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Light attenuation by pawpaw (*Asimina triloba* L.) in a midwestern upland forest[1]

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Abstract. Pawpaw (*Asimina triloba* L. Dunal) occurs across a wide geographic range in eastern North America, forms clonal patches that can dominate the shrub/small-tree stratum, and has been associated with lower tree seedling density, survival, and growth, potentially due to light interception. However, relatively little research has been done on alteration of light regimes by shrubs in mesic forests compared with the impacts of overstory and understory trees, and there are no data on light attenuation by *A. triloba* on the basis of direct irradiance measurements. Photosynthetic photon flux density (PPFD) patterns were measured simultaneously above (3 m) and below (0.25 m) the *A. triloba* canopy in summer 2016 at eight locations along transects through each of eight patches of varying size and ramet/foliar density in an old-growth deciduous forest in west-central Indiana. Six-second readings across eight 14-hr sample days per patch were analyzed in numerous ways to quantify light regimes above and below the *A. triloba* canopies, to relate transmission to foliar density, and to compare PPFD levels inside patches with previous measurements in the surrounding understory. *A. triloba* patches in this system received $<$ 1.5% full sun (mean 22.0 μmol m^{-2} sec^{-1}) on the upper canopy and transmitted 40–50% overall. The result was very low mean daily PPFD irradiance near the ground on both sunny (9.3 μmol m^{-2} sec^{-1}) and cloudy (3.5 μmol m^{-2} sec^{-1}) days. Foliar density indices (leaf area index, leaf area volume) were mostly not correlated with percent transmission on the basis of mean or median PPFD on selected days with comparable open-site PPFD and wind conditions. Sunny days produced higher mean PPFD both above and below the canopy and more variable percent transmission than cloudy days, but overall mean percent transmission (41.5 *versus* 42.9%, respectively) did not differ with sky conditions. Sunfleck regimes near the ground were significantly reduced in terms of total daily fleck number (58% lower), total daily duration (67% lower), and total daily fluence (65% lower) compared with above the canopy. Mean daily below-canopy PPFD (9.0 μmol m^{-2} sec^{-1}) across all patches and sample days was approximately 45% lower than in the surrounding understory outside *A. triloba* patches (13.1 μmol m^{-2} sec^{-1}) measured in 2012. The results confirm that light attenuation by patches in this upland forest poses substantial challenges for leaf-level carbon gain by seedlings of most tree species, especially on cloudy days, and suggest that sunfleck utilization may be critical for seedling survival and growth overall.

Key words: clonal shrub, forest understory, photosynthetic photon flux, sunfleck

Shade-tolerant shrub and small-tree taxa play numerous roles in the understory of mesic, closed-canopy forests. They provide habitat structure and food for animals, they alter microclimates and resource availability above and below ground, and they compete with herbs, other shrubs, and juvenile trees (*e.g.*, Lei *et al*. 2002; Beckage *et al*. 2008; Jensen *et al*. 2011). Understory shrub taxa differ inherently in their stature, architecture, and clonality, and they also differ in their phenotypic plasticity in response to local environments (Nicola and Pickett 1983; Valladares *et al*. 2000). All shrubs intercept light transmitted through the overstory as a function of their shoot architecture, total leaf area, leaf orientations, and leaf optical properties. The impacts of clonal shrubs on light attenuation may grow over time as genets establish and spread, as ramets proliferate internally and become taller, and as total foliar area per unit ground area (leaf area index, LAI) or per unit volume (leaf area density, LAD) increases.

Considerable research has been done on light transmission through mesic forests (*e.g.*, Brown and Parker 1994; Canham and Burbank 1994; Lieffers *et al*. 1999; Messier *et al*. 1998; Montgomery and Chazdon 2001; Beaudet *et al*. 2004; Niinemets 2010). Some of this work has specifically emphasized the impacts of herbs or shrubs (George and Bazzaz 1999; Clinton 2003), but there has generally been a greater emphasis on attenuation by overstory and understory trees than by lower strata (Aubin *et al*. 2000; Montgomery

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2004). Numerous studies have examined the growth and architectural and physiological responses of understory shrubs to light (*e.g*., Pearcy and Yang 1996; Luken *et al*. 1997; Kawamura and Takeda 2004), but there has been comparatively little work on how temperate understory shrubs attenuate light except for the broadleaved evergreen *Rhododendron maximum* L. (Nilsen *et al*. 2001; Clinton 2003, Lei *et al*. 2006).

Pawpaw (*Asimina triloba* L Dunal.) is a native deciduous understory shrub/small tree that establishes distinctive clonal patches in temperate deciduous forests across much of the eastern USA. *Asimina triloba* has been shown through observation and experiment to be associated with lower densities of tree seedlings (Baumer and Runkle 2010). The general hypothesis is that it reduces tree seedling growth or survival through competition for light or other resources in ways analogous to the impact of *Rhododendron* (Nilsen *et al*. 2001, 2009; Lei *et al*. 2002; Beckage *et al*. 2008).

Asimina triloba leaves and buds are rarely consumed by white-tailed deer (*Odocoileus virginianus*), so its absolute and relative abundance can increase in forests with high deer densities as other shrubs, herbs, and juvenile trees are reduced by herbivory (Baumer and Runkle 2010; McGarvey *et al*. 2013; Slater and Anderson 2014). Deer may therefore inhibit forest regeneration not only directly by consumption but indirectly by favoring *A. triloba* and its resulting impacts on resource availability, especially light. Hochwender *et al*. (2016) have suggested that deer browsing selectivity plus *A. triloba*'s shade tolerance and clonal dominance potential may allow it to become a "recalcitrant" understory layer (*sensu* Royo and Carson 2006) and reduce juvenile tree success on a sustained basis. Other research has documented complex interactions among deer browsing, competition with native or invasive shrubs, and canopy disturbance on juvenile trees (Ward *et al*. 2018; Walters *et al*. 2020). These studies focused on shrub species other than *A. triloba*, but similar kinds of interactions could occur in browsed forests where *A. triloba* is well established.

Research at Allee Memorial Woods (AMW), an old-growth preserve in west-central Indiana, has shown very low densities of juvenile trees (defined here as seedlings and small saplings 0.25–1.0 m) in several mature and successional forest stands (Sipe and Yamulla 2021). Deer populations have increased in AMW and the surrounding region over the last 40+ yr. Controlled hunts conducted at two state parks within 25 km of AMW for more than 2 decades clearly demonstrated substantial impacts on tree seedling populations and herb/shrub biodiversity in mature forests similar in composition and structure to AMW (Jenkins *et al*. 2015).

Deer are likely not the only factor affecting juvenile tree populations at AMW, however. *Acer saccharum* L. (sugar maple) and *Fagus grandifolia* Ehrh. (American beech) have developed strong dominance of both the mid-sized (7.6–50.7-cm diameter at breast height [DBH]) and sapling (1 m tall to 7.6 cm DBH, hereafter 1 m–7.6 cm) strata in older stands across the last 50 yr (Sipe and Yamulla 2021) in a pattern consistent with the widespread transformation of the understory in eastern forests due to changing disturbance regimes (Nowacki and Abrams 2008). Photosynthetic photon flux density (PPFD) levels measured in the herb/tree seedling stratum (< 50 cm) in summer 2012 were very low and strongly related to the density of sugar maple and beech saplings (Sipe and Yamulla 2021). These previous PPFD measurements were intentionally done outside *A. triloba* patches to focus specifically on sapling density impacts.

There are no published data for PPFD transmission through *A. triloba* canopies, so the primary objective of this study was to determine how patches affect PPFD patterns under nongap conditions and to speculate on the degree to which this may be contributing to regeneration limitation at AMW. Five attributes of PPFD patterns above *versus* below the *A. triloba* canopy were examined: (a) mean and median PPFD values, (b) percentile distributions, (c) percent transmission from above to below, (d) diurnal variation in (a) and (c), and (e) sunfleck regimes. The following specific questions were addressed by analyzing these patterns:

- What are the overall impacts of *A. triloba* foliage on PPFD patterns when measured across numerous patches under varying sky and wind conditions?
- Is there a significant relationship between PPFD attenuation and patch LAI or LAD when measured under comparable sky and wind conditions?
- How do *A. triloba* effects on PPFD patterns differ on sunny *versus* cloudy days?
- How do sunfleck regimes differ above and below the *A. triloba* canopy on sunny days?

