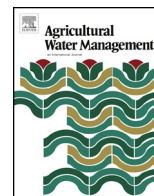




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Nutritional responses to soil drying and rewetting cycles under partial root-zone drying irrigation

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ABSTRACT

Repeated soil drying and rewetting (DRW) cycles occur in rainfed and irrigated agriculture. The intensity and frequency of DRW cycles regulate both microbial physiology and soil physical processes, hereby affecting the mineralization and immobilization of soil nutrients and their bioavailability. Partial root-zone drying irrigation (PRI) irrigates half of the soil zone, while the other half is allowed to dry, and the two halves is alternately irrigated. PRI outweighs conventional deficit irrigation in further improving water use efficiency (WUE) by enhancing the root-to-shoot chemical signaling that regulates stomatal aperture. PRI induced soil DRW cycles and more soil water dynamics in the root zone enhance soil nutrient mineralization process and thus increase the bioavailability of soil nutrients, resulting in improved nitrogen (N) and phosphorus (P) uptake, in which soil microbial processes play a key role. Studies investigating how soil DRW cycles and water dynamics under PRI on nutrient transport in soil solution, soil microbe mediated P transformation, interactions between phytohormones and nutrient uptake, root morphological and architectural traits for nutrient acquisition, and PRI-integrated fertigation are still lacking. In addition, the positive nutritional effect may be varied in terms of climatic conditions and intensity and frequency of precipitation or irrigation, and these merit further in-depth studies.

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1. Introduction

Soil undergoes a complex of physi-biochemical changes under repeated soil drying and rewetting (DRW) cycles in natural ecosystems as well as in rainfed or irrigated agricultural lands. These cycles affect plant water and nutrient uptake, and the activity of soil microbes involved in the transformation of soil nutrients during the mineralization and immobilization turnover processes, leading to varied soil nutrient bioavailability. Increasing shortage of freshwater for agriculture and more frequent and severe drought due to climate change have stimulated research into water-saving irrigation strategies (Dodd, 2009; Du et al., 2015). To meet the increasing food demand for growing population, the arable land area under irrigated agriculture is continuously increasing in order to secure crop production. Meanwhile, global nitrogen (N) and phosphorus (P) fertilizer consumptions have increased seven- and 3.5-fold between 1960 and 1995, and which are expected to rise further in the future decades. However, at present only 30–50% of the applied

N and about 45% of P is taken up by crops (Tilman et al., 2002), and the rest of those nutrients are lost into the environment causing contaminations to both surface- and ground-water resources. To cope with these challenges, there is an urgent need to develop strategies to use irrigation water, N and P nutrients more efficiently in line with principles of sustainable development.

Water use efficiency (WUE) can be defined in different ways. Essentially, it is a ratio between two physiological (*i.e.*, transpiration and photosynthesis) or agronomic (*i.e.*, yield and crop water use) entities (Blum, 2005). Apparently, to sustain crop yield under water scarcity will require producing more ‘crop per drop’. Thus, the question arises as to whether it is possible to achieve the dual goal of increasing crop yield and saving irrigation water through improvement of WUE in crop production. Basically, crop WUE is species dependent (*e.g.* C₃ vs. C₄ crops) and physically limited; therefore it is fairly constant for a crop under a given climate and cannot be easily modified significantly by any genetic strategies (Tardieu, 2005). Rather, WUE can be enhanced by application of less amount of irrigation water. However, evidence has demonstrated that a higher WUE is often a trade-off against lower biomass production; therefore breeding for high WUE alone often results in slow plant growth and low yield (Zhang and Yang, 2004). It is clear that the regulation of stomatal aperture is central to WUE of plants. The environmental

