

Effects of headwater wetland restoration on the demography and ecology of the federally threatened White Fringeless Orchid (*Platanthera integrilabia*) in the Cumberland Plateau of Kentucky, USA

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Abstract

Wetlands are critical biodiversity hotspots that support numerous rare species, including orchids. Over half of North America's terrestrial orchids depend on wetlands, and more than a quarter are threatened with extinction (G1-G3), with global rarity concentrated in the southeastern U.S. Despite this, effective restoration strategies for wetland orchids remain poorly understood. The white fringeless orchid (*Platanthera integrilabia*), a federally threatened species, is restricted to Appalachian wetlands and has suffered widespread declines due to habitat destruction and hydrologic alterations. In Kentucky, populations remain predominately vegetative with few flowers, with most populations persisting in shaded, closed-canopy conditions. This 11-year study evaluated the effects of canopy and shrub reduction and debris dam installation on *P. integrilabia* and its associated plant communities in a Kentucky nature preserve. Long-term monitoring revealed increased inundation rates, soil saturation, orchid viability, and enhanced floristic diversity. Flowering increased by over 1000% two to four years post-manipulation, along with an increase in fruit production, indicating increased reproductive potential. While white-tailed deer (*Odocoileus virginianus*) browsing increased post-management, the percentage of aborted flowers declined. Despite browsing pressure (~ 50% of orchids browsed), the substantial increase in flowering plants still resulted in higher fruit and seed production at restored sites. Our results highlight the importance of active management, including reduction of woody encroachment and hydrological restoration through debris dam construction, for conserving *P. integrilabia* and improving overall wetland biodiversity. This research expands our knowledge of rare wetland orchids in the region and contributes to broader efforts to restore imperiled orchids and their associated habitats.

1. INTRODUCTION

Wetlands are critical ecosystems that are important for carbon storage, water filtration, flood control, and support high biodiversity (Lang 2024). The diversity of plants can serve as an important measure of wetland condition, and orchids (Orchidaceae), among the most ecologically specialized plants, can serve as an indicator of health for these ecosystems. Orchidaceae account for nearly 10% of all plant species, with over 800 genera and 28,000 + species worldwide (Sheviak 2023; Givnish et al., 2015). While most diversity occurs in the tropics, North America supports 196 terrestrial orchid species, more than half of which are wetland-dependent (obligate and facultative wetland species) (NatureServe 2024; USACE, 2023; Weakley et al., 2024).

Orchids are known for their unique and complex relationships with pollinators, mycorrhizal fungi, and habitat conditions. Darwin's early studies (1899) and recent work by Houlihan et al. (2019) have recognized orchids for their specialized pollination mechanisms. However, the ecology of pollinators remains poorly understood, even within *Platanthera*, North America's most diverse genus of terrestrial orchids (Janes et al., 2024). In addition, their dependence on mycorrhizal fungi for seed germination is also understudied yet critical to their survival. Declines in wetland orchids coincide with broader ecosystem degradation, signaling alterations in habitat integrity that contribute to biodiversity losses. The ecological sensitivity and charismatic appeal of orchids highlight the interconnectedness and collective importance of conserving diverse wetland communities without diminishing the critical ecological roles of other wetland plants and animals.

Globally, 40% of plant species face extinction risks (Antonelli et al., 2020; Enquist et al., 2019). In the U.S., 34% of native plants and 41% of ecosystems are at risk of collapse, with wetlands and orchids among the most imperiled (Fay & Hinsley, 2024; Fay, 2018; Antonelli et al., 2020; NatureServe, 2023; Lang et al., 2024). Half of the

wetlands in Europe, the United States, and China, have been lost over the past 300 years, with many European countries' wetlands such as Ireland, Germany, the UK, and Italy declining > 75% (Fluet-Chouinard et al., 2023). Wetlands currently cover less than 6% of the lower 48 states in the U.S., concentrated in the Southeast, Great Lakes, and Prairie Pothole regions (Lang et al., 2024). Alarming, wetland loss rates have increased by 50% since 2009 due to development, agriculture, and silviculture (Lang et al., 2024). In Kentucky, wetlands and grasslands represent most of the state's rare natural communities tracked by the Office of Kentucky Nature Preserves (OKNP 2024).

Orchids are disproportionately threatened compared to other plant groups, making them key indicators of ecological integrity and conservation priorities, especially within wetland and fire-dependent ecosystems. Major drivers of orchid decline include habitat loss and degradation, herbivory, fire suppression, climate change, poaching, and invasive species (Knapp & Wiegand, 2014; NAOCC, 2024; Noss et al., 2021; Fay & Hinsley, 2024; Fay, 2018; Swarts & Dixon, 2009). The southeastern United States (SE-US) harbors 69% of North America's wetland orchids, 25% of which are globally rare, G1-G3 (NatureServe, 2024; USACE, 2023; Weakley et al., 2024). Additionally, at least 28 terrestrial orchids in the SE-US are associated with both wetlands and fire-dependent habitats, with nearly half of these species being globally rare and primarily found in fire-maintained pine ecosystems (NatureServe, 2024; USACE, 2023; Weakley et al., 2024). Kentucky has 44 species of orchids, of which 43% are state-listed, 44% are wetland-associated, and 30% occur in imperiled grassland and wetland habitats (OKNP, 2024). Among the 47 *Platanthera* species documented in North America, 68% are wetland-associated, 14 are globally rare, and four are federally listed under the U.S. Endangered Species Act (NatureServe, 2024; USACE, 2023; NAOCC, 2024).

Despite the urgency for wetland orchid conservation, few species have been studied to determine their habitat requirements and best management practices for restoring degraded habitats. Much of the terrestrial orchid conservation literature is based in Europe and Australia, underscoring the need for increased research in North America—particularly in the southeastern U.S., where most globally rare wetland orchids are concentrated. This lack of knowledge about North American wetland orchids hinders effective conservation efforts (Swarts & Dixon, 2017; Swarts & Dixon, 2009; Fay et al., 2015; Krupnick et al., 2013; Sheviak 1990; Whigham & Willems, 2003; Weakley et al., 2024).

European studies have shown that mowing, grazing, and canopy removal mitigate woody plant invasion and restore heliophytic (sun-loving) orchid habitat (Willems 1989; Hutchings 1987; Whigham & Willems, 2003; Djordjević et al., 2023, 2016; Wotavova et al., 2004; Janekova et al., 2005; Hurskainen et al., 2017). However, there is still limited understanding of how best to manage North American wetland orchids. Additionally, the complexities of wetland hydrology and weather patterns highlight the importance of long-term monitoring to evaluate orchid responses to different management practices. This lack of understanding about the impact of wetland hydrology on orchid populations hinders effective conservation efforts (Sletvold et al., 2013; Pfeifer et al., 2006; Bell et al., 2021; Bleho et al., 2015).

While some research has examined North American terrestrial wetland orchid ecology (Sieg & King, 1995; Brown & Scott, 1997; Shefferson et al., 2019; Wotavova et al., 2004), few studies have assessed management effects in wetland habitats. Previous research on facultative wetland heliophytic orchids, such as *Platanthera leucophaea* and *P. praeclara*, suggests mixed responses to fire and grazing (Bell et al., 2021; Bleho et al., 2015; Bowles & Jones, 2013; Wilson et al., 2006; Cavan 2022; Bowles et al., 2005; Bowles 1983; Alexander et al., 2010).

Additionally, studies on mowing in *Platanthera ciliaris* habitats have demonstrated positive effects on this facultative wetland orchid population size and viability (Knapp & Wiegand 2014). *Isotria medeoloides* studies highlight the importance of canopy thinning for improving orchid conditions, but this research is focused on an upland forest species, not a wetland orchid (Dibble et al., 2019; Whigham & Willems, 2003; Whigham et al., 2021; Brumback et al., 2011). Consequently, research on wetland orchid management—including fire, mowing, and grazing—remains limited to just a handful of species, primarily *Platanthera leucophaea*, *P. praeclara*, and *P. ciliaris*. Studies on the effects of wetland management and restoration on floristic composition, hydrology, and biodiversity of intact high-quality wetlands also remain scarce (Abella et al., 2020; Warren et al., 2007; Bowles 2013; Bentley et al., 2022; Barton et al., 2008, Lopez & Fennessy, 2002, Mushet et al., 2002).

As such, this 11-year study aims to fill in knowledge gaps by evaluating restoration strategies on the population dynamics of *Platanthera integrilabia*, a federally threatened species, and associated wetland plant communities in headwater wetlands in the Cumberland Plateau of Kentucky.

1.1 Study Species

The white fringeless orchid (*Platanthera integrilabia*) is a federally threatened wetland, globally imperiled (G2) orchid restricted to acidic upland headwater wetlands (referred to as seeps for the remainder of the article), seepage slopes, and streamside bogs in the Appalachian region of the southeastern United States (Zettler & Fairey III, 1990; USFWS 2021; Correll 1950; Luer 1975; NatureServe 2024; Ettman & McAdoo, 1979). This species can grow up to 81 cm (32 inches) tall in its peak flowering state, producing 3–19 fragrant white flowers on a light-green stalk in July–August. Its vegetative leaves are green, strap-like, and vary in size depending on plant age.

This orchid possesses thickened tuber-like roots that contribute to localized vegetative reproduction and may facilitate gradual plant movement within wetland habitats. It is suspected to be a short- to medium-lived perennial capable of surviving up to 20 years as a vegetative plant under shaded conditions. *P. integrilabia* relies on Lepidoptera (butterflies and sphinx moths) for pollination (Zettler et al., 1996; Littlefield et al., 2025 in prep.) and depends exclusively on *Tulasnella inquilina* fungi for seed germination. Increased light availability enhances seed viability (Currah et al., 1997; Zettler & McInnis Jr., 1992, 1994).

Habitat loss from development, agriculture, logging, and invasive species has driven significant population declines (USFWS 2021). Federally listed as threatened in 2016, *P. integrilabia* now persists in fewer than 60 known populations across five states, primarily in the Cumberland Plateau of Kentucky and Tennessee (USFWS 2021; NatureServe, 2024). Historically, this species was described as “fairly common in the plateau region of Kentucky and Tennessee” in 1941 (Correll 1941). The uplands of the Cumberland plateau region where *P. integrilabia* wetlands occur were part of a broader landscape shaped by fire and animal activity (Stambaugh et al., 2020). The abundance of rare, declining fire-adapted plants, animals, and shortleaf pine-oak grassland communities known from the region, coupled with the lack of natural firebreaks between the seeps and uplands, mean that fire historically would have burned through the seeps, contributing to open conditions (OKNP 2024). However, fire suppression, logging, ungulate loss, and shortleaf pine (*Pinus echinata*) decline have disrupted these disturbance regimes and the connectivity of these upland habitats.

