# Title Page

**Manuscript title:** Genetically based variation in fitness and carbon assimilation among bur oak populations

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**Key words/phrases:** local adaptation; reciprocal transplant; tree ecophysiology; Quercus macrocarpa; plasticity

# Abstract

Ongoing climate change will negatively impact tree populations unless they are able to acclimate to the changes in their local environment. Effective planning for climate adaptation management requires an understanding of the current state of local adaptation and physiological performance to assess whether populations are at risk of local extinction, determine if assisted migration is appropriate, and to select appropriate seed sources if intervention is needed. We established a new reciprocal transplant experiment (ACE, Adaptation to Climate and Environment) across a latitudinal gradient in North America to examine the impacts of warming on three bur oak (*Quercus macrocarpa*) populations across much of the species range. We established common gardens in Minnesota, Illinois, and Oklahoma with seedlings grown from seeds collected within 50 km of each of those locations from a total of sixty maternal families . We aimed to 1) assess local adaptation in each of the populations using survival and size as fitness metrics, and 2) evaluate physiological responses to different environments along the latitudinal gradient. We found that northern populations are maladapted to hotter climates as evidenced by their low survival, growth, and photosynthetic rates in the warmest common garden. The southernmost population had the highest survival rate, growth rate, and fitness of the three populations in the southernmost garden, providing evidence for local adaptation to the warmest site. However, conditions in the middle garden resulted in the highest fitness and best physiological performance for all populations. Growth and survival were correlated in the middle garden but were decoupled in the northern and southern gardens. This decoupling is likely due to stress associated with the relatively extreme climates in the gardens at the ends of the gradient that led to greater resource allocation to survival than growth. Our results suggest that southern seed sources may perform well in warmer conditions in the north brought on by climate change,

which has important implications for managers assisting broadly ranged tree species in adapting to climate change.

# Introduction

Climate change is rapidly shifting the global climate to historically unprecedented conditions, as evidenced by the warmest years on record occurring in the past ten years, (Tierney et al., 2020). With warming comes other related climatic issues, including increasing intensity and frequency of drought events (Seneviratne et al., 2023). Such shifts in climate are likely to alter species ranges and ecosystem boundaries (Chen et al., 2011). Ranges of many tree species have already contracted in response to warming and drought stress (Zhu et al., 2012). Their long lifespan and sessile nature force tree populations to plastically acclimate or adapt to new climate conditions, shift to higher latitudes with similar climate conditions that they evolved in, or become locally extinct in the face of climate change (Aitken et al., 2008). Historical rates of tree migration based on life history and dispersal data backed by molecular data indicate migration at a maximum rate of 100 meters per year (McLachlan et al., 2005), though evidence suggests that modern rates of northern range edge migration for *Quercus* species may average 500 to 1200 meters per year (Sittaro et al., 2017; Tang et al., 2024), which is slower than the current rates of climate change and may lead to maladaptation at species range edges. Dispersal limitations on the movement of tree species will necessitate population-level responses to novel climates through phenotypic plasticity or adaptation (Franks et al., 2014; Hoffmann & Sgrò, 2011; Huntley, 1989). Knowledge of local adaptation and plasticity in response to changes in climate are critical to managing tree populations and ecosystems for future climates conditions.

Climate change will likely impact the survival and fitness of individuals, which will have implications for the long-term persistence of locally adapted populations. Populations that have

higher fitness in their local environment than other populations, or higher fitness in their home environment than away from their home environment are said to be locally adapted (Kawecki & Ebert, 2004; Williams, 1966). Local adaptation in large populations of widespread species can help maintain genetic variation within the species, which is critical in species' persistence through changing climatic conditions. However, with climate change, populations may perform better at higher latitudes than in their current environment leading populations to be maladapted to their home environment (Browne et al., 2019; Etterson et al., 2020; Gorton et al., 2022; Sáenz-Romero et al., 2017). Such adaptational lags to climate coupled with dispersal limitations may necessitate anthropogenic intervention to ensure survival of populations that cannot tolerate novel climate regimes in their current environment.

One conservation management goal to maintain tree species through climate change is to enhance genetic diversity to improve ecosystem resilience through strategies such as favoring existing genotypes that are better adapted to future climates (Butler et al., 2012). This management strategy is commonly referred to as "assisted population migration", where genetic material (i.e., seeds or pollen) from southern, warm adapted populations is transferred northward through human intervention to improve persistence of species in a changing climate (Williams & Dumroese, 2013). For successful assisted migration of populations in the face of climate change, it is critical to ensure that plasticity and genetic effects that may lead to maladaptation in the transferred populations are accounted for prior to migration (Nagamitsu & Shuri, 2021). It is worth noting that what we now call "assisted migration" has been historically practiced by indigenous people by moving seeds and plant material to create desirable landscapes (Krech et al., 2004). Assisted migration can be a critical strategy in helping to prevent species extinction

and economic losses and to maintain ecosystem services (Abrams et al., 2021; Krech et al., 2004; Williams & Dumroese, 2013).

Changes in growing season length along with increased stresses of heat and aridity may lead to maladaptation in photosynthetic and growth rates and shifts in carbon allocation. Carbon allocation is a trade-off amongst various carbon pools including growth, reproduction, defense, symbionts in the rhizosphere, and secondary compounds or increased storage in response to cold acclimation, and drought response (Herms & Mattson, 1992). At lower latitudes, growing seasons are longer and cold stress is reduced. Slow life history strategies, in which plants grow slowly but steadily, are often found at lower latitudes, and have long-lived leaves with slow, prolonged carbon fixation over a longer time (Chabot & Hicks, 1982; Kikuzawa, 1991; Wright et al., 2004). Slow life history strategies may be better adapted to drought associated with climate change, as species with slow strategies are more resistant to drought and can maintain productivity through intense drought (Oram et al., 2023).

At higher latitudes with shorter growing seasons, growth may compete with investment in cold tolerance (MacArthur, 1984). Shorter growing season length in higher latitudes is thought to select for higher carbon assimilation rates, allowing plants to compensate for the shorter period favorable for growth and reproduction (Bosiö et al., 2014). Cold temperatures in higher latitudes also increase the allocation to nonstructural carbohydrate reserves, which are critical for spring bud break after the long, cold winter (Klein et al., 2016; Körner, 2003). The conversion of photosynthetic carbon to biomass is mediated by other carbon demands that shift with changing environmental conditions, including drought and freezing, that may affect growth rate (Körner, 2015; Reich & Oleksyn, 2008). Therefore, we expect higher photosynthetic rates and lower relative growth rates in higher latitudes. These combined expectations lead to contrasting

predictions about how photosynthetic rates and growth rates should vary with growing season length (see Fig. S1).

