes 2009).

References

Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., Ogle, K., Shaw, J.D., Shevliakova, E., Williams, A.P., Wolf, A., Ziaco, E., and Pacala, S. 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science 349, 6247: 528-532. DOI: 10.1126/science.aab1833

Bogdziewicz, M. 2022. How will global change affect plant reproduction? A framework for mast seeding trends. New Phytologist 234: 14-20. DOI: 10.1111/nph.17682

Bogdziewicz, M., Ascoli, D., Hacket-Pain, A., Koenig, W.D., Pearse, I., Pesendorfer, M., Satake, A., Thomas, P., Vacchiano, G., Wohlgemuth, T., and Tanentzap, A. 2019. From theory to experiments for testing the proximate mechanisms of mast seeding: an agenda for an experimental ecology. Ecology Letters 23, 2: 210-220. https://doi.org/10.1111/ele.13442

Buechling, A., Martin, P.H., Canham, C.D., Shepperd, W.D. and Battaglia, M.A. 2016. Climate drivers of seed production in *Picea engelmannii* and response to warming temperatures in the southern Rocky Mountains. Journal of Ecology 104: 1051-1062.

Bunn, A.G., Graumlich, L.J., and Urban, D.L. 2005. Trends in twentieth-century tree growth at high elevations in the Sierra Nevada and White Mountains, USA. The Holocene 15, 4: 481-488. https://doi.org/10.1191/0959683605hl827rp

Caignard, T., Kremer, A., Firmat, C., Nicolas, M., Venner, S., and Delzon, S. 2017. Increasing spring temperatures favor oak seed production in temperate areas. Nature Scientific Reports 7, 8555. DOI:10.1038/s41598-017-09172-7

D'Arrigo, R., Wilson, R., Liepert, B., and Cherubini, P. 2008. On the 'divergence problem' in northern forests: A review of the tree-ring evidence and possible causes. Global and Planetary Change 60: 289-305.

Eis, S., Garman, E.H. &Ebell, L.F. 1965. Relation between cone production and diameter increment of douglas fir (*Pseudotsuga menziesii (mirb.) franco*), grand fir (*Abies grandis (dougl.) lindl.*), and western white pine (*Pinus monitcola dougl.*). Canadian Journal of Botany 43: 1553-1559.

Fisher, R. A., Koven, C. D., Anderegg, W. R. L., Christoffersen, B. O., Dietze, M. C., Farrior, C. E., Holm, J. A., Hurtt, G. C., Knox, R. G., Lawrence, P. J., Lichstein, J. W., Longo, M., Matheny, A. M., Medvigy, D., Muller-Landau, H. C., Powell, T. L., Serbin, S. P., Sato, H., Shuman, J. K., … Moorcroft, P. R. 2018. Vegetation demographics in Earth System Models: A review of progress and priorities. Global Change Biology 24, 1: 35–54. https://doi.org/https://doi.org/10.1111/gcb.13910

Girona, M.M., Rossi, S., Lussier, J., Walsh, D., And Morin, H. 2017. Understanding tree growth responses after partial cuttings: a new approach. PLos ONE 12, 2: e0172653. doi:10.1371/journal.pone.0172653

GLISA. "Regional maps produced by the Great Lakes Integrated Sciences and Assessments (**glisa.umich.edu**) using data from the University of Wisconsin Nelson Institute Center for Climatic Research."

Godman, R.M., Yawney, H.W., and Tubbs, C.H. 1990. *Acer saccharum* Marsh. Sugar Maple. From Burns, Russell M., and Barbara H. Honkala. "Silvics of North American trees. Vol 2, hardwoods." *US Department of Agriculture, Washington, DC.*

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43: 69-78.

Holmsgaard, E. (1958) The effect of seed-bearing on the increment of the European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst). *Proceedings of the 12th International Union of Forestry Research Organizations Conference,* Oxford, UK, 158-161

Houle, G. 1999. Mast seeding in *Abies balsamea, Acer saccharum,* and *Betula alleghaniensis* in an old growth, cold temperate forest of north-eastern North America. Journal of Ecology 87: 413-422.

Ibáñez, I., Katz, D.W. and Lee, B.R. 2017. The contrasting effects of short-term climate change on the early recruitment of tree species. Oecologia 184: 701-713. DOI: 10.1007/s00442-017-3889-1

Isagi, Y., Sugimura, K., Sumida, A., and Ito, H. 1997. How does masting happen and synchronize? Journal of Theoretical Biology 187: 231-239.

Kelly, D. 1994. The evolutionary ecology of mast seeding. Tree 9, 12: 465-470.

Knops, J.M.H, Koenig, W.D. & Carmen,W.J. 2007. Negative correlation does not imply a tradeoff between growth and reproduction in California oaks. PNAS 104: 16982-16985.

Koenig, W.D., Knops, J.M.H., and Carmen, W.J. 2020. Can mast history be inferred from radial growth? A test using five species of California oaks. Forest Ecology and Management 472: 118233.