Kentucky has 15 documented occurrences of *P. integrilabia* from Bell, Laurel, McCreary, Pulaski, and Whitley Counties, of which nine are extant, one is historic, and five are extirpated (OKNP 2024). They are known from

several wetland types, primarily restricted to the Cumberland Plateau, with one known from the Cumberland Mountains. (OKNP, 2024). Most populations occur in small (< 0.5 hectares) degraded forested headwater acidic seeps, typically located near broad ridges. These wetlands are suspected to be primarily fed by precipitation, but little research has been performed to characterize hydrologic control in these systems (Hoy, 2012).

Past logging practices, including headwater cuts, have been shown to disrupt hydrology, leading to lowered water tables and increased evapotranspiration from regenerating hardwood and shrub thickets, exacerbating wetland drying (Warren et al., 2007; OKNP, 2024). Disrupted hydrology of these wetlands throughout the range of the species is assumed to be a significant cause of population declines that were made worse by coinciding increases in canopy cover with the loss of landscape-level disturbances like fire and megafauna that kept the canopy open (OKNP, 2024). In Kentucky, most sites are heavily shaded (> 90% canopy cover), resulting in predominantly vegetative orchids. In contrast, populations in open (0–30% canopy cover) to semi-open conditions (30–80%), such as powerline rights-of-way—exhibit higher flowering rates and greater species richness of associated plants (OKNP, 2024). This pattern differs from a range-wide study that found no significant correlation between light, soil moisture, and flowering (Boyd et al., 2014). However, the optimal canopy cover and hydrologic conditions for sustaining *P. integrilabia* while maintaining high floristic quality remain unknown (Wooten et al., 2021; Boyd et al., 2014; USFWS 2021).

This study examines wetland restoration strategies for improving population dynamics of *P. integrilabia* and its associated wetland plant communities in Kentucky. Our objective is to evaluate the effectiveness of practical management recommendations that could enhance wetland hydrology while reducing shade (e.g., hardwood thinning and debris dam creation). This contributes to ongoing *P. integrilabia* conservation strategies and broader efforts to restore imperiled wetland ecosystems.

2. METHODS

2.1 Study Site

The study was conducted in a Kentucky State Nature Preserve in the Cumberland plateau region of Kentucky (Fig. 1). The property consists of 101-ha of young to medium aged maple-oak-pine forests that had been selectively logged in the 1990's. While the upland forests were generally depauperate, with little plant diversity due to the regenerating hardwoods and increased shading, the site still contained three small headwater seeps (West, Center, East) ranging in size from 0.1 acre to 0.5-ha that harbored rare orchids such as *Platanthera integrilabia*, *Platanthera cristata*, and historic populations of *Calopogon tuberosus* (OKNP, 2024)

Common species in the seeps prior to management included ferns such as *Osmunda spectabilis* and *Osmundastrum cinnamomum*; graminoids such as *Chasmanthium laxum*, *Dichanthelium macrocarpon*, and *Leersia virginia*; and Forbs such as *Doellingeria umbellata*, *Eupatorium pilosum*, and *Lycopus virginicus*, along with *Sphagnum palustre*. Orchids present before management included small populations of *Platanthera integrilabia*, *Platanthera cristata*, *Platanthera ciliaris*, and *Platanthera clavellata* (OKNP, 2024).

The Center and East seeps contained dense shrub thickets of *Ilex verticillata* and *Aronia melanocarpa*, along with young regenerating hardwood trees, including *Liriodendron tulipifera*, *Acer rubrum*, and *Quercus alba*. *Ilex opaca*, an evergreen shrub, was common in the shrub layer. The Center and East seeps were more heavily disturbed during the logging event in the 1990s, as evidenced by tire ruts caused by skid steers (OKNP, 2024). By

2007, the once abundant flowering populations of *P. integrilabia* declined to just a few flowering individuals. Although mature vegetative orchids were still present in the East and Center seeps, overall population numbers had declined greatly since the population was first discovered (OKNP, 2024). In addition, the center seep contained a small population of the state endangered *Calopogon tuberosa* that was discovered in the 1990's but had disappeared from the site in 2003.

The West seep had an overstory of mature *Acer rubrum* and *Nyssa sylvatica* and was less disturbed in the past logging event compared to the other seeps. It previously had a small *P. integrilabia* and *Calopogon tuberosa* (state endangered orchid) population, although flowering and vegetative plants had not been seen in the west seep since 2003 (OKNP, 2024).

2.2 Study Design and Field Methods

2.2.1 Monitoring Plot Establishment

In August 2009, four permanent monitoring plots were established in the seeps that contained custom layouts of 10 × 10 m plots that were installed along a grid that encompassed the entire *P. integrilabia* population. The seep layouts were: West seep - one 10 × 40 m plot, Center seep - one 20 × 50 m plot, and East seep - one 20 × 30 m plot and one 10 × 30 m plot. The monitored area for each seep was 400 m² (West Seep), 1,000 m² (Center Seep), and 900 m² (East Seep), with a total of twenty-three monitoring modules at the preserve (2300 m²). Photo monitoring points were also installed along the center line of the plots and photos were taken at cardinal directions annually during plant surveys to visually track change over time.

2.2.2 *P. integrilabia* demographic monitoring

The plots were sampled annually in August from 2009–2020, with data collection focused on flowering plants, vegetative plants, individual flowers and browsed plants. Data was also collected on additional orchids or rare plants found within the plot. Aborted orchids, defined as an *P. integrilabia* plants that attempted to flower but failed to fully develop, were also counted and tallied in each seep.

Every *P. integrilabia* flowering plant in the monitoring plots was numbered and flagged, and individual flowers were counted and recorded. Once fruits formed in late September-October, they were counted on each plant and additional browsed plants were recorded. Vegetative orchids were also counted and tallied in each plot. Large aggregations of vegetative leaves were sometimes difficult to count due to density and other species of *Platanthera* vegetative leaves, such as *P. ciliaris* and *P. cristata*, may have mistakenly been included in the counts since these *Platanthera* species share similar leaf morphology. All size classes of *P. integrilabia* leaves were collectively counted as a part of this study and are reflected in the vegetative plant count.

2.2.3 Vegetation structure and floristic composition

The vegetation of each plot module was sampled using the Carolina Vegetation Survey (CVS) Level IV methodology (Peet et al., 1998; Lee et al., 2008). Within each 10 x 10-meter plot module, cover was estimated for all vascular plants rooted in the plot across three strata: herb (all herbaceous species and woody species under 0.5 m in height), shrub (woody species 0.5-5 m), and tree (trees > 5m). were visually estimated using CVS cover classes (1 = < 0.1%; 2 = 0–1%; 3 = 1–2%; 4 = 2–5%; 5 = 5–10%; 6 = 10–25%; 7 = 25–50%; 8 = 50–75%; 9 = 75–95%; 10 = 95–100) and level IV CVS methodology Carolina Vegetation Survey (CVS) methodology (Peet, 1998; Lee, 2008). Cover estimates followed the CVS Level IV methodology, using percentage classes ranging from < 0.1 –

100% (Peet et al., 1998; Lee et al. 2008). Unknown plants were collected and photographed for identification. Vascular plant taxonomy followed the Flora of the Southeastern United States (Weakley et al., 2024). *Sphagnum palustre*, a non-vascular bryophyte, was also measured using cover classes because of its strong association and suspected importance in these wetlands.

2.2.4 Canopy Cover

A spherical densiometer was used to estimate canopy closure within the established plots, with four readings taken at every 10 x10 meter plot within the West, Center, and East seeps in 2009 and 2014. Measurements were taken in cardinal directions within each plot and then averaged for each seep following the methods of Lemmon (1956). Canopy cover was then remeasured post management in 2019 along the center line of the seeps using a Delta-T Devices (Cambridge, U.K.) HemiView canopy analysis system. The system included a self-leveling mount that was equipped with a Nikon (Nikon Corporation, Japan) COOLPIX 4500 camera with a fish-eye lens. Canopy images were analyzed using HemiView Version 2.1 software in Photoshop (Adobe, San Jose, CA) following the methods outlined by Barton and Karathanasis (2002) and Sena et al. (2018).

2.2.5 Soils

At each site, soils were excavated from a central location with a bucket auger and described and sampled by horizon following standard procedures (Schoeneberger et al., 2002). Subsequently, a 40 cm in depth pit was also excavated at each site to confirm the presence of restrictive soil horizons (Hoy 2012). Each soil sample from each horizon was sent to the University of Kentucky's Regulatory Services Testing Laboratory to test physical and chemical properties. Air-dried sieved samples were analyzed for particle size by the pipette method (Sheldrick and Wang, 1993) and soil pH was measured in a 1:1 soil/water paste following methods outlined by the Soil and Plant Analysis Council (2000). Soil organic matter (SOM) was measured using a LECO CHN analyzer (Nelson and Sommers, 1982).

2.2.6 Wetland hydrology

Hydrology was monitored using piezometers, tensiometers, and pressure transducers to assess groundwater fluctuations, soil moisture, and vertical hydraulic gradients were measured following Barton et al. (2008) and Karathanasis et al. (2003). Hoy (2012) used piezometers to measure hydraulic head, which were constructed of 2.5 cm diameter PVC piping with a 15 cm section of slotted (0.005 cm) PVC well casing on the submerged end. The pipes were bored at 30, 60, 90, and 120 cm depths. For each piezometer, the annulus was filled with sand and in-situ soil above the slotted pipe and sealed with a bentonite plug. The remaining annulus was filled with in-situ soil and the hydraulic head was manually recorded in centimeters using the equation: hydraulic head = (distance from casing top to ground) – (distance from casing top to water level).

Hoy (2012) also used tensiometers to measure soil matric potential. These were constructed of a porous ceramic cup attached to a water column and vacuum gauge (Schwartz & Zhang, 2003). A SW-010 tensiometer (Soil Measurement Systems, Tucson, AZ) was used to read the pressure in the tensiometer and the number was recorded in millibars; the more negative the reading, the drier the soil (Yocubal et al., 2004). Tensiometers were installed at 30, 60, 90, and 120 cm depths and backfilled with native soil around the ceramic cup and cement was used at the soil surface to hold tensiometers in place and prevent short-circuiting.

Using a 150 cam (0.005 cm) slotted PVC pipe, groundwater levels were continuously recorded at wells constructed of 2.5 cm diameter piping. In-Situ MiniTROLL PSIG (In-Situ, Inc. Fort Collins, CO) pressure

transducers recorded water levels at 15-minute intervals. Data were downloaded and transferred to Excel, creating continuous hydrographs for each seep.

Vertical hydraulic gradient (VHG) was calculated to determine groundwater flow direction by comparing hydraulic head in wells and piezometers (Barackman & Brusseau, 2004) using the equation $VHG = (\Delta h_{\text{piezometer}} - \Delta h_{\text{well}}) / \text{depth to piezometer screen}$ (Lee & Cherry, 1978). Aquifer discharge (upwelling) was indicated by positive VHG, while negative VHG indicated aquifer recharge (downwelling) (Moorhead, 2001). Long-term (2010–2019) monthly precipitation information was obtained from the Automated Surface Observing System (ASOS) station located at the nearby London/Corbin. Airport.

