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Dynamic responses of wheat to drought and nitrogen stresses during re-watering cycles

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ABSTRACT

Temporal responses to drought and nitrogen stresses were studied on wheat (*Triticum aestivum*) seedlings subjected to drying and re-watering cycles. Growth traits were monitored in a soil column experiment conducted with two water and two nitrogen levels. Leaf area, dry weight, carbon and nitrogen mass, root/shoot ratio, specific leaf nitrogen, photosynthesis, transpiration, and water and nitrogen use efficiencies dynamically responded to water and nitrogen stresses as a function of the degree of specific stress over the growing period. Specific leaf nitrogen was critical for improving photosynthetic activity, and influenced water use efficiency positively but nitrogen use efficiency negatively, indicating a distinct trade-off between water and nitrogen use efficiencies. Subsequent to irrigation and the immediate alleviation of severity of water and nitrogen stresses, photosynthesis and transpiration recovered gradually over a period of 3–4 days. Extent of recovery was influenced by the degree of stress prior to re-watering and the re-watering cycles. Ignoring the dynamics of recovery from stress led to notable errors in numerical simulations of the dynamics of soil water and plant transpiration.

1. Introduction

Drought is a major limiting factor for global agriculture and the limitation is greatly aggravated by nitrogen (N) deficiency (Heitholt, 1989; Shangguan et al., 2000; Gonzalez-Dugo et al., 2010). Growers are challenged to optimize plant growth and enhance water and N use efficiencies (WUE and NUE, respectively) under drought and N stresses (Reich et al., 1989; Wu et al., 2008).

Morphological and physiological responses of plants to soil water and/or N availability have received considerable attention in the past decades. Although there are some disagreements (Heitholt, 1989; Ashraf et al., 2001), an enhancement in plant dry weight (DW) ratio of roots to shoots (RR/S) has been widely reported under water and/or N stress conditions (Wilson, 1988; Skinner and Comas, 2010). Both photosynthesis and transpiration are understood to be significantly inhibited by water and/or N stress in a variety of species at both leaf and whole plant scales, as well as in terms of leaf area (LA) and DW (Shimshi, 1970; Hsiao, 1973; Nagarajah, 1981; Borghi, 2000; Wu et al., 2008). Less attention has been paid concerning the effects of the stressers on carbon (C) and N uptake and allocation (Peichl et al., 2012).

Regulation of photosynthesis and transpiration is expected to directly influence WUE and NUE, which are, respectively, defined as net C assimilation per transpiration volume and leaf N mass during a given growth period (Reich et al., 1989). Under drought conditions, WUE is widely reported to increase (Shangguan et al., 2000; Liu et al., 2005), but to decrease under N deficiency (Heitholt, 1989; Shangguan et al., 2000; Brueck and Senbayram, 2009). However, this is not universal, as a number of studies demonstrated the opposite case when water (Monclus et al., 2006; Wu et al., 2008; Li et al., 2009; Galle et al., 2011) or N (Hubick, 1990; Wu et al., 2008) is limiting. Comparatively, there is better agreement

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Abbreviations: DAP, days after planting; DW, dry weight; HN, high nitrogen; HW, high water; LA, leaf area; LN, low nitrogen; LW, low water; LTR, leaf transpiration rate; NUE, nitrogen use efficiency; PR, photosynthesis rate; RR/S, ratio of roots to shoots; SLN, specific leaf nitrogen; SNC, soil nitrogen content; SWC, soil water content; WUE, water use efficiency.

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concerning NUE: repression is usually found under drought, and strong enhancement of NUE is universally induced by N deficiency (Reich et al., 1989; Fredeen et al., 1991; Van den Boogaard et al., 1995).

Besides plant species and varieties (Galle et al., 2011), the referred discrepancies may be credited to the fact that the studies were conducted over diverse growth stages and environmental conditions (Flexas et al., 2004; Brueck and Senbayram, 2009). Even under stable water and/or N stress, plant responses might vary during different growth stages. For example, in sunflower, Cechin and Fumis (2004) found that leaf transpiration rate (LTR) under N stress was reduced only at the beginning of leaf growth. Except in limited cases (Jose et al., 2003; Cechin and Fumis, 2004; Wu et al., 2008; Achten et al., 2010), most of the previous studies were subjected to few individual samplings, and plant dynamic characteristics under water and/or N stress were seldom examined. Furthermore, due to the overall interest in grain yield, relatively little effort focused on plant vegetative development, in spite of the fact that vegetative development is expected to considerably influence grain yield potential (Wilhelm et al., 1993).

Wheat is the world's most widely grown crop and its cultivation embraces approximately one sixth of the total arable land globally (Slafer and Satorre, 2000). While wheat is mainly cropped under rainfed conditions, irrigation has been found enable or raise production, especially in arid or semi-arid areas (Shangguan et al., 2000). Wheat development is characterized by three phases: a short vegetative phase in which number of leaves is determined, a reproductive stage beginning with spikelet initiation and finishing with the initiation of the terminal spikelet in which the number of fertile florets is determined, and a grain-filling phase (Miralles and Slafer, 2000). These developmental changes are accompanied by increased assimilation and nutrient demands of the vegetative organs. During the vegetative phase, N undergoes continuous translocation within plants, back and forth from roots to shoots (Borghi, 2000).