Local adaptation can be tested with reciprocal transplant experiments which separate genetic from environmental (plastic) influences on phenotypes (Kawecki & Ebert, 2004; Schwinning et al., 2022). We established a reciprocal transplant experiment using the deciduous, broad-leaved tree species *Quercus macrocarpa L.* across a latitudinal gradient by collecting seeds from maternal families across the gradient to establish the ACE (Adaptation to Climate and Environment) experiment. *Quercus macrocarpa* is a useful species for such an experiment because it has a broad latitudinal and ecological range. Consequently, it is likely to show adaptive differentiation across its range of contrasting climatic conditions. Furthermore, *Q. macrocarpa* is an ecologically important tree species that is an important food source for birds, insects, and mammals (Tallamy, 2021). *Quercus macrocarpa* is also an important species in oak savannas, a rare and threatened ecosystem, due to its fire resistance capabilities (Hoekstra et al., 2005). We collected acorns from individual trees (half-sib families) within three populations (Minnesota, Illinois, and Oklahoma) across a climatic gradient which spans a mean annual temperature gradient of 6-16 $^{o}$C. ACE was designed to reciprocally plant seedlings from each family within each population into gardens in those three states using a quantitative genetics design, such that seedlings from all families were randomized in replicated blocks in each garden.

Previous predictions of the response to climate change are mixed for *Q. macrocarpa* in Minnesota: the species is predicted to have high capacity to cope with low levels of climate change, but high climate change levels are expected to decrease suitable habitat (Iverson et al., 2019). Climate change may provide some benefit for populations in Minnesota due to the

expected longer growing seasons (Handler et al., 2014) leading to increased growth, as has been shown in other temperate tree species (Pretzsch et al., 2014). There is a general consensus that there will be changes in the amount and timing of precipitation in Minnesota, likely leading to periods of high aridity coupled with increased temperature as well as periods of heavy rainfall and flooding. Trees in Minnesota may be maladapted to these changes, which could result in mortality (Galatowitsch et al., 2009; Handler et al., 2014). To develop clear management strategies for ecologically important tree species such as *Q. macrocarpa*, it is critical to study seedling survival and function to understand the future of tree populations because seedlings often have a narrower climatic niche compared to adult trees (Dobrowski et al., 2015). Seedlings may be more vulnerable to climate change, but their survival and establishment are critical to the regeneration and survival of tree populations (Williams, 2021).

In this study, we tested for local adaptation and adaptive differentiation by reciprocally transplanting seedlings from three populations in field conditions. We used components of fitness and integrated measures of fitness using Aster models (Geyer et al. 2007, Shaw et al. 2008) to test for adaptative differences among populations across gardens. We acknowledge that common garden sites vary both climatically and edaphically and in many other respects, and are experiencing ongoing climate change. We addressed the overarching questions: Do *Q. macrocarpa* progeny from three bur oak tree populations have higher fitness and physiological performance in the garden closest to their origin, or are they better adapted to a climate that has shifted northward due to warming with climate change? If populations are locally adapted, we expect them to have higher fitness and adaptive physiological performance when they are in their home garden (home vs. away), and to have higher fitness than other populations in their home garden (local vs. foreign) (Fig. S2). On the other hand, if populations are adapted to a climate

that has shifted northward due to the 1.1 °C warming in the past century (IPCC, 2023), we expect them to have higher fitness and physiological performance in the more northern (higher latitude) gardens compared to the hotter and drier southern (lower latitude) gardens, but northern populations to exhibit lower fitness and higher physiological stress responses in the southern garden. Because seedling transplants were grown in natural field conditions, there may be edaphic differences among sites that can offer more favorable soil resource conditions at some sites relative to others and complicate interpretations of local adaptation in relation to climate.

# Methods

**Reciprocal transplant experimental design**

The Adaptation to Climate and Environment (ACE) experiment was designed to test for local adaptation by reciprocally transplanting bur oak seedlings from known families into three garden sites across a latitudinal gradient. The design was based on prior work from Etterson and Shaw (2001), Etterson (2004a, 2004b), Deacon and Cavender-Bares (2015), and Ramirez-Valiente et al. (2018). Acorns from Minnesota, Illinois, and Oklahoma populations were collected in 2018 and 2019 from individual mother trees at least 100 feet apart to minimize the likelihood of shared pollen among trees. Acorns collected from mothers in the same parkland area were grouped into sub-populations. Both 2018 and 2019 collections were germinated outdoors in the ground in a common environment in Vallonia, Indiana at the Vallonia State Nursery through the Indiana Department of Natural Resources (see appendix S1:Methods for supplemental details on acorn processing). In March 2021, seedlings were lifted from the common nursery, sorted, and sent to be planted in the common gardens in tilled former grasslands in Minnesota (Cedar Creek Ecosystem Science Reserve, East Bethel MN), Illinois (Morton Arboretum, Lisle IL), and Oklahoma (Kessler Atmospheric and Ecological Field

Station, Purcell OK). In each of the common gardens we planted ten individuals from twenty families from each of the three populations (Minnesota, Illinois, and Oklahoma) 1 m apart in a randomized block design, with at least one individual from each family planted in each block (Fig. 1a). Gardens were weeded or mowed to remove small herbs and grasses that were growing around the trees, then mulched at the end of the first growing season or beginning of the second to suppress herbaceous understory growth. The seedlings were irrigated for the first two years after planting to ensure the gardens were established.

**Climate data**

Monthly temperature data from 1940 to 2023 were acquired from ERA5 data (Hersbach et al., 2023) using garden coordinates, and extracted the data from the raster file using QGIS (*QGIS Geographic Information System*, v3.34, 2024). Temperature data for each year were averaged to calculate the mean annual temperature (MAT) and were averaged over the months of May to September to calculate the growing season temperature for each year. To find the change in MAT and growing season temperature since the middle of the 21$^{st}$ century, we calculated the past mean for the years 1940-1960 and the recent mean 2003-2023 then subtracted the past mean from the recent mean for each garden. We used a similar approach to extract precipitation data for the years of 2021-2023, while the garden was planted.

To estimate differences in aridity between the gardens, we calculated an index of moisture (IM) for each of the gardens following Ramírez-Valiente & Cavender-Bares (2017), where the index of moisture is equal to the difference between monthly precipitation and monthly potential evapotranspiration (PET). The IM reflects the monthly water balance for an area and indicates water deficit with negative values and water surplus with positive values. We

calculated PET with the Thornthwaite (1948) method, using monthly mean temperature and average day length per month.

**Soil nutrients and texture**

To document differences in soil properties among sites, we sampled soil from the center of each garden block to 10 cm depth and conducted tests for soil nutrients (carbon-nitrogen ratios (C:N), total nitrogen content) and soil texture. To measure soil nutrients, we dried the soil and sieved it with a 2 mm mesh sieve to remove large rocks and organic matter. To measure total soil carbon and nitrogen concentration, we ground the soil to a homogenous fine powder and analyzed with a Costech ECS4010 elemental analyzer (Valencia, California, USA). We approximated the soil texture using the "texture by feel" method (Thien, 1979).

