ISSN 1536-7738

Oklahoma
Native Plant Record

Journal of the Oklahoma Native Plant Society
Volume 21, December 2021

Oklahoma Native Plant Record

Journal of the Oklahoma Native Plant Society
P. O. Box 14274
Tulsa, Oklahoma 74159-1274
Volume 21, December 2021

ISSN 1536-7738
http://ojs.library.okstate.edu/osu/

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https://doi.org/10.22488/okstate.22.100000

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Cover photo:
Eryngium leavenworthii (Leavenworth's eryngo) 2004 Photo Contest entry by Ellen Jonsson

Foreword

This issue of the *Oklahoma Native Plant Record* contains two dendrochronology reports, a phenological study of Oklahoma Asteraceae, and a study of the effect of cold stratification on germination of seeds of a native plant. These studies provide evidence of how land-use changes and abiotic factors affect Oklahoma plant communities and native species as well as provide insight into how future changes could impact our native flora.

Chad King from the University of Central Oklahoma investigated the growth patterns and ages of trees at Martin Park Nature Center in north Oklahoma City. He reports that some trees in this park are approaching a century in age. Through the analysis of tree-rings, he was able to determine when trees of various species became established, and document variation in annual growth over time, indicating periods of growth suppression and growth release that might be due to land-use practices after the park was established in 1963.

John Unterschuetz and Abigail Moore from the University of Oklahoma, and Jennifer Messick from the University of Central Oklahoma investigated the flowering phases of herbarium specimens of four native Asteraceae (sunflower family) species that had been collected since the early 1900s. Their goal was to determine if there was evidence of shifts in flowering times related to changing climatic conditions.

Carmen Esqueda and Chad King of the University of Central Oklahoma provide a literature review of dendrochronological research conducted solely within the state of Oklahoma, beginning almost 100 years ago. Common research topics included age-diameter/growth rate, stand dynamics, climate, fire history, and some combinations of these topics. Post oak, blackjack oak, and eastern redcedar were the most frequently studied species. The authors identify understudied species and research topics that might stimulate additional dendrochronological research in the state.

Samantha Coplen from the University of Central Oklahoma investigated the effect of cold stratification on germination of seeds of the pitcher sage, *Salvia azurea* var. *grandiflora*. Studies such as this, by documenting the germination probability of seeds exposed to different lengths of cold stratification, can give insight into whether climate change could reduce germination probability in the future.

This issue's Critic’s Choice essay was written by Paul Buck for the Fall 1998 *Gaillardia*. It describes his attempts to verbalize what I suspect we all experience when we take time to reflect on the immense beauty of Oklahoma landscapes. He encourages us to extend our observations past dusk to experience the transition in sights, sounds, and scents from daylight to dark.

Please consider publishing your work in the *Oklahoma Native Plant Record.* It is listed in the Directory of Open Access Journals, is abstracted by the Centre for Agricultural Bioscience International, and can be accessed by researchers around the world.

Gloria Caddell
Managing Editor

Oklahoma Native Plant Record
Volume 21, December 2021

GROWTH PATTERNS AND AGES OF TREES FROM MARTIN PARK NATURE CENTER, OKLAHOMA COUNTY, OKLAHOMA

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Keywords: dendrochronology, Quercus, Celtis, Ulmus

ABSTRACT

This paper provides insight into ages and patterns of radial growth from mature trees at Martin Park Nature Center, Oklahoma County, Oklahoma. A total of 80 trees were sampled and crossdated using dendrochronology from the three most common genera at Martin Park Nature Center: *Quercus*, *Celtis*, and *Ulmus*. The oldest trees at the park were *Q. macrocarpa* and *C. laevigata* with individuals dating back to the 1920s and 1930s. A pulse of *C. laevigata* recruitment occurred in the 1960s that likely reflected changes in land-use as the property transitioned from private ownership to the City of Oklahoma City. A sequence of growth suppressions and releases was identified in *C. laevigata* that is related to park maintenance and forest development at the park.

INTRODUCTION AND STUDY AREA

Martin Park Nature Center (MPNC) is an approximately 54.8 ha area owned and managed by the City of Oklahoma City. The property was purchased by the City in 1962, converted to a park in 1963, and named after Dr. J.T. Martin (N. Garrison, former naturalist MPNC, personal communication 2022). Prior to 1963, the property was privately owned and was originally homesteaded in 1895 (General Land Office Records 2022).

Martin Park Nature Center is within the Cross Timbers Transition (Level IV) ecoregion (Woods et al. 2005) in central Oklahoma (Figure 1). This ecoregion is known as an ecotone between the grasslands of the Central Great Plains ecoregion to the west and Cross Timbers ecoregion to the east. Common trees within the Cross Timbers Transition ecoregion include *Juniperus virginiana* L. (eastern redcedar), species of *Quercus* including *Q. marilandica* Muenchh. (blackjack oak), *Q. stellata* Wangenh. (post oak), and *Q. macrocarpa* Michx. (bur oak), and species of *Ulmus* including *U. americana* L. (American elm) and *U. rubra* Muhl. (red elm).

Soils at MPNC reflect the presence of streams and periodic flooding. A pair of creeks, Spring Creek and Bluff Creek, dissect MPNC. Soil classifications include Ashport silt loam, Pulaski fine sandy loam, and Lawrie silt loam that are alluvium derived from sedimentary rock associated with floodplains (Web Soil Survey 2022). Elevations at MPNC range from 331.3 m at the north side of the park to 334.9 m at the south side of the park. Mean annual temperature for Oklahoma County is 60.3°F and mean annual precipitation is 84.8 cm (National Centers for Environmental Information 2022).

In collaboration with William Hagenbuck, Martin Park Nature Center naturalist, I identified trees at MPNC as part of a plan to create educational materials for park guests about the ages of trees along the

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10.22488/okstate.22.100001

trails at MPNC. The focus of tree aging was on the common tree species at MPNC, including *Q. macrocarpa*, *U. americana*, *U. rubra*, and *Celtis laevigata* Willd. (sugarberry). This manuscript reports tree ages, estimates of tree establishment dates, and patterns of radial growth that provide insight into land-use patterns at MPNC.

Figure 1 The forested landscape at Martin Park Nature Center, Oklahoma County, Oklahoma. Photo is from the central portion of MPNC. Photo by C. King.

METHODS

To build an educational portfolio about tree ages at MPNC for the general public, common native tree species were selected for sampling during Fall 2018 and Spring 2019 to estimate age and establishment dates. Specifically, *Q. macrocarpa*, *U. americana*, *U. rubra*, and *C. laevigata* trees that were > 8 cm diameter at breast height (DBH) were identified for sampling, with the assumption that the oldest members of each species would be > 8 cm DBH. Increment cores were collected as close to the base of each tree as possible using a 5.15 mm (diameter) Haglof increment borer. Increment core samples were collected low on the tree bole in order to estimate a more accurate establishment date for each tree. Trees were selected along trails at MPNC and within the southern third of the park because of the presence of large diameter *Q. macrocarpa* within the floodplain. These larger diameter trees were selected at the request of MPNC. Increment cores were stored in plastic drinking straws for return to the TREELab at the University of Central Oklahoma (UCO) for processing and crossdating. Additional data collected for each increment core included species and diameter at breast height (DBH).

Each individual increment core was glued on wooden mounts at the TREELab. Increment cores were sanded with progressively finer sandpaper (80-grit to 1200-grit) in order to identify individual cells under a binocular microscope (Stokes and Smiley 1996). To determine age at coring height for each increment core, tree-ring widths were measured to the nearest 0.001 mm using a Velmex TA Measuring System (Velmex, Inc., Bloomsfield, NY), a binocular boom microscope, and recorded using Measure J2X software (VoorTech Consulting, Holderness, NH). Tree-ring series of each increment core were crossdated to assign calendar years to each tree-ring using COFECHA (Holmes 1983) and graphical visualization. In the event that the increment core missed the pith, the number of tree-rings missing to the pith were estimated using Speer (2010). This method uses the 10-year pattern of growth closest to the pith to estimate the number of tree-rings missing to estimate pith date.

RESULTS AND DISCUSSION

A total of 80 increment cores were collected from *Q. macrocarpa* (n = 23), *U. americana* (n = 6), *U. rubra* (n = 4), and *C. laevigata* (n = 47). The largest diameter tree that was sampled was a *Q. macrocarpa* (DBH = 96.3 cm). The oldest trees sampled for each species include 93 years (*Q. macrocarpa*), 87 years (*C. laevigata*), 53 years (*U. americana*), and 43 years (*U. rubra*) (Figure 2). Several large diameter *Q. macrocarpa* exist within the floodplain of MPNC along the south side of the park. A few of these were selected for sampling that resulted in the oldest trees found at MPNC.

Approximately 40% (n = 32) of trees sampled began growing in the 1960s (Figure 3). The species that established during the 1960s were *C. laevigata* and *U. americana*. A possible explanation for the establishment of the 1960s tree cohort was likely the transition from private ownership to the City of Oklahoma City. This may have resulted in changes in land-use patterns that promoted the natural establishment of trees. Trees of several species were planted at MPNC after the City of Oklahoma City developed the park but did not include *C. laevigata* and *U. americana* (N. Garrison, former naturalist MPNC, personal communication January 2022). I was unable to find information pertaining to previous land-use before the development of MPNC. Previous research at E.C. Hafer Park in Edmond, Oklahoma County, Oklahoma (King and Cheek 2015) documented farming land-use prior to the City of Edmond purchasing the property. Following the purchase of the future E.C. Hafer Park property, King and Cheek (2015) identified a pulse of tree recruitment in the 1950s that corresponded to a change in land-use from farming practices to minimal use. A similar pattern may have occurred at MPNC following the purchase of the property by the City of Oklahoma City.

Patterns of annual growth in tree-rings can provide important insight into events that may have been occurring around the tree at the time of tree-ring formation (Fritts 1976; Orwig and Abrams 1997; Speer 2010; Cowdon et al. 2014) or provide information about tree senescence (Cailleret et al. 2016). An interesting set of radial growth patterns emerged in several *C. laevigata* that were not observed in the other species at MPNC (Figure 4). I noted that approximately 49% (n = 23) of *C. laevigata* demonstrated a rapid growth suppression (Figure 5). The initiation of growth suppression varied from the mid-1970s (n = 9; Figure 4D), mid-1980s (n = 5; Figures 4A and 4B), and mid-1990s (n = 9; Figure 4C). For eight trees, the growth suppression was sustained through 2018. The other *C. laevigata* (n = 15) exhibited increased annual growth following growth suppression. All but two trees were part of the 1960s cohort.

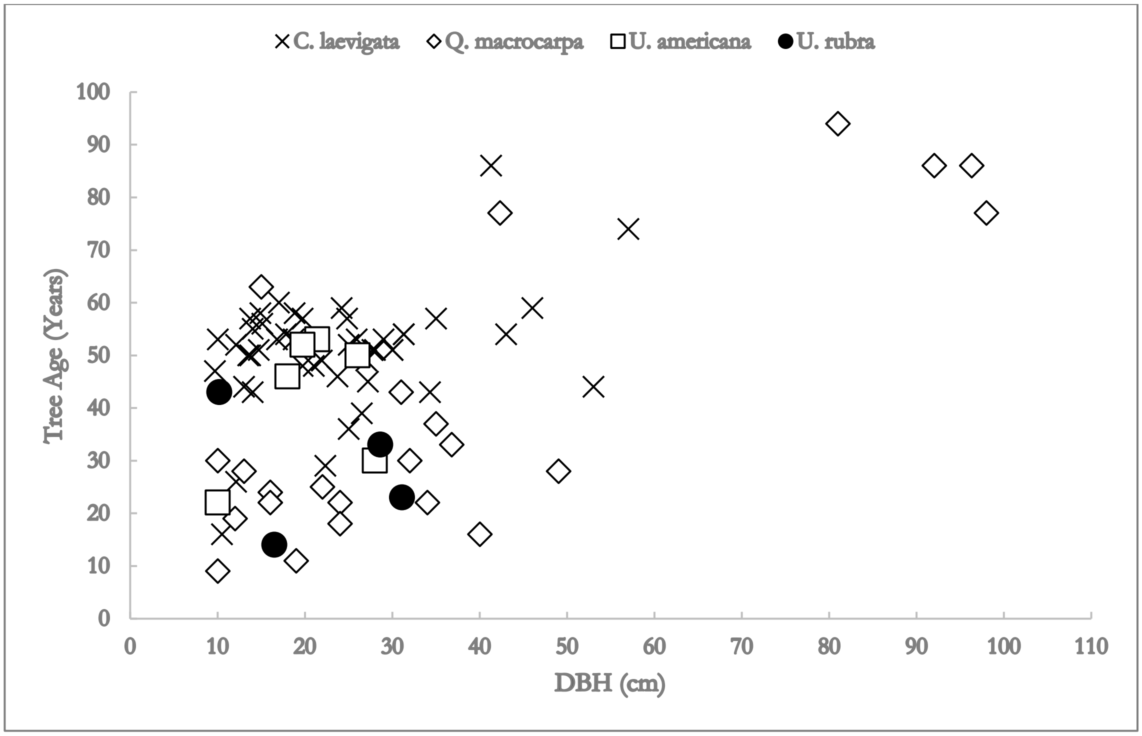

Figure 2 Diameter at breast height (DBH) and tree age for trees cored in Fall 2018 and Spring 2019.

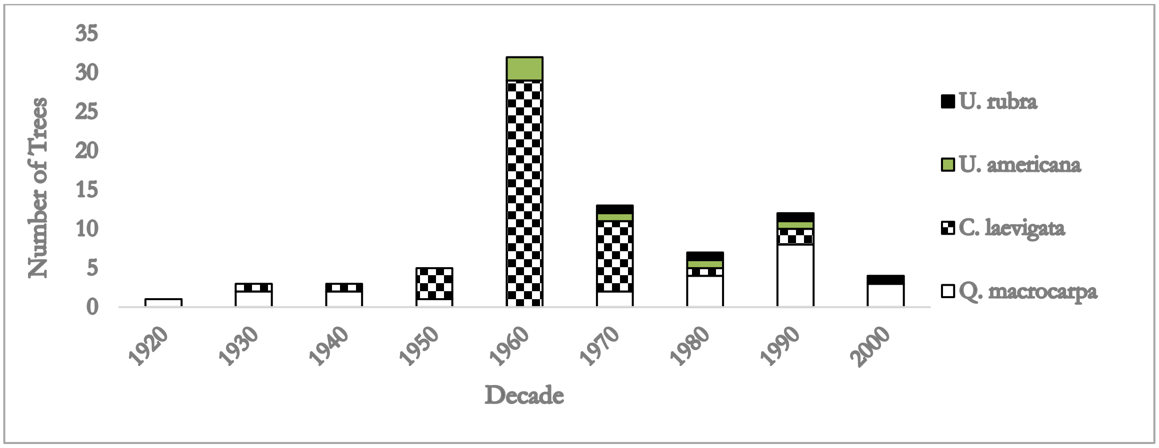

Figure 3 Number of trees that established by decade. Approximately 38% of the trees sampled established during the 1960s. The oldest tree sampled was a bur oak that dated to 1925 (93 years old at time of sampling). A sugarberry also dated to 1931 (87 years old at time of sampling). A large cohort of sugarberry established during the 1960s (29 trees).

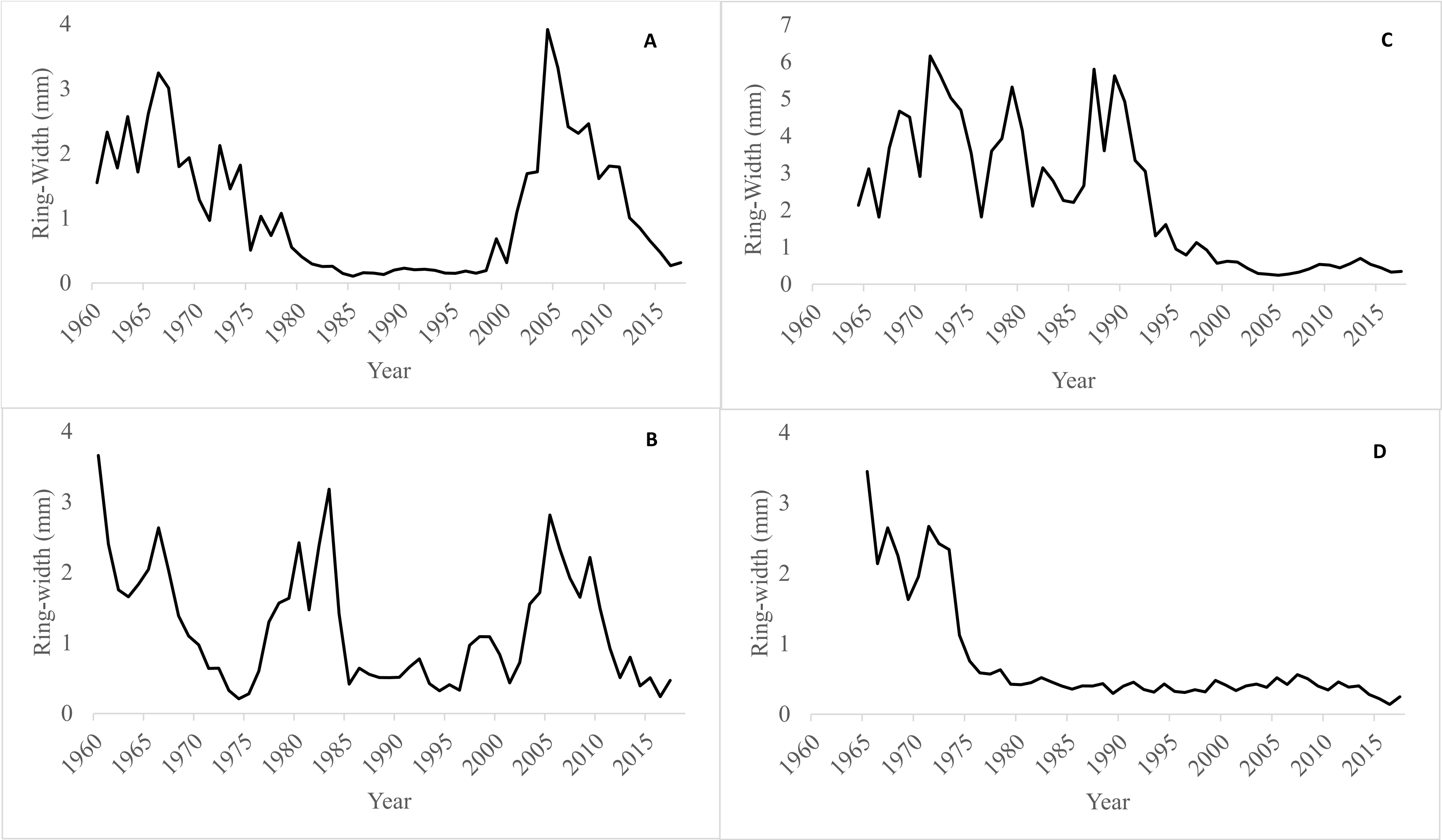

Figure 4 Examples of radial growth patterns in *C. laevigata* at Martin Park Nature Center, Oklahoma County, Oklahoma. Samples A and B represent examples of trees that exhibited declining radial growth with a subsequent growth release in 2002 (A) and 2003 (B). Samples C and D demonstrate sustained growth suppression beginning in 1993 (C) and 1975 (D). Please note different y-axis range in C.

