EFFECTS OF SHADING ON THE RARE PLANT SPECIES, *PHYSOSTEGIA CORRELLII* (LAMIACEAE) AND *TRILLIUM TEXANUM* (MELANTHIACEAE)

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ABSTRACT

Rare plant species that are constrained by shading may be threatened by a lack of natural disturbance that removes overhanging vegetation. The original distribution of the study species *Physostegia correllii* (Lundell) Shinners included freshwater floodplains of large rivers in the southcentral U.S. (Colorado, Rio Grande, and Mississippi rivers). A second species, *Trillium texanum* Buckley was found in seep spring baygalls in east-central Texas and extreme northwestern Louisiana. Experiments to determine the effects of shading on *P. correllii* and *T. texanum* were conducted using short-term shade cloth treatments (full sunlight vs. 30% shading for 2–3 weeks), and a dryness treatment for *T. texanum* (moist vs. less moist). Mean height and cover responses of individuals for both species were determined in conservation gardens located in Lafayette, Louisiana. *Physostegia correllii* grown in shaded environments for 2.5 weeks had shorter mean height than if grown in full sunlight. Half of the shaded plants in shaded plots had died by the mid-summer. For *T. texanum*, shading reduced the mean height and cover of plants. Therefore, management to remove overhanging ground vegetation to mimic natural disturbance might revive *P. correllii* and/or *T. texanum* populations where overhanging vegetation is increasing due to lack of natural disturbance (e.g., flood pulsing, grazing, burning).

Key Words: climate drying; disturbance fugitive; rare, endangered and threatened species; floodplain; ruderal species; seed bank; shade experiment; seep spring drying

RESUMEN

Las especies de plantas raras que están afectadas por el sombreado pueden estar amenazadas por la falta de perturbación natural que elimina la vegetación sobresaliente. La distribución original de la especie de estudio *Physostegia correllii* (Lundell) Shinners incluyó llanuras de inundación de agua dulce de grandes ríos en el centro-sur de los Estados Unidos (ríos Colorado, Río Grande y Mississippi). Una segunda especie, *Trillium texanum* Buckley se encontró en las baygalls de filtraciones primavera en el centro-este de Texas y el extremo noroeste de Luisiana. Los experimentos para determinar los efectos del sombreado en *P. correllii* y *T. texanum* se llevaron a cabo mediante tratamiento de sombreado con tela a corto plazo (luz solar completa frente a un sombreado del 30% durante 2-3 semanas) y un tratamiento de sequia para *T. texanum* (húmedo vs. menos húmedo). La altura media y las respuestas de cobertura de los individuos para ambas especies se determinaron en jardines de conservación ubicados en Lafayette, Louisiana. *Physostegia correllii* cultivada en ambientes sombreados durante 2,5 semanas alcanzó una altura media menor que cultivada a plena luz del sol. La mitad de las plantas en parcelas sombreadas habían muerto a mediados del verano. Para *T. texanum*, el sombreado redujo la altura media y la cobertura de las plantas. Por lo tanto, la gestión para eliminar la vegetación del suelo para imitar la perturbación natural podría revivir las poblaciones de *P. correllii* y / o *T. texanum* donde la vegetación está aumentando debido a la falta de perturbación natural (por ejemplo, inundaciones, pastoreo, quema).

INTRODUCTION

Some rare plant species are declining as the nature of natural disturbance changes. In particular, if disturbance fugitives rely on disturbance to reduce overhanging vegetation, a reduction in the frequency or intensity of natural disturbance can threaten their existence if shade increases (Lavorel et al. 1994). Such species may also be negatively affected by climate changes in air temperature, soil temperature, and precipitation, but are particularly vulnerable to landscape-level changes or land management that decrease the frequency and intensity of natural disturbance (Middleton 2013; García-Girón et al. 2021) and allow increased shading (e.g., limited fire: Fowler et al. 2012; Leonard & Van Auken 2013). Sun-adapted species may grow much more slowly in the

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shade (Valladares & Niinemets 2008). For example, the rare *Streptanthus bracteatus* was likely more common in the open central Texas woodland in the past because of frequent fire disturbance, which kept the woodland habitat more open (Fowler et al. 2012; Leonard & Van Auken 2013).

We propose that the rare species *Physostegia correllii* and *Trillium texanum* may be declining due to changes in natural disturbance regimes within narrow distributions mostly in Texas and Louisiana. Natural disturbance is important in creating gaps in the thatch of dominant species, thereby supporting the short-term establishment of fugitive species (Lavorel et al. 1994). Note that "thatch" is an overtopping of living and dead stems, between actively growing plants and the soil surface. In wetlands, disturbances capable of removing thatch include fire (Anderson & Menges 1997), water movement of wrack (Elsey-Quirk et al. 2019), soil digging by crayfish or animals (Brewer et al. 1998; Krupa et al. 2021), flood pulsing (Middleton 1999; Mettler et al. 2001), and disturbance interactions (Kirkman & Sharitz 1994). Local biodiversity is supported in open environments of high light and moisture, especially if these fugitive species can regenerate from seeds in the seed bank (Brown & Cahill 2020).