Many experiments have been conducted on plant growth under drought conditions and as soil water content (SWC) increases following re-watering (Boyer, 1971; Heckathorn et al., 1997). Some of the studies showed that plant growth measured as LA and DW was remarkably stimulated by re-watering following drought (Liu et al., 2001; Reynolds et al., 2004; Siopongco et al., 2006), while other researchers found that plant growth characteristics such as leaf photosynthesis rate (PR) and LTR recovered gradually (Miyashita et al., 2005; Galmés et al., 2007). Furthermore, recovery can be incomplete and its extent is apparently influenced by plant species, variety, plant or leaf age, severity of stress prior to re-watering, and number of consecutive drying cycles (Flexas et al., 2004; Miyashita et al., 2005; Galmés et al., 2007; Xu et al., 2009). Plant recovery from drought after re-watering has not been fully clarified and has been attributed to various morphological, physiological and biochemical mechanisms, including maintenance of membrane stability, osmotic adjustment, phytohormone accumulation, delay in leaf rolling during stress and increased C partitioning and carbohydrate storage in plant organs (Xu et al., 2009; Hu et al., 2010). In most wheat growing regions, rainfall and irrigation patterns dictate drought and re-watering cycles that can occur at any of the different stages during the plant life cycle (Borghi, 2000). As compared to trees, grasses or other crops (Flexas et al., 2004; Miyashita et al., 2005; Siopongco et al., 2006; Xu et al., 2009), less attention regarding plant recovery from drought has been paid regarding wheat (Liu et al., 2001). Furthermore, root-water-uptake models, incorporating soil water flow equations, are commonly applied to simulate soil water flow as well as plant transpiration (Feddes et al., 1976; Wu et al., 1999; Shi and Zuo, 2009). However, plant recovery from drought is hardly considered in the published root-water-uptake models.

The main objective of this study was to examine the dynamic responses of plant traits to water and N treatments on wheat subjected to drought and re-watering cycles, and to test whether the processes could be accurately reflected by simulation of plant transpiration using a popular root-water-uptake model.

2. Material and methods

2.1. Soil column experiment for winter wheat

Winter wheat (*Triticum aestivum* L. cv. Jingdong 8) was grown in 53 cm high soil columns in a greenhouse experiment (Shi and Zuo, 2009; Shi et al., 2013). The following four treatments were initiated at 20:00 on 10 DAP, and subsequently irrigated every 6 days: (1) high water high N (HWHN), (2) high water low N (HWLN), (3) low water high N (LWHN), and (4) low water low N (LWLN). The average root zone SWC for high water (HW) treatments was designed to be no less than 80% of field water capacity. The irrigation quantity for low water (LW) treatments was designed to be half that of HW treatments. The high nitrogen (HN) treatments were irrigated with half-strength Hoagland solution with NO_3^-–N = 0.105 mg cm^{-3}, while the low nitrogen (LN) treatments were irrigated with modified half-strength Hoagland solution having NO_3^-–N = 0.011 mg cm^{-3}.

Sampling was conducted twice every 6 d (0.5 and 5.5 days after each irrigation event), for a total of 16 samplings between 10 and 57.5 DAP under each treatment. Two columns of each treatment were selected randomly for shoot removal and were opened to sample soil from surface to rooting depth (2 cm thick layer for the first two samplings and 4 cm layer for the later 14 samplings). A portion of each soil sample was used to determine soil water content and the rest was extracted with 0.01 mmol cm^{-3} $CaCl_2$ solution and analyzed with a continuous flow analyzer (TRAACS 2000, Bran + Luebbe, Norderstedt, Germany) to determine soil solution N concentration (N mass per unit soil solution volume, mg cm^{-3}). The opened soil columns were cut into layers at the same intervals as for soil samples, and each layer was washed via a 0.05 cm diameter sieve to collect roots. The roots from each soil layer were dried to a constant weight at 70 °C to determine DW, and tissue C and N concentrations (C or N mass per unit DW, mg g^{-1}) were measured with an element analyzer (CHNSO EA 1108, Carlo Erba, Italy). The shoots were scanned (SNAPSCAN 1236, AGFA, Germany) and analyzed for LA, and then DW, tissue C and N concentrations were measured.

Two soil columns for each treatment were chosen to measure net canopy PR from 8:00 to 10:00 in the morning every day, with a stirred canopy chamber operated as a closed system (Held et al., 1990; Steduto and Hsiao, 1998). The chamber was made of a Perspex cuvette (50 cm high, 0.6 cm thick and 30 cm in diameter; internal volume = 0.04 m^3), and was sealed with a Perspex cover at the top. A fan was located under the cover to mix the air in the chamber. A small hole at the top of the chamber was used to connect a gas-exchange system (Li-6400; Li-Cor, Lincoln, NE, USA). At the bottom of the chamber, a Perspex cover with a 16 cm diameter hole was affixed with rubber sealing where it could be joined to the upper soil boundary in the soil column. The decrease of CO_2 concentration during a period was monitored as soon as the chamber was placed over the soil column. In order to mitigate the effect of the increase of humidity and the decrease of CO_2 concentration on plant photosynthesis in the chamber, a short period was set as 30 s. The measurements were repeated four times for each soil column, with the chamber removed from the soil column and aired for at least 60 s between successive measurements. Additionally, two soil columns from each treatment without plants were