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- How do PPFD levels below the *A. triloba* canopy compare with broader PPFD regimes measured previously outside the patches?

Materials and Methods. STUDY SITE. Allee Memorial Woods is an 80-ha preserved site containing old-growth areas (*sensu* Parker 1989) located (39.863°N, 87.280°W) near the boundary of the central hardwoods and forest–prairie ecoregions in west-central Indiana (Petty *et al.* 1961). Details about AMW physiography and history are reported in Sipe and Yamulla (2021). Climate data measured across 1991–2020 at the nearest National Weather Service station 46 km to the south of AMW show a mean annual temperature of 19.7 °C (monthly range 4.4–32.4 °C) and a mean total annual precipitation of 113.5 cm (monthly range 6.3–12.9 cm). The frost-free growing season averages approximately 188 days, April 19–October 13 (Indiana State Climate Office, 2022).

The *A. triloba* patches used in this study are located across three older AMW stands (A, B, C). Forest structure and composition measured during 2011–12 in permanent grids of 1.2 to 3.2 ha within the stands are described in detail in Sipe and Yamulla (2021). The overstories are dominated by varying proportions of *Quercus alba* L. (white oak), *Quercus rubra* L. (northern red oak), *Quercus velutina* Lam. (black oak), *Liriodendron tulipifera* L. (tulip poplar), *Ac. saccharum* L., and *F. grandifolia* Ehrh. Both the mid-sized (7.6–50.7 cm DBH) and sapling (1 m tall to 7.6 cm DBH, hereafter 1 m–7.6 cm) strata are dominated by *Ac. saccharum* and *F. grandifolia*. Very little canopy disturbance occurred in the three stands between 2012, when stand structure, composition, and understory PPFD outside *A. triloba* patches were measured, and 2016, when the patch PPFD patterns were quantified. Two other shrub species occur with varying frequency and abundance across AMW, *Lindera benzoin* L. (spicebush) and *Dirca palustris* L. (leatherwood). The herbaceous community is diverse and dense on the gorge slopes and bottoms, but considerably reduced in the uplands. Invasive herb and shrub species are relatively uncommon across the preserve, especially in the upland stands.

PATCH CHARACTERISTICS. Stands A, B, and C were surveyed to identify all *A. triloba* patches in or near the permanent study grids, and eight patches were selected for further study in undisturbed upland locations. The goal was to include intact patches showing wide variation in in foliar height, patch area, and ramet and foliar densities (T. Sipe in press). The eight patches have distinctive boundaries and are isolated from other patches. The patches show important differences relevant to their potential impacts on PPFD attenuation. Ramet density ranges from 1.7 to 6.7 stems m^{-2}, maximum foliar height from 0.83 to 1.88 m, LAI from 0.42 to 1.28 m^2 m^{-2}, and LAD from 0.53 to 1.12 m^2 m^{-3}. These variables do not change in parallel across patches, however, which produces a greater diversity of patch foliar structures and potential impacts on PPFD attenuation.

A 2-m-wide belt transect was positioned through the center of each patch parallel to its longest axis and divided into contiguous 2 × 2 m quadrats placed 0–2, 2–4, 4–6 m, etc. on either side of the patch midline. Within each quadrat, the minimum and maximum foliar heights were measured and total leaf area (m^2) per quadrat was estimated using leaf area scaling relationships developed previously on the basis of counting leaf clusters projected over each 2 × 2 quadrat (T. Sipe in press). Leaf area index (m^2 m^{-2}) per quadrat was then calculated by dividing total leaf area by four and LAD (m^2 m^{-3}) was calculated by dividing total leaf area by the volume of space defined by the quadrat's 2 × 2 m footprint and its maximum and minimum foliar heights.

OPEN-SITE PPFD/WIND SPEED AND PATCH PPFD MEASUREMENTS. Photosynthetic photon flux density and wind speed were measured 2.5 m above ground in an open area outside AMW approximately 1 km from the *A. triloba* patch locations during May 27–July 16, 2016, spanning the duration of PPFD measurements in *A. triloba* patches. A LI-190 quantum sensor (Li-Cor, Lincoln, NE) and three-cup anemometer (model 12012, R.M. Young, Traverse City, MI) were connected to a data logger (model 23X, Campbell Scientific, Logan, UT) programmed to read every 10 sec and store 1-min averages continuously during all daylight hours.

Incident PPFD above the *A. triloba* canopy (3 m) and transmitted PPFD near the ground (0.25 m) were measured simultaneously using two LI-190 quantum sensors mounted on rods extending 0.25 m from each of eight 5-cm-diameter polyvinyl chloride (PVC) towers affixed vertically to steel

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stakes and distributed along the 2-m-wide belt transects in patches. The 0.25-m sampling height was used because pawpaw foliage often occurs down to this level. Herb, other shrub, and seedling foliage were sparse to absent within the eight patches and thus had little impact on PPFD at 0.25 m. The horizontal distances between sensor towers differed among patches since eight towers were used in all cases but belt transect lengths varied by threefold (8–24 m).

All sensors were calibrated against a factory-certified LI-190 sensor before the field sampling. The 16 sensors in each patch were connected to two data loggers (model 21X, Campbell Scientific) that were programmed to read and store PPFD every 6 sec during 14-hr days (0600–2000 Central Standard Time) centered approximately around solar noon for at least 10 days to span a range of weather conditions. Only two patches could be measured simultaneously because of limited numbers of sensors (32) and data loggers (4). Therefore four pairs of patches were measured during successive periods of 10–14 days between May 30 (Julian 151) and July 15 (Julian 197) in 2016.

The open-site and *A. triloba* patch data were screened to identify data gaps due to sensor or data-logger problems. Eight full 14-hr days of measurements were identified per patch pair for which open-site data were complete. One-way parametric ANOVA was used to determine whether the four patch-pair sampling periods differed significantly for open-site weather variables to guide sample day selection for *A. triloba* patch PPFD analyses. Daily mean PPFD ($P = 0.012$), mean wind speed ($P = 0.018$), and median wind speed ($P = 0.032$) differed significantly overall across the four sampling periods, whereas median PPFD did not (Kruskal–Wallis one-way ANOVA, $P = 0.062$). Tukey pairwise comparisons for the first three variables showed that the second period (June 11–20) was both brighter and windier compared with the fourth period (July 3–12), whereas the first (May 31–June 9) and third (June 22–July 1) periods were intermediate.

PPFD Analysis. Photosynthetic photon flux density means and medians are both reported here because of the highly skewed nature of understory irradiance regimes caused both by long periods of low PPFD in morning and evening and by sunflecks. Interpretations of PPFD regimes on the basis of means alone may overestimate photosynthetically usable photons while simultaneously underrepresenting the extent and photosynthetic impact of shaded conditions.

Photosynthetic photon flux density readings above and below the *A. triloba* canopy were not combined for any analysis. Unless otherwise noted, “patch” refers to *A. triloba* patches, and “canopy” refers to *A. triloba* patch foliage. Several additional terms are used throughout the paper for different hierarchical levels of data averaging. “Sensor” calculations denote a statistic for an individual sensor across an entire individual sample day (*e.g.*, daily sensor mean or median). Patch values denote averages across all sensors at one of the measurement heights for either individual 6-sec readings or all-day sensor means. “Grand patch” values refer to statistics calculated across all sample days for a given patch, using the patch means or patch medians as inputs. Finally, the term “all-patch” is used for some analyses that involve descriptive statistics or inferential tests calculated across all patches for selected sample days. A “full sun” value of 2,000 μmol m^{-2} sec^{-1} has often been used as a referential constant for temperate latitudes, corresponding to incident PPFD in the open on a horizontal surface at solar noon on a clear day near summer solstice. Photosynthetic photon flux density values are sometimes expressed below as “percent full sun” using this 2,000 μmol m^{-2} sec^{-1} baseline. All statistical inference tests and percentile distributions were done with Sigmastat (v. 12.5, Systat, San Jose, CA) or SPSS (v. 27, IBM, Armonk, NY).

All Patches and Sample Days. For each patch, the grand patch mean, grand patch median, and their standard deviations were calculated separately above and below the canopy and presented in a single bar graph for comparison across the entire PPFD data set. Patch percent transmission values based on the patch means or medians were also calculated for each patch. All-patch descriptive statistics were then calculated across the eight patches for above-canopy PPFD, below-canopy PPFD, and percent transmission. Inference tests were not done for these variables to determine whether patches differed significantly since they were measured during periods with different sky and wind conditions. The data are presented because they collectively represent the strongest expression of the overall impact of pawpaw patches on near-ground PPFD levels across the

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Table 1. Daily statistics for open-site weather station photosynthetic photon flux density (PPFD; μmol m^{-2} sec^{-1}) and wind speed (m/s) during (a) the 4 days used for direct comparison of PPFD patterns across all eight patches and (b) the days used to contrast PPFD patterns under sunny *versus* cloudy conditions for four patches.