**Survival and growth surveys**

To determine seedling performance and fitness, the seedlings were surveyed for survival and size after planting and yearly from 2021 to 2023 at the end of the growing season. The height of the tallest living bud and basal diameter measured with a caliper 5 cm from the ground were used as metrics of size. Stem volume (SV) was estimated using a conoid equation as a proxy for aboveground biomass.

We used conoid volume (CV):

(1) $CV = H \times \pi \times D_{rc}^2 / 12$

where H is the height of the tree from the root collar to the apical meristem, and $D_{rc}$ is stem diameter at the root collar.

Relative growth rate was calculated as

(2) $RGR = \ln(V_{final}) - \ln(V_{initial})/T_{final} - T_{initial}$

where V is stem volume and T is time in total days. We calculated percent survival of maternal family groups in each garden as the number of trees alive out of the total trees originally planted in each family group.

**Phenology**

In 2023, to determine growing season length, we tracked spring and fall phenology using protocols established by the National Phenology Network (Denny & Crimmins, 2023). In the spring, approximately weekly, we surveyed the trees in each garden and tracked if the trees were breaking leaf bud. Leaves were considered to be breaking leaf bud if a green leaf tip was visible at the end of the bud. At similar intervals in the fall, we tracked leaves that were browning and/or falling after changing color as senescence. We considered senescing leaves to have late-season color that were actively falling or had recently fallen from the tree.

We used the budburst and the senescence data to estimate the growing season length of canopy foliage persistence, or how long foliage was present on the trees in a growing season. We calculated this as the difference between the mean initial budburst date and the mean initial senescence date to find the total length of the canopy foliage growing season.

**Gas exchange**

To measure photosynthesis rates and stomatal conductance, we conducted measurements of leaf-level gas exchange on every living tree in each of the three gardens using a LI-6800 Portable Photosynthesis System (LI-COR, Lincoln NE, USA) to determine $CO_2$ assimilation (A) and intrinsic water use efficiency (iWUE) (see appendix S1:Methods for supplemental details on settings and parameters used for measurement). This data was collected in both 2022 and 2023 at similar points in the growing season and using the same settings and approach. We calculated

iWUE as a ratio of $CO_2$ assimilation over stomatal conductance, which is the rate of photosynthetic $CO_2$ assimilation against the water loss from open stomata. Because A and iWUE change over the course of the day with stomatal closure, we found the maximum for A, stomatal conductance, and iWUE by excluding measurements after stomatal closure occurred (see Fig. S3 for cutoff times in each garden for each year).

**Spectral indices**

We collected hyperspectral reflectance measurements at the leaf level on every living tree in each garden to add additional, nondestructive metrics of chlorophyll content and nitrogen content. We measured leaf reflectance on the uppermost, fully expanded, undamaged leaf on each tree using a portable field spectrometer (SVC HR-1024i; Spectra Vista) and a leaf clip with an internal light source (LC-RP PRO; Spectra Vista) (see appendix S1:Methods for supplemental details on spectral data and processing). Using the spectra, we calculated the chlorophyll normalized difference index (ChlNDI)

$$(3) \qquad \left(\frac{R750-R705}{R750+R705}\right)$$

and the normalized difference nitrogen index (NDNI)

$$(4) \qquad \left(\frac{log(1/R1510)-log(1/R1680)}{log(1/R1510)+log(1/R1680)}\right).$$

The ChlNDI is positively correlated with chlorophyll a content with minimal influence of chlorophyll fluorescence (Gitelson & Merzlyak, 1994). The NDNI is positively correlated with percent nitrogen of vegetation (Serrano et al., 2002).

**Trait variance partitioning**

We partitioned the variance of relative growth rate, spectral indices, and gas exchange traits between population, sub-population (the site of acorn collection), and maternal family for

each garden. We used linear mixed models implemented with the lme4 package in R (Bates et al., 2024). We specified the model with population, sub-population nested within population, and maternal family nested within sub-population within population. We then extracted the variance components and the residual variance and calculated the percent of the total variance explained by each component.

## Statistical analysis

### *Aster modeling of fitness*

We used aster models to estimate fitness for each population in each garden. Aster models are useful to estimate fitness as they enable integration of fitness components with different statistical distributions by modeling the dependence of fitness components expressed later in life on earlier fitness components (Geyer et al., 2007; Shaw et al., 2008). We modeled fitness using survival to 2023 and height conditional to survival to the last year of measurements, as our nodes, depicted graphically as:

(5) Planted→ Survival to 2023→ Height

We chose height as the fitness estimate because it fit a normally distribution, and is a useful predictor of eventual fecundity (Cornelius, 1994; Gamache & Payette, 2004). Survival to 2023 was modeled with a binomial distribution and height was modeled with a normal distribution. As predictors in the aster models, we included population (P), garden (G) and the interaction between them, as well as the height at the time of planting (S) as a covariate to account for variation in size that could influence fitness, as:

(6) $F = P \times G + S$

We used the anova() function in the R software v. 4.3.0 (R Core Team, 2023) to compare models with and without the interaction effect to test for significance of the interaction effect. Once we

settled on the model (equation 6), we obtained means and standard errors for each population in each garden using the aster predict function for a dummy dataset with an "average individual" representing each population-garden combination.

*Statistical testing*

We evaluated differences in $A_{max}$, ChlNDI, survival, and growth among and within gardens for all populations using ANOVAs followed by Tukey post-hoc tests with a population by garden interaction effect. Number of individuals in each population in each garden varied due to survival and the number of measurements we were able to obtain (see supplemental Table S1 for number of individuals included in each measure). We also tested relationships between photosynthetic physiology ($A_{max}$ and ChlNDI) with fitness components (survival and growth) using linear models to understand the relationship between physiology and fitness components. All analyses were conducted in R software v. 4.3.0 (R Core Team, 2023).

# Results

**Site climate differences**

The ERA5 dataset, indicated that the average monthly temperature decreased latitudinally, with the Minnesota garden having the lowest average temperatures each month and Oklahoma having the highest (Fig. 1b). Notably, the Oklahoma garden never had a monthly average below freezing (0 °C), whereas the Minnesota and Illinois gardens did in the winter months. We found that since 1940, temperatures have increased at each of the garden sites. Mean annual temperature (MAT) has increased by over 1°C in each garden from averaged 20-year periods of 1940-1960 to 2003-2023, and the amount of temperature change increased with latitude, with the greatest change in MAT occurring in the northernmost, Minnesota garden, and

the lowest change in temperature in the southernmost garden, Oklahoma (Table S2). Over the same period, the average growing season temperature has also increased. Like MAT, the greatest change in growing season temperature was in Minnesota. However, unlike MAT, the change in growing season temperature was lowest in Illinois, the middle garden.

