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Interactive effects of CO_2 concentration elevation and nitrogen fertilization on water and nitrogen use efficiency of tomato grown under reduced irrigation regimes

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ABSTRACT

The interactive effects of CO_2 concentration elevation, N fertilization, and reduced irrigation regimes on water and nitrogen use efficiency (WUE and NUE) of tomato (*Solanum lycopersicum* L.) plants at both leaf and whole plant scales were investigated in a split-root pot experiment. The plants were grown in two separate climate-controlled greenhouse cells at atmospheric $[CO_2]$ of 400 ($a[CO_2]$) and 800 ($e[CO_2]$) ppm, respectively. In each cell, plants were fertilized at either 1.5 or 3 g N per pot. The leaf physiological parameters, C and N content in stem, leaf and fruit were determined, and both WUE and NUE were evaluated. Plants harvested from 3 g N per pot associated with $e[CO_2]$ environment possessed the greatest photosynthetic rate (P_n) and lowest stomatal conductance (g_s) and transpiration rate (T_r), resulting in the highest WUE at stomatal and leaf levels. Especially alternate partial root-zone irrigation (PRI) strategy coupled with $e[CO_2]$ had the potential to synergistically reduce g_s and T_r while sustain P_n and leaf water status, and further improve tomato leaf WUE. $e[CO_2]$ combined with sufficient N fertilization enhanced the biomass, C accumulation and N uptake of plants under reduced irrigation; yet the WUE and NUE at whole plant scale were affected solely by the N supply being greater in low N fertilizer. These findings provide useful knowledge on efficient irrigation and N management for adapting to the future water-limited and CO_2-enriched environment.

1. Introduction

Atmospheric carbon dioxide (CO_2) concentration has been constantly increasing and is predicted to reach nearly 800 ppm at the end of this century (IPCC, 2013). The elevated CO_2 concentration ($e[CO_2]$) in atmosphere could stimulate global warming, induce severe declining freshwater resources in agricultural regions around the world (Pazzagli et al., 2016). This has led to increased attention into the research of developing novel irrigation strategies for improved crop water use efficiency (WUE) (Wang et al., 2010a). On the other hand, $e[CO_2]$ could decrease mineral contents, particularly nitrogen (N) in plants (Li et al., 2016), mostly due to dilution effect, and potentially exacerbate the prevalence of 'hidden hunger' (Loladze, 2002; Myers et al., 2014). Therefore, it is of great interest to understand the influences of reduced irrigation and limited N fertilizer on plant physiological response and nutrient status in $e[CO_2]$ condition, which may provide further insights into the regulatory mechanisms of water and N availability as well as CO_2 environment effects on water and N use efficiency (WUE and NUE) of plants.

It is widely accepted that alternate partial root-zone irrigation (PRI) and deficit irrigation (DI) are effective irrigation techniques, which have been extensively studied throughout the world (Davies et al., 2002; Du et al., 2015). DI is a method that irrigates the entire root zone with an amount of water less than the potential evapotranspiration and the mild stress that develops minimal effects on the yield (Dodd, 2009). PRI is a further refinement of DI, which has been demonstrated to maintain crop product quality and allows considerable water savings. The underlying mechanisms for the improved WUE from leaf to plant scale under PRI are to alternately allow one part of the root system to be irrigated to keep the leaves hydrated while the other part is exposed to soil drying, triggering stronger root-to-shoot abscisic acid (ABA) hormonal signaling, inducing partial closure of stomata and reduction in leaf expansion growth, thereby curtailing the transpirational water loss larger than photosynthesis (Davies et al., 2002; Kang and Zhang, 2004; Liu et al., 2006; Loveys et al., 2000; Wang et al., 2010a; Wei et al., 2016). In addition to enhancing crop WUE, recent studies have

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indicated that PRI could improve N nutrition as well as NUE as compared to DI with the same degree of water saving (Hu et al., 2009; Shahnazari et al., 2008; Wang et al., 2009, 2010a,b,c, 2012, 2013). The greater accumulated N nutrient accompanied with modified dry matter and N allocation of the plant might have increased leaf photosynthetic capacity, contributing to the higher WUE in the PRI plants (Wang et al., 2009, 2010a,b,c). The improved plant N nutrition of PRI treatment could be predominantly ascribed to an enhanced root N uptake capacity associated with an increased mineral N availability caused by the intensive drying and wetting cycles of the soil (Sun et al., 2013a; Wang et al., 2010a,c, 2012).

