REVIEW PAPER

The importance of soil drying and re-wetting in crop phytohormonal and nutritional responses to deficit irrigation

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Abstract

Soil drying and re-wetting (DRW) occurs at varying frequencies and intensities during crop production, and is deliberately used in water-saving irrigation techniques that aim to enhance crop water use efficiency. Soil drying not only limits root water uptake which can (but not always) perturb shoot water status, but also alters root synthesis of phytohormones and their transport to shoots to regulate leaf growth and gas exchange. Re-wetting the soil rapidly restores leaf water potential and leaf growth (minutes to hours), but gas exchange recovers more slowly (hours to days), probably mediated by sustained changes in root to shoot phytohormonal signalling. Partial rootzone drying (PRD) deliberately irrigates only part of the rootzone, while the remainder is allowed to dry. Alternating these wet and dry zones (thus re-wetting dry soil) substantially improves crop yields compared with maintaining fixed wet and dry zones or conventional deficit irrigation, and modifies phytohormonal (especially abscisic acid) signalling. Alternate wetting and drying (AWD) of rice can also improve yield compared with paddy culture, and is correlated with altered phytohormonal (including cytokinin) signalling. Both PRD and AWD can improve crop nutrition, and re-wetting dry soil provokes both physical and biological changes which affect soil nutrient availability. Whether this alters crop nutrient uptake depends on competition between plant and microbes for nutrients, with the rate of re-wetting determining microbial dynamics. Nevertheless, studies that examine the effects of soil DRW on both crop nutritional and phytohormonal responses are relatively rare; thus, determining the cause(s) of enhanced crop yields under AWD and PRD remains challenging.

Key words: ABA, alternate wetting and drying, partial rootzone drying, soil phosphorus dynamics, root-to-shoot signalling, xylem sap.

Introduction

Plants in natural ecosystems, and rainfed or irrigated agriculture, are exposed to fluctuating soil water availability, characterized by repeated soil drying and re-wetting (DRW) cycles. These cycles affect both plant water uptake and the activity of soil microbes involved in nutrient cycling, thereby affecting soil nutrient availability. Nevertheless, many soil drying experiments reported in the plant physiological literature expose plants to a single drying cycle (often until loss of plant turgor), usually to evaluate relationships between soil and plant water status and physiological responses such as leaf growth

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and gas exchange. In contrast, the irrigation science community is concerned with using such information to optimize crop yields and water use efficiency (WUE) by understanding when and how much to irrigate. Exploiting our knowledge of how plants and soils respond to DRW cycles seems critical to optimize resource use efficiency in agriculture, especially given global concerns such as dwindling supplies of fresh water for irrigation (Elliot *et al.*, 2014), and the limited availability and high cost of synthetic fertilizers to boost crop yields (Cordell *et al.*, 2009).

Rapid and continued human population growth, combined with global economic growth, has placed increasing pressure on agricultural systems worldwide to deliver sufficient food. Where water resources permit, a solution adopted in many parts of the world has been to increase the land area under irrigated agriculture, since crop yields typically outstrip those of rainfed agriculture. Sometimes, this expansion of irrigation usage has been supported by farmers pumping aquifer water to supplement natural rainfall, and exploitation of aquifers has resulted in falling water table levels (Qin *et al.*, 2013) and increased costs to the farmer of pumping water. Consequently, improving crop WUE (the harvested yield per unit of irrigation water supplied) while maintaining or even improving yield may conserve valuable water resources while allowing farmers to maintain their economic livelihoods.

