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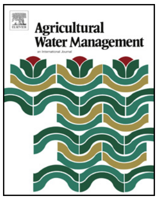

Carbon isotope discrimination shows a higher water use efficiency under alternate partial root-zone irrigation of field-grown tomato

Zhenhua Wei[a], Taisheng Du[a,*], Juan Zhang[a], Shujun Xu[a], Paul J. Cambre[b], William J. Davies[b]

[a] Center for Agricultural Water Research in China, China Agricultural University, Beijing 100083, China
[b] Lancaster Environment Centre, Lancaster University, Bailrigg, Lancaster LA1 4YQ, UK

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ABSTRACT

Experiments of alternate partial root-zone irrigation (APRI) on tomato plants were conducted in the field with three different water application rates via furrow irrigation (*i.e.*, AFI) during 2011–12 and drip irrigation (*i.e.*, ADI) during 2013–14 in the arid region of northwest China. Leaf carbon isotope discrimination (ΔL), fruit carbon isotope discrimination (ΔF) and fresh yield (Y) were determined at fruit maturation stage. The impacts of irrigation treatments on water use efficiency (WUE) were evaluated at leaf and yield scales. The results showed that APRI usually resulted in a higher WUE improvement with no significant difference in yield but 33.3% less irrigation water. Compared with conventional irrigation (CI), APRI regulated leaf photosynthetic processes and stomatal aperture more efficiently and induced a lower ΔL and higher WUE at leaf scale. Δ^{13}C of tomato leaf and fruit at fruit maturation stage could be used as an important, quick and suitable indicator for phenotype of high WUE at both leaf and field scales to some extent, irrespective of which APRI method was applied. Our results suggest that APRI, especially ADI, have some potential to be used as an efficient water-saving irrigation strategy in arid region of northwest China where tomato production is threatened by insufficient irrigation water for agriculture.

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1. Introduction

A worldwide water shortage and more severe drought has promoted research on water-saving irrigation strategies to increase crop water productivity (Wang et al., 2010). The irrigation area is continuously increasing in order to meet the food demand of growing population, and in fragile ecological arid areas, more additional water supply is needed to increase food production in the coming decades (Kang and Zhang, 2004; Li et al., 2014), therefore, appropriate water-saving irrigation techniques must be explored for both food security and environment.

In recent years, alternate partial root-zone irrigation (APRI) or partial root-zone drying (PRD) has been shown to be an effective irrigation technique in many regions of the world (Loveys et al., 2000; Davies et al., 2002; Kang and Zhang, 2004; Dodd, 2009). APRI involves alternating irrigation in space and time in two halves of the root system, which are alternately irrigated in a frequency according to crop varieties, growth stages and soil water balance (Du et al., 2006). Plant responses induced include partial stomata closure, reduced leaf initiation and expansion rate and decreased inefficient transpiration without significant reduction in photosynthesis, thus increasing WUE. These responses have been demonstrated to depend on bio-chemical signalling, which involves plant growth regulators and other chemical spp., either sourced from the roots or recirculated from shoots to varying extents in response to the drying soil (Davies et al., 2002; Kang and Zhang, 2004; Wilkinson

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Abbreviations: WUE, water use efficiency; APRI, alternate partial root-zone irrigation; CI, conventional irrigation; FI, furrow irrigation; DI, drip irrigation; M, conventional full irrigation water quota; AFI-1 (ADI-1), alternate furrow irrigation (drip irrigation) with 100% of M; CFI-1 (CDI-1), conventional furrow irrigation (drip irrigation) with 100% of M; AFI-2 (ADI-2), alternate furrow irrigation (drip irrigation) with 66.7% of M; CFI-2 (CDI-2), conventional furrow irrigation (drip irrigation) with 66.7% of M; AFI-3 (ADI-3), alternate furrow irrigation (drip irrigation) with 50% of M; CFI-3 (CDI-3), conventional furrow irrigation (drip irrigation) with 50% of M; ABA, abscisic acid; P_n, photosynthetic rate (μmol m^{-2} s^{-1}); T_r, transpiration rate (mmol m^{-2} s^{-1}); g_s, stomatal conductance to water vapour (mol m^{-2} s^{-1}); Y, fresh yield (g m^{-2}); DY, dry yield (g m^{-2}); ET, crop evapotranspiration (mm); WUE$_{\text{ins}}$, instantaneous water use efficiency at leaf scale (μmol mmol^{-1}); WUE$_{\text{int}}$, intrinsic water use efficiency at leaf scale (μmol mol^{-1}); WUE$_{\text{Y}}$, water use efficiency at fresh yield scale (kg m^{-3}); WUE$_{\text{DY}}$, water use efficiency at dry yield scale (kg m^{-3}); C_i, intercellular CO_2 concentration; C_a, atmospheric CO_2 concentration; δ^{13}C, carbon isotope composition; Δ^{13}C, carbon isotope discrimination; ΔL, Δ^{13}C of leaf tissue (‰); ΔF, Δ^{13}C in fruit (‰); *R*, correlation coefficient.