Julian date	Patches sampled	Mean PPFD	Median PPFD	Maximum PPFD	Minimum PPFD	Mean wind speed	Median wind speed
Direct comparison, similar conditions, all patches							
152	B8, C7	808	810	2,452	16	0.66	0.57
167	B9, C10	766	284	2,084	6	0.77	0.77
180	A1, C1	791	681	2,167	13	0.81	0.80
190	C2, C3	782	739	1,864	17	0.60	0.55
Sunny- *versus* cloudy-day contrast, four patches							
156	B8, C7 (cloudy)	217	114	1,294	12	0.71	0.39
160	B8, C7 (sunny)	1,142	1,323	2,140	10	0.52	0.44
184	A1, C1 (cloudy)	295	312	716	8	0.38	0.13
181	A1, C1 (sunny)	1,044	1,195	2,112	35	0.53	0.44

study site, even though all eight patches were not sampled simultaneously.

All Patches on Similar Individual Days. Weather differences among the four sampling periods constrained the ability to compare all eight patches directly and to relate PPFD patterns to *A. triloba* LAI and LAD. Therefore scatterplots of open-site daily PPFD *versus* daily wind speed for all 32 sample days (4 periods × 8 days/period) were examined to identify a set of days that would allow direct comparison of all patches. Four days (one per patch pair) with similar average light and wind conditions of intermediate magnitudes were identified (Table 1).

These PPFD data were analyzed several ways. First, within each patch, the daily sensor means were used to determine through paired t tests or Wilcoxon signed-rank tests whether above-canopy means or medians differed significantly from their respective below-canopy values ($N = 8$ sensors per height). Second, individual patch means at the two measurement heights were used to test for the overall difference in above- *versus* below-canopy PPFD across all patches ($N = 8$ patches). A paired t test was used for patch means and a Wilcoxon signed-rank test for patch medians since the latter were nonnormal and heteroscedastic. Third, Kruskal–Wallis one-way ANOVA was used to determine whether the eight patches differed among themselves in patch means or medians above or below the canopy (four separate tests, $N = 8$). Dunn's test was used for pairwise patch differences if the overall Kruskal–Wallis result was significant. Fourth, within-patch spatial variation was explored by plotting means and medians both above and below the canopy for all sensor towers in each patch.

Attenuation versus LAI and LAD across All Patches. The relationship between foliage density and PPFD transmission was explored at the whole-patch scale, rather than the finer 2 × 2 m quadrat scale, because of the complexity with which both direct and diffuse radiation interact with three-dimensional patch structure inside and outside the 2-m belt transect across the day. Patch percent transmission values calculated previously using patch means or medians were plotted against mean patch LAI and LAD values separately for all eight patches on the days with similar open-site PPFD and wind conditions. A linear regression was fit to each of the four scatterplots to determine whether there were predictable impacts of LAI or LAD on light attenuation.

Effects of Sunny versus Cloudy Skies on Patch Attenuation. Four days were identified that allowed direct comparison of the impacts of sunny *versus* cloudy conditions on PPFD patterns for four of the eight patches (A1, B8, C1, C7; Table 1). Sunny *versus* cloudy contrasts could not be made for the remaining four patches, since the second sampling period (patches B9, C10) did not include any sufficiently cloudy days, whereas the fourth period (patches C2, C3) did not include any sufficiently clear days. These sunny and cloudy designations are defined on the basis of mean daily PPFD and do not represent completely clear or overcast days, respectively.

The impacts of sky conditions were examined in numerous ways. First, the difference in average grand patch mean PPFD above *versus* below the *A. triloba* foliage was tested separately for sunny and cloudy days using paired t tests ($N = 4$), and the results were compared between sky conditions. Second, the difference in mean percent transmis-

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sion between sunny and cloudy days was tested directly using paired *t* tests ($N = 4$). Third, within each patch, PPFD differences above *versus* below the *A. triloba* foliage were examined with a paired *t* test or Wilcoxon test ($N = 8$) and the results were compared between sky conditions.

Finally, diurnal PPFD patterns were generated by (a) converting 6-sec means across sensors to 30-min means above and below the canopy within each patch, (b) calculating mean percent transmission for each of these half-hour intervals, and (c) plotting the resulting values *versus* time of day.

Sunfleck Regimes. Sunflecks were quantified above and below the canopy for the same four patches used for sunny- *versus* cloudy-day comparisons above. Within each patch, three of the eight sensors were selected at each height for which their mean daily PPFD values were closest to (a) the overall mean at that height, (b) the mean + 1 SD, and (c) the mean − 1 SD. The goal was to distribute the sampling across most of the PPFD range at each height in a consistent way across patches. For one patch (B8), the sensor daily means above the canopy were unusually bimodal, with no single sensor sufficiently close to the patch mean (32.1 μmol m^{-2} sec^{-1}). Therefore the closest sensors higher (55.0 μmol m^{-2} sec^{-1}) and lower (16.3 μmol m^{-2} sec^{-1}) than the mean were both included so their joint contribution to the overall patch mean would substitute for a single sensor. This yielded a total of 25 sensors for the sunfleck analyses (13 above, 12 below).

Sunflecks are usually identified as transient PPFD occurrences above a fixed threshold (*e.g.*, 50 μmol m^{-2} sec^{-1}). Defining the appropriate threshold is challenging given that the diffuse background at each understory location changes diurnally and can vary considerably within and across forest stands. The goal here was not to determine a "correct" sunfleck regime, but to contrast sunfleck patterns above *versus* below the canopy using appropriate fixed threshold(s) determined through careful examination of diurnal PPFD traces. Six-second PPFD readings were plotted *versus* time of day for each of the 25 sensors above and below the canopy, and the peak diffuse background at midday was estimated visually from the graph for each sensor in a manner similar to the procedure used by Brantley and Young (2009) to define thresholds for different plant communities. High and low estimates were averaged in a few cases where it was difficult to select a single value. The midday peak diffuse PPFD per sensor spanned 8.0–18.0 μmol m^{-2} sec^{-1} (overall mean 11.7, $N = 13$) above the canopy and 3.0–11.0 μmol m^{-2} sec^{-1} (mean 6.0, $N = 12$) below the canopy. A sunfleck threshold of 20 μmol m^{-2} sec^{-1} was then selected since it was sufficiently high for the brightest diffuse background above the canopy (18 μmol m^{-2} sec^{-1}) and represents ~ 1% full sun. Careful examination of the diurnal trace plots showed that a 20-μmol m^{-2} sec^{-1} threshold was a suitable compromise between a higher threshold, which would exclude too many distinctive fleck events, and a lower threshold, which would include too many minor PPFD transients above the diffuse background.

A sunfleck event was identified if 6-sec readings exceeded the 20-μmol m^{-2} sec^{-1} threshold for at least three measurements and ended when there were at least three successive readings below the threshold. Readings < 20 μmol m^{-2} sec^{-1} during the event were included so long as there were no more than two in a row.

Four variables were calculated for each fleck event, including the duration, mean PPFD, maximum PPFD, and fluence (mean PPFD × duration). Descriptive statistics were then calculated for these same four variables across all fleck events for that sensor on that day. The total number of fleck events, total daily fluence (mean PPFD × 14 hr × 3,600 sec/hr), total daily fleck duration (sum of all fleck-event durations), and total daily fleck fluence (sum of all fleck-event fluences) were also calculated for each sensor. Finally, the percentage of the day and the percentage of total fluence represented by all fleck events were calculated.

The analysis above was repeated for each of the 25 sensors. Means were calculated across the three (or four, for B8 above canopy) sensors per height per patch, yielding four data points above and below the patch canopies for statistical tests. Paired *t* tests (two-tailed, d.f. = 3) were used for each of the 10 variables above to determine whether and to what degree the *A. triloba* canopy significantly altered sunfleck regime components.

