

SEASONAL LIGHT RESPONSE CURVES OF *LIGUSTRUM SINENSE*: A TEST OF EXTENDED LEAF PHENOLOGY

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ABSTRACT

Chinese privet (*Ligustrum sinense*, hereafter: privet) is an invasive shrub common throughout the Eastern and Southeastern United States. The foremost concern of privet is its highly competitive nature; it displaces native plants, their associated pollinators, and wildlife communities. Extended leaf phenology (ELP) is an adaptation which allows understory plants in deciduous forests to take advantage of higher sunlight levels during the dormant season when canopy foliage is absent and has been associated with many invasive plant species. To measure the ELP potential of privet, we created light response curves for privet along two habitat types (forest edge and forest interior) using a gas exchange analyzer. Privet actively photosynthesized after native canopy leaf-off, and carbon assimilation rates did not differ between habitats. We observed habitat and seasonal variability in privet leaf shedding and leaf replacement with privet retaining leaves in both habitats throughout October 2019 to February 2020. Individuals along the forest edge shed leaves in November 2020, and privet in the interior habitat did not shed leaves until February 2021. Our results provide evidence of the competitive ELP potential of privet and suggest potential issues for planning winter foliar herbicide applications based on current management recommendations.

INTRODUCTION

Invasive species are an economic concern, costing more than \$26 billion per year since 2010 and totaling more than \$34 billion in the forest sector from 1960 to 2017 (Crystal-Ornelas and others 2021). They are also an ecological concern, wreaking havoc on native species abundance and diversity (Crystal-Ornelas and others 2021). Additionally, the horticulture industry's \$38 billion economic contribution in 2021 suggests an increase in the propagule pressure of many invasive plant species land managers try to control, such as privets (*Ligustrum*), silverberries (*Elaeagnus*), and Callery/Bradford pear (*Pyrus calleryana*), as well as many others (Beaury and others 2021, Wei and others 2023).

Chinese privet (*Ligustrum sinense*, hereafter: privet) is a common invasive shrub in the Eastern and Southeastern United States that is still sold worldwide in nurseries and online as a

hedgerow shrub for its attractive white flowers. The foremost concern about the invasion of privet is its ability to outcompete native plants for resources in the invaded range. Like many invasive plants, privet thrives in edge habitats where disturbances are common and light availability is high, such as roadsides and along stream systems or in depressions where moisture supply is abundant (Ward 2002). However, its high shade tolerance also allows it to live in deciduous hardwood understories and develop dense thickets that disrupt native species' growth and prevent tree regeneration (Merriam and Feil 2002), but it seldom invades upland evergreen conifer forests such as natural or plantation pine (*Pinus* spp.) stands (Tiller 2015).

Understanding the physiology of an invasive plant is vital to determine best management practices for control and eradication. Several hypotheses have been proposed to explain the relative success of nonnative plant species; for

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example, intermediate disturbance, empty niche, enemy release, and novel weapons (Callaway and Ridenour 2004, Eggeling 1947, Elton 1927, Grinnell 1917, Watt 1947). One such hypothesis unique to plants is extended leaf phenology (ELP). ELP is an adaptation of evergreen and semi-evergreen plants growing under the forest canopy, which allows them to take advantage of the absence of deciduous canopy foliage during their dormant season (Smith 2013, Smith and Hall 2016). While not unique to invasive plants, ELP allows them to gain carbon (C) through photosynthesis during what is traditionally the dormant season, giving these species an advantage over those that do not photosynthesize during this time. The measurement of C production of plants requires a measure of photosynthetic activity (Lazar 2003) and determining the seasonal change in photosynthetic rates throughout the year for invasive plants may indicate how these plants compete with native flora by acquiring C when the native overstory canopy is absent (Feng and others 2007).

