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Characteristics of canopy structure and contributions of non-leaf organs to yield in winter wheat under different irrigated conditions

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ABSTRACT

Non-leaf green organs of wheat plants may have significant photosynthetic potential and contribute to grain yield when the plants are subjected to stress at late growth stages. Canopy structure, change of green non-leaf organ area (e.g., ear, peduncle, sheath), the proportion of green non-leaf organs area to total green area and the contribution proportion from different organs' photosynthate to grain yield in winter wheat (*Triticum aestivum* L.) were studied at Wuqiao Experiment Station of China Agricultural University, Hebei, China, in 2001–2002 and 2002–2003 using two winter wheat cultivars, Shijiazhuang8 (SJZ-8) and Lumai21 (LM-21). Four irrigation treatments used were W0 (no water applied during spring), W1 (750 m^3 ha^{-1} water applied at elongation), W2 (1500 m^3 ha^{-1} applied 50% at elongation and 50% at anthesis) and W4 (3000 m^3 ha^{-1} applied 25% at upstanding, booting, anthesis and grain filling), respectively. Results showed that the area of top three leaf blades decreased and the proportion of green non-leaf organ area to the total green area at anthesis increased with the decreasing of water supply. Root weight increased in the 0–100 cm soil layer and decreased in the 100–200 cm layer when water supply increased, suggesting reducing irrigation enhanced root weight in deep soil layer. The photosynthetic contribution of non-leaf organs above flag leaf node to grain yield increased with decreasing water supply, and was significantly higher than that of the flag leaf blade contribution. Winter wheat grain yield increased, but water use efficiency (WUE) decreased, with increase in water supply. Higher light transmission ratio in the canopy after anthesis was achieved with smaller size and high quality top leaf blades, higher grain-leaf ratio and larger proportion of green non-leaf area, which lead to higher canopy photosynthetic rate and WUE after anthesis. Irrigation of 1500 m^3 ha^{-1} applied in two parts, 750 m^3 ha^{-1} applied at elongation and another 750 m^3 ha^{-1} applied at anthesis, was the best irrigation scheme for efficient water use and for high yield in winter wheat.

1. Introduction

Leaf tissue is the main photosynthetic organ of plants. However, non-leaf organs, such as stem (Nilsen, 1995), inflorescence and developing fruit (Weiss et al., 1988), also have actual or potential photosynthetic capability (Guido and Hardy, 2003). Many studies have indicated that non-leaf organs of wheat (ear, inter-node and sheath) showed the capability of assimilating CO_2 by the C_4 pathway of photosynthesis, or C_3–C_4 intermediate type of photosynthesis (Singal et al., 1986; Blanke and Lenz, 1989; Ziegler-Jons, 1989). The various photosynthetic parts of the ear together with the flag leaf make major contributions to wheat grain carbohydrates (Singal et al., 1986). Luo (1965) demonstrated an equivalent contribution between wheat flag leaf and its sheath. Kriedemann (1966) stated that the ear contributed 10–44% of total wheat photosynthesis, depending on variety, environment and experimental procedures. Maydup et al. (2010) also reported the contribution of ear photosynthesis to grain yield differed depending on the experimental approach used (from about 12–42%). Araus et al. (1993) proved with C isotope technology that ≥59% of the materials in wheat grain came from photosynthesis in ear tissue, especially under drought conditions where the ears may become the main photosynthetic contributor to grain filling (Bort et al., 1994; Abbad et al., 2004; Tambussi et al., 2007).

In response to drought and high temperature, wheat non-leaf organs, sheath, glume and awn showed advantages in resisting stress and resulted in higher WUE than leaves (Araus et al., 1993; Wang et al., 2001; Xu and Wang, 2001; Martinez et al., 2003;

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Tambussi et al., 2005). Under conditions of water stress, spikelets maintained higher water potential than leaves (Morgan, 1977; Xu and Ishii, 1990; Bort et al., 1994; Tambussi et al., 2005). CO_2 fixed by ear parts make a greater contribution to canopy photosynthesis in cereals experiencing post-anthesis drought than in well-watered plants (Johnson and Moss, 1976; Bort et al., 1996; Gebbing and Schnyder, 2001; Reynolds et al., 2005). Blum (1986) suggested that awns are important for wheat production in semiarid regions, both in terms of their high WUE and their favorable temperature response. Ali et al. (2010) demonstrated that awn length was positively and significantly correlated with grain yield. The ear assumes a greater role than flag leaves in supplying assimilate to grain when water stress develops (Johnson and Moss, 1976; Abbad et al., 2004; Tambussi et al., 2007). The extent of depression in photosynthesis resulting from water deficit was larger in the leaf blades than in ear, leaf sheath and stem (Xu and Ishii, 1996). The greater ability of ears, compared to leaves, to supply assimilate to the grain under conditions of water stress depends partly on the greater availability to the grain of ear assimilate than that of flag leaf assimilate (Carr and Wardlaw, 1965; Tambussi et al., 2007). Martinez et al. (2003) and Tambussi et al. (2005) suggested that the photosynthetic parts of the ear have physiological and morphological traits that make them more tolerant to water deficit.