.2.2.7 Management Implementation-Seeps

Center Seep. In February 2013, a 10-person crew felled several large and pole-sized trees and many saplings and shrubs including *Ilex opaca* and *Ilex verticillata* thickets within the Center Seep. Stumps were treated with Garlon 3A (Corteva Agriscience, Indianapolis, IN) to prevent sprouting. Seedlings that emerged from the seed bank and stump sprouts were subsequently controlled every 2–3 years by cutting the new vegetation with loppers and treating it with Garlon 3A. Measurements on the quantity of thinning were not made during management, but the basal area was reduced considerably, and canopy openings and reduction of the midstory and shrub layers were evident. Several of the large, felled *Quercus alba* were used as wood for the creation of debris dams. Two dams were constructed across the seep's central and widest sections (Fig. 2). One was placed in the central portion of the seep (approximately 5 m downgradient of the well cluster), and the other was toward the seep's end near the ephemeral channel's origin. Logs were placed on the surface and borrow soil from the uplands was used to “seal” openings between the ground and logs and between stacked logs. The final structures were approximately 10 m long by 0.5 m high. The structures were not intended to prevent water movement but rather to slow flow and enhance ponding (Fig. 2)

East Seep. In February 2017, a seven-person crew felled several large and pole-sized trees, *Ilex verticillata* thickets, and many saplings within the east seep following methods utilized in the Center Seep. As performed previously, several of the large, felled *Quercus alba* trees were used for the creation of debris dams. In this case, dams were positioned in individual ditches, actively conveying water to downstream ephemeral channels, thereby partially draining the wetland.

2.3 Data Analysis

Values for *P. integrilabia* life history traits were averaged per site and year, with select descriptive statistics mean, median and standard errors reported. Percentages of browsed plants were calculated for each seep, with the following equation: % browsed plants = total browsed plants/Total flowering plants (flowering + aborted). Percentages of aborted plants were also calculated using a similar equation: % aborted plants = total aborted plants/total flowering plants (flowering + browsed). To assess the impact of management on *P. integrilabia*, population metrics including 1) total flowering count, 2) number of flowers per plants (mean and median), 3) plant/flower ratio, 4) vegetative plants, 5) number of browsed and aborted plants and 6) the percentage of population browsed or aborted was averaged for pre management and post management metrics, and then compared using paired t-tests to look at management effects. Population growth rates were calculated by the equation: population growth rates = [(average of post management flowering plants - average of pre

management flowering plants) / (average of pre management flowering plants)] x 100. Percentage of increase/decrease of other population metrics was also calculated. Statistical significance was set at $p < 0.05$.

Impacts of management on the vegetation were accessed by calculating changes in percent cover of native and non-native plants, species richness, mean Coefficient of Conservatism (Mean C), Floristic Quality Index (FQI), coefficient of wetness score and the Floristic Heliophytic Index to assess shifts in community composition and ecological integrity. The geometric mean (median of the upper and lower limits) of the cover classes were used in the species composition analysis.

Mean C and FQI were derived from the Floristic Quality Assessment (FQA) method developed by Swink & Wilhelm (1979) which rely on the Coefficient of Conservatism (C-value) scores, which range from 0 to 10, where 0 represents non-native species, and 1–10 assigned to native species, with higher values indicating 'conservative' species associated with quality habitats with high biodiversity and lower values representing "weedy" species that can tolerate many disturbances in low quality habitat. C-values used in this study were compiled and refined by OKNP from the previously published C-value list (OKNP, 2024).

The floristic heliophytic index was calculated pre- and post-management using a 1–10 scale that quantifies species' tolerance and preference for different light conditions, from deep shade to full sun (Weakley et al., 2024). Mean wetness coefficient scores were calculated by converting the wetland indicator codes (USACE, 2023) into numeric values (OBL = -5; FACW = -3; FAC = 0; FACU = +3; UPL = +5). Scores with negative values indicate wetland conditions, whereas positive values indicate more upland conditions. The following equations were used to calculate the floristic metrics: richness = number of native species; Mean C = (sum of C-values)/richness; FQI = Mean C/($\sqrt{\text{richness}}$); Mean coefficient wetness = (sum of coefficient wetness coefficient scores)/richness; and mean heliophytic index = (sum of heliophytic index values)/richness.

3. RESULTS

3.1 Orchid Population Metrics and Response to Management

3.3.1 Flowering, Fruiting, and Vegetative Plants

Prior to management, *P. integrilabia* was present in both the East and Center seeps, but flowering individuals were rare, with most plants vegetative (Table 1, Fig. 4). The West seep had already lost its *P. integrilabia* population, with no vegetative or flowering plants present (Table 1). Following management, the number of flowering plants increased substantially in both restored seeps. In the center seep, flowering plants increased significantly within four growing seasons, with over a 2000% increase by the seventh-year post-management ($p = 0.03$; Table 1, Fig. 4). Similarly, the east seep demonstrated flowering increases within two growing seasons, approaching a 1000% increase three years after management ($p = 0.07$). High variability, indicated by large standard deviations, inherently reflected this delayed orchid response. Consequently, statistical significance was primarily detectable only when substantial increases in orchid flowering occurred.

Table 1

Platanthera integrilabia Demographic Data in three seeps over 11 years. M1 = management Woody Removal and Debris dam installation. Standard deviation is denoted ().

Center Seep	Pre management (2009–2013)	Post management (2014–2020)	T test P value (alpha 0.05)	% increase
# flowering plants (mean)	5.2 (2.01)	125.6 (42.25)	0.03	2314
total individual flowers (mean)	34.4 (12.85)	944.0 (336.45)	0.04	2644
total individual fruits (mean)	13.4 (4.63)	416.9 (196.54)	0.09	3010
flowers per plant (mean)	7.43 (0.28)	8.26 (0.1)	0.01	11
flowers per plant (median)	8	8	n/a	n/a
plant/flowers ratio	0.14 (0.0055)	0.13 (0.0019)	0.52	2.8
vegetative plants (mean)	1074 (157.8)	1412.5 (158.09)	0.16	32
aborted orchids (M1)	8.0 (2.19)	8.3 (4.63)	0.96	3
% population aborted (M1)	60.6 (7.55)	18.3 (9.8)	0.01	-70
% population browsed (M1)	16.2 (7.28)	45.4 (7.64)	0.02	180
East Seep	Pre management (2009–2017)	Post management (2017–2020)	T test P value (alpha 0.05)	% increase
# flowering plants (mean)	6.1 (2.47)	62.0 (15.59)	0.07	914
total individual flowers (mean)	44.1 (18.88)	486.0 (177.24)	0.13	1428
total individual fruits (mean)	17.9 (11.28)	214.0 (130.54)	0.27	1096
flowers per plant (mean)	7.63 (0.35)	9.15 (0.23)	0.0005	20
flowers per plant (median)	7.5	9	n/a	n/a
plant/flowers ratio	0.15 (0.0089)	0.12 (0.0034)	0.0038	24.3
vegetative plants (mean)	2055.5 (151.24)	1232.7 (65.57)	< 0.01	-40
aborted orchids (M1)	15.9 (5.0)	4.5 (2.5)	0.08	-72
% population aborted (M1)	72.8 (8.68)	6.2 (3.97)	< 0.01	-92

Center Seep	Pre management (2009–2013)	Post management (2014–2020)	T test P value (alpha 0.05)	% increase
% population browsed (M1)	26.4 (10.24)	43.3 (11.21)	0.31	64
West Seep	Pre management (2009–2020)	n/a	n/a	n/a
Flowering plants (mean)	0	n/a	n/a	n/a
# flowering plants (mean)	0	n/a	n/a	n/a
total individual flowers (mean)	0	n/a	n/a	n/a
total individual fruits (mean)	0	n/a	n/a	n/a
flowers per plant (mean)	0	n/a	n/a	n/a
flowers per plant (median)	0	n/a	n/a	n/a
plant/flowers ratio	0	n/a	n/a	n/a
vegetative plants (mean)	0	n/a	n/a	n/a
aborted orchids (M1)	0	n/a	n/a	n/a
% population aborted (M1)	0	n/a	n/a	n/a
% population browsed (M1)	0	n/a	n/a	n/a

Prior to management, the number of flowers on each plant averaged 7.43 in the center and 7.63 in the east seep, with a median of 8 and 7.5 flowers per plant, respectively (Table 1). Post management, flower numbers per plant significantly increased in the center (8.26, $p = 0.01$) and East seeps (9.15, $p = 0.0005$), with a range of 3–19 flowers per plant. The plant-to-flower ratio decreased post-management at both seeps, indicating increased floral productivity per plant. Increased flowering plants significantly increased total flowers—over 2500% in the center seep—and a positive trend in the east seep (Table 1, Fig. 4). Fruit set increased post-management but varied considerably, reflecting existing challenges such as herbivory, temperature, and precipitation fluctuations (Table 1, Fig. 4).

Vegetative plant counts, however, showed contrasting responses between restored seeps. In the center seep, vegetative plants increased post-management, though not significantly (32% increase, $p = 0.16$, Table 1). The east seep experienced a significant decline (40% reduction, $p = 0.0007$). Potential causes attributed to vegetative decline include competitive interactions, fungal abundance, or observer error in data collection.

3.1.2 Herbivory and Aborted Orchids

White-tailed deer (*Odocoileus virginianus*) referred to as deer for the remainder of paper) were the most significant herbivore threat to *P. integrilabia*, where browsing impacted approximately half the flowering orchids annually and contributed to reduced fruit set (Fig. 4). Aphids, weevils, caterpillars, and crayfish also were documented on or damaging *P. integrilabia*, but the impact was considered minor relative to other existing threats (Littlefield et al., in prep, 2025). Post-management, browsing increased significantly in the center seep, with nearly 50% of flowering orchids annually browsed (Table 1). Browsing intensity varied yearly, with some extreme cases notable in 2017, where 100% of flowering orchids in the east seep and 66% in the center seep were browsed, the highest recorded impact year. In 2020, the significant increase in individual flowers in the center seep was followed by a sharp decline in fruits due to the browsing of 55% of flowering plants (Fig. 4).

Aborted orchids—plants that initiated flower stalks but failed to complete flowering—were monitored during the monitoring period (excluding 2016–2019). Before management, sites with low flowering rates exhibited higher numbers of aborted plants (Table 1). After management, the number of aborted orchids significantly declined in both the Center and East seeps. However, the exact mechanisms behind what causes flowering stems to abort remains uncertain but likely involves a combination of climatic factors and insect interactions (Littlefield et al., in prep, 2025).