The 20-μmol m^{-2} sec^{-1} threshold is appropriate given the unusually low midday diffuse background peaks, and it is consistent with the PPFD patterns measured outside *A. triloba* patches across the site (Sipe and Yamulla 2021). However, it is nontrivially lower than the 50- to 100-μmol m^{-2} sec^{-1} range of values that have been used in some studies of forest understory sunfleck regimes

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(Nilsen *et al*. 2001; Brantley and Young 2009). To determine whether and how a higher threshold would affect the contrast in sunfleck regimes above *versus* below the *A. triloba* canopy, all the analyses described above were repeated for a fixed threshold of 40 µmol m^{-2} sec^{-1} (~ 2% full sun).

PPFD Comparison Inside versus Outside Patches. A key focus of this study is whether *A. triloba* canopies reduce incident PPFD for tree seedlings to levels below that in the surrounding understory outside *A. triloba* patches. This question was addressed by comparing extensive PPFD measurements at a height of 0.5 m outside *A. triloba* patches across all three stands in 2012 with values measured at 0.25 m below the *A. triloba* canopy in 2016.

Details concerning the 2012 sampling are in Sipe and Yamulla (2021) and are summarized here. Nine sensor arrays, including three arrays in each stand (A, B, C), were placed in upland areas outside *A. triloba* patches with no canopy gap influence. Each array included eight LI-190 sensors mounted on PVC stakes at 0.5 m inside a 14-m radius circle attached to a data logger, with two sensors randomly positioned within each 90° quadrant. One array was set up in each stand and PPFD was measured simultaneously in the three stands for 14 consecutive days (May 30–June 12). Readings were taken every 6 sec and 1-min means were recorded across 14-hr days. The arrays were then moved to a second location in each stand and measured as before (June 15–28), and this was repeated for a third set of arrays (June 30–July 13). Thus the entire 2012 data set included nine arrays (designated A1–A3, B1–B3, and C1–C3) with eight sensors each, measured across a total of 42 days.

Photosynthetic photon flux density percentile distributions were generated for the 2012 array data using the 1-min mean data values. For each array, the mean across the eight sensors was calculated for each minute during each sample day ($N = 840$). These means were then collated across the 14 sample days ($N = 11{,}760$ total) and percentiles were calculated for each array from the collated data. To make the temporal resolutions comparable between *A. triloba* patches and arrays, the below-canopy 6-sec means across sensors from the patch measurements were condensed to 1-min means for each day ($N = 840$). These condensed sets were collated across sample days for each patch ($N = 6{,}720$), and a percentile distribution was generated for each patch.

This percentile calculation process yielded similarly structured data sets for 1-min mean PPFD measurements in *A. triloba* patches and in the surrounding understory arrays across diverse sky and wind conditions. There were eight *A. triloba* patches with eight sensors each at 0.25 m measured over 8 days, nine arrays with eight sensors each measured at 0.5 m over 14 days, and the two data sets were measured on similar spatial scales (*i.e*., 14-m radius circular arrays *versus* 8- to 24-m patch transects) with the same instruments. Therefore the arrays and patch patterns were compared in two ways. First, PPFD percentile distributions were averaged across the nine arrays to produce a mean (± SD) percentile distribution for the arrays, and the eight *A. triloba* below-canopy distributions were averaged to produce a mean (± SD) distribution for the patches. Second, the 25th, 50th (median), 75th, 85th, and 95th percentiles were calculated for each data set, averaged (± SD) across all the arrays or patches, and graphed. Differences between the array and patch data were not tested statistically since they were measured in different years and at slightly different heights.

Results. Patterns across All Patches and Sample Days. All-patch mean PPFD calculated across all sensors, patches, and sample days was reduced by over half from above the *A. triloba* canopy (22.0 µmol m^{-2} sec^{-1}) to below the canopy (9.0 µmol m^{-2} sec^{-1}) and the difference was significant (paired *t* test: $t = 5.02$, $P = 0008$, d.f. $= 7$) (Fig. 1). All-patch mean PPFD was approximately 1% full sun above the canopy and less than 0.5% below the canopy. All-patch median PPFD values were approximately half that of means, the medians differed significantly on average above (9.3 µmol m^{-2} sec^{-1}) *versus* below (3.7 µmol m^{-2} sec^{-1}) the canopy overall (paired *t* test: $t = 9.96$, $P < 0.0001$, d.f. $= 7$), and they showed a slightly lower overall transmission percentage (average 40%, range 27–53%) compared with PPFD means (average 44%, range 28–96%).

Individual patch means above the canopy varied by 2.3-fold, from 15.8 to 36.0 µmol m^{-2} sec^{-1}, and were over twice the magnitude of patch means below the canopy, which showed even greater relative variation (5.2–15.2 µmol m^{-2} sec^{-1}, 2.6-

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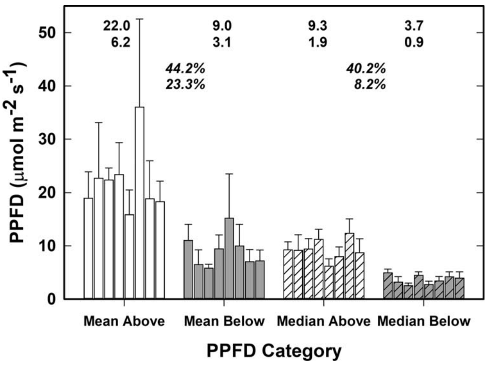

FIG. 1. Grand patch mean and median photosynthetic photon flux density (PPFD) above and below the *Asimina* canopy across all sample days for each patch (+ SD, $N = 7$–8 sensors per patch). The pairs of numbers above each of the four sets of bars are the all-patch mean and SD across the patches ($N = 8$) in that set. The italicized numbers are the all-patch mean and SD for percent transmission from above to below the canopy, calculated separately for patch means and patch medians. The bars represent (left to right) patches A1, B8, B9, C1, C2, C3, C7, and C10.

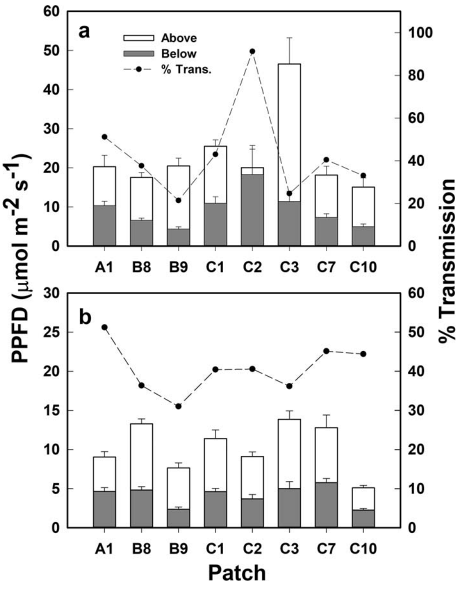

FIG. 2. Average (± 1 SE, $N = 7$–8 sensors per patch) patch mean (a) and patch median (b) photosynthetic photon flux density (PPFD) above and below the *A. triloba* canopy for all patches on selected days with similar mean daily open-site PPFD and wind speed. Percent transmission from above to below the canopy is also plotted. Note *y*-axis scale differences for means *versus* medians.

fold) (Fig. 1). Patch medians showed about the same relative variation among patches above (6.2–12.54 μmol m^{-2} sec^{-1}, 2.0-fold) and below (2.8–5.0 μmol m^{-2} sec^{-1}, 1.8-fold) the canopy.

ALL-PATCH COMPARISON ON DAYS WITH SIMILAR CONDITIONS. Average PPFD across all patches differed significantly above *versus* below the *A. triloba* canopy for both patch means (Wilcoxon signed-rank test: $z = -2.521$, d.f. = 7, $P = 0.008$) and patch medians (paired *t* test: d.f. = 7, $P < 0.0001$) (Fig. 2). The eight patches differed significantly from each other in above-canopy mean PPFD (Kruskal–Wallis $H = 23.23$, d.f. = 7, $P = 0.002$), below-canopy mean PPFD ($H = 23.65$, d.f. = 7, $P < 0.001$), above-canopy median PPFD ($H = 41.18$, d.f. = 7, $P < 0.001$), and below-canopy median PPFD ($H = 31.15$, d.f. = 7, $P < 0.001$).

Patch means above *versus* below the canopy differed significantly within every individual patch (paired *t* tests: $t = 4.3$–10.0, $P < 0.001$ to 0.004, d.f. = 7) except C2 (Wilcoxon signed-rank test, $z = -1.40$, $P = 0.195$), whereas patch medians differed above *versus* below in every patch (paired *t* tests: $t = 5.1$–11.0, $P < 0.001$ to 0.008, d.f. = 7). The transmission percentage averaged 43% (range 25–91%) for means and 41% (range 31–51%) for medians (Fig. 2).