Koenig, W.D. & Knops, J.M.H. 1998. Scale of mast seeding and tree-ring growth. Nature 396: 225-226.

Little, E.L. 1999. Digital representation of 'Atlas of United States Trees.' United States Geological Survey.

Martin, D., Vazquez-Pique, J., Carevic, F.S., Fernandez, M., and Alejano, R. 2015. Trade-off between stem growth and acorn production in holm oak. Trees 29: 825-834. DOI: 10.1007/s00468-015-1162-y

McKenzie, D., Hessl, A.E., and Peterson, D.L. 2001. Recent growth of conifer species of western North America: assessing spatial patterns of radial growth trends. Canadian Journal of Forest Research 31, 3. https://doi.org/10.1139/x00-191

Miyazaki, Y. 2013. Dynamics of internal carbon resources during masting behavior in trees. Ecological Research 28: 143-150. DOI: 10.1007/s11284-011-0892-6

NOAA National Centers for Environmental information, Climate at a Glance: Divisional Mapping, published March 2023, retrieved on February 3, 2023 from https://www.ncei.noaa.gov/access/monitoring/climate-at-a-glance/divisional/mapping

Nussbaumer, A., Gessler, A., Benham, S., de Cinti, B., Etzold, S., Ingersley, M., Jacob, F., Lebourgeois, F., Levanic, T., Marjanovic, H., Nicolas, M., Ostrogovic Sever, M.Z., Priwitzer, T., Rautio, P., Roskams, P., Sanders, T.G.M., Schmitt, M., Sramek, V., Thimonier, A., Ukonmaanaho, L., Verstraeten, A., Vesterdal, L., Wagner, M., Waldner, P., and Rigling, A. 2021. Contrasting resource dynamics in mast years for European beech and oak- A continental scale analysis. Frontiers in Forests and Global Change 4: 689836. DOI: 10.3389/ffgc.2021.689836

Nussbaumer, A., Meusburger, K., Schmitt, M., Waldner, P., Gehrig, R., Haeni, M., Rigling, A., Brunner, I., and Thimonier, A. 2020. Extreme summer heat and drought lead to early fruit abortion in European beech. Scientific Reports 10: 5534.

Nussbaumer, A., Waldner, P., Etzold, S., Gessler, A., Benham, S., Thomsen, I.M., Jorgensen, B.B., Timmermann, V., Verstraeten, A., Sioen, G., Rautio, P., Ukonmaanaho, L., Skudnik, M., Apuhtin, V., Braun, S., and Wauer, A. 2016. Patterns of mast fruiting of common beech, sessile and common oak, Norway spruce and Scots pine in Central and Northern Europe. Forest Ecology and Management 363: 237-251. doi: 10.1016/j.foreco.2015.12.033

Overgaard, R., Gemmel, P., and Karlsson, M. 2007. Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. Forestry: An International Journal of Forest Research 80, 5: 555-565. https://doi.org/10.1093/forestry/cpm020

Plantico, M., Goss, A., Hammer, G., Love-Brotak, L., and Owen, T. 2005. Selected Maps from the Climate Atlas of the United States. *National Climatic Data Center, Asheville, NC.*

Redmond, M.D., Forcella, F. & Barger, N.N. 2012. Declines in pinyon pinecone production associated with regional warming. Ecosphere 3: 1–14.

Sork, V.L., Bramble, J. & Sexton, O. 1993. Ecology of mast-fruiting in threes species of North American deciduous oaks. Ecology 74: 528-541.

Speer, J.H. 2001. Oak mast history from dendrochronology: A new technique demonstrated in The Southern Appalachian region. [Unpublished doctoral dissertation]. University of Tennessee, Knoxville.

Sykes, M.T. 2009. Climate change impacts: vegetation. Encyclopedia of Life Sciences. https://doi.org/10.1002/9780470015902.a0021227

Walters, R.S. and Yawney, H.W. 1990. *Acer rubrum* L. Red Maple. From Burns, Russell M., and Barbara H. Honkala. "Silvics of North American trees. Vol 2, hardwoods." *US Department of Agriculture, Washington, DC.*

Wang, X. and Ibáñez, I. 2022. The contrasting effects of local environmental conditions on tree growth between populations at different latitudes. Forests 13, 429. doi.org/10.3390/f13030429

Way, D.A. and Montgomery, R.A. 2015. Photoperiod constraints on tree phylogeny, performance, and mitigation in a warming world. Plant, Cell, and Environment 38: 1725-1736.

Way, D.A. and Oren, R. 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. Tree Physiology 30: 669-688. doi:10.1093/treephys/tpq015

Zyweic, M. and Zylonka, T. 2013. Does a heavy fruit crop reduce the tree ring increment? Results from a 12-year study in a subalpine zone. Trees 27: 1365-1373. DOI: 10.1007/s00468-013-0884-y

Table 1. Characteristics of the six study sites where tree growth and reproduction data were collected. Basal area per hectare were calculated based on a census conducted at the sites in the summer of 2022. *Acer saccharum* was present in all sites expect for Balsam Fir. *A. 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.