3.2. Vegetation and floristic composition

3.2.1 Pre and Post-Management Changes

Over the study period, we documented 117 vascular plants and one nonvascular bryophyte (*Sphagnum palustre*) within the vegetation plots. A complete floristic list with associated metrics is provided in the online resource 1. Although classified as wetlands, the seep plant species composition reflects various moisture conditions and light preferences, from obligate wetland species to upland generalists and shade-tolerant to heliophytic species. Common species present in the seeps prior to management aligned with original inventories. Orchids documented in and adjacent to the seeps included small populations of wetland species such as *Platanthera ciliaris*, *Platanthera clavellata*, and *Platanthera cristata*, as well as more upland-associated species like *Cypripedium acaule*, *Isotria verticillata*, *Tipularia discolor* and *Cleistesiosis bifaria*, which was found just outside the study plots.

Pre-management richness and quality (mean C and FQI) in the East and Center seeps were slightly higher compared to the West seep due to the presence of conservative species such as *P. integrilabia* and vegetative upland heliophytic species such as *Coreopsis tripteris*. The coefficient of wetness was lower in the West seep compared to the East and Center seeps (Table 2). Post management, the floristic richness and quality increased in both managed seeps, while the West seep showed minimal changes (Table 2). The coefficient of wetness scores became wetter in the Center seep, drier in the East seep, and unchanged in the West seep (Table 2). The heliophytic index scores increased in both the managed seeps. The vegetation structure of the seeps post-management shifted from a tree and shrub dominated strata to an herbaceous dominated stratum (Table 2). Grasses, forbs, ferns, and sphagnum increased significantly. (Table 2).

Table 2

Floristic metrics of the three seeps pre and post management. Total cover was per strata and determined by adding the dominant species cover classes. Dominant species were listed in the vegetation structure, with a full floristic list provided in the online resource 1.

		West Seep		Center Seep		East Seep	
		2009	2020	2009	2020	2009	2020
VEGETATION METRICS							
Coefficient of Wetness		-0.125	-0.29	0.56	-0.07	0.18	0.46
Mean C (Coefficient of Conservatism)		5.42	5.61	5.73	5.44	5.5	5.39
Floristic Richness		48	49	59	84	56	93
Floristic Quality Index (FQI)		37.53	39.29	44	49.86	41.16	51.95
Heliophytic Index		5.35	5.39	5.37	5.93	5.32	5.42
VEGETATION STRUCTURE							
Herbaceous	Scientific name	36.75	61.375	24.25	121.05	13.83	102.43
% total cover							
herbaceous	<i>Chasmanthium laxum</i>	4.5	1.25	9.3	45	3.58	19.5
herbaceous	<i>Dichanthelium microcarpon</i>	1.75	0.75	0.65	17.6	1.041	32.67
herbaceous	<i>Doellingeria umbellata</i>	1.25	1	1.05	3.15	1.38	2.88
herbaceous	<i>Eupatorium pilosum</i>	1.25	0.125	0.45	1.65	0.042	0.083
herbaceous	<i>Osmunda spectabilis</i>	15	43.75	6.65	18.45	1.83	17
herbaceous	<i>Osmundastrum cinnamomeum</i>	7.5	10	4.4	17.7	4.5	25.42
herbaceous	<i>Sphagnum palustre</i>	5.5	4.5	1.75	17.5	1.46	4.88
Tree canopy		90.11	91.29	85.8	29.35	83.77	36.45
% total cover							
Tree canopy	<i>Acer rubrum</i>	45.8	44.19	48.5	12.75	35.78	7.92
Tree canopy	<i>Liriodendron tulipifera</i>	0.83	3.75	2.2	0	7.5	0.42
Tree canopy	<i>Magnolia macrophylla</i>	4.38	4.88	1.5	0.2	0.25	0
Tree canopy	<i>Nyssa sylvatica</i>	5.5	4.5	5.5	2.5	19.92	8.56
Tree canopy	<i>Oxydendrum arboreum</i>	4.38	4.63	1.35	0.1	8.75	3.75
Tree canopy	<i>Quercus alba</i>	29.22	29.34	26.75	13.8	11.57	15.8
Shrub % Total Cover		24.33	25.89	57.58	5.9	58.95	12.17

		West Seep		Center Seep		East Seep	
		2009	2020	2009	2020	2009	2020
VEGETATION METRICS							
Shrub	<i>Acer rubrum</i>	0.75	0.94	11.45	0.6	5.5	0.6
Shrub	<i>Aronia melanocarpa</i>	1.63	0.75	1.25	0.425	4.25	1.1
Shrub	<i>Ilex opaca</i>	6.63	10.88	15.8	0.95	7.27	1.65
Shrub	<i>Ilex verticillata</i>	3.25	8.31	23.75	1.35	22.38	0.48
Shrub	<i>Liriodendron tulipifera</i>	4.19	1.063	0.18	0.3	10.27	1.19
Shrub	<i>Magnolia macrophylla</i>	1.88	0.88	0.35	0.55	0.083	0.083
Shrub	<i>Nyssa sylvatica</i>	4.69	1.94	3.95	0.5	3.71	0.52
Shrub	<i>Oxydendrum arboreum</i>	1.31	1.13	0.85	1.225	5.49	3.17
Vine % Total Cover		2.125	1.125	1.8	7.45	4.12	5.62
vine	<i>Apios americana</i>	0.125	0.375	0.5	6.7	0.083	2.08
vine	<i>Smilax glauca</i>	1.125	0.25	0.15	0.1	1.04	0.79
vine	<i>Smilax rotundifolia</i>	0.875	0.5	1.1	0.65	3	2.75
Invasives % Total Cover		0	0.1	Trace	0.2	Trace	0.04
invasives	<i>Lonicera japonica</i>	0	0.1	0	0	0	0
invasives	<i>Microstegium vimineum</i>	0	0	trace	0.1	trace	0.04
invasives	<i>Rosa multiflora</i>	0	0	0	0.1	0	0

Conservative obligate and facultative wetland species increased notably post-management, increasing the floristic quality index and contributing to a lower coefficient of wetness score. Several wetland species appeared, such as *Calopogon tuberosus*, *Lobelia nuttallii*, *Rhynchospora capitellata*, *Calmagrostis coartata*, *Ludwigia alternifolia* and *Juncus canadensis*. Weedy conservative wetland natives also increased, including *Cyperus acuminatus* and *Boehmeria cylindrica*, affecting the floristic quality scores. In contrast, there was also an increase in heliophytic conservative upland species, such as *Eurybia surculosa*, *Coreopsis tripteris*, and *Helianthus strumosus*, that contributed to a higher coefficient of wetness (drier) and higher floristic quality index. At the same time, an increase in weedy, low-conservative upland species such as *Rhus copallinum* var. *latifolia* and *Sassafras albidum* also influenced the vegetation metric scores.

The east seep experienced similar increases in wetland and upland conservative and weedy species. The narrower shape of the east seep and the removal of a large *Ilex verticillata* thicket in the lower end of the seep may have contributed to more weedy upland influence post management, such as the arrival of *Erechtites hieraciifolia*, *Parthenocissus quinquefolia*, and *Dichanthelium boscii*. Additionally, more upland hummocks within the seep likely influenced the positive wetness index. The west seep, the unmanaged control, exhibited minimal

changes in floristic quality and coefficient of wetness. However, the percent cover of *Osmunda spectabilis* increased substantially in the herbaceous layer in 2019, likely due to high amounts of precipitation experienced in 2018 and 2019 (Table 2, Fig. 9).

Before management, *Microstegium vimineum* was present in small quantities in both seeps and expanded slightly post-management, with species being actively controlled through hand pulling during floristic surveys. In addition, the invasive shrub *Rosa multiflora* was present in the Center seep in low abundance and expanded into both seeps post-management. This invasive shrub was actively controlled by hand pulling or cut stump treatment. In the surrounding uplands, additional invasive species such as *Paulownia tomentosa* and *Mosla dianthera* were also identified as existing threats and are actively being removed.

The reappearance of the state-endangered *Calopogon tuberosus* in the center seep in 2017, five years post-management, after a 15-year absence—suggests that seed bank dormancy or root persistence played a role in restoration success. Similarly, the state-threatened *Lobelia nuttallii* emerged six years post-management, likely from the seed bank. Additionally, several conservative wetland species that had previously persisted in vegetative form began flowering post-management, including *Lilium canadense*. Several weedy, non-conservative native species increased significantly in areas with the most significant canopy reduction, including *Dichanthelium macrocarpon* (0.65% cover to 17.6% cover in the center seep; 1% cover to 32.67% cover in the east seep) and *Erechtites hieraciifolia* (0 to 8% cover in the east seep) (Table 2).

3.3 Canopy Cover Changes

Canopy cover was measured at all three wetlands in 2009, 2014, and 2019 (Table 3). Before management, all three seeps exhibited dense canopy cover (ranging from 93.2–97.2%). After thinning at the central seep in 2013, mean canopy cover decreased to 81.9%, while the East and West seeps became denser, with only 2.6% and 1.9% open canopy, respectively. Mean open canopy cover increased in 2019 at the east seep to 18.9% following thinning, comparable to that after thinning at the center seep. Canopy openness at managed seeps increased by 12.1–14.9%. Areas directly above flowering orchids had slightly more open canopy—about 1–2% higher—than areas without orchids, suggesting a possible link between light availability and orchid flowering.

Table 3

Mean percent open canopy (± standard deviation) [†] within 10 x 10-meter plots modules (2009 and 2014 readings) and along the central axis line (2019 readings) in the East, Center and West seeps.

Year	East Seep (%)	Center Seep (%)	West Seep (%)
2009	6.8 (5.2)	4.6 (2.2)	2.8 (2.0)
2014	2.6 (3.7)	18.1 (9.4)	1.9 (1.9)
2019	18.9 (3.0)	19.5 (5.1)	1.1 (1.9)
[†] Canopy cover estimated with a spherical crown densiometer in 2009 and 2014. A Delta-T hemispherical camera and analysis system was used in 2019 for estimating percent open canopy. The center seep was thinned in 2013. The east seep was thinned in 2017.			

3.4 Wetland Soils

Soil characterization was conducted at all three wetlands, with results summarized in Table 4. Soils at all sites were classified in the Lindside (ponded) series (Fine-silty, mixed, active, mesic Fluvaquentic Eutrodepts). Each

site exhibited similar texture, structure, matrix colors and redox features. The A-horizons extended to depths of 10–11 cm, below which a weak fragic horizon (B_{xg}) was present between 10 and 30 cm. Soil horizons below the B_{xg} horizon exhibited higher chroma values, suggesting improved drainage conditions. As such, the fragic horizon likely resulted from physical compaction, forming a fragipan—a conclusion supported by visible rutting, ponding, and other logging-related disturbances.

Table 4
Field classification and characteristics of soils in the three wetlands.