The overall goal of this study was to understand the competitive ability of using ELP by privet to improve management recommendations. For example, further understanding privet's photosynthetic activity and physiological adaptations should allow land managers to plan herbicide applications seasonally to align with the time when the plants translocate resources via the phloem for foliar application or xylem for soil applications (Cobb and Reade 2010, Higgins and Richardson 2014). Our objectives were to 1) measure the photosynthetic activity of privet during the native deciduous dormant season (October through March), 2) compare light saturation points (LSP) and light concentration points (LCP) between interior and edge habitats containing privet, and 3) compare the monthly photosynthetic rate of privet as the canopy closes in the spring.

MATERIALS AND METHODS

Study Species

Privet is a member of the Oleaceae family and is native to southeast China, Taiwan, and Vietnam. There are several *Ligustrum* species in the

United States and the following is a description for *L. sinense*. It is a shrub or tree reaching average heights of 1.5 to 4.5 m but it can grow as tall as 9 m. The leaves are oppositely arranged approximately 2.5 cm along the stem and are evergreen or semideciduous. Leaf blades are elliptical with entire margins, up to 2.5 cm wide and 5 cm long. Flowers occur prolifically throughout the shrub in 5- to 10-cm-long panicles. Each flower has four white to off-white petals and two stamens attached to a fused petal that make up the corolla. A blue-black, berry-like fruit is formed from a single pistil (Kirkman and others 2007). While privet produces a large mast of berries that are consumed and spread primarily by birds, it also spreads by reproducing asexually via root sprouting (Wang and Grant 2012).

Study Area

We selected two sites within the Clemson Experimental Forest (CEF), a 7,082-ha multi-use forest for recreation, research, and timber management in upstate South Carolina. Historically, the land was used for cotton farming until land reclamation attempts occurred in 1934, when timber and kudzu were planted (Sorrells 1984). Both sites consisted of native deciduous forests with an actively spreading infestation of privet in the understory. Site 1 was in the New Hope (NH) Wildlife Management Area (WMA) and site 2 was in the Fant's Grove (FG) area of the CEF at the Butch Kennedy's Trail Head (fig. 1). Both sites were split into an understory (interior: >15 m from forest road or trail) and a forest edge (<15 m from road or trail) plot. The soil type for the interior NH was Pacelot, fine sandy loam, and Cecil clay loam for the exterior plots; the soil type for the FG area included Cecil, sandy loam for the interior and exterior sites (USDA NRCS 2020). The common overstory species at each location were oaks (*Quercus*), hickories (*Carya*), yellow-poplar (*Liriodendron tulipifera*), sweetgum (*Liquidambar styraciflua*), loblolly pine (*Pinus taeda*), and Virginia pine (*P. virginiana*). Midstory species included red maple (*Acer rubrum*), river birch (*Betula nigra*), American holly (*Ilex opaca*), and winged elm (*Ulmus alata*). Other invasive species at both sites included silverthorn (*Elaeagnus pungens*), chinaberry (*Melia azedarach*), Japanese honeysuckle (*Lonicera japonica*), sacred bamboo