The gardens also differed in precipitation and aridity over the year. The Oklahoma garden peaked in precipitation in the springtime around April and May (Fig. 1c). The Minnesota garden also had a small peak in precipitation at that time, however the highest monthly precipitation occurred in late summer for the Minnesota garden around August and September. Precipitation in the Illinois garden peaked mid-summer in June and July and was the highest precipitation of the year among the three gardens. The Illinois garden was also the least arid of the three gardens during the growing season, though the index of moisture was negative for all the gardens, indicating a water deficit during the growing season (Fig. 1d). Notably, the index of moisture was negative year-round for the Oklahoma garden, suggesting it was in an atmospheric water deficit for the entirety of the year while the gardens were planted, though some of the water stress may have been alleviated by irrigation in the first two years of growth.

**Fitness components**

We assessed two main components of fitness: survival and plant size. Survival rates of family groups were most disparate in the Oklahoma garden, where survival of the Minnesota population (MN), was significantly lower than the Illinois (IL) and Oklahoma (OK) populations . The higher survival of OK compared to MN is in line with local vs. foreign local adaptation. (Fig 2a). Survival for MN and IL was highest overall in the Illinois garden. In the Minnesota garden,

survival was similar across populations and was similar to OK in the Oklahoma garden and to all populations in the Illinois garden.

Trends in tree size growth varied depending on the aspect of size observed. Stem volume combines the effects of diameter and height growth. The OK population had the highest stem volume RGR in the Oklahoma garden but was similar to the IL population in the Illinois garden (Fig. 2b). In the Minnesota garden, the stem RGR was similar among all populations. Stem volume RGR was highest in the Illinois garden for all populations.

**Fitness**

We found significant ($p<0.001$) interaction effects of population and garden on fitness using omnibus tests. Our model showed that aster fitness was highest in the Illinois garden for all populations, with the OK population having the highest fitness, in line with our hypothesis of climate change having shifted ranges northward. (Fig. 2c). In the Oklahoma garden, the OK population had higher fitness than the northern populations, as expected with local vs. foreign local adaptation. Fitness in the Minnesota garden was about the same for all populations.

**Physiology**

We evaluated photosynthetic responses in the different climates of each garden. The maximum $CO_2$ assimilation ($A_{max}$) was highest for the MN and IL populations in the Illinois garden (Fig. 2d). The MN and IL populations had similar $A_{max}$ rates to each other in all gardens and were lower in the Oklahoma garden than in the northern gardens, as we hypothesized given the aridity stress in the Oklahoma garden. The OK population had lower $A_{max}$ rates in both the Minnesota and Illinois gardens compared to the northern populations but had higher $A_{max}$ rates in

the Oklahoma garden compared to the MN population. The OK population also had lower chlorophyll content (as detected by the chlorophyll normalized difference spectral index (ChlNDI)) in the Illinois and Minnesota gardens compared to the MN population (Fig. 2e). The IL population generally was in between the OK and MN populations, with no significant differences detected between populations. We found that spectral normalized difference nitrogen index (NDNI) was highest for all populations in the Illinois garden, indicating higher leaf nitrogen content (Fig. 2f). The OK population had lower leaf nitrogen content than the northern populations in the Illinois garden. The NDNI was similar for all populations in the Oklahoma and Minnesota gardens. Data from 2022 was significantly different from 2023 data, but indicated similar though less strong trends, which may be an effect of irrigation or ontogeny. We include 2023 data here as the effects are stronger and indicate responses in natural conditions without irrigation (see Fig. S4 for 2022 results).

**Soil quality**

Soils in Oklahoma and the Illinois gardens were very similar in carbon (C) and nitrogen (N) concentrations, though concentrations in Oklahoma were a bit higher on average (table 2.1). Soils in the Minnesota garden had low soil percent nitrogen and percent carbon. Minnesota had the highest soil C:N, followed by the Illinois and then the Oklahoma gardens. The soils also differed texturally in terms of silt, clay and sand fractions. Oklahoma garden soils were classified as silty clay loam, Illinois as sandy clay loam, and Minnesota as sandy loam.

**Correlations of survival, growth, and physiology**

Stem volume growth was significantly positively correlated with survival for all populations in the Illinois garden, but not in the Minnesota or Oklahoma gardens (Fig. 3a). We

found significant positive relationships of $A_{max}$ with stem volume growth for the OK and IL populations in all the gardens, and for the MN population in the Illinois garden (Fig. 3b). We also found positive correlations of ChlNDI with stem volume growth in the Illinois garden for all populations, and for the MN and IL populations in the Minnesota garden (Fig. 3c). We did not find significant relationships with survival for $A_{max}$ or ChlNDI, except for a negative relationship between ChlNDI and survival for the MN population in Minnesota.

**Phenology and growing season**

Budburst was recorded earliest in the Oklahoma garden, and latest in the Minnesota garden, on average. Of the three populations, the OK population tended to break bud earliest on average, except in the Minnesota garden where all populations broke bud at similar times (Fig. 4a). The Minnesota garden had the earliest date of senescence, whereas the Oklahoma garden was the latest (Fig. 4b). The OK population also tended to senesce later than the northern populations, particularly in the Illinois garden. The Oklahoma garden had the longest growing season length for all three populations, whereas Minnesota was the shortest (Fig. 4c).

**Variance partitioning of traits**

When we partitioned the variance for traits in each garden, we found that variance attributable to population-level differences was distributed heterogeneously among traits and differed among gardens. Generally, variance attributable to population-level differences was greater in the Oklahoma and Illinois gardens, whereas in the Minnesota garden variation was often more attributed to subpopulation or maternal family-level variance, with the exception of ChlNDI (Fig. S5). One consistency in the variance partitioning was for $A_{max}$, population-level variance accounted for the greatest percent of the variance compared to subpopulation or

maternal family-level variance. In the Oklahoma garden the majority of the variance in relative growth rate (RGR_Vol) was attributed to population-level variation, whereas in the Minnesota garden most of the variance was attributable to maternal family variation. In the Illinois garden, stomatal conductance (gswMAX) had the highest population-level variance.