Horizon	Depth (cm)	Matrix Color	Redox Feature Color [†]	Texture [‡]	Structure ^Δ	pH	SOM (%) [*]
<i>East Seep</i>							
A	0–11	10YR 5/2	f,f, 10YR 4/4	sil	gr	4.74	4.88
B _{xg}	11–30	2.5Y 6/2	m,d, 7.5YR 5/6	sil	b,abk	4.66	1.17
B _{w1}	30–52	2.5Y 6/4	m,d, 7.5YR 6/8	sil	sbk	4.78	0.55
B _{w2}	52–90	2.5Y 6/6	m,d, 7.5YR 5/8	sil	sbk	4.91	0.43
C/R	90+						
<i>Center Seep</i>							
A	0–10	10YR 4/2	f,f, 10YR 4/4	sil	gr	4.52	6.52
B _{xg}	10–25	2.5Y 6/2	f,d, 5YR 5/8	sil	b,abk	4.59	2.87
B _{w1}	25–40	2.5Y 6/3	m,f, 7.5YR 6/8	sil	sbk	4.74	1.03
B _{w2}	40–70	2.5Y 7/3	m,d, 10YR 5/8	sil	sbk	4.78	0.58
B _{w3}	70–95	2.5Y 7/2	m,f, 7.5 YR 6/8	sil	sbk	4.87	0.60
C/R	95+						
<i>West Seep</i>							
A	0–10	10YR 4/2	f,f, 10YR 4/4	sil	gr	4.55	6.45
B _{xg}	10–25	2.5Y 6/2	m,d, 7.5YR 5/8	sil	b,abk	4.62	1.63
B _{w1}	25–40	2.5Y 6/3	m,f, 7.5YR 6/8	sil	sbk	4.75	0.79
B _{w2}	40–60	2.5Y 6/3	m,d, 7.5YR 7/8	sil	sbk	4.80	0.60
B _{w3}	60–95	2.5Y 6/3	m,d, 7.5YR 5/8	l	sbk	4.81	0.41
C _g	95+	2.5Y 6/2	m,d, 7.5YR 5/8	l	ma	4.80	0.26
[†] Abundance: f = few, m = many; Brightness: f = faint, d = distinct.							
[‡] Texture: sil = silt loam, l = loam.							
^Δ Structure: b = brittle, gr = granular, abk = angular blocky, sbk = subangular blocky, ma = massive.							
[*] SOM = soil organic matter							

Soil pH ranged from 4.52 to 4.91, which aligns with the acidic conditions typically observed in headwater seeps (Soulsby et al., 2007; Weakley & Schafale, 1994; O'Driscoll & DeWalle, 2010). Soil organic matter (SOM) was highest in the A horizon, a typical feature of wetlands where anaerobic conditions limit decomposition (Collins & Kuehl, 2001). Redoximorphic features (such as mottling) below the A horizon and a Bxg horizon with a chroma of 2 indicate that these soils meet hydric criteria.

3.5 Hydrology

3.5.1 Hydrology Pre-treatment

Continuous monitoring of the water table in the wells showed that each wetland maintained saturated conditions over the 18-month pretreatment monitoring period, suggesting similar hydrologic regimes among the three sites (Hoy 2012). From the beginning of December through the end of May, the water level usually stayed between +/- 10-cm of the soil surface. Following saturation, during the growing season from June until November, there was a significant dry-down period during much of the growing season, where the water table was below the maximum recording depth of 120-cm. Occasional rain events during the growing season caused temporary saturation of the soil and were consistent between the hydrographs (Hoy 2012). The wetlands did not exceed a maximum water level of approximately 10-cm, with a few exceptions during large rain events in the center and west seeps.

Manual water level measurements taken from piezometers during bi-monthly visits to the wetlands during the pre-treatment showed a similar seasonal pattern as seen in the monitoring wells (Fig. 6). VHG calculated from piezometers during the winter, spring, summer, and fall showed on average - 0.013 cm (east), -0.060 cm (center), and - 0.005 cm (west). The tight fit between the piezometer and well measurements, as seen in Fig. 6, suggests that groundwater does not influence the hydrology of the wetlands. Near zero VHG calculations indicate a lack of influence of groundwater discharge or recharge.

Tensiometer measurements document changes in soil moisture. As soil dries, measurements become more negative due to more negative pressure in the tensiometer. Data from the tensiometers were similar to those observed in piezometers, showing wet and dry periods at similar times of the year. Unlike the piezometers, data from the tensiometers show soil saturation (readings of 0 mbar) in the wetlands on multiple occasions during the summer of 2010 (Fig. 7). Although the water table was below our monitoring capability depth for most of the 2010 growing season, the tensiometers detected high soil saturation levels during summer precipitation events.

Using tensiometer data, Hoy (2012) showed a restrictive layer in the soil between 30 and 60 cm. (Fig. 7). A distinct separation in the readings between the 30cm tensiometer and the 60, 90, and 120 cm tensiometers supported this. Greater negative readings at the 60, 90 and 120 cm tensiometers compared to the 30 cm tensiometer indicated soil was wetter at the surface and potentially contained a perched water table near the soil surface.

Hoy (2010) calculated water yield for the site as the difference between precipitation input and ETr output following methods of Sun et al. (2011). During the winter, precipitation was generally higher than ETr, while growing season evapotranspiration was generally higher than precipitation. The pattern of wet and dry months coordinates well with piezometer and tensiometer data. From these estimates, approximately 58% of precipitation was removed through Etr, while 42% exited as surface runoff in downgradient ephemeral streams

or infiltrated the soil. Sheet and channelized water flow out of the wetlands was observed during the winter and spring when soils were saturated.

3.5.2 Hydrology Post-treatment

Hydroperiods, or percent of time ponded, were calculated each year and for the growing season to determine differences in wetland hydrology between seeps and establish whether ponding frequency changed due to forest thinning. Soil saturation occurred when the water level was 30 cm below the soil surface or closer. Soil saturation was calculated annually and seasonally (Table 5). Annual precipitation varied, with 2010, 2012, 2014, and 2016 below the 30-year average while the remaining years were above average (Fig. 8). The growing seasons of 2012 and 2014 were particularly dry, resulting in no ponding during the growing season in any of the seeps. Wetter years (2011, 2013, 2017, 2018, and 2019) resulted in longer hydroperiods and saturated soil conditions in all wetlands for annual and growing season periods.

Table 5

Wetland hydroperiods (% of time ponded) and periods of inundation (% of time soil is saturated) for annual and growing season periods in three wetland seeps.

Year	East Seep		Center Seep		West Seep	East Seep		Center Seep		West Seep		
-----% Ponded [†] -----					-----% Saturated [‡] -----							
	Annual	GS*	Annual	GS	Annual	GS	Annual	GS	Annual	GS	Annual	GS
2010	<i>32[◇]</i>	<i>6[◇]</i>	<i>41</i>	<i>7</i>	<i>45</i>	<i>11</i>	<i>45</i>	<i>21</i>	<i>50</i>	<i>30</i>	<i>45</i>	<i>31</i>
2011	<i>50</i>	<i>30</i>	<i>50</i>	<i>30</i>	<i>50</i>	<i>30</i>	<i>64</i>	<i>50</i>	<i>64</i>	<i>50</i>	<i>64</i>	<i>50</i>
2012	<i>nd</i>	<i>0</i>	<i>nd</i>	<i>0</i>	<i>nd</i>	<i>0</i>	<i>nd</i>	<i>0</i>	<i>nd</i>	<i>0</i>	<i>nd</i>	<i>0</i>
2013	<i>66</i>	<i>25</i>	<i>46</i>	<i>27</i>	<i>45</i>	<i>21</i>	<i>74</i>	<i>45</i>	<i>58</i>	<i>45</i>	<i>57</i>	<i>46</i>
2014	<i>28</i>	<i>0</i>	<i>44</i>	<i>0</i>	<i>34</i>	<i>0</i>	<i>51</i>	<i>31</i>	<i>60</i>	<i>46</i>	<i>57</i>	<i>22</i>
2015	<i>nd</i>	<i>21</i>	<i>nd</i>	<i>16</i>	<i>nd</i>	<i>12</i>	<i>nd</i>	<i>29</i>	<i>nd</i>	<i>31</i>	<i>nd</i>	<i>35</i>
2016	<i>nd</i>	<i>nd</i>	<i>nd</i>	<i>nd</i>	<i>nd</i>	<i>nd</i>	<i>nd</i>	<i>nd</i>	<i>nd</i>	<i>nd</i>	<i>nd</i>	<i>nd</i>
2017	<i>41</i>	<i>22</i>	<i>48</i>	<i>71</i>	<i>41</i>	<i>72</i>	<i>45</i>	<i>30</i>	<i>27</i>	<i>45</i>	<i>23</i>	<i>52</i>
2018	<i>32</i>	<i>34</i>	<i>61</i>	<i>73</i>	<i>37</i>	<i>60</i>	<i>59</i>	<i>62</i>	<i>31</i>	<i>47</i>	<i>20</i>	<i>48</i>
2019	<i>nd</i>	<i>71</i>	<i>nd</i>	<i>34</i>	<i>nd</i>	<i>45</i>	<i>nd</i>	<i>90</i>	<i>nd</i>	<i>54</i>	<i>nd</i>	<i>79</i>
†Percent of time that ponding conditions were present.												
‡Percent of time that soil was saturated 30 cm below the surface.												
*GS = Growing season: April 21 – October 17.												
◇Numbers in italics were calculated from manual measurements collected monthly; numbers in normal font were calculated from pressure transducer data that was logged on a 15-minute interval.												
nd = not enough data to determine.												

Understanding the effect of thinning on wetland hydrology was complicated by the relationship between precipitation events and quantity. All of the wetlands were ponded or saturated during the non-growing season. Growing season saturation levels correlated with annual precipitation ($r^2 = 0.53$ East, 0.67 Center, and 0.87 West) and growing season precipitation ($r^2 = 0.33$ East, 0.44 Center, and 0.54 West). During the pre-treatment period (2010–2011), ponding and soil saturation were similar in the three seeps. A dry winter and spring in 2012, followed by only 9.9 mm of rain in June (128.5 mm normal for June), led to the complete drying of all three seeps during that growing season. Above-normal precipitation in 2013 recharged all the seeps with ponding and soil saturation at levels similar to what was observed prior to 2012. Although thinning and debris dams were constructed in 2013 at the Center Seep, a hydrologic response was not observed, likely due to the high precipitation. Drier conditions in 2014 elicited an increased annual time of ponding and growing season soil saturation in the Center Seep over that seen in the East or West Seep. Similarly, the East Seep exhibited a substantial increase in soil saturation during the growing season after treatment in 2017, reaching levels above both the Center and West Seep. Unusually wet conditions in 2018 and 2019 contributed to a higher time of ponding and soil saturation in all seeps over previous years.

