THE EFFECT OF HEIGHT AND SEED PROVENANCE ON EARLY FLOWERING IN BUR OAKS (*QUERCUS MACROCARPA*)

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Abstract. Bur oaks (*Quercus macrocarpa*) are long-lived trees that often require two to three decades to mature from seedlings. The rate at which they do so may depend on how rapidly they grow, as maturity is often correlated with height. Many woody monoecious species, like pines and birches, often produce only staminate flowers in their first year of maturity. Using our common garden of 600 bur oak trees from three states (Oklahoma, Illinois, and Minnesota), we asked how long it took for trees to reach maturity, whether maturity was correlated with height, and what types of flowers trees produced early in maturity. We found that 18% of trees flowered after six years of growth and 40% after seven years of growth. Within each population, height was positively correlated with flowering. However, the population with the tallest trees (Oklahoma) had the smallest percentage of trees flowering. Surprisingly, many of the trees produced only pistillate flowers. Our findings suggest that the relationship between maturity and height differs genetically in the Oklahoma population compared to the Illinois or Minnesota populations. Additionally, our finding that bur oaks from all three populations produced pistillate flowers prior to staminate flowers raises questions about the generality of trade-offs between resource availability and allocation to reproduction in flowering plants, in which pistillate flowers are generally assumed to be more costly.

Keywords: acorn, common garden, maturity, pistillate flowers, staminate flowers

Time to reproductive maturity can vary widely among long-lived tree species and among individuals of the same species (Bonner and Karrfalt, 2008; Goelz and Carlson, 1997). This time period—the age of first seed set—has a wide range of biological effects, including migration rates, adaptability, and fitness. Tree maturity and seed set may shape a tree's fitness through their impact on the number of reproductive years and offspring. The time to maturity also has important applications, from estimating the time needed for breeding new cultivars (Cecich, 1993) to estimating migration rate under different climate variation models (e.g., Chen et al., 2021; Leroy et al., 2020). Earlier acorn production also leads to earlier ecosystem services in the form of food for wildlife, which can be a motivating factor for tree planting (Burns and Honkala, 1990; Whittemore, 2004).

Long-lived oaks (*Quercus* L.) are generally presumed to take two to three decades or longer to reach first seed set (e.g., Ducousso et al., 1993), and authors have commonly used 50 years as the average generation time in oak population genetic studies (e.g., Chen et al., 2021; Leroy et al., 2020). The USDA's influential *Woody Plant Seed Manual* (Bonner and Karrfalt, 2008; United States, 1948) reports 35 years as the minimum seed-bearing age (with the older 1948 publication using the term "minimum commercial seed-bearing age" although this was never defined) for bur oak (*Quercus macrocarpa* Michx.) and a range of 15–25 years for most other eastern North American oak species (with

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one exception: *Q. texana* Buckley has a reported minimum seed-bearing age of 5 years). These estimates from the horticultural literature are largely supported by studies in natural populations. In natural forests in Louisiana and Texas, for example, oaks (cow, white, post, blackjack, sandjack, southern red, and water oaks) less than 20 years old produced few, if any, acorns (Goodrum et al., 1971)—which matched minimum seed-bearing ages reported in Bonner and Karrfalt (2008). However, variation among populations is not known.

More broadly, height is directly correlated with maturity in some tree species and is often used as a proxy for fitness (Alía et al., 2024). Consequently, environmental conditions that increase growth can incidentally lead to faster maturation. This plasticity in time to maturity has been used to speed up selection and breeding trials (Cecich, 1993). However, time to maturity also has a genetic component (Cecich, 1993; Johnsson, 1949). For example, in natural forests on western Honshu Island, Japan, smaller trees in two species of *Q.* sect. *Cerris* Loudon did not produce flowers, whereas in two species of *Q.* sect. *Quercus* even the smallest trees produced flowers (Hirabayashi et al., 2023). Teasing apart the effects of plasticity and genetic variation on maturation is essential for understanding how young trees may respond to transplanting or shifts in environment and climate.

Monoecious species such as oaks may regulate pistillate and staminate flower production separately in response to the environment. Previous research suggests that pistillate flower production can be affected by changes in growing conditions, while staminate flower production remains constant. In *Quercus alba* L. and California white oaks (*Quercus* subsection *Dumosae* (Trel.) A.Camus), the number of pistillate flowers varied annually, whereas staminate flowers showed little variation (Cecich, 1993; Knops and Koenig, 2012), suggesting that pistillate flower production may be more influenced by the environment than staminate flower production. Similarly, for the western North American *Q. gambelii* Nutt., trees in xeric habitats produced fewer pistillate flowers than trees in mesic habitats while the number of staminate flowers remained the same (Freeman et al., 1981). In a study plot of genetically precocious *Betula verrucosa* Ehrh., 431 trees produced staminate flowers only, 31 were monoecious, and two produced pistillate flowers

