Relationship between photosynthetically active radiation and understory productivity across a forest-savanna continuum

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ABSTRACT

Conversion of closed-canopy forests to open woodland and savanna structure is an important objective related to ecosystem restoration and management of wildlife habitat. Our objective was to determine how aboveground net primary production (ANPP) of the understory at the forest-prairie ecotone of the Southern Great Plains, USA is affected by availability and interception of photosynthetically active radiation (PAR) as modified by overstory tree cover. The study site included a continuum from closed-canopy *Pinus echinata*/*Quercus stellata* dominated forest to savanna. More open-canopy treatments were created by harvesting and thinning trees in 1984 and implementation of fire return interval between one and four years (1985-2013). During the 2013 growing season, we measured PAR interception by the overstory using repeated hemispherical photographs ($fIPAR_o$), calculated total PAR available to the understory ($TAPAR_u$), and measured PAR intercepted by the understory ($TIPAR_u$) using repeated ceptometer measurements. ANPP of grasses, forbs, legumes, and woody plants in the understory was measured by clip plots at the end of the growing season and correlated to $TAPAR_u$ and $TIPAR_u$. ANPP increased as $TAPAR_u$ increased (less than $25 \text{ g m}^{-2} \text{ y}^{-1}$ in closed-canopy forest to $> 300 \text{ g m}^{-2} \text{ y}^{-1}$ in savanna areas) and dominance within the understory shifted from woody plants to C4 grasses along the forest to savanna continuum. However, the relationship between ANPP per $TAPAR_u$ shifted lower in the forested treatments ($28.9 \text{ g ANPP m}^{-2} \text{ y}^{-1}$ at $1486 \text{ MJ PAR m}^{-2} \text{ y}^{-1}$) compared to the savanna treatments ($66.8 \text{ g ANPP m}^{-2} \text{ y}^{-1}$ at $1486 \text{ MJ PAR m}^{-2} \text{ y}^{-1}$). In contrast, the relationship between ANPP and $TIPAR_u$ was consistent across the forest-savanna continuum. The net effect was that where trees occur in greater abundance they exert additional negative effects on ANPP beyond the capture of PAR. Stand

level basal area of approximately $10 \text{ m}^2 \text{ ha}^{-1}$ or lower appears sufficient to shift ANPP per
TAPAR_u upwards.

1. Introduction

Lack of disturbance, primarily fire exclusion, has caused the transition of open woodlands and savannas to closed-canopy forests in the southeastern USA. While aboveground productivity and carbon storage increase with tree dominance, understory productivity declines (e.g., Reich et al., 2001). The understory is a major biomass component of savanna systems, but generally contributes a small amount towards total biomass in forest ecosystems (Gilliam, 2007; Gonzales et al., 2013). However, in both savanna and forest ecosystems, the understory layer is important regarding energy flow and nutrient cycling (Likens and Bormann, 1970; Wise and Schaefer, 1994; Lapointe, 2001). In addition, a productive and diverse understory is important for many wildlife species as it provides forage and vegetation structure for species requiring early successional habitat.

Given this shift to closed-canopy forest, an important objective for forest managers is to restore woodlands and savannas. For instance, the USDA Forest Service has restored over 100,000 ha of closed-canopy pine-oak forest back to *Pinus echinata* - *Schizachyrium scoparium* (shortleaf pine – little bluestem) woodland/savanna habitat in the Ouachita Mountains of Arkansas and Oklahoma, USA. Based on this success, similar efforts in the southeastern USA are underway on additional national forests and are being undertaken by organizations such as The Nature Conservancy and US Department of Defense or advocated to private landowners by groups such as the Longleaf Pine Alliance, Longleaf Pine Initiative, Shortleaf Pine Initiative, etc.

A better understanding of the relationship between tree cover and understory productivity will increase the ability to achieve desired conditions in woodland/savanna restoration efforts because light availability to the forest floor can be manipulated to control understory productivity and composition.

Interception of photosynthetically active radiation (IPAR) by plant canopies is a primary determinant of plant productivity (Monteith, 1977). Therefore, productivity of the understory is reduced when PAR is captured by taller trees and shrubs (e.g., Brezeanu et al., 1973; Belsky, 1994). Within forested systems, understory plant yield increases with higher light availability resulting from the reduction in tree canopy cover and basal area (McConnell and Smith, 1970; Blair, 1971). Understory productivity decreases along the continuum from savanna to closed-canopy forest and is associated with PAR reaching understory (Reich et al., 2001). In addition to differences related to availability of PAR, the efficiency of converting IPAR to biomass within the understory may vary across the forest-savanna continuum because the conversion may be affected by the availability of resources or characteristics of different vegetation types (Sinclair and Horie, 1989; Earl and Davis, 2003).

Light is probably the most variable environmental resource (spatial and temporal) that affects plants (Pearcy, 1999). The availability and heterogeneity of light influences distribution of plants (Monsi and Saeki, 2005), regeneration of tree species (e.g., Nuñez and de Gouvenain, 2015), and productivity (Gardiner and Hodges, 1998; McGuire et al., 2001). In particular, the light environment reaching the understory in savanna ecosystems is very heterogeneous due to the presence of scattered trees and shrubs. Due to this heterogeneity, the controls of understory productivity in savannas are more complex and poorly understood even though herbaceous plants generally contribute more than 50% of the total NPP (Lloyd et al., 2008). While there

have been numerous studies examining the interaction between isolated trees and nearby understory plants in savannas (e.g., Jackson et al., 1990; Belsky, 1994; Scholes and Archer, 1997; Ludwig et al., 2004), the relationship between IPAR and understory productivity is still unclear, as compared to that of other ecosystems (Pearson and Ison, 1997).