* Corresponding author. Fax: +86 10 62737611.
E-mail address: dutaisheng@cau.edu.cn (T. Du).

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and Davies, 2010; Ghanem et al., 2011; Dodd, 2013). Accumulated studies have shown that APRI allows considerable crop water savings, maintains yield and improves WUE at field scale compared to conventional irrigation (CI) using alternate furrow or drip irrigation on cotton (Du et al., 2006, 2008), maize (Kang et al., 2000; Liang et al., 2013), grapevine (Loveys et al., 2000; Romero and Martinez-Cutillas, 2012), pomegranate (Parvizi et al., 2014), potato (Yactayo et al., 2013) and tomato (Davies et al., 2000; Zegbe et al., 2004; Kirda et al., 2004; Campos et al., 2009; Wang et al., 2010).

WUE can be expressed as instantaneous water use efficiency (WUE_{ins}, photosynthetic rate/transpiration rate, P_n/T_r), intrinsic water use efficiency (WUE_{int}, photosynthetic rate/stomatal conductance to water vapour, P_n/g_s) at the leaf scale, and WUE_Y (yield/crop evapotranspiration, Y/ET) at a yield scale (Pascual et al., 2013). WUE_{int} could be enhanced either by maintaining the P_n or lowering the g_s (Wang et al., 2010). Many studies have suggested that APRI induced partial stomatal closure, decreased transpiration and, therefore increased WUE (Loveys et al., 2000; Davies et al., 2002; Liu et al.,2006; Campos et al., 2009; Yang et al., 2012; Akhtar et al., 2014). However, carbon gain has to be maintained at a high level in parallel with reduced g_s (Liu et al., 2006; Du et al., 2006) and variation in g_s commonly explains more variation in WUE than in P_n (Easlon et al., 2014), implying that the regulation of gas exchange under APRI is tightly linked to the environment (de Souza et al., 2005). WUE_{ins} and WUE_{int} by gas exchange measurement can be used to reflect the dynamic physiological response of crop water use process to environmental factors (Cui et al., 2009), and carbon isotope composition ($\delta^{13}C$) of plant tissues, which is frequently expressed as discrimination from the source air ($\Delta^{13}C$), provides a time integrated measurement of the C3 crop's WUE over the life time during which dry biomass is assimilated (Farquhar and Richards, 1984; Farquhar et al., 1989).

A robust negative linear relationship between $\Delta^{13}C$ and WUE_{int} has been shown (Farquhar et al., 1982) under conditions where partial mesophyll conductance is very high while respiratory ^{13}C discrimination is negligible (Werner et al., 2012). Although WUE_{ins} indicates the actual transpiration efficiency, WUE_{int} is a more reliable metric for comparison, as it standardizes vapor pressure deficit, which makes it less variable between measurements and instruments (Seibt et al., 2008). The carbon isotope discrimination ($\Delta^{13}C$) of crop tissue is influenced by crop photosynthesis and stomatal aperture under water stress throughout the growth period (Farquhar and Richards, 1984), as the leaves can discriminate against the heavier carbon isotope (^{13}C) during photosynthesis. The extent of this fractionation depends on the ratio between the intercellular (C_i) and the atmospheric (C_a) CO_2 concentration (i.e., C_i/C_a) and is largely driven by the amount of the primary carboxylating enzyme (Rubisco) and stomatal behaviour (Farquhar et al., 1982, 1989; Brugnoli and Farquhar, 2000; Condon et al., 2002).

