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Root-sourced signal and photosynthetic traits, dry matter accumulation and remobilization, and yield stability in winter wheat as affected by regulated deficit irrigation

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A B S T R A C T

Regulated deficit irrigation (RDI) is important water-saving technique. Although some positive effects of RDI have been confirmed in earlier results, more knowledge is still need on how RDI can affect grain growth and drought ability of crops. A micro-plot field experiment was conducted under a movable transparent rain-shelter from October 2011 to June 2012. Three RDI treatments designed to subject the plants to soil water deficit at different stages: tillering-the beginning of the spring-growth stage (RS1), the beginning of the spring-growth to the end of stem elongation stage (RS2), and booting-heading stage (RS3). The results showed that RDI treatments improved the non-hydraulic root-sourced signal (nHRS) sensitivity and photosynthetic capacity of winter wheat. The soil water content (SWC) of RS1, RS2 and RS3 treatments when the nHRS was triggered and net photosynthetic rate (P_N) declined significantly was significantly lower than the control during progressive soil drying. After flowering stage, RS1 and RS2 treatments had significantly lower post-flowering accumulated dry matter (ADM), and but increased pre-flowering dry matter remobilization (DMR) in well-watered group, and both significantly increased DMR and ADM of wheat in dried group compared to the control. RS1 and RS2 had no significant effect on grain yield in well-watered group, but significantly increased grain yields in dried group. In addition, RS1 and RS2 also increased water use efficiency (WUE) and yield stability of winter wheat compared to the control. Above all, the results of this study showed that RS1 and RS2 treatments significantly increased drought resistance ability of winter wheat through improving the nHRS sensitivity of plants during progressive soil drying, and increased grain yield through increasing both current photosynthesis and the remobilization of pre-anthesis carbon reserves.

1. Introduction

Water shortage is the major bottleneck that limits sustainable development of agriculture in north China. Efficient use of water by irrigation is becoming increasingly important. Apparently, the only method to maintain cereals production sustainable in this area is to develop water-saving agriculture and improve water use efficiency (WUE). Regulated deficit irrigation (RDI) is an important water-saving technique to improve WUE of crops (Du et al., 2010). RDI has been tested to minimize water use, decrease vegetative growth, increase yield and WUE (Leib et al., 2006; dos Santos et al., 2007). In China, it has been successfully used in cereals and tested that RDI improved crop water use efficiency in maize production in loess plateau of northwest China (Kang et al., 2000) and wheat

Abbreviations: RDI, regulated deficit irrigation; nHRS, non-hydraulic root-sourced signal; HRS, hydraulic root-sourced signals; P_N, net photosynthetic rate; ADM, post-flowering accumulated dry matter; DMR, pre-flowering dry matter remobilization; WUE, water use efficiency; GYS, grain yield stability; Gs, stomatal conductance; LRWC, leaf relative water content.

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production in North China Plain (Zhang et al., 1998). Different from the traditional irrigation method, RDI is a modern irrigation technology based on plants' adaptive and specific responses to drought (Fabeiro et al., 2001; Kang et al., 2002). Although some positive effects of RDI have been confirmed in earlier results, more knowledge is needed on how RDI can affect the grain yield and what the consequences are for plant production in different water regimes.

To cope with environmental drought stresses, plants have evolved with some mechanisms for quickly perceiving stresses and actively regulating their stress tolerance reactions. Roots play important roles through various adaptive responses specific to the soil moisture. Understanding root system's adaptive responses specific to drought stress in stress-prone environments will provide important opportunities to reveal the mechanism of action on RDI. However the current study on root system is far from satisfactory. The crucial reason – other than the difficulty of its research method – is that we could not find a good way in combining soil drought, root reactions and ground adjustment, which makes it tough to continue this research. The theory of root-sourced signaling has been raised and attracted considerable interest in recent years. The previous studies have ascertained the course of reaction on root-to-shoot communication signal, in which root-sourced signals fall into two types: non-hydraulic root-sourced signals (nHRS, i.e. chemical signals) and hydraulic root-sourced signals (HRS). Roots in progressively drying soil first produce nHRS, which are transported through the transpiration stream to the shoots where shoot physiology (mainly leaf expansion rate and stomatal opening) is regulated (Blackman and Davies, 1985; Xiong et al., 2006, 2007). Thus, nHRS may substantially reduce the water loss through stomata, when no water deficit is yet detectable in the shoots; this is a first defense against possible drought (Davies et al., 1994; Xiong et al., 2007). Continuing drought sets up a hydraulic gradient between the leaf and the drying soil. This hydraulic gradient speeds up the development of leaf water deficit by reduction in leaf turgor pressure (Croker et al., 1998) and further lowers stomatal conductance, weakening gas exchange with the atmosphere, and this eventually retards plant growth. That point is typically defined as the commencement of the HRS (Blackman and Davies, 1985). Ober and Sharp (2003) argued that early triggering of nHRS is important for crop production during periods of decreasing soil moisture. In addition, root sourced signal also played important role in regulating root growth and its development, adjusting root/shoot ratio, and optimizing assimilation allocation. It is a new way to carried out the studies of water-saving agriculture by improving root-sourced signals traits of plants with appropriate agriculture measure in agriculture production practice (Li and Zhao, 1997). Some effective irrigation approaches, such as deficit irrigation (DI) (Jensen et al., 2010), partial root zone drought (PRD) (Dry and Loveys, 1998) and alternate partial root zone irrigation (APRI) (Kang and Zhang, 2004) were profited from the mechanism of shoot water status regulation by the root-sourced signal. Recent studies (Xiong et al., 2006, 2007) found that nHRS may also contribute to yield maintenance during drought. The previous studies (Fan et al., 2008, 2009) also showed that the nHRS varies among species, like other drought response characteristics (e.g. osmotic adjustment). RDI could increase drought resistant ability of some crops (Zhang et al., 2012), which could also change root-sourced signal properties of crops. Therefore, we also need to know if RDI changed nHRS traits of plant and how nHRS integrates with the whole system for plants experiencing progressive drying.