The goal of this study was to determine how aboveground net primary production (ANPP) of different functional groups in the understory along the forest-prairie ecotone of the Southern Great Plains, USA is affected by availability and interception of PAR as modified by overstory tree cover. Specifically, we measured the seasonal patterns of IPAR by the trees (overstory) and the understory, aboveground productivity for different herbaceous plant functional groups (grass, legume, forb, sedge) and woody plants shorter than 1.4 m, and the ability of understory plants to convert IPAR to aboveground biomass. Different ecosystems were created by mechanical treatments and fire, then sustained by varying fire return interval. The replicated experimental treatments were randomly assigned among a contiguous set of plots thus eliminating potentially confounding effects of soil type, climate, and weather conditions.

Because PAR provides the energy for photosynthesis, we hypothesized that understory productivity would be linearly related to PAR availability and interception by the understory plants across the various ecosystems. If understory productivity is proportional to PAR availability, productivity can be readily predicted and managed by manipulating the canopy density of trees and shrubs. In contrast, if understory ANPP exhibits a threshold to reducing PAR availability or interception, then there is a range of tree canopy coverage that does not significantly interfere with understory productivity. Alternatively, if overstory tree presence has additional negative effects on understory ANPP beyond those due to PAR capture, then reducing stem density, as well as canopy cover, may be important to maximize understory productivity.

2. Methods

2.1. Study site

The study was conducted at the Pushmataha Forest Habitat Research Area (FHRA) (34°31'40" N, 95°21'10" W), established in 1982 by Oklahoma Department of Wildlife Conservation to evaluate woody and herbaceous vegetation response to different treatments of harvesting timber and fire regimes (Masters and Waymire, 2012). The study area comprised 53 ha on the 7690 ha Pushmataha Wildlife Management Area located in the Kiamichi Mountains on the western border of the Ouachita Highland Province, southeastern Oklahoma, USA. Soils were formed from shale and sandstone (Masters et al., 1993) and are an association of soil series Carnasaw (fine, mixed, semiactive, thermic Typic Hapludults) and Stapp (Fine, mixed, active, thermic Aquic Hapludults) with slopes between 8 to 12 percent (Web Soil Survey). Across the study area, depth of the surface horizon ranges from 0-21 cm with a texture of stony fine sandy loam with coarse fragments greater than 7.6 cm of 5 to 30%.

The climate is semi-humid to humid with hot summers and moderate winters (Masters, 1991). The overall mean annual precipitation and temperature for the 10 years prior to the study (2003 – 2013) were 1040 mm and 17.5 °C (Oklahoma Climatological Survey – Clayton Station). Within this period, 2003 and 2009 were the driest and wettest years with annual totals of 778 mm and 1500 mm, respectively. The hottest and coldest years were 2012 and 2004 with mean temperatures of 18.1 °C and 13.3 °C. During 2013, when this research was conducted, total annual precipitation was 1308 mm with April and May receiving the most precipitation. The hottest and coldest months in 2013 were August (26.8 °C) and December (3.3 °C) (Oklahoma Climatological Survey).

The overstory was mainly composed of *P. echinata* (55% of overstory basal area), *Quercus stellata* (post oak), and *Carya tomentosa* (mockernut hickory) (Masters et al., 1993). The understory was mainly composed of *Andropogon gerardii* (big bluestem), *S. scoparium*, different species of *Panicum* spp., *Carex* spp., and *Scleria* spp. (Masters and Waymire, 2012). Frequent woody understory species found in this area were *Vaccinium arboreum* (sparkleberry), *Toxicodendron radicans* (poison ivy) and *Smilax* spp. (Masters et al., 1993). Plants of genus of *Dichanthelium* and *Aster* were also common in the area (Crandall and Tyrl, 2006). In this present study, we considered the herbaceous and woody plants shorter than 1.4 m to be the understory.

2.2. Treatments

In 1983, 28 adjacent units were established in a randomized experimental design with each unit area ranging in size between 0.8 and 1.6 ha (Masters and Waymire, 2012). Before treatment the experimental area was a homogenous closed-canopy forest and treatments were imposed to units randomly within the area. This study used 23 units that represented eight cultural treatments with three replications of each (except for HT3 which had two replicates). The treatments consisted of different combination of harvesting *P. echinata* sawtimber (H), thinning of hardwoods (T) and fire return interval (1-4 years as well as no fire) (Table 1). From all treatments except the Control and Rough Reduction Burn (RRB), the *P. echinata* greater than 11.4 cm dbh was harvested and the selected hardwoods were killed using injection of 2,4-Dichlorophenoxyacetic acid during the summer of 1984. Fire return intervals (dormant season burns) were maintained 1985 through 2013. The different treatments resulted in conditions ranging from closed-canopy forests of different stages of development and age structure to savanna. In the spring before the 2013 growing season (growing season for this current study)

all treatments that included fire were burned, except the HT3 treatment that was burned the year before.