Although the whole crop $\Delta^{13}C$ is dominated by CO_2 assimilation and diffusion into leaves, internal partitioning and metabolism of primary assimilates may produce differences in $\Delta^{13}C$ for different tissues (Brugnoli and Farquhar, 2000). Research on grape showed that $\Delta^{13}C$ of leaf tissue (ΔL) represented the C_i/C_a and reflected the impact of water availability and other variables on carbon assimilation and allocation through the growing season, and the $\Delta^{13}C$ in fruit (ΔF) can be used to reflect the impact of soil water availability in the field late in the growing season, as the dry biomass of fruits integrates leaf photosynthetic isotopic discrimination of carbon during fruit ripening (de Souza et al., 2005). Thus, water status has significant and various effect on fractionation of $\Delta^{13}C$ in different tissues of plants. However, there are few studies on field-grown horticultural crops to estimate WUE at different scales with $\Delta^{13}C$ in different crop tissues over several years.

In order to further illuminate the effect of varying water deficit on crop WUE and to assess the possibilities of combining carbon stable isotope technology and conventional measurements of crop physiology for high WUE, field experiments were conducted on tomato by applying alternate partial root-zone irrigation (APRI) and conventional irrigation (CI) with three water levels. Both furrow and drip irrigation methods were trialed. The objectives of this study are to (1) evaluate the response of physiological characteristics, yield, WUE at different scales, ΔL, ΔF and interannual variation of tomato plants subjected to APRI under three levels of water deficit. These treatments are compared with CI applied by different irrigation methods between years; (2) investigate the relationship between ΔL, ΔF and WUE_{ins}, WUE_{int}, WUE_Y and yield of tomato plants respectively, which may be helpful to clarify the water use mechanism on phenotyping of different WUE under APRI and CI at fruit maturation stage; (3) assess the reliability and practicability to use $\Delta^{13}C$ of various tomato tissues to indicate WUE under APRI and CI by furrow and drip irrigation, respectively.

2. Materials and methods

2.1. Experimental site

Field experiments were carried out during 2011–14 at Shiyanghe Experimental Station of China Agricultural University located in Wuwei City, Gansu Province of northwest China (37°52′N, 102°50′E, altitude 1581 m), which is in the typical continental temperate arid zone, with an average annual sunshine duration over 3000 h, an mean annual temperature of 8 °C, an annual accumulated temperature (higher than 0 °C) of more than 3350 °C, a mean annual precipitation of 164 mm and a mean annual evaporation from a free water surface of 2000 mm. The groundwater table is consistently below 30 m. The soil type is sandy loam with soil saturated water conductivity of 1.62 ± 0.11 cm/d, organic matter content of 0.74 ± 0.06 %, field capacity of 0.263 ± 0.009 m in the upper 1.0 m of the soil profile (0.263 ± 0.009 cm^3/cm^3) and bulk density of 1.53 ± 0.08 g/cm^3.

2.2. Experimental design

In 2011, two furrow irrigation methods, i.e., alternate partial root-zone furrow irrigation (AFI, each of the neighbouring two furrows alternately watered) and conventional furrow irrigation (CFI, all neighbouring furrows watered), were applied with three levels of irrigation (100%, 66.7% and 50% of conventional full irrigation quota) (M), i.e., 23.5, 15.7 and 11.8 mm for each irrigation, coded with 1, 2 and 3, respectively, with AFI and 37.0, 24.6 and 18.5 mm for each irrigation, coded with CFI-1, CFI-2 and CFI-3, respectively. In 2012, treatments included AFI-1, AFI-2, AFI-3 (42.6, 28.4 and 21.2 mm for each irrigation, respectively) and CFI-1 corresponded to AFI-1. The field experiments had totally 12 plots in both years, arranged in a randomized block design with two and three replicates per treatment in 2011 and 2012, respectively. Each plot area was 19.6 m^2 (4.0 m × 4.9 m) with a 4 furrow ditch with a width of 0.5 m, a depth of 0.25 m per furrow and four ridges with a width of 0.5 m per ridge. Two rows of tomato seedlings were planted in a similar way to the local tomato production method and evenly transplanted along the edge of each furrow side with row spacing of 0.50 m and interplant spacing of 0.35 m in both growing seasons. A furrow of 0.5 m width was taken as buffer to avoid lateral water flow between two neighbouring plots. The layout of the partial root-zone furrow irrigation experiment is shown in Fig. 1. In each plot, the central two ridges of plants were sampled. The irrigation amount was recorded by water meters (Accuracy of 0.1 L) at the end of the pipes for each furrow. Plants were irrigated eleven times in AFI treatment and seven times in CFI treatment in 2011, showing that more water was applied to CFI for each irrigation time. Over

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