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Cotton responds to different plant population densities by adjusting specific leaf area to optimize canopy photosynthetic use efficiency of light and nitrogen

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ABSTRACT

Appropriate plant population density (PPD) is an important crop management practice for optimizing canopy light distribution and increasing canopy photosynthetic capacity in field-grown cotton (*Gossypium hirsutum* L.). A 2-year field experiment was conducted to determine how the PPD (7.5, 19.5 or 31.5 plants m^{-2}) of cotton affects canopy photosynthetic capacity and photosynthetic use efficiency of light and N. The results indicated that PPD significantly affected both leaf morphology and canopy photosynthetic characteristics. As PPD changed, cotton maximized canopy apparent photosynthetic light use efficiency (CAP_{LUE}) and photosynthetic capacity by adjusting specific leaf area (SLA), which in turn affected leaf N distribution in the canopy. The SLA of all three canopy layers increased as PPD increased. In the upper canopy, canopy light interception and canopy apparent photosynthetic N use efficiency (CAP_{NUE}) rose as SLA increased, but CAP_{LUE} declined. As PPD increased, SLA in the mid- and lower-canopy layers increased significantly. This caused canopy apparent photosynthesis rate per leaf area (CAP_{Leaf}) and CAP_{NUE} to decline. Medium-PPD had the highest canopy apparent photosynthesis rate (CAP) and CAP_{LUE} in the mid- and lower-canopy layers. As a result, medium-PPD had the highest whole-canopy photosynthetic capacity and CAP_{LUE} in this study. Overall, the results indicated that optimal spatial distribution of both light and specific leaf area is key for efficient utilization of light and N in cotton canopies.

1. Introduction

Photosynthetically active radiation (PAR) is the major driver of plant photosynthetic processes (Meir et al., 2002). Previous studies have shown that PAR affects not only leaf morphological traits (e.g., specific leaf area, SLA) (Niinemets, 1999; Niinemets and Sack, 2006; Feng et al., 2008), but also leaf physiological traits (e.g., leaf N content and leaf N allocation to the photosynthetic system) (Feng and Fu, 2008; Yao et al., 2015). Leaves with low SLA and high leaf N allocation to photosynthesis usually have high leaf-level photosynthetic capacity (Niinemets and Sack, 2006; Feng et al., 2008; Feng et al., 2009; Yao et al., 2015). Canopy photosynthetic capacity is a function of leaf-level photosynthetic capacity, which varies among canopy layers.

Nitrogen is an essential resource driving the accumulation of plant C. Leaf N content at different positions in the canopy is positively correlated with the light environment during leaf development (Werger and Hirose, 1991; Anten et al., 1998). Plants adjust SLA in response to changes in PAR to optimize N investment in leaves (Hirose et al., 1988; Cornelissen et al., 1997). Yao et al. (2015) observed significant negative linear correlation between SLA and leaf N content per unit area in cotton canopies. Thus, SLA is an important determinant of the spatial distribution of leaf N within canopies (Cornelissen et al., 1997; Yao et al., 2015).

Ecological studies show that SLA is significantly influenced by light distribution from the top to the bottom of plant canopies (Niinemets et al., 1998; Meir et al., 2002). In deep shade environments, thin leaves enhance light harvesting because there is more leaf area per unit dry mass (Gutschick and Wiegel, 1988). In general, SLA is negatively related to leaf-level photosynthetic capacity per unit leaf area (Terashima et al., 2001; Niinemets, 2007). Hence, regulation of SLA can affect canopy photosynthetic capacity.

Improvements in canopy photosynthetic capacity are necessary to increase yield (Zhang et al., 2003; Dong et al., 2012; Mao et al., 2014; Dai et al., 2015). Crop management practices have

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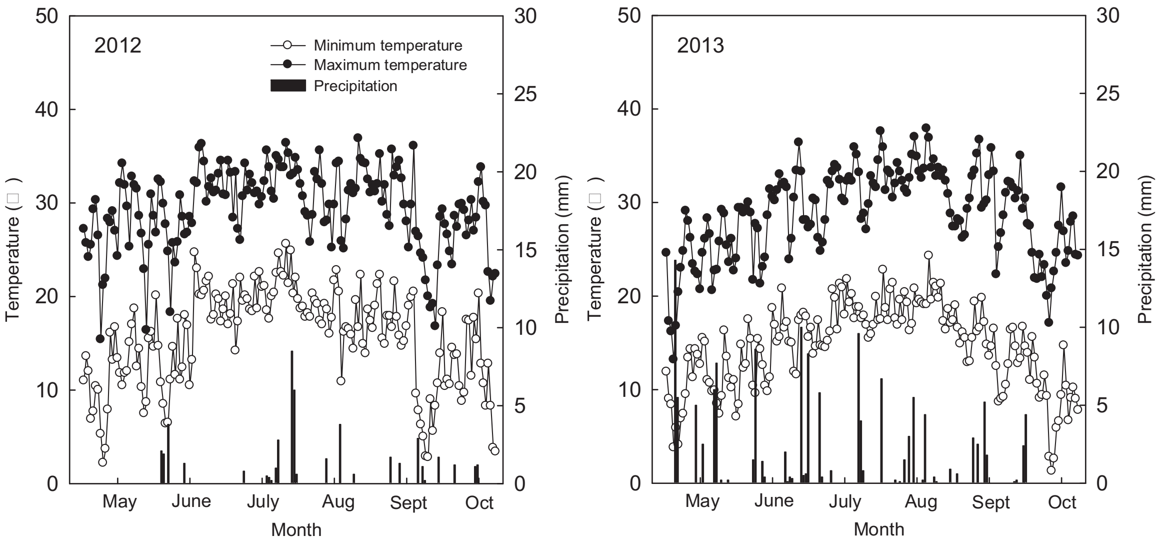