Region	Site Name	Soil Texture	Dominant Species	Basal area cm^2/ha
North	Aspen	Coarse-textured, well-drained	*Acer saccharum* Marshall, *Acer rubrum* L., *Fagus grandifolia* Ehrh.	48.45
	Northern Hardwood	Coarse-textured, well-drained	*Acer saccharum* Marshall, *Fagus grandifolia* Ehrh., *Populus grandidentata* Michx.	32.25
	Balsam Fir	*Data not collected*	*Abies balsamea* (L.) Mill., *Acer rubrum* L., *Thuja occidentalis* L., T*suga canadensis*	52.67
South	ESGR Wet	*Data not collected*	*Acer saccharum* Marshall, *Hamamelis virginiana* L., *Prunus serotina* Ehrh.	34.35
	Stinchfield	Coarse-textured, well-drained	*Quercus alba* L.*, Quercus velutina* L'Her. ex A.DC., *Acer saccharum* Marshall, *Acer rubrum* L.	35.30

Radrick	Fine-textured, well-drained	*Quercus rubra* L.*, Quercus alba* L.*, Acer nigrum* Michx. F.*, Acer saccharum* Marshall	36.34
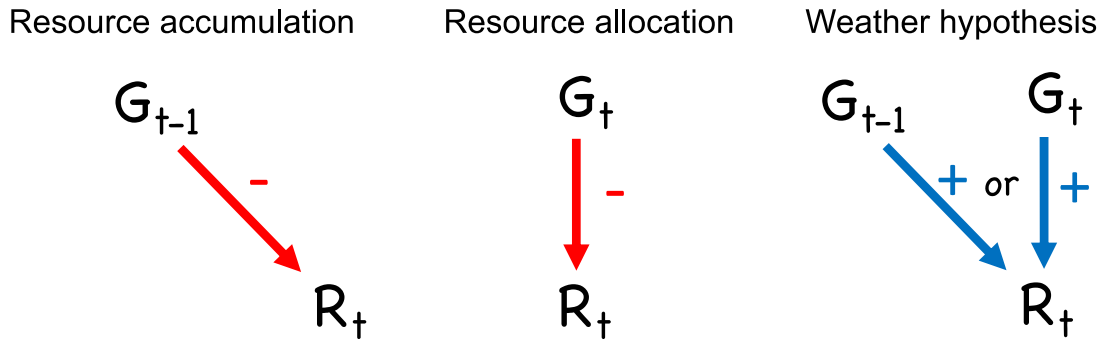