In northern China, water is a limiting factor for the improvement in winter wheat grain yield because drought always occurs during winter wheat growth season. Additional water must be supplied to winter wheat for the achievement of high grain yield. However, more irrigation in traditional farming systems has led to serious environment problems (Lan and Zhou, 1995). In order to use the water stored in soil and enhance water use efficiency (WUE), researchers at China Agricultural University have developed a water-saving farming system at Wuqiao Experimental Station, Hebei, China (Li and Zhou, 2000). Only 750–1500 m^3 ha^{-1} water was applied in this system to winter wheat, which developed an optimal canopy structure and mainly used water in the upper 2-m soil layer. Water use efficiency of this system reached $\geq$16.5 kg ha^{-1} mm^{-1}.

There is limited information available on the photosynthetic characteristic of the ear parts during grain development. It is a challenge to maximize the photosynthesis potential of wheat non-leaf organs under water-saving conditions. Our previous work showed that one of the most important cultivation technologies for water-saving and high yield winter wheat was to develop population structure with high density, small phylliform morphology, high photosynthetic capacity and low water consumption (Wang et al., 2001; Zhang et al., 2003). Moreover, the population structure of water-saving and high yield winter wheat, especially non-leaf organs' structure characteristics need to be revealed further. The objectives of this study were: (1) to investigate the changes of photosynthetic areas composition in the canopy and single plants; (2) to investigate the distribution of wheat root with different irrigation amounts; (3) to determine how the canopy structure changes were correlated with yield under water-saving conditions; and (4) to investigate the contribution of different photosynthetic organs above flag leaf node to grain weight of wheat under different irrigation schemes.

2. Materials and methods

2.1. Experimental field and meteorological conditions

Two years of winter wheat experiments were conducted at Wuqiao Experiment Station of China Agricultural University at Cangzhou, Hebei province, China, in the 2001–2002 and 2002–2003 growing seasons. Soil was clay-loam with an average bulk density of 1.5 g cm^{-3} in the upper 100 cm layer. The underground water level was 6–9 m. Maximum water storage in the upper 200-cm soil layer was 640 mm, and available water storage was 420 mm. Soil moisture at maximum field capacity was 21.7%. The wilting coefficient was 7.6%. The total rainfall in wheat growth period during 2001–2002 was 53.5 mm, only 39.3% of the long term average rainfall (136 mm). The total rainfall in wheat season during 2002–2003 was 112.1 mm.

2.2. Plant materials and experimental design

In 2001–2002, Lumai21 (LM-21), a commonly used variety in Hebei province, was sown on October 12, 2001 with a row space of 20 cm. Seedling density after emergence was 6×10^6 plant ha^{-1}. Experimental fields were irrigated with 75 mm water before sowing. No irrigation was applied before upstanding. Four irrigation treatments were established, i.e. W0, no water applied during spring; W1, 750 m^3 ha^{-1} applied at elongation; W2, 1500 m^3 ha^{-1}, 50% applied at elongation and 50% at anthesis; and W4, 3000 m^3 ha^{-1}, 25% of which applied at upstanding, booting, anthesis and grain filling, respectively. Specifically, W4 was taken as the control that was a sufficient irrigation scheme applied in the traditional wheat production by local farmers, and W2 was a water-saving irrigation scheme for high WUE and high yield, which had been clarified through many years' research (Lan and Zhou, 1995; Li and Zhou, 2000).

In 2002–2003, two wheat cultivars, LM-21 and Shijiazhuang8 (SJZ-8), were sown on October 13, 2002. Three irrigation treatments were established in this year, W0 (no water applied during spring; W2 (1500 m^3 ha^{-1}, 50% applied at elongation and 50% at anthesis) and W4 (3000 m^3 ha^{-1}, 25% of which was applied at upstanding, booting, anthesis and grain filling, respectively).

A completely randomized block design (CRBD) with three replications was used in both experiments. The plot size was 50 m^2. In both years, all experiments received 225 kg N ha^{-1} (as urea), 300 kg P ha^{-1} (as ammonium monoacid phosphate), 150 kg K ha^{-1} (as potassium sulfate), 15 kg Zn ha^{-1} (as zinc sulfate) and 30 m^3 ha^{-1} organic fertilizer (as chicken manure) before sowing. No fertilizer was applied during growth.

2.3. Data acquisition and analysis

2.3.1. Green areas of plant organs

Wheat photosynthetic organs areas were measured six times during the growing season (Table 5). Samples were collected from double rows 50 cm long. Leaf blade area was calculated as leaf length × leaf width × 0.82. Whole ear area was determined according to Teare and Peterson (1971), Qiu and Zhai (1985) as the equation below:

$$\text{Whole ear area} = \text{ear length} \times \text{ear width} \times 3.8\ (\text{glumes surface area}) + \text{total awn length of top third spikelet} \times \text{fruit spikelet number} \times 0.1\ (\text{awn surface area})$$

Areas of culms and sheath were measured as the equation below:

$$\text{Culms or sheath area} = \text{culms or sheath length} \times \pi \times D\ (\text{culms or sheath diameter})$$