Previous evidence has demonstrated that *e*[CO_2] could increase leaf photosynthetic rate (P_n) but decrease stomatal conductance (g_s) and transpiration rate (T_r) (Ainsworth and Long, 2005; Leakey et al., 2009) as well as modify the morphology of stomata (Haworth et al., 2016), hereby maintaining a better leaf water status (Tausz-Posch et al., 2015; Wullschleger et al., 2002) and resulting in an improvement of WUE at leaf scale (da Silva et al., 2017; Li et al., 2017; Kang et al., 2002; Pazzagli et al., 2016; Yan et al., 2017). The higher photosynthesis and lower stomatal aperture are predominantly induced by stronger Rubisco activity and depolarization of guard cell membrane potential, respectively (Ainsworth and Rogers, 2007), probably leading to declined leaf transpiration and plant water consumption, therefore, further enhancing WUE of plant (da Silva et al., 2017; Kaminski et al., 2014; Pazzagli et al., 2016).

Despite improving WUE at both leaf and plant scale at *e*[CO_2], there is generally a reduction in N concentration of plant, partly having an impact on the leaf photosynthetic and carbohydrate metabolic process (da Silva et al., 2017; Li et al., 2016; Sanz-Sáez et al., 2010), and such phenomenon has been proposed to attribute primarily to the dilution of N by increased biomass, altered root architecture and physiology, and changed requirement for N as protein cofactors or in other organic complexes as well as reduced root N uptake due to limited transpiration mass flow of plant resulting from partial stomatal closure (Taub and Wang, 2008; Loladze, 2002; McGrath and Lobell, 2013; Myers et al., 2014). Furthermore, NUE is commonly observed to enhance in plant harvested from *e*[CO_2] environment resulted from the increased C and decreased N content in dry matter (Reddy et al., 2010). Nevertheless, to date no studies are available to elucidate the mechanism and response of combined effects of N fertilization and reduced irrigation regimes on plant WUE and NUE under *e*[CO_2] environment.

In this study, tomato plants were grown in two atmospheric CO_2 concentrations (400 and 800 ppm) combined with two N fertilizer rates (1.5 and 3.0 g pot^{-1}) and subjected to three different irrigation regimes (FI, DI, and PRI) during flowering to fruiting stages. It was hypothesized that both *e*[CO_2] and reduced irrigation would improve WUE from leaf to plant level simultaneously; moreover, *e*[CO_2] would increase C and decrease N concentration, whilst PRI and greater N fertilization could improve plant nutrients uptake and may further enhance plant N nutrition and NUE at *e*[CO_2]. The objective was to investigate whether the interactive effects of *e*[CO_2] and reduced irrigation could synergistically improve WUE at leaf and plant scales and NUE simultaneously of tomato under increased N fertilization in a future drier and CO_2-enriched environment.

2. Materials and methods

2.1. Experimental setup

The experiment was conducted in a climate controlled greenhouse at the experimental farm of the Faculty of Science, University of Copenhagen, Taastrup, Denmark. The tomato seeds (*Solanum lycopersicum* L., cv. Elin) were sown on 26th Sept. 2016. The seedlings were transplanted into 1.5 L pots at the fourth leaf stage. From sowing, half of the plants (24) were grown in a greenhouse cell with ambient CO_2 concentration of 400 ppm (*a*[CO_2]), and another half were grown in a cell with elevated CO_2 concentration of 800 ppm (*e*[CO_2]). In both greenhouse cells, the [CO_2] was sustained or achieved by emission of pure CO_2 from a bottled tank, released in one point and distributed evenly in the cells through internal ventilation. The [CO_2] in the glasshouse cells was monitored every 6 s by a CO_2 Transmitter Series GMT220 (Vaisala Group, Helsinki, Finland). The climatic conditions in the two glasshouse cells were set at: 23/16 ± 2 °C day/night air temperature, 60% relative humidity, 16 h photoperiod, and > 500 $\mu mol\ m^{-2}\ s^{-1}$ photosynthetic active radiation (PAR) supplied by sunlight plus LED lamps.