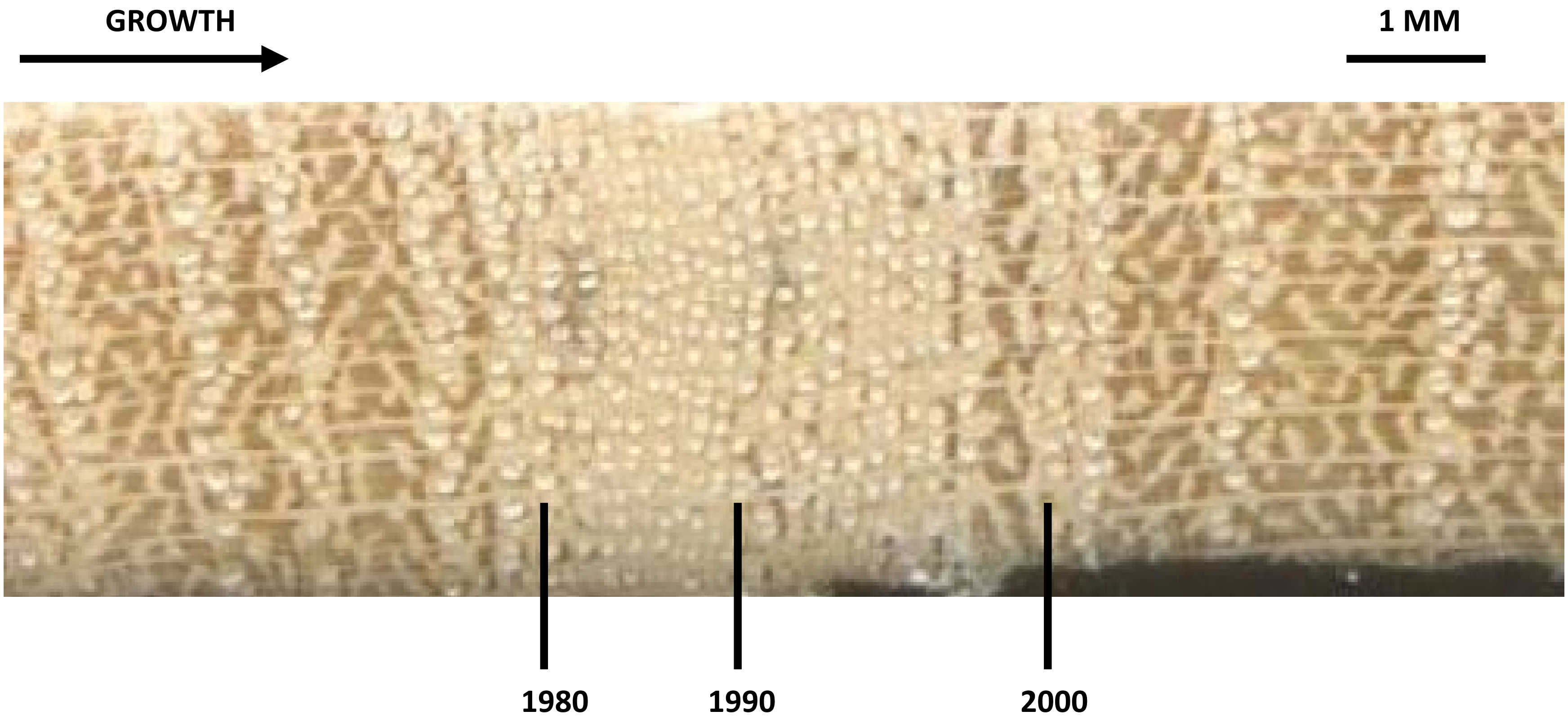

Figure 5 Example of growth suppression in *C. laevigata* at Martin Park Nature Center. Annual growth is from left to right. This sample corresponds to the suppressed growth seen in Figure 3A. Note prior to 1979, ring-widths were wider than the period 1979 through 1998. Subsequent to 1998, ring-widths returned to similar widths when compared to pre-1979.

Several factors likely contributed to this variability in *C. laevigata* growth not seen in the other species that were sampled at MPNC. One explanation is that rapid growth changes are due to regular trail maintenance that resulted in periodic removal of trees near the trails. Damage due to falling stems and/or trees removed leaf area that reduced growth rates of retained *C. laevigata* (Figures 4C and 4D). Maintenance could have also opened the canopy that facilitated some *C. laevigata* to be released from competition that resulted in sustained increases in annual growth until the tree reached an overstory position in the canopy (Figures 4A and 4B). Previous research at E.C. Hafer Park, that is approximately 14 km from MPNC, noted growth releases of trees that was attributed to the development of trails (King and Cheek 2015). Growth releases and suppressions of surviving trees are a common response to canopy disturbances (wind, human activities), particularly in the Eastern Deciduous Forest (Abrams and Orwig 1996; Stan and Daniels 2014; King and Muzika 2014). Suppressions in growth (Figure 4C and 4D) can also be attributed to canopy closure that resulted in reduced light availability to understory *C. laevigata*. This species is considered shade tolerant but responds favorably to being released from a suppressed position in the understory (Kennedy, Jr. 1990). It is not surprising, therefore, that *C. laevigata* is exhibiting suppressed growth but also can rapidly increase growth rates when released. The other species that were sampled are shade tolerant (*U. americana*, *U. rubra*) or intermediately shade tolerant (*Q. macrocarpa*) and may have had responses similar to *C. laevigata*. The numbers of each of the other species sampled was limited relative to *C. laevigata*, so it's possible that, by chance, I did not capture growth responses similar to those seen in *C. laevigata*.

I document ages of trees found at Martin Park Nature Center in Oklahoma City, Oklahoma County. *Quercus macrocarpa* are the oldest trees with the oldest individual dating back to 1925. Additionally, a *C. laevigata* individual dates to 1931, which is currently the oldest representative that I have found in Oklahoma. *Celtis laevigata* is a largely unstudied tree species in dendrochronology and older individuals are likely present in Oklahoma due to their ability to survive in shaded environments while still developing annual growth rings.

ACKNOWLEDGMENTS

I would like to thank Christian Hart for assistance at Martin Park Nature Center in collecting increment cores. I graciously thank William Hagenbuck for permission to collect increment cores from trees at Martin Park Nature Center. Thanks to reviewers of this manuscript for their constructive comments and suggestions.

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Oklahoma Native Plant Record
Volume 21, December 2021

MEASURING CHANGES IN PHENOLOGY OF OKLAHOMA ASTERACEAE USING HERBARIUM SPECIMENS

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Keywords: climate change, phenological shift, phenophase, temperature

ABSTRACT

Analyzing shifts in plant flowering times (flowering phenology) in response to changing climate is crucial to understanding the impacts of climate change on plants. Herbaria contain the physical record of reproductive events from past seasons, making them an important source of long-term data for studies of phenology. We measured changes in flowering phenology of four Oklahoma native plants in the Asteraceae (sunflower) family: *Grindelia ciliata*, *Liatris punctata*, *Ratibida columnifera*, and *Vernonia baldwinii*. These species were selected to represent the morphological and phylogenetic diversity of the Asteraceae in Oklahoma and were represented in the Robert Bebb Herbarium (OKL) with over 100 specimens each. We created novel protocols for scoring the flowering phenology of these species into numeric categories, called phenophases. We looked for correlations between the collection date and both the year of collection and the temperature in that year. There was a significant relationship between collection date and year only in peak flowering specimens of *G. ciliata*. There was a significant relationship between statewide annual temperature and collection date only in peak flowering specimens of *V. baldwinii*. There was a significant relationship between the annual temperature of the climate division of the state where the plants were collected and collection date for peak flowering in *G. ciliata*, *R. columnifera*, and *V. baldwinii*, for first flowers in *V. baldwinii*, and for last flowers in *L. punctata*. More precise temperature data thus lead to an improvement of the model, but in all cases temperature or year explained relatively little of the total variation in flowering time.

10.22488/okstate.22.100002

INTRODUCTION

Phenology is the study of the timing of recurring biological events. Analyzing shifts in flowering times in response to changing climatic conditions is crucial to comprehending and forecasting the impacts of climate change on the world's plants. Climate and phenology are physiologically linked and changes in the climate have the potential to alter phenological responses (Kooyers et al. 2019). In the Rocky Mountains, for example, many alpine plant species have shifted their flowering times earlier in the year in response to a 1°C rise in temperature since the mid-1990s (Munson and Sher 2015). The change in flowering phenology for these species has been steady since the late 1800s, leading them to flower over a month earlier than they once did, which has massive consequences for the ecosystem (Munson and Sher 2015). Other studies have found mixed results with increased temperature; some taxa in Oklahoma flowered later than in the past and others flowered earlier (Messick 2017). A study in the Netherlands found a similar result (Van Vliet et al. 2014). Pearson (2019) found that fall flowering taxa flowered later with increasing July temperatures, while spring flowering taxa flowered earlier in response to rising March temperatures. Species within the same genus in the same geographic range may have different responses, as was the case in a British study, with *Geranium rotundifolium* L. delaying its first flowering date and *Geranium dissectum* L. advancing its first flowering date in response to increasing temperature over time (Fitter and Fitter 2002). These different responses may be due to a delay in flowering with less winter cold by plants that require vernalization before flowering (Gremer et al. 2020; Messick 2017). The way that climate change links to phenology varies between taxa and environments, depending on the most important abiotic factors in each environment. For example, Matthews and Mazer (2016) found that with greater precipitation, the mean date of flowering moved later along the Pacific Coast of North America. In addition, plants in xeric environments tend to have greater phenological changes than plants in more mesic environments and are at a higher risk for changes in community composition (Park 2014).

These changes in flowering phenology will alter ecosystem functioning and productivity, as well as ecological interactions across trophic levels (Pearson 2019). A study on broad-tailed hummingbirds in Colorado and their preferred nectar sources revealed that changes in the flowering phenology of food sources in northern breeding grounds, if they continue at current rates, would lead to hummingbirds eventually arriving after flowering begins (McKinney et al. 2012). This projected mismatch in ecological timing may result in flowering of some important species ending their flowering before the hummingbirds raise their young, which would lower reproductive success (McKinney et al. 2012). In some cases, these phenological shifts may also increase competition for pollinators if the changes in phenology cause taxa that used to flower at different times to flower at the same time (Park and Mazer 2019). Differential changes in flowering phenology may also allow co-occurring species of *Viburnum* to hybridize, which was previously prevented by non-overlapping flowering periods (Spriggs et al. 2019).

Many studies of plant phenology are based on herbarium specimens. Herbaria contain longer consistent records of phenological events than are available from observational data from historical documents like newspapers or journals (e.g., Aono and Kazui 2008; Haggerty et al. 2013b) or detailed observations on flowering from individual observers (e.g., McKinney et al. 2012; Jánosi et al. 2020).

Herbarium specimens also allow us to examine changes in all stages of flowering, instead of being limited to the specific stage(s) previous observers chose to record (generally the date of first flowering; Amano et al. 2010). The advantage to dividing flowering specimens according to their phenological phase, or phenophase, is that it has the potential to uncover changes in phenology in more detail. Treating all flowering individuals as a single category is much less precise (e.g., Bowers 2007). Careful delineation of specific phenophases is a challenge for phenological research (Love et al. 2019). This must be done in a consistent manner, so that different researchers will score the phenology in the same way (Love et al. 2019; Yost et al. 2019).

We used records from the Robert Bebb Herbarium (OKL) at the University of Oklahoma to investigate the flowering periods of four members of the Asteraceae that are native to Oklahoma: *Grindelia ciliata* (Nutt.) Spreng., *Liatris punctata* Hook., *Ratibida columnifera* (Nutt.) Wooton & Standl., and *Vernonia baldwinii* Torr. We chose taxa that belonged to different tribes of the Asteraceae to capture more of the evolutionary variation in the family. In addition, we chose taxa with different inflorescence types. We were interested in answering the following questions: 1) Are there significant shifts in flowering periods? 2) If so, has flowering shifted earlier or later through time? 3) Which flowering stages show the largest shifts?

MATERIALS AND METHODS

Selected Species

Grindelia ciliata is in the tribe Astereae (Figure 1B). It is a fall-flowering annual with clusters of one to a few heads at the ends of each stem. While many individuals have only one stem and are 45 cm tall or less, plants can be up to 2 m tall. These larger plants have many side branches, which are often branched again, and each branch ends in a group of heads. Each individual head contains 100–200 disk florets and 25–40 ray florets (Strother and Wetter 2006), both of which produce fruit in this species.

Liatris punctata is in the tribe Eupatorieae (Figure 2B). It is a fall-flowering, long-lived perennial that comes from a corm or rhizome. It has many, small heads borne in an elongated cyme-like inflorescence that flowers from the top to the bottom. Each individual head contains 3–8 disk florets and no ray florets (Nesom 2006).

Ratibida columnifera is in the tribe Heliantheae (Figure 3B). It is a summer-flowering perennial from a rosette. Each plant bears 1–15 heads, with individual heads consisting of 4–12 ray florets and 200–400 disk florets borne on a columnar receptacle, with only the disk florets producing fruits in this species (Urbatsch and Cox 2006).

Vernonia baldwinii is in the tribe Vernonieae (Figure 4B). It is a late summer-flowering perennial, which forms rhizomatous clumps. Each individual stem has many heads in a corymbose arrangement, with each clump having many stems. Individual heads consist of 20–25 disk florets and no ray florets (Strother 2006).

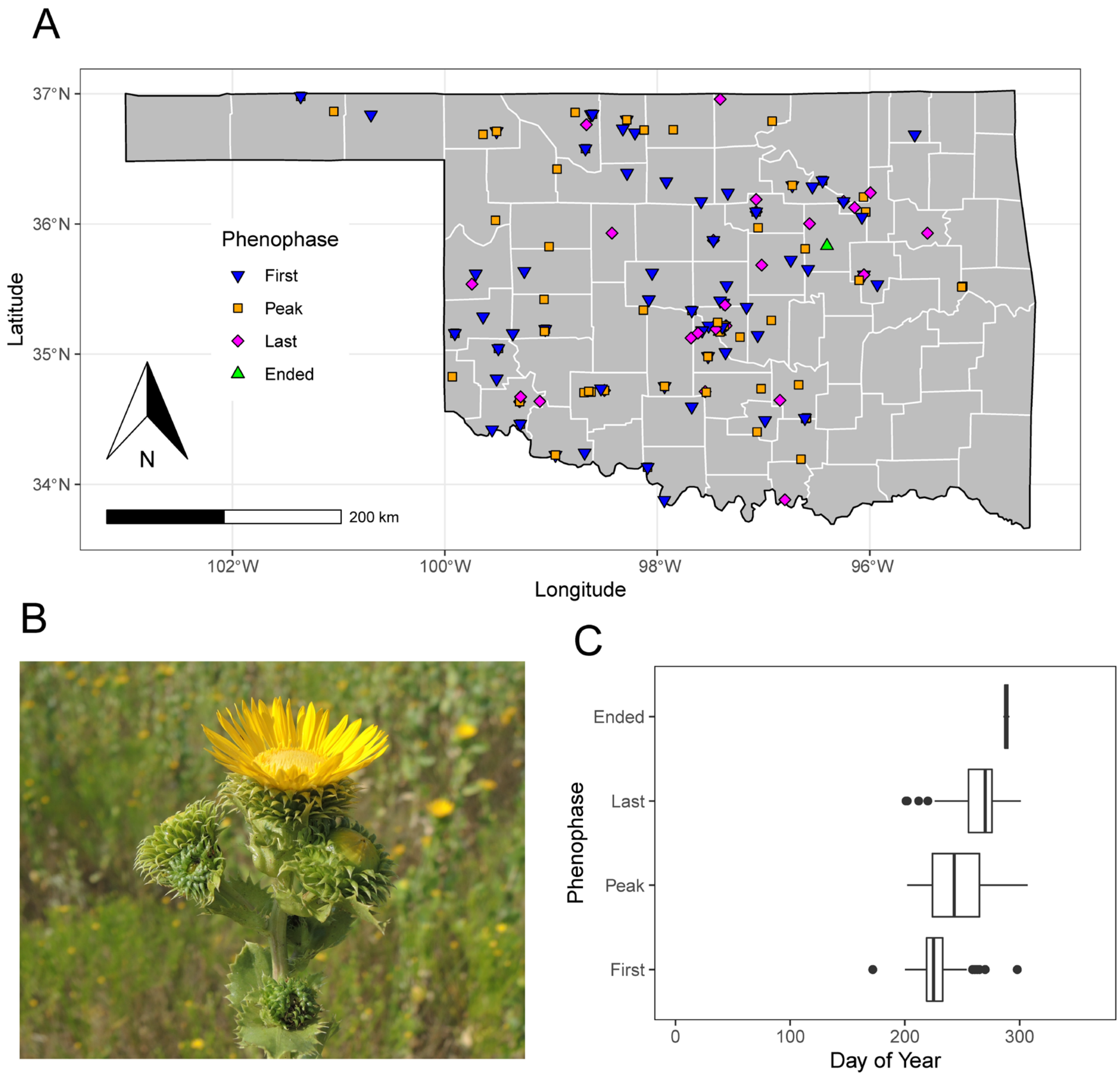

Figure 1 *Grindelia ciliata* (Astereae). A) Distribution map of specimens examined in this study, all from OKL. B) Plant from Sutton Urban Wilderness, Norman, Cleveland Co., Oklahoma. C) Boxplot showing the range of date of collection (DOY) for each of the four phenophases: First (First Flowers, 1), Peak (Peak Flowering, 2), Last (Last Flowers, 3), and Ended (Flowering Finished, 4).

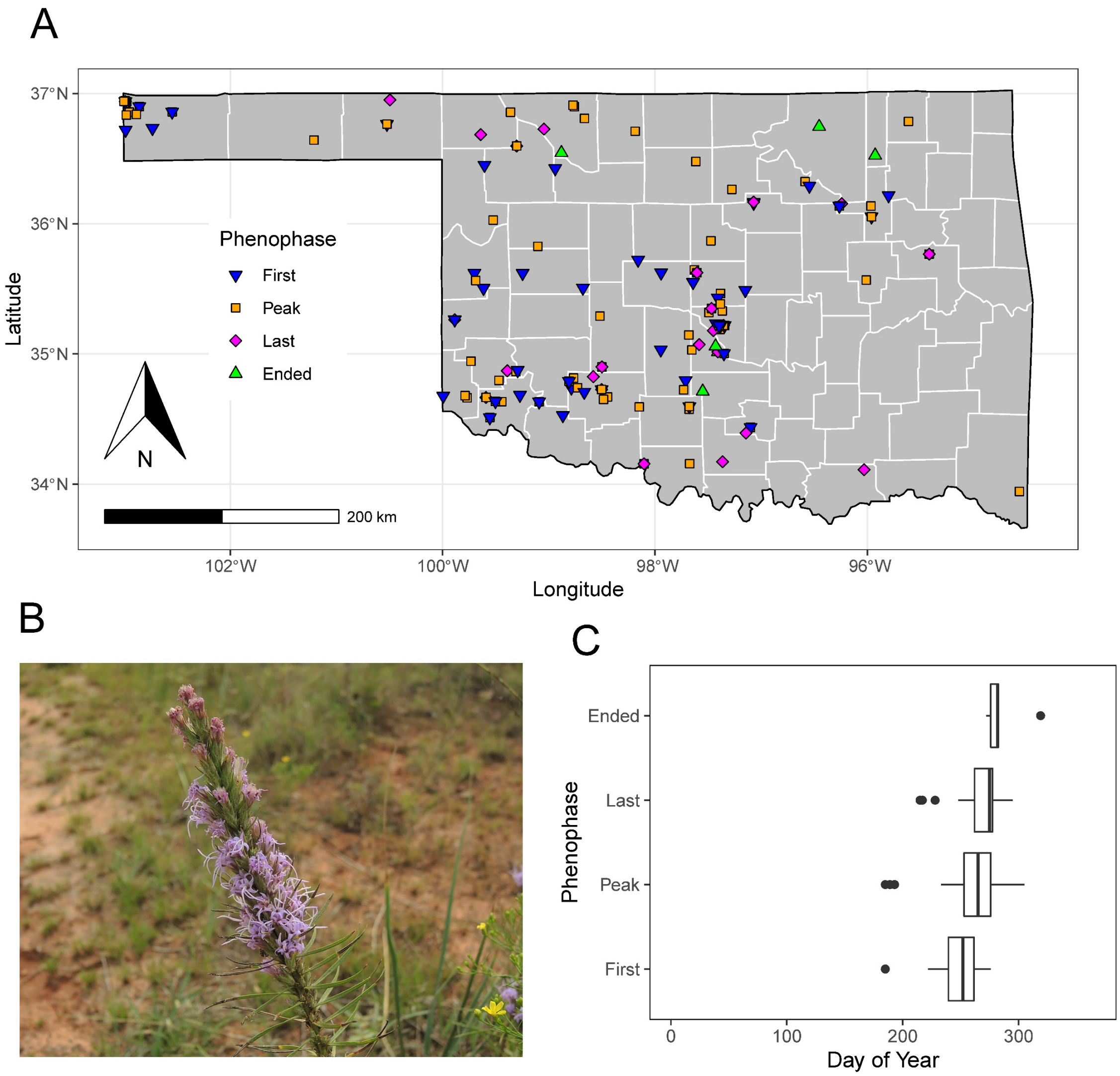

Figure 2 *Liatris punctata* (Eupatorieae). A) Distribution map of specimens examined in this study, all from OKL. B) Plant from Lake Thunderbird State Park, Cleveland Co., Oklahoma. C) Boxplot showing the range of date of collection (DOY) for each of the four phenophases. Labeling of phenophases following Figure 1.