2.3. PAR transmission to understory

Ten 4 x 4 m (16 m²) permanent plots were established in each treatment unit for detailed measurements. They were installed at 20 m intervals on two randomly, north-south oriented lines perpendicular to the edge of the unit. Hemispherical photographs were taken to estimate overstory IPAR and PAR transmission to the understory. They were taken monthly from March to November of 2013 with a digital camera (Model E8400, Nikon, Tokyo, Japan) and fisheye lens in each permanent plot. The camera was positioned in the middle of each plot 1 m above the ground. Photos were taken near dusk and dawn or during cloudy days to avoid interference of direct sunlight. Photos were analyzed using the program WinScanopy Version 2006a (Regent Instruments Inc. Quebec, Canada). The maximum zenith angle used for the analyses was 75°. Zenith angles larger than 75° were not used as they often included areas outside the units.

The fraction of overstory IPAR ($fIPAR_o$) was calculated by Equation 1. Overstory PAR (PAR_o) above was the theoretical maximum (direct + diffuse) reaching the top of the canopy calculated by WinScanopy based on day of year and latitude. PAR_o under was the amount of PAR transmitted to the understory based on the path of the sun for a given day and canopy coverage along the corresponding suntrack. The $fIPAR_o$ was calculated for each day of 2013 by interpolating estimates between measurement dates.

$$fIPAR_o = \frac{PAR_o \text{ above} - PAR_o \text{ under}}{PAR_o \text{ above}} \quad (1)$$

The daily overstory IPAR (DIPAR_o) was then calculated by multiplying the $fIPAR_o$ by incident PAR for each day from nearby empirical measurement. The total solar radiation incoming was obtained from Clayton Mesonet station which is 25 km from the study site (Oklahoma Climatological Survey). Total incident radiation was multiplied by 0.5 to estimate incoming PAR (Weier and Cahalan, 2003).

2.4. PAR intercepted by the understory

We established 0.25 m² subplots adjacent to each of the 10 permanent plots within each unit to measure biomass and PAR interception by the understory. The HT treatment was not measured due to lack of understory vegetation in most subplots. The fraction of understory IPAR ($fIPAR_u$) was measured using a ceptometer (SunScan, Delta-T, UK) and estimated by Equation 2. In each understory sampling subplot, PAR was measured twice above and twice below the understory arranged to form an 'X' across the subplot. Measurements were taken each month under diffuse light conditions from May 2013 until the vegetation was clipped for biomass determination in October. The $fIPAR_u$ for each day was estimated by interpolating between monthly measurements.

$$fIPAR_u = \frac{PAR \text{ above understory} - PAR \text{ under understory}}{PAR \text{ above understory}} \quad (2)$$

The daily PAR available at the top of the understory (DPAR_u) was calculated by subtracting DIPAR_o from the empirically measured incident PAR for each day. The total PAR available (TAPAR_u) and intercepted (TIPAR_u) by the understory were calculated by summing daily values during the 2013 growing season (May 15th to November 12th). This period started

when the grasses began to grow (based on observation) and ended when the minimum temperature dropped below -2 °C (measured on site).

2.5. Understory ANPP

Between October 12th and 20th 2013, understory ANPP was measured using clip plots. Aboveground vegetation was clipped by hand from the same 0.25 m² subplots that were used to measure *f*IPAR_u. Understory vegetation was separated into woody, grass, forb, sedge, and legume (legume kept separate from forb because of nitrogen fixing ability). The woody vegetation below 1.4 m was clipped and only the current year growth was collected (leaves plus current year shoots). In addition, litter (dead understory plant material as well as bark, leaves, and branches <2.5 cm diameter) was collected under each subplot. The samples for each subplot and functional group were kept separate and dried at 60 °C and weighed.

We conducted our sampling in October before the first frost. While we did not conduct sampling at other times during the growing season as a comparison, October represents the maximum for forb and grass biomass in our region (Blair et al. 1977). Likewise, previous percent cover estimates comparing July vs October at our study site did not show a difference for either grasses or forbs (unpublished data). We did not sample spring ephemerals. Given the relatively xeric conditions of our study site associated with the combination of moderate precipitation, high potential evapotranspiration, and sandy textured soils with high stone content, spring ephemerals are a minor component of total understory ANPP for all of our treatments. Peak understory interception of PAR occurred before biomass sampling in October (see below). This was likely due to senescence or changes in structure of the understory vegetation between

late summer and fall. In either case, current-year biomass was captured and accurately estimated. While herbivory might have reduced understory biomass before sampling, Masters et al. (1993) previously found that herbivory little effect on understory biomass estimates.

2.6. Statistical Analysis

Data were analyzed with SAS 9.3 (SAS Institute Inc. 2008) using Proc Mixed (seven treatments with three replications and one treatment with two replications). To compare whether seasonal trends in $fIPAR_o$ differed among treatments, a repeated measures analysis was conducted using the measured dates. For treatments with different seasonal trends, i.e., significant time x treatment interaction, an analysis of simple effects was conducted with the slice option using all treatments simultaneously to determine which months the various treatments significantly differed from one another ($p \leq 0.05$).

Differences among treatments within functional groups and for total understory aboveground productivity (ANPP) were analyzed using Proc Mixed with data log transformed [$\log(\text{value} + 1)$] to meet the assumption of homogenous variance. Total understory ANPP was the sum of forbs, grass, legume, sedge, and woody. Analysis of covariance was used to determine if the relationship between total understory ANPP and $TAPAR_u$ and the relationship between total understory ANPP and $TIPAR_u$ differed ($p \leq 0.05$) among treatments (both slope and differences in least squares means were tested).