Patches differed substantially in the degree and pattern of spatial variation among sensor locations (Fig. 3). There was more spatial variation in absolute terms above the canopy than below, both within and across patches, and this contrast was stronger for PPFD means than medians. Below values paralleled the above values in many patches (*e.g.*, B8) but not in others (*e.g.*, B9). Only two patches (B8, C7) showed complete separation of the mean and median data ranges, with no crossovers of above *versus* below means for any location. In contrast, four of the eight sensor towers in C2 showed mean PPFD below the canopy that was equal to or greater than mean PPFD above, which is consistent with its unusually high percent transmission for means (Fig. 2a). Patch C3 showed the highest incident PPFD overall, but it varied substantially across sensor locations.

ATTENUATION VERSUS FOLIAR DENSITY. Scatterplots of percent transmission *versus* average LAI or LAD across the eight patches were noisy, with a distinctive outlier (patch C3) (Fig. 4). Linear

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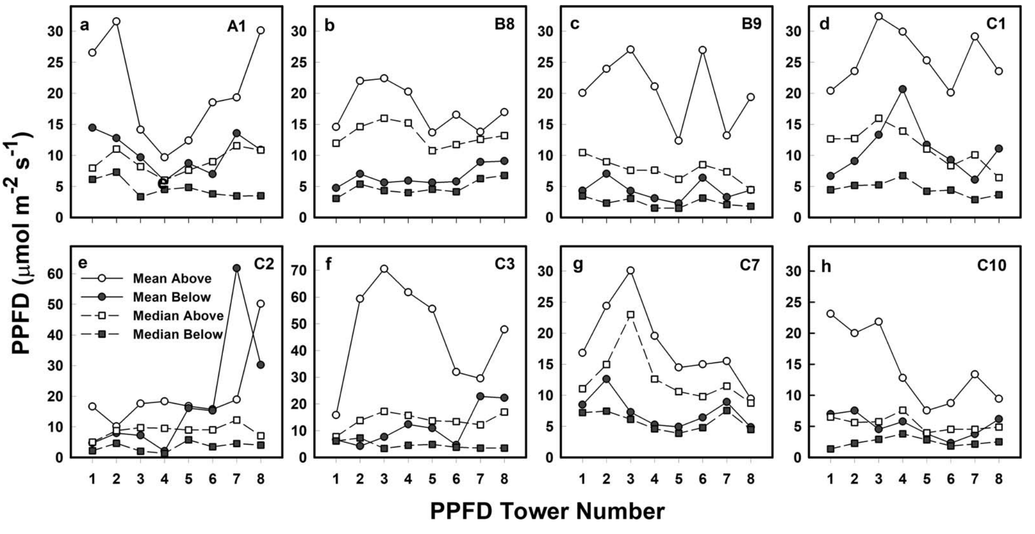

FIG. 3. Spatial variation among sensors ($N = 8$) within patches for patch mean photosynthetic photon flux density (PPFD; open symbols) and patch median PPFD (closed symbols) above (solid lines) and below (dashed lines) the *Asimina triloba* canopy, calculated for sample days with similar open-site daily mean PPFD and wind speed. Note different *y*-axis scales for patches C2 and C3 compared with the other patches.

regressions for percent transmission based on patch means were insignificant for both LAI ($P = 0.340$, $R^2 = 0.152$, d.f. = 1,7) and LAD ($P = 0.699$, $R^2 = 0.027$, d.f.= 1,7). Removing the C3 outlier improved the correlation for mean transmission, but the relationship was still insignificant ($P = 0.133$, $R^2 = 0.391$, d.f. = 1,7). Scatterplots based on patch medians were generally similar, except that C3 was no longer an outlier (Fig. 4b). The regression for percent transmission *versus* LAD was very insignificant ($P = 0.828$, $R^2 = 0.009$, d.f. = 1,7); however, percent transmission *versus* LAI showed a significant negative slope with a moderate correlation ($P = 0.030$, $R^2 = 0.570$, d.f. = 1,7).

EFFECTS OF SUNNY VERSUS CLOUDY SKIES. *Overall Patterns*. Comparing the four patches on sunny *versus* cloudy days produced both expected and unexpected results. The contrast between sky conditions was substantial for mean PPFD values, but much less so for median PPFD (Fig. 5). The average of the four patch means above the canopy (25.1 µmol m^{-2} sec^{-1}) was significantly greater than below the canopy (9.3 µmol m^{-2} sec^{-1}) on clear days (paired *t* test: $t = 4.26$, d.f. = 3, $P = 0.020$), but there was no difference on cloudy days (8.0 *versus* 3.5 µmol m^{-2} sec^{-1}; Wilcoxon signed-rank test: $z = 1.83$, d.f. = 3, $P = 0.125$). In contrast, the average of the four patch medians differed above *versus* below the canopy on both sunny days (paired *t* test: $t = 7.77$, d.f. = 3, $P = 0.004$) and cloudy days (paired *t* test: $t = 3.19$, d.f. = 3, $P = 0.050$).

Calculations of percentile distributions showed that 95% of the readings on cloudy days were < 20 µmol m^{-2} sec^{-1} above the canopy and < 10 µmol m^{-2} sec^{-1} below. Photosynthetic photon flux density means were higher on sunny days, as expected, but 65% of the readings above the canopy and 95% below were still < 10 µmol m^{-2} sec^{-1}.

Percent transmission ranged from 20% to 60% across all patches and days and showed no consistent contrasts, either between sky conditions or between means and medians (Fig. 5). Mean percent transmission across the four patches was nearly the same on sunny days (41.5%) *versus* cloudy days (42.9%), with somewhat higher patch-to-patch variation for sunny skies (SD = 10.5% *versus* 8.7%, respectively) As a result, average percent transmission across patches did not differ significantly between sunny *versus* cloudy days for either mean PPFD (paired *t* test: $t = 0.83$, d.f. = 3, $P = 0.467$) or median PPFD (paired *t* test: $t = 2.54$, d.f. = 3, $P = 0.085$). The four patches showed a similar pattern in the rank order of their transmission percentages for both sky conditions and for both means and medians.

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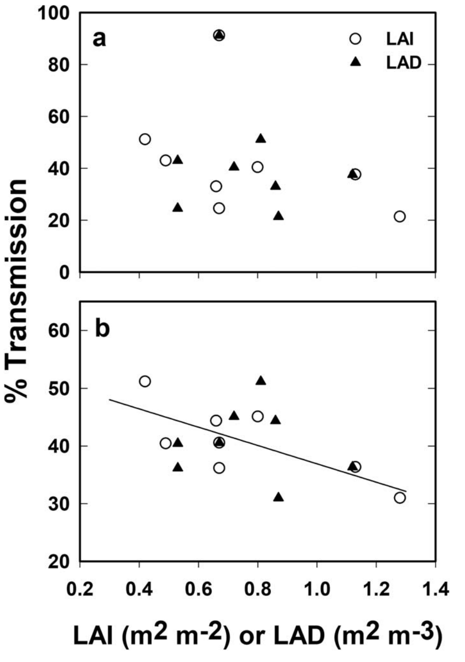

FIG. 4. Overall patch percent transmission plotted against patch leaf area index (LAI) or leaf area density (LAD) separately for patch means (a) and patch medians (b) on sample days with comparable open-site mean photosynthetic photon flux density and wind-speed conditions. Linear regressions were insignificant for all scatterplots except percent transmission of medians *versus* LAI in panel (b) ($P = 0.030$, $R^2 = 0.57$, d.f. = 1,7). The LAI and LAD values are nearly identical within two of the patches (overlapping symbols).