# Discussion

**Evidence for local adaptation**

We established the ACE (Adaptation to Climate and Environment) experiment, a reciprocal transplant experiment along a latitudinal gradient, to test for local adaptation and adaptive differentiation among populations of *Q. macrocarpa* from contrasting climates. Results of this work can inform ongoing efforts to manage forests and assist population migration. For all populations, we expected that local adaptation would be demonstrated by higher fitness of the local population relative to other populations (local vs foreign) and higher fitness of each population in its home location relative to its fitness in other locations (home vs. away). We found evidence supporting local adaptation based on the local vs. foreign comparison in the lowest latitude garden with the hottest climate. The OK source population had higher survival, growth, and fitness in the Oklahoma garden, compared to the MN population. In addition, the OK population had the highest maximum carbon assimilation rate ($A_{max}$) of the three populations in the Oklahoma garden. The lower $A_{max}$ rate of the northern populations in the Oklahoma garden indicate they were stressed in the hotter climate. The relative rates of $A_{max}$ reversed in both of the northern gardens where the OK population had lower $A_{max}$ than the northern populations. Drought is known to reduce stomatal conductance, which limits carbon assimilation (Boyer, 1976). Previous findings from oaks have shown that $A_{max}$ is reduced when exposed to

chronic drought (Gimeno et al., 2008). Higher survival of the OK population in the Oklahoma garden, which has the hottest climate relative, to the MN population provides evidence that the OK population is better adapted to warm temperatures. Under the expected 2 °C warming with climate change, the OK population may be better suited for the emerging warmer climates with potential to expand northward (IPCC, 2023). Conversely, the decline in assimilation rates in seedlings from the IL and MN populations in the hotter and drier Oklahoma climate suggests that these populations may experience declines in survival and fitness in their current environments.

While we found evidence of a local survival advantage relative to foreign populations in the Oklahoma garden, all populations expressed highest fitness in the Illinois garden. Consequently, we did not find evidence for local adaptation based on home vs. away comparisons. We also did not find clear statistical evidence for local vs. foreign local adaptation in the two northern populations after three years of growth. However, these patterns of local adaptation could still emerge through time. The OK population had higher absolute growth rate, which could be due in part to its larger acorn size (Table S3) with larger seed size supporting growth and survival in its early years (Bischoff et al., 2006; Deacon & Cavender-Bares, 2015). In addition, ontological differences in growth may have impacted our ability to observe signal of local adaptation. We monitored seedlings transplanted to the gardens after germination in a common nursery. Consequently, we were not able to measure all critical lifetime components of fitness. For example, we did not account for differences in germination rates of the populations in different gardens, nor could we observe fecundity as our trees had not reached reproductive maturity. Observing differences in fitness components relevant at an older, reproductively mature life stage might still reveal evidence of local adaptation not evident at the seedling life stage (Wadgymar et al., 2022).

Our alternative hypothesis for the observation of high performance outside of populations' local garden was that ongoing climate change has shifted suitable ranges of different populations northward, leading southern populations to be better adapted to northern gardens. While we saw that the OK population did perform better in the Illinois garden, which could be a consequence of both edaphic and climatic factors, we did not see evidence that the IL population performed better in the Minnesota garden compared to in its home garden, nor did it outperform the local MN population in Minnesota. This result indicates that there may be additional conditions or stressors in the Minnesota garden, such as freezing, nutrient deficiencies, and/or insect herbivory, that influence performance of non-local populations.

**Adaptive differentiation in phenology and function**

We found differences in phenology and plant function in line with adaptive differentiation, though the amount attributable to population-level differences versus subpopulation or maternal family-level differences varied among gardens. Both bud break and senescence differed significantly among populations in the Illinois garden. The OK population broke bud earlier and senesced later in the Oklahoma and in Illinois gardens relative to other populations, consistent with findings in other oak common gardens (Papper & Ackerly, 2021; Wright et al., 2021). In the Minnesota garden, where the growing season was shortest, all populations broke bud later and began senescence earlier compared to southern gardens (Fig. 4).

Population explained most of the variance in $A_{max}$, indicating that there are population-level differences in $A_{max}$ that are evident across environments. We found evidence supporting adaptive differentiation in photosynthetic rate in the OK population, which had lower $A_{max}$ values than the northern populations in the northern gardens but had highest $A_{max}$ values in its home garden. $A_{max}$ was highest in the least arid Illinois garden, indicating that alleviation of

467 aridity, cold stress, and soil nitrogen limitation improved photosynthetic rates, as we
468 hypothesized. On the other hand, low $A_{max}$ in the Oklahoma garden indicated low performance.
469 The differences in $A_{max}$ likely were due to high temperature stress inhibiting photosynthesis
470 through increased enzyme inhibition and RuBisCo oxygenation (Moore et al., 2021). The $A_{max}$
471 was greater for the OK population in its home garden and provides evidence for adaptive
472 differentiation and heat tolerance in the OK population.

473 We expected that populations from more arid climates would have greater water use
474 efficiency and drought tolerance, however $iWUE_{max}$ differed little among populations, and had
475 more differentiation among gardens, and at the garden level, $iWUE_{max}$ in Oklahoma was
476 explained less by population-level differences, but rather maternal family-level differences were
477 most important. Similarly, variation in NDNI was accounted for by subpopulation (mother tree
478 site) level differences to a higher degree than the population level differences. The variation in
479 NDNI may be attributed to adaptation to local nutrient availability of the mother tree. Genetic
480 differentiation in drought related traits in oak common gardens has previously been indicated to
481 be lower than for phenological traits, consistent with our results (Torres-Ruiz et al., 2019). NDNI
482 and $iWUE_{max}$ in Oklahoma were explained less by population-level differences, but rather
483 maternal family-level differences were most important for $iWUE_{max}$, and NDNI was partially
484 accounted for by subpopulation (mother tree site) level differences. The variation in NDNI may
485 be attributed to adaption to local nutrient availability of the mother tree.

486 **Growth and photosynthetic traits were correlated with survival in the middle garden**

487 Higher survival, growth rates and fitness in the Illinois garden for all populations were
488 likely a consequence of productive soil conditions and intermediate climate that alleviate stress
489 found in more extreme ends of the species' range. Previous work in another North American

temperate oak species (*Quercus rubra*) suggests that autumn frost damage at northern range limits leads to reduced growth in southern seed sources (Lindback et al., 2023), which is likely the cause of the negative growth observed in *Q. macrocarpa* from Oklahoma planted in the Minnesota garden, and we did indeed observe top-down dieback of stems in the Minnesota garden, particularly for the OK population. The lower growth rates of all populations observed in the Minnesota and Oklahoma gardens compared to Illinois may be also explained by reduced absolute rates of carbon fixation over the growing season. Photosynthetic rates are lower for the MN and IL populations in the Oklahoma garden, likely in response to stressful climatic conditions—such as increased aridity stress (Chaves, 1991).

Stressful conditions can also shift carbon allocation away from growth toward drought stress responses, and defense (Wang et al., 2024). We found correlations between growth and survival in Illinois garden, in which all populations expressed highest fitness, likely due to its relatively mild climate and loamy soils. Previous work in the European pedunculate oak, *Quercus robur,* indicates that differences in soil conditions and water availability across sites with similar climate regimes lead to variation in productivity (Buras et al., 2020). Growth and survival were not correlated in Oklahoma, where drought and high temperature stress were highest, and the fine textured silty-clay soils in Oklahoma may be less conducive to nutrient access. Growth was also not correlated with survival in Minnesota, which has the longest, coldest winters of the three gardens, along with nutrient-poor sandy soils. This decoupling of growth and survival in the hottest and coldest gardens may be a consequence of resource allocation trade-offs under increased stress that improves survival at the expense of growth rates (Bazzaz et al., 1987; Willi & Van Buskirk, 2022).