Each day, a plant transpires more than its actual water content. When water resources are ample, complete replacement of crop evapotranspirational losses may be an appropriate management technique. Increasingly, due to scarcity of water resources, applying less water than crop evapotranspiration (termed 'deficit irrigation'; DI) has been implemented by various techniques that vary either the timing or the spatial distribution of irrigation (or both). Sustained DI applies a fraction of crop evapotranspiration to the entire rootzone throughout the growing season. Regulated DI applies a fraction of crop evapotranspiration to the entire rootzone, but varies the timing of deficit periods throughout the growing season to ensure that more water is supplied during sensitive phenological stages (e.g. during reproductive development) and less at other times. Partial rootzone drying (PRD) irrigates only part of the rootzone (e.g. one side of a row of vines or alternate furrows), although the fraction of crop evapotranspiration applied can vary. The irrigated and drying parts of the rootzone can remain fixed throughout the growing season (fixed PRD) or be regularly alternated (alternate PRD) at variable frequency. Alternate wetting and drying (AWD) is mainly applied to paddy rice, and involves alternate inundation and soil drying of the entire rootzone. These techniques have usually improved crop WUE, and sometimes either actual and/or economic yields (Fereres and Soriano, 2007; Dodd, 2009; Davies *et al.*, 2011), but results may be inconsistent and there is still a knowledge gap between our understanding of agronomic responses that integrate crop performance over the entire growing season, and of physiological responses that may be restricted to specific tissues at specific times of the growing season.

The irrigation frequency applied in such techniques will determine the degree and depth of soil drying, and

subsequent plant physiological responses to both drying and re-irrigation. Interestingly, both alternate PRD and AWD explicitly impose DRW cycles, and the agronomic impacts of these cycles can be substantial. Figure 1 compares the yield response of plants supplied with the same irrigation volumes, but exposed to either fixed (part of the rootzone allowed to dry and the other part irrigated) or alternate (drying and irrigated parts of the rootzone are frequently swapped) PRD. Alternate PRD consistently outyielded fixed PRD, and it is tempting to speculate that physiological responses to repeated DRW cycles during alternate PRD are responsible.

This paper reviews changes in plant physiological responses (emphasizing root to shoot phytohormonal signalling affected by soil water availability; Davies and Zhang, 1991; Dodd, 2005) and soil nutrient availability induced by DRW cycles. Whether these changes in soil nutrient availability affect crop nutrition and root to shoot signalling of soil water availability is also explored. Although it may be premature to attribute the yield response identified in Fig. 1 to specific processes, further understanding of soil–plant interactions may inform management decisions that aim to improve the efficiency of irrigated agriculture.

Root to shoot signalling of soil drying and re-wetting

Entire rootzone drying and re-wetting

As the soil dries, plants initiate adaptive responses that regulate yield-determining processes such as leaf expansion and leaf gas exchange (including photosynthesis). Understanding
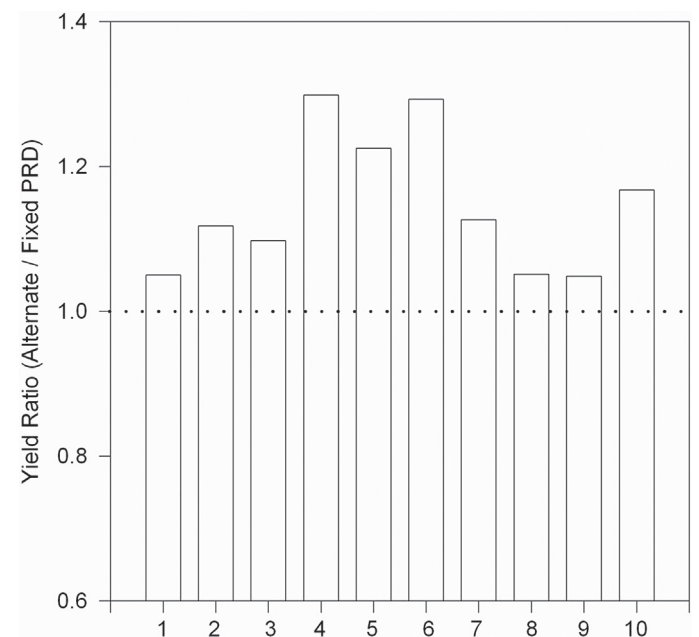
Fig. 1. Crop yield ratio of alternate to fixed PRD at similar irrigation volumes (a ratio of 1 indicates that yield with both techniques is equivalent). Studies are numbered thus: (1) Grant *et al*. (2006) raspberry *Rubus idaeus* cvs Glen Ample and Glen Prosen, (2–4) Du *et al*. (2006) *Gossypium hirsutum* comprising three irrigation volumes, (5) Tang *et al*. (2005) *Gossypium hirsutum* cv. Xin K4, (6, 7) Kang *et al*. (2001) *Capsicum annum* comprising two irrigation volumes, (8–10) Kang *et al*. (2000) *Zea mays* cv. Duanyu 13 comprising three irrigation volumes.