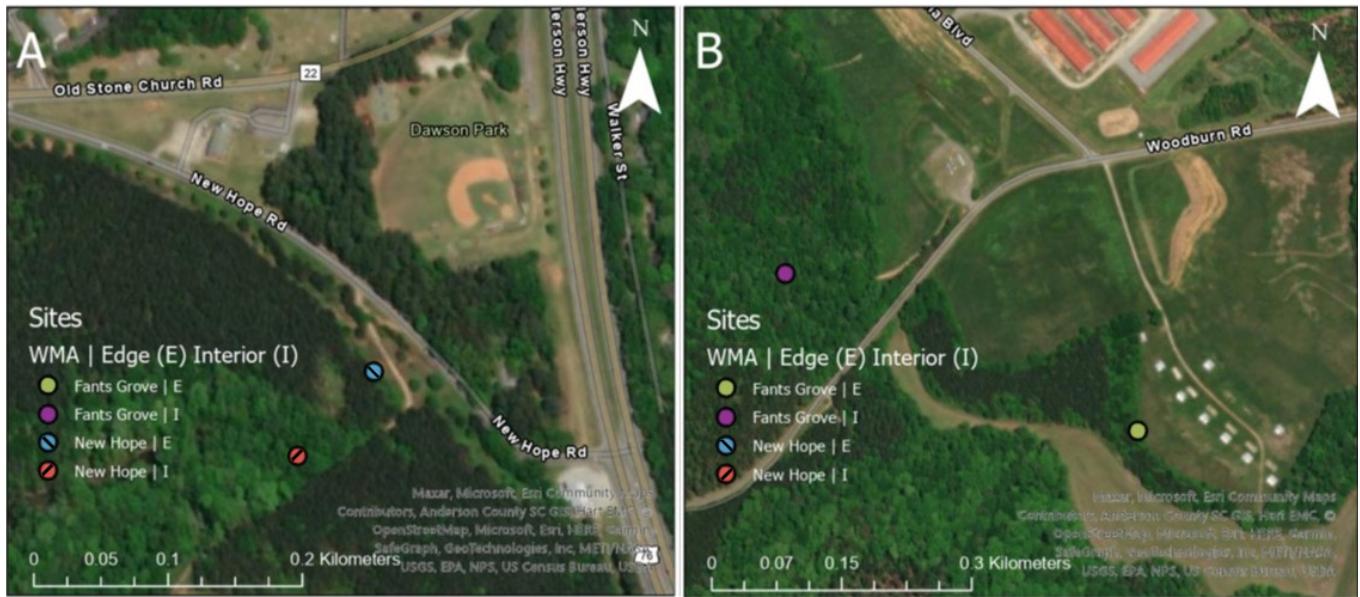


Figure 1—Site locations in the Clemson Experimental Forest of (a) New Hope (NH) and (b) Fant's Grove (FG) edge and interior habitats.

(*Nandina domestica*), and multiflora rose (*Rosa multiflora*).

Gas Exchange Measurements

Gas exchange was measured using the CIRAS-2 with the PLC cuvette attachment (P.P. Systems, Amesbury, MA). A total of six privet shrubs were selected at each site, three in the interior plot and three in the edge plot, with each shrub within a plot 10–20 m apart. The CIRAS-2, via the PLC-6U cuvette, was attached to an individual leaf, free of defects and securely attached to the stem, near the top of the canopy of each of the six shrubs per site once per month. For accurate measurements, and to prevent water damage to the equipment, gas exchange recordings were taken only on sunny days from November 2019 to January 2021. The cuvette, stabilized by a tripod, served to maintain a constant CO₂, temperature, and relative humidity around the leaf to standardize photosynthetic rate measurements (Lazar 2003). The selected leaf was acclimated for 2 minutes to the cuvette chamber conditions before measurement. The CIRAS-2 then measured the photosynthetic rate (P_N [μmol (CO₂) m⁻² s⁻¹]) at light transmittance levels [photosynthetic active radiation (PAR)] from high to low [2000, 1500, 1000, 500, 100, 50, 25, 0 μmol (photon) m⁻² s⁻¹] with an acclimation period of 60 seconds between recordings (Ralph and Gademann 2005). CO₂ was set as nonlimiting based on the atmospheric CO₂ levels at the time of

the study (410 ppm, NOAA 2019). Relative humidity was held constant at 50 percent and temperature was held constant at 25 °C.

Statistical Analysis

All analyses were conducted using R (version 4.3.0, R Core Team 2023). We fit light response curves using a nonrectangular hyperbola-based model (equation 1) (Marshall and Biscoe 1980).

$$P_N = \frac{\Phi_{(I_0)} \times PAR + P_{gmax} - \sqrt{(\Phi_{(I_0)} \times PAR + P_{gmax})^2 - 4\theta \times \Phi_{(I_0)} \times PAR \times P_{gmax}}}{2\theta} - R_D \quad (1)$$

where

P_N = net photosynthetic rate [μmol (CO₂) m⁻² s⁻¹]

$\Phi_{(I_0)}$ = quantum yield with irradiance equal to 0 [μmol (CO₂) μmol (photon)⁻¹]