3. Results

3.1. Stand structure

The treatments resulted in a wide range in the dominance of overstory trees. The total (conifer + hardwood) overstory basal area ranged from 3.2 m² ha⁻¹ in the HT1 treatment to 35.2 m² ha⁻¹ in the HT treatment (Table 2). The Control treatment was a closed-canopy forest with larger diameter *P. echinata* (13.7 cm diameter at breast height; DBH) and a mix of large and medium sized hardwood trees. Basal area of the RRB treatment was not statistically different from the control. The harvesting of *P. echinata* and thinning of hardwoods 29 years previous in the HT treatment resulted in an even-aged, *P. echinata* - dominated forest that had smaller trees than the Control (conifer DBH 8.7 cm), but the greatest basal area. The harvesting of *P. echinata* and thinning of hardwoods plus inclusion of fire at a four-year return interval in the HT4 treatment, resulted in a developing uneven-aged forest (conifer DBH 6.8 cm). Overstory basal area of the HT4 treatment was significantly lower than Control, HT, and RRB treatments, but greater than the treatments with more frequent fire return intervals. Fire return interval of three years was a threshold that slowed the development of forest structure and kept basal area of overstory trees low. The HT3 and HT2 treatments had savanna-like structure and the HT1 was mostly prairie with just a few scattered trees per hectare. Because hardwoods were not initially thinned in the HNT1 treatment, these stands had savanna structure dominated by large *Q. stellata* that were established prior to imposition of treatments.

3.2. Overstory *fIPAR*

The fraction of incident PAR intercepted by the overstory (*fIPAR_o*) of all treatments increased beginning in April and decreased towards the end of the growing season in September (Fig. 1a). Three of four forested treatments (HT, Control, RRB) and one savanna treatment (HNT1) followed the same trend (defined by no treatment x month interaction; $p > 0.05$). The overall means of HT, RRB, and Control were similar to each other and greater than HNT1. The remainder of the savanna treatments (HT1, HT2, and HT3) and the remaining forested treatment (HT4) followed the same trend. The overall mean *fIPAR_o* of the HT4 was greater than the HT1, HT2, and HT3 treatments which were in turn similar to one another. When each month was tested separately to compare means of treatments that interacted with one another (analysis of simple effects using the slice option in SAS), the forested treatments (Control, HT, RRB) had greater *fIPAR_o* than savanna treatments (HT1, HT2, HT3) for all months. *fIPAR_o* of HT4 was significantly less than the other forested treatments (Control, HT, RRB) for all months except for April.

3.3. Understory *fIPAR*

In general, ranking of *fIPAR_u* was opposite that for overstory, being greater in savanna than in forested treatments (Fig. 1b). *fIPAR_u* increased for all treatments beginning in May. The RRB and Control treatments reached a peak in July while the HNT1, HT1, HT2, HT3, and HT4 treatments reached a peak in August. Given these different trends, there were significant treatment x month interactions. *fIPAR_u* of the savanna treatments followed the same trend (no treatment x time interaction; $p > 0.05$) and their overall means were not statistically different

from one another. The HT4 treatment had a trend that was not statistically different than the savanna treatments, but had a lower overall mean. $fIPAR_u$ of RRB and Control followed the same trend and had overall means that were not statistically different. Comparing each month separately, $fIPAR_u$ of RRB and Control treatments were lower than the savanna treatments on all dates and lower than HT4 for all months except May.

3.4. Aboveground net primary productivity (ANPP)

Total understory ANPP in savanna treatments (HNT1, HT1, HT2, HT3) and the HT4 treatment was significantly greater than the Control, RRB, and HT treatments (Fig. 2a). ANPP for each functional group of understory vegetation significantly varied across the treatments except for sedge which contributed the least to ANPP and ranged from only 0.0 to 0.05 g m⁻² y⁻¹ among treatments. Overall grass composed the highest ANPP among functional groups, ranging from 0.4 to 308.7 g m⁻² y⁻¹ (Fig. 2b). The greatest grass ANPP occurred in treatments with one, two, and three year fire frequency (HT1, HNT1, HT2 and HT3). Grass biomass for the HT4 was greater than for other forested treatments. Forb ANPP varied among the treatments with biomass ranging from 0.2 to 13.7 g m⁻² y⁻¹ (Fig. 2c) and declined as fire return interval lengthened. Legume ANPP varied from 0.03 to 6.2 g m⁻² y⁻¹ (Fig. 2d) and was lowest in the treatments without fire. Woody plants in the understory had ANPP that ranged from 3.6 to 83.4 g m⁻² y⁻¹ across the treatments (Fig. 2e). Woody plant ANPP in the understory was lower for the HT, RRB, and HNT1 than the HT2, HT3, and HT4 treatments. Litter accumulation ranged from 105 to 1672 g m⁻² (Fig. 2f) and was lower with more frequent the fire return interval.