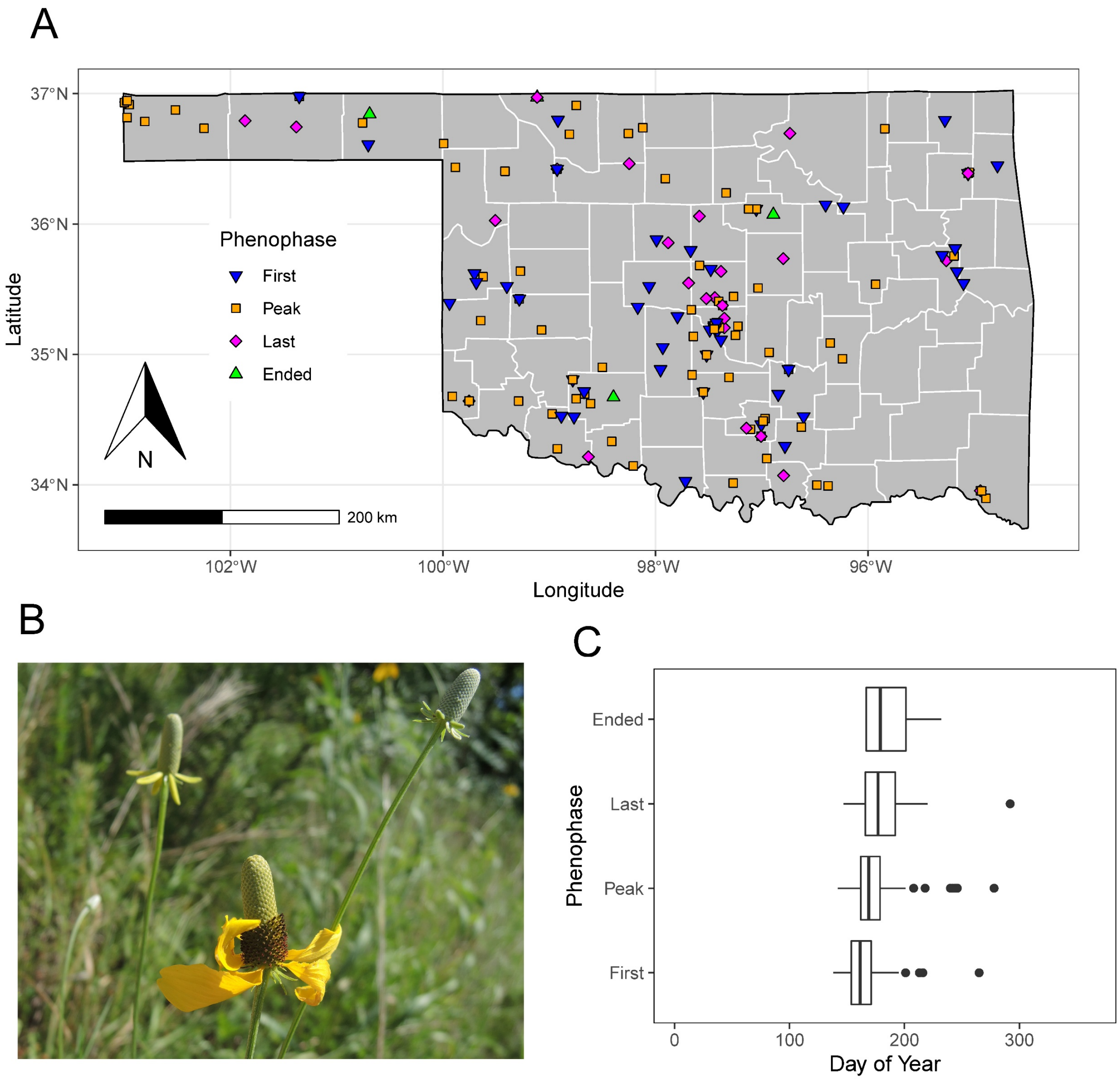

Figure 3 *Ratibida columnifera* (Heliantheae). A) Distribution map of specimens examined in this study, all from OKL. B) Plant from Sportsman Lake, Seminole Co., Oklahoma. C) Boxplot showing the range of date of collection (DOY) for each of the four phenophases. Labeling of phenophases following Figure 1.

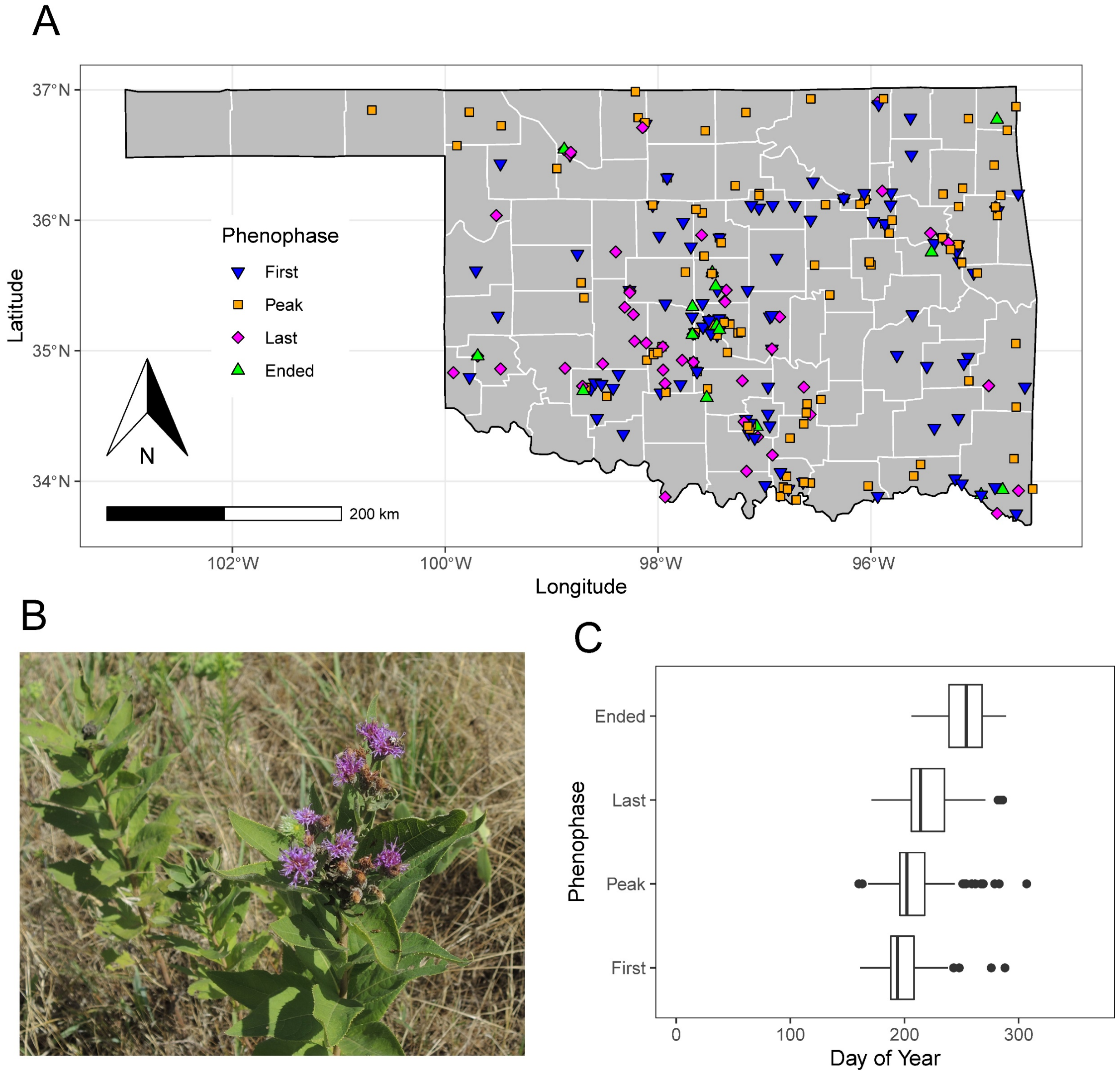

Figure 4 *Vernonia baldwinii* (Vernonieae). A) Distribution map of specimens examined in this study, all from OKL. B) Plant from US-412, Major Co., Oklahoma. C) Boxplot showing the range of date of collection (DOY) for each of the four phenophases. Labeling of phenophases following Figure 1.

Dataset Selection

We selected taxa that were present in the Bebb Herbarium (OKL) in high numbers, with at least 100 useable herbarium specimens per taxon. Specimens were only included in the analyses if their phenophase could be determined. Specimens were excluded if they did not include precise locality information or had no date. Multiple plants on the same herbarium sheet were treated as separate data points, because they often had different phenophases. In this case, each plant would receive a different phenophase score and would be included in the analysis as an independent data point from the same location with the same date.

We used the Oklahoma Vascular Plants Database (OVPD; Hoagland et al. 2019) to access dates and localities of specimens for georeferencing. This database includes each specimen's label information. Collection date was converted to day of year (DOY) with January 1 as day one and with DOY adjusted for leap years. We used Google Earth Pro (Google, Mountain View, California) to manually georeference the specimens. The accuracy of the georeferencing was checked by ensuring each specimen mapped to the county in which it was collected.

Determination of Phenophases

We based our strategy for determining phenophases on the primer by Haggerty et al. (2013a). There were four phenophases, based on how many open florets were present on the specimen and whether there were fruits present. Category 1 (first flowers) was assigned to specimens with at least one and up to 25% of the florets on the plant open. "Open" referred to visible stamens and pistil. Category 2 (peak flowering) applied to any specimen with 25%–75% open flowers, with more flowers than fruits. Category 3 (last flowers) corresponded to specimens with more fruits than flowers, but with at least some open flowers. Finally, category 4 (flowering finished) included specimens completely in fruit. For each taxon, the protocol for assigning a specific phenophase changed due to changes in morphological characters (Appendix).

Statistical Analyses

Data on the mean annual temperature for Oklahoma as a whole (henceforth statewide annual temperature) and for each of the nine climate divisions within Oklahoma (henceforth climate division annual temperature) were obtained from NOAA National Centers for Environmental Information (2021a, 2021b; procedure similar to that used by Calinger et al. 2013). In addition, both statewide and climate division temperature data were obtained for each of the four seasons separately from the same source (NOAA National Centers for Environmental Information 2022a, 2022b). Specimens were classified into climate divisions based on their counties (as each county was only in one climate division). This allowed us to investigate flowering responses on a broad statewide scale and on a finer scale which could be more informative in the potential flowering response to temperature changes.

All data analysis was performed in R, version 4.1.1 (R Core Team 2021). We performed simple linear regressions between DOY and various predictor variables: calendar year (year), statewide and climate division mean annual temperature, and statewide and climate division mean seasonal temperatures, with the specimens grouped by phenophase in all cases. Graphs and maps were plotted with ggplot2 (Wickham 2009) and sf (Pebesma 2018). The Bonferroni correction was applied to the p-values to account for multiple tests. (All seasons were tested for each species, as significance of the tests did not vary when only the season of flowering and the season prior to flowering were included.)

The R code, the datasets for each of the four species, and the table with the results from the analyses of all variables are available on ShareOK (https://hdl.handle.net/11244/336289).

RESULTS

The 203 examined specimens of *Grindelia ciliata* were found in approximately the western two-thirds of Oklahoma (Figure 1A). They were rather evenly scattered throughout the state, with clusters in Cleveland County (the location of the Bebb Herbarium) and in Comanche County (Wichita Mountains National Wildlife Refuge). They were collected from 1916 to 2020 (Figure 5). The median day of year (DOY) for peak flowering specimens of *G. ciliata* was 243 (31 August, Figures 1C, 5). There were no significant trends for first flowers or last flowers or for peak flowering with year (Figures 5, 6). There were only two specimens in the Flowering Finished category, so trends in this category could not be examined. The DOY for peak flowering was significantly correlated with statewide summer temperature ($p = 0.024$) and climate division summer temperature ($p = 0.050$; Figure 6). Both relationships were positive, showing that flowering became later by 4.81 and 3.75 days for each degree increase in temperature for statewide and climate division temperature, respectively, although temperature explained a relatively small amount of variation in flowering in both cases ($r^2 = 0.167$ for statewide summer temperature and $r^2 = 0.149$ for climate division summer temperature; Figure 6).

The 211 examined specimens of *Liatris punctata* were also found in approximately the western two-thirds of Oklahoma and were collected from 1913 to 2013 (Figures 2A, 7). They were not randomly distributed in the state, with clusters in Cleveland and McClain Counties, in southwestern Oklahoma, and in Cimarron County. The median DOY for peak flowering specimens of *L. punctata* was 265 (22 September, Figure 2C). There were no significant trends for the relationship of any flowering category with year or any of the temperature categories after correction for multiple tests (Figure 7).

The 191 examined specimens of *Ratibida columnifera* were found throughout the state, although there was a gap in collections in southeastern Oklahoma (Figure 3A), and a cluster of specimens in Cleveland County. They were collected from 1906 to 2015 (Figure 8). The median DOY for peak flowering specimens of *R. columnifera* was 169 (18 June, Figure 3C). There were no significant trends for any flowering category for year or any of the statewide temperature datasets (Figure 8). There were significant relationships between peak flowering DOY and three of the climate division datasets: annual ($p = 0.0057$), spring ($p = 0.0081$), and summer ($p = 0.0020$; Figure 9). In all cases, flowering advanced in response to an increase in temperature (by 3.6 days for annual temperature, 2.46 days for spring temperature, and 4.31 days for summer temperature), with temperature explaining a relatively small amount of the variation in the data ($r^2 = 0.132$ for annual, $r^2 = 0.126$ for spring, and $r^2 = 0.148$ for summer; Figure 9).

The 309 examined specimens of *Vernonia baldwinii* were spread throughout the body of the state, with clusters in Cleveland County, Comanche County, Marshall County, and Murray County (Figure 4A). They were collected from 1903 to 2013 (Figure 10). The median DOY for peak flowering specimens of *V. baldwinii* was 202 (21 July, Figure 4C). There were no significant trends in the relationship of any flowering category with year or any of the temperature categories after correction for multiple tests (Figure 10).

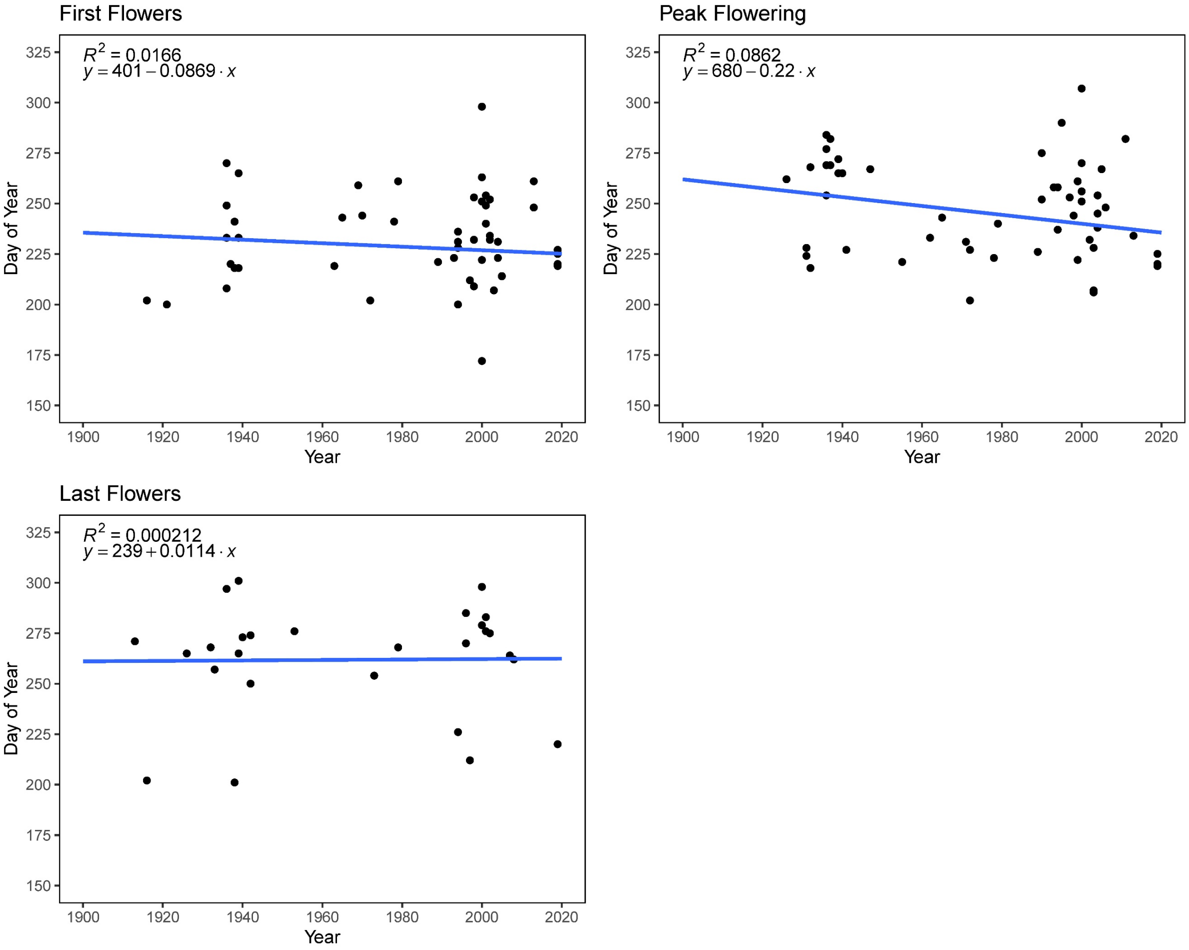

Figure 5 Scatterplot of day of year of collection for each of the three phenophases versus year of collection for *Grindelia ciliata*. (Too few specimens in the Ended category were present to analyze the relationship of day of year and year for that category.) Labeling of phenophases following Figure 1.

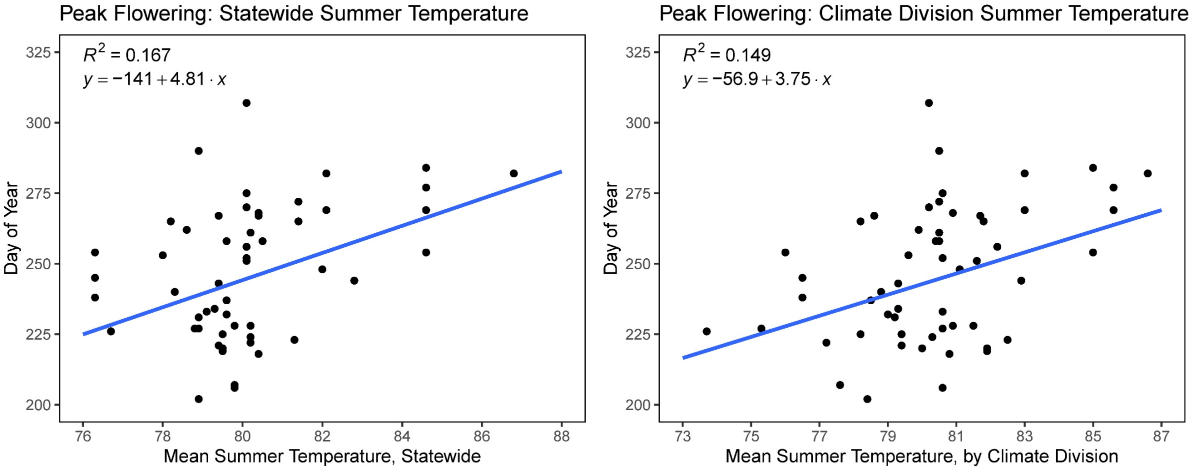

Figure 6 Scatterplot of the significant relationships between day of year of collection for *Grindelia ciliata*: Peak Flowering with yearly mean summer temperature statewide ($p = 0.024$) and yearly mean summer temperature in the climate division in which the specimen was collected ($p = 0.050$).