In addition, we found that $A_{max}$ was correlated with growth but not survival in all of the gardens. Leaf chlorophyll content was also correlated with growth in the Illinois garden, indicating that carbon assimilation and light energy acquisition through photosynthesis were important for growth, particularly in Illinois. In fertile sites, relative growth rates and photosynthetic rates tended to be higher, as was the case in the Illinois garden, where conditions were favorable (Lambers & Poorter, 1992). Survival and growth were higher in the less stressful Illinois garden compared to the Oklahoma or Minnesota garden. Moreover, the two most stressful gardens exhibited little difference from each other in growth or survival between the two, further supporting the Illinois garden as a favorable habitat for bur oaks, where aridity and cold stress are alleviated. In the Illinois garden, the oaks were able to allocate most of their carbon toward aboveground growth, which in turn improved survival. On the other hand, in the less favorable conditions of Minnesota and Oklahoma, survival likely depended on allocating carbon elsewhere, such as root growth or defense against herbivory (Coley et al., 1985; Poorter et al., 2012).

**Variation in season length helps explain carbon assimilation and growth patterns**

Differences in growing season lengths along the latitudinal gradient also played a role in the populations' photosynthetic and growth responses. The Oklahoma garden has the longest growing season which allowed the trees ample time to acquire carbon and grow. However stresses during the growing season such as drought may reduce carbon acquisition by forcing stomatal closure and decreasing carbon assimilation (Flexas et al., 2004; McDowell et al., 2008). The Oklahoma population had higher fitness in the Oklahoma garden compared to other populations and was likely adapted to the hot conditions during the prolonged growing season there , sustaining carbon assimilation at relatively higher rates compared to the other populations.

On the other hand, the northern populations that originated from shorter growing seasons tended to have higher $A_{max}$ rates than the Oklahoma population in the northern gardens, which is similar to findings in a *Betula pendula* providence trial in which northern populations had greater net photosynthesis (Tenkanen et al., 2021). The northern populations showed reduced growth and photosynthesis in the high aridity and heat in the Oklahoma garden, which prevented them from taking advantage of the longer growing season. In this study, we estimated growth in aboveground biomass, however it is also plausible that the northernmost population from Minnesota allocated more biomass to root growth than to aboveground biomass, leading to smaller trees with lower aboveground growth, as has been shown in *B. pendula* (Tenkanen et al., 2021). The Oklahoma population tended to maintain a relatively low rate of carbon assimilation across gardens; compared to the other populations in the northern gardens, it showed the lowest carbon assimilation rate, in accordance with leaf economic expectations where leaves with longer life spans are theoretically expected and empirically demonstrated to have slower rates of photosynthesis across species (Chabot & Hicks, 1982; Wright et al., 2004). $A_{max}$ and relative growth rate peaked at intermediate growing season lengths found in the Illinois garden likely due to trade-offs in optimizing carbon dynamics for leaf economics and stress tolerance in the other gardens (Fig. S6).

**Multiple environmental factors vary across gardens**

An outdoor common garden experiment such as ours, with unmanipulated soils, cannot isolate climate as the sole factor that varies among sites. Edaphic factors, as well as unmeasured factors such as the microbial environment, also vary substantially. The Illinois garden had high soil nitrogen  and organic matter content. Leaves from plants across populations in the Illinois garden had higher spectrally detected nitrogen content (NDNI). Nitrogen is a major component

of photosynthetic chemistry, including RuBisCo, and chlorophyll, and is correlated with higher photosynthetic rates (Ellis, 1979; Evans, 1989; Luo et al., 2021). Total soil nitrogen concentration was similar between the Illinois and Oklahoma gardens, but the less arid and slightly cooler climate in the Illinois garden combined with the high soil nitrogen and soil organic matter of the loamy soil as an environment that is conducive to bur oak carbon assimilation and fitness. We also note that of the three gardens, Illinois had the least change in growing season temperature since 1940. The fertile soil and relatively stable, mild climate of the region near the Illinois garden may provide important habitat for bur oak populations to grow with ongoing climate change. Controlled environment experiments that isolate climate as the driving variable for performance changes in bur oaks are an important next step in predicting response of bur oak populations to climate change.

## Conclusion

Findings from the ACE reciprocal transplant experiment provide context for assisted migration aimed at improving resilience of northern tree populations in the face of climate change. Our results indicate that northern bur oak populations may suffer increasing mortality in the face of climate change. We found evidence that the northern population was poorly adapted to hotter conditions in the south, but populations originating from warmer southern climates performed better than the northern population in the hottest garden. These findings indicate that southern locations may provide valuable seed sources to augment exisiting genetic variation in northern regions in the face of ongoing climatic warming. Consideration of current climate conditions alongside future climate conditions are important in decisions to move locally adapted populations. It may be beneficial to ensure seeds are sourced from locations with varied climates to accommodate fluctuations in climate. We found that in the coldest, most northern climate, the

southern population performed the worst, suggesting that assisted migration of southern populations northward must be timed with the pace of climate change. The lack of evidence for local adaptation in northern populations indicates that the expected change in climate may be within the tolerance limits of existing populations in the north. Mild climate warming akin to that experienced by the MN populations in the Illinois garden may even improve performance and fitness in the case of bur oak. In addition, other environmental factors that can impact growth and survival must be accounted for in assisted migration planning. For example, limitations in soil nutrient availability, and variation in competitive ability in different soil types may impact growth and survival, even if seed sources and climates are well matched. We did not test performance under competition with other species nor explicitly vary edaphic environments across climates, however, the performance of oaks across contrasting edaphic environments in competition with other tree species is an important area of investigation for future studies.

## Acknowledgements

We would like to thank those without whom the work presented here could not have been done. We thank Kris Bachtell, Cathy Bechtoldt, Brett Fredericksen, Marlene Hahn, Troy Mielke, Maria Park, Senna Robeson, Allison Scott, Nick Stoynoff, the Cedar Creek Ecosystem Science Reserve, Morton Arboretum Facilities and Natural Resources staff, The Kessler Atmospheric and Ecological Field Station staff for help establishing the common garden. We thank the Indiana Department of Natural Resources Vallonia Nursery for use of their facilities and help with harvesting seedlings. Field assistants including Iris Cessna, Isaiah Clark, Allison Collins, Nick Duncan, Rachel Gowett, Jennifer Hamann, Leah Hill, Keion Mackey, and Morton Arboretum volunteers were assisted with data collection. Ruth Shaw provided instruction on aster modelling and provided edits on an earlier version of the manuscript. We acknowledge funding from

ASCEND Biological Integration Institute (NSF DBI 2021898), the National Science Foundation Dimensions of Biodiversity grant (NSF DEB 2129312 (UMN), 2129281 (MOR), and 2129236 (UO)), the Morton Arboretum Center for Tree Science, and Cedar Creek Ecosystem Science Reserve Long Term Ecological Research Program through NSF DEB 1831944.