Figure 1. Framework for the strategies connecting growth (G) and reproduction (R). In resource accumulation, there is a tradeoff between growth in previous years and reproduction (negative sign). In Resource allocation, there is a tradeoff between growth and reproduction in the same year. Expectations 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).
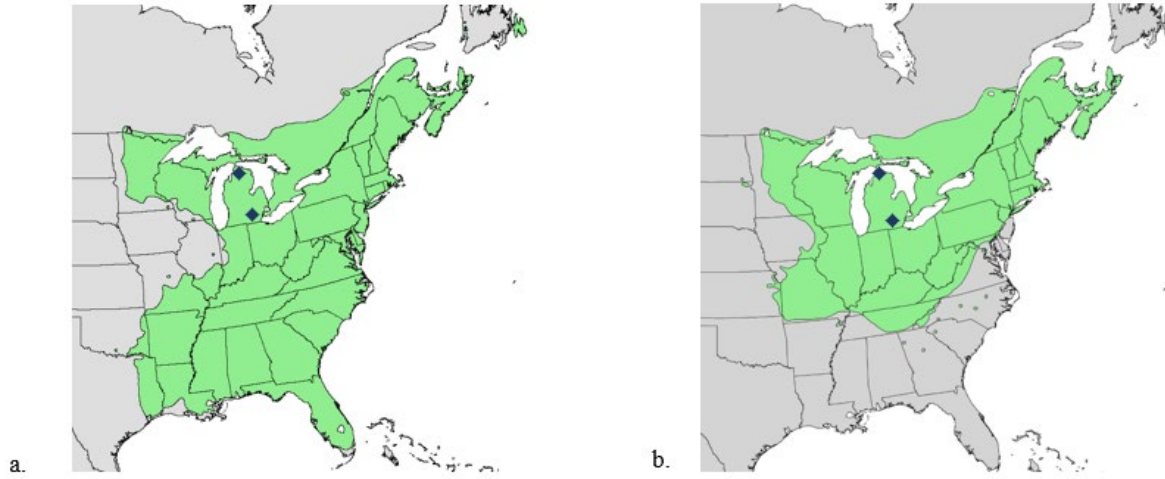
Figure 2. Native distribution of study species (green), a. *Acer rubrum* and b. *Acer saccharum*, and location of study sites (blue diamonds).
Range maps from Elbert L. Little, Jr. 1999. Digital representation of 'Atlas of United States Trees.' United States Geological Survey.
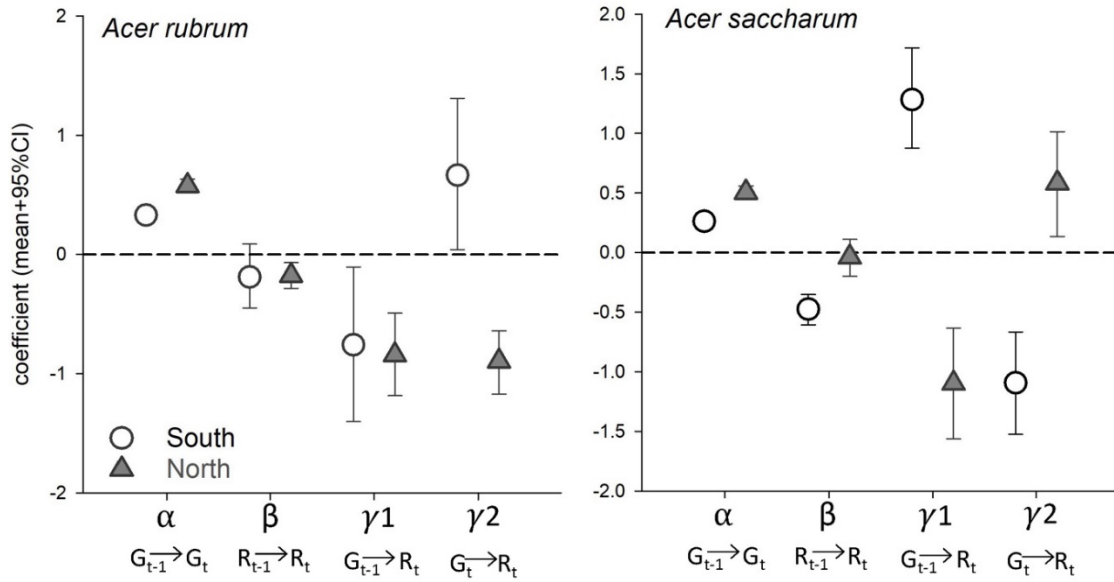
Figure 3. Parameter values, means and 95% CI, from the integrated analysis of growth and reproduction data, of the two studied species, *A. rubrum* (left) and *A.saccharum* (right) at two latitudes (south and north). Parameters indicate the following relationships: γ1, effect of previous year's growth on reproduction, and γ2, effect of current year's growth on reproduction.