Ultimately, the long-term success of disturbance fugitives may depend on the presence of viable seeds via dispersal and seed bank storage. Seed longevity in the soil varies by species, environment, and the frequency and intensity of natural disturbances that allow germination, establishment, and successful reproduction for replenishment of the seed bank (Middleton 1999; Baskin & Baskin 2014). For example, federally threatened *Boltonia decurrens* are uncommon on the banks of the Illinois River; however, the species expanded temporarily following the Great Flood of 1993. This flood removed the thatch of dominant vegetation with subsequent *B. decurrens* recruitment and reseeding of the seed bank (Mettler et al. 2001). Short-lived disturbance events can help fugitives persist by supporting temporary adult occupation and seed bank replenishment (Lavorel et al. 1994).

Other factors may also limit populations of *P. correllii* and *T. texanum*. Both species are geographically isolated and mostly limited to Louisiana and Texas, which could limit their access to any specialized pollinators. Climate warming may contribute to phenology changes in spring ephemerals such as *Trillium erectum* creating asynchronous flowering, which may result in decreased gene flow to pollen and seeds between separated populations (Rivest et al. 2021).

The objectives of this study were to determine if the rare species *P. correllii* and *T. texanum* may be affected by changes in shading and moisture levels in the environment. The hypotheses tested were as follows.

Physostegia correllii.—**1)** Shading is related to the decreased height of individuals and seed production.
Trillium texanum.—**1)** Shading is related to decreased height and cover of individuals, **2)** a lower moisture environment is related to decreased height and cover of individuals, and **3)** seeds are found in the seed banks of current populations in Angelina National Forest, Texas.

The outcome of this study can help to illuminate if these rare species might benefit from management actions to reduce the effects of shading or lack of moisture.

MATERIAL AND METHODS

Study species background. *Physostegia correllii* and *T. texanum* are rare species listed by NatureServe (2021). *Physostegia correllii* is rare but was once widespread in small populations from southern Louisiana to northeastern Mexico (Fig. 1; Cantino 1982). The species has indeterminate growth with secondary and tertiary horizontal rhizomes of up to 50 cm long, which emerge from primary rootstocks (Cantino 1982). Rosettes can be generated either from the rhizome or by stem internodes (Middleton, pers. obs.). The flowers mature from the base toward the tip of the spike (Middleton, pers. obs.) and are attractive to a wide variety of pollinators, especially native bees (Cantino 1982).

Only a small number of populations of *P. correllii* remain in Louisiana, Texas, and northern Mexico (Cantino 1980) including a recently documented population along the Rio Grande (Owens et al. 2005). In a

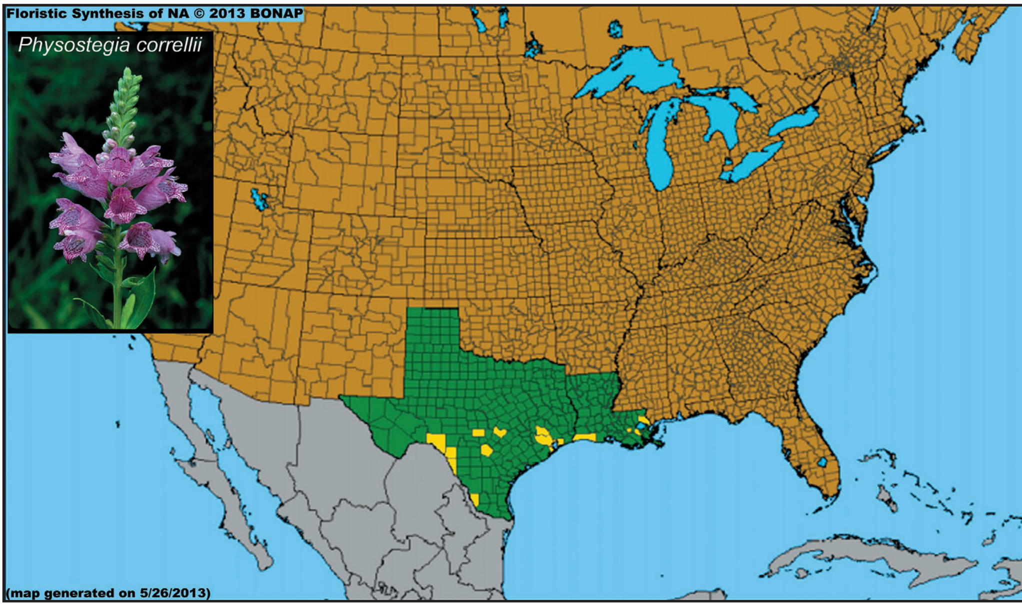


Fig. 1. ***Physostegia correllii*** **distribution in North America (from Kartesz 2015). Inset photo from USDA Plants Database (2021a). The states of Texas and Louisiana appear in green; yellow indicates counties (Texas) and parishes (Louisiana) where *P. correllii* occurs.**