PAR = photosynthetic active radiation [μmol (photon) m⁻² s⁻¹]

P_{gmax} = asymptotic estimate of the max gross photosynthetic rate [μmol (CO₂) m⁻² s⁻¹]

θ = convexity (dimensionless)

R_D = dark respiration rate [μmol (CO₂) m⁻² s⁻¹]

We confirmed that our data did not violate the assumptions of normality and equal variance using a Shapiro-Wilk test and equal variance F-test, respectively ($\alpha = 0.05$). We then compared curve coefficients from the nonrectangular

hyperbola-based model (equation 1) and individual light levels between sites and habitat (i.e., forest edge and forest interior), and among months using analysis of variance and Tukey's posthoc test for pairwise comparisons.

Unfortunately, data from November 2019 through September 2020 had to be removed from the analysis due to issues with the gas exchange analyzer needing to be calibrated and troubleshooting that throughout the study period. Continuous measurements were attempted from November 2019 to February 2020 on all samples because leaves were present and in good standing to be measured. However, we were unable to

have consistent measurements for an entire year to compare spring and summer photosynthetic activity with fall and winter.

RESULTS

There were significant differences in P_N between sites for interior habitats with NH having lower P_N than FG but no significant P_N difference between sites for the edge habitats in October 2020 ($F = 8.333$ and 0.021 ; $P = 0.006$ and 0.885 , respectively; fig. 2). We also saw a significant difference between sites for all interior plots with NH having lower P_N than FG ($F = 51.324$, $P < 0.001$). Thus, the sites were analyzed separately for individual PAR