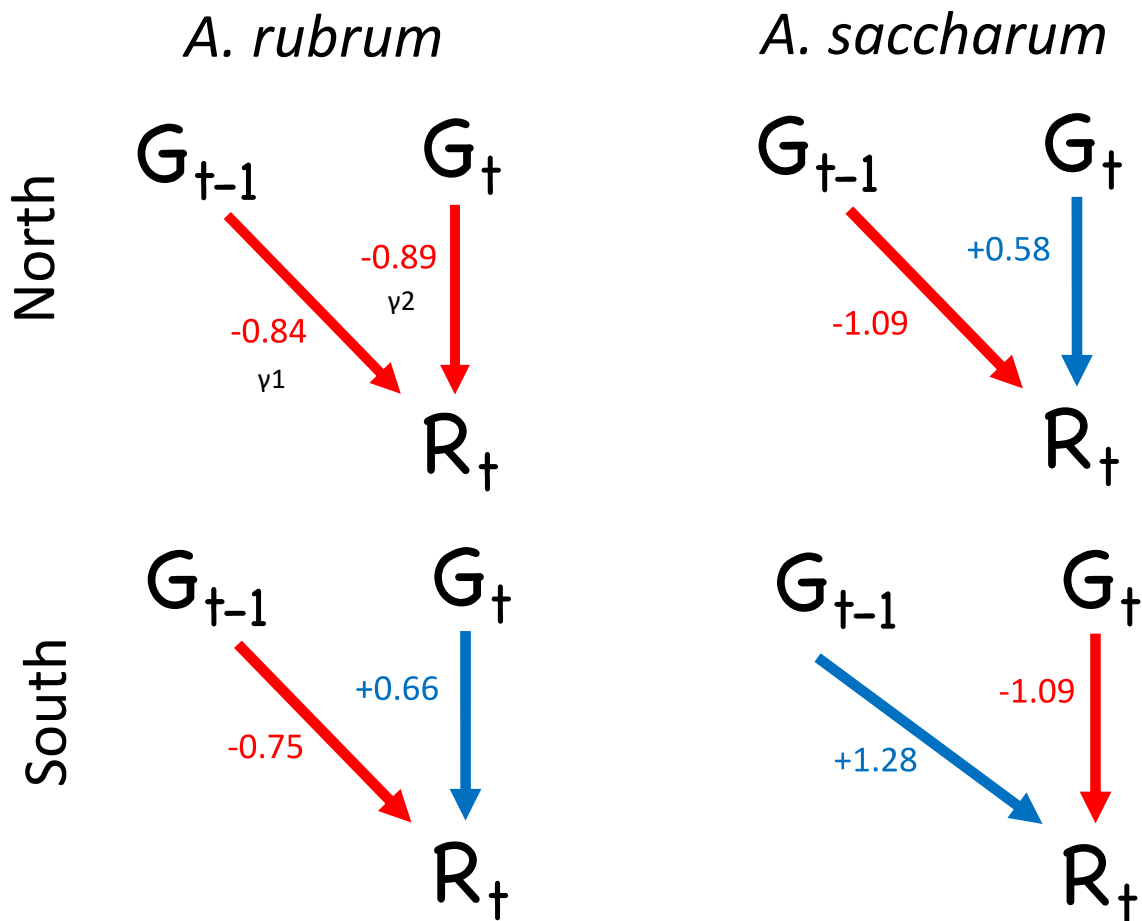
Figure 4. Integrated representation of results showing the nature of the relationship (red negative, blue positive) between growth (G) and reproduction (R) across years (t) for each species (right and left panels) and regions (top and down panels). Values represent the parameter means, all parameters 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).
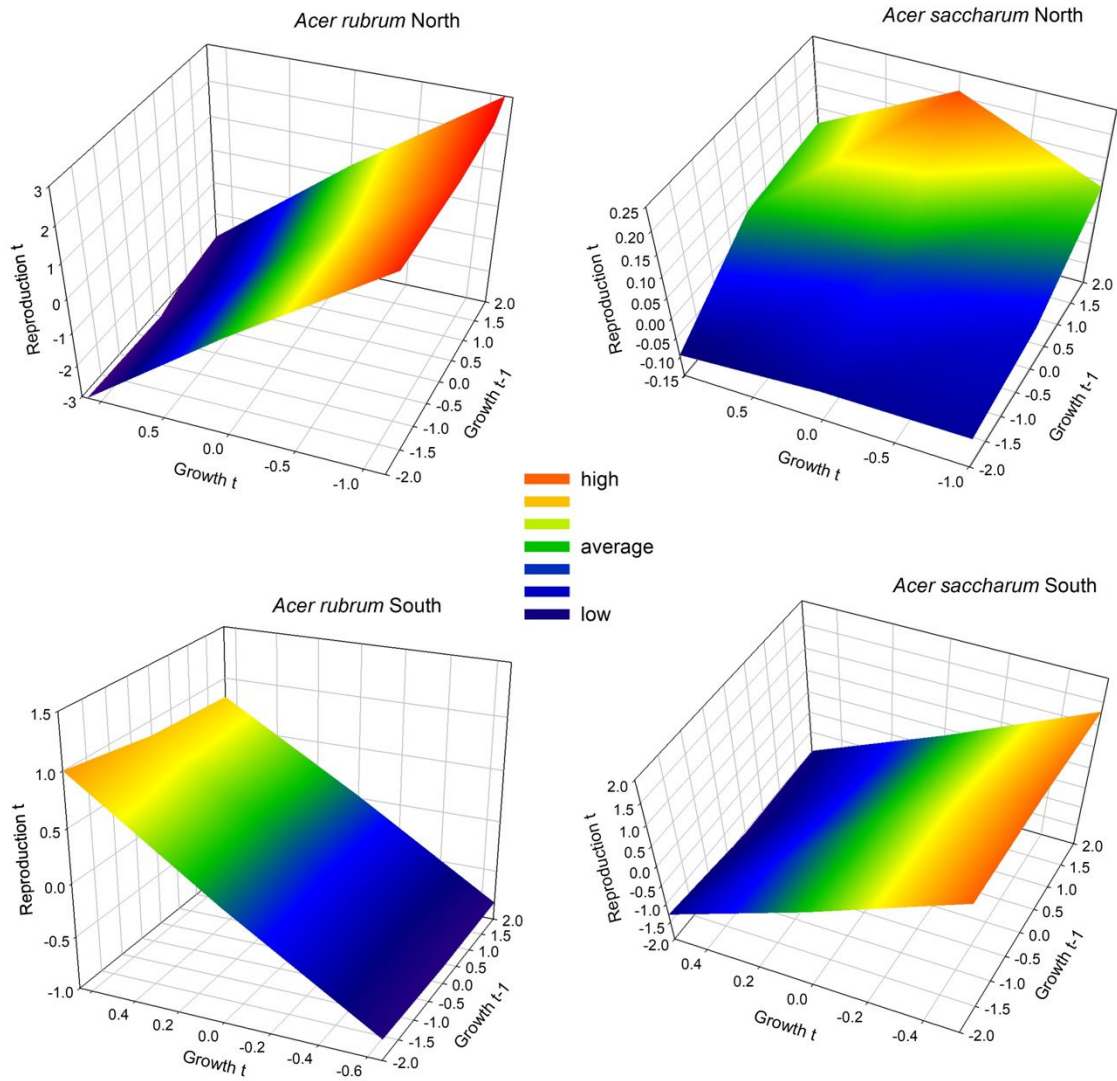
Figure 5. Simulated growth and reproduction at time t as a function of growth at time t-1 using the covariance structure of the parameters estimated in the analysis. Growth at time t-1 was gradient between -2 and 2, representing average growth for that species and region and a 2 SD range. All values are standardized, zero represents average performance.