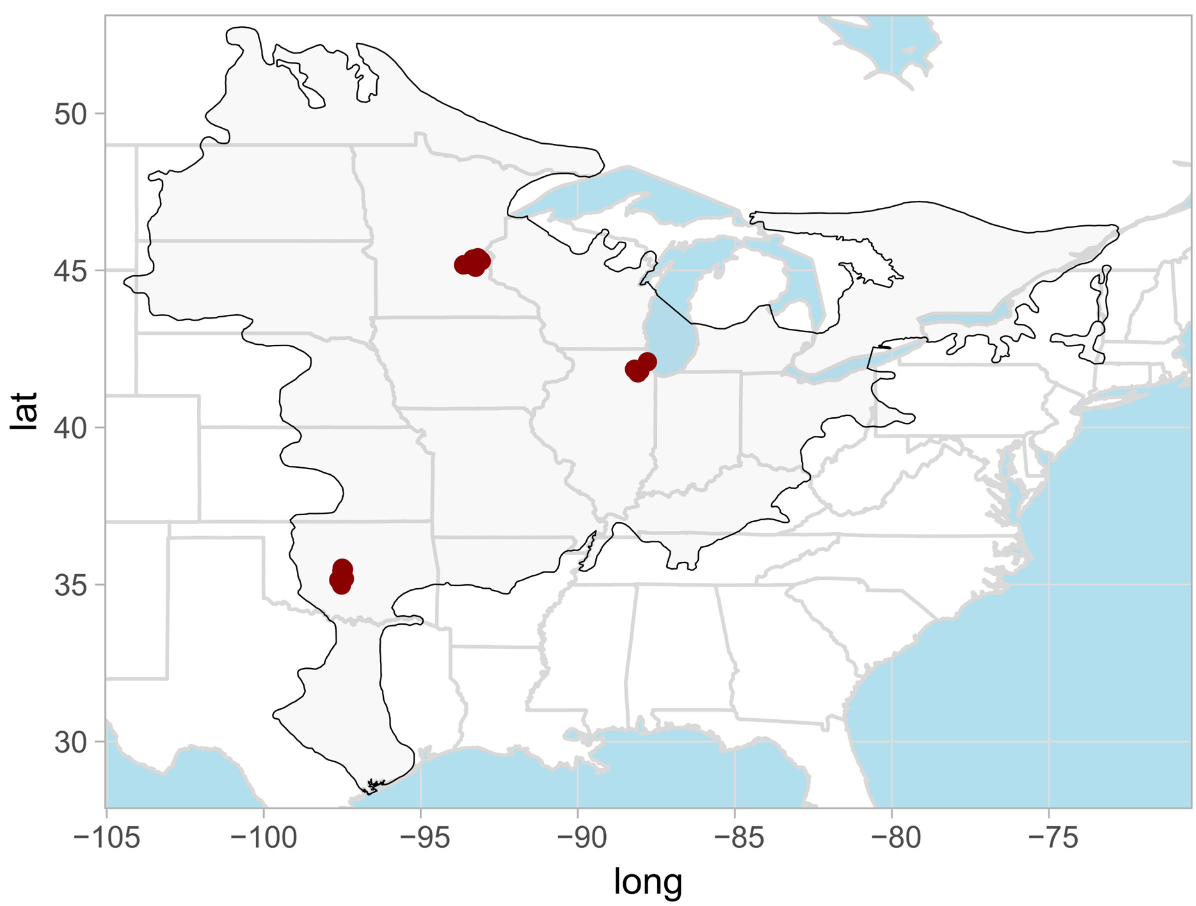

FIGURE 1: Common garden acorns were sourced from roughly 20 trees in Minnesota, Illinois, and Oklahoma (red dots) within the species range of *Quercus macrocarpa* (black outline).

only (Johnsson, 1949). In dioecious species, male *Ilex opaca* Aiton matured in fewer years than female trees (Clark and Orton, Jr., 1967), and small, young *Bischofia javanica* Blume produced staminate flowers, whereas large mature trees tended to produce pistillate flowers (Yamashita and Abe, 2002). Given the trends of consistent pollen production each year in oaks, young birch producing staminate flowers only, and faster maturation of male than female dioecious trees, we might anticipate that younger trees would produce only staminate flowers or both pistillate and staminate flowers.

Alternatively, taller, older trees might be better pollen dispersers, which, coupled with the phosphorus (P) and nitrogen (N) costs of pollen production, might lead to selection for greater pistillate flower production when trees are younger and shorter. While pistillate flowers of *Q. gambelii* vary with growing conditions, taller stems in clonal stands of the same species had a larger increase in staminate flowers per branch than pistillate flowers (Freeman et al., 1981). Additionally, staminate flowers of Asian oaks exhibit 3–4 times higher concentrations of P and N by weight than the fruiting structures (Wang et al., 2023). However, interpretation of this difference in P and N concentrations is limited by the lack of data on the weight of staminate flowers versus acorns produced.

Reports of trees that produce only female reproductive structures in the first year of maturity are limited to pines, another genus with wind-dispersed pollen. Some pines (*Pinus L.*) produce female cones on younger growth, which results in female cone production before pollen cone production (Giertych, 1976; Wareing, 1959). Occasionally, precocious pollen cone production occurs before seed cone production (Giertych, 1976). Young *Pinus halepensis* Mill. produces female cones before male cones, possibly as an adaptation to the risk of mortality due to canopy fires (Ne'eman et al., 2004; Santos-del-Blanco et al., 2010). Young, potentially isolated trees that produce seed cones can receive pollen from distant mature trees that escaped the fire and thereby produce seed and maintain the population before another fire occurs (Ne'eman et al., 2004). Such limitations of pollen dispersal might result in trees producing female flowers or cones first when they are small, understory trees. Male flowers or cones might develop once the trees are larger or have established canopy dominance. Despite staminate and pistillate flowers potentially arising in separate years, trees are generally considered to be mature upon the first production of a reproductive structure (Giertych, 1976).

Quercus macrocarpa is a long-lived, widespread, eastern North American tree (Fig. 1) valued for its wood and ability to tolerate dry conditions and poor air quality (Burns and Honkala, 1990; Fowells, 1965). In addition, its acorns provide food for rodents, deer, birds, and insects (Burns and Honkala, 1990). This species dominates or co-dominates in oak savannas, especially in the upper Midwest (Cavender-Bares and Reich, 2012; Leach and Givnish, 1999), where pollen movement appears to interconnect even distant populations (Craft and Ashley, 2007, 2010). Like all members of the genus, bur oak is monoecious and wind-pollinated, bearing staminate flowers on dangling catkins that emerge from the base of new growth, and pistillate flowers in the leaf axils (Fig. 2). Bur oak pistillate flowers mature into the iconic mossy-cupped acorns in the same season in which they are pollinated (Fig. 2). Generally, acorns from northern populations must be cold-stratified before emerging the following spring, while those from southern populations produce a radicle immediately (Bonner and Karrfalt, 2008; Burns and Honkala, 1990; Fowells, 1965).