4. DISCUSSION

4.1 Orchids, Hydrology, Soils and Canopy

This study assessed practical management techniques in headwater acid seep wetlands and their impacts on declining populations of the federally threatened *Platanthera integrilabia*. Long-term monitoring in the restoration sites revealed that orchid population size and floristic richness increased significantly following the reduction of 12.1–14.9% canopy, the shrub layer to less than 10%, and installation of debris dams. These actions enhanced water retention, which resulted in increased inundation and soil saturation, in turn benefiting the orchids and habitat.

Soils across the three wetlands were similar in structure and texture, and contained a fragipan horizon at 10–30 cm, restricting water movement and creating perched water tables (Hall et al., 2001; McDaniel et al., 2008). This was supported by tensiometer data indicating higher saturation at 30 cm than at deeper layers—despite minimal surface ponding. Tensiometers are sensitive instruments, effectively documenting soil saturation even when surface water is not evident (Karathanasis et al., 2003). Although visible surface ponding was largely absent during the growing season, tensiometer data confirmed soils were sufficiently saturated to support obligate and facultative wetland species. This seasonal drying explains the coexistence of both upland and wetland species in the seeps, as well as microsite topography and upland hummocks present within the seeps.

Pretreatment hydrologic characterization determined that wetlands were seasonal and ombrotrophic—primarily precipitation-fed, with evapotranspiration as the dominant water loss mechanism during the growing season. Data from wells and piezometers indicated substantial fluctuations in water levels across the year, suggesting limited groundwater influence. Typically, wetlands strongly connected to groundwater exhibit more stable hydroperiods (Thompson et al., 2007). Data from wells, piezometers, and isotopic analyses (Hoy, 2012) consistently indicated limited groundwater influence. Hoy (2012) revealed strong similarities ($r^2 = 0.92$) between the isotopic composition (deuterium and O^{18}) of precipitation and surface water in each wetland, reinforcing the conclusion that the hydrology is dominated by precipitation. Water budget calculations revealed that evapotranspiration accounted for approximately 58% of annual precipitation losses, with the remaining 42%

attributed to infiltration or surface runoff. This highlights the sensitivity of these wetlands to vegetation cover, as evapotranspiration plays a dominant role in regulating seasonal wetting and drying cycles.

Consequently, changes in canopy structure through tree removal could substantially influence hydrologic dynamics, particularly during the growing season. After canopy thinning, shrub layer reduction and debris dam installation, both the Center and East seeps experienced subtle increases in growing season ponding and soil saturation. However, all three seeps exhibited increased wetness during the study period due to frequent, higher precipitation, with three (2011, 2018, 2019) of Kentucky's five wettest recorded years (1895–2020) that occurred during this decade and annual rainfall averaging 188 mm above historical norms since 2011 (Runkle et al., 2022).

Silvicultural practices alter wetlands, typically decreasing evapotranspiration and increasing hydroperiods and nutrient fluxes (Sun et al., 2000; 2001; 2002; Amataya et al., 2006a, 2006b; Barton et al., 2008). Post-harvest hydroperiod increases in Carolina Bay wetlands resulted from reduced transpiration and infiltration due to soil compaction (Barton et al., 2008), with similar findings documented in northern Florida cypress-pine flatwoods (Sun et al., 2000).

However, wet conditions post-logging are often temporary. Woody plant invasion during dry periods can reduce hydroperiods and floristic quality (Mitsch and Gosselink, 1993; DeSteven, 1991; Warren et al., 2007; DeSteven et al., 2010; Martin and Kirkman, 2009; Stine et al., 2011). Post-logging hardwood encroachment likely contributed to orchid declines prior to management by increasing water demand and shading. Subsequent thinning and debris dams improved orchid and plant community conditions, but ongoing management remains essential to control hardwood resurgence. Maintaining prolonged hydroperiods may deter hardwood regeneration (Moser et al., 2012), and buffer from extremes in climate predicted, emphasizing their importance for long-term seep conservation.

4.2 Orchid demography, Associated Species and Habitat Restoration

Our results clearly indicate a marked improvement in *P. integrilabia* populations and reproductive success after canopy reductions of just 12–15%, to an average of 80% canopy cover, and reducing the shrub cover to < 10% but further studies are required to examine orchid populations under more open canopies (e.g., powerline right-of-ways with < 30% canopy) and to assess how increased herbaceous and shrub competition influences orchid recruitment. Unlike the findings of Boyd et al. (2016), our study found clear correlations between orchid population size and improved light and moisture conditions, suggesting the importance of active management. However, the reduction of woody competition in the herb and shrub layer may also be driving the trend of increased orchids with decreased canopy cover. Methods used for measuring canopy (densiometer and fish eye lense) likely underestimated canopy openness effects. Physical removal of seedlings significantly increased understory light levels beyond what was captured by these methods, but it was detected in the change in stratum percent cover estimations.

Vegetative orchid responses varied due to factors like microsite variability, competition, fungal interactions, and observational errors from difficult identification of vegetative leaves. Nonetheless, increased reproductive output and reduced flower abortion indicate demographic improvement. Improving vegetative orchid identification

methods and examining age-class demographics are important next steps to understand orchid demographic response to seedling recruitment.

Browsing of *P. integrilabia* by deer remained a significant threat post management. Fluctuations in browsing rates and herbivory by these ungulates are likely influenced by a variety of factors, including food availability, predation, disease and habitat changes. Browsing of woody plants and forest succession can also be influenced by deer, helping to maintain open habitats. Their role in the uplands can be viewed as a double edged sword, with negative impacts to palatable plants such as orchids and lilies, but positive effects of reducing woody vegetation contributing to maintenance of open habitats. Historically, migrating ungulates such as the functionally extinct American bison (*Bison bison*) that were known from this region would have had a direct impact on the development of grassland communities in the uplands of the Cumberland Plateau, including wetlands. Nonetheless, additional deer management strategies, whether through controlled hunting or habitat diversification at a landscape scale, are needed to continue recovering the orchids and their habitats.

Additionally, the decline in aborted orchids post management is notable, especially considering the large percentage of potential flowering populations ultimately aborting its stem. However, research is needed to fully understand the underlying causes of aborted flowers, with factors including climate and insect interactions, and their long-term implications for orchid viability.

4.3 Orchid habitat vegetation change

This is the first known study examining the vegetation responses to canopy and shrub layer reduction and debris dam installation specifically within headwater acid seeps containing *Platanthera integrilabia*. The overall trend towards more heliophytic and more hydrophytic vegetation is predictable with the increase in light availability and longer hydroperiod resulting from debris dams and reduced evapotranspiration of the wetland. Post management, species richness and floristic quality improved significantly, though this increase was moderated by the presence of both conservative and weedy species.

The recovery of other wetland orchids and rare and/conservative plants alongside *P. integrilabia* and the connections of the seep and adjacent upland communities supports the notion that this orchid can serve as a flagship species for wetland and grassland restoration in the Cumberland Plateau. Notably, the reappearance of the state endangered *Calopogon tuberosus* (S1/G5), after remaining dormant either through seed or corm for over 15 years, represents a major restoration success. The new arrival of the state threatened *Lobelia nuttallii* also is also a sign of habitat recovery. Seed from this short lived perennial most likely persisted in the seed bank and returned when conditions became favorable. *P. ciliaris* also increased post management, though not to the population sizes of *P. integrilabia*. *P. cristata* persisted through management but showed minimal increases in the restored sites. This orchid can tolerate and persist under lower light conditions compared to *P. integrilabia*, *P. ciliaris* or *C. tuberosus* as noted by its lower heliophytic index. *P. clavellata* also showed similar trends as *P. cristata*, with minimal increases post management due to greater shade tolerance and potential increased competition in the restored seeps. These conservation successes highlight the role of seed banks and vegetative persistence, and the urgent need to increase conservation action to open these habitats for these declining species.

The findings from this study suggest many rare species could take several years to respond to improvement habitat conditions, especially in hydrologically degraded or successional advanced wetlands, but within a

decade the recovery of the wetland and associated species as a whole is possible. However, management disturbance also introduced new invasive species challenges, emphasizing the need for continual monitoring and removal of species that can further degrade the habitats.

Prior to this study, the existing seep wetlands in the uplands of the Cumberland Plateau of Kentucky with *P. integrilabia* existed on opposite ends of a successional spectrum with some occurring in closed canopy forested seeps and others occurring in completely open seeps in powerlines (OKNP, 2024). These represent extremes in disturbance with one type having an artificially heavy anthropogenic disturbance by occasional bush-hogging and the other type having artificially little to no disturbance. There are records of more open seep vegetation persisting into the late 20th century in shortleaf pine grasslands of Kentucky's Cumberland Plateau, but they were poorly documented and are now rare to non-existent (Campbell et al., 1989; OKNP 2024). This study provides an example of seeps with a moderate level of disturbance, something that was likely much more common in the past with intact disturbance regimes when *P. integrilabia* was not as imperiled. These moderate disturbances were likely caused by a combination of animal browsing, windstorm damage and tree tip up mounds, or fire on the landscape.

4.4 Managing Wetlands as Dynamic, integrated systems

Effective wetland restoration requires integrating hydrologic management, vegetation dynamics and natural disturbance analogues. The decline of *P. integrilabia* in the undisturbed West seep contrasts sharply with the dramatic increase in managed seeps, reinforcing the importance of periodic disturbance in preventing successional canopy closure and maintaining wetland conditions. Given that the West seep had remained undisturbed for over 50 years—compared to the 25 + years post-logging disturbance of the East and Center seeps—this suggests that periodic disturbance may be necessary to maintain conditions favorable for orchid flowering. Historical disturbances such as fire, animal activity, and storm events are critical for maintaining favorable wetland conditions. Mimicking these disturbances through targeted canopy thinning, prescribed fire, or debris dam installation remains essential for long-term orchid conservation. The study revealed a potential connectivity between upland and wetland processes. Adjacent upland conditions have the potential to influence light conditions, hydrology, orchid viability and floristic composition of the wetlands. Future research focusing on the role of prescribed fire as a tool to manage both the upland forest and wetland communities and its impacts on orchid viability is needed.

This research affirms that adaptive, disturbance-based management is essential in maintaining and restoring floristic biodiversity and orchid viability in headwater wetlands of the region. By implementing practical wetland management strategies, combined with ongoing monitoring for invasive species, this research contributes to conservation planning for this orchid and other rare orchids in similar habitats in the southeastern United States.