Fig. 1. Daily maximum temperature (filled circles), daily minimum temperature (open circles), and precipitation (bars) at the study site in 2012 and 2013.

significant effects on canopy photosynthetic capacity (Dong et al., 2010, 2012; Mao et al., 2014; Dai et al., 2015). For example, plant population density (PPD) affects canopy structural characteristics (e.g., leaf area index, canopy openness, and especially light distribution). All of these factors significantly influence canopy photosynthetic capacity (Zhang et al., 2003; Dong et al., 2006). Relatively little is known about how PPD affects SLA in cotton canopies or how SLA influences canopy apparent photosynthetic light use efficiency (CAP_{LUE}) and canopy apparent photosynthetic N use efficiency (CAP_{NUE}). The objectives of this study were to investigate (i) the influence of PPD on leaf morphology and leaf N distribution within the cotton canopy; (ii) the effects of these morphological and physiological factors on CAP_{NUE} and CAP_{LUE}; and (iii) the key characteristics which could contribute to the improvement of canopy photosynthetic capacity.

2. Materials and methods

2.1. Experimental design and field management

The field experiment was conducted in 2012 and 2013 at the Shihezi University Experiment Station in Xinjiang Province, China (45°19′N, 86°03′E). The experimental field has a fine clay loam soil (fine-loamy, mixed, mesic). Cotton (*cv.* Xinluzao 33) was sown through holes in plastic film mulch on April 18, 2012 and April 22, 2013. 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, the cotton in each plot was thinned so that there was one vigorous plant per hill. The resulting PPDs were 7.5, 19.5, and 31.5 plants m^{-2} (referred to as low-PPD, medium-PPD, and high-PPD, respectively). The experiment was arranged in a completely randomized design with three replications. Canopy photosynthetic capacity at boll-setting is a major determinant of cotton yield (Zhang et al., 2002, 2003). Therefore, the measurements described in the following sections were made at the boll-setting stage (100–110 days after sowing) in both years. The experiment has been previously described in detail (Yao et al., 2015). Thus, only the main features are described here.

2.2. Determination of photosynthetically active radiation

Photosynthetically active radiation (400–700 nm) was measured at four heights in each plot using a SunScan Canopy Analysis System (Delta, UK; 100 cm line quantum sensor). The heights were as follows: at the soil surface (I_1), one-third of canopy height (I_2), two-thirds of canopy height (I_3), and 0.1 m above the canopy (I_4). The measurements were all made on the same day. At least ten readings of photosynthetic photon flux density (PPFD) were taken at each height. The line quantum sensor was held in different directions but always parallel to the earth's surface. The PAR interception (PAR_i) of each canopy layer was then calculated using the equation:

$$PAR_i = I_{t+1} - I_t$$

where I_t is the incident radiation at one of the four heights described above.

2.3. Determination of canopy apparent photosynthesis

Canopy apparent photosynthesis (CAP) was measured 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 CAP measurements were made between 12:30 and 13:30 h on clear days (immediately after determining PAR). The PPFD was at its daily maximum during this time, with values at I_4 averaging $1750 \pm 25\ \mu mol\ m^{-2}\ s^{-1}$. The assimilation chamber was placed over two rows in the center of each plot. There was a 10-cm-wide space between the two cotton rows. There were 5–6, 12–13 and 20–21 plants inside the chamber in the low-, medium-, and high-PPD treatments, respectively. Two assistants held the chamber tightly against the plastic film mulch to prevent air leakage from around the bottom of the chamber. Gas exchange rates in each plot were measured during at least three 60 s intervals using a LI-8100 Soil CO_2 Flux System (LI-COR Inc., Lincoln, NE, USA). We began recording the values when the CO_2 concentrations inside the chamber began to drop steadily. The CO_2 concentrations inside the chambers ranged from 350 to 400 ppm during the gas sampling times. The air temperature within the chamber was less than 3 °C above ambient. The relative humidity remained near ambient levels.

After measuring CAP, 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