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The physiological processes and mechanisms for superior water productivity of a popular ground cover rice production system

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ABSTRACT

Ground cover rice production systems (GCRPS) have been shown to both save water and increase yields compared to traditional paddy rice production systems (TPRPS). Physiological processes and mechanisms explaining the superiority of a popular GCRPS were investigated in a series of hydroponic, soil column and field experiments. Soil water, temperature and nitrogen, leaf gas exchange, plant water and nitrogen, growth and yield, transpiration, and water productivity were analyzed. Compared to TPRPS, plant available soil inorganic nitrogen was generally improved under GCRPS due to a combination of higher soil temperature and less nitrogen loss through non-physiological water consumption, especially during the early growing season. Consequently, more nitrogen was absorbed by plants under GCRPS except serious drought conditions, accompanied by higher nitrogen contents in plant tissues. Preferable specific leaf nitrogen might lead to higher leaf photosynthetic rate under optimal water conditions and less decrease relative to leaf transpiration rate under water stress. Therefore, rice under GCRPS grew faster with much more biomass and grain yield while transpiration consumption was limited in spite of the fact that the number of tillers and therefore leaf area were increased relative to TPRPS, resulting in superior water productivity. Compared to TPRPS, the root system under GCRPS was limited, but it could absorb enough water and nutrients (especially nitrogen) to support a relatively large canopy even when under water stress, which might be attributed to its higher nitrogen content and thus stronger activity.

1. Introduction

Rice is the major staple food for more than 50% of the world's population, accounting for approximately 20% of total energy intake, and an annual increase of 8–10 million t is estimated as necessary to meet future needs (Seck et al., 2012). Asia produces about 75% of the world's rice while consuming 45% of its total fresh water resources (Bouman and Tuong, 2001; Bouman et al., 2007). It is estimated that about 15–20 million ha of irrigated rice will suffer from water scarcity by 2025 (Tuong and Bouman, 2003). As the largest rice producer in the world, China cultivates 29 million ha of rice, representing about 30% of its total farmland and consuming about 70% of its total agricultural water resources (Zhang, 2007). Water shortage in China is estimated to reach 400 billion m^3 by 2050, roughly corresponding to 80% of its current annual capacity (Tso, 2004). Global rice production predominantly depends on traditional paddy rice production systems (TPRPS), where a standing water layer is always maintained except during the drying field periods and water consumption per unit area is about 3–5 times that of alternative dry-land crop production systems (Bouman and Tuong, 2001). Therefore, exploring a high-efficient rice production technology, to meet the requirements of increasing production coupled with decreasing water consumption, is necessary.

Designed to promote water conservation, one kind of ground cover rice production system (GCRPS) with some strip soil beds, mulched by plastic film and on which there is not a standing water layer even when irrigation is implemented through the surrounding furrows, has been successfully applied in more than 4 million ha in China (Lin et al., 2002; Liu et al., 2013; Tao et al., 2014). This popular GCRPS was initially introduced in the mountainous regions of Central China in 1980s to overcome both limitations of low temperatures during the early growing season and seasonal water shortages (Lin et al., 2002). Compared with TPRPS, the significant differences for GCRPS lie in the transformation of root zone soil water status from completely saturated and anaerobic to unsatu-

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rated and aerobic, and an increased temperature in the near surface soil layer, especially during the early growing season (Tao et al., 2015). In recent years, with the rapid expansion of GCRPS, efforts have been made by many researchers to investigate this novel system regarding water consumption, plant growth, yield formation, leaf gas exchange, water use efficiency (WUE), etc. Except for cases when temperature was not the main limitation for rice growth at the beginning of vegetation period such as in Southeast China (Xu et al., 2007a, b; Zhang et al., 2008; Zhang et al., 2009), previous studies have indicated significant promotion of shoot growth and grain yield under GCRPS while non-physiological water losses (the sum of runoff, deep drainage and evaporation) and even transpiration consumption were reduced in comparison to TPRPS (Liu et al., 2005b; Li et al., 2007; Fan et al., 2012; Qu et al., 2012; Liu et al., 2013; Liu et al., 2014; Tao et al., 2014, 2015; Jin et al., 2016). The superior water productivity of GCRPS, especially resulted from the increased yield while decreased transpiration consumption, is inspiring since it is completely different from most dryland crops production systems. Water productivity can be improved under appropriate water stress conditions when plant growth and thus grain yield are reduced at a lower rate than transpiration. However, its attractiveness is offset and discredited as the accompanying economic costs of the reduced yields become inhibitory (Liu et al., 2005a; Zhang et al., 2008; Lei et al., 2009; Matsuo et al., 2010).

The superior water productivity of rice under GCRPS is likely due to the integrated effects of soil water and temperature conditions. Firstly, under GCRPS, increased soil temperature and decreased soil water content might directly impact rice tillering and root lengthening (Shimono et al., 2002; Nagasuga et al., 2011). Secondly, the changed soil water and temperature conditions and therefore the changed soil nutrient (e.g. nitrogen) conditions under GCRPS, might also influence water and nutrient uptake and their contents in the plant itself (Liu et al., 2003; Fan et al., 2005). For many kinds of plant such as wheat and American elm, positive correlation has been found between WUE evaluated on transpiration and specific leaf nitrogen (Morgan, 1984; Heitholt, 1989; Reich et al., 1989; Shi et al., 2014), as well as between root uptake activity and nitrogen content in roots (Shi and Zuo, 2009; Shi et al., 2013). However, the physiological processes and mechanisms driving rice under GCRPS to produce more biomass and even grain yield along with less transpiration are not clear and have yet to be determined. This study consequently was driven by the hypothesis that the higher water productivity under GCRPS could be attributed to preferable nitrogen contents in soil and thus in plant tissues resulting from the corresponding soil water and temperature conditions. Taking TPRPS as a control, three experiments (hydroponic, soil column and field) were conducted to explore possible physiological processes and mechanisms for the water-saving and yield-increasing characteristics of GCRPS by analyzing the dynamics of soil water and temperature conditions, root and shoot growth, water and nitrogen uptake, soil and plant nitrogen contents, gas exchange, and their interrelationships.