In this study, we used a bur oak common garden to ask (1) whether provenance has a direct effect on time to first reproduction after accounting for height and (2) what sex of flowers were produced in the first year of flowering (staminate, pistillate, or both). To answer these questions, we measured tree height and diameter at breast height (dbh) in the fall of 2024 and collected weekly observations of flower presence in spring 2025 for approximately 600 six- to seven-year-old *Q. macrocarpa* trees. These trees were sourced from acorns collected in Oklahoma, Minnesota, and Illinois and grown in a common garden in Illinois. We hypothesized that the presence of flowers would be positively correlated with height, that more trees would flower in the population with taller trees (Oklahoma), and that more staminate-only rather than pistillate-only trees would be observed.

Materials and Methods

Garden Establishment

As described in Rea et al. (2024), we established a bur oak (*Q. macrocarpa*) common garden in Illinois. Briefly, in 2018 and 2019, acorns were collected from mother trees at sites in central Minnesota, northern Illinois, and central Oklahoma (Fig. 1). For ease of cultivation and transplanting, acorns were planted in sand in the Indiana DNR Vallonia Nursery (Vallonia, Indiana, USA) the same year they were collected and grown together for one to two years in beds labeled by mother tree. (Hereafter in this manuscript, trees will be referred to as "2018 trees" or "2019 trees" according to the collection year of the acorns from which they were grown.) In 2021, the seedlings were harvested, and 2018 seedlings were trimmed to be the same height as 2019 seedlings. A median of 10 seedlings (3–12) from each mother tree, totaling 200 trees from each state, were planted into a common garden at the Morton Arboretum (41°49'12" N, 088°05'34.8" W, Illinois, USA), spaced 1 m on center. Seedlings were watered each week for the first two growing seasons after transplanting in weeks when there was less than an inch of rain. They were also mulched and weeded. Replicate reciprocal transplant gardens were established in

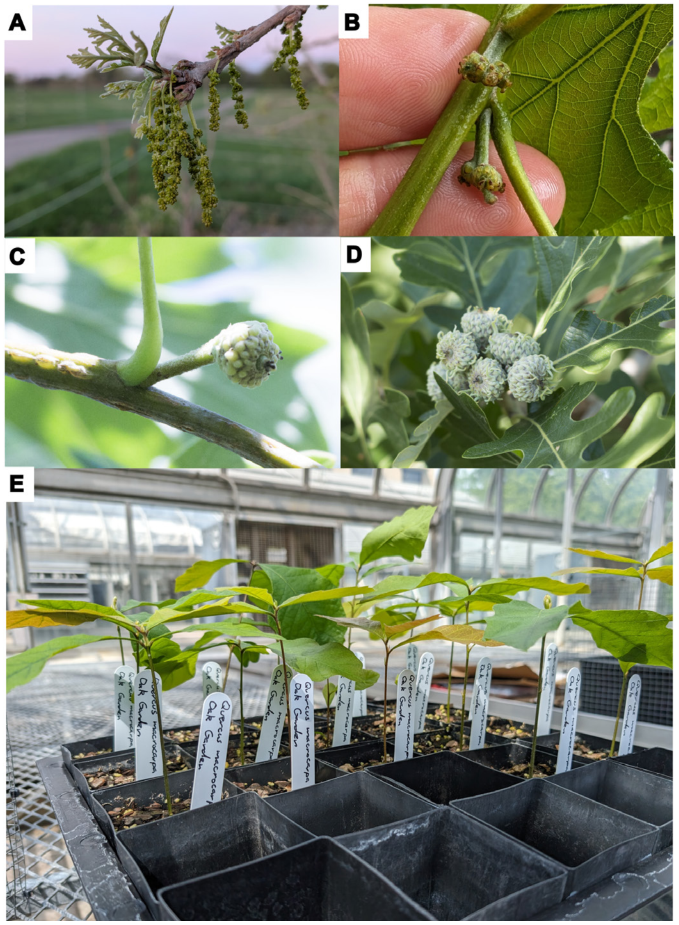

FIGURE 2: Reproductive cycle in *Quercus macrocarpa*: A, staminate catkins before pollen release (12 May 2025); B, pistillate flowers (16 May 2025); C and D, developing acorns (3 July 2025); E, young seedlings from 2023 acorns (21 May 2024).

central Minnesota and central Oklahoma, but these gardens were not included in this study, as they had not produced flowers at the time of writing.

A small number of plants (<5%) were identified visually in summer 2021 as having symptoms of *Phytophthora* de Bary, an oomycete that causes root rot. The pathogen was confirmed by culturing a subset of roots in August 2021. The soil around all 600 trees was treated using Subdue Maxx granular fungicide (Syngenta Global AG, Basel, Switzerland) in September 2021, with a repeat treatment in spring 2022.

In 2023, trees that had died in 2021 and 2022 were replaced, but only trees surviving from the original 2021 planting were considered in this analysis.

Growth Data Measurements

Height, diameter, and dbh of each tree were measured between 24 September and 8 October 2024. Height was measured in centimeters with a retractable tape measure, from the top of the root crown to the top apical bud. The diameter was measured in millimeters 5 cm above the ground with a Mitutoyo Digimatic caliper for trees less than 150 mm in diameter and rounded to the nearest 0.5 mm. Additionally, we measured dbh for trees taller than 4.5 ft (1.37 m) also using the Mitutoyo Digimatic caliper. Five trees were removed from the analysis due to evidence of transcription error, either because the diameter in millimeters was greater than the height in centimeters or because there was a recorded dbh despite the reported height being less than 1.37 m, suggesting that either the dbh or the height was incorrect.

Flower Data Collection

The trees were inspected for the presence or absence of pistillate and staminate flowers by trained observers once a week from 12 May 2025 to 9 June 2025. This ensured that trees that flowered at different times were not missed. Since pistillate flowers are much smaller and easier to miss than staminate flowers, trees with only staminate flowers were inspected an extra time for young acorns in July 2025. Any trees found to have acorns in this second inspection were then recorded as having staminate and pistillate flowers. All trees, regardless of flower presence, were monitored weekly for acorn development throughout the season.