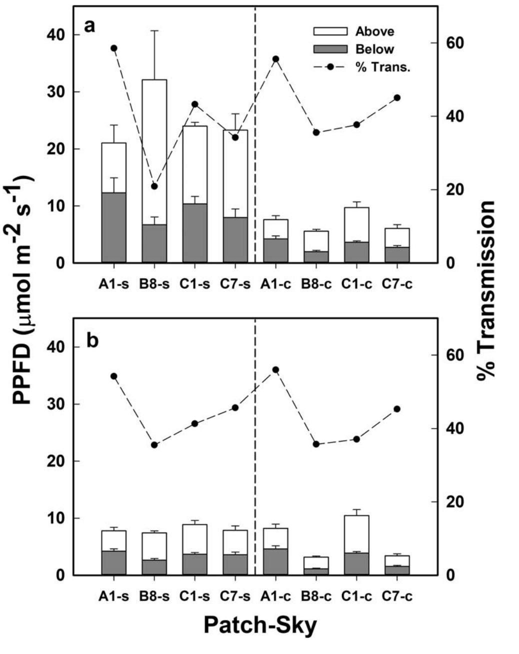

FIG. 5. Average (± 1 SE, $N = 8$ sensors per patch) mean (a) and median (b) photosynthetic photon flux density (PPFD) above and below the *A. triloba* canopy for four patches that could be contrasted on sunny days (left of the vertical dashed line) *versus* cloudy days (right of the dashed line). The percent transmission from above to below the canopy is also plotted for each patch.

Diurnal Variation. Mean PPFD both above and below the *A. triloba* canopy showed substantial variation over time on sunny days, particularly during midday hours, due to scattered cloud occurrence or to heterogenous overstory alteration of incident PPFD on the *A. triloba* canopy (Fig. 6). Patch-level percent transmission also fluctuated considerably in patterns that differed among patches and sample days. Cloudy days contrasted dramatically in these patterns, with very strong parallels for above and below means and nearly constant percent transmission between 30% and 40%.

SUNFLECK REGIMES. A total of 727 sunfleck events were identified across the 25 sensor days using a threshold of 20 μmol m^{-2} sec^{-1}, with more than twice as many ($N = 522$) above the canopy as below ($N = 205$). Locations below the canopy experience an average of 17 flecks per day that collectively represent 5.3% of the 14 daytime hours but 51% (0.253 mol day^{-1}) of the total daily fluence (Table 2). Statistics calculated across all recorded flecks below the canopy show that mean fleck duration is just over 2.5 min (155 sec), with an average of the mean PPFD within individual flecks of just 54.4 μmol m^{-2} sec^{-1} and an average of the maximum PPFD within individual flecks of 115 μmol m^{-2} sec^{-1}. Frequency distributions for these three variables below the canopy are skewed toward shorter, dimmer flecks, however, with 75% lasting less than 3.1 min and corresponding mean and maximum PPFDs of 57.5 and 122 μmol m^{-2} sec^{-1}, respectively.

For fleck-event statistics, only the average maximum duration ($P = 0.031$, 1.6-fold) and average maximum PPFD ($P = 0.021$, 1.9-fold) differed between sample heights (Table 2, upper half). The averages for fleck duration, mean PPFD, and fluence were also greater above the canopy by 9, 16, and 64%, respectively, but these differences were not significant. The means for all daily total variables were significantly greater above the canopy, as expected (Table 2, lower half). This occurred despite the modest sample size ($N = 4$)

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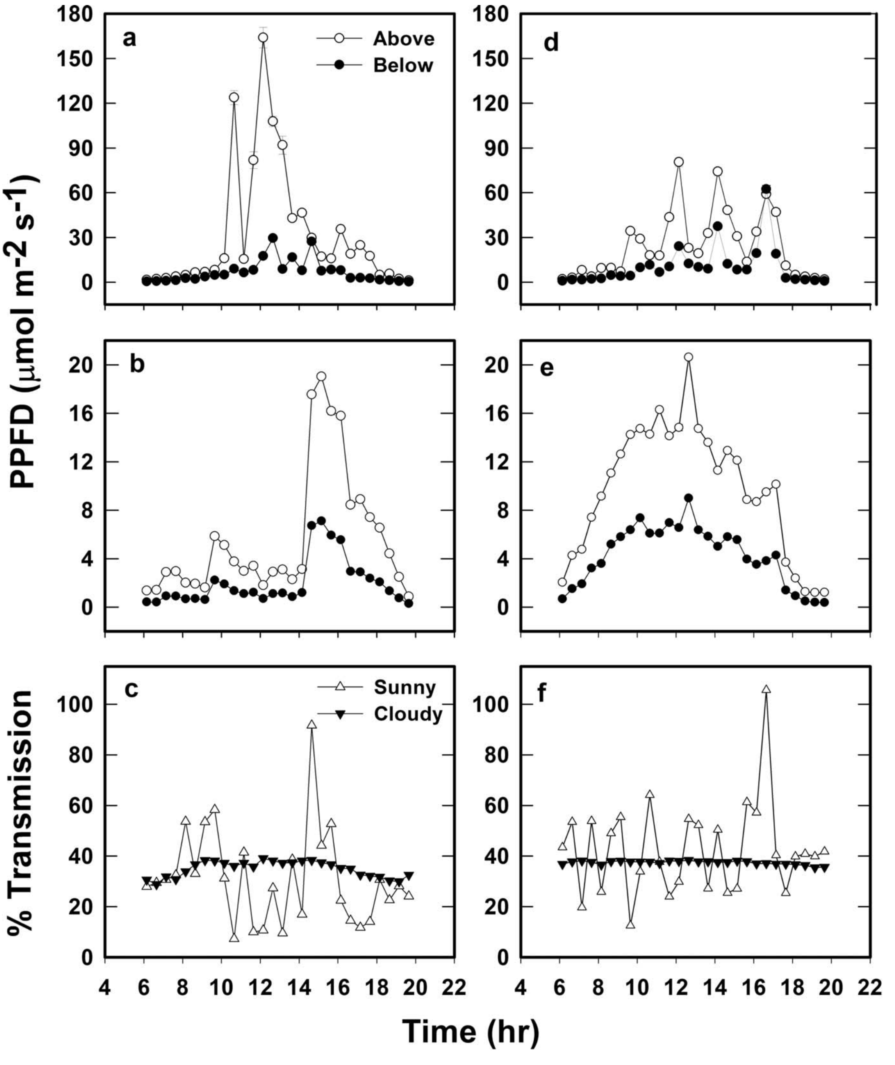

Fig. 6. Examples of diurnal time courses on sunny *versus* cloudy days for mean photosynthetic photon flux density (PPFD) above the canopy (open circles), below the canopy (closed circles), and for percent transmission (triangles). The input data are based on sensor averages calculated across half-hourly intervals, and the plotted data points are patch means across the eight sensors at each measurement height. Panels (a) through (c) correspond to patch B8 and panels (d) through (f) to patch C1. For each patch, the upper graph is for the sunny day, the middle graph is for the cloudy day, and the third shows percent transmission on both days. The diurnal patterns for patches A1 and C7 were similar to those presented here for C1 and B8, respectively.

because of the highly consistent pattern across individual patches. Every patch showed greater mean values above than below the canopy for all variables except mean fleck duration. The percentage of total daily fluence in flecks was 38% higher above the canopy, and the contrast for the remaining five variables ranged from 2.4-fold (mean number of flecks) to 3.8-fold (total fleck fluence). The same pattern of significant *versus* insignificant statistical test outcomes occurred for all 10 variables described above when the 40 μmol m^{-2} sec^{-1} sunfleck threshold was used instead of 20 mol m^{-2} sec^{-1} (data not shown).

PPFD Comparison Inside versus Outside *A. triloba* Patches. Mean PPFD below the *A. triloba* canopy was consistently lower by 31–45% than outside patches for both the mean and for all percentiles from the 25th to the 85th (Fig. 7). Only the 95th percentile appeared to show an

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Table 2. Descriptive statistics and paired *t* test results for sunflecks above and below the *A. triloba* canopy in four patches (A1, B8, C1, C7) on individual sunny days using a threshold of 20 μmol m^{-2} sec^{-1}. Each patch was represented by one input value, so $N = 4$ and d.f. = 3 in all cases. The eight input values were based on 727 total fleck events across the four patches (522 above, 205 below). Bold-faced *P* values are significant on the basis of two-tailed tests. One-tailed tests for mean duration, mean photosynthetic photon flux density (PPFD), and mean fluence of flecks produced the same outcomes. See Methods for explanations of data processing for individual fleck events and for aggregation to single patch-level input values used for calculations and tests below.

