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Effects of CO_2 elevation and irrigation regimes on leaf gas exchange, plant water relations, and water use efficiency of two tomato cultivars

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ABSTRACT

We investigated the effects of elevated CO_2 concentration ($[CO_2]$), different irrigation regimes, and their interactions on leaf gas exchange, water relations, biomass production, and water use efficiency in tomato plants. In spring 2014, two tomato cultivars (CV1, which is potentially drought tolerant, and CV2 which is potentially heat tolerant) were grown in two separate greenhouse cells at $[CO_2]$ of 380 and 590 μmol L^{-1} (ppm) located at the experimental farm, Taastrup, Denmark. Plants were either irrigated to 18% of volumetric soil water content (FI, full irrigation), or irrigated with 70% water of the fully-irrigated control, delivered to either the whole pot (DI, deficit irrigation) or alternately to only half of the pot (PRD, partial root-zone drying). The experiment was a completed factorial design with four replications per treatment. The two cultivars showed a similar response to soil water deficits, but their water consumption responded differently to high $[CO_2]$. Intrinsic water use efficiency (WUE_i, photosynthetic rate/stomatal conductance) and plant water use efficiency (WUE_p, aboveground biomass/plant water use) were both significantly increased by reduced irrigation treatments and elevated $[CO_2]$, although no significant reduction of stomatal conductance was detected under high $[CO_2]$. There was a positive interaction between CO_2 enrichment and water deficits on plant water use efficiency. Root water potential was negetatively affected by reduced irrigation but positively influenced by elevated $[CO_2]$, while leaf water potential was significantly decreased only by reduced irrigation. CO_2 enrichment increased flower number without affecting fruit number, thereby reducing fruit set. Reduced irrigation in combination with elevated $[CO_2]$ caused a significant improvement in plant water use efficiency in both tomato cultivars.

1. Introduction

The patterns of changes in climate and the mechanisms driving plant responses to such changes are important for the development of agricultural practices and crops that are better adapted to future growing conditions (Ainsworth et al., 2008). It is predicted that atmospheric CO_2 concentration ($[CO_2]$) will rise globally to 550 ppm in the middle of the present century (Kirtman et al., 2013). On the other hand, the short- and long-term projected changes in temperature and precipitation patterns show a great regional – and sometimes seasonal – variability (Kirtman et al., 2013). Mid-latitude regions, including large parts of Europe, are likely to experience reductions in summer precipitation and increases in temperature, which will result in higher frequency of seasonal drought (Christensen et al., 2007). Therefore, an understanding of plant responses to rising $[CO_2]$ and limited water availability is necessary for maximizing crop yield and quality under future climate scenarios.

Declining freshwater resources have stimulated research into developing novel irrigation strategies to use the water more efficiently. Alternate partial root-zone drying irrigation (PRD) and deficit irrigation (DI) are water-saving irrigation techniques being intensively studied in many regions on different crop species, including tomatoes (Sun et al., 2013). Deficit irrigation consists of delivering plants a reduced amount of water (typically 30–50% less) relative to full irrigation (FI) that usually compensates 100% plant evapotranspiration (Sezen et al., 2008). Although photosynthetic rates are often lowered in deficit-irrigated plants (Liu et al., 2006), the reduction of irrigation water generally improves water use efficiency (WUE), either at the stomatal level (photosynthetic

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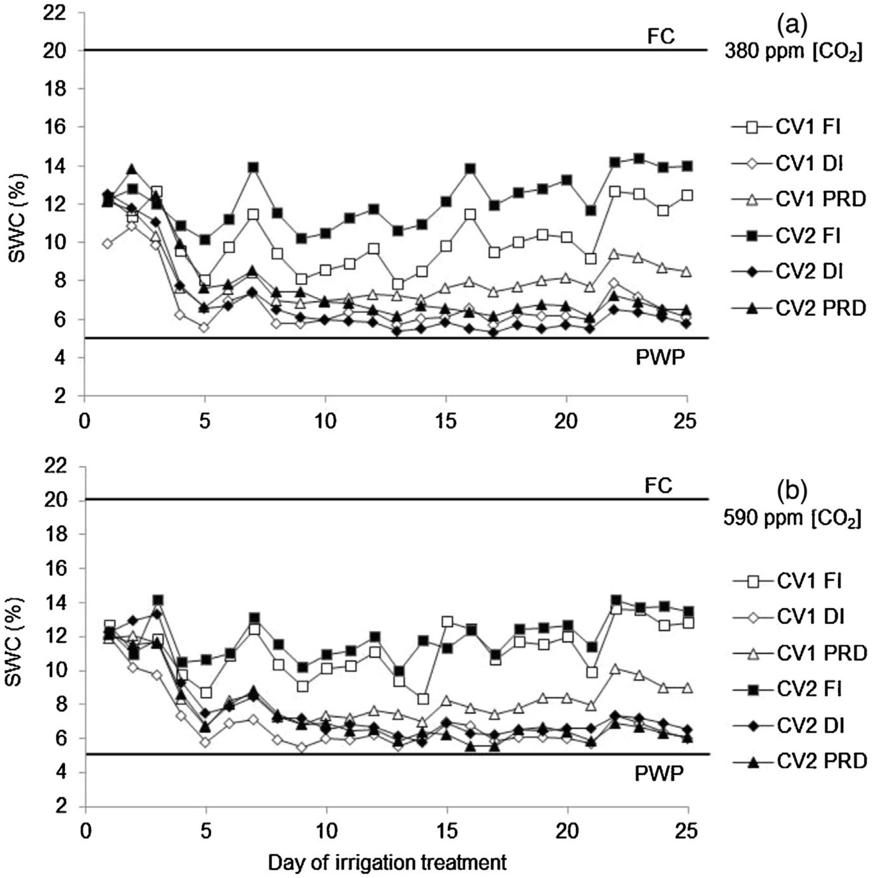