Statistics

We tested whether Oklahoma trees had more flowers, whether trees that flowered were taller, and whether flower production was correlated with provenance and height. First, we used an odds ratio test (Fisher's exact test; fisher.test function in R v. 4.4.3; R Core Team, 2025) on all three state pairs—Oklahoma versus Illinois, Illinois versus Minnesota, and Minnesota versus Oklahoma—to test which state in each pair produced more flowers overall among 2018 and 2019 trees, as well as which state produced more trees with flowers, more trees with pistillate flowers, and more trees with staminate flowers among 2018 and 2019 trees separately. Next, to provide a heuristic of whether trees that flowered were significantly taller, we performed Tukey's test on an analysis of variance (ANOVA) in R to summarize differences between state, flower type, and height. To test whether flower production (presence or absence) was correlated significantly with provenance and height, we used the function glmer in the R package lme4 v. 1.1-36 (Bates et al., 2015) to fit generalized linear mixed-effects models with a logit (binomial) link to fit the binary flower production data. For each flower type (any flowers, catkins, and pistillate flowers), we tested four models with combinations of fixed effects: just scaled height, just state of origin, both scaled height and state of origin, and both scaled height and state of origin with the interaction term. For all four models, we included garden block and year collected as separate random effects. Mother tree identity was not used as a random effect, as it resulted in a warning. The Anova function in R package car v. 3.1-3 (Fox and Weisberg, 2019) was used to calculate ANOVA tables for the fitted glmer objects. We calculated AIC values for models using the AIC function from the base R stats package (Sakamoto et al., 1986). The AIC values were compared within flower type, and AIC*w* values were calculated following Burnham and Anderson (2002). To visualize the impact of height on reproduction in trees from the three states, the percentage of trees flowering was plotted against height binned into 50 cm height classes, using ggplot2 v 3.5.1 (Wickham, 2016). Further, we tested the significance of the percentage of trees flowering per bin with an odds ratio, Fisher's exact test for each size class between 125 and 325 cm.

Acorn Data Collection

Between 8 July 2025 and 19 August 2025, acorns developing on trees in the experiment were distinguished from aborted acorns and counted. Some acorns were eaten by squirrels before we were able to harvest, but the remaining acorns were collected upon ripening. Half of the trees were removed at the end of September, so at that time, any remaining acorns on their branches were collected regardless of whether they were ripe. Up to three acorns from each tree, depending on availability, were extracted from their caps and their height and diameter were measured. These were used to calculate volume using $V = 0.75\pi 0.5h(0.5w)^2$, where V is volume, h is acorn height, and w is acorn cross-sectional diameter. As a proxy for acorn biomass produced, we multiplied acorn volume by the number of acorns counted per tree.

Acorns collected in 2023 and 2024 were stored at approximately 4.4 C in moist sand until they were ready to be sown. In November of the same year, they were sown into potting media and left in a hoop house kept above 0 C to stratify over winter. In May, they were transferred to a greenhouse with temperatures kept between 15 C and 20 C to encourage germination. Acorns observed to be growing by the end of the growing season were considered viable.

Results

In 2023, we observed acorns developing on six bur oak trees in the Illinois common garden, but on four of those trees all the acorns aborted (Fig. 3). In 2024, we observed pistillate flowers on 12 trees in May and early June. In late June and the end of July, we found acorns developing on four additional trees, for a total of 16 trees that produced pistillate flowers. Even though staminate catkins are much larger and more obvious than pistillate flowers in bur oak (like all oak species), and despite the fact that we conducted careful, systematic phenology observations tree-by-tree throughout each spring of this study, no catkins were observed on any of the trees in 2023 or 2024. In spring 2025, we observed flower production on 49 of 121 (40%) 2018 trees and 76 of 417 (18%) 2019 trees, of which 57 trees had staminate flowers (with or without pistillate) and 118 had pistillate flowers (with or without staminate flowers). Later in the season as acorns developed, nine additional trees were found to have acorns (1 Illinois 2018, 1 Minnesota 2018, 2 Oklahoma 2019, 4 Illinois 2019, and 1 Minnesota 2019), but these were not included in analyses, except for reflowering (Fig. 3). Seventeen of the 20 trees that had flowered in 2023 or 2024 reflowered in 2025 (Fig. 3).

Flower Type

Of the 125 trees with flowers observed in spring 2025, 53 (41%) had both pistillate and staminate flowers and 67 (52%) had pistillate flowers only (Table 1). Nine trees (2%) were originally documented as having only staminate flowers during the 2025 flowering season, but two of these were later found to have young fruit, leaving seven trees with only staminate flowers. A higher percentage of Minnesota and Illinois 2018 trees had both pistillate and staminate flowers (18% and 29% respectively) than just pistillate

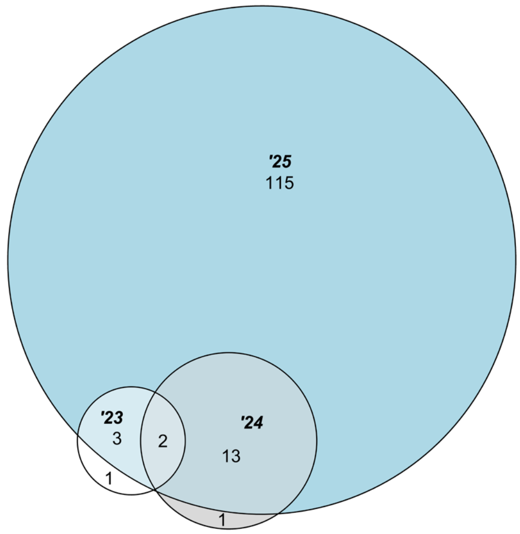

FIGURE 3: The overlap of trees flowering each year from 2023 to 2025. Five of six trees that bloomed in 2023 and 15 of 16 trees that bloomed in 2024 rebloomed in 2025.

flowers (14% and 21% respectively; Table 1). Oklahoma 2018 trees and all 2019 trees had more trees with pistillate flowers only (2019 Minnesota: 18%, 2019 Illinois: 8%, 2019 Oklahoma: 8%, 2018 Oklahoma: 13%) than trees with both pistillate and staminate flowers (2019 Minnesota: 8%, 2019 Illinois: 7%, 2019 Oklahoma: 4%, 2018 Oklahoma: 7%; Table 1).