In grain crops, both current assimilation transferred directly to kernels and remobilization of assimilates stored in vegetative plant parts contribute to grain yield (Gebbing et al., 1999; Arduini et al., 2006) and may buffer the yield against unfavorable climatic conditions during grain filling (Tahir and Nakata, 2005). Zhang et al. (1998) proposed that increased remobilization of reserved carbon from stems and sheaths under water stress may contribute to increased harvest index in deficit irrigation treatments. Previous research indicated that proper water deficit exerted purposefully by RDI in some growth stages are helpful to optimize distribution of photosynthetic matter in tissues and organs, thus resulting in high grain yield, and reduction of proportion of nutrient organs in total organic matter (Cai et al., 2002). However, no study has been conducted to investigate RDI effect on remobilization of pre-anthesis carbon reserves.

The adaptive strategies selected for plants suffering from drought not only affect crop survival but also crop production, while different physiology effects vary with different field managements. In the present study, plants were exposed to 3 RDI treatments under a movable transparent rain-shelter. The objective of this study was to (1) understand the physiological mechanism for determinations of drought resistance ability and WUE under RDI; and (2) investigate effect of RDI on yield stability, photosynthetic traits, dry matter accumulation and remobilization of pre-anthesis carbon reserves during grain filling.

2. Materials and methods

2.1. Plant materials and experimental design

A micro-plot field experiment was conducted from October 2011 to June 2012 at the Farmland Irrigation Research Institute, Chinese Academy of Agricultural Sciences, Xinxiang, China (35°18′N, 113°54′E). All micro-plots were arranged under a movable transparent rain-shelter. The micro-plot measured 0.5 m × 0.5 m, its frame and bottom is made of metal plate, and the height is 1.3 m. Before sowing of seeds, dig a square pit with a depth of 1.2 m in the field first and then put the micro-plot into the pit and filled the soil into the micro-plot just as it was in levels of original soil profiles. Eighty seeds of winter wheat (*Triticum aestivum* L. cv. Yumai 49) per micro-plot were sown at a depth of 2 cm and thinned to 40 seedlings per plot at the 3-leaf stage. Chemical fertilizers (N, P and K) were applied to the micro-plots at 120, 60 and 48 kg ha^{-1}, respectively, to ensure sufficient nutrition. Randomly selected plants were subjected to RDI treatments at three different stages: tillering—the beginning of the spring-growth stage (RS1), the beginning of the spring-growth to the end of stem elongation stage (RS2), and booting-heading stage (RS3). During regulated deficit irrigation (RDI), plants were maintained at 45–55% FWC (field water capacity). After treatment, plants were re-watered to 70–75% FWC until anthesis. The control plants (CK) were maintained at 70–75% FWC until heading stage. There were 18 replications (micro-plots) per treatment and all micro-plots were arranged randomly under a movable transparent rain-shelter. Soil water levels were determined gravimetrically by weighing method and irrigating every day. At the heading stage, plants in every treatment were divided into two groups: Group A plants (9 replications) were maintained at 70–75% FWC; Group B plants (9 replications) were deprived of water and dried naturally to 45% FWC, nHRS and HRS were measured in the process of drought. Group B plants were maintained at 45–50% FWC after nHRS and HRS measurements.

2.2. Experimental methods

Photosynthetic rate (P_N), stomatal conductance (*Gs*) and leaf relative water content (LRWC)

At the anthesis stage, the instantaneous photosynthetic rate (P_N) and stomatal conductance (*Gs*) of the flag leaf was measured using a LI-6400 portable photosynthesis system (LI-Cor, Inc., Lincoln, Nebraska, USA) during 9:00–11:00 am and 2:00–4:00 pm daily after