	Above	Below	Paired *t* test results	
	Mean ± 1 SD	Mean ± 1 SD	t	Two-tailed *P*
Fleck events				
Mean duration (sec)	188.2 ± 37.5	172.1 ± 48.5	0.63	0.573
Maximum duration (sec)	1070 ± 299	684 ± 241	3.85	**0.031**
Mean PPFD (μmol m^{-2} sec^{-1})	65.7 ± 21.3	56.5 ± 7.5	1.19	0.319
Maximum PPFD (μmol m^{-2} s^{-1})	407.1 ± 85.2	209.9 ± 63.2	4.48	**0.021**
Mean fluence (μmol m^{-2})	26,754 ± 11,577	16,355 ± 3,293	2.25	0.110
Daily totals				
Mean no. flecks	40.7 ± 6.5	17.1 ± 5.0	8.72	**0.003**
Total fleck duration (min)	135.6 ± 19.7	44.1 ± 9.7	15.90	< **0.001**
% day in flecks	16.1 ± 2.3	5.3 ± 1.2	15.89	< **0.001**
Total fluence (mol day^{-1})	1.265 ± 0.311	0.445 ± 0.080	4.23	**0.024**
Total fleck fluence (mol day^{-1})	0.964 ± 0.306	0.253 ± 0.045	4.09	**0.027**
% total fluence as flecks	70.7 ± 6.2	51.1 ± 3.4	9.47	**0.003**

insignificant difference, most likely due to the large variance around the below-canopy average. Mean PPFD was 0.45% full sun below the *A. triloba* foliage (9.0 μmol m^{-2} sec^{-1}) compared with 0.65% outside patches (13.1 μmol m^{-2} sec^{-1}), whereas medians were 0.25% (5.0 μmol m^{-2} sec^{-1}) and 0.48% (9.5 μmol m^{-2} sec^{-1}) full sun, respectively.

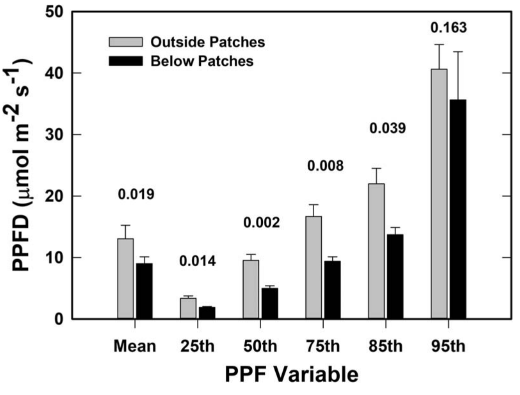

FIG. 7. Mean (± 1 SE) photosynthetic photon flux density (PPFD) at 0.25 m below *Asimina triloba* patch canopies in 2016 *versus* comparable statistics for PPFD measured at 0.5 m in sensor arrays outside *A. triloba* patches across stands A, B, and C in 2012. Variables include the PPFD mean and values corresponding to the 25th, 50th (median), 75th, 85th, and 95th percentiles. $N = 8$ for patches and $N = 9$ for the arrays.

Discussion. OVERALL PPFD LEVELS AND ATTENUATION. *Asimina triloba* patches of the size and foliar density typical of this mature upland forest significantly and substantially reduced available light in the lower 3 m by 50–60% to levels below 1% or even 0.5% full sun. This strong impact occurs in nearly all patches, across sunny and cloudy days, and holds across numerous categories of analysis.

Mean percent transmission varied considerably among patches on similar days and within patches under sunny skies. However, fairly consistent background attenuation levels were discernible within patches, especially on cloudy days but also on sunny days, where a baseline transmission level was overlain by higher and lower increases in response to direct beam dynamics. The background attenuation levels presumably correspond to the interception of diffuse radiation on both types of days.

Regressions of patch percent transmission using PPFD means or medians *versus* LAI or LAD produced negative relationships overall, but only median percent transmission *versus* LAI was significant. An inverse relationship between LAI/LAD and transmission is generally expected, but has not always been found since variation in leaf vertical distributions, orientations, and optical properties among taxa can influence interception by plant canopies with similar LAI (Pearcy *et al.*

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2005). The relationship is usually stronger under the diffuse conditions of cloudy skies because clear skies generate a complex interaction between solar movement (azimuth and elevation), the resulting solar beam path angles and lengths through the heterogeneous plant community, and the three-dimensional foliar structure closer to the point(s) of PPFD measurement. The 4 days used for testing this relationship across *A. triloba* patches at the AMW study site were chosen because of their similar mean daily PPFD, but they had variable cloud cover within and across days. The 2-m-wide belt transects were large enough to quantify patch LAI and LAD well, given the moderate sizes of most of the patches and thus the fraction of total patch area represented by the transects (mean = 22%, range = 6–31%). However, foliage both elsewhere inside and outside the transect would influence PPFD in a specific 2 × 2 m quadrat, particularly at the low 0.25-m measurement height. This lateral attenuation impact increases with patch stature and is more pronounced in morning or early evening because of lower solar path angles, especially under clear skies. A larger number of patches measured simultaneously under differing sky conditions would be required to determine with greater confidence the relationship between transmission and LAI/LAD for *A. triloba* patches.

Comparison with Other Studies of Shrub Impacts on Light. The few published papers reporting the effects of shrubs or small trees on understory PPFD patterns in temperate mesic forests differ considerably in their study systems, objectives, and methods, so direct comparison with *A. triloba* effects at AMW is challenging. The results of the present study are mostly applicable to undisturbed, mature forests on upland sites with moderate-quality soils. *Asimina triloba* can produce a much taller, denser, nearly monospecific stratum in moister, more fertile uplands, on lower slopes, or in bottomlands, particularly in sites that are younger successionally, have experienced canopy disturbance, or in which the mature overstory is dominated by less shade-tolerant species. This type of system is represented in controlled experiments by Cole and Weltzin (2005) on the competitive impacts of *A. triloba* on the invasive grass *Microstegium vimineum* (Trin.) A. Camus in a mixed-deciduous floodplain forest in eastern Tennessee. They measured PPFD with an integrating line sensor at 10 locations inside and outside each of three *A. triloba* patches on one clear day in mid-May to determine PPFD levels to use in the experiments. Photosynthetic photon flux density averaged 249 ± 132 μmol m^{-2} sec^{-1} outside patches and 15 ± 1 μmol m^{-2} s^{-1} inside patches, representing 6% transmission overall. The PPFD levels inside their patches are generally consistent with the AMW results, but their understory outside patches is brighter than at AMW by over an order of magnitude.

Nilsen *et al*. (2001) measured light and soil resources inside and outside areas with a 3- to 4-m-tall *R. maximum* L. subcanopy in a mature, mixed-deciduous forest dominated in the overstory by *Q. rubra* L. on a north-facing slope in western North Carolina. The motivation for their research was similar to that of the present study, which was to quantify the impact of the shrub canopy on juvenile tree performance. They measured PPFD at 0.5 m using fixed sensors over an extended period and with spatial arrays of eight sensors on single days. Total daily fluence inside and outside the *R. maximum* subcanopy averaged 0.729 and 0.141 mol m^{-2}, respectively, for an average transmission of 19.3%. Sunflecks, which they defined as PPFD occurrence above a threshold of 100 μmol m^{-2} sec^{-1}, averaged 18.3/day (total duration ∼ 3 hr) outside *R. maximum* and just 0.8/day inside (total duration ∼ 8 min). Average maximum daily PPFD measured by the fixed sensors and recorded as 10-min means generally ranged from 10 to 15 μmol m^{-2} sec^{-1} outside *R. maximum* and 2 to 4 μmol m^{-2} s^{-1} inside during the growing season (∼ 24% transmission). No information was provided on the structure of the *R. maximum* subcanopy in their site, but their PPFD results suggest important differences compared with *A. triloba* patches at AMW. Average patch transmission levels (∼ 35–45%) were about twice as high compared with the *R. maximum* subcanopy (∼ 18–24%), and total daily fluence below the *A. triloba* patches on sunny days was approximately three times greater than under *R. maximum* (0.445 *versus* 0.141 mol day^{-1}). Lei *et al*. (2006) extended the analysis of light regimes in the same study site, particularly through hemispherical photo analysis across seasons. They confirmed the very low mean PPFD levels inside *R. maximum* thickets and stressed the year-round impact of the evergreen foliage on tree seedling carbon gain, which contrasts with the seasonal influence of deciduous *A. triloba*.