Source of Tree

Across all years, trees sourced from Illinois or Minnesota had significantly more flowers than those from Oklahoma (Tables 1 and 2). Among the 2018 trees, Illinois trees had a significantly higher percentage of individuals flowering (54%) than Minnesota trees (34%). However, 2019 Minnesota trees (29%) had a significantly higher percentage of individuals flowering than 2019 Illinois or Oklahoma trees.

Height of Tree

Within each of the three tree sources (Minnesota, Oklahoma, and Illinois), flowering trees were significantly taller than non-flowering trees (Fig. 4). While Oklahoma trees were significantly taller overall (Fig. 4), a lower percentage of Oklahoma trees flowered (Tables 1 and 2).

To evaluate the significance of a correlation between flowering and tree height/state, we used linear mixed models that accounted for random effects of tree year and block. Generalized linear mixed models in which state and height together predicted the presence of any flower without an interaction term (AIC = 466.2, AIC*w* = 0.711) had similar support to the more complex models that included the interaction term (AIC = 468.0, AIC*w* = 0.289; Table 3). Models with just state (AIC = 561.8, AIC*w* = 1.24×10^{-21}) or just height (AIC = 507.6, AIC*w* = 7.20×10^{-10}; Table 3) as predictors were very poorly supported. Likewise, according to AIC estimates, the best model for pistillate flower presence included state and height without an interaction term (AIC = 439.8, AIC*w* = 0.871; Table 3). For staminate flowers, as for any flowers, the model without an interaction term (AIC = 313.9, AIC*w* = 0.630) had similar support to the model with an interaction term (AIC = 314.9, AIC*w* = 0.368; Table 3). R reported singular boundary warnings with the staminate flower models for both the full model with the interaction term and the model with height alone. The height + state model without the interaction term produced no warnings and, as the simplest model with a low AIC value for all flower types, was used to estimate the fixed effects. In all height + state models, the presence of flowers was positively correlated with height (any-flowers effect estimate = 1.51 [± 0.19 S.E.M.]; pistillate-flowers effect estimate = 1.67 [± 0.20]; staminate-flowers effect estimate = 1.25 [± 0.22]; Table 4). After taking height into account, Minnesota and Illinois trees did not differ significantly in catkin production. For all other flower types, Oklahoma had significantly fewer and Minnesota had significantly more trees with flowers present than Illinois (the intercept; Table 4). The difference between Oklahoma and Illinois was greater than that between Minnesota and Illinois (Table 4).

While trees sourced from Oklahoma were taller on average, less than 50% of trees in any height size class flowered. Alternatively, at least 50% of Minnesota trees in the size classes greater than 225 cm and Illinois trees in the size classes greater than 275 cm flowered (Fig. 5). This corresponds to significantly higher odds of flowering in Minnesota trees between 125–275 cm and Illinois trees between 225–325 cm compared to Oklahoma trees (Table 5).

Acorn Production and Viability

Even in their first, second, or third year of flowering, a few trees produced 100–500 acorns (Fig. 6). Although Oklahoma had the fewest trees flowering, the acorns produced were significantly larger than those from Minnesota and Illinois (Fig. 6), while Illinois trees produced significantly larger acorns than those from Minnesota. Despite this discrepancy in size, all states produced a similar volume of acorns (Fig. 6).

In 2023, 17 acorns were planted from one tree, which had an Illinois provenance, and all of them germinated (Fig. 2E). In 2024, a total of 19 acorns were planted—from two Minnesota, one Illinois, and four Oklahoma trees—and 12 of them germinated. The seven acorns that failed to germinate were from a single Oklahoma tree.

Discussion

After only six or seven years of growth, 42% (for 2018 trees) and 20% (for 2019 trees) of bur oak trees grown in the Illinois common garden produced flowers or acorns. However, less than half of the trees observed with flowers produced both staminate and pistillate flowers. Instead, the majority (54%) produced only pistillate flowers (Table 1). While height was correlated with flower production overall, the source population with taller trees (Oklahoma) had a smaller percentage of individuals flowering. This leads us to reconsider our hypotheses about the roles of height, pollen

	Count	OK		IL		MN		Totals	
		Count	Percent	Count	Percent	Count	Percent	Count	Percent
2018 Trees	Only pistillate flowers	2	13%	12	20%	7	14%	21	17%
	Only staminate flowers	1	7%	1	2%	0	0%	2	2%
	Both pistillate and staminate flowers	1	7%	16	27%	9	18%	26	21%
	Subtotal: Trees with flowers	4	27%	29	49%	16	32%	49	40%
	Subtotal: Trees without flowers	11	73%	30	51%	34	68%	75	60%
	Total Trees	15	100%	59	100%	50	100%	124	100%
2019 Trees	Only pistillate flowers	13	8%	10	8%	23	18%	46	11%
	Only staminate flowers	3	2%	0	0%	2	2%	5	1%
	Both pistillate and staminate flowers	6	4%	9	7%	10	8%	25	6%
	Subtotal: Trees with flowers	22	13%	19	15%	35	27%	76	18%
	Subtotal: Trees without flowers	147	87%	108	85%	93	73%	348	82%
	Total Trees	169	100%	127	100%	128	100%	424	100%

Table 1: Number flowering trees by origin in the Illinois common garden.*

*Note: Most trees with flowers present had either pistillate flowers or both pistillate and staminate flowers. Numbers of trees in the Illinois common garden in 2025 are given by state of origin (Illinois [IL], Minnesota [MN], or Oklahoma [OK]) and flower type. Percentages were calculated as the number of trees in each category divided by the total number of trees from the state and acorn collection year. See Table 2 for comparisons of flower type per year.