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

Tara Littlefield and Chris Barton contributed to the study conception and design. Orchid, floristic and in part canopy data preparation, data collection and analysis was performed by Tara Littlefield and hydrology and soils data preparation, data collection and analysis was performed by Chris Barton. The first draft of the manuscript was written by Tara Littlefield and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Figures

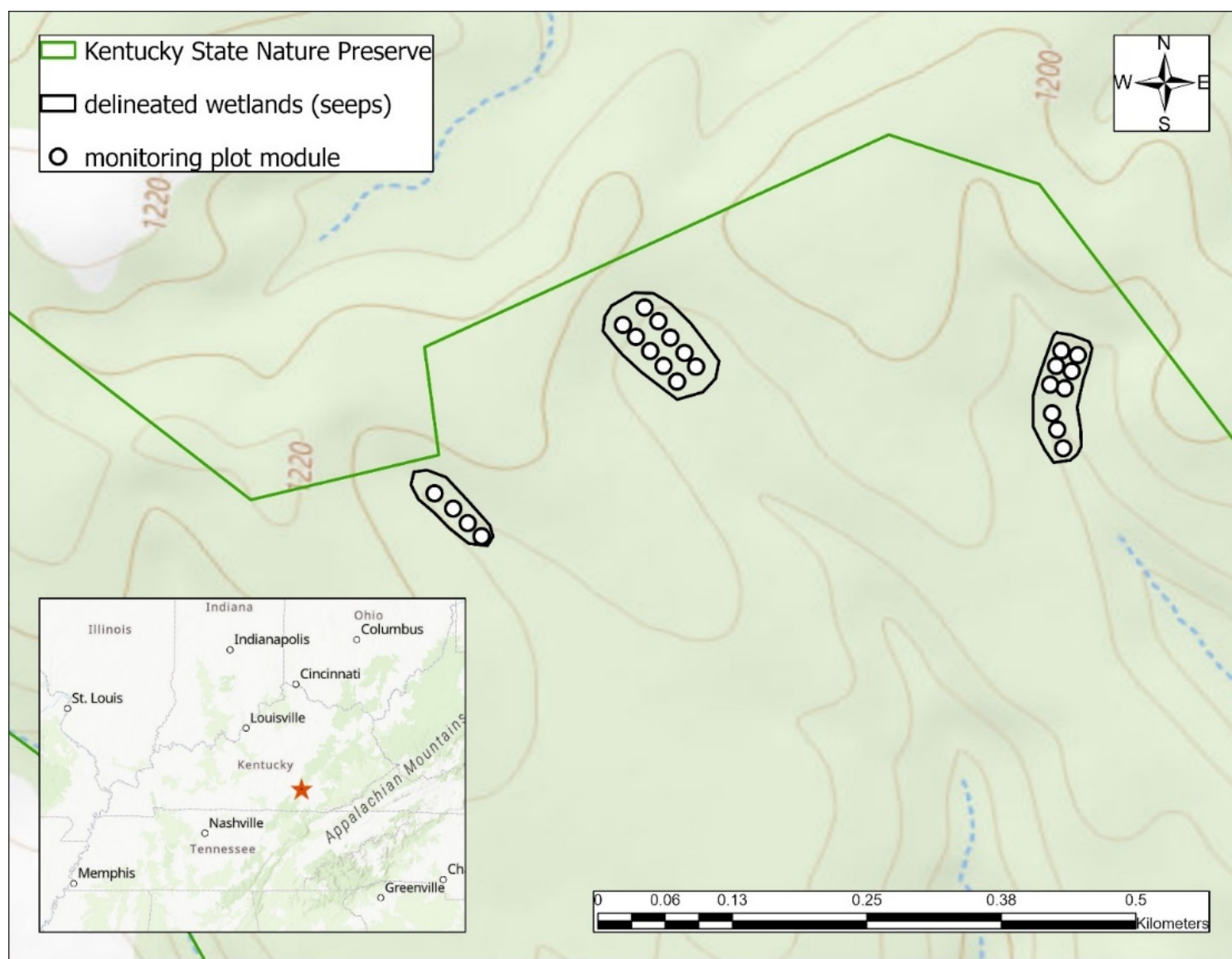


Figure 1

Map of the study site, with white dots representing the 23 permanent 10 × 10 m monitoring plots modules across the West, Center, and East seeps.



Figure 2

Debris dam in the lower portion of the Center seep.

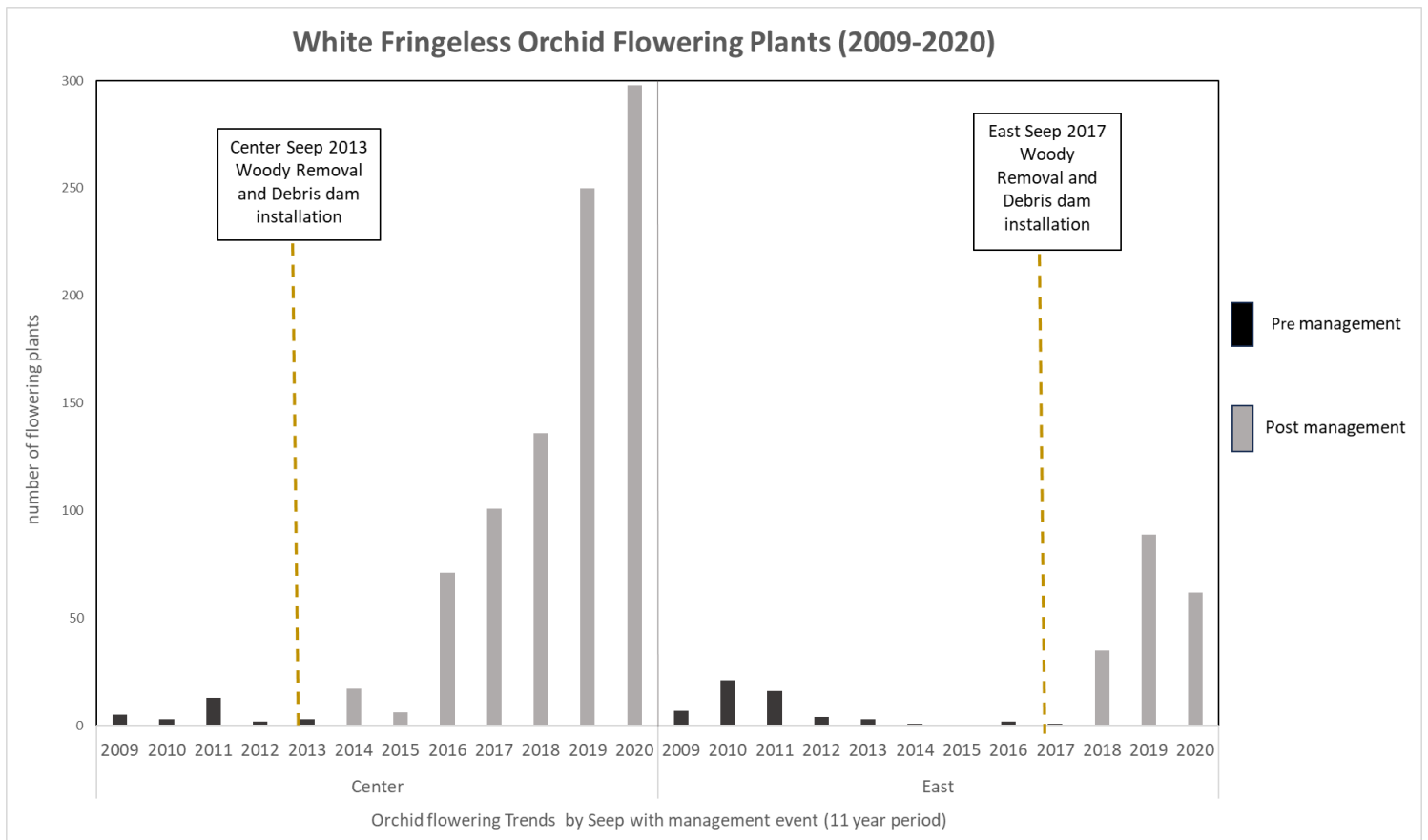


Figure 3

Platanthera integrilabia flowering plants (2009-2020) pre and post management.

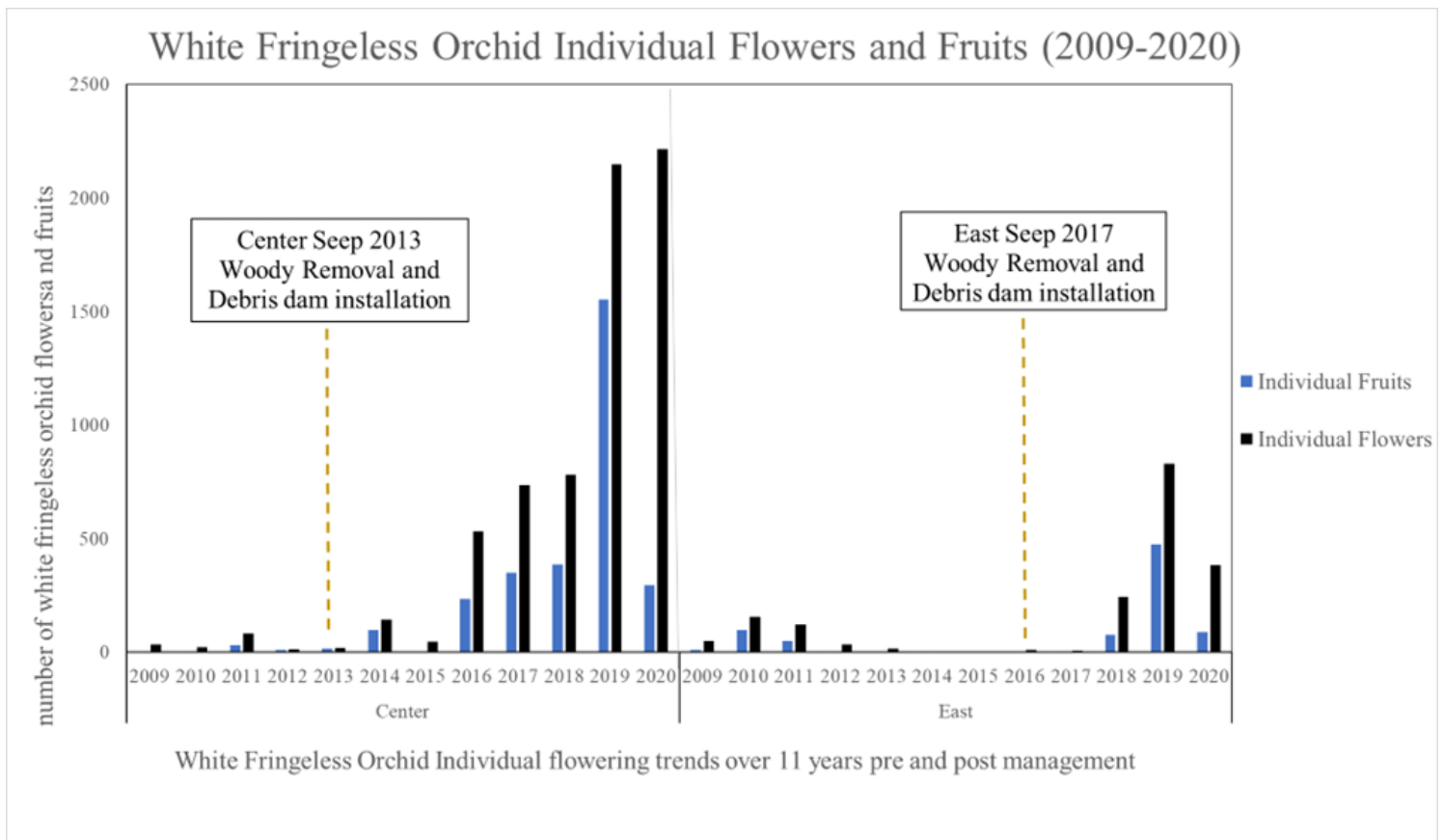


Figure 4

Platanthera integrilabii individual flowers and fruits (2009-2020) pre and post management.