**Author Contribution Statement**

All authors contributed intellectually to the study. JCB designed the ACE experiment and managed its implementation. JCB, AH, HRM managed the collaboration and secured funding for the study. LMSR lead data collection, analysis and interpretation, and writing of the manuscript. JCB led nursery planting. CL, LW, and MG led planting efforts in the gardens. LO, RM, MG, LW, and CL collected data. JCB, AH and HRM edited early versions of the manuscript. All authors provided critical revision of the article and provided final approval of the version to be published.

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# Tables

*Table 2.1.* Soil properties in each of the three gardens.

| Garden | % Nitrogen | % Carbon | C:N | Soil texture |
|---|---|---|---|---|
| MN | 0.06 | 1.04 | 21.32 | Sandy loam |
| IL | 0.25 | 3.54 | 14.12 | Sandy clay loam |
| OK | 0.30 | 3.33 | 11.21 | Silty clay loam |

## Figure captions

*Figure 1.* Reciprocal transplant garden design and climate information. In the top panel (a), the experimental design of the Adaptation to Climate and Environment (ACE) experiment is depicted. Three common gardens are located across a latitudinal gradient in Minnesota (Cedar Creek Ecosystem Science Reserve), Illinois (Morton Arboretum), and Oklahoma (Kessler Field Station). In each garden, 600 seedlings were planted representing the three populations from Minnesota (blue), Illinois (green) and Oklahoma (orange). Each population was comprised of 20 half-sibling maternal families, with half-sibling acorn progeny collected from one known mother tree. Ten progeny from each family were planted in each garden. Photos in each site were taken in summer of 2022 after one year of planting. In the bottom panel, ERA5 monthly climate data averaged over the years 2021-2023 is shown for temperature (b), total precipitation (c), and the index of moisture (d). Colored lines indicate gardens: Minnesota (blue), Illinois (green) and Oklahoma (orange).

*Figure 2.* Fitness, fitness components, and physiology in each garden. Each panel represents the common garden located in Oklahoma (OK), Illinois (IL), or Minnesota (MN). Progeny from each source population are represented by orange circles for OK, green triangles for IL, and blue squares for MN, with larger points indicating population means. Distinct letters denote statistical significance ($p<0.05$) for each population group. Percent survival is represented by a point for each maternal family (a), and was highest for the local OK population in OK, but was similar among all populations in the northern gardens. The relative growth rate of stem volume for individuals (b) was also highest for the local population in OK, with the lowest growth rates occurring in MN. Aster expected fitness (c) is represented by a point for each population, and was highest in the Illinois garden. Aster fitness significance was determined by omnibus tests of population*garden interactions. Maximum CO2 assimilation ($A_{max}$) (d) of the local populations was highest for the OK and MN garden, but overall the IL garden had the highest $A_{max}$. Spectral chlorophyll normalized difference index (ChlNDI) (e) was also higher overall in the IL garden for all populations, though the local MN population was highest in the MN garden. Normalized difference of the nitrogen index (NDNI) (f) indicates that leaf nitrogen was highest in the Illinois garden.

*Figure 3.* Comparisons of growth, survival, and physiology to understand shifts in carbon allocation. Each panel represents a common garden located in Oklahoma (OK), Illinois (IL), or Minnesota (MN). The populations are represented by an orange circle for OK, a green triangle for IL, and a blue square for MN, with significant trendlines (with standard errors) in matching colors. a) Percent survival by maternal family is significantly positively correlated with relative stem volume growth for all populations in the Illinois garden, but not in the OK or MN gardens.

$A_{max}$ has significant relationships with growth (b) for OK and IL populations in all gardens, and for the MN population in the IL garden. Chlorophyll normalized difference index (ChlNDI) was significantly positively correlated with relative growth rate (c) in IL for all populations, and was significantly correlated with growth in the MN garden for the IL and MN populations.

*Figure 4.* Phenology and growing season length in each of the gardens. Each panel represents a common garden located in Oklahoma (OK), Illinois (IL), or Minnesota (MN). The populations are represented by an orange circle for OK, a green triangle for IL, and a blue square for MN. Budburst (a) occurs earlier in the OK and IL garden for all populations than in the MN garden, and senescence (b) occurs latest in the OK garden. The growing season length (c) is shortest in the MN garden and longest in the OK garden.