	Odds ratio by flower type		
	IL:OK (p-value)	**IL:MN (p-value)**	**MN:OK (p-value)**
2018 any pistillate flowers	3.60 (0.073)	2.25 (0.049)	1.61 (0.739)
2018 any staminate flowers	5.57 (0.096)	2.22 (0.111)	2.51 (0.670)
2018 any flowers	3.87 (0.070)	2.41 (0.031)	w1.61 (0.739)
2019 any pistillate flowers	1.33 (0.483)	0.49 (0.029)	2.70 (0.002)
2019 any staminate flowers	1.30 (0.630)	0.72 (0.502)	1.81 (0.253)
2019 any flowers	1.12 (0.737)	0.45 (0.014)	2.48 (0.003)
Any flowers	2.14 (0.006)	0.88 (0.635)	2.43 (0.001)

TABLE 2: Odds ratio (p-value in parentheses) for flowering types between populations in Illinois (IL), Minnesota (MN), and Oklahoma (OK). Flower production varied significantly based on tree year and state.

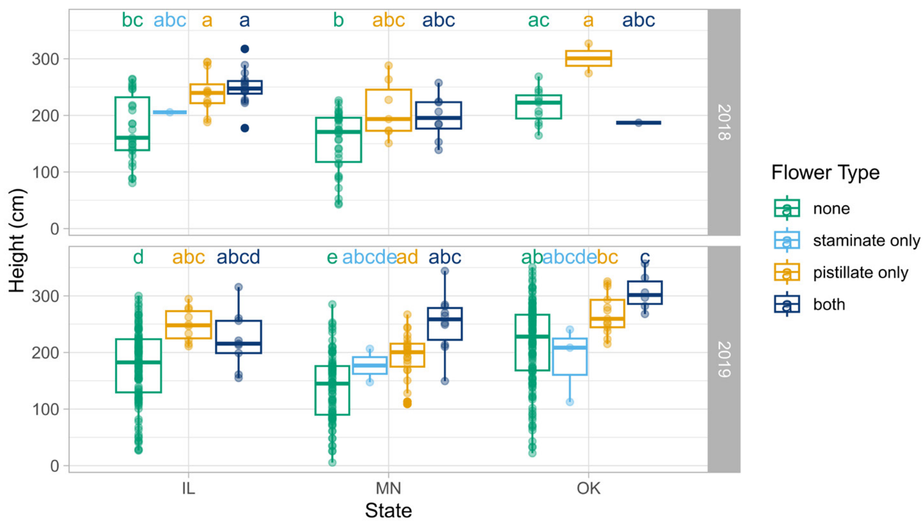

FIGURE 4: Flowering trees trend taller. Distribution of tree height by flower type in 2025. Letters indicate significant differences within each year. None of the Minnesota (MN) 2018 trees, Oklahoma (OK) 2018 trees, or Illinois (IL) 2019 trees had staminate flowers without pistillate flowers.

dispersal, climate, and environmental cues in controlling the timing of maturation and order of flower production in *Q. macrocarpa*.

Quercus macrocarpa Trees Can Mature and Produce Viable Acorns in Less Than 10 Years Under Ideal Growing Conditions

In previous studies of natural populations of two eastern North American white oak species, *Q. alba* and *Q. stellata* Wangenh., acorn production in trees less than 20 years old was negligible (Goodrum et al., 1971). For the minimum dbh size class (7–8.9 in for *Q. alba* and 3–4.9 in for *Q. stellata*), 38% and 41% of trees produced acorns and were expected to yield on average 0.5 lbs. or 51 acorns and 0.7 lbs. or 197 acorns, respectively. By contrast, some of our *Q. macrocarpa* trees matured and produced viable acorns at only five years old. Of the seven-year-old *Q. macrocarpa* trees—all of which have less than 2-in dbh—42% produced flowers, and 14 of these yielded over 51 acorns each (Fig. 6). We suspect that this is not due to a younger minimum seed-bearing age in *Q. macrocarpa* (reported to be 35 years) relative to *Q. alba* (reported to be 20 years; Bonner and Karrfalt, 2008), but rather to the effect of growing conditions on age of maturation. The importance of growing conditions is further supported by the replicate common gardens planted in Minnesota and Oklahoma. Both were planted with the same design, at the same time, and from the same source trees as the Illinois garden. YYet, thus far neither the Minnesota nor the Oklahoma garden has observed any flower production. Tellingly, trees planted in the Minnesota and Oklahoma gardens average 28% and 49% the height of the trees in the Illinois garden, respectively. The faster growth in the Illinois garden is likely a factor of moderate abiotic factors, such as warmer winters than Minnesota, cooler summers than Oklahoma, and richer soils and fewer weeds than both Minnesota and Oklahoma. Despite being long-lived and considered slow-growing (Fowells, 1965), *Q. macrocarpa* is able to reach maturity and produce viable acorns quickly in ideal conditions. Similar rapid maturation under cultivated and transplant conditions has been observed in *Quercus rubra* L. (Kormanik et al., 2004).

Height Plus Population Predicts Flowering in Q. macrocarpa

We observed a positive correlation between flowering and height within each population. This supports the hypothesis of an ontogenetic effect regulating flowering within each population—that faster growth leads to faster maturity (Cecich, 1993). However, population of origin also had a significant effect on flowering (Tables 3 and 4), as illustrated by the fact that the tallest population (Oklahoma) produced significantly fewer flowers than the other two populations (Table 2). In other words, we found that, at a young age, tree height and tree state of origin together predicted flower presence better than height alone, which highlights the importance of long-term studies on seed source location and fitness.

A positive correlation between height and onset of flowering has also been documented in several pines, including *Pinus banksiana* Lamb. (Cecich, 1993), *P. pinaster* Aiton (Santos-del-Blanco et al., 2010, 2012), and *P. halepensis* (Santos-del-Blanco et al., 2010). Similar to our findings (Fig. 5), Santos-del-Blanco et al. (2010) found that the threshold size for reproduction varied with population of origin. These findings suggest that there are genetic differences regulating the time to tree maturity. In bur oaks, genetic differences observed between the north and south subpopulations of *Q. macrocarpa* (Ribicoff et al., 2025) may include functional differences in age to first flower. However, we did not rule out a potential maternal effect in height causing this difference (i.e., that the large acorns in Oklahoma resulted in the height difference).