Five weeks after sowing, tomato seedlings were transplanted into 10 L pots (17 cm diameter and 50 cm depth) in the greenhouse, filled with 14.5 kg of air-dried soil. The pots were divided vertically into two equal-sized compartments with plastic sheets such that the water exchange between the two compartments was prevented. The soil used was classified as sandy loam, with a pH of 6.7, total C 10.3 g kg^{-1}, total N 1.0 g kg^{-1}, $NH_4{}^+$- N 0.1 mg kg^{-1}, $NO_3{}^-$- N 5.3 mg kg^{-1}. The soil was sieved through 5 mm mesh before filling the pots. The soil had a volumetric soil water content (% vol.) of 18.0% and 5.0% at pot water holding capacity and permanent wilting point, respectively. 0.7 g P and 0.88 g K fertilizers were applied as KH_2PO_4 into the soil of each pot. In each [CO_2] greenhouse cell, 1.5 g N was applied as NH_4NO_3 per plant into half of the pots, and 3.0 g N per plant was applied into the other half.

2.2. Treatments

The experiment was conducted in two CO_2 concentration greenhouse cells, one with ambient CO_2 concentration (*a*[CO_2], 400 ppm) and the other with elevated CO_2 concentration (*e*[CO_2], 800 ppm). Two N fertilizer rates in each cell, that is N1 (1.5 g N pot^{-1}) and N2 (3.0 g N pot^{-1}).

The tomato plants were well-watered in the first three weeks after transplanting. Thereafter, the plants were subjected to three irrigation treatments: (1) full irrigation (FI) where both soil compartments were watered daily at 15:00 h to water content of 18% to compensate the full evapotranspiration water loss during the previous day; (2) alternative partial root-zone irrigation (PRI), where half of the root system was watered to 70% of the FI irrigation volume while the other half was allowed to dry to ca. 6%, then the irrigation was shifted between the two soil compartments; and (3) deficit irrigation (DI) where the same amount of water for PRI was evenly irrigated to the two soil compartments. The experiment was a complete randomized design with four replicates in each treatment. The water used for the irrigation was tap water with negligible concentrations of nutrients. The irrigation treatments lasted 40 days and each soil compartment of the PRI plants had experienced five drying/wetting cycles. The average soil water content in the pot was monitored by a time domain reflectometer (TDR, TRASE; Soil Moisture Equipment Corp., Santa Barbara, USA) with probes (35 m in length) installed in the middle of each soil compartment. The changes of soil water content in the pots were presented elsewhere (Wei et al., unpublished).

2.3. Measurements

On days 1, 4, 8, 12, 16, 24 28 and 40 after initiation of the irrigation treatment with four replicates in each treatment during each measurement, leaf gas exchange rates, including photosynthetic rate (P_n), stomatal conductance (g_s), transpiration rate (T_r) were determined on upper canopy fully expanded leaves around 10:00 h with a portable photosynthetic system (LiCor-6400XT, LI-Cor, NE, USA). Measurements were performed on one leaf per plant at 20 °C chamber temperature and 1200 $\mu mol\ m^{-2}\ s^{-1}$ photon flux density, and at a [CO_2] of 400 ppm for *a*[CO_2] and 800 ppm for *e*[CO_2] treatment, respectively. Intrinsic water use efficiency (WUE_i, $\mu mol\ mol^{-1}$) was calculated as the ratio of P_n ($\mu mol\ m^{-2}\ s^{-1}$) to g_s ($mol\ m^{-2}\ s^{-1}$) and instantaneous water use