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Plant density alters nitrogen partitioning among photosynthetic components, leaf photosynthetic capacity and photosynthetic nitrogen use efficiency in field-grown cotton

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ABSTRACT

Plant population density (PPD) is an important practice for optimizing canopy structure and improving canopy photosynthetic capacity of field-grown cotton (*Gossypium hirsutum* L.). A 2-yr field experiment was conducted to determine if and how PPD (7.5, 19.5 or 31.5 plants m^{-2}) affects the light-saturated photosynthetic rate and photosynthetic nitrogen use efficiency in cotton leaves, with a focus on the key canopy characteristics for efficient utilization of light and nitrogen. The results showed that leaf N allocation and partitioning among different components of the photosynthetic apparatus were significantly affected by PPD. As PPD changed, cotton optimized photosynthetic N use efficiency and photosynthetic capacity by adjusting leaf mass per area, which in turn affected leaf N allocation to the photosynthetic apparatus. In the upper canopy layer, leaf N allocation to the photosynthetic apparatus increased as PPD increased, resulting in an increase in leaf photosynthetic N use efficiency. In contrast, in the mid- and lower-canopy layers, leaf N allocation to the photosynthetic apparatus decreased as PPD increased, resulting in declines in leaf light-saturated photosynthetic rate and photosynthetic N use efficiency. The overall results indicated that high photosynthetic capacity of leaves in the upper-canopy layer and high leaf N allocation to the photosynthetic apparatus and photosynthetic use efficiency of photosynthetic nitrogen in the mid- and lower-canopy layers were two key canopy characteristics for efficient utilization of light and nitrogen by cotton. The medium-PPD is the optimum plant density due to high light utilization efficiency, superior spatial distribution of leaf N allocation to the photosynthetic apparatus and photosynthetic use efficiency of photosynthetic N in leaves within the canopy.

1. Introduction

Improvements in canopy photosynthetic capacity have long been considered to be necessary for improving yield formation (Heitholt, 1994; Bednarz et al., 2000; Zhang et al., 2002, 2003; Dong et al., 2012; Mao et al., 2014). Canopy photosynthetic capacity varies widely, depending not only on leaf-level photosynthetic capacity but also on growing conditions such as photosynthetically active radiation (PAR). These growing conditions strongly influence leaf morphology and physiology within the canopy (Field and Mooney, 1986; Hikosaka et al., 1993; Niinemets et al., 1998, 2014; Meir et al., 2002; Pearcy et al., 2004; Valladares and Niinemets, 2008).

Leaf N is an essential element for leaf photosynthesis and canopy development (Wullschleger and Oosterhuis, 1990). The photosynthetic apparatus is the largest N sink in plants and leaf photosynthetic capacity is positively correlated with leaf N (Evans and Seemann, 1989; Poorter and Evans, 1998). Leaf N concentrations at different positions within the canopy are positively correlated with the light environment during leaf development (Werger and Hirose, 1991). Numerous studies have demonstrated that leaf N concentration per unit area (N_A) and leaf N concentration per unit mass (N_M) are both proportional to irradiance during the development of the leaf (Werger and Hirose, 1991; Warren and Adams, 2001; Niinemets, 2007; Niinemets et al., 2014). Canopy photosynthesis is maximized when N is preferentially distributed to upper leaves rather than uniformly distributed throughout the canopy (Leuning et al., 1995). Therefore, the light environment is

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an important determinant of leaf N partitioning within the canopy. Plant population density (PPD) significantly influences the light environment in plant canopies (Hirose et al., 1988), especially in cotton (*Gossypium hirsutum* L.) (Zhang et al., 2003; Dong et al., 2005; Kaggwa-Asiimwe et al., 2013). Hence, it is important to study the effect of PPD and light distribution on N allocation and utilization efficiency.

Cotton is one of the most important textile-fiber crops. The indeterminate growth habit of cotton causes a variety of adaptations to PPD. One of the most important adaptations is the alteration of canopy structure (Zhang et al., 2003; Mao et al., 2014), which significantly influences light conditions within the canopy. Ecological studies show that light harvesting is of paramount importance for plants growing in a light competitive environment such as a dense stand (Pearcy et al., 2004; Valladares and Niinemets, 2008). Light affects not only leaf N content but also leaf N allocation to different components of the photosynthetic apparatus, e.g., light-harvesting (N_L), electron transport (bioenergetics, N_B) and carbon reduction (carboxylation, N_C) (Field and Mooney, 1986; Evans, 1989a). Furthermore, Feng et al. (2009b) reported that leaf N allocation to the photosynthetic apparatus (N_P) plays a crucial role in determining light-saturated photosynthetic rate (P_{max}) and photosynthetic N use efficiency (PNUE). However, neither the effects of light conditions on the distribution of leaf N among the components of the photosynthetic apparatus nor the influences of these changes on leaf P_{max} and PNUE in cotton were well determined. The objectives of this study were to determine, (i) the effects of PPD on leaf morphology, leaf N distribution, leaf N allocation to photosynthesis and N partitioning among components of the photosynthetic apparatus; (ii) how these morphological and physiological factors affect leaf P_{max} and PNUE within the cotton canopy; and (iii), most importantly, the key canopy characteristics for efficient light and N utilization.