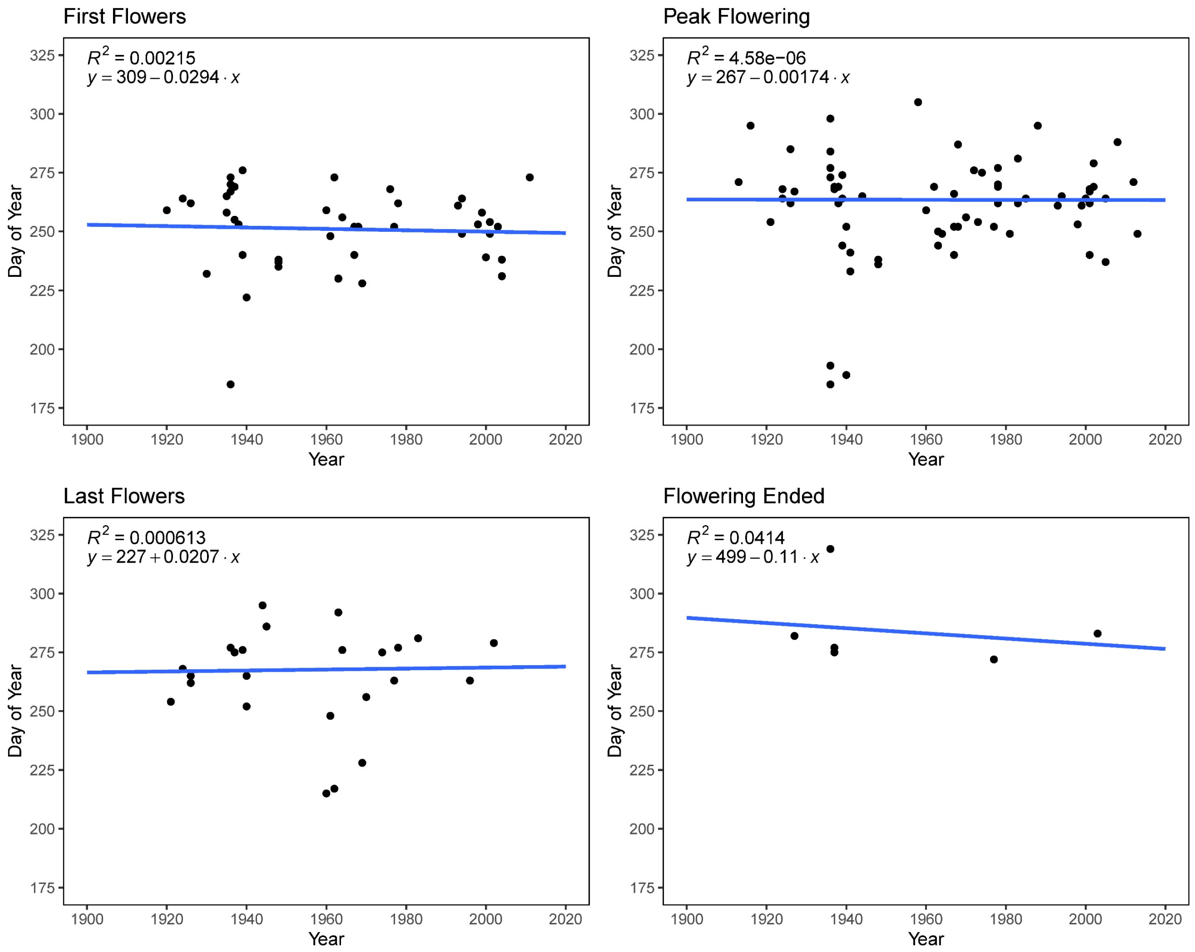

Figure 7 Scatterplot of day of year of collection for each of the four phenophases versus year of collection for *Liatris punctata*. Labeling of phenophases following Figure 1.

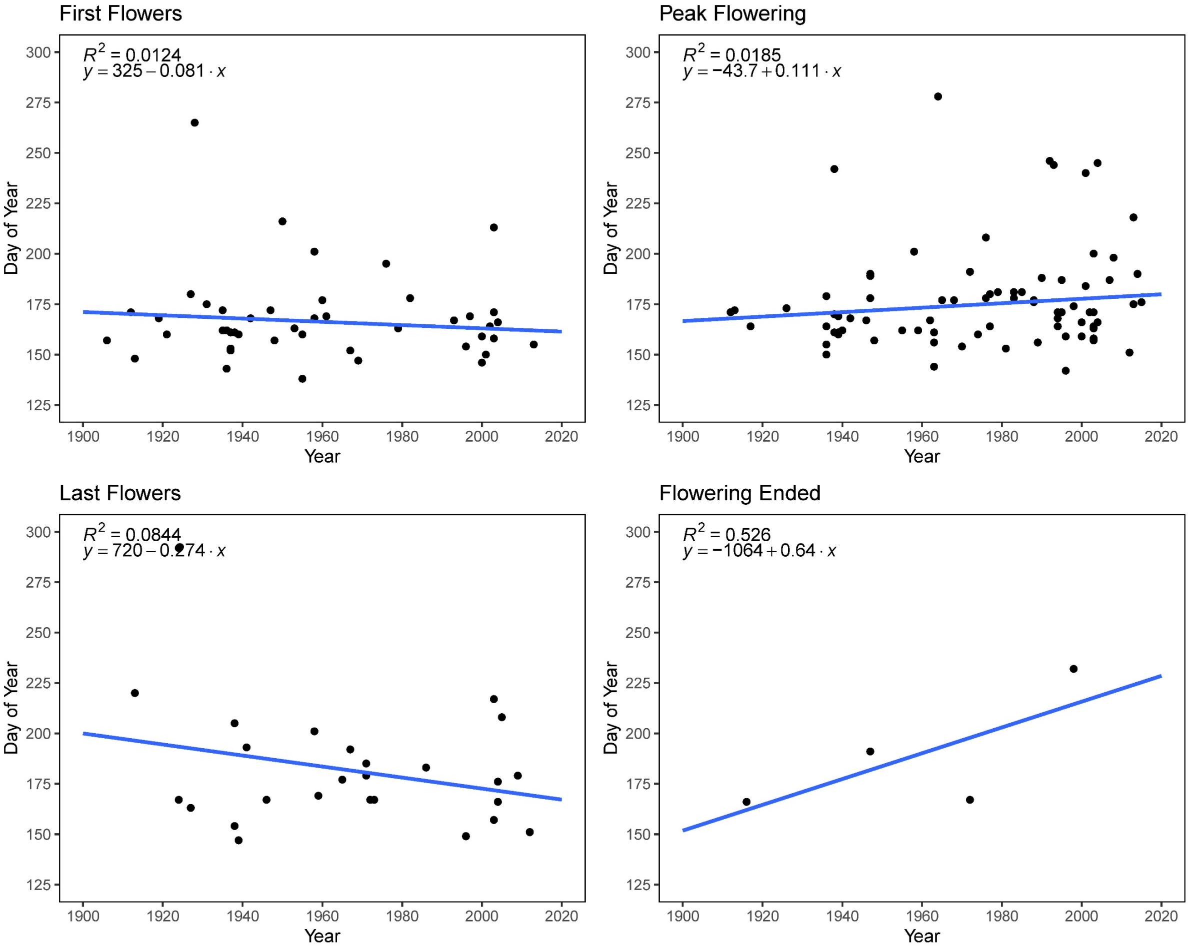

Figure 8 Scatterplot of day of year of collection for each of the four phenophases versus year of collection for *Ratibida columnifera*. Labeling of phenophases following Figure 1.

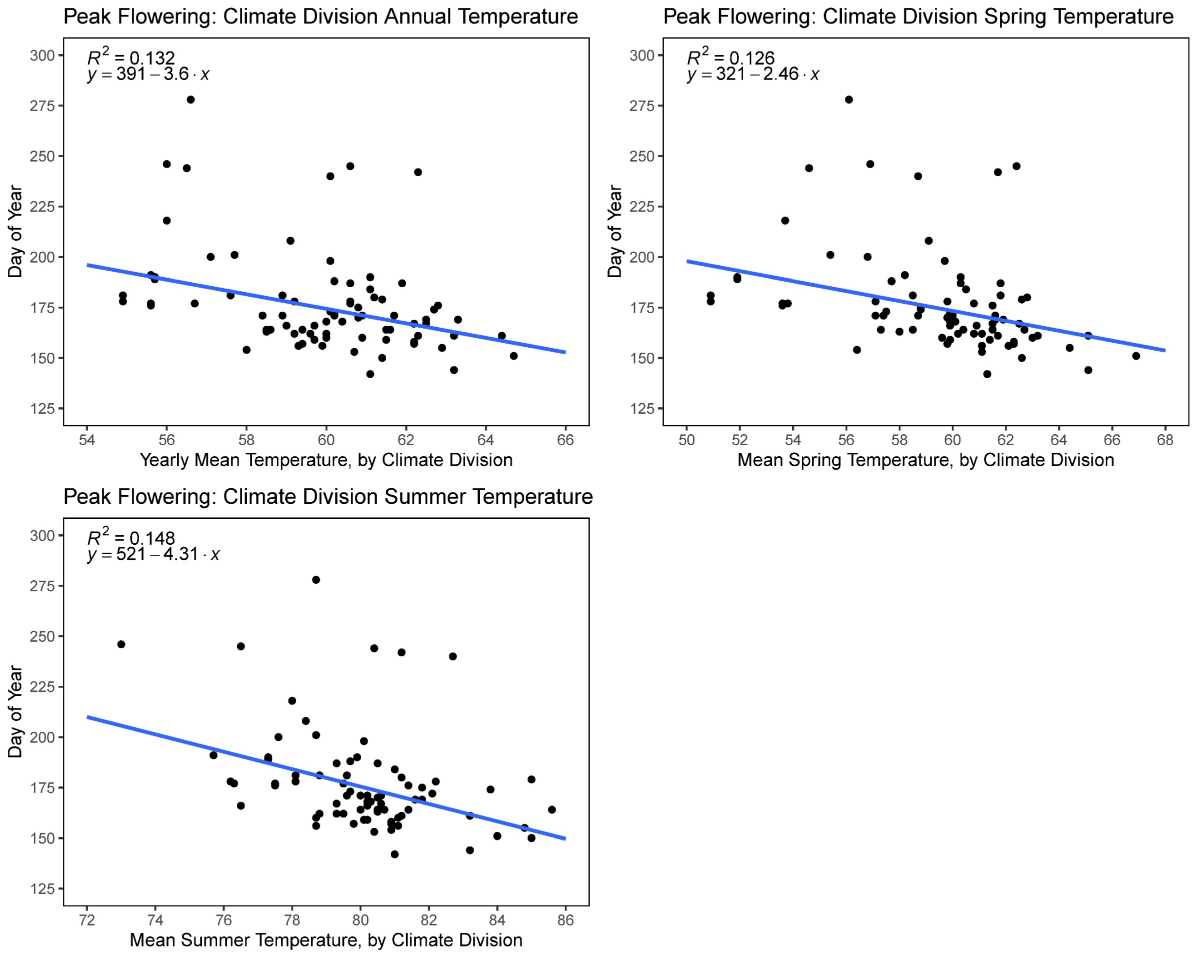

Figure 9 Scatterplot of the significant relationships between day of year of collection for *Ratibida columnifera*: Peak Flowering with the yearly mean annual temperature (p = 0.0057), yearly mean spring temperature (p = 0.0081), and yearly mean summer temperature (p = 0.0020), all for the climate division in which each plant was collected.

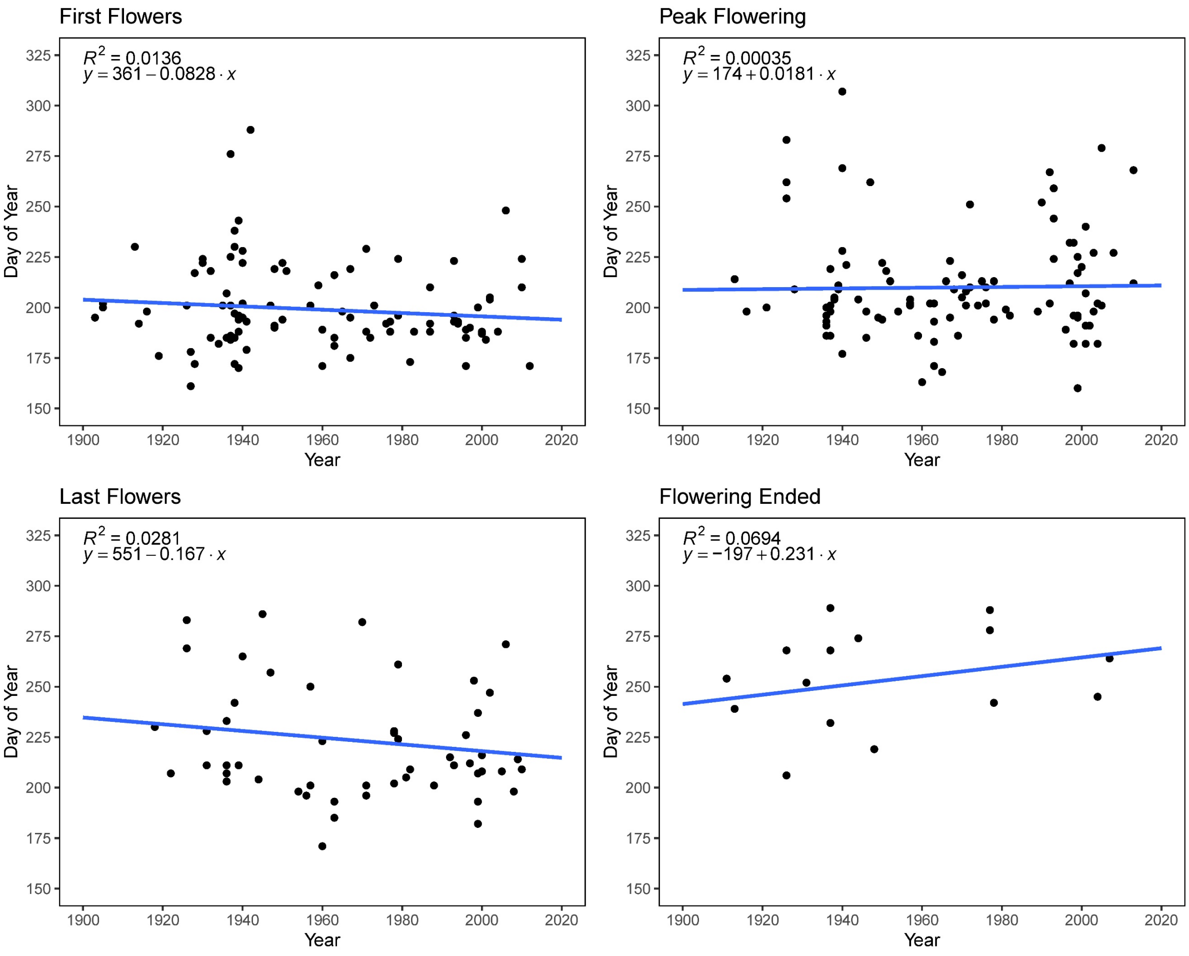

Figure 10 Scatterplot of day of year of collection for each of the four phenophases versus year of collection for *Vernonia baldwinii*. Labeling of phenophases following Figure 1.

DISCUSSION

We did not detect a significant relationship between collection date of year (DOY) and year in any of the species/phenophase combinations after correcting for multiple tests (Figures 5, 7, 8, and 10). In some cases, these species/phenophase combinations did show weak directional trends of earlier or later flowering through time. A lack of significant relationship between DOY and year of collection has been found in other multi-species phenology studies. Calinger et al. (2013) analyzed peak flowering of 141 species and found 66 species to show significant changes, either advances or delays, in flowering times. Messick (2017) found 10 of 20 species to show a significant change in flowering while the other species showed no trend or weak non-significant trends when year and DOY were regressed. Within this same study (Messick 2017), a mix of significant and non-significant trends were found when analyzing the same phenophases as in the present study. Three possible explanations for this lack of relationship found in the current study are that flowering is not strongly related to temperature, year and temperature are not strongly related, or that the selected species simply have not had enough time to show a significant response to temperature changes.

As noted in the results for each species, sampling is not evenly spread throughout the state, with sampling often concentrated in Cleveland County (where the Bebb Herbarium is located). This clumping of samples could have an effect on the results if the climate is different in different parts of the state or if plants are responding differently to climate in different parts of the state. While we corrected for differences in climate across the state by using the climate division datasets, the data to test how plants are responding to the climate across their ranges do not currently exist for these species.

Statewide annual temperature in Oklahoma does not show a steady warming trend over the period of this study (Oklahoma Climatological Survey 2021). The annual temperature has been warmer than the long-term average since the mid-1990s, but it was colder than the long-term average from the mid-1960s to the mid-1990s. The relationship between statewide annual temperature and DOY was not significant for any of the species. Two possible explanations for this lack of relationship are that flowering is not strongly related to temperature and that statewide annual temperature is not the most pertinent temperature variable for plant flowering.

When we looked at the data at a finer scale, either by dividing Oklahoma into its nine climate divisions or by dividing the temperature by season, more of the relationships were significant. Summer temperature, both statewide and divided by climate division, was significantly related to DOY for peak flowering in *G. ciliata* (Figure 6), while annual, spring, and summer temperature divided by climate division were significantly related to DOY for peak flowering in *Ratibida columnifera* (Figure 9). The remaining relationships did not show significant trends.

It is possible that flowering time may be governed strictly by temperature, but that annual or seasonal temperature is too coarse of a measure, even when it is for a specific climate division. For example, Jánosi et al. (2020) found that even monthly mean temperatures were too coarse to predict flowering accurately and that instead snowfall anomaly a certain number of days prior to flowering was the most pertinent variable governing the start of flowering for numerous cultivated bulb species. Messick (2017) found several species of Brassicaceae and Lamiaceae were responding to mean temperatures one to three months prior to date of collection with either an advance in flowering times or contractions in flowering period length.

Even if annual or seasonal temperature for their climate division is what plants are responding to, it may be that they are responding to temperature in a complex way. There is often a relationship between flowering time and temperature for spring-flowering species or for budburst (e.g., Bowers 2007; Miller-Rushing and Primack 2008; Amano et al. 2010; Munson and Sher 2015), with strong trends in earlier flowering over the last hundred years for these species. However, the plants we examined are summer- or fall-flowering species, and flowering time in these species may not be governed, or may not be governed exclusively, by the start of spring. Pearson (2019) found that warming temperatures made spring flowering earlier but delayed fall flowering, with summer-flowering species showing intermediate responses. Except for *L. punctata*, which was fall-flowering with a median DOY for peak flowering of September 22, all of our species began flowering in mid- to late-summer, so they could be experiencing conflicting signals which would lead to no overall change in flowering time. In addition, for taxa that require vernalization (a period of cold before they are able to germinate, grow, or flower), warmer winters may delay sprouting or flowering, because the plants may wait to start to grow until they have experienced a certain number of cool or cold days (e.g., Hepworth et al. 2018; Gremer et al. 2020; Jánosi et al. 2020). However, while the only annual, *G. ciliata*, typically germinates in the fall (Kistenmacher and Gibson 2016), it does not require a cold period to flower after germination (A. J. Moore, pers. obs. of greenhouse plants). The other three species are perennials, and the vernalization requirements to induce flowering in adult plants do not appear to have been investigated.

Other factors besides temperature may be equally important for the timing of flowering in these plants. On its own, the influence of precipitation on flowering times has shown a mix of responses. Some species have not changed flowering times in response to increased precipitation (Abu-Asab et al. 2001; Matthews and Mazer 2016), while other species have delayed flowering with increased precipitation (Von Holle et al. 2010; Mazer et al. 2013), and yet other species advanced flowering with increased precipitation (Crimmins et al. 2010; Lambert et al. 2010). Precipitation has been shown to interact with temperature to determine the timing of various phenological events (e.g., Lesica and Kittelson 2010; Xie et al. 2015; Matthews and Mazer 2016). Messick and Hoagland (in prep.) found that budburst in *Quercus marilandica* Münchh. and *Q. stellata* Wangenh. responded to the interactions of temperature (chilling period followed by warming period), cumulative precipitation, and increasing photoperiod from February through April.

In Oklahoma, precipitation or available soil moisture is highly variable year to year. Drought may delay flowering, and abundant precipitation could prolong flowering. In the annual *G. ciliata*, plants in dry years or dry sites remain quite short and produce only a few flower heads, while plants growing in wetter years or more mesic sites can become tall and branched, producing many more heads (A. J. Moore, pers. obs.). These taller plants would also be classified as at peak flowering for longer, both because they would have a large number of open heads for a longer period and because botanists are likely to preferentially collect flowering branches of plants that are too large to collect and press in their entirety, thus further biasing the data to increase the length of time a plant is at peak flowering (Willis et al. 2017; Daru et al. 2018).

Even for species that do not have longer flowering with increased precipitation, variability in flowering within a population would mean that some individuals were flowering while others were either pre-flowering or in fruit. These flowering specimens are more likely to be collected than pre-flowering or mainly fruiting specimens (Daru et al. 2018), in part because they better represent the ideal herbarium specimen, in part because they have the characters needed to identify the plant, and in part because plants that are still green can be pressed more easily than plants that have already completely dried out. Therefore, in the absence of notes on the phenological stage of the population as a whole, we assume that the specimen is representative of the population, when that might not be the case.

It is also possible that some of the species are not able to respond to climatic cues to change their flowering time, but instead respond to day length (e.g., Song et al. 2015). If this is the case, then these taxa may be at risk of declining, because they cannot track their optimal flowering period (Hulme 2011). In a prairie ecosystem, where one or more members of the Asteraceae are in flower throughout the summer, the selection for a particular flowering time may not be that strong. However, if some species track climate while ecologically similar species do not, then their formerly non-overlapping flowering times could begin to overlap, allowing for hybridization or increased competition for pollinators (Park and Mazer 2019; Visser and Gienapp 2019).

We found few significant results in our search for correlations between DOY and year, statewide annual temperature, and annual temperature of the climate division in which specimens were collected across four Oklahoma members of the Asteraceae. This result could be due to annual temperature being too coarse of a measure, to a lack of information on precipitation, or to a bias towards collecting specimens in full flower—artificially extending the time plants were considered to be in Peak Flower or Last Flowering stages. It is also possible that the flowering phenology of these taxa has not shifted with climate change, like it has for so many other taxa.

ACKNOWLEDGMENTS

Special thanks go to Amy Buthod for helping determine phenophases and advice about locations. Thanks to Bruce Hoagland for starting the Oklahoma Vascular Plants Database and to Todd Fagin for providing the localities and numbers of each specimen in the Bebb Herbarium. We thank the MPBIO department at the University of Oklahoma for supporting John Unterschuetz with the George L. and Cleo Cross Endowed Scholarship as an undergraduate student researcher during this investigation. We would like to thank two anonymous reviewers and the editor for valuable comments that improved the manuscript.