2. Materials and methods

2.1. Field experiment (Exp. 1)

A field experiment in a randomized block design with three replications, described in detail by Jin et al. (2016), was conducted to investigate the superior water productivity of ground cover rice production system (GCRPS) at Fangxian Agricultural Bureau Farm in Shiyan, Hubei province, China. Before transplanting, basal fertilizers (150 kg N ha^{-1} as urea, 45 kg P ha^{-1} as calcium superphosphate and 45 kg K ha^{-1} as potassium chloride) were applied for 9 independent plots (9 m wide by 10 m long), and each plot was separated into five strip soil beds (1.56 m in width and 9.4 m in length) surrounded by 0.15 m wide and 0.15 m deep furrows. Six plots were randomly chosen for GCRPS, where the soil beds were covered with 5 μm thick and 1.7 m wide plastic film. Twenty-five-day old rice seedlings (*Oryza sativa* L. *cv. Yixiang* 3728) were transplanted into soil beds on 28 April 2013 and 29 April 2014, and were harvested on 10 September (135 days after transplanting, 135 DAT) and 19 September (143 DAT), respectively.

The three plots without plastic film were prepared for traditional paddy rice production system (TPRPS), where irrigation was applied to maintain an average water layer on the soil beds between 2 and 5 cm thick. The three plots with plastic film for $GCRPS_{sat}$ were irrigated intermittently through the furrows to keep the average root zone (0–40 cm soil layer) soil water content close to saturation while without a standing water layer on the soil beds. The remaining three plots with plastic film were managed identically to $GCRPS_{sat}$ until mid-tillering and afterwards transient irrigation was intermittently implemented to fully fill the furrows when the measured average root zone water content reached approximately 80% of field water capacity ($GCRPS_{80\%}$). For all the three treatments, irrigation was forbidden during the drying field periods (66–72 and 113–135 DAT in 2013; 78–85 and 121–143 DAT in 2014).

Soil water content under GCRPS was measured every 2 days with a capacitance probe (Diviner 2000, Sentek Inc., Australia) at 10 cm intervals from surface to 60 cm depth. Soil temperature at the depths of 5 (with 3 replications), 10 and 20 cm (only one replication) was measured hourly by a multipoint temperature instrument (CB-0221, Yaxin, China) for each treatment. After 85 DAT in 2014, some failure of the temperature probes at 10 and 20 cm occurred, resulting in incomplete data. Plants were sampled during the mid-tillering, max-tillering, panicle initiation, anthesis, and maturity stages (34, 53, 78, 99 and 135 DAT in 2013; 34, 51, 78, 99 and 143 DAT in 2014). Plant parameters, measured as described in Jin et al. (2016), included leaf area, shoot biomass, stomatal conductance, leaf transpiration and photosynthetic rates, root growth and distribution, and grain yield. Water potential of sampled flag leaves under each treatment was measured using a Dewpoint Potential Meter (WP4, Decagon Inc., USA). Nitrogen contents in shoots and roots were measured by an element analyzer (EA1108, Fisons Instruments, Italy) with their samples powered by a ball mill (MM200, Retsch Inc., Germany). Specific leaf nitrogen (mg N cm^{-2}) was estimated by dividing nitrogen mass in shoots with leaf area (Shi et al., 2014), and specific root nitrogen (mg N m^{-1}) was determined by dividing nitrogen mass in roots with root length. The increase of total nitrogen mass in both shoots and roots was taken as plant nitrogen uptake between two sampling events. Inorganic nitrogen concentrations in sampled soil solution and runoff water were measured with a continuous flow analyzer (TRAACS 2000, Bran + Luebbe, Norderstedt, Germany). Field-scale transpiration was estimated through water balance calculation (Jin et al., 2016). Water use efficiency (kg m^{-3}) was evaluated in two ways, first by dividing the increase of total biomass with the corresponding transpiration between two sampling events (WUE_{T_B}), and secondly by dividing grain yield with total transpiration over the growth season (WUE_{T_Y}).

According to the data regarding plant nitrogen uptake, transpiration, and inorganic nitrogen concentration in soil solution, dimensionless root nitrogen uptake factors (δ) were estimated for various growth stages as follows (Shi et al., 2007; Shi and Zuo, 2009; Zhu et al., 2010; Shi et al., 2013):

$$\delta = \frac{100M_u}{T_aC_N} \tag{1}$$

where M_u is plant nitrogen uptake during any distinct stage (kg ha^{-1}); T_a is transpiration (mm); and C_N is inorganic nitrogen concentration in soil solution (mg L^{-1}). A value of $0 < \delta \le 1$ indicates passive uptake, while $\delta > 1$ indicates coexisting passive and