Appendix I
JAGS Code Used in the Analysis

```
model{
    for(i in 1:N){ #tree
        #missing baisS values at time 1
        baiS[i,1]~dnorm(0,1)
        for(t in 2:23){ #time
    baiS[i,t]~dnorm(G[i,t],tau[species[i]]) #likelihood
    baiS.pred[i,t]~dnorm(G[i,t],tau[species[i]]) #predicted
    G[i,t]<-alpha[species[i],region[i]]*baiS[i,t-
1]+YRE[species[i],region[i],t] #process model
    } #time
    } #tree

#stand level predictions
for(t in 2:23){ #times
  #acru
Gstand[1,1,t]<-mean(G[1:18,t])
Gstand[1,2,t]<-mean(G[19:36,t])
Gstand[1,3,t]<-mean(G[37:61,t])
Gstand[1,4,t]<-mean(G[62:95,t])
Gstand[1,5,t]<-mean(G[96:106,t])
Gstand[1,6,t]<-0
  #acsa
Gstand[2,1,t]<-mean(G[107:126,t])
Gstand[2,2,t]<-mean(G[127:150,t])
Gstand[2,3,t]<-mean(G[150:172,t])
Gstand[2,4,t]<-mean(G[173:195,t])
Gstand[2,5,t]<-0
Gstand[2,6,t]<-mean(G[196:219,t])
} #times

#seed model
for(i in 1:NN){#traps
  #missing values at time 1
  seed[i,1]~dnorm(0,1)
  for(t in 2:15){ #times
    seed[i,t]~dnorm(S[i,t],tau[species[i+2]]) #likelihood
    seed.pred[i,t]~dnorm(S[i,t],tau[species[i+2]]) #predictions
    S[i,t]<-beta[speciesS[i],regionS[i]]*seed[i,t-1]
+gamma1[speciesS[i],regionS[i]]*Gstand[species[i],regionS[i],t+8]+gamma
2[speciesS[i],regionS[i]]*Gstand[species[i],regionS[i],t+8-1]
  }#times
}#traps

#priors
#priors
for(i in 1:2){ #species
  for(r in 1:2){#regions
  alpha[i,r]~dnorm(0,0.1)
  beta[i,s]~dnorm(0,0.1)
  gamma1[i,s]~dnorm(0,0.1)
  gamma2[i,s]~dnorm(0,0.1)
  }#regions
  for(r in 1:2){ #regions
```

```
      for(t in 2:23){ #times
      YRE[i,r,t]~dnorm(0,tauRE[i,r])
      }#times
   }#regions
}#species
for(i in 1:4){
tau[i]~dgamma(1,1)
v[i]<-1/tau[i]
}
for(i in 1:2){#species
   for(r in 1:2){ #regions
tauRE[i,r]~dgamma(1,1)
vRE[i,r]<-1/tauRE[i,r]
   }#regions
}#species
}
```