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APPENDIX

Scoring Protocols

General Protocol

This protocol is based on the protocol of Haggerty et al. (2013a), with the same four categories and metrics for splitting them up. The First Flowers phenophase (1) indicates specimens with up to 25% open flowers, the Peak Flowering phenophase (2) indicates specimens that have between 25% and 75% open flowers with few fruits present, the Last Flowers phenophase (3) is for specimens with fruits present and more than 50% closed flowers, and the Flowering Finished phenophase (4) is for specimens that are fully in fruit.

If the herbarium sheet includes multiple individual plants or multiple pieces of plants that are not currently connected (even though they may have come from the same plant originally), each plant or plant piece gets its own score and is a separate data point. To score the individual plants or parts, it is important to take all of the flowering heads on that plant into consideration. The entire plant should not be scored based on the state of just one part of the plant. Each head on a branch or each part of the inflorescence can be scored separately, and those scores can be averaged to get the score of the entire plant.

Grindelia ciliata Protocol

Grindelia ciliata has radiate heads with yellow ray florets and many disk florets. The ray florets produce seeds and thus factor into the higher scores that indicate fruits (3 or 4). The presence of relatively long ray florets (up to about 4 cm) makes the interior disk florets much harder to investigate and also indicates a mature inflorescence. Because the disk florets are so tiny, they are often pressed into the page and harder to view from the side in a dissection scope. When the disk florets are flowering, they will have prominent yellow anthers. The achene is a brown color with a pappus of long bristles, which can be seen without peeling back the ray florets.

Without developed ray florets, if the plant does have any open disk florets, it would be in the First Flowers (1) category. If a head has ray florets, they must be gently pulled back to look for the prominent anthers that each open disk floret will produce. The proportion of disk florets with visible anthers will allow the plant to be scored. If more than 25% of the florets have conspicuous anthers and there is not a lot of pappus sticking out of the receptacle, the plant is likely in the Peak Flowering (2) category. If more than 75% of the florets are open and there are fruits present (with prominent pappus bristles), the plant belongs in the Last Flowers (3) category. Last flowers specimens have lots of pappus, but they also have some open florets that must be confirmed by using a dissection probe to carefully sift through the pappus to search for conspicuous anthers. If no yellow anthers are seen, the specimen is in the Flowering Finished (4) category.

Liatris punctata Protocol

Liatris punctata has discoid heads, which only have purple disk florets. The inflorescence is a spike-like cyme with many heads. The heads at the top (distal) end of the inflorescence open first and those at the lower (proximal) end of the spike open last. When the disk florets are open, their light purple stigmas will be visible. If the florets do not have a visible stigma the dissection probe can be used to manually open a "closed" floret to see if it is a bud or a developing achene. The achenes appear slightly pinkish and are very hard to the touch with the dissection probe.

Scores are determined by starting at the top of the inflorescence in this species. If there are achenes in the proximal heads, then the specimen must be in either the Last Flowers (3) or

Flowering Finished (4) category. While, if the terminal heads are still developing and their florets are all not fully open, then the plant would be in the First Flowers (1) category, since the heads on the rest of the inflorescence will open later than the top heads. If the top heads have open florets or fruits, then the rest of the inflorescence must be examined to see how open the other florets are and keeping a rough count to estimate percentages. It is crucial to count the emerging heads that may only appear as buds to get accurate percentages to differentiate between First Flowers (1) and Peak Flowering (2) categories.

Ratibida columnifera Protocol

Ratibida columnifera has radiate heads, with the ray florets that are dark red with yellow edges or entirely yellow and the ray corollas that are dropped when the heads are in fruit. The disk florets are borne on an elongated, column-like receptacle, where they open from bottom to top of the receptacle, so florets on the top of the head can be assumed to be younger. The receptacles and florets are green when they are immature and, as the heads develop, they turn brown. Individual florets must sometimes be investigated with a dissection probe, because they are very small and hard to see inside of. Florets in fruit are much larger in diameter and harder to break open with a dissection probe than undeveloped florets. The achenes are dark brown to black in color.

Plants with many green immature heads will be in the First Flowers (1) category. Plants in this category must also have some open florets. Individual heads should be scored from bottom to top, noting the number of florets with pollen visible. In most plants in the Peak Flowering (2) category, the ray florets will be colorful, and the disk florets will also appear yellow because of their pollen. The fruits that will be present in the Last Flowers (3) category cannot be broken with the dissection probe, while undeveloped buds can be. Specimens that are in the Flowering Finished (4) category have all of their florets in fruit or will have some missing florets, because the fruits have already been dispersed.

Vernonia baldwinii Protocol

Vernonia baldwinii has discoid heads, with purple disk florets. The heads form a cyme in this species, with each section of the cyme flowering at roughly the same time. For example, if upon investigation of a specimen, a certain group of heads in the cyme contains an achene, the other heads in that branched group should be checked for achenes. The cyme has a more developed, longer, and thicker main branch, with shorter, younger branches coming from the bottom. Undeveloped florets are much smaller and green in color, while open florets are purple and have visible anthers and styles. The filaments are white, and the style extends beyond the corolla tube. When the plant is in fruit, the achenes produce a pappus with brown bristles. These florets developing into achenes are harder to the touch with a dissection probe.

The presence of many smaller, green, undeveloped florets on a specimen would indicate the First Flowers (1) category. When 25–75% of all florets on a plant, after considering each branched group, appear purple and the corolla containing stigma and anthers can be seen appearing out of the pappus, the plant is in the Peak Flowering (2) category. If many branched groups within the cyme inflorescence are found with maturing or mature achenes and there are only a few purple corolla tubes present, the plant would be in the Last Flowers (3) category. Plants with fully developed inflorescences with no open florets and all achenes with visible brown pappus would be in the Flowering Finished (4) category.

Oklahoma Native Plant Record
Volume 21, December 2021

LITERATURE REVIEW OF DENDROCHRONOLOGY RESEARCH IN OKLAHOMA, U.S.A.

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Keywords: Quercus, tree-ring, climate, stand dynamics, fire, land-use history

ABSTRACT

Dendrochronology, the study of tree-rings to help understand events of the past, is a growing body of research that has become well-established in scientific literature within the last century. Oklahoma is a distinct resource to dendrochronology as it exists at the eastern deciduous forests and western prairies/grasslands transition. The extent of dendrochronological research conducted in Oklahoma has not yet been determined. A literature review was performed to catalogue and quantify dendrochronological research for Oklahoma. Thirty-seven written works were identified ranging through years 1923 to 2018. Nine research topics were developed to aid publication synthesis, with climate reconstruction, fire history, and stand dynamics being the most frequently encountered topics. Reviewed publications indicated that humans and climate, specifically drought, largely impacted Oklahoma forests historically, and remain a current threat. Results provide a detailed resource of dendrochronological applications within Oklahoma that spans the past century. Presented literature can be referenced for future Oklahoma dendrochronology studies, with presented knowledge also benefiting studies of similar forest types elsewhere.

INTRODUCTION

North American forests have undergone species compositional changes and remain susceptible to further change (Bürgi et al. 2000; Hall et al. 2002; Dyer 2006, Pederson et al. 2014). Factors contributing to forest changes include climate change, anthropogenic effects, biotic interactions, and natural disturbances (Wallin et al. 1996; Radeloff et al. 1999; Gerhardt and Foster 2002; Guyette et al. 2003). Oklahoma contains an estimated 12.2 million acres (4.9 million ha) of forestland which amounts to 27% of total land area (Dooley 2018). The Great Plains and eastern deciduous forest complex converge within Oklahoma, resulting in a central forest-grasslands ecotone (Robinson et al. 2019). Oklahoma's earliest U.S. Geological Survey was conducted on eastern Indian Territory from 1895 to 1898 and documented an estimated 12 million forested acres in eastern Oklahoma (Johnson et al. 2015). Land-use practices by Native Americans and Euro-American settlers largely affected Oklahoma's forests (Johnson et al. 2015; Oklahoma Forestry Services 2019a). Native Americans cleared forests for agriculture/ rangeland and performed intentional burning (Oklahoma Forestry Services 2019a). Euro-American settlement in Oklahoma which began in the early 1800s also impacted forests through agriculture, intentional burning, lumber harvesting, commercial logging, incentivized planting, and fire suppression/exclusion (Smola 1985; Johnson et al. 2015; Oklahoma Forestry Services 2019a). Consequences of

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historic land-use practices are still observable within Oklahoma's forests.

Historic and current abiotic factors such as topography, soil nutrient availability, wildfire, and climate also affect Oklahoma forestland (DeSantis et al. 2010a; DeSantis et al. 2010b; Johnson et al. 2015). Precipitation and temperature gradients contribute to an observed pattern of decreasing forest cover from east to west as well as tree species distribution (Kloesel et al. 2018). Oklahoma's largest forest-type group is oak-hickory (*Quercus* L.-*Carya* Nutt.), comprising more than half (55.5%) of all Oklahoma forestland as defined by the United States Department of Agriculture Forest Service (Dooley 2018). Other notable forest-type groups are much smaller in proportion: elm-ash-cottonwood (*Ulmus* L.-*Fraxinus* L.-*Populus* L.; 11.5%), loblolly-shortleaf pine (*Pinus taeda* L.-*Pinus echinata* Mill.; 10.0%), oak-pine (*Quercus-Pinus* L.; 7.8%), and other eastern softwoods (4.5%) (Dooley 2018). The oak-hickory forest-type group includes one of Oklahoma's major forest types, the post oak-blackjack oak forest type, or "Cross Timbers", which is centrally located from north to south within Oklahoma (Oklahoma Forestry Services 2019b). Post oak (*Quercus stellata* Wangenh.), blackjack oak (*Quercus marilandica* Münchh), and black hickory (*Carya texana* Buckley) dominate the overstory of the Cross Timbers, which exists as a matrix of prairie, deciduous forest, and savanna (Johnson et al. 2015; Oklahoma Forestry Services 2019b). The Cross Timbers, which also extends into Kansas and Texas, is one of the least disturbed forest types in the eastern United States (Johnson et al. 2015). Tree-ring research within Oklahoma's Cross Timbers has revealed the presence of undisturbed ancient forest tracts (Therrell and Stahle 1998). Encroachment of native *Juniperus virginiana* L. has become a threat to the Cross Timbers, woodlands, grasslands, and bottomland hardwoods of Oklahoma, impacting hardwood recruitment and wildlife habitat (Johnson et al. 2015).

Additional threats to Oklahoma forests include invasive plant species, invasive insects/fungi and associated diseases, natural disturbances, urbanization, severe weather, and climate change (Johnson et al. 2015; Kloesel et al. 2018; Oklahoma Invasive Plant Council 2019; Oklahoma Forestry Services 2020). Climate change will likely impact all the beforementioned threats to Oklahoma forests (Kloesel et al. 2018). Natural ranges of floral and faunal species are already limited within Oklahoma's forest-grassland transitional landscape, and small changes to the environment may have consequential effects (Kloesel et al. 2018). A clearer understanding of what factors have previously affected and shaped Oklahoma forests is essential for future conservation efforts involving forest management.

Identifying variables that have previously affected forests can be explained using dendrochronology: the study of tree-ring structure to examine past events in time (Fritts 1976). Trees grow in response to the surrounding environment, and when site history is known, influencing factors can be defined by examining patterns of tree-ring width (Speer 2010). Climate impact on annual tree-ring width has been well documented (Fritts 1976; Swetnam 1993; Guyette et al. 2004; Stambaugh et al. 2009; Brose et al. 2013). Narrow tree-rings represent limited growth and wide tree-rings represent ample growth under favorable environmental conditions (Stokes and Smiley 1996). When accurately dated using accepted methods and statistical techniques, tree-ring widths can provide long records of environmental conditions going back thousands of years (Schulman 1954; Stahle et al. 2019), vital knowledge that would have otherwise remained unknown.

Dendrochronology data remains limited in many regions across the United States. Although dendrochronology research has increased significantly in the past century, with over 11,000 publications as of 2010, assessing new geographic regions can help expand this scientific field (Speer 2010). Dendrochronology research has been conducted in Oklahoma, but a comprehensive review of Oklahoma dendrochronology literature has not yet been performed. This literature review aims to discover tree-ring research studies performed in Oklahoma. Cataloguing and discussing Oklahoma dendrochronology publications (ODP) discloses what subdisciplines of dendrochronology have been previously investigated and reveals topics where research is lacking. Species and locations utilized in studies were also catalogued to help identify areas with future research potential.

METHODS

Peer-reviewed, full-text articles published in scientific journals relating to dendrochronology in Oklahoma were collected using academic databases available online through the Max Chambers Library (MCL) at the University of Central Oklahoma (UCO), Edmond, Oklahoma. Digital libraries (Ebscohost, JSTOR, and ProQuest) and scientific literature databases (Biological Abstracts, BioOne, Environment Complete, ScienceDirect, and Sci-Tech Premium Collection) were searched for article retrieval using the keywords “dendrochronology,” “tree-ring,” “climate reconstruction,” and “fire history” in conjunction with “Oklahoma”. The inter-library loan program through MCL was used to retrieve articles that were unavailable via academic databases. Referencing citations within recovered articles helped locate additional literature. During the review process, theses, reports, bulletins, and conference proceedings were also encountered, and when found relevant, were included within the literature review. The written works collected, although not all are published literature, will be hereafter referred to as the Oklahoma Dendrochronology Publications (ODP), for clarification.

The focus of the literature review was to highlight how dendrochronology research has been conducted exclusively within Oklahoma over time and which tree species were utilized. For this reason, dendrochronology research articles that combined Oklahoma with other states/regions were not included. Unpublished individual tree-ring records were also not quantified. Tree-ring records and regional studies are still highly pertinent to dendrochronology overall, in and out of Oklahoma, and a few notable publications are mentioned within the Discussion.

Retrieved ODP were assigned to “research topics” to clarify literature review results. Research topics were also catalogued with supplementary information into Appendix A to serve as an efficient resource for future dendrochronology investigations in Oklahoma and surrounding regions. Reviewed literature will have presented more information/data than discussed here as methods utilizing tree-ring analysis were explored primarily. The succeeding literature review was performed during the years 2019 and 2020, and it should be disclosed that there was likely additional literature published and produced since its development and publication.

RESULTS

Thirty-seven publications were found that performed dendrochronological analyses within Oklahoma (Table 1, Appendix A). Twenty-four publications were journal articles which were published among 19 scientific journals (Table 1; Literature Cited). Publication years ranged from 1923 to 2018, although Sellards (1923), the earliest written work discovered, was not represented graphically (Figure 1). Following the two earliest publications (Sellards et al. 1923; Harper 1960), at least one publication per decade was observed (Figure 1).

Table 1 A total of 37 written works involving dendrochronological analysis within Oklahoma were found among seven types of literature.

Oklahoma Dendrochronology Publication Types	
journal articles	24
master's theses	4
conference publications	3
doctoral theses	3
bulletin	1
honors thesis	1
report	1
Total	**37**

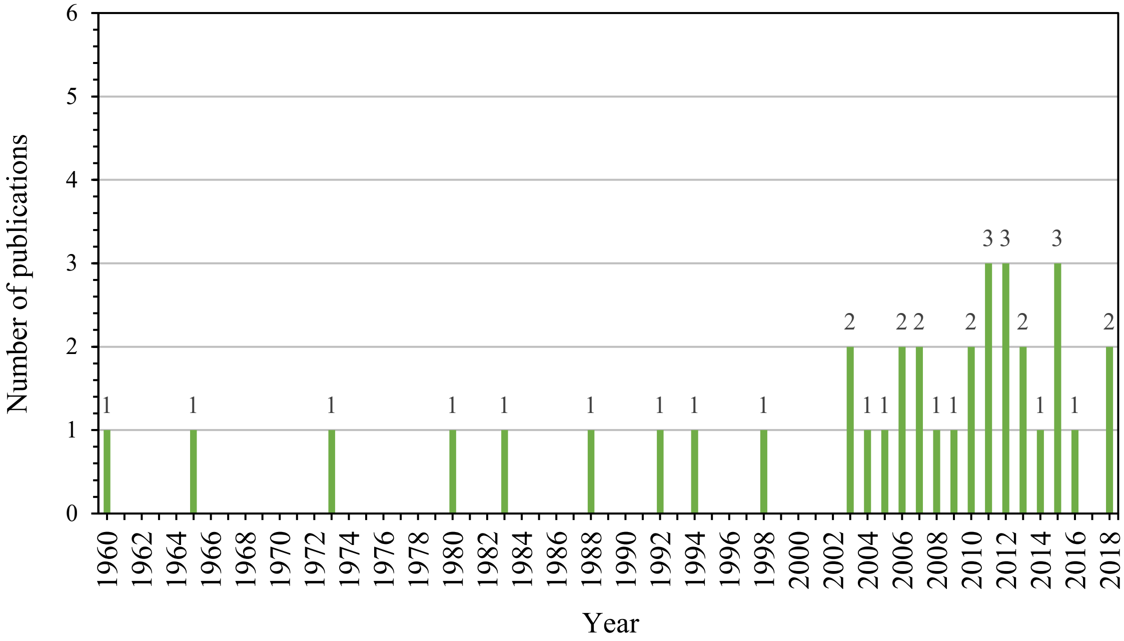

Figure 1 Thirty-six publications published between 1960 and 2018 each presented dendrochronological research conducted in Oklahoma (Sellards et al. [1923] not shown).

Sellards et al. (1923) was part of a Supreme Court ruling for which the boundary line between Oklahoma and Texas, originally defined by the Red River's natural course, needed to be reestablished. Physiographical, geological, and ecological evidence was used to help date the land area surrounding the Red River valley/riverbanks, which included determining age structure for trees of the area (Sellards et al. 1923). The most recent publication retrieved was Hoff et al. (2018). Earliest ODP were shorter, had smaller sample sizes, and typically focused on one variable affecting tree-ring width (Harper 1960; Johnson and Risser 1973). Variability in study site locations was observed, but some areas were subject to repeated study over time.

Study sites

Thirty-one ODP focused on research within the Cross Timber and 18 studies investigated forest reserves and management areas: Wichita Mountains Wildlife Refuge/Wichita Mountains, Keystone Ancient Forest Preserve, Tallgrass Prairie Preserve, Okmulgee Game/Wildlife Management Area, and Nickel Family Nature and Wildlife Preserve. Six ODP evaluated counties, ecoregions, and other areas throughout Oklahoma: Oklahoma/Texas boundary, Bryan County, Oklahoma County, Payne County, Harper County, Ellis County, and Ozark Highlands. Areas of repeat investigation resulted in some tree genera/species explored more often than others among the ODP (Figures 2 and 3).

Genera and species

Species from 12 families and 13 genera were investigated among the 37 publications with *Quercus* being the most frequently examined genus and *Juniperus* being second (Figure 2; Appendix B). Twenty-one tree/shrub species of 12 genera were analyzed dendrochronologically for various purposes specific to each publication (Figure 3). Sellards et al. (1923) did not specify trees at the species level and Hoff et al. (2018) grouped some species by genus for analyses. Only trees where species were known were included in Figure 3.

Although an array of genera and species were investigated, *Quercus* showed the highest presence within the ODP (Figure 2), particularly *Q. stellata* and *Q. marilandica* (Figure 3; Appendix B). Some tree species were investigated less frequently as main species within the ODP: *Fraxinus pennsylvanica* Marshall (King and Buck 2018), *Pinus echinata* Mill. (Taylor 1965, Stambaugh et al. 2013a, Cerny et al. 2016) and *Prunus angustifolia* Marshall (Dunkin et al. 2008). *Juniperus virginiana* L. was the third most examined species and the main study species for six ODP (Butler and Walsh 1988; Engle and Kulbeth 1992; Edmondson 2006; Dunford et al. 2007; Hammer 2012; Bode 2015; Figures 2 and 3). In seven ODP, *Q. marilandica*, *Q. stellata*, and *J. virginiana*, were main study species collectively (Clark 2003; DeSantis 2010; DeSantis et al. 2011; Hallgren et al. 2012; Stambaugh et al. 2013b; Stambaugh et al. 2014; King and Cheek 2015).

Research topics

Oklahoma dendrochronology publications (ODP) were assigned to nine research topics based on each study's objectives, methods, and results (Figure 4). The task of assigning publications to one topic was at times problematic due to occasional overlap in studies' hypotheses, results, and discussions. Complexity of research goals for some studies required the assignment of a combination of research topics. Research topics were developed during the literature review based on types of dendrochronological investigations encountered among the ODP. The nine research topics are Age-diameter/Growth rate, Age-diameter/Growth rate & Stand dynamics, Climate, Climate and Stand dynamics, Fire history, Fire history and Stand dynamics, Geomorphology, Oil extraction, and Stand dynamics (Figure 4, Appendix A).