Among functional groups in the understory, grasses and woody plants made the largest contributions to ANPP (Fig. 3). Grasses contributed between 71.9% and 92.5% of total ANPP in the understory among the savanna treatments. In the forested treatments, the contribution of grass to ANPP increased with fire, i.e., HT, Control, HT4, and RRB, had contributions to total ANPP from grasses of 7.4%, 17.7%, 69.3%, and 76.6% respectively. Woody plants made the largest contribution to ANPP in the understory (>80%) in the non-burned, forested treatments (RRB and Control). Among burned treatments, the percent of ANPP of the understory composed of woody vegetation was lowest in the annual burn treatments (HT1, HNT1). Regarding the contributions of the other plants to ANPP, in forested treatments, forbs contributed between 5.5% and 1.1%, legumes between 3.1% and 0%, and sedge between 1.9 and 0%. In savanna treatments, forbs contributed between 4.2% and 1.3% while sedges contributed less than 0.04% and legumes contributed less than 1.8% to the total understory biomass.

3.5. Radiation utilization

The total PAR available at the top of the understory ($TAPAR_u$) ranged from 811 $MJ\ m^{-2}\ y^{-1}$ in the HT to 2112 $MJ\ m^{-2}\ y^{-1}$ in the HT1 treatment (Table 3). Overall, forested treatments had less PAR reaching the understory than savanna treatments. $TAPAR_u$ was not statistically different among savanna treatments. $TAPAR_u$ in the HT4 treatment was intermediate, i.e., lower than the HT1, HT2, and HT3 savanna treatments and greater than other forested treatments (HT, RRB, and Control).

The slopes of relationships between total understory ANPP and $TAPAR_u$ were positive and did not differ among treatments ($p = 0.07$). However, the intercept of the forested treatments was more negative than the savanna treatments (Fig. 4) resulting in different relationships ($p < 0.0001$). The intercept of savanna treatments ($-42 \text{ g m}^{-2} \text{ y}^{-1}$) did not differ statistically from zero ($p = 0.74$) while the intercept of forested treatments ($-75 \text{ g m}^{-2} \text{ y}^{-1}$) was more negative than zero ($p < 0.0001$). As a result of the shift downward in the relationship between total understory ANPP and $TAPAR_u$ for forested treatments, understory ANPP estimated at a common $TAPAR_u$ (Least squares means at $1486 \text{ MJ m}^{-2} \text{ y}^{-1}$) was greater for the savanna treatments than forested treatments ($p < 0.0001$) (Table 3).

Total understory intercepted PAR ($TIPAR_u$) ranged from $48.1 \text{ MJ m}^{-2} \text{ y}^{-1}$ in the Control treatment to $915.9 \text{ MJ m}^{-2} \text{ y}^{-1}$ in the HT1 treatment (Table 3). $TIPAR_u$ of the savanna treatments was greater than the forested treatments. Among the forested treatments, the HT4 treatments had greater $TIPAR_u$ than the Control or RRB treatments. $TIPAR_u$ was positively correlated with total understory ANPP ($r^2 = 0.65$) and the slopes of the various treatments were not statistically different from one another ($p = 0.35$) (Fig. 4b). The intercepts of the treatments did not statistically differ ($p = 0.82$). The intercept was $-19.6 \text{ g m}^{-2} \text{ y}^{-1}$ and not statistically different than zero ($p = 0.25$). Total understory ANPP estimated at a common $TIPAR_u$ (expressed as Least squares means, ANPP at $536 \text{ MJ m}^{-2} \text{ y}^{-1}$) was not statistically different among the treatments ($p = 0.82$) and ranged from $46.8 \text{ g m}^{-2} \text{ y}^{-1}$ to $59.1 \text{ g m}^{-2} \text{ y}^{-1}$ (Table 3). Understory plants in forested treatments, i.e., Control, RRB, and HT4, intercepted 5%, 8%, and 29%, respectively, of the total

PAR available. Among the savanna treatments, the percent of PAR intercepted by the understory plants varied between 40 and 43%.

4. Discussion

4.1. Overstory fIPAR

All the treatments exhibited an increase in $fIPAR_o$ due to foliage growth with the onset of the growing season and a decline towards the end due to abscission. This seasonal fluctuation affects transmittance of light to the understory (Ross et al., 1986; Constabel and Lieffers, 1996) and the development of the understory (Uemura, 1994). Even though all the treatments showed an increase in April, those with more deciduous tree basal area had a steeper increase in $fIPAR_o$, i.e., Control, RRB, HT, and HNT1. In comparison, *P. echinata* maintains foliage all year, although it increases due to needle development during the growing season and decreases with abscission of the previous year's needle cohort in fall/winter. Seasonal fluctuations in $fIPAR_o$ were less pronounced for canopies dominated by *Pinus* spp. in previous studies (Pangle et al., 2009), and in this study. For instance, the HT4 treatment had basal area that was 75% *P. echinata* and showed very little annual change in $fIPAR_o$.

4.2. Understory fIPAR

The grass-dominated savanna treatments exhibited a large increase in $fIPAR_u$ in the beginning of growing season that corresponded to the development of warm season grasses at (Gautam et al., 2014). The peak in $fIPAR_u$ for savanna treatments occurred in late summer when

the grasses typically reach maximum leaf area index (Madakadze et al., 1998) and then began to decline due leaf senescence and onset of dormancy. The HT4 treatment showed a similar pattern to the savanna treatments probably because the abundance of understory biomass and the dominance by grasses in this treatment (69% of total understory biomass) were more similar to savanna treatments than the other forested treatments.