Fig 1. Daily volumetic soil water content (SWC, %) before irrigation in the pots of the two tomato cultivars exposed to three irrigation regimes (FI, DI, and PRD) and two atmospheric [CO_2] (380 and 590 ppm) treatments. FC indicates field capacity and PWP denotes permanent wilting point.

rate/stomatal conductance, WUE_i) or the plant level (aboveground biomass/plant water use, WUE_p). Indeed, stomatal conductance (g_s) is more sensitive than photosynthetic rate (A_n) to decreases in water availability, leading to higher WUE_i under moderate soil water deficits (Liu et al., 2005). Similarly, under mild and moderate droughts, the proportional reduction in biomass production is often consistently lower than that in delivered water, and WUE_p is therefore increased (Liu et al., 2006).

PRD is an irrigation strategy based on the delivery of water (usually 50–70% of the full irrigation requirements) to only one half of the root system, while the other is left to dry. The irrigated side is generally alternated during the treatment in order to avoid death of the roots, and to maintain root-to-shoot signaling (Liu et al., 2008). The intensity of drought-signaling was reported to be larger in PRD than in DI for various species, and many studies describe benefits of PRD relative to DI in increasing WUE (Wang et al., 2010). The alternation of drying and re-wetting cycles in the soil under PRD leads to increased root production (Liu et al., 2006; Mingo et al., 2004) and to an increased release of inorganic N into the soil solution (Birch effect—Birch 1958) resulting in beneficial effects on plant N nutrition (Wang et al., 2010; Wang et al., 2013).

A number of experiments have been conducted in this sense during the last two decades, involving different CO_2 concentrations and ranges of irrigation reduction (*e.g.* Fleisher et al., 2013; Nackley et al., 2014; Xu et al., 2013). The increase in internal CO_2 concentration (C_i) caused by a rise in ambient [CO_2] leads to a reduction in stomatal aperture (Ainsworth and Rogers, 2007), and a positive interaction between elevated [CO_2] and drought in decreasing g_s is generally reported (Kang et al., 2002). In C_3 plants, an increase in atmospheric [CO_2] increases the CO_2:O_2 ratio at the chloroplast, improving the efficiency of net carbon gain through acceleration of the carboxylation reaction and inhibition of the oxygenation reaction (Ogren, 2003). Significant enhancement of photosynthesis and growth by elevated [CO_2] occurs in C_4 plants only under water stress conditions (Conley et al., 2001; Leakey et al., 2006; Morgan et al., 2011), and in C_3 plants the relative stimulation under drought is generally larger than in well-watered conditions (*e.g.* Poorter and Pérez-Soba 2001). Indeed, CO_2 enrichment may extend assimilation periods during moderate (Nackley et al., 2014) and temporary (Vu and Allen 2009) drought. Therefore, elevated [CO_2] may further increase WUE of plants under reduced irrigation (Kumar et al., 2014).

The objective of this study was to investigate the independent and combined effects of CO_2 enrichment and reduced irrigation on two tomato cultivars with potentially different responses to drought and heat stress. Three different irrigation regimes (FI, DI, and PRD) in combination with two CO_2 concentrations (380 and 590 ppm) were investigated for the two tomato cultivars. We hypothesized that both reduced irrigation and elevated [CO_2] will increase WUE, and that the combination of the two factors would further enhance WUE of tomato plants.

2. Materials and methods

2.1. Plant material and growth conditions

The experiment was conducted from March to June 2014 at the experimental farm of University of Copenhagen located in Taastrup, Denmark (55N40′6.61″; 12E18′25.62″). Tomato plants were grown in two cells (50 m^2 each) of a recently built greenhouse, designed