detailed survey of colonies along the shoreline of Lady Bird Lake of the Colorado River, Austin, Texas, twenty-two colonies were found in 2014 (Williams and Manning 2020). By 2018, only sixteen of these colonies were relocated; twenty-two colonies were observed in 2018 because new colonies appeared after the flooding of 2015–2016 in Lady Bird Lake (Williams, pers. obs.). In July 2021, the number of colonies had decreased to eleven in Lady Bird Lake (Williams, Middleton, and John David (Volunteer, U.S. Geological Survey, Wetland and Aquatic Research Center, July 26, 2021), pers. obs.). By 2019, the colonies in Gillespie County Texas (Williams, pers. obs.) and Cameron Parish Louisiana (Middleton, pers. obs.) could not be relocated and were presumed extirpated. As of 2021, the historical colonies along the Rio Grande in Del Rio TX, Val Verde County had not been relocated due to lack of private property access (Williams, pers. comm. 2021). In short, only a few populations may still remain in Louisiana and Texas (U.S.D.A. 2021a), where it is considered critically imperiled and imperiled, respectively (NatureServe 2021). Known populations include only those in Texas at Lady Bird Johnson Lake (last observed in 2021; Williams & Middleton, pers. obs.), and along the Rio Grande in Kinney County (Owens et al. 2005). *Physostegia correllii* is under consideration for listing by the U.S. Fish and Wildlife Service under the Endangered Species Act of 1973.

Physostegia correllii is likely a disturbance fugitive (following Mettler et al. 2001) because it tends to grow along periodically flooded river floodplains, and along irrigation ditches, roadsides, and creek beds, especially on the edge of forested wetlands (NatureServe 2021), typically in isolated populations with natural or human disturbance (Cantino 1982). A species with a similar niche that occupies occasionally disturbed areas along riverbanks is *Pedicularis furbishiae* (Furbish's lousewort), which requires erosion by both water flow and ice scour to reduce shading by woody species (Day 1983; NBCFWRU 2022). After seed germination, *P. correllii* forms a rosette, which bolts and flowers in the second year. The flowering stalks die back after one year, and then new rosettes arise from belowground rhizomes and aboveground stolons (Middleton & Williams, pers. obs.). *Physostegia correllii* grows in open sunlight on newly deposited sediment with associates such as *Alternanthera philoxeroides*, *Colocasia esculenta*. *Physostegia correllii* often has yellowing leaves, insect damage, and decreased flowering under dense vegetation (Williams & Manning 2020).

Trillium texanum is a rare species found in isolated populations in thirteen counties/parishes in east Texas and Louisiana (Figs. 2; Singhurst et al. 2002; Shilling et al. 2017; U.S.F.W.S. 2021); its distribution limit in northwest Louisiana is near Rodessa (MacRoberts 1970; Doffitt & Middleton, pers. obs., 2020). This species is listed as imperiled (G2) by Nature Serve (2021). Closely related to *T. texanum* are *Trillium pusillum* and *Trillium georgianum*, which are geographically disjunct. *Trillium texanum* and *T. georgianum* both produce single and three-leaved stems from a single rhizome, with stomata on the upper leaf surface unlike other species that are closely related to *T. pusillum* (Farmer 2006; Schilling et al. 2017). However, linear-leaved *T. georgianum* is found in a single disjunct location in Georgia and differs in morphology from *T. texanum* with its narrowly ovate leaves.

Trillium texanum grows in hillside seepages in elevated areas around the bases of trees (Shilling et al. 2017) in creek bottom baygalls (Singhurst et al. 2002), especially in crevices of shallow-soiled surface roots of woody trees and shrubs with a high dense overcanopy and little understory; these wet shallow root crevices formed by species such as *Magnolia virginiana* are filled with up to 2 cm of decomposing leaf/twig litter and moss (Middleton, pers. obs.). Stands of *T. texanum* are often a part of hillside seepages and springs with individuals located in the middle slope of forested oak or pine uplands and riparian baygalls comprised of *Taxodium distichum*, *Nyssa biflora*, *Magnolia virginiana*, *Liquidambar styraciflua*, *Osmunda regalis*, *Osmunda cinnamomea* and *Woodwardia areolata* (U.S.F.W.S., 2021), and, *Acer rubrum*, *Myrica serifera,* and *Alnus serrulata* (Singhurst et al. 2002).