The lower and more consistent seasonal values in $fIPAR_u$ of the Control and RRB treatments, compared to savanna treatments, occurred because the understory was sparser, probably limited by overstory development and PAR interception (Constabel and Lieffers, 1996; Fournier et al., 2004). The earlier peak of understory $fIPAR$ that occurred in July, and subsequent small decrease during the remainder of the growing season in forested treatments might partly have been due to ephemeral spring plants in the understory which take advantage of higher light conditions at the forest floor available in the early spring (Lapointe, 2001). These plants usually undergo leaf senescence and dormancy about the same time that overstory canopy closure occurs (Vezina and Grandtner, 1965). Our sampling for understory plant biomass conducted in October did not include spring ephemerals. However, the relatively xeric conditions of our study site limit the prevalence of these types of plants.

4.3. Aboveground net primary productivity

In general, total understory ANPP differed among treatments in a predictable manner and was positively associated $TAPAR_u$ such that savanna treatments had approximately seven times greater understory ANPP ($>3000 \text{ kg ha}^{-1} \text{ y}^{-1}$) than forest treatments. Similarly, previous studies in forest and woodland systems found an inverse relationship between tree canopy cover and

understory productivity (Pieper, 1990; Reich et al., 2001; Peterson et al., 2007). Almost all grasses collected were C4 (*A. gerardii*, *S. scoparium*, and *Sorghastum nutans*). C4 grasses occur in greater abundance where there is plenty of radiation available, such as subtropical savannas and temperate grasslands (Knapp and Medina, 1999). Plants with the C4 photosynthetic pathway are largely absent in forests where the solar radiation available for the understory drops below 20% of the total incident radiation (Pearcy, 1990). In an analogous ecosystem in Wisconsin, i.e., tallgrass prairie understory with drought, fire tolerant *Quercus* overstory, overstory canopy cover explained 70% of grass cover (inverse relationship) when measured across a savanna-forest continuum (Peterson et al., 2007).

In addition to availability of PAR, fire also may have contributed to dominance of grasses in savanna treatments (Peterson et al., 2007). Fire reduces the litter layer, kills less fire-tolerant species, and releases nutrients. Because fire regime is a major factor controlling midstory and overstory trees in our study, the effects of PAR on ANPP might be confounded by other effects associated with fire return interval. One factor that probably limited confounding fire regime with PAR on the ANPP response in our study within the burned treatments was that all treatments, except the HT3, were burned before the 2013 growing season which eliminated differences in time since fire. When comparing total understory plant ANPP to overstory cover and fire frequency, Reich et al. (2001) found a better correlation with overstory cover ($r^2 = 0.95$) than fire return ($r^2 = 0.56$). Likewise, Peterson et al. (2007) found that greater variation in grass cover was explained by overstory cover than fire return interval.

In contrast to grass-dominated savanna treatments, understory ANPP of the Control and HT treatments was dominated by woody plants. Woody plants have a C3 photosynthetic pathway which is better adapted for shadier conditions that occur near the forest floor. Peterson

et al. (2007) found that woody plant cover in the understory was maximum between 60 and 90% overstory tree cover. Even though the percentage of the understory composed of woody plants was higher in the forested treatments than the savanna treatments, absolute woody plant ANPP in the understory decreased as PAR availability decreased across the savanna-forest continuum.

Another reason for the dominance of woody plants in the understory of forested treatments could be that fire exclusion favors their establishment under the forest canopy (Peterson et al., 2007). However, the inclusion of regular fire did not have a negative effect on woody plant ANPP in the understory in our study when comparing savanna to forested treatments. While the fires topkilled seedlings and low stature trees, they resprouted. Even annual burning in the HT1 treatment did not significantly reduce woody biomass ANPP compared to other treatments after approximately 30 years of annual dormant season fire.

4.4. Influence of PAR available and IPAR on understory ANPP

The presence of trees had a negative effect on ANPP beyond just reducing PAR available to the understory as evidenced by the shift downward in the relationship between $TAPAR_u$ and understory ANPP for forest treatments. In addition to capturing radiation, overstory trees compete with understory plants for water and nutrients. Forest canopies transpire water and can intercept as much as 36% of incoming precipitation along the forest-grassland ecotone (Zou et al., 2015) which reduces plant available water. At our study site, soil moisture was significantly lower in the forested treatments than in the savanna treatments and decreased more quickly after rainfall events (unpublished results). Nutrient cycling and mineralization are faster under forests than savannas or grasslands which may increase nutrient availability. At our study site, nitrogen

availability and mineralization were higher under forest areas than grass-dominated areas (Daly, 2015). However fine root turnover is faster in forests (Reich et al., 2001) which may increase nutrient uptake and soil exploration by tree roots.

Trenching studies that eliminated root competition between trees and understory vegetation demonstrated the importance of belowground competition on understory ANPP (e.g., Riegel et al., 1992). In a trenching study in the southeastern USA examining the response of herbaceous plants analogous to those in our study found that *P. palustris* competition from above and belowground factors was approximately similar in magnitude (Harrington et al., 2003). Therefore, in addition to controlling PAR reaching the top of the understory, trees reduce understory productivity by using water and nutrients at the expense of understory plants. This competition for belowground resources from trees is probably the major reason for the shift downward in the intercept of the understory ANPP x $TAPAR_u$ relationship in forested treatments. Because we did not find any difference among treatments in the relationship between PAR intercepted by the understory and total understory ANPP, the reduction in ANPP per $TAPAR_u$ of forested treatments was due to less cover of understory plants per unit ground area rather than a decrease in the efficiency of converting IPAR to ANPP.