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factors act in some way either directly or indirectly on regulating stomatal aperture, together with internal circadian rhythms, leaf water status and xylem-borne signals (e.g. abscisic acid (ABA), cytokinins, etc.). Water could be saved by manipulation of stomatal behavior, and this is because stomatal conductance (g_s) for water vapour is more sensitive than photosynthesis (A) to soil drying; thus during mild soil water deficits intrinsic water use efficiency (i.e. A/g_s) may increase when stomata are partially closed while A is kept at high levels (Liu et al., 2005). When soil water availability falls below a certain level, root water potential and turgor become low, stimulating the synthesis of several plant growth regulators including ABA (Wright, 1977; Davies and Zhang, 1991). This hormone is synthesized in root-tips as root water potential decreases and being transported through the transpiration stream to the shoots where it causes reductions in stomatal opening (Sauter et al., 2001; Davies et al., 2002; Liu et al., 2006). By exploiting this root-to-shoot ABA signaling in regulation of stomatal aperture, a novel water-saving irrigation technique called alternate partial root-zone drying (PRD) or partial root-zone irrigation (PRI) has been developed as a further refinement of conventional deficit irrigation (DI). In DI the entire root zone is watered with an amount of water less than the potential evapotranspiration during the non-sensitive growth stages and the mild stress has minimal effects on the yield (English and Raja, 1996). PRI involves irrigating only half part of the root zone in order to keep the leaves hydrated while the other half is allowed to dry to a predetermined level before alternating irrigation between the drying and rewetting zone to sustain the root-to-shoot ABA signaling for controlling stomatal opening. Both PRI and DI can induce the ABA-based root-to-shoot chemical signaling regulating stomatal conductance and leaf expansion growth (Dodd, 2007; Wang et al., 2010a). Nonetheless, at a similar degree of water saving, PRI can intensify ABA signaling relative to DI, resulting in a better control of plant transpiration causing further improvement of WUE (Dodd, 2009; Wang et al., 2010a).

In addition to increasing crop WUE, recent studies have found that PRI induced soil DRW cycles affect plant N and P acquisition. Fig. 1 compares the N or P accumulation of plants supplied with the same irrigation volume, but exposed to either DI or PRI. It can be seen that in most cases PRI outperforms DI in enhancing N or P accumulation in plants, and this could be largely attributed to high soil nutrient bioavailability under PRI. Such knowledge is critical for a better understanding of how plants and soils respond to DRW cycles and soil moisture heterogeneity to concurrently optimize water and nutrient use efficiencies. Given the same amount of irrigation water, PRI is superior to DI in terms of yield maintenance and increase of WUE at both single leaf and the whole plant levels as reviewed by Dodd (2009), Sadras (2009), Jensen et al. (2010), Dodd et al. (2015) and Du et al. (2015). To further exploit the beneficial effect of PRI technique on crops, the aim of this review is to highlight soil processes affecting nutrients (mainly N and P) bioavailability and plant uptake when irrigated with PRI strategy as illustrated in Fig. 1.

2. Soil nutrient responses to soil drying and rewetting cycles

Birch (1958) firstly reported the contribution of soil DRW cycles to organic matter decomposition and mineralization upon rewetting a dry soil. Later, this phenomenon has been defined as the 'Birch effect'. In the last decade, accumulated studies have shown that soil DRW cycles could cause 'Birch effect', leading to a flush of plant bioavailable N (Mikha et al., 2005; Xiang et al., 2008; Butterly et al., 2009) or P into soil solution (Turner et al., 2003; Lovieno and Bååth, 2008; Blackwell et al., 2009). The magnitude of the pulse effect is determined by the intensity and frequency of soil DRW cycles. The