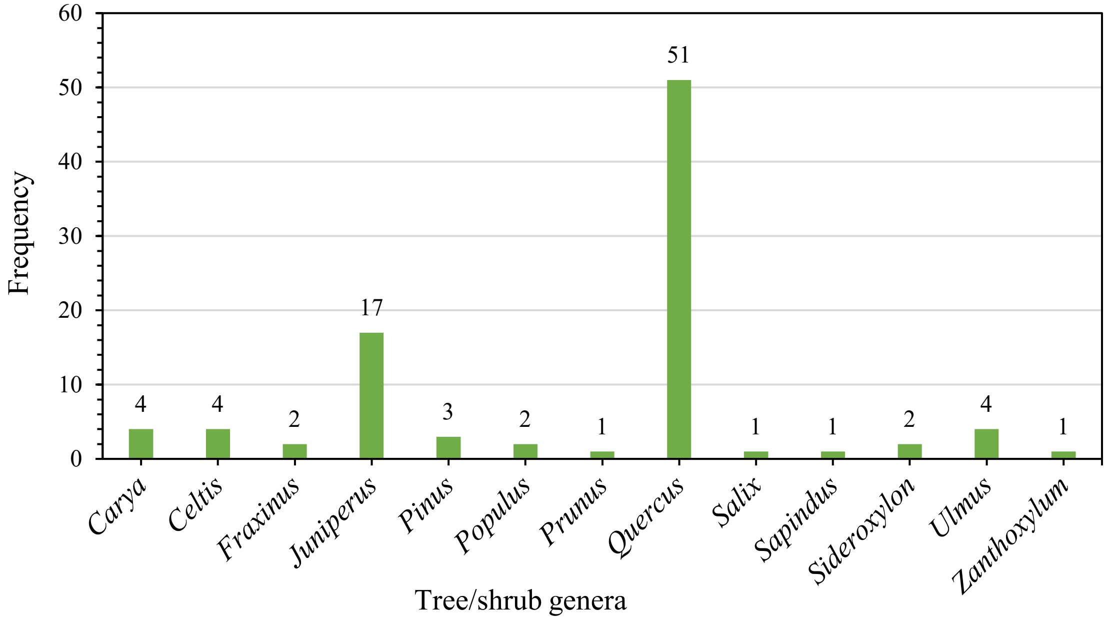

Figure 2 Thirteen genera were researched among the 37 Oklahoma dendrochronology publications.

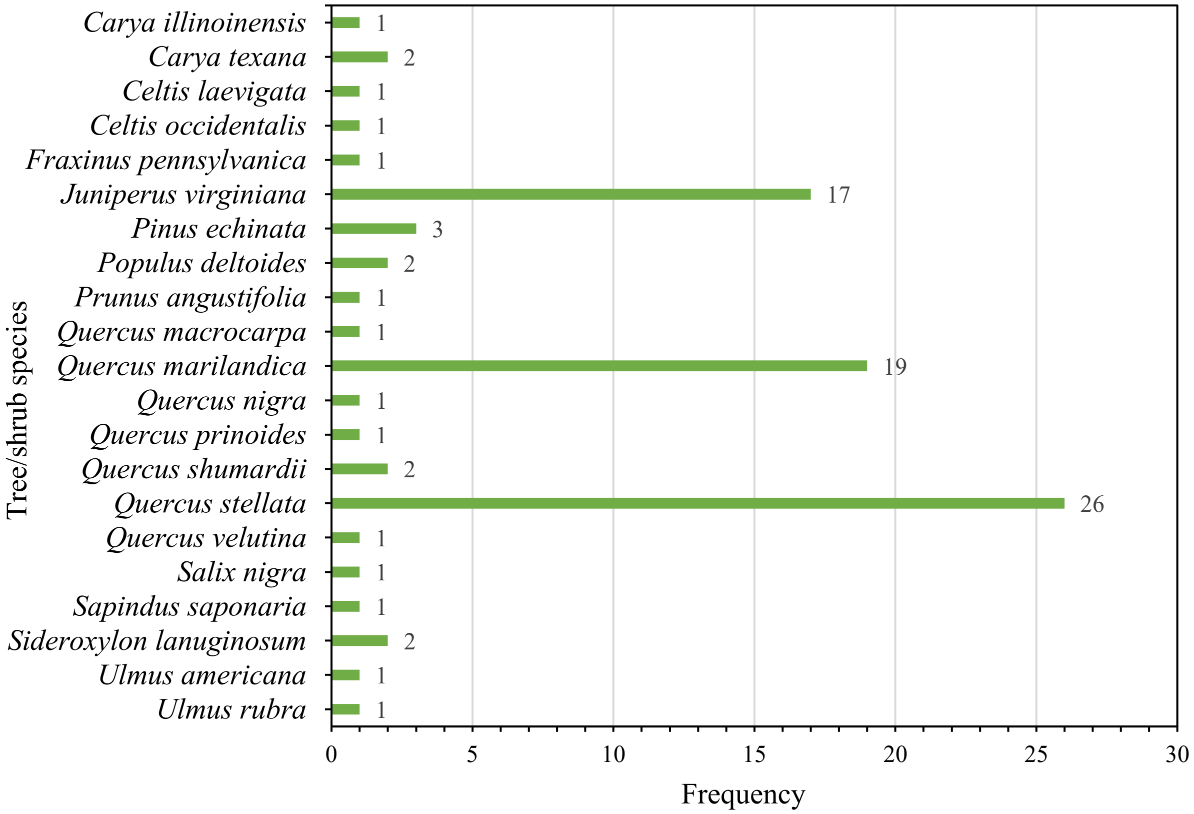

Figure 3 Twenty-one species were researched among the 37 Oklahoma dendrochronology publications.

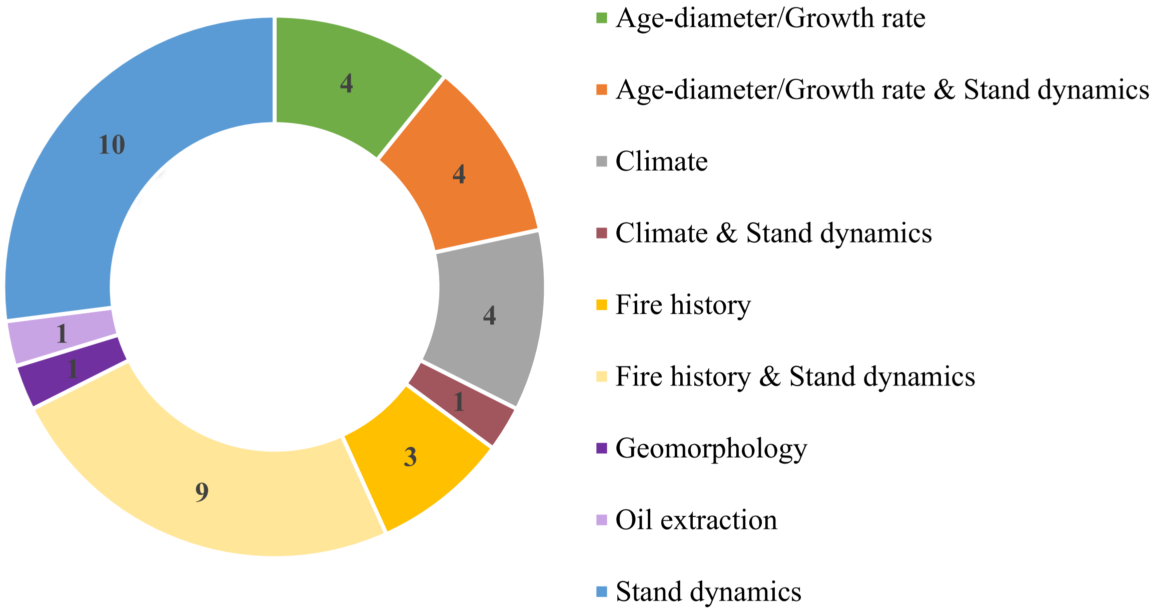

Figure 4 The 37 Oklahoma dendrochronology publications were designated into nine research topics based on the primary study objectives of each publication.

Appendix A chronologically discloses assigned research topics for the 37 ODP and the species used for dendrochronological analysis. Research topics were assigned to the ODP based on how tree-rings were specifically analyzed to answer questions posed by investigators. Specific results and analysis of publications within some research topics was suitably reserved for the Discussion. The least investigated topics were Geomorphology, Oil Extraction, and Climate & Stand Dynamics (Figure 4). Stand Dynamics was the most investigated subject as it was the broadest category by collectively including ODP that performed tree-ring analyses to assess temporal patterns/changes in forest composition: competition, conversion, distribution, disturbance, encroachment, recruitment, regeneration, and succession (Figure 4). Climate and Fire History were the next most investigated subjects. Of the 37 ODP, 31 involved Climate, Fire History, and Stand Dynamics at varying degrees (Figure 4). These heavily investigated research topics are historically and ecologically connected.

DISCUSSION

This literature review granted an overview of the progression and use of dendrochronology research in Oklahoma over time (Figure 1). Sellards et al. (1923) was a distinct and historically significant application of tree-ring analysis in Oklahoma. As the amount of dendrochronology literature increased in Oklahoma, methods were refined, information became more accessible, and dendrochronological studies occurred more frequently and were conducted at a larger scale (Clark et al. 2007; Stambaugh et al. 2009; Stambaugh et al. 2014; Figure 1).

Publications generally increased in complexity over time regarding objectives, methods, and results. Tree-rings, false-rings, and fire scars were analyzed using a variety of living and dead sample types: cores, stem/root cross-sections, and fallen trees/snags. As seen in Figures 2 and 3, two genera and three tree species dominated the Oklahoma dendrochronology literature during the observed temporal period. These species were encountered the most among the ODP for numerous reasons.

Quercus stellata and *Q. marilandica* are dominant species in the Cross Timbers, the largest forest type in Oklahoma (Dooley 2018; Oklahoma Forestry Services 2019b). Encroachment of *J. virginiana* is also occurring within the Cross Timbers (Dooley 2018; Johnson et al. 2015; Oklahoma Forestry Services 2019b). Results show that *Q. stellata* has had greater population stability than *Q. marilandica* for the past half-century considering increased drought and *J. virginiana* encroachment (Johnson and Risser 1973; Powell and Lowry 1980; Dooley 1983; Shirakura et al. 2006; Hammer 2012; Stambaugh et al. 2013b). However, McGrath (2012) observed stable *Quercus* recruitment was lacking despite absence of mesophication and *J. virginiana* invasion. Hammer (2012) researched within the Wichita Mountains National Wildlife Refuge and found that all dominant tree species (*Quercus* and *Juniper*) were experiencing ample reproduction despite temporal anthropogenic/environmental changes. *Quercus stellata* and *J. virginiana* are long-lived species, making them ideal for climate reconstructions, and *Q. stellata* has been shown to produce the best climate signal of trees of this region (Stahle and Cleaveland 1988; Therrell 2000).

Assigning publications to research topics helped illustrate what scientific areas were explored most often. Some research topics were assessed only once, such as Geomorphology which included Sellards et al. (1923), and Oil Extraction, which included Dunford et al. (2007) who quantified oil distribution in heart/sapwood based on age for urban *J. virginiana* trees (Figure 4). Age-diameter/Growth Rate literature is still currently relevant, with Powell and Lowry (1980), Engle and Kulbeth (1992), and Dunkin et al. (2008) providing rangeland management recommendations and Rosson (1994) assessing *Q. stellata* growth characteristics/stand structure as a commercial resource. Age-diameter/Growth Rate & Stand Dynamics consisted of Dooley (1983), McGrath (2012), Hammer (2012), and Hoff et al. (2018) who all investigated species compositional changes in the Cross Timbers. Dooley (1983) observed stable *Quercus* establishment while McGrath (2012) observed a lack of stable *Quercus* recruitment coupled with a lack of mesophication, likely due to an enacted prescribed burning regime. Hammer (2012) examined anthropogenic, topography, and fire exclusion effects on *J. virginiana* expansion, distribution, and age. Results from Hoff et al. (2018) offered evidence that *Quercus*-dominated forests may be experiencing a compositional transition due to fire exclusion (early 1900s) and mesophication (post 1950s), a change also occurring in other parts of the U.S. (Abrams 1992).

Further research is needed to help determine why some but not all Cross Timbers forests are experiencing a dominant species transition. Some areas experience prescribed burnings while others do not, and other disturbances/environmental factors have been removed/added within the last century, which can also influence forest stand dynamics. Investigating publications from the literature review revealed the greatest factors influencing Oklahoma forest stand dynamics involved climate and fire.

Determining the most limiting environmental factor affecting tree-ring width at the stand-level is a recurrent goal for dendrochronologists (Fritts 1976; Speer 2010). Many ODP offered evidence that drought was a significant variable affecting Oklahoma tree growth. Climate ODP of different decades focused on drought reconstruction (Harper

1960; Johnson and Risser 1973; Butler and Walsh 1988; and Bode 2015). Harper (1960) determined drought frequency and Johnson and Risser (1973) assessed drought effects by evaluating annual tree-ring variation in *Quercus*. Butler and Walsh (1988) and Bode (2015) both demonstrated innovative applicability of *J. virginiana* in dendroclimatology despite the species being difficult to cross-date due to false-ring formation. Bode (2015) discovered false-ring events were more likely to occur in areas with the most variable precipitation. In the sole publication of Climate and Stand Dynamics, DeSantis et al. (2011) showed that species compositional changes such as reduced *Quercus* recruitment in central Oklahoma forests was due to factors associated with fire exclusion and drought.

Fire occurrence in Oklahoma was historically common (Oklahoma Forestry Services 2019a). Fire History ODP helped establish the impact of humans and drought on historic fire regimes (16th to 21st centuries) by dating fire scars to develop fire chronologies (DeSantis et al. 2010b; Allen and Palmer 2011; Stambaugh et al. 2013a). Removal of Native Americans, influx of Euro-Americans, and fire exclusion were all found to correlate with historic fire regime changes; humans had a more significant effect on fire regimes compared to drought.

Fire, drought, and human habitation/land-use were further explored in the Fire History and Stand Dynamics ODP, which developed fire histories to better understand current forest conditions (Shirakura 2006; Clark et al. 2007; Stambaugh et al. 2009; DeSantis 2010; DeSantis and Hallgren 2011; Hallgren et al. 2012; Stambaugh et al. 2013b; Stambaugh et al. 2014; and King 2015). Factors in addition to fire history were explored, such as topography (Clark et al. 2007), sprout regeneration (DeSantis and Hallgren 2011), and sapling age structure (King 2015). While scale of studies varied, *Q. stellata, Q. marilandica,* and *J. virginiana* were the main species for all publications of this topic. Altered temporal fire regimes within central Oklahoma forests were more often linked to anthropogenic activity rather than drought (Clark et al. 2007; DeSantis et al. 2010b; Allen and Palmer 2011; Stambaugh et al. 2013b; Stambaugh et al. 2014; King 2015). These ODP revealed that historic/current fire regimes have affected successional processes of Oklahoma forest ecosystems, particularly by removal of fire from the landscape and mesophication.

The Stand Dynamics research topic contained the highest number of ODP with the most diverse main study species: *P. echinata* (Taylor 1965; Cerny et al. 2016), *J. virginiana* (Edmondson 2006), *Quercus* (Therrell and Stahle 1998; Clark 2003; Clark and Hallgren 2003; Clark and Hallgren 2004; Clark et al. 2005; King and Cheek 2015), and *F. pennsylvanica* (King and Buck 2018). Numerous forest types/locations were assessed: upland *Quercus-Pinus* stand (Taylor 1965), Shortleaf Canyon (Cerny et al. 2016), upland Cross Timbers (Therrell and Stahle 1998; Clark 2003; Clark and Hallgren 2003; Clark and Hallgren 2004; Clark et al. 2005; Edmondson 2006), an urban forest (King and Cheek 2015), and a lakeside bottomland hardwood forest (King and Buck 2018). Many factors leading to forest composition changes were evaluated in the Stand Dynamics research topic.

Stand Dynamics ODP's methodologies and results were distinct from all other ODP. Taylor (1965) was the first analysis of *P. echinata* in Oklahoma at its western range and Cerny et al. (2016) documented its range expansion. Therrell and Stahle (1998) developed a GIS model that identified soil type to help predict ancient Cross Timbers forest tract locations: a new utilization of dendrochronology. The thesis by Clark (2003) was published successively as journal articles and provided a high amount of information on *Quercus* forest dynamics and Oklahoma Cross Timbers ecology. *Quercus* primarily reproduced by stump sprouting based on root age structure (Clark and Hallgren 2003), methods to correct age estimates were introduced (Clark and Hallgren 2004), and old-growth *Quercus* forests (~200 years) successfully regenerating among mesophytic species was documented (Clark et al. 2005). Edmondson (2006) developed the first *J. virginiana* tree-ring chronology (~360 years) and a false-ring chronology. Investigating directly in an urban area, King and Cheek (2015) demonstrated that disturbed urban forests are an important dendrochronological resource. Due to urbanization, drought, fire exclusion, and lack of management, *Quercus* recruitment decreased as non-*Quercus* recruitment increased, with *J. virginiana*, mesic species, and invasive *Ligustrum sinense* Lour. (Chinese privet) dominating the midstory and understory. King and Buck (2018) described characteristics of bottomland hardwood forest and obtained baseline data for *F. pennsylvanica* in case of an invasive insect outbreak by *Agrilus planipennis* Fairmaire (emerald ash borer). The diverse dendrochronology applications observed in the Stand Dynamics ODP showed analyzing tree-rings can go far beyond studying tree age.

Major ecological questions were addressed by the Stand Dynamics ODP. What is the state of Oklahoma's old-growth forests? How is *Quercus* reproducing? What impact does fire exclusion have? How can laboratory methods be refined to provide more accurate results, and can we analyze false-rings instead of dismissing them? How are forests changing considering urbanization and climate change? Comparing late Stand Dynamics publications to the earliest Oklahoma dendrochronological studies demonstrates how this body of knowledge has advanced over time.

A recurring topic for many ODP were two leading factors affecting forest stand dynamics: historical land-use and drought. Land-use changes over time due to population movements of Native Americans and settlement by Euro-Americans showed a gradual effect on forest ecosystems and disturbance patterns as both groups cleared forests for agriculture, grazing, and logging, and changed fire regimes (Taylor 1965; Clark 2003; Allen and Palmer 2011; and Stambaugh et al. 2013b). More recent effects due to urbanization include fire exclusion, *J. virginiana* encroachment, and introduction of non-native plant species (King and Cheek 2015; Hoff et al. 2018; King and Buck 2018). Several ODP established new techniques and foundspecies applicable to the field of dendrochronology beyond Oklahoma (Therrell and Stahle 1998; Clark and Hallgren 2004; Edmondson 2006; Bode 2015; King and Cheek 2015). Studies that comprised the ODP are significant to forests within Oklahoma, but also to the international field of dendrochronology.

CONCLUSION

From early studies estimating age structure to fire history reconstructions that spanned centuries, there are still more inquiries for Oklahoma forests that can be addressed using dendrochronology. Future dendrochronology studies could examine understudied research topics as revealed by this review, such as Geomorphology and Age-diameter/Growth rates. Field sites from some of the earliest ODP could also be revisited to assess compositional changes. There was also a lack of diversity in tree species utilized in the ODP. Sensitive tree species, such as *Q. stellata*, *Q. marilandica*, and *J. virginiana*, were researched more frequently than others, even though Oklahoma has many other species suitable for dendrochronology studies.

Three ODP included *Pinus* as a main study species (Taylor 1965, Stambaugh et al. 2013a; Cerny et al. 2016). *Taxodium distichum* (L.) Rich. (bald cypress) is also native to Oklahoma but was not a main species in any ODP despite its longevity (>2000 years) and reconstruction capability (Stahle et al. 2019; United States Department of Agriculture 2021). Both *P. echinata* and *T. distichum* are known to produce long tree-ring chronologies which makes them highly applicable for future denchrochronological studies in Oklahoma (Grissino-Mayer and Butler 1993; LaForest et al. 2005-6; Stahle et al. 2019). Long tree-ring chronologies are essential for reconstructions, but analyses of young trees and invasive trees can also provide valuable information. Fast-growing, invasive *Pyrus calleryana* Decne. (Callery pear) is invading Oklahoma open prairies, woodlands, and urban/rural forests (Oklahoma Invasive Plant Council 2019). *Pyrus calleryana* can outcompete native tree species and its eradication is difficult. Dendrochronology could be used to help validate the impact planting this species as an ornamental has on Oklahoma forests.

Oklahoma dendrochronology studies can positively impact dendrochronology research elsewhere. Tree-ring records for species studied in Oklahoma could potentially be submitted to the International Tree-Ring Databank (ITRDB), which is the world's largest tree-ring data repository that is readily available for research (National Oceanic and Atmospheric Administration 2021). The ITRDB is a global resource of tree-ring chronologies containing over 2000 chronologies that spans six continents with the aims to preserve tree-ring data and encourage international research collaborations (Speer 2010). Increasing the diversity of Oklahoma tree-ring records will help expand species representation within this reputable international database. Various historical and potential impacts to Oklahoma forests were recognized within the ODP, many of which likely impact forests outside of Oklahoma.