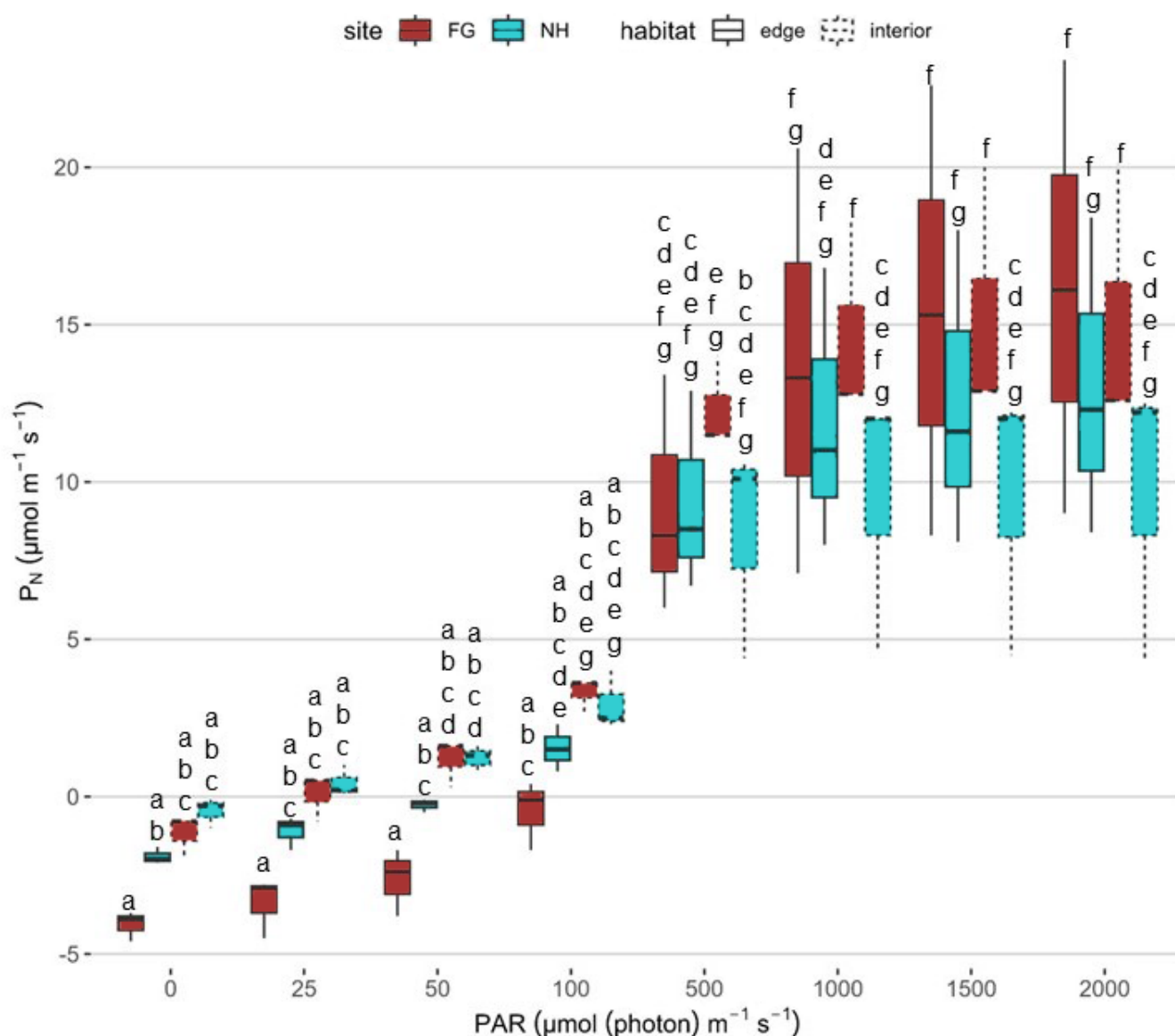


Figure 2—October 2020 light level comparisons of each site, New Hope (NH) and Fant's Grove (FG) for interior and edge habitat types. There was a significant difference among sites for interior habitat ($P = 0.006$) but no difference among sites for edge habitats ($P = 0.885$). Different letters represent significant differences with $\alpha = 0.05$.

[0–2000 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$] levels. When examining each PAR level for the NH site, P_N differed among months with October having greater P_N rates than December and January ($F = 3.051$, $P = 0.035$, fig. 3) and all others not significantly different. At the FG site, individual PAR level P_N did not differ among months ($F = 1.802$, $P = 0.176$, fig. 4).

The calculated curve coefficients using the nonrectangular hyperbola model (equation 1) showed no significant differences between sites or habitats for the month of October for LSP ($P_{g_{\text{max}}}$) ($F = 3.654$ and 2.254 ; $P = 0.088$ and 0.167 ,

respectively), LCP ($\phi_{(10)}$) ($F = 3.271$ and 1.965 ; $P = 0.104$ and 0.195 , respectively), curve convexity (θ) ($F = 0.081$ and 2.277 ; $P = 0.783$ and 0.166 , respectively). There was a significant difference in curve coefficients for dark respiration (R_d) with NH having a lower value than FG ($F = 12.625$, $P = 0.006$) and interior habitat having a lower value than edge habitat ($F = 31.096$, $P < 0.001$).

The interior habitat curve coefficient for LSP ($P_{g_{\text{max}}}$) had significant differences between sites with NH having a lower LSP value than the FG site ($F = 10.460$, $P = 0.005$) with no differences among months ($F = 0.236$, $P = 0.870$). There was