In addition to PAR availability and competition, other factors may affect understory productivity. Air temperature and wind speed are lower while relative humidity is higher under a forest canopy than in more open environments. As discussed above, fire can affect understory ANPP by removing litter, increasing nutrient availability, and shifting community composition. Fire as a direct agent did not appear to have a large effect on ANPP per $TAPAR_u$ because the HT4 and RRB treatments both had periodic fire and were burned immediately before the 2013

growing season, yet the understory productivity per $TAPAR_u$ of these treatments was most similar to the nonburned HT and Control treatments.

Litter accumulation is a very important factor that can affect understory productivity (Sydes and Grime, 1981; Facelli and Pickett, 1991), particularly in forest ecosystems. Forest floor microsite conditions can be the dominant driver of understory productivity. In a *P. palustris* forest in northern Florida, USA, Hiers et al. (2007) found that leaf litter from midstory *Quercus* spp. suppressed understory plants more than shading. In tallgrass prairie, reduction of grass litter accumulation by fire increases PAR available to actively growing grass (Knapp, 1984) and increases productivity (Hulbert, 1969). In our study, however, the litter layer biomass of the forested HT4 was more similar to the savanna treatments, but understory ANPP per $TAPAR_u$ of the HT4 treatment was lower than the savanna treatments and similar to the forested treatments, implying that litter biomass was not a primary determinant of understory ANPP.

Grass and forb species richness and percent cover decrease with tree canopy cover and increase with fire frequency while woody plants respond in the opposite way (Peterson et al., 2007; Peterson and Reich, 2008). These changes in functional groups may affect ANPP per $TIPAR_u$ as the species vary in their growth rates, specific leaf area, canopy architecture, and resource use efficiencies. However, we did not find any differences in the relationship between understory ANPP and $TIPAR_u$ even though the understory species composition shifted from woody plants to grasses and productivity increased more than six fold comparing forest to savanna treatments. The fact that understory ANPP per $TIPAR_u$ was consistent across the various treatments with very different species assemblages and productivities may indicate a

convergence in light use efficiency among treatments related to their habitat preferences and physiology of the various species found in each environment.

IPAR is well correlated to productivity and is often a better predictor of productivity than leaf area index (e.g., Will et al., 2005). However, a causal link between $TIPAR_u$ and ANPP is impossible to prove in our study. While it is intuitive that energy capture ($TIPAR_u$) is driving ANPP, plots with greater ANPP also intercept more radiation due to greater leaf area. In any case, $TIPAR_u$ was a robust predictor that accounted for nearly 2/3 of the variation in understory ANPP across sites ranging from closed-canopy forest to open savanna and supports indirect methods using canopy light capture to estimate understory biomass (Reich et al., 2001). The fraction of unexplained variation could be from factors such as microsite soil water and nutrient availability, presence of surface rocks, or slope differences. Our results are from only one growing season. Variation in growing season precipitation is likely correlated to the response of understory ANPP to PAR, i.e., greater ANPP per $TIPAR_u$ when precipitation is greater.

5. Conclusions and Management implications

Understory productivity increased and there was a shift in the understory from woody plants to C4 grasses as $TAPAR_u$ increased across a savanna-forest continuum. However, understory ANPP per $TAPAR_u$ was higher in savanna than forest treatments, probably due to the addition of belowground competition associated with greater dominance of trees within the forest treatments. To achieve management objectives related to increasing understory ANPP,

therefore, it is most effective to conduct treatments that increase PAR through tree removal or mortality as there is a synergy between reduced tree dominance and increased PAR availability. The threshold of tree dominance that caused a shift upward in understory productivity per $TAPAR_u$ was approximately basal area of $10 \text{ m}^2 \text{ ha}^{-1}$ because the minimum basal area of a forested treatment plot was $12.0 \text{ m}^2 \text{ ha}^{-1}$ and the maximum from a savanna treatment plot was $8.8 \text{ m}^2 \text{ ha}^{-1}$. At higher basal area in the forested treatments, competition provided by the matrix of trees appears to be sufficient to shift productivity downward even where gaps occur to allow for greater PAR. In this study, burning alone (RRB treatment) was not enough to significantly increase understory ANPP relative to the untreated control which further emphasizes the need for initial mechanical treatments that reduce canopy cover and tree dominance. Therefore, to increase herbaceous food and cover for wildlife or achieve restoration objectives that involve an abundant and productive understory, thinning trees should be incorporated as more herbaceous biomass is produced per unit of IPAR when trees are removed as opposed to other treatments, such as burning without thinning. Burning, however, is necessary to maintain an open forest structure and was required every three years or less at this site to maintain a savanna structure.

The efficiency of understory ANPP produced per PAR intercepted by the understory was not affected by overstory treatments so it can be used to predict ANPP across the full range of condition along the forest-savanna continuum regardless of species composition, understory productivity, or canopy architecture. This implies a convergence in light use efficiency among the various treatments and permits the estimation of understory ANPP using relatively simple and fast techniques (compared to clip plots for biomass).