Shade effects on growth of *Physostegia correllii*.—The experiment tested the effects of two light levels (full sunlight vs. 30% shading) on the height and cover of individuals grown in an experimental garden. Each plot of plants was grown from a single seed collected at Lady Bird Lake (Blunn Creek and Metz Park) in Austin Texas on September 11, 2013 (Minnettte Marr, Lady Bird Johnson Wildflower Center, written communication, July 9, 2021). The seeds were kept in dry storage at room temperature until the beginning of the experiment. In March 2018, fifty seeds were placed into fifty separate peat pots, but these seeds did not germinate for almost two years (March 2020). Only about twenty seeds grew into seedlings, which were placed in twenty plastic pots (15.2 cm radius). Of these, only five seedlings survived, and in June 2020 these seedlings were planted more than 2 meters apart along the edge of a yard in Lafayette Louisiana (i.e , five plots were established, each with a single seedling). The seedlings grew slowly from basal rosettes into full-sized plants after one year. Shade experiments were conducted on fully established plants starting on March 20, 2021. Of the five plots, two were randomly assigned to 30% shade cloth treatment for 2.5 weeks, when the experiment ended (April 15, 2021). We removed the shade cloth from the shaded treatments at that time because the plants had begun to die back.

Before and after the shade treatment, plant height, percent cover of plants, and the number of *P. correllii* stems were assessed in each of four quadrants in a 1-m^2 area marked in the center of the plot by a fiberglass pole in four adjacent 1/4 m^2 quadrants (NE, NW, SW, SE). Light levels were measured with and without shade cloth over each plot using a Licor 250A at mid-day on a nearly cloudless day (April 10, 2021).

Shade and drying effects on *Trillium texanum*.—Individuals were established from short, intact rhizomes (~2 cm long) transferred from Nagoniche Creek in Texas. Three *Trillium* rhizomes bearing trifoliate leaves with a single growing point, and 3 to 5 rhizomes of plants with single leaves were planted in each tray (5 × 6.5 × 2 cm) at the beginning of the non-flowering/dormant season (May 18, 2019); a total of 28 trays was used in the experiment. Within the trays, the rhizomes were placed on a shallow (~1-2 cm) layer of sand and tree leaves, which had been collected adjacent to a seep spring with *T. texanum* in Angelina National Forest. To document plant height under field conditions, five plants at the collection site were randomly selected by tossing an object and their height was measured above the tree root layer. The experiment tested the effects of two light levels (full sunlight vs. 30% shading) and moisture levels (moist and less moist) on the growth of *T. texanum*.

The prepared trays were placed over a bed of sand, small branches, and tree leaves (30 cm deep), and these trays were positioned between timbers to hold them in place in an outdoor conservation garden (U.S.

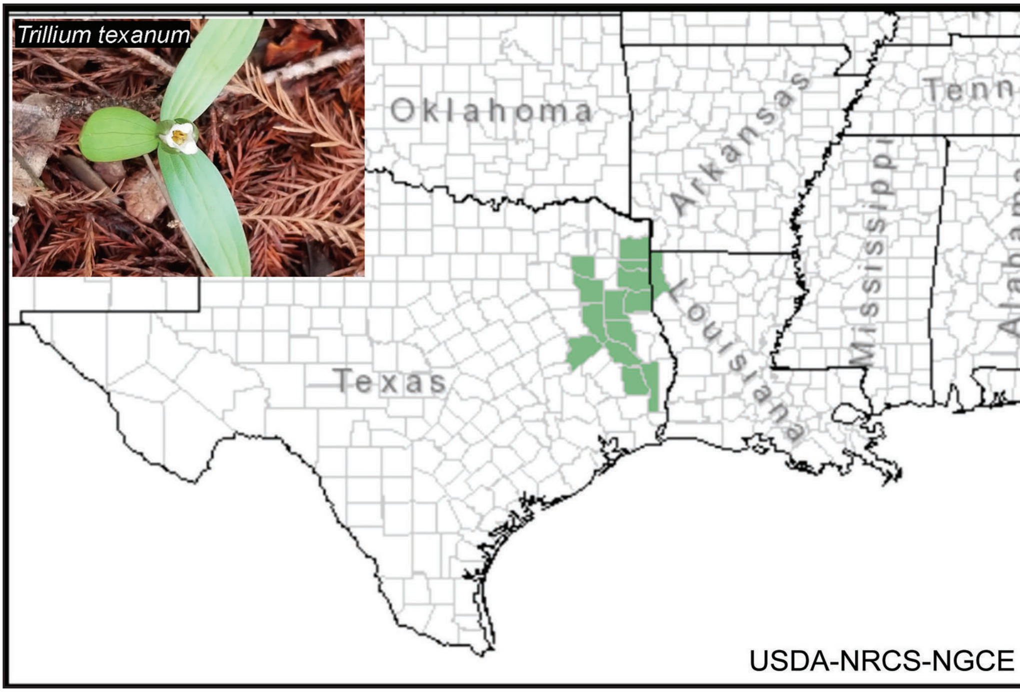


Fig. 2. *Trillium texanum* distribution in northwestern Louisiana and eastern Texas (U.S.F.W.S. 2021 and USDA Plants Database 2021a). Inset photo by Beth Middleton.

