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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 (*f*IPARo), 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 g m^{-2} y^{-1} in closed-canopy forest to >300 g m^{-2} 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 g ANPP m^{-2} y^{-1} at 1486 MJ PAR m^{-2} y^{-1}) compared to the savanna treatments (66.8 g ANPP m^{-2} y^{-1} at 1486 MJ PAR m^{-2} 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 m^2 ha^{-1} or lower appears sufficient to shift ANPP per $TAPAR_u$ upwards.
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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; Gonzalez 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

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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 and 12% (Web Soil Survey). Across the study area, depth of the surface horizon ranges from 0 to 21 cm with a texture of stony fine sandy loam with coarse fragments greater than 7.6 cm of 5–30%.

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

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