Appendix II

Table A1. Expressed population signals of samples at each study site.

Site	Species	Expressed Population Signal (EPS)
North-Aspen	*Acer rubrum*	0.934
	Acer saccharum	0.900
North-Balsam Fir	*Acer rubrum*	0.789
North-Northern Hardwood	*Acer saccharum*	0.927
South-ESGR Wet	*Acer rubrum*	0.926
	Acer saccharum	0.916
South-Radrick	*Acer rubrum*	0.943
	Acer saccharum	0.914
South-Stinchfield	*Acer rubrum*	0.957
	Acer saccharum	0.925

Appendix III

Analysis Parameter Values

Table A2. List of parameters estimated in the analyses of growth and seed production.

Species	Region	Parameter	Mean	SD	95% CI
Acer rubrum	South	α $G_{t-1} \rightarrow G_t$	0.330	0.025	0.280,0.381
		β $R_{t-1} \rightarrow R_t$	-0.194	0.135	-0.463,0.062
		γ_1 $G_{t-1} \rightarrow R_t$	-0.770	0.338	-1.484, -0.132
		γ_2 $G_t \rightarrow R_t$	0.662	0.330	0.048,1.298
	North	α $G_{t-1} \rightarrow G_t$	0.577	0.028	0.521,0.631
		β $R_{t-1} \rightarrow R_t$	-0.178	0.0568	-0.293, -0.066
		γ_1 $G_{t-1} \rightarrow R_t$	-0.845	0.179	-1.207, -0.499
		γ_2 $G_t \rightarrow R_t$	-0.897	0.145	-1.206, -0.629
Acer saccharum	South	α $G_{t-1} \rightarrow G_t$	0.263	0.025	0.215,0.312
		β $R_{t-1} \rightarrow R_t$	-0.472	0.065	-0.597, -0.339
		γ_1 $G_{t-1} \rightarrow R_t$	1.290	0.219	0.869,1.719
		γ_2 $G_t \rightarrow R_t$	-1.096	0.234	-1.559, -0.646
	North	α $G_{t-1} \rightarrow G_t$	-0.036	0.079	-0.188,0.117
		β $R_{t-1} \rightarrow R_t$	0.504	0.030	0.446,0.561
		γ_1 $G_{t-1} \rightarrow R_t$	-1.104	0.256	-1.651,-0.635
		γ_2 $G_t \rightarrow R_t$	0.586	0.229	0.142,1.041

Appendix IV.

Goodness of fit for the analyses performed in this study.

Figure A1. Predicted vs Observed plots, goodness of fit, for the analysis of standardized growth and seed production data in the two studied species.
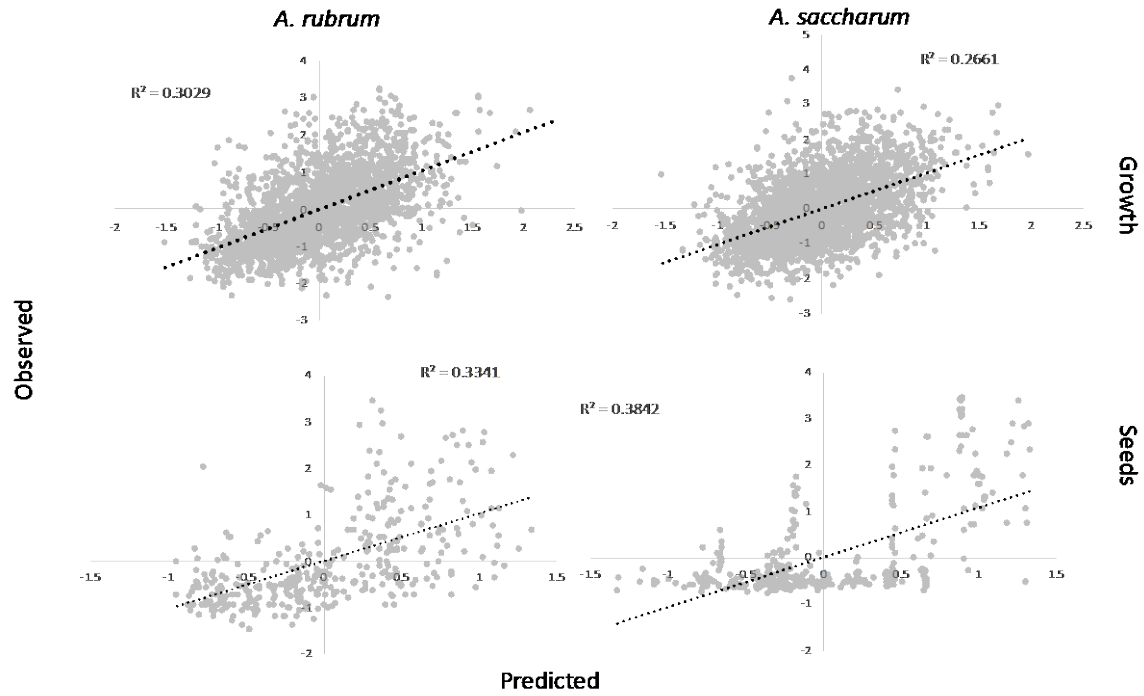
Appendix V

Year random effects in the growth model and correlations with climatic variables.

Table A3. Year random effects calculated in the analysis of growth.

Species	Region	Year	Mean	SD
Acer rubrum	South	2001	0.339	0.102
		2002	0.030	0.103
		2003	-0.393	0.103
		2004	-0.598	0.103
		2005	0.190	0.103
		2006	0.685	0.103
		2007	-0.344	0.104
		2008	0.011	0.078
		2009	0.037	0.074
		2010	0.682	0.076
		2011	0.221	0.070
		2012	0.259	0.085
		2013	-0.665	0.084
		2014	-0.602	0.079
		2015	-0.066	0.081
		2016	0.275	0.073
		2017	-.099	0.065
		2018	-0.469	0.081
		2019	0.430	0.098
		2020	-0.042	0.071
		2021	0.664	0.084
		2022	0.398	0.101
	North	2001	-0.049	0.115
		2002	0.138	0.115
		2003	-0.173	0.115
		2004	-0.153	0.116
		2005	-0.096	0.115
		2006	0.044	.115
		2007	0.097	0.115
		2008	-0.045	0.115
		2009	0.301	0.114
		2010	0.082	0.115
		2011	0.155	0.115
		2012	0.267	0.115
		2013	0.044	0.115
		2014	-0.258	0.115
		2015	0.138	0.115
		2016	-0.376	0.115
		2017	0.038	0.115
		2018	-0.272	0.116
		2019	0.247	0.117
		2020	0.038	0.119
		2021	0.533	0.121