More work is needed to disentangle what drives differences in height of flowering individuals between trees of different state origins. It could be influenced by several factors, including differences in investment in acorns affecting the size of the resulting trees, flowering allocations that are adaptive to present environments, past selection (for example due to migration during glaciation), or a site-specific phenomenon resulting from environmental cues unique to the Illinois garden replicate. If selection during rapid migration northward were driving the difference in age to first reproduction, we might expect a higher variance in the age of first flowering in Oklahoma and less variance in northern populations. If climate selected for height at reproductive age, we might expect lower variance in time to maturation in more extreme climates and no change in time to maturation among more northern or southern

Model (year collected and block are random effects for all models)	**AIC**	**AIC*w***
flowers ~ state + height	**466.2**	**7.11×10^{-1}**
flowers ~ state + height + state * height	**468.0**	**2.89×10^{-1}**
flowers ~ height	507.6	7.20×10^{-10}
flowers ~ state	561.8	1.24×10^{-21}
pistillate ~ state + height	**439.9**	**8.71×10^{-1}**
pistillate ~ state + height + state * height	443.6	1.29×10^{-1}
pistillate ~ height	487.5	3.72×10^{-11}
pistillate ~ state	544.9	1.28×10^{-23}
catkins ~ state + height	**313.9**	**6.30×10^{-1}**
catkins ~ state + height + state * height	**314.9**	**3.68×10^{-1}**
catkins ~ height	325.8	1.60×10^{-3}
catkins ~ state	351.8	3.64×10^{-9}

Table 3: AIC and AIC*w* values for state and height models for the presence of flowers, pistillate flowers, and catkins*

* Note: The presence of any flowers, pistillate flowers, and catkins is best explained by state + height models. All models evaluated included tree year and block as random effects. Generalized linear mixed models with a logit regression were evaluated, and the AIC was calculated to compare models. Models supported by AIC are in bold.

Model	height		(Intercept)		Oklahoma state		Minnesota state		1|block n = 6		1|year n = 2	
	est.	SE	est.	SE	est.	SE	est.	SE	var.	SD	var.	SD
flowers ~ state + height	1.51	0.19	-1.34	0.37	-1.43	0.33	0.91	0.29	0.05	0.22	0.17	0.41
pistillate ~ state + height	1.67	0.20	-1.45	0.39	-1.65	0.35	0.96	0.30	0.05	0.22	0.19	0.43
catkins ~ state + height	1.25	0.22	-2.14	0.43	-1.40	0.44	0.35	0.36	0.00	0.00	0.23	0.47

TABLE 4: Estimates of fixed effects and variance of random effects for the state + height models.*

* Note: The simplest model among the AIC-inferred best models for each flower type (Table 3) show that height has a positive effect estimate on flower presence. All models were tested with a generalized linear mixed models and a logit regression with tree year and block included as random effects. Estimates (est.) and standard error (SE) are presented for fixed effects and variance (var.), and standard deviation (SD) are presented for random effects.

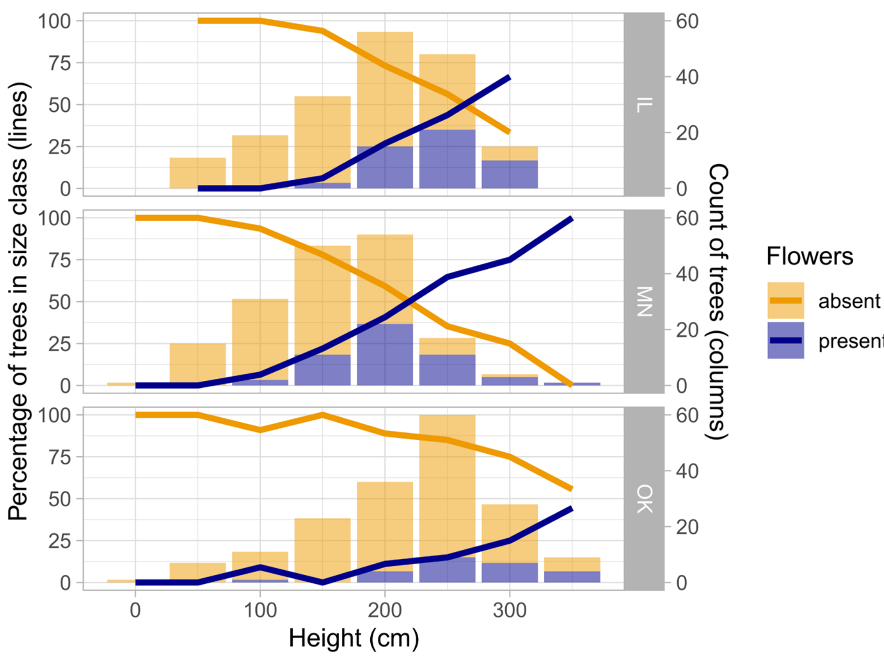

FIGURE 5: Percentage of trees flowering in 50 cm height classes (lines) and the total number of trees in each size class (columns). Illinois (IL) and Minnesota (MN) trees, despite being shorter on average than Oklahoma (OK) trees, have height classes where ≥ 50% of trees are flowering (IL 300 cm; MN 225 cm), while no OK size class reaches 50% flowering. For significance, see Table 5.

common gardens. If differences between the environmental conditions and the required cues resulted in differences between populations in the Illinois garden, we would expect to see changes in which locally-provenanced trees flowered first in the Oklahoma and Minnesota common gardens.

Pistillate Flower Production Early in Maturity

Our finding of pistillate-only flower production by young *Q. macrocarpa* did not meet our expectations based on previous studies. *Quercus alba* and *Q. gambelii* both vary in pistillate flower production but not staminate flower production depending on year and habitat respectively (Cecich, 1993; Freeman et al., 1981), and a multispecies study (Hirabayashi et al., 2023) found both pistillate and staminate flower production in small oak trees. This raises the question: what, if anything, distinguishes *Q. macrocarpa* from other oak species such that it produces pistillate flowers first?