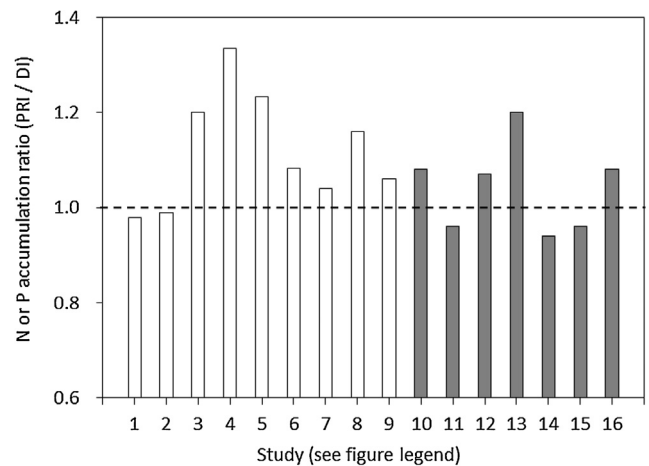


Fig 1. Plant N or P accumulation ratio of PRI to DI at same or similar irrigation volumes (a ratio of 1 indicates that N or P accumulation under both irrigation techniques is equivalent). Unshaded columns indicate N accumulation ratio of PRI and DI, and shaded columns denote P accumulation ratio of PRI and DI. Studies are numbered thus: (1) Kirda et al., 2005; *Zea mays* cv. Sele; (2) Shahnazari et al., 2008; *Solanum Tuberosum* cv. Folva; (3) Wang et al., 2009; *Solanum Tuberosum* cv. Folva; (4–5) Liu et al., 2015; *Solanum Tuberosum* cv. Folva, (4) with mineral N but without mineral P fertilization, (5) with mineral N and P fertilization; (6) Topcu et al., 2007; *Lycopersicon esculentum* cv. F1 Fantastic; (7) Wang et al., 2010a; *Lycopersicon esculentum* cv. Cedrico; (8) Wang et al., 2010b; *Lycopersicon esculentum* cv. Cedrico; (9) Wang et al., 2013; *Lycopersicon esculentum* cv. Cedrico; (10–13) Liu et al., 2015; *Solanum Tuberosum* cv. Folva, (10) with mineral N and P fertilization on 30 days after irrigation treatment (DAT), (11) with mineral N and P fertilization on 52 DAT, (12) with mineral N but without mineral P fertilization on 30 DAT, (13) with mineral N but without mineral P fertilization on 52 DAT; (14) Sun et al., 2015; *Solanum Tuberosum* cv. Zhongshu 3#; (15–16) Wang et al., 2012b; *Lycopersicon esculentum* cv. Cedrico, (15) with mineral N and P fertilization, (16) with organic N and mineral P fertilization.

microbial stress and substrate supply processes occur and influence soil nutrient dynamics during soil DRW cycles (Mikha et al., 2005; Wu and Brookes, 2005; Xiang et al., 2008). The microbial stress process results from microbial drought tolerance physiology. When progressive soil drying gradually confines soil water to smaller films around soil particles, this leads to increasingly negative soil water potentials. Some microbial cells die because of this passive equilibration, and microbial cells that do not survive desiccation are considered to be a part of soil organic matter (SOM) (Marumoto et al., 1977). Microbes that are survived can equilibrate internal water potential to the surrounding soil by cellular plasmolysis, decreases in internal water potential or the accumulation of intercellular organic solutes (Harris, 1981; Killham and Firestone, 1984; Kempf and Bremer, 1998; Halverson et al., 2000; Schimel et al., 2007). While the desiccation process usually proceeds slowly, allowing time for microbial accumulation of intracellular solutes. Cells that have passively equilibrated to the dry conditions will rehydrate during rewetting (Kieft et al., 1987). The microbial stress process should reduce microbial biomass and inhibit microbial function, as the resources needed to survive stress are depleted and stress-sensitive microbes die (Harris, 1981; Halverson et al., 2000). The rewetting of dry soil by precipitation or irrigation usually occurs rapidly as a wetting front penetrating dry soil microsites (Kieft et al., 1987). Microorganisms typically respond by expelling these accumulated intracellular osmolytes into extracellular environment, resulting in the release of intracellular organic solutes, such as amino acids, ammonium compounds and glycerol. These readily degradable organic compounds could be utilized by surviving soil microorganisms, thus contributing to the pulse of C, N or P pools after rewetting (Bottner, 1985; Kieft et al., 1987; van Gestel et al., 1991, 1993; Grierson et al., 1998; Halverson et al.,

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