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Aubin *et al*. (2000) measured percent open-site PPFD at several heights between 5 m and 0.05 m, calculated light extinction coefficients across the profile, and related extinction to vegetative cover by five shrub and herbaceous community components in six coniferous, deciduous, and mixed stands in the southern boreal forest of Quebec. The open-site PPFD averaged 15.3% (range 7.1–38.7) above the understory strata and 3.3% (range 0.8–6.6) below across the stands, both of which are considerably higher than for *A. triloba* patches at AMW. The most important connection between the studies is the impact of *Acer spicatum* Lam. (mountain maple) on light transmission in their system, which parallels *A. triloba*'s role at AMW. *Acer spicatum* typically produces multiple shoots from the base and has limited clonality (by lower branch layering). However, its structure and ecology are otherwise similar to *A. triloba* in several other ways, including shrub/small-tree variability in growth form, stature, plagiotropic branching and leaf orientation, overall shade tolerance, the ability to form dense thickets, the ability to respond quickly to canopy gaps, and its preference for fertile soils on slopes or stream bottoms. Aubin *et al*. (2000) concluded that *Ac. spicatum* played the dominant role in lower-strata light extinction in three of their six forest types. This is linked to the impact of *Ac. spicatum* on forest regeneration (Bourgeois *et al*. 2004; Raymond *et al*. 2018), a characteristic it also shares with *A. triloba* (Baumer and Runkle 2010).

Potential Impacts on Juvenile Trees and Regeneration Processes. Forest composition measurements in AMW during 2012 included seedling surveys and showed that seedling population densities were extremely low. A census of all seedlings in four height classes up to 1.0 m tall in 130 1 $\times$ 1 m plots distributed randomly across the three stands (24–72 per stand) showed only 1,088 total seedlings (83,692/ha), of which 76% were $<$ 10 cm tall and only 4 were $\geq$ 25 cm. The populations were very young (mean = 2.7 yr) and very small (mean = 8.4 cm tall) on average. Increased deer browsing had affected the juvenile tree populations by 2012, but it is likely that increasing abundance of *Ac. saccharum* and *F. grandifolia* in the sapling and mid-sized strata was also playing a role by attenuating light (Sipe and Yamulla 2021).

Asimina triloba patches appear to reduce near-ground light levels even further compared with PPFD measured under variable sapling densities outside patches, and this holds true for nearly the entire PPFD range. The overall difference between patch and array grand means is only 4.1 μmol m^{-2} sec^{-1} (9.0 *versus* 13.1, 31%), but the effects of this apparently small absolute reduction on juvenile tree survival may be magnified at such low PPFD levels overall and depend on species-specific photosynthetic efficiencies below 0.5% full sun, the ability to use sunflecks, or both.

There are no data on comparative seedling abundance, growth, or survival inside *versus* outside the *A. triloba* patches at AMW. The potential impact of PPFD attenuation by *A. triloba* can be explored by comparing published data on leaf-level photosynthetic light compensation points (LCPs) with below-patch PPFD values at AMW. Light compensation point is only one of many variables that affect survival in low light, but its role in leaf carbon economy makes it a key reference point for interpreting the consequences of understory PPFD measurements. Light compensation point data collated by Walters and Reich (1999) from experimental studies include 17 temperate tree species of varying shade tolerance, of which 16 are native to North America. The average LCP across these taxa is 10.5 μmol m^{-2} sec^{-1} (SD = 7.4, range 1.1–28.2). Nine of these species, including representatives from across the entire shade tolerance spectrum, had LCPs lower than the below-canopy mean PPFD at AMW not only for all patches on all days (9.0 μmol m^{-2} sec^{-1}) but also for four patches on sunny days (9.3 μmol m^{-2} sec^{-1}). These mean daily PPFD values mask the differing impacts of diffuse background light and sunflecks, however. The former show midday peaks averaging just 6.0 μmol m^{-2} sec^{-1} (range 3.0–11.0) across four patches on sunny days, and the diffuse levels are considerably lower than this most of the time. Only five of the 17 species had LCPs below the 6.0 μmol m^{-2} sec^{-1} midday diffuse mean, and even these species would show negative net photosynthesis much of the day.

Thus one of the key impacts of *A. triloba* patches on juvenile tree performance is to increase the importance of species responses to sunflecks for net daily carbon gain, as is also the case for *R. maximum* thickets (Lei *et al.* 2006; Nilsen *et al.* 2009). It is unclear whether the more common modest flecks or the rarer, longer-duration brighter flecks under the *A. triloba* canopy would produce

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greater contributions to total daily carbon gain by juvenile trees. The answer depends on species-specific sunfleck induction/induction loss dynamics and on fully induced saturation irradiances (which set the upper limit on photosynthetic conversion during flecks) in the field, for which considerably more research like that reported by Nilsen *et al*. (2009) is needed.

Impact of *A. triloba* versus Other Tree Species. The increasing dominance of *Ac. saccharum* and *F. grandifolia* at AMW in the sapling and mid-sized tree strata over the last 50 yr represents an altered competitive environment not only for juvenile trees but for shrub and herb taxa as well, including *A. triloba*. Selective logging at AMW during 1890–1920 opened up stands A and C and likely favored some *A. triloba* expansion along with enhanced regeneration of many tree taxa. However, substantial losses of saplings of nearly all tree taxa have occurred since 1960 for many species in stands B and C during a time when both *Ac. saccharum* and *F. grandifolia* have increased their dominance (Sipe and Yamulla 2021). The small-tree losses include major reductions in three shade-tolerant understory species: *Carpinus caroliniana* Walt. (American hornbeam), *Cornus florida* L. (flowering dogwood), and *Ostrya virginiana* (Mill.) K. Koch. (ironwood). Some of the decline for *Co. florida* may be due to disease (dogwood anthracnose, *Discula destructiva* Redlin), but the simultaneous losses of *Ca. caroliniana* and *O. virginiana* suggest an impact of increasing shade caused by *Ac. saccharum* and *F. grandifolia*. There is no reason to suspect that *A. triloba* has not been affected as well.

Daily mean incident PPFD on the *A. triloba* canopies at 3 m is low overall, generally in the 10–40 μmol m^{-2} sec^{-1} range among patches and individual sample days. Grand patch means across all sample days above the canopy ranged from 15.8 to 23.3 μmol m^{-2} sec^{-1}, with an outlier (patch C3) at 36.0 and an overall mean of 22.0 μmol m^{-2} sec^{-1}. The corresponding values on days with similar sky/wind conditions were nearly the same (range 15.0 to 25.5, overall mean 23.0). This is consistent with previous 2- to 7-m vertical PPFD profile measurements at AMW (Sipe and Yamulla 2021) and reflects substantial attenuation by the overstory trees, mid-sized trees, and larger saplings ($>$ 2 m tall). Published data on *A. triloba* photosynthetic performance in the field includes the maximum photosynthetic rate but not full light response curves (Augspurger *et al*. 2005), so *A. triloba* LCPs are unknown. The greater number, duration, and fluence of sunflecks above the canopy may offset the low background PPFD levels somewhat. However, it is likely the *A. triloba* canopy itself is often light limited, and additional intraspecific self-shading may constrain total foliage production and LAI across much of the study site. This in turn will affect the impact of *A. triloba* PPFD attenuation on juvenile trees and regeneration patterns.

Conclusions. With respect to the original study questions, the results confirm the following. (a) *Asimina triloba* patches intercept substantial fractions (50–60% on average) of incident PPFD in a spatially heterogeneous and temporally variable manner, resulting in very low light availability overall near the ground. (b) The relationship between transmission and total foliar area expressed as LAI or LAD across patches is weak at best, perhaps due to the variable sky conditions used for quantifying the relationship across patches. (c) Photosynthetic photon flux density levels are higher both above and below the canopy on sunny days compared with cloudy days, percent transmission is highly variable during sunny days but nearly constant under cloudy skies, and mean percent transmission does not differ overall between sky conditions. (d) Sunfleck regimes based on thresholds of either 20 or 40 μmol m^{-2} sec^{-1} are substantially reduced by the canopy in terms of total daily fleck number, duration, and fluence. (e) Photosynthetic photon flux density levels inside *A. triloba* patches are significantly reduced compared with the already low irradiances measured in the understory outside patches. (f) Light attenuation by *A. triloba* poses substantial challenges for leaf-level carbon gain and survival by seedlings of most tree species, particularly on cloudy days; sunfleck utilization may be especially important for seedlings given the very low diffuse backgrounds near ground; and the impact of *A. triloba* attenuation on regeneration in the future may depend on its ability to survive under increasing dominance by saplings and mid-sized trees of shade-tolerant species, particularly *Ac. saccharum* and *F. grandifolia*.

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