Geological Survey, Wetland and Aquatic Research Center, Lafayette, LA). The sand, small branches, and tree leaves were mostly from Angelina National Forest (see above), but were augmented with twigs and leaves (mostly *Taxodium distichum*) in the vicinity of a conservation garden. The conservation garden was established in a grove of high canopy *Taxodium distichum* with an understory of roughly mown lawn. Two separate beds were created in the conservation garden with one in the center of a planted stand of *T. distichum* trees (Bed A; more moist) and the other in a more open area at the edge of the *T. distichum* stand and a pond (Bed B; less moist), noting that both beds were watered with two 5 gallon buckets of distilled water after 7 days of no rain. The experimental beds were set up to resemble a seep spring and watered with either distilled water or rainwater after seven days with no precipitation.

The shade experiment began on March 21, 2021, after the plants had begun to grow, but before the maximum flowering period. Four of fifteen total trays were randomly selected in Bed A and Bed B, and covered with 30% shade cloth for three weeks, and height of stems, number of plants, and percent cover were measured on March 21, 2021, and April 10, 2021. The environments of Bed A and Bed B were monitored for soil moisture and photosynthesis using a CSA Hydrosense II and Licor 250A, respectively. Light measurements were taken at mid-day on nearly cloudless days. One measurement of soil moisture and light level was taken over each tray without shade cloth, and two measurements in shaded plots were taken one each with and without shade cloth taken on April 10, 2021.

Regeneration of local populations via seed banks

Trillium texanum (only).—Soil seed banks were lifted from root crevices of organic matter with a small kitchen spoon at a depth of less than 2 cm (volume ~ 14.8 cm^3) within 0.5 m of five plots of *T. texanum* in Angelina National Forest. The soil was transferred into a 12.7 × 16.5 × 5.1-cm tray filled to about 4 cm with sand and leaf

Fig. 3. Comparison of *Physostegia correllii* grown in full sunlight (left) vs. 30% shade (right) (Plot 4 vs. Plot 1, respectively). The cloth covering over Plot 1 was removed for this photo. Plot 1 died back about one month after the experiment even though the shade cloth was removed after three weeks. Photo by Beth Middleton.

litter material collected from a nearby location; the trays were placed into a bed of sand in an outdoor conservation garden (U.S. Geological Survey, Wetland and Aquatic Research Center, Lafayette, LA). The conservation garden was established in a grove of planted *Taxodium distichum* set up to resemble a seep spring, and watered with distilled or rainwater (see above). Seedling emergence was examined for two years.

Pollinators.—Insects were casually observed and recorded while visiting flowering *Physostegia correllii* and *Trillium texanum* from January 2019 to June 2022. A wildlife camera was set up in Bed A of the *T. texanum* conservation garden to observe insects visiting flowers in March 2022.

Seed production.—Phystostegia correllii. Seeds were collected weekly throughout the growing season from mature coccyx. These were collected into a single marked envelope and marked by plot number. At the end of the season, the seeds from each plot were counted.

Trillium texanum.—The seedpods and any seeds disappeared before the fruits were fully developed because they were cut off by some unknown animal or insect.

Statistical analysis

Physostegia correllii.—To analyze differences in mean plant height and cover related to treatments of shade vs. no shade, a General Linear Model was conducted to do repeated measures ANCOVA using PROC GLM in SAS (2018) to test responses of mean height and cover per quadrant by nesting quadrant, and treatment using time (before/after) and treatment (shade/no shade). Covariates tested in the model included light levels. The residuals were checked for normality and homogeneity (Shapiro-Wilk =0.981356, P= 0.7652) (SAS 2018).

Trillium texanum.—To analyze differences in plant height and percent cover, a repeated measures ANCOVA with a Proc Mixed model (SAS 2018) was used to test response variables including a) mean height per tray and b) percent cover per tray with Bed (i.e., randomized block replicated) as a block variable of the independent variables of treatment. The mean height of plants per tray was used as a response variable, and not the number of plants per tray because the rhizomes that were planted in the trays were very short, and usually with only one growth point included. Time (before/after the treatment) was a repeated measures effect. The variables light, soil moisture, and total plant number were not significant and were dropped from the model based on AICc comparisons ($p > 0.05$). The residuals were checked for normality and homogeneity; percent cover was arcsine square-root transformed with test results: Mean height per tray; Shapiro-Wilk =0.965008, P=0.0829; Arcsin square root percent cover per tray: Shapiro-Wilk=0.9767, P=0.3053) (SAS 2018).