Figure 5

Visual changes in canopy and vegetation structure from 2009-2020 in West, Center and East seeps.

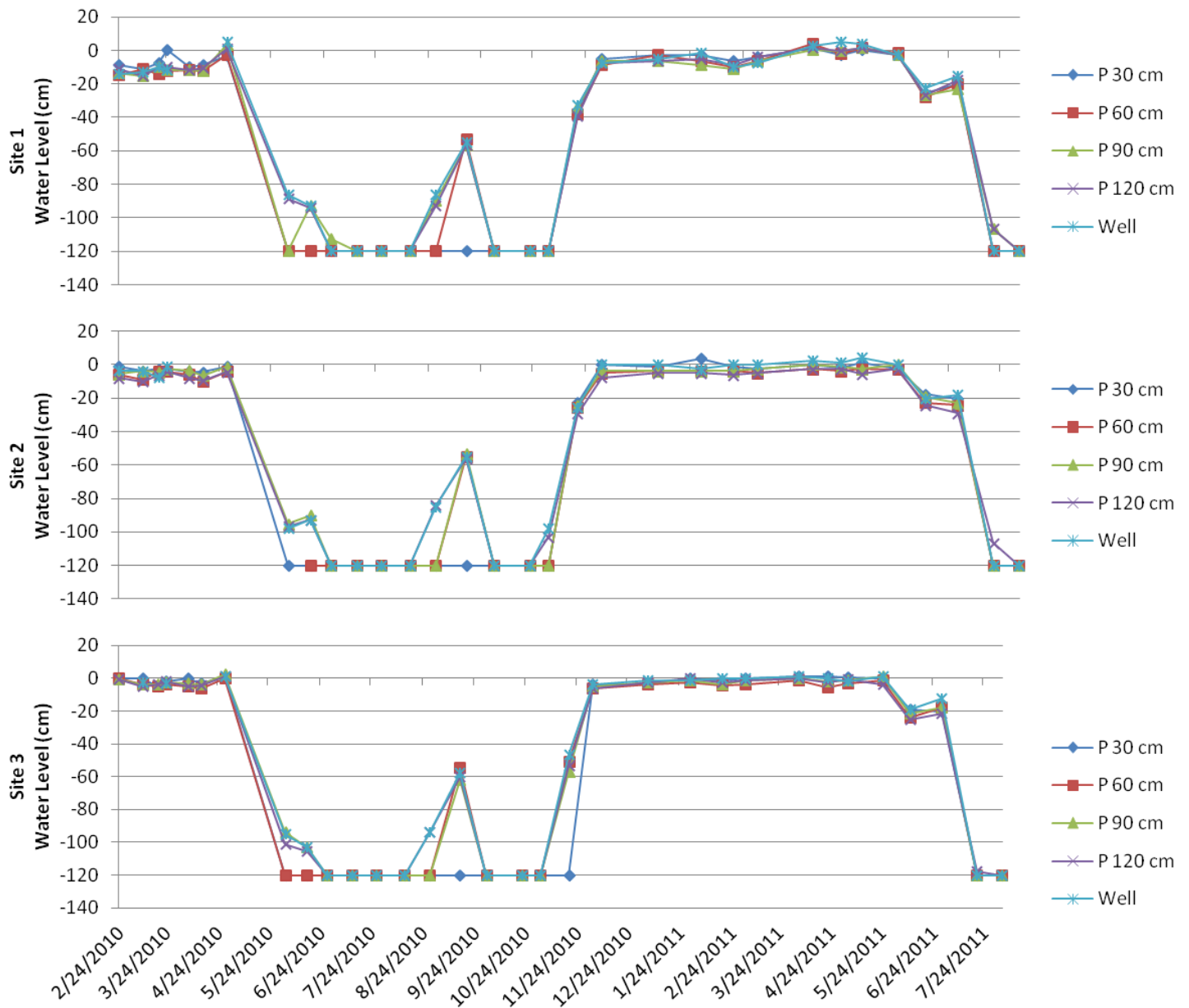


Figure 6

Manual piezometer and well readings from February 24, 2010 to August 4, 2011.

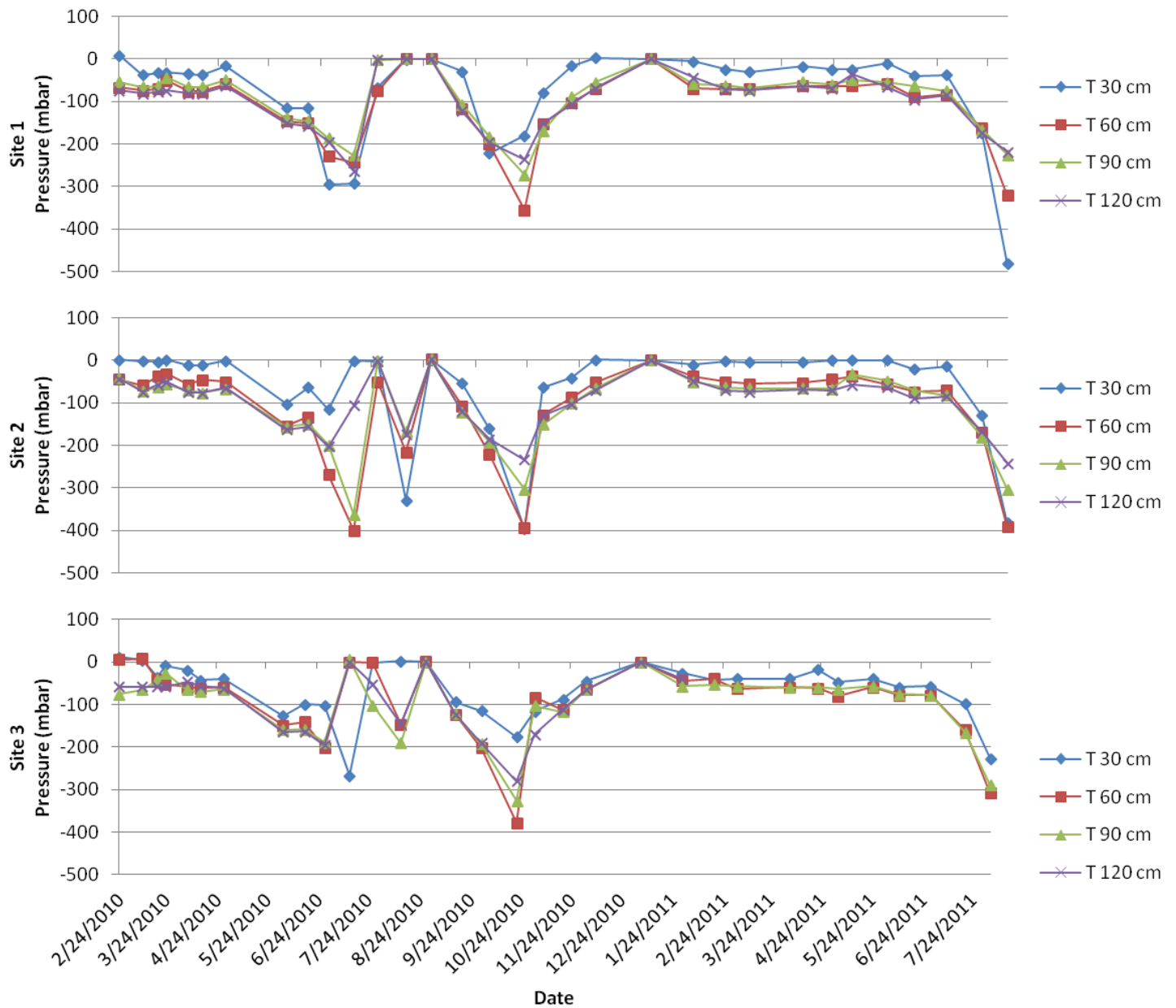


Figure 7

Tensiometer readings from February 24, 2010, to August 4, 2011.

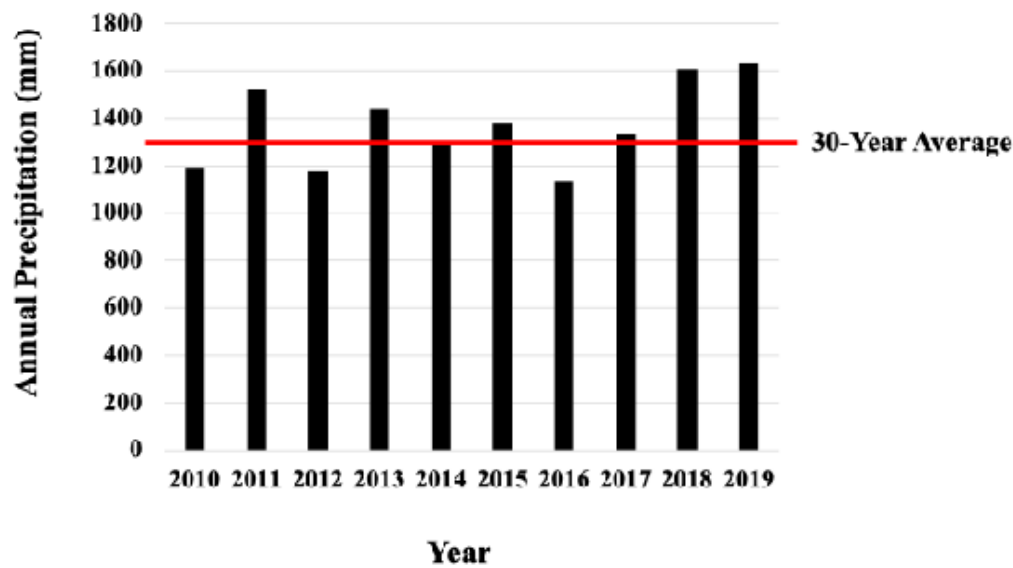


Figure 8

Annual precipitation from the London-Corbin, KY airport which is sixteen miles due east of the project location. Precipitation normal (1992-2021) is 1305 mm.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplimentalinfovegetationplotspecieslistperseepandyearLittlefield.xlsx](#)