Multi-state/regional dendrochronology publications that included Oklahoma were not reported in the literature review but are still relevant to dendrochronology research in Oklahoma and elsewhere. Notable research that involved Oklahoma within more comprehensive studies offers substantial findings regarding climate relationships/reconstructions (Stahle and Hehr 1984; Stahle 1990; Cook et al. 1999; Edmondson 2010; LeBlanc and Stahle 2015; Guyette et al. 2015), dendrohydrology (Cleaveland and Stahle 1989), and fire frequency (Guyette et al. 2015; Rooney and Stambaugh 2019). These studies used larger field sites and sample sizes, that increased the significance of results from there research. Oklahoma's inclusion within these multi-state studies demonstrates the role it serves within the larger field of dendrochronology. Future research could include developing a second literature review that catalogues regional/multi-state dendrochronology studies that include Oklahoma. Larger, regional studies, along with the reviewed Oklahoma dendrochronology publications, will likely help uncover the continuous impacts of increased urbanization and climate change on North American forests.

Dendrochronology is one of few environmental proxies that allows researchers to reconstruct environmental conditions of the past with great confidence, offering an outlook into how forests may develop in the future under similar conditions. Compared to other regions in the U.S., there are still a limited number of dendrochronological studies for Oklahoma forests. Discovering new locations, species, and applications within Oklahoma that hold potential for dendrochronological studies is needed to help expand this body of literature within and outside of Oklahoma.

Dendrochronology has helped researchers understand what dominating factors have affected forest stand dynamics in Oklahoma: people and climate. Drought is predicted to increase in length and frequency due to climate change. Urban areas are growing as human populations continue to increase, a contributing variable to climate change. The need for further dendrochronological research remains exceedingly important as climate and humans, the factors that have the greatest impact on Oklahoma forests, are also likely to affect forests worldwide.

ACKNOWLEDGMENTS

We would like to thank the University of Central of Oklahoma for providing the resources necessary to complete this literature review. We would additionally like to thank the reviewers and editorial committee.

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APPENDIX A
Chronological Inventory of Oklahoma Dendrochronology Publications (ODP)

Publication Type Abbreviations	Research Topic Abbreviations
B = bulletin	AD/GR = age-diameter/growth rate
CP = conference proceedings	AD/GR & SD = age-diameter/growth rate & stand dynamics
DT = doctoral thesis	C = climate
HT = honors thesis	C & SD = climate and stand dynamics
JA = journal article	FH = fire history
MT = master's thesis	FH & SD = fire history and stand dynamics
R = report	GM = geomorphology
	OE = oil extraction
	SD = stand dynamics

In-text citation*; Publication type	Research topic	Main study genera/species
Sellards et al. (1923); B	GM	*Carya illinoinensis, Celtis* spp., *Fraxinus* spp., *Populus deltoides*, *Ulmus* spp., *Sideroxylon lanuginosum* ssp. *oblongifolium, Zanthoxylum* spp.
Harper (1960); JA	C	*Quercus macrocarpa, Quercus nigra, Quercus stellata*
Taylor (1965); JA	SD	*Pinus echinata*
Johnson and Risser (1973); JA	C	*Quercus marilandica, Quercus stellata*
Powell and Lowry (1980); JA	AD/GR	*Quercus marilandica, Quercus prinoides, Quercus stellata*
Dooley (1983); DT	AD/GR & SD	*Quercus stellata*
Butler and Walsh (1988); JA	C	*Juniperus virginiana*
Engle and Kulbeth (1992); JA	AD/GR	*Juniperus virginiana*
Rosson (1994); CP	AD/GR	*Quercus marilandica, Quercus stellata*
Therrell and Stahle (1998); JA	SD	*Quercus stellata*
Clark (2003); DT	SD	*Juniperus virginiana, Quercus marilandica, Quercus stellata*
Clark and Hallgren (2003); JA (originally in Clark 2003)	SD	*Quercus marilandica, Quercus stellata*
Clark and Hallgren (2004); JA (originally in Clark 2003)	SD	*Quercus marilandica, Quercus stellata*
Clark et al. (2005); JA (originally in Clark 2003)	SD	*Carya texana, Juniperus virginiana, Quercus marilandica, Quercus shumardii, Quercus stellata, Quercus velutina*

In-text citation*; Publication type	Research topic	Main study genera/species
Shirakura (2006); MT	FH & SD	*Quercus marilandica, Quercus stellata*
Edmondson (2006); HT	SD	*Juniperus virginiana*
Clark et al. (2007); CP (originally in Clark 2003)	FH & SD	*Carya texana, Juniperus virginiana, Quercus marilandica, Quercus shumardii, Quercus stellata*
Dunford et al. (2007); JA	OE	*Juniperus virginiana*
Dunkin et al. (2008); JA	AD/GR	*Prunus angustifolia*
Stambaugh et al. (2009); JA	FH & SD	*Quercus stellata*
DeSantis (2010); DT	FH & SD	*Juniperus virginiana, Quercus marilandica, Quercus stellata*
DeSantis et al. (2010b); JA (originally in DeSantis 2010)	FH	*Quercus stellata*
DeSantis et al. (2011); JA (originally in DeSantis 2010)	C & SD	*Juniperus virginiana, Quercus marilandica, Quercus stellata*
Allen and Palmer (2011); JA	FH	*Quercus stellata*
DeSantis and Hallgren (2011); JA (originally in DeSantis 2010)	FH &SD	*Quercus marilandica, Quercus stellata*
Hallgren et al. (2012); CP	FH & SD	*Juniperus virginiana, Quercus marilandica, Quercus stellata*
Hammer (2012); MT	AD/GR & SD	*Juniperus virginiana*
McGrath (2012); MT	AD/GR & SD	*Quercus marilandica, Quercus stellata*
Stambaugh et al. (2013b); R	FH &SD	*Quercus stellata, Juniperus virginiana*
Stambaugh et al. (2013a); JA	FH	*Pinus echinata*
Stambaugh et al. (2014); JA	FH & SD	*Juniperus virginiana, Quercus marilandica, Quercus stellata*
King and Cheek (2015); JA	SD	*Juniperus virginiana, Quercus marilandica, Quercus stellata*
King (2015); JA	FH& SD	*Celtis laevigata, Celtis occidentalis, Juniperus virginiana, Quercus marilandica, Quercus stellata, Sapindus saponaria* var. *drummondii*, *Sideroxylon lanuginosum* ssp. *oblongifolium, Ulmus americana, Ulmus rubra*
Bode (2015); MT	C	*Juniperus virginiana*
Cerny et al. (2016); JA	SD	*Pinus echinata, Quercus stellata*
King and Buck (2018); JA	SD	*Fraxinus pennsylvanica, Populus deltoides, Salix nigra*
Hoff et al. (2018); JA	AD/GR & SD	*Carya* spp., *Celtis* spp., *Juniperus virginiana, Quercus marilandica, Quercus stellata*, *Ulmus* spp.

APPENDIX B
Index of Tree/Shrub Species Reviewed in Oklahoma Dendrochronology Publications

Main tree/shrub genera and species assessed in the ODP are listed below alphabetically by family/scientific name along with common names and status (N=native, I=introduced) (http://plants.usda.gov; United States Department of Agriculture 2020).

Family name	Scientific name	Common name	Status
CELTIDACEAE	*Celtis* L.	hackberry	N
	Celtis laevigata Willd.	sugarberry	N
	Celtis occidentalis L.	common hackberry	N
CUPRESSACEAE	*Juniperus virginiana* L.	eastern redcedar	N
FAGACEAE	*Quercus macrocarpa* Michx.	bur oak	N
	Quercus marilandica Münchh.	blackjack oak	N
	Quercus nigra L.	water oak or black oak	N
	Quercus prinoides Willd.	dwarf chinkapin oak	N
	Quercus stellata Wangenh.	post oak	N
	Quercus shumardii Buckley	Shumard's oak	N
	Quercus velutina Lam.	black oak	N
JUGLANDACEAE	*Carya* Nutt.	hickory	N
	Carya illinoinensis (Wangenh.) K. Koch	pecan	N
	Carya texana Buckley	black hickory	N
OLEACEAE	*Fraxinus* L.	ash	N, I
	Fraxinus pennsylvanica Marshall	green ash	N
PINACEAE	*Pinus echinata* Mill.	shortleaf pine	N
ROSACEAE	*Prunus angustifolia* Marshall	Chickasaw plum	N
RUTACEAE	*Zanthoxylum* L.	pricklyash	N, I
SALICACEAE	*Populus deltoides* W. Bartram ex Marshall	eastern cottonwood	N
	Salix nigra Marshall	black willow	N
SAPINDACEAE	*Sapindus saponaria* L. var. *drummondii* (Hook. & Arn.) L.D. Benson	western soapberry	N
SAPOTACEAE	*Sideroxylon lanuginosum* Michx. ssp. *oblongifolium* (Nutt.) T.D. Penn	gum belly or chittamwood	N
ULMACEAE	*Ulmus* L.	elm	N, I
	Ulmus americana L.	American elm	N
	Ulmus rubra Muhl.	slippery elm	N

COLD STRATIFICATION OF *SALVIA AZUREA* VAR. *GRANDIFLORA* BENTH. (LAMIACEAE) SEEDS TO BREAK DORMANCY

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Keywords: germination, pitcher sage

ABSTRACT

Seed dormancy and its maintenance rely on a range of environmental signals and cues such as light, temperature, soil pH, and moisture. A significant contributor to the cycle of dormancy and germination is temperature. *Salvia azurea* var. *grandiflora* Benth. is an Oklahoma native perennial that produces blue flowers with one seed per flower. Seeds were collected from four sites in Oklahoma and Cleveland Counties, OK, and randomly assigned to one of three treatment groups: no cold stratification, 3-week cold stratification, and 6-week cold stratification. Seeds were monitored daily, and seed germination date was recorded for analysis. Survival analysis indicated there was a significant correlation between the amount of time in a cold stratification environment and number of seeds that germinated. Seeds in the 6-week cold stratification treatment group exhibited increased germination compared to the other two treatment groups.

INTRODUCTION

Environmental temperature and climate variability are dominant influences for many species' life-history traits (Bernareggi et al. 2016; Fernandez-Pascual 2019). Plant reproductive phases, such as seed germination and seedling establishment and survival, are more sensitive to variation in climatic conditions (Bernareggi et al. 2016; Nonogaki 2017) than other phases of the plant life cycle. Seed dormancy is an adaptation that allows for persistence of a population during seed dispersal or impact by climatic conditions, including temperature extremes and drought (Baskin and Baskin 2001; Messick and Hoagland 2018). This mechanism is dominated by an intricate balance between the phytohormones gibberellins and abscisic acid (Footitt et al. 2014; Nonogaki 2014; Hradilova et al. 2019). Balance continues to be maintained through cohorts of genes that regulate the hormones' perception, sensitivity and metabolism through the use of complex signaling pathways necessary for seed dormancy and the control of germination (Footitt et al. 2014; Nonogaki 2017; Tudela-Isanta et al. 2017; Fernandez-Pascual 2019). Cold affects dormancy levels and cycling by affecting levels of abscisic acid and making environmental temperature an important signal for numerous plant species (Footit et al. 2014; Nonogaki 2014), and has been studied in molecular detail in relation to dormancy induction and cycling control by hormones. Warmer temperatures (above 15°C) are generally related to lower levels of dormancy (Footit et al. 2014), whereas cooler temperatures (10-15°C) induce higher dormancy levels in seeds and are correlated with strongly enhanced abscisic acid levels.

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Seeds may exhibit physiological dormancy, physical dormancy, or a combination of both (Baskin and Baskin 2001). The most observed type of dormancy, physiological dormancy, is regulated mainly by the relative levels of hormones that either inhibit or promote germination. It produces seeds with distinct and valuable advantages. Physiological dormancy ensures germination will not occur in an adverse climatic environment, although short periods of favorable conditions may present themselves (Carrera-Castano et al. 2020). It also provides for maximum dispersal of seeds, which decreases competition between the parent plant and offspring (Baskin and Baskin 2001; Carrera-Castano et al. 2020). Physiologically dormant seeds also exhibit dormancy cycling, which is the alleviation and re-induction of dormancy (Baskin and Baskin 2001; Long et al. 2015) in response to changing environmental signals and cues. Physical dormancy is when a seed coat is impermeable to water and gases needed for germination. Physically dormant seeds are unable to exhibit dormancy cycling because the change in seed coat permeability cannot be reversed (Baskin and Baskin 2001; Long et al. 2015).

Salvia azurea var. *grandiflora* Benth. (pitcher sage), a member of the Lamiaceae (Mint Family), is a native perennial with a distribution range from the eastern U.S. to New Mexico and Colorado (Figure 1).

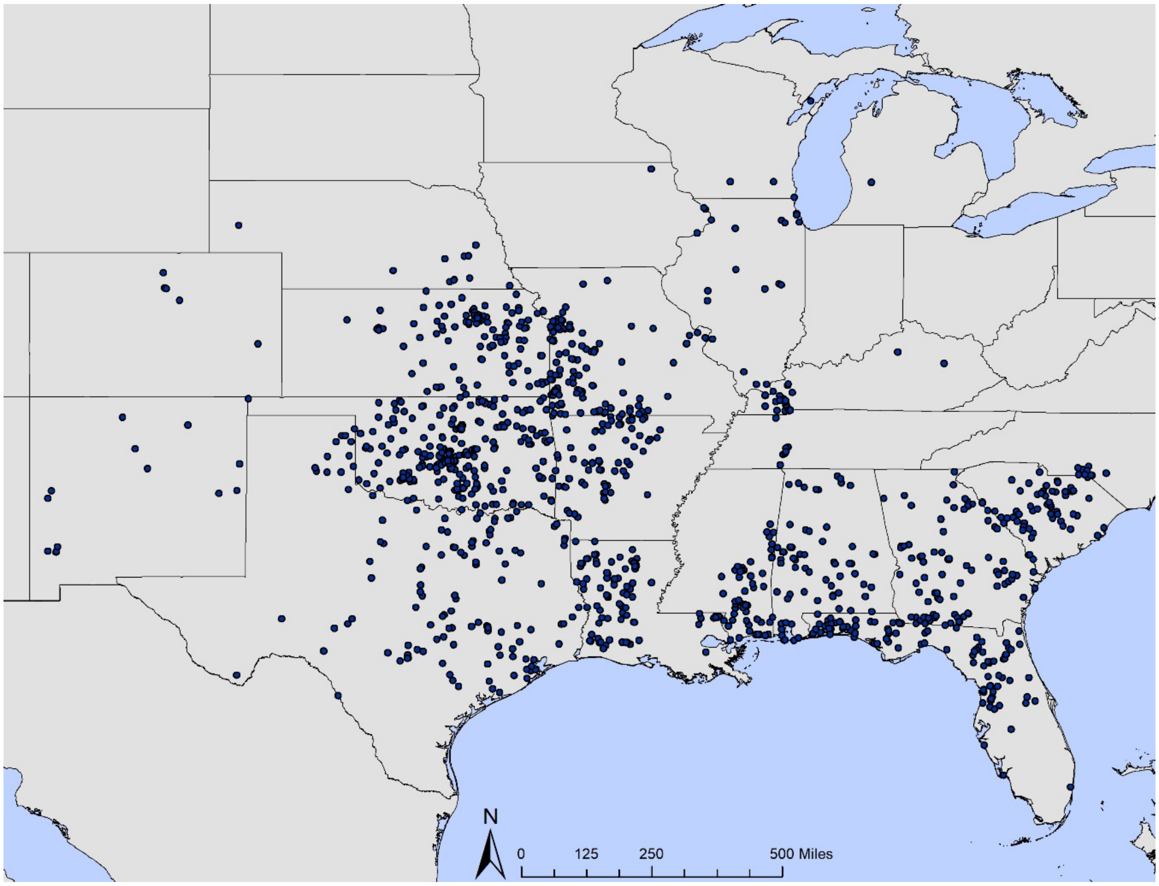

Figure 1 *Salvia azurea* var. *grandiflora* distribution range in the United States.

It reaches 50-150 cm in height with leaves averaging 3-7 cm long and 1-2.5 cm wide (McGregor et al. 1986). *Salvia azurea* var. *grandiflora* produces blue flowers (occasionally white), from July through October (McGregor et al. 1986), with one seed per flower. It is an important resource for generalist pollinators, including monarch butterflies (Figure 2), which use *S. azurea* var *grandiflora* as a nectar source during their fall migration (Xerces Society for Invertebrate Conservation 2021). One specialist bee, *Tetraloniella cressoniana* (blue sage bee), has coevolved with *S. azurea* var. *grandiflora* and depends on the nectar of *S. azurea* var. *grandiflora* as its sole source of nutrition (LaBerge 2001; Schuette 2016).

Understanding the seed germination requirements of *S. azurea* var. *grandiflora* is important to study because the data have the potential to contribute to our knowledge of climate change and its effect on environmental temperature and the cycle of dormancy. The goal of this study was to determine the relative length of cold stratification required to produce an increased rate of germination for *S. azurea* var. *grandiflora.* My null hypothesis was that cold stratification would have no effect on germination probability.

Figure 2 *Salvia azurea* var. *grandiflora* in northwestern Oklahoma with monarchs nectar feeding. Photo credit: Amy Buthod 2018, Oklahoma Biological Survey, Norman, OK.

METHODS

Salvia azurea var. *grandiflora* seeds were collected from four sites (Figure 3; Table 1) located using the Oklahoma Vascular Plant Database (OVPD; Hoagland et al. 2021). A total of 270 seeds were obtained from among these sites, with the number of plants from each site varying dependent upon availability. Then seeds were pooled and randomly assigned to one of three treatment groups: no cold stratification (no cold), three weeks of cold stratification at 4°C (3-week cold), and six weeks of cold stratification at 4°C (6-week cold). Each treatment consisted of three replicates each having 30 seeds per petri dish for a total of 90 seeds per treatment. The seeds were placed in standard (90 mm x 15 mm) petri dishes containing a thin layer of vermiculite and moistened with deionized water. This helped to maintain consistent moisture levels and aided in controlling potential mold growth. The no cold treatment group was placed on a lab bench at room temperature under lights set for 12 hours on and 12 hours off. The 6-week cold treatment group was placed in a standard refrigerator for the stratification period. Three weeks into this stratification period, the 3-week treatment group was placed in the same cold stratification environment.

Table 1. Latitude and longitude of sample sites.

Collection Site	Latitude	Longitude
Mitch Park	35.65085	-97.47227
Myriad Gardens	35.46651	-97.5145
John Saxon Park	35.18675	-97.39542
Sutton Wilderness	35.20141	-97.43688

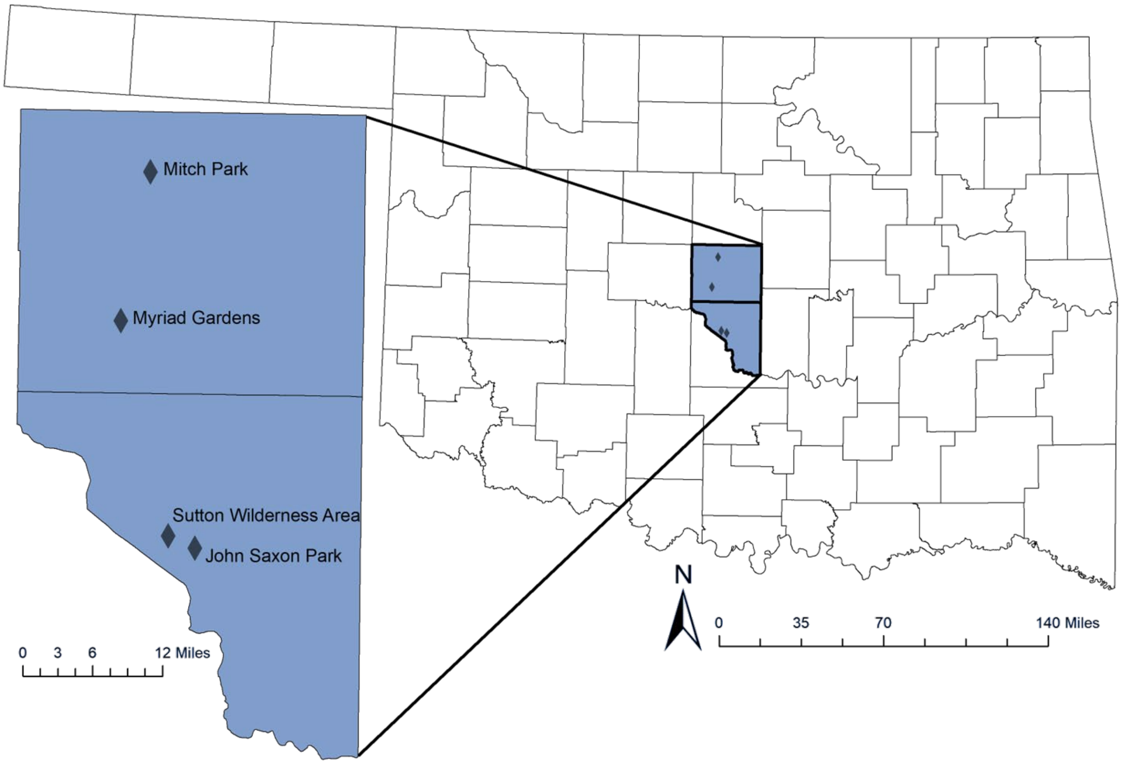

Figure 3 Collection sites in Oklahoma and Cleveland counties, OK.