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Table 1

Description of treatments. The harvesting of *P. echinata* and thinning of hardwoods was completed at time of treatment installation (1984). Fire return intervals were maintained since 1985. Treatment RRB is Rough Reduction Burn.

Treatment	Current Condition	Harvest Pine	Thin Hardwoods	Fire return interval (years)
Control	Forest	No	No	No Fire
HT	Forest	Yes	Yes	No Fire
RRB	Forest	No	No	4
HT4	Forest	Yes	Yes	4
HT3	Savanna	Yes	Yes	3
HT2	Savanna	Yes	Yes	2
HT1	Savanna	Yes	Yes	1
HNT1	Savanna	Yes	No	1

Table 2

Means and standard error of conifer, hardwood, and total overstory basal area. Means (within conifer, hardwood, or total) with the same letter are not significantly different ($p > 0.05$).

Treatment	Conifer (m ² ha ⁻¹)	Hardwood (m ² ha ⁻¹)	Total (m ² ha ⁻¹)
Control	16.7 ± 2.8 <i>ab</i>	12.5 ± 0.9 <i>a</i>	29.3 ± 3.7 <i>ab</i>
HT	24.3 ± 6.7 <i>a</i>	10.9 ± 3.6 <i>a</i>	35.2 ± 2.8 <i>a</i>
RRB	15.3 ± 1.4 <i>ab</i>	10.4 ± 1.5 <i>ab</i>	25.7 ± 2.6 <i>b</i>
HT4	12.9 ± 4.6 <i>cb</i>	4.8 ± 0.3 <i>c</i>	17.1 ± 4.6 <i>c</i>
HT3	2.6 ± 0.9 <i>d</i>	3.0 ± 0.6 <i>c</i>	5.6 ± 0.3 <i>d</i>
HT2	3.5 ± 0.7 <i>cd</i>	3.7 ± 0.4 <i>c</i>	7.2 ± 0.9 <i>d</i>
HT1	1.1 ± 0.5 <i>d</i>	2.1 ± 0.5 <i>c</i>	3.2 ± 0.9 <i>d</i>
HNT1	0.6 ± 0.2 <i>d</i>	6.9 ± 1.1 <i>bc</i>	7.5 ± 1.2 <i>d</i>

Table 3

Mean total photosynthetically active radiation (PAR) available (TAPAR_u) at the top of the understory layer and total intercepted PAR (TIPAR_u) by the understory for 2013 growing season. Least Squares Means of total understory aboveground net primary production (ANPP) at a common TAPAR_u and a common TIPAR_u for 2013 growing season (May – Nov). See Table 1 for treatment descriptions. Similar letters indicate means are not statistically different ($p > 0.05$). Total PAR incident was $2546 \text{ MJ m}^{-2} \text{ y}^{-1}$ for each treatment. HT does not have values for TIPAR_u because of negligible understory development.

Treat.	TAPAR_u ($\text{MJ m}^{-2} \text{ year}^{-1}$)	TIPAR_u ($\text{MJ m}^{-2} \text{ year}^{-1}$)	ANPP at TAPAR_u of $1486 \text{ MJ m}^{-2} \text{ y}^{-1}$ ($\text{g m}^{-2} \text{ y}^{-1}$)	ANPP at TIPAR_u of $536 \text{ MJ m}^{-2} \text{ y}^{-1}$ ($\text{g m}^{-2} \text{ y}^{-1}$)
Cont	864 <i>a</i>	48.1 <i>a</i>	26.8 <i>a</i>	59.1 <i>a</i>
HT	811 <i>a</i>	-	27.0 <i>a</i>	-
RRB	963 <i>a</i>	81.1 <i>a</i>	24.8 <i>a</i>	57.5 <i>a</i>
HT4	1477 <i>b</i>	421.3 <i>b</i>	37.0 <i>a</i>	49.7 <i>a</i>
HT3	2070 <i>cd</i>	839.1 <i>c</i>	67.9 <i>b</i>	48.4 <i>a</i>
HT2	1965 <i>c</i>	843.9 <i>c</i>	64.8 <i>b</i>	46.8 <i>a</i>
HT1	2112 <i>c</i>	915.9 <i>c</i>	64.9 <i>b</i>	48.9 <i>a</i>
HNT1	1825 <i>bc</i>	765.2 <i>c</i>	69.7 <i>b</i>	55.8 <i>a</i>

Fig. 1. Fraction of intercepted photosynthetically active radiation (IPAR) for the overstory (a) and understory layer (b) during the 2013 growing season. Solid symbols represent forest treatments. Open symbols represent savanna treatments. Similar lines (dashed or solid) indicate same trends over the growing season. See Table 1 for treatment description.

Fig. 2. Total (a) and plant functional group (b-e) aboveground net primary production (ANPP) of the herbaceous layer for the 2013 growing season as well as litter (f). Vertical bars represent standard error. Means with the same letter are not statistically different ($p > 0.05$). Statistical analysis based on log transformed data. See Table 1 for treatment descriptions.

Fig. 3. Percent contribution of different plant functional groups to aboveground net primary production for the 2013 growing season. See Table 1 for treatment descriptions.

Fig. 4. Relationship between total understory aboveground net primary production (ANPP) and photosynthetically active radiation (PAR) available at the top of the understory layer (a) and the relationship between total understory ANPP and PAR intercepted by the understory layer (b) during the 2013 growing season. See Table 1 for treatment descriptions.