Flower/fruit production costs, though similar between observed species, differ by mass between pistillate and staminate flowers (Wang et al., 2023). This is evidenced by the fact that staminate flowers of four species of Asian oaks, representing both *Q.* subgen. *Quercus* and *Q.* subgen. *Cerris*, exhibit 3–4 times higher concentrations of phosphorus (P)

	Odds ratio by tree size		
All Years Size Category (cm)	**IL:OK (p-value)**	**IL:MN (p-value)**	**MN:OK (p-value)**
125–175	Inf (0.507)	0.23 (0.066)	Inf (0.013)
175–225	2.68 (0.113)	0.50 (0.104)	5.40 (0.004)
225–275	4.34 (0.001)	0.43 (0.166)	9.95 (<0.001)
275–325	5.16 (0.020*)	0.62(1.000)	8.29 (0.079)

TABLE 5: P-values for odds ratios of flowering by size classes among populations from Illinois (IL), Minnesota (MN), and Oklahoma (OK). Because no Oklahoma trees had flowers 125–175 cm, the odds ratio is infinite (Inf).

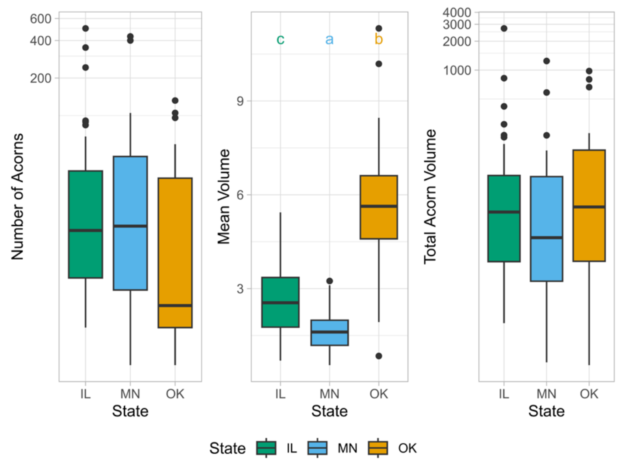

FIGURE 6: Acorn size but not acorn production varies significantly between populations: A, some trees produced large numbers of acorns despite their young age. B, Oklahoma trees produce significantly larger acorns than Illinois trees, which produce significantly larger acorns than Minnesota trees (volume in cm³). C, the approximate total acorn volume (cm³) per tree is not significantly different across states.

and nitrogen (N) by weight than their seeds, cupules, and pericarps (Wang et al., 2023). However, the difference in total acorn mass and total staminate inflorescence mass per tree has not been documented. Moreover, this is unlikely to explain the difference between *Quercus* species as the costs of building an inflorescence were not significantly different between species of Asian oaks.

An additional factor may be that young, short trees are likely better pollen receivers than pollen donors, as pollination success likely increases with the height of the tree and taller trees can disperse pollen more widely (Burd and Allen, 1988). In clonal stands of *Q. gambelii*, taller stems had a larger increase in staminate flowers per branch than pistillate flowers (Freeman et al., 1981). Effectiveness of pollen dispersal may be different in *Q. macrocarpa* compared to *Q. alba, Q. gambelii* and Asian *Quercus* species (Cecich, 1993; Freeman et al., 1981; Hirabayashi et al., 2023), as *Q. macrocarpa* is adapted to fire-prone oak savannas where young trees may be isolated (Abrams, 2006; Sieg and Wright, 1996). Long-distance pollen dispersal in *Q. macrocarpa* (Craft and Ashley, 2007, 2010) may enable a small tree to receive pollen even before that tree can produce enough pollen of its own to disperse. Interestingly, while *Betula* L. species produced catkins first (Johnsson, 1949) and Asian oaks produced both pistillate and staminate flowers early in maturity (Hirabayashi et al., 2023), one species documented to undergo female reproduction first is a fire-adapted pine (*Pinus halepensis*; Santos-del-Blanco et al., 2010). Pistillate-first reproduction in *P. halepensis* has been proposed to ensure reproductive success for young, isolated trees in fire-prone plant communities (Santos-del-Blanco et al., 2010). The production of acorns instead of catkins in young trees of *Q. macrocarpa*, a fire-adapted species, may similarly increase the fitness of small, isolated trees and enable reproduction before fire damages aboveground growth of young trees.

Alternatively, environmental and developmental factors may influence which flowers develop first in a tree's life or most abundantly in a given year. Some literature has suggested that pistillate and staminate flowers are initiated at different times of the year in *Q. alba* and *Q. suber* L. (Merkle et al., 1980; Sobral et al., 2020). If pistillate and staminate flowers in *Q. macrocarpa* also differ in the seasonal time of initiation, pistillate-only production could be due to ideal conditions at the time of pistillate flower initiation but not at staminate flower initiation. Freeman et al. (1981) found in *Q. gambelii,* as well as other species, that individuals in xeric habitats produced fewer pistillate flowers (fewer than staminate flowers) than individuals in mesic habitats, which produced more pistillate flowers than staminate flowers. While in their study the total number of pistillate and not staminate flowers differed between trees and sites (Freeman et al., 1981), our study showed dramatic differences in staminate flower production among individuals, with more than 98% of flowering individuals producing pistillate flowers. This suggests that we are observing different processes than found by Freeman et al. (1981) in *Q. gambelii*.

Further work is needed to determine whether *Q. macrocarpa* always produces pistillate flowers first or whether flower type in the first year of maturity is environmentally regulated. If the former, it could be an adaptation to young trees being poor pollen donors as small, potentially isolated individuals but effective pollen recipients. If the latter and pistillate flowers are not more prevalent in the first year of flower production in the Minnesota or Oklahoma gardens, it could be that flowering is affected by their more xeric habitats or the climate timing of these sites compared to the Illinois garden.

In conclusion, we observed that *Quercus macrocarpa* can mature quickly under ideal growing conditions, that pistillate flowers alone are often produced on young trees in *Q. macrocarpa,* and that Oklahoma trees—despite their greater height—had a smaller percentage of flowering individuals than Illinois- or Minnesota-sourced trees. Future work should further explore what affects flowering type and maturation processes in *Quercus macrocarpa.*

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