Prior to cold stratification, only the no cold treatment group was exposed to light, but because the seeds were covered with vermiculite, there might have been little exposure. Upon removal from cold stratification, all three treatment groups received 12 hours of light and 12 hours of dark. Moisture levels of all the treatment groups were monitored every day to ensure continued proper moisture maintenance and seeds were lightly misted as needed. Observations of each treatment group were made at that time and any germination was recorded. Seeds were considered to have germinated upon emergence of the radicle from the seed. All three treatment groups were observed every day for six weeks to allow for latent germination of seeds that still appeared to be dormant. Germinated seeds were carefully removed, transplanted, and allowed to grow.

Data analysis consisted of survival analysis, as this test is a powerful methodology for analyzing seed germination (McNair et al. 2012; Manso et al. 2013; Messick and Hoagland 2018; Sanchez-Toledano et al. 2018). Although initially intended to estimate the survival of patients in medical studies, survival analysis can be applied to seed germination studies, as it effectively estimates the failure rate of the seed to survive as a seed (McNair et al. 2012; Manso et al. 2013; Messick and Hoagland 2018; Sanchez-Toledano et al. 2018). In other words, it estimates the probability that a seed will not germinate. The probability of not germinating can then be converted to the probability of germinating by simply subtracting the probability estimate of not germinating from one (Messick and Hoagland 2018; Romano and Stevanato 2020).

Survival analysis consists of Kaplan-Meier survival curve estimation which is then compared using the semiparametric Cox proportional hazards (PH) model. The Cox PH model estimates the proportional hazard for germination to *not* occur. As most, if not all, seed germination data involving cold stratification treatments violate the proportional hazard ratio assumption, a stratified Cox PH model is run instead (McNair et al. 2012; Messick and Hoagland 2018; Romano and Stevanato 2020), where the data are then split into their respective cold stratification treatments and the stratified model is run to compare treatments and a hazard ratio is obtained (McNair et al. 2012). A hazard ratio of 1.00 indicates there is an equal probability of germination between treatments, while a hazard ratio greater than 1.00 indicates the first treatment in the comparison has that many times greater probability of germinating (McNair et al. 2012; Messick and Hoagland 2018).

Survival analysis was run using the survival package (v. 2.44-1.1; Therneau 2019) in R version 3.6.1 (R Core Team 2019). Kaplan-Meier survival estimates were calculated and converted into germination curves. A stratified Cox PH model was then run to obtain the hazard ratios between treatments. Additionally, we tested for potential "tray effects" between each petri dish within a treatment by adding frailty to the stratified Cox PH models (McNair et al. 2012; Messick and Hoagland 2018).

RESULTS

In the no cold treatment, no seeds germinated, and all 90 seeds exhibited continued dormancy for the duration of the study. Relative to the other two treatment groups, the additional light to which this group was exposed did not promote germination as all seeds in the no cold stratification group-maintained dormancy. The 3-week cold treatment had a total of 14 seeds (15.5%) that germinated, while the 6-week cold treatment had a total of 54 (60%) germination events. The Kaplan-Meier survival estimates (Figure 4) showed increased germination probability for the 3-week and 6-week cold, with the 6-week

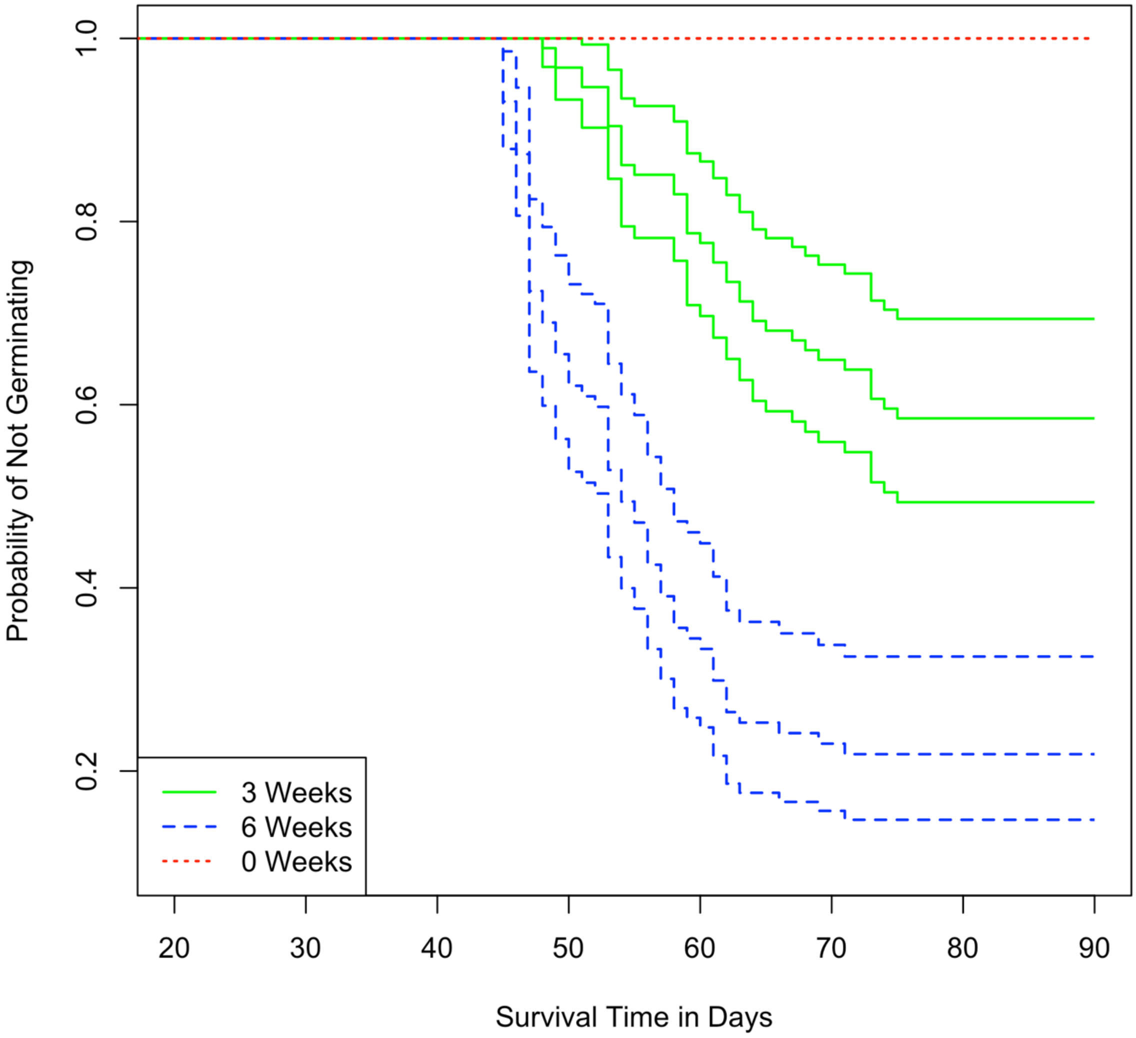

Figure 4 Kaplan-Meier survival time (as a seed) estimates by stratification treatment with 95% confidence intervals.

cold having the highest probability of germination. The converted Kaplan-Meier estimates are presented as germination curves in Figure 5. The stratified Cox PH model results, comparing the 3-week cold to the no cold were not significant, indicating there was no difference in the likelihood of germination within the allotted time interval between these two treatments, even though germination events did not occur in the no cold treatment. The stratified Cox PH models indicated that 6-week cold was 3.4 times more likely (as indicated by the hazard ratio of 3.4; p-value < 0.001) than the 3 week cold to germinate within that given time interval. This indicated that there was a significant correlation between length of time exposed to a cold stratification treatment and the probability of germination to occur. Frailty analysis results also showed a significant difference between cold stratification treatments (p-value < 0.001) but no significant effect (p-value = 1.00) on germination with regards to petri dish designation.

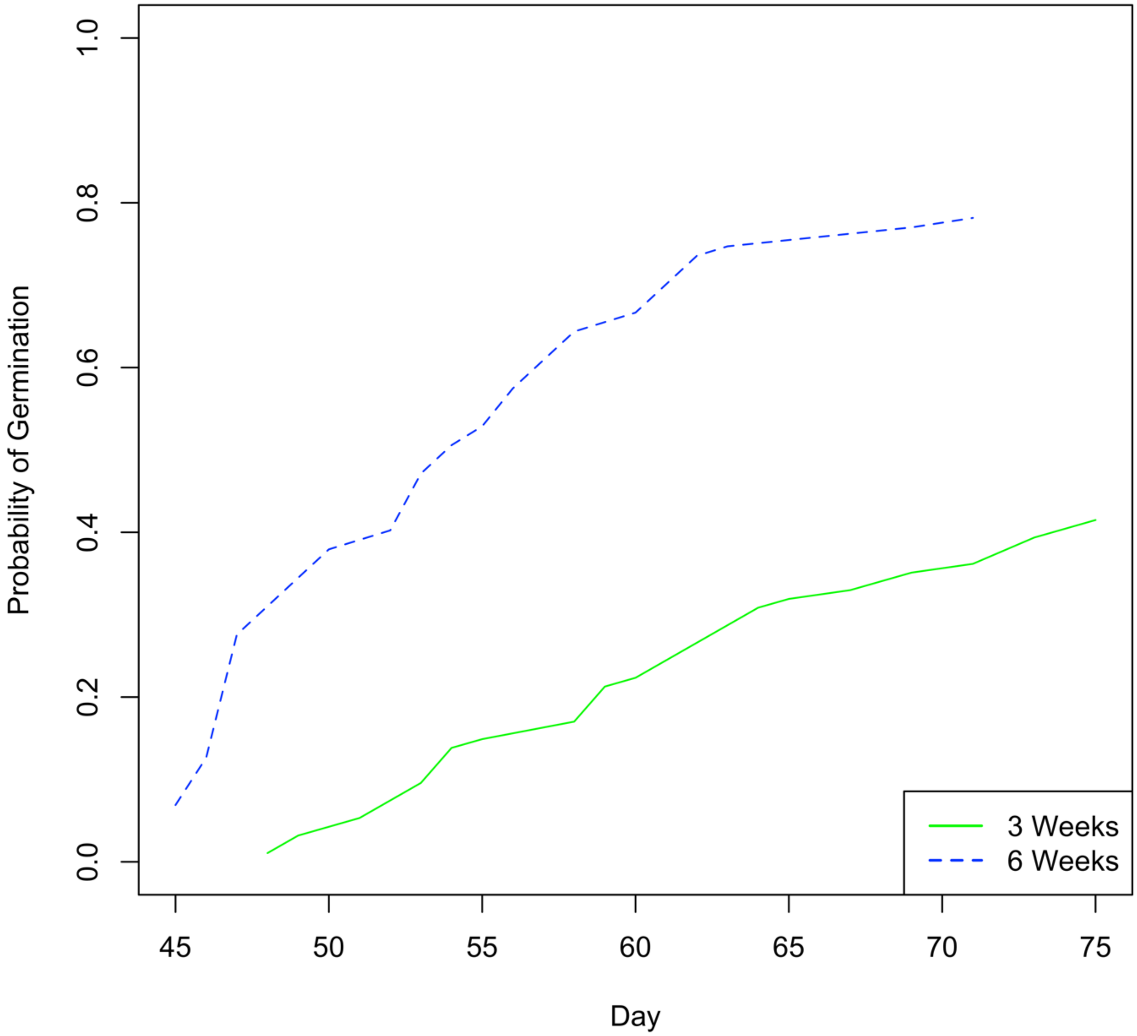

Figure 5 Germination curves by stratification treatment, calculated as one minus the Kaplan-Meier estimate. No cold treatment not shown, as zero seeds germinated.

DISCUSSION AND CONCLUSIONS

Salvia azurea var. *grandiflora* seeds germinated in larger numbers after a 6-week cold stratification period compared to the other treatments indicating that a period of cold stratification is necessary to obtain higher germination. The 6-week cold stratification treatment group responded to induced environmental cues in accordance with natural environmental cues it would receive outdoors in Oklahoma, its native cold-stratification environment. From approximately December to February (6-10 weeks), the average temperature in central Oklahoma ranges from 4.2°C to 5.1°C (Oklahoma Climatological Survey 2021), which correlates to the length of time and temperature stratification implemented in this study. I reject my null hypothesis that cold stratification would have no effect on germination.

Seed dormancy is a remarkable evolutionary adaptation to help promote species *continuation* and survival. The ability of a species to persist temporally and spatially, particularly throughout unfavorable climatic conditions, helps to ensure their continuation. Climate change can have an immense influence on plant regeneration, seed dormancy and cycling, survival, and diversity, changing natural biological ecosystems throughout our planet (Chhettri and Rawal 2017). Germination defines the intricate, high-risk transition phase between seed, radicle emergence and seedling establishment, during which environmental temperatures strongly influence germination success (Chhetri and Rawal 2017; Hradilova et al. 2019). Climate change can alter environmental signals including temperature, soil moisture and composition, radiation and humidity that may prevent, hinder or enhance the release of dormancy and implementation of the germination process (Bernareggie et al. 2016; Chhettri and Rawal 2017). This could in turn present a risk to species fecundity (reproductive success).

Specialist pollinators such as *Tetraloniella cressoniana* (blue sage bee), that have evolved to inhabit a *single* niche in the local ecosystem and rely on one species of flora for survival could be adversely affected by an alteration in the natural seed dormancy and release cycle. This could result in a seed germination phenological shift which would ultimately affect species continuation, composition and diversity (Footitt et al. 2014; Bernareggi et al. 2016; Chhetri and Rawal 2017). A phenological shift in seed germination could alter flowering time (Mo et al. 2017) which could adversely affect Monarch butterflies in their annual migration, as they rely on numerous flower sources for nectar feeding during that time. As climate change reshapes our global environment, the ability of plant species to persist will depend on their seeds' ability to adapt to continuing environmental fluctuation in local and global temperature.

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Critic's Choice Essay

MUSINGS AT DUSK

Reprinted from *Gaillardia*, Fall 1998

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When I get into the field, I find myself overwhelmed by the profound spirit of Nature and am driven to locate a secluded space from which to observe the world around me and contemplate questions of life. It is comforting to settle at the base of a rock or tree or simply recline on the open ground and mull over questions of 'what' and 'why' and at the same time experience visions, sounds, scents, and the physical contacts of Nature. Chief Standing Bear, a Sioux, said "...to sit or lie upon the ground is to be able to think more deeply and feel more keenly...see more clearly into the mysteries of life and come closer to kinship to other lives...."

How does one translate these personal experiences into words? Most of us lack that talent and it is at this time the ability to communicate via the written word that is so important. When beautiful passages such as Standing Bear's come to mind I, once again, offer a sincere prayer of thanks to Mother for the hours spent at her side as she read to her children, cultivating our love of reading.

While surrounded by the tranquility of Nature I have watched the world about me and searched through the reaches of my mind for those special words appropriate for the experiences of the moment. Once a careless vole, caught momentarily away from the security of its burrow, had its life quickly snuffed out. The approach of the hawk was silent, and it appeared the vole's first awareness may have been talons piecing its flesh. I had just witnessed the end of a life. But what is life? Yes, we biologists have a detailed definition steeped in technical terminology but at that moment I found the final words [attributed to] Crowfoot, a Blackfoot spokesman, more meaningful.

"What is life? It is the flash of a firefly in the night. It is the breath of a buffalo in the wintertime. It is the little shadow which runs across the grass and loses itself in the Sunset."

It has become impossible to walk across a hot, dry, Oklahoma prairie in August without reflecting on a passage from *The Way to Rainy Mountain* by N. Scott Mornady as he described part of a journey to the grave of his grandmother:

“A single knoll rises out of the plain in Oklahoma, north and west of the Wichita Range. For my people, the Kiowas, it is an old landmark, and they gave it the name Rainy Mountain. The hardest weather in the world is there. Winter brings blizzards, hot tornadic winds arise in the spring, and in summer the prairie is an anvil's edge. The grass turns brittle and brown, and it cracks beneath your feet. There are green belts along the rivers and creeks, linear groves of hickory and pecan, willow and witch hazel. At a distance in July or August the steaming foliage seems almost to writhe in fire. Great green and yellow grasshoppers are everywhere in the tall grass, popping up like corn to sting the flesh, and tortoises crawl about on the red earth, going nowhere in the plenty of time. Loneliness is

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an aspect of the land. All things in the plain are isolate; there is no confusion of objects in the eye, but one hill or one tree or one man. To look upon that landscape in the early morning, with the sun at your back, is to lose the sense of proportion. Your imagination comes to life, and this, you think, is where creation was begun."

Some of my more gratifying experiences have involved finding an isolated spot on a ridge shortly before sunset and sitting quietly until the sun has disappeared below the horizon. Often it is difficult to willfully break the spell as Nature swiftly changes her face. With darkness the creatures of the day settle down, replaced by those of the night. During that magic transition, as the shadows creep toward me, I think of a small book of nature essays, *From the Stump*, by Bob Jennings of the Tulsa Oxley Nature Center and his interpretation of that moment:

"From the scrubby trees along the dry ridge, the first tentative notes of a whip-poor-will's song emerge. The bird will make a false start or two, checking to make sure the tone is just right, that the acoustics are perfect. Soon it will start the evening concert, unbroken strings of notes calling the shadows out of the woods and across the grassland, weaving night out of the remnants of shady places."

You know, we of the Native Plant Society may be approaching our field activities wrong by scheduling the mid-day. That time has probably been selected for convenience, the dew is gone, insect activity low, the sun is high, and flowers open. But perhaps we should get out in the early evening, botanize until near dusk and then close the day, as a group, with a silent sunset vigil: an approach which might place each of us in closer harmony with Nature.

ONPS

Paul Buck

EDITORIAL POLICIES AND PRACTICES

Oklahoma Native Plant Record is published annually by Oklahoma Native Plant Society. Submission for publication in the journal is open to all. Manuscripts will be accepted on topics related to Oklahoma's regional botany, including historical research reports, current research articles, site record species lists, and descriptions of new or important species sightings in Oklahoma. Oklahoma's environmental gradients of human impact, climate, and elevation make the *Record* a prime resource for research on habitat edges, species ranges, and edge species. Articles of other themes may be included as well. Local research overlooked by journals of broader geographic regions will be considered for publication in the *Record*.

Manuscripts will be reviewed for content and appropriateness by at least two reviewers. Papers must not have been published previously or accepted for submission elsewhere and should represent research conducted in accordance with accepted procedures and scientific ethics. All authors retain copyright of their articles. Submission of the manuscript implies granting Oklahoma Native Plant Society permission to publish it. We ask only for the right to publish articles. We do not seek to own them. In return, we require our authors to allow their work to be used freely for non-commercial purposes, allowing each individual to make, gratis, a single copy of the published manuscript whether from its print or its internet version; instructors to make, gratis, multiple copies available for non-commercial teaching purposes; and libraries to make copies available, gratis, for interlibrary loan. Authors are responsible for supplying reprints upon request.

The title page should state the affiliation and complete addresses of all authors and telephone number or email address for the corresponding author. Provide four key words not in the title. Research and technical papers should include a one-paragraph abstract of not more than 250 words. It should concisely state the goals, principal results, and major conclusions of the paper. All references, figures, and tables should be cited in the text. Site descriptions should include latitude, longitude, total area, and elevation. Measurements should be in SI units (metric). Use no headers, no footers, nor auto page numbering. Proof-read and verify taxa and taxa numbers before submission. Color photos may be submitted.

Common names should be referenced to a scientific name using nomenclature that has been revised according to the Integrated Taxonomic Information Service (ITIS) database (http://www.itis.gov). Abbreviations of authorities for scientific names should follow *Authors of Plant Names* (Brummitt, R.K. and C.E. Powell. 1992. Richmond, Surrey, England: Royal Botanic Gardens Kew). Titles of periodicals should be abbreviated following Botanico-Peridoicum-Huntianum and its supplement, except in historic publications when original format may be used.

Authors are encouraged to submit manuscripts to the editor as an email file attachment to the email address below, preferably by August 1 for publication in December.

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Volume 20

Oklahoma Native Plant Society
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