RESULTS

Plant height and cover in various shading and/or moistness environments

Physostegia correllii.—Unshaded plants were taller than shaded plants (height intercepts of unshaded at time 0 and time 3: $F = 155.0$, $p < 0.0001$; Table 1; Appendix 1a; Middleton et al. 2022a). The mean height per plot at the beginning of the study was 17.9 ± 2.9 cm. The majority of the plants in the shade-treated plots had died back after three weeks (April 15, 2021). Light levels with and without cloth in the experiment on March 20, 2021 were: shade vs. sun: 128.5 ± 13.2 cm vs. 250.6 ± 30.7 µmol m^{-2} s^{-1}, respectively; one measurement was taken over each plot without shade cloth, and two measurements in shaded plots one each with and without the shade cloth.

Trillium texanum.—The mean height of the individuals in the conservation garden ranged from 8-10 cm tall, but at Nagoniche Creek mean height ranged from 3-5 cm above the root crevice. The mean height per tray and percent cover per tray of the *Trillium* at the beginning of the experiment was 8.7 ± 0.3 cm and 23.3 ± 2.3 percent cover per tray (Middleton et al. 2022b). In the shading study in the conservation garden, the intercept of our predicted equations for mean height per tray was higher after the study in unshaded treatments (Intercept of Time 0 and Time 3: 8.47191 vs. 8.74394); however, the intercept decreased after the shading treatment in the study (Intercept of Time 0 and Time 3: 9.6805 vs. 8.72006, respectively; Table 2a; Appendix 1b). The intercept of the arcsin square root percent cover per tray was related to time and increased after the study (arcsin square root intercept at Time 0 vs. Time 3: 0.10468 vs. 0.24138, respectively; Mean percent cover at intercept Time 0 vs. Time 3: 18.5% vs. 30.3% cover, respectively; Table 2b; Appendix 1c) was not related to shading ($p < 0.05$).

Seed number, and pollinators

Physostegia correllii.—Seed number produced in shaded plots B1 and B2 were 0 and 850 seeds m^{-2}, respectively, and in unshaded plots B3, B4, and Front were 78, 1370 and 269 seeds m^{-2}, respectively. Southern carpenter bees and other unidentified insects were observed to pollinate *P. correllii* (Appendix 2), with certain species working as nectar robbers by cutting holes from the outside of the corolla (Middleton, pers. obs.).

Trillium texanum.—Seedling emergence was examined for two years, but no *T. texanum* seedlings emerged from the seed banks. Seeds in seed pods remain undocumented because the immature seed pods were cut off and carried away by an unknown organism. Wildlife cameras did not resolve the question of why the pods disappeared. Certain pollinators were captured on video camera on flowers of *T. texanum* including Dorantes longtail (*Thorybes dorantes* (likely)), a beetle, and a bee (Appendix 3).

DISCUSSION

Certain rare plant species may be hindered by an increase in overhanging species and shade if natural disturbance dynamics are altered (Lavorel et al. 1994; Valladares & Niinemets 2008; Fowler et al. 2012; Leonard & Van Auken 2013). Our study shows that the rare *P. correllii* (likely disturbance fugitive) and *T. texanum* grew taller in less shaded experimental conditions. Also, *P. correllii* produced fewer seeds in shaded conditions. The *P. correllii* in the shading treatments almost completely died back after three weeks of shade cloth treatment, but one or two plant in these plots resprouted from rhizomes during Fall 2021 from the shaded plots. These individuals overwintered, and then grew into full-sized plants during Spring 2022 (Middleton, pers. obs.). The challenge for the improvement of management for these rare species may be to find approaches to mimic the intensity and frequency of disturbances to support growth and reproduction (Middleton 1999).

The forest at Angelina National Forest is managed with fire and was logged historically (U.S.D.A. 2021b) and although fragmented, these forests have a number of stands of *T. texanum* (Singhurst et al. 2002; Shilling et al. 2017). It may be that fire is reducing shade by removing low overhanging vegetation in these forests, but it is not known if this disturbance supports populations of *T. texanum*. While shade was an important limiter of *T. texanum* in our study, soil moisture was not (Table 2a, 2b). Nonetheless, other studies with a wider range of moisture observations indicate that *T. texanum* may be sensitive to changes in moisture supply. On hillside baygalls of the Angelina National Forest *T. texanum* was most numerous in the middle section of seep springs,

Table 1. ANCOVA Model of *Physostegia correllii* testing outcomes of an experiment by nesting quadrant within Plot ID as well as fitting treatment(shade cloth/no shade cloth) and time(before/after) as main effects and light level as a covariate. AIC model comparison was used to get the final model. Note that plants were adjusted for their starting mean heights based on the Plot ID and quadrant. The Percent cover of the plants per quadrant was not related to the treatment factors, their interactions, or their covariates, adjusting for Light level, time 0 < time 3. The test type is an F statistic.