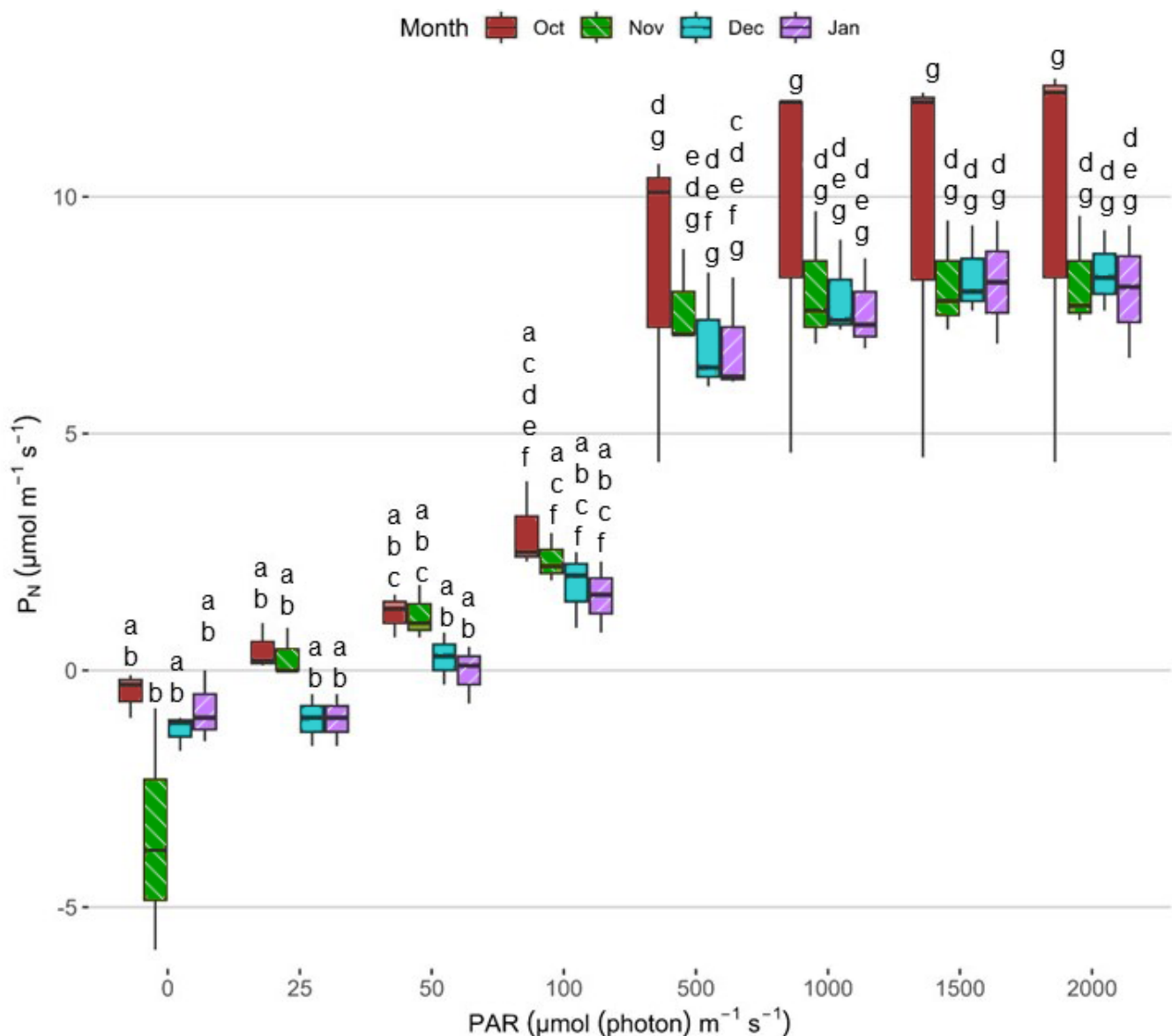


Figure 3—Light level comparison for New Hope (NH) interior habitats from October 2020 to January 2021. P_N rates were not significantly different other than between October and December ($P = 0.043$) and October and January ($P = 0.022$) with October having significantly higher P_N rates than December and January. Different letters denote significant differences with $\alpha = 0.05$.