		2022	-0.151	0.124
		2001	0.041	0.101
		2002	-0.144	0.101
		2003	-0.460	0.102
		2004	0.001	0.101
		2005	0.461	0.101
		2006	0.567	0.101
		2007	0.125	0.102
		2008	-0.152	0.102
		2009	0.192	0.101
		2010	0.729	0.101
	South	2011	0.353	0.103
		2012	0.052	0.102
		2013	-0.370	0.101
		2014	-0.502	0.102
		2015	0.033	0.101
		2016	0.083	0.101
		2017	-0.055	0.102
		2018	-0.728	0.102
		2019	-0.011	0.106
		2020	-0.219	0.105
		2021	0.004	0.114
Acer saccharum		2022	-0.033	0.118
		2001	0.089	0.121
		2002	-0.061	0.119
		2003	0.117	0.120
		2004	0.321	0.120
		2005	0.297	0.121
		2006	0.113	0.120
		2007	-0.421	0.120
		2008	0.149	0.118
		2009	0.009	0.118
		2010	0.012	0.118
	North	2011	-0.333	0.118
		2012	0.272	0.118
		2013	-0.246	0.118
		2014	-0.392	0.117
		2015	0.429	0.119
		2016	-0.049	0.117
		2017	-0.221	0.118
		2018	0.107	0.124
		2019	-0.254	0.125
		2020	-0.389	0.127
		2021	-0.136	0.131
		2022	0.421	0.136

Table A4. Pearson's correlation values of year random effects with climate variables, including monthly average, minimum, and maximum temperatures (°C) and total monthly precipitation (cm).

Species	Region	Climate Variable	Correlation current year	Correlation previous year
Acer rubrum	South	April Average Temperature	0.430	-0.125
		May Minimum Temperature	0.005	0.017
		May Maximum Temperature	-0.129	-0.018
		May Average Temperature	-0.072	-0.004
		June Minimum Temperature	0.281	0.359
		June Maximum Temperature	0.255	0.121
		June Average Temperature	0.287	0.241
		June Precipitation	0.012	0.177
		July Minimum Temperature	0.511	-0.143
		July Maximum Temperature	0.450	-0.183
		July Average Temperature	0.494	-0.169
		July Precipitation	0.264	0.102
		August Maximum Temperature	0.563	0.096
		August Average Temperature	0.516	0.177
		September Maximum Temperature	-0.211	0.089
		September Average Temperature	-0.048	0.189
	North	May Minimum Temperature	-0.181	-0.010
		May Maximum Temperature	-0.122	0.006
		May Average Temperature	-0.153	-0.003
		June Minimum Temperature	0.168	0.079

		June Maximum Temperature	0.020	0.190
		June Average Temperature	0.101	0.145
		June Precipitation	0.403	0.105
		July Minimum Temperature	0.116	0.315
		July Maximum Temperature	0.012	0.268
		July Average Temperature	0.062	0.299
		July Precipitation	0.134	0.216
		August Maximum Temperature	-0.030	0.183
		August Average Temperature	-0.034	0.169
		September Maximum Temperature	-0.138	-0.576
		September Average Temperature	-0.203	-0.509
Acer saccharum	South	April Average Temperature	0.592	0.094
		May Minimum Temperature	0.015	-0.058
		May Maximum Temperature	-0.112	-0.0849
		May Average Temperature	-0.058	-0.079
		June Minimum Temperature	0.184	0.022
		June Maximum Temperature	0.148	-0.196
		June Average Temperature	0.175	-0.113
		June Precipitation	-0.031	0.220
		July Minimum Temperature	0.289	-0.289
		July Maximum Temperature	0.236	-0.336
		July Average Temperature	0.269	-0.326
		July Precipitation	0.418	0.251

		August Maximum Temperature	0.137	-0.098
		August Average Temperature	0.150	-0.018
		September Maximum Temperature	-0.154	-0.096
		September Average Temperature	-0.080	-0.021
	North	May Minimum Temperature	0.189	-0.319
		May Maximum Temperature	0.233	-0.421
		May Average Temperature	0.224	-.401
		June Minimum Temperature	-0.080	0.191
		June Maximum Temperature	-0.124	0.151
		June Average Temperature	-0.106	0.177
		June Precipitation	-0.113	-0.014
		July Minimum Temperature	-0.084	-0.468
		July Maximum Temperature	0.052	-0.455
		July Average Temperature	-0.008	-0.475
		July Precipitation	-0.210	0.189
		August Maximum Temperature	-0.061	-0.207
		August Average Temperature	-0.040	-0.126
		September Maximum Temperature	0.298	0.322
		September Average Temperature	0.314	0.223