2. Materials and methods

2.1. Experimental design and field management

The field experiment was conducted in 2012 and 2013 at an experiment station near Shihezi University, Shihezi City, Xinjiang, China (45°19′N, 86°03′E). The experimental field has a fine clay loam soil (fine-loamy, mixed, mesic).

Plastic film mulch and drip irrigation were used in the experiment. Before sowing, the experiment plots were covered with 1.2-m-wide sheets of transparent plastic film. There was a 0.3-m-wide strip of bare soil between each sheet. Drip irrigation lines were installed beneath the plastic. Cotton (*cv.* Xinluzao 33) was sown through holes in the plastic film mulch on April 18, 2012 and April 22, 2013. Three to four seeds were planted in each hill. The row spacing was 66 cm–10 cm–66 cm–10 cm. The intrarow spacings between cotton hills were 8.4, 13.5, or 35 cm. After full emergence, each plot was thinned by leaving one vigorous plant per hill. The resulting PPDs were 7.5, 19.5, and 31.5 plants m^{-2}, which were referred to as low-PPD, medium-PPD, and high-PPD, respectively. The experiment was arranged in a completely randomized design with three replications.

The plots were drip-irrigated with 585 mm in 2012 and 600 mm in 2013. The plots were fertilized before sowing each year with 240 kg N ha^{-1} (urea), 170 kg P_2O_5 ha^{-1} [$(NH_4)_3PO_4$], and 1500 kg ha^{-1} organic fertilizer (235 g kg^{-1} organic matter, 18 g kg^{-1} total N, 14 g kg^{-1} total P, and 22 g kg^{-1} total K). An additional 120 kg N ha^{-1} (urea) was applied by drip irrigation to each plot during both growing seasons. The fertilizer amounts are typical in the region. Plant topping was conducted at peak flowering (80–85 days after sowing). Mepiquat chloride (*N*, *N*-dimethylpiperdinim chloride) was applied six times during the growing season (300–350 g ha^{-1} per application) to regulate cotton growth.

The measurements described in following sections were made at the boll-setting stage (100–110 days after sowing) in both years.

2.2. Determination of photosynthetically active radiation

The PAR (400–700 nm) interception was determined near the center of each plot at solar noon with a SunScan Canopy Analysis System (Delta, UK; 100 cm line quantum sensor). All of the measurements were made on the same day. At least five readings were taken at each position within the canopy. The PAR interception (PARI) of the upper-, mid-, and lower-canopy layer was then calculated using the equation:

$$\mathrm{PARI} = I_{t+1} - I_t$$

where I_t is the incident radiation at one of four positions (I_1, incident radiation at the soil surface; I_2, incident radiation at one-third of canopy height; I_3, incident radiation at two-thirds of canopy height; I_4 incident radiation 0.1 m above the canopy)

The fraction of PAR intercepted by each canopy layer (FIPAR) was calculated using the equation:

$$\mathrm{FIPAR} = \left[\frac{\mathrm{PARI}}{I_4 - I_1}\right] \times 100\%$$

The fraction of PAR intercepted by the whole canopy (WFIPAR) was calculated using the equation:

$$\mathrm{WFIPAR} = \frac{(I_4 - I_1)}{I_4} \times 100\%$$

2.3. Determination of canopy apparent photosynthesis and canopy respiration

Canopy apparent photosynthesis (CAP) and canopy respiration rate (CR) were measured on the same day as the measurement of FIPAR using the assimilation chamber method described by Acock et al. (1978) and Reddy et al. (1995). The assimilation chamber (90 cm long × 76 cm wide × 110 cm high) was covered with acrylic film, which transmitted more than 95% of solar radiation. Two fans were installed inside the chamber to mix the air. The air temperature within the chamber was less than 3 °C above ambient.The CAP measurements were made between 12:30 and 13:30 h on clear, windless days. The chamber was placed over two rows in the center of each plot. There was a 10-cm-wide space between the two cotton rows. Two assistants held the chamber tightly against the plastic film mulch to prevent air leakage from around the bottom of the chamber. The CO_2 concentration inside the chamber was determined with a LI-8100 Soil CO_2 Flux System (LI-COR Inc., Lincoln, NE, USA). Gas exchange rates in each plot were measured during at least three 60 s intervals. We began recording the values when the CO_2 concentrations inside the chamber began to drop steadily.

After measuring CAP, the chamber was lifted above the canopy to refresh the air. The chamber was then returned to its original position and covered with a double-layered cloth. The outer layer of the cloth was black and the inner layer was red. The CR was then determined in the same way as described above for CAP.

After measuring CR, the plants within the chamber were cut off at ground level and removed. The chamber was returned to its original position and the gas exchange measurements were repeated in order to determine soil respiration. The CAP and CR values were corrected to account for the contribution of soil respiration.