Variable	df	F	p	Significance
Mean individual height per quadrant				
Whole model	21	15.0	**<0.001**	***
Plot ID	4	20.4	**<0.0001**	***
Quadrant[Plot ID]	15	2.0	0.0841	n.s.
Time (before/after)	1	155.0	<0.0001	***
Light level (covariate)	1	8.2	**0.0111**	*

Table 2. A repeated measure ANCOVA using a Proc Mixed model to test experimental responses of a) mean height per tray and b) percent cover per tray for *Trillium texanum*. An AIC model comparison was used to get the final model, which consisted of a fixed block effect of Bed and a covariable of the total number of plants per tray. The final mean response per tray ± S.E. is given. The total number of individuals per tray depended on the mean height per tray. The covariates of light and soil moisture as well as Treatment, time*Treatment, and the fixed block of Bed*treatment were not significantly related to the model ($p > 0.05$). Because Time*treatment was not significant, the outcome implies that the mean height and percent cover at time 0 were the same for shaded vs. unshaded treatments. "*" indicates a Z test from Chi-square. Mean height had a significant repeated measures effect whereas percent cover did not. "‡"indicates an F test.

Variable	df	Test type	p	Significance
a) Mean plant height per tray				
Overall model	5	31.2^{*}	**<0.0001**	***
Bed	1	**$0.4^{\ddagger}$**	**0.0149**	*
Time (before/after)	1	$1.3^{\ddagger}$	0.8506	n.s.
Total number of individuals per tray [covariate]	1	$17.7^{\ddagger}$	**0.0004**	***
b) Percent cover per tray				
Overall model	3	41.3^{*}	**<0.0001**	***
Time (before/after)	1	$23.4^{\ddagger}$	**0.0002**	***
Bed	1	$0.6^{\ddagger}$	**<0.0001**	***
Total number of individuals per tray [covariate]	1	$36.1^{\ddagger}$	0.0002	***

and absent both in the drier upper baygall/longleaf pine upland and under the dense canopy of the lower mucky section (MacRoberts & MacRoberts 2005). In the middle section of a hillside seep population observed by Doffitt and Middleton in 2021 near Rodessa, Louisiana, *T. texanum* grew in open habitats with shallow root crevices filled with organic matter, water from constantly seeping springs, and a high tree canopy with little overhanging vegetation.

We had other noteworthy observations regarding pollinators. We observed carpenter bees both pollinating and nectar-robbing *P. correllii* flowers from 2019 to 2022. Cantino (1982) observed twenty-nine species of insects and hummingbirds pollinating *P. correllii*, with species of bumblebees noted as especially effective pollinators. Unlike bumble bees, carpenter bees can remove nectar without pollination by chewing holes in the base of the corolla (Cantino 1982). *Physostegia correllii* is self-compatible so the incidence of self-pollination may be high regardless of any nectar-robbing activities by insects (Cantino 1982).

While details on pollinators for *T. texanum* have been largely unknown, we videoed the pollination of this species by Dorantes longtail (*Thorybes dorantes* (likely)), a beetle, and a bee using a wildlife camera (Appendix 3). We also noted that the *T. texanum* flowers have a delicate scent on the first day or two of flowering (Middleton, pers. obs.). We noted that the fruiting pods of *T. texanum* disappeared at the time of maturation, perhaps cut off by a small mammal, bird, or insect; subsequently, we were not able to do a full accounting of reproductive status with respect to shading and moisture. It is possible that the seed pods were cut off by ants; *Trillium* spp. have elaisomes that are fed by ants to juvenile stages, and the seed is subsequently carried away from the nest to the seed bank (Miller & Kwit 2018). We did not detect any ants on *Trillium* in our wildlife camera footage.

A few *T. texanum* produced flowers in January 2021 and 2022. In 2021, these plants did not produce seed pods, but in 2022, a single frozen individual produced a seed pod in a season with no sign of pollinators. We observed that shoots of both *T. texanum* and *P. correllii* could be covered in ice for several days during winter storms in 2021 and 2022, and then subsequently grow again after the ice melted (Middleton, pers. obs.).

MANAGEMENT IMPLICATIONS

In addition to the species in this study, other wetland disturbance fugitives may grow better in more open environments such as *Drosera capillaris* of bog habitats (Brewer 1998). An increase of light following the removal of low plant cover was followed by an increase in the density of *Drosera capillaris* seedlings. Both the seedlings and adults of this species were denser in untreated open areas away from low shrub canopies (Brewer 1998). For *Pedicularis furbishiae*, management to reduce woody dominance has improved the prospects of this endangered species along riverbanks in Maine and New Brunswick (Day 1983; NBCFWRU 2022). To reduce shading for *P. correllii* along the shores of Lady Bird Lake, Austin, Texas, experimental cutting of ground vegetation began on July 24, 2021 to observe the effect of increasing sunlight on declining *P. correllii* stands (Appendix 4).