*Figure 1.*

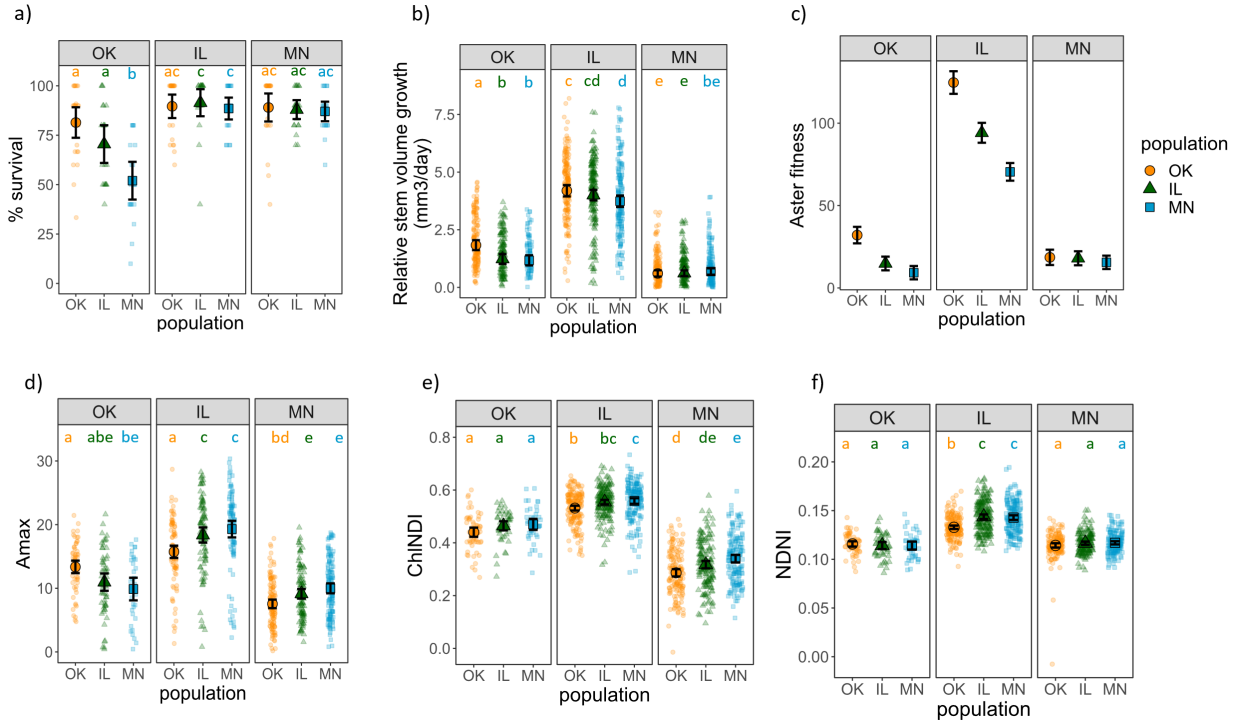
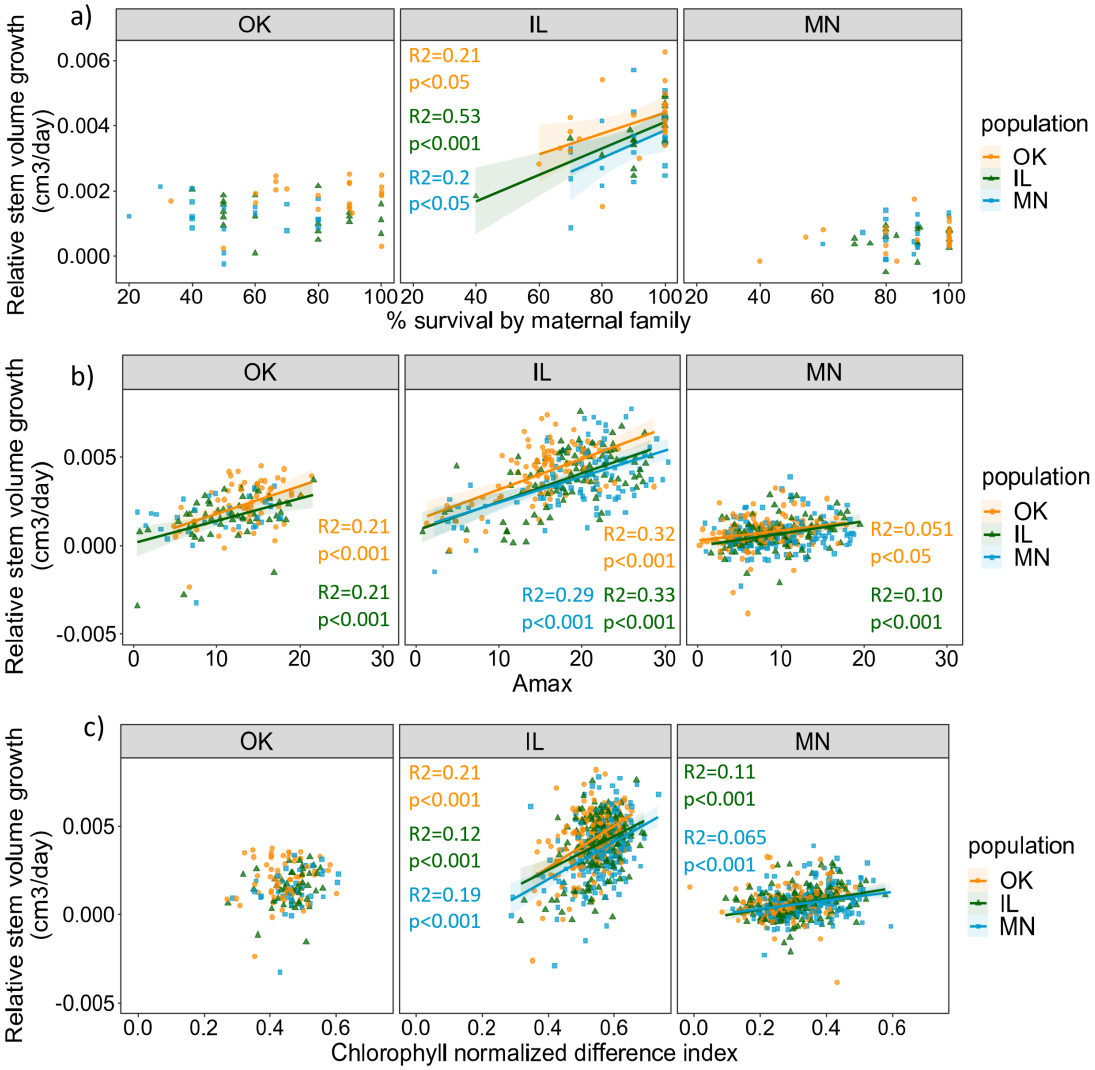
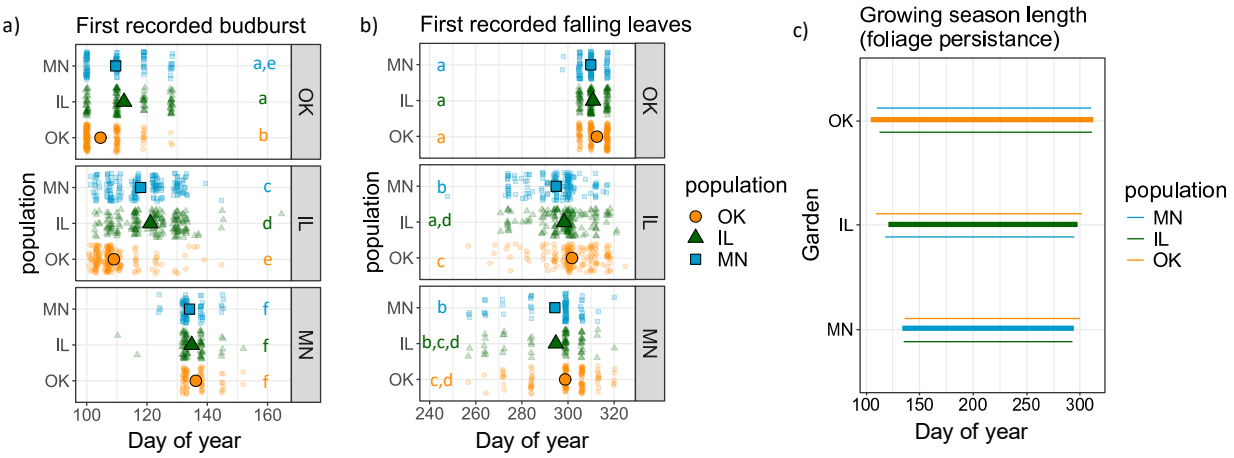



*Figure 2.*




933

934 *Figure 3.*

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936 *Figure 4.*