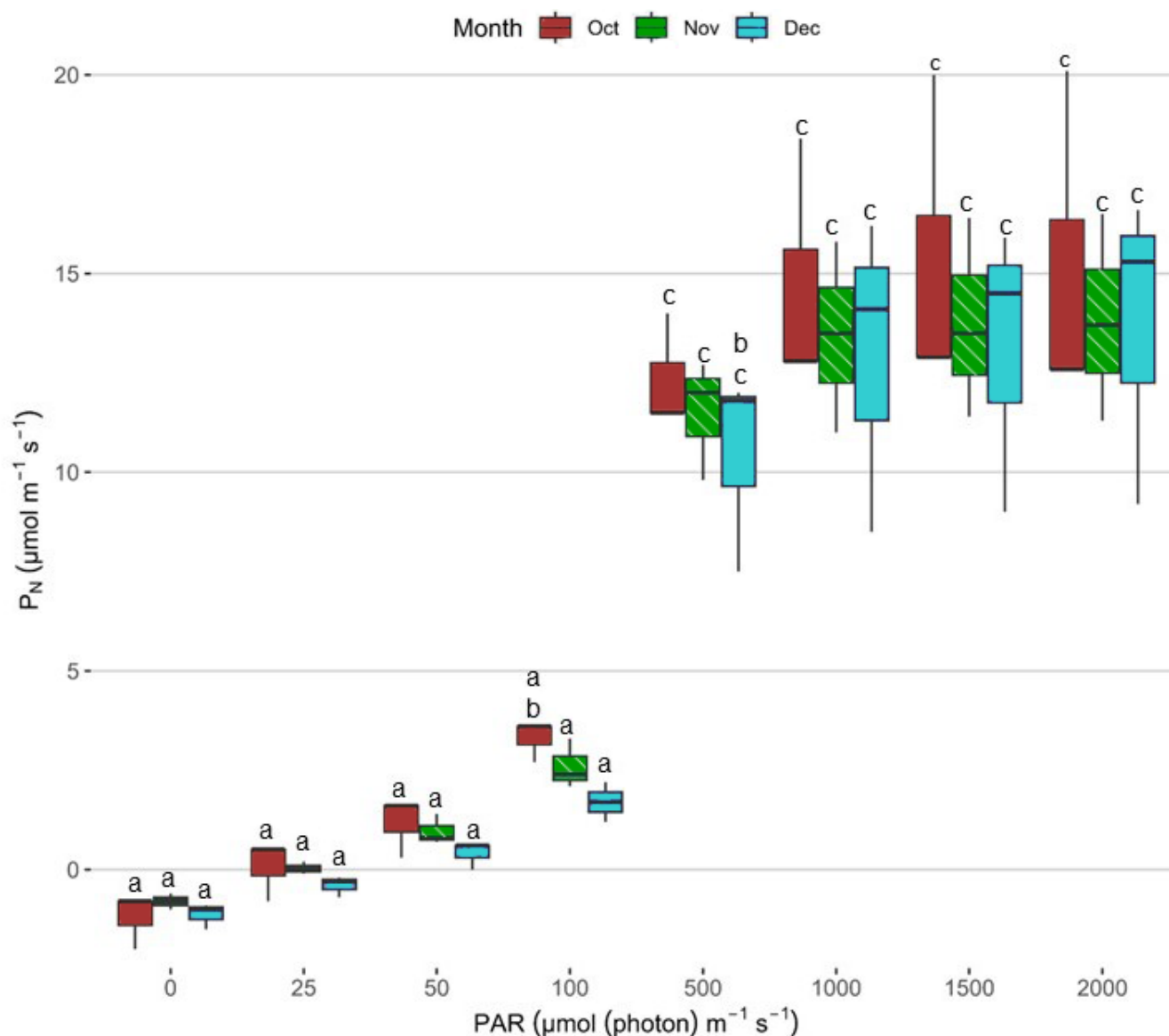


Figure 4—Light level comparison for Fant's Grove (FG) interior habitats from October 2020 to January 2021. P_N rates did not significantly differ among months ($P = 0.176$). Different letters denote significant differences with $\alpha = 0.05$.

no significant difference between sites or among months for LCP ($\phi_{(10)}$) ($F = 1.212$ and 1.970 ; $P = 0.287$ and 0.159 , respectively), curve convexity (θ) ($F = 3.399$ and 1.526 ; $P = 0.839$ and 0.246 , respectively), and dark respiration (R_p) ($F = 1.530$ and 1.236 ; $P = 0.0234$ and 0.330 , respectively).