CONCLUSIONS

For the likely disturbance fugitive, *Physostegia correlli*, the loss of recurring natural disturbances such as flood pulsing along large rivers such as the Colorado, Mississippi, and the Rio Grande may be threatening the success of populations, based on the fact that the height and cover of plants were reduced under experimental shade treatment in our study. Management to remove overhanging ground vegetation and mimic natural disturbance might revive populations of *P. correllii*, especially if soil seed banks are present in current and historical populations along the Colorado River at Lady Bird Lake in Austin Texas. For *Trillium texanum*, overhanging thatch may also reduce the size of individuals. In addition, the lack of a constant source of seeping water may threaten endemic species as springs dry because of climate warming and/or decreased groundwater discharge following drought or freshwater over-extraction.

APPENDIX 1

Final model estimates (intercept, block, lsmeans, and/or covariance estimates for mean height (a) *Physotegia* per quadrant, (b) *Trillium* per tray, and, (c) arcsin (square root percent cover) per tray. Note that time 0 was less than time 3. T. For *Physostegia*, the repeated measures assumption (for *Trillium*) was dropped due to the lack of samples. For *Trillium*, the effect of the repeated measures was not significant and pooled into the error.

a)

Effect	PatchID	quad	time	Estimate	StError	DF	t Value	Pr > |t|
Intercept				39.3054	7.3110	16	5.38	<.0001
time			**0**	-28.1615	2.2619	16	-12.45	<.0001
time			**3**	0	.	.	.	.
Light_noc				-0.02696	0.009394	16	-2.87	0.0111
PatchID	**BC9**			0.1395	8.3706	16	0.02	0.9869
PatchID	**BD5**			27.8248	8.3706	16	3.32	0.0043
PatchID	**MP10**			28.4181	8.3825	16	3.39	0.0037
PatchID	**MP3**			11.1903	9.0132	16	1.24	0.2323
PatchID	**MP8**			0	.	.	.	.

b)

Effect	Bed	time	Estimate	StError	DF	t Value	Pr > |t|
Intercept			6.1714	0.9219	28	6.69	<.0001
TotPlNumb			0.4488	0.1120	28	4.01	0.0004
Time		**0**	0.07307	0.3844	28	0.19	0.8506
Time		**3**	0	.	.	.	.
Bed	**BedExter**		-1.2699	0.4895	28	-2.59	0.0149
Bed	**BedInter**		0	.	.	.	.
				c)			
Intercept			0.2469	0.06898	56	3.58	0.0007
TotPlNumb			0.05289	0.008139	56	6.50	<.0001
time		**0**	-0.1367	0.03429	56	-3.99	0.0002
time		**3**	0	.	.	.	.
Bed	**BedExter**		-0.1562	0.03530	56	-4.42	<.0001
Bed	**BedInter**		0	.	.	.	.

APPENDIX 2

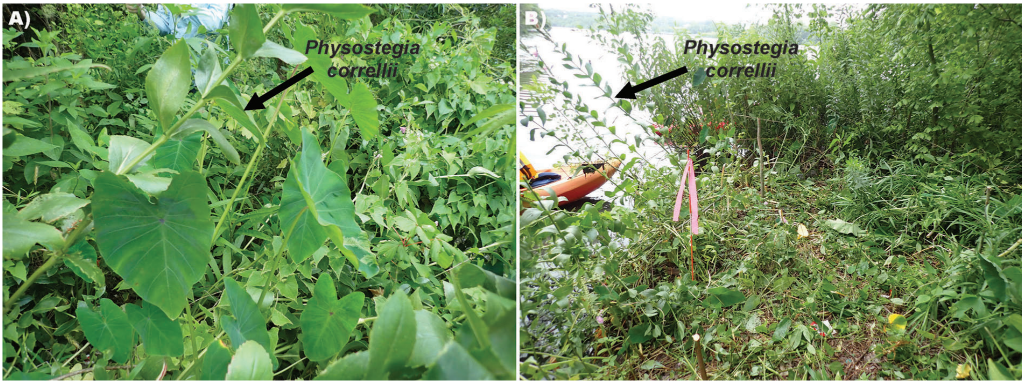
A) Corolla with nectar guides in flowers of *Physostegia correllii* and a, **B)** *Xylocarpa micans* (carpenter bee) pollinating a flower.

APPENDIX 3

Pollinators of *Trillium texanum* detected with a wildlife camera in the conservation garden of the U.S. Geological Survey, Lafayette LA including **A)** Dorantes longtail (*Thorybes dorantes* (likely)), **B)** beetle, and **C)** bee. Photos and ID by Charles Battaglia and Hannah Gonzales, Louisiana Department of Fisheries and Wildlife.

APPENDIX 4

Physostegia correllii at Waller Creek, Lady Bird Lake, TX **A)** before, and **B)** after herb and small woody shade species removal on, July 24, 2021.



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Data Availability Statement.—Data for this study are available in Middleton et al. 2022a,b.

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