In March 2020, leaf senescence and new leaf emergence occurred for all sites and habitats. Edge shrub leaf senescence occurred in November 2020, thus excluding data for this habitat from November 2020 through January 2021 and leaves were too small to measure in February 2021. The interior habitat leaves were in good standing until leaf senescence occurred in February 2021.

DISCUSSION

Our data provides evidence that privet actively photosynthesizes in the fall and winter months when the canopy is absent in deciduous forests. Photosynthetic rates continued in the FG sites as the winter progressed, and senescence eventually occurred in January. However, photosynthetic rates fell in December and January in the NH interior habitat until senescence occurred in February 2021. Still, any C assimilation occurring while most native species are dormant gives invasive plants a competitive advantage via ELP (Smith and Hall 2016). Privet seedling survival can occur at light levels as low as 1 to 5 percent

full sun but long-term survival is limited (Wang and Grant 2014). Winter photosynthesis would be significant to the success of privet as an invasive shrub and may explain why the species is more common in deciduous forests than in pine forests (Tiller 2015).

There was variability in when the plant was considered evergreen to semi-evergreen. Based on visual observations throughout the study in the winter of 2019–2020, privet was evergreen whereas in the winter of 2020–2021, all sampled privet were semi-evergreen, with the plants in the edge sites behaving more like deciduous species (i.e., most leaves dropped in November 2020). Species with the ability to adapt to various site characteristics will show differences in morphology, assimilation rates, and chemical production, which explains privet's ability to switch from evergreen to semi-evergreen based on environmental conditions (Fan and others 2019, Oduor and others 2016, Xiong and others 2021).

Seasonal variability in photosynthetic rates of semi-evergreen and evergreen species is expected (Rothstein and Zak 2001). Rothstein and Zak (2001) saw variability in photosynthesis and found limited growth in privet during canopy closure, while growth increased when the canopy opened. Photosynthetic rates depend on several factors, including water availability, temperature, and humidity, which cause the seasonal variability of assimilation rates. However, some species are better adapted to withstand the season's variability, allowing them to be highly competitive with deciduous species (Feng and others 2007). By having extended winter phenology (i.e., becoming semi-evergreen) or remaining evergreen during the entire winter, privet could accumulate a significant amount of carbon at a time when light is readily available due to the absence of canopy foliage given that air and soil temperatures are above freezing (Ensminger and others 2006).

Understanding the seasonal photosynthetic rates and morphological differences in privet can help determine management solutions for invaded ranges and sensitive ecosystems.

Current management recommendations for privet include broad-spectrum application of foliar glyphosate in the fall (late October to early November) after desirable plants have senesced (Enloe and others 2018). Foliar herbicides are transported throughout the plant via C assimilation, having a better understanding of photosynthetic capabilities during the winter aids in recommendations for application timing and chemical formulation and rate (Draber and others 1991, Tiaz and others 2015). Results from our study suggest the phenology of privet may vary from year to year, and close monitoring of phenology is warranted when foliar herbicide applications are prescribed as treatment. Glyphosate can kill nontarget native evergreen species that grow in the forest understory [e.g., American holly, Christmas fern (*Polystichum acrostichoides*)]. Attempting to control privet with native evergreen species present may complicate control efforts. Finally, a further understanding of the photosynthetic ability of privet may also assist in finding more targeted herbicides for its control.

CONCLUSIONS

This study could only complete measurements for part of the year, thus preventing comparisons of understory privet photosynthetic rates in open- versus closed-canopy conditions. However, the snapshot of information gathered during the project did show that privet actively photosynthesizes during canopy absence. Additionally, this study discovered a variability in leaf senescence from one year to the next, posing issues with current herbicide prescription recommendations for homeowners and land managers and reducing the economic impact of treating privet. This study can be further improved by adding more elements to data collection, including measuring the growth rate, soil water availability, precipitation, ambient air and soil temperature, and environmental light levels during the time of measurement. The scope of the study would also benefit by comparing photosynthetic rates of privet with native and invasive species at each site to better understand its competitive ability.

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