the regulation of these processes may improve agronomic and breeding approaches to tune their sensitivity to mitigate the impacts of water deficits on crop yields. One of the most enduring controversies in plant water relations (Kramer, 1988; Passioura, 1988a; Christmann *et al.*, 2007) is whether leaf growth and gas exchange are regulated hydraulically [via changes in leaf water potential (Ψ_{leaf}) or turgor] or chemically [via changes in ionic and phytohormonal signals originating from the roots or shoots). Several lines of evidence suggest that trying to distinguish the effects of each in the shoot is somewhat artificial, as the effect of the plant hormone abscisic acid (ABA) on stomatal aperture is mediated by Ψ_{leaf} (Tardieu and Davies, 1992), and ABA affects stomatal conductance (g_s) both directly by acting on the stomatal guard cells and also indirectly by decreasing leaf hydraulic conductance (Pantin *et al.*, 2013). Nevertheless, it is useful to consider that both forms of regulation can alter crop responses to soil DRW.

One of the earliest pieces of evidence provided for the existence and importance of root to shoot chemical signals were experiments that frequently measured leaf water relations, leaf growth, and gas exchange in response to soil drying. In some experiments, g_s and leaf growth declined before any change in Ψ_{leaf} (Blackman and Davies, 1985; Henson *et al.*, 1989). Indeed, many plant species (termed 'isohydric') maintain Ψ_{leaf} as the soil dries as a result of stomatal closure (Tardieu and Simonneau, 1998). Nevertheless, the relationship between g_s and Ψ_{leaf} in a single species can be positive, negative, or even absent according to the duration of soil drying (cf. Dodd *et al.*, 2006; Kudoyarova *et al.*, 2007), suggesting that stomatal closure cannot always be attributed to decreased Ψ_{leaf}.

Another set of experiments applied a pneumatic pressure to the roots of plants to prevent any loss of leaf turgor during soil drying. Root pressurization was unable to prevent or reverse stomatal closure and leaf growth inhibition in some (Gollan *et al.*, 1986; Passioura, 1988b) but not all (Saliendra *et al.*, 1995; Fuchs and Livingston, 1996; Mencuccini *et al.*, 2000; Yao *et al.*, 2001) species. Stomatal closure when plants were maintained at full turgor has been interpreted as evidence for the existence of root-supplied chemical signals regulating shoot responses, while reversal of stomatal closure by applying pressure to the roots suggests the primacy of leaf water relations in regulating shoot responses. Clearly, both types of signal can play important regulatory roles as the soil dries and either may be more or less effective in different species and according to the time of day (Mencuccini *et al.*, 2000).

Unlike this inconsistency in the effects of Ψ_{leaf}, there is surprising consistency in some phytohormonal responses to soil drying, as assessed by determining xylem sap composition of plants exposed to drying soil. A brief literature survey (four separate studies: Masia *et al.*, 1994; Hansen and Dörffling, 2003; Megat Wahab, 2007; Alvarez *et al.*, 2008) revealed that xylem concentrations of ABA (a potent antitranspirant) increased 2- to 100-fold as the soil dried, while concentrations of the cytokinins zeatin and zeatin riboside declined compared with well-watered plants (Perez-Alfocea

et al., 2011). In contrast, xylem ionic (nitrate, phosphate, sulphate, chloride, calcium, sodium, magnesium, and potassium) responses were much more variable (in another five studies: Munns and King, 1988; Trejo, 1994; Goodger *et al.* 2005; Megat Wahab 2007; Ernst *et al.*, 2010). This suggests that some xylem phytohormone concentrations provide a more consistent 'measure' of the degree of soil drying than xylem ion concentrations. If there is no change in xylem loading (movement of ions and phytohormones from root cells into the xylem lumen) as xylem sap flow rates decrease (as a result of stomatal closure), it is predicted that the concentrations of all xylem sap constituents should increase as the soil dries (Jackson, 1993). However, increases and decreases in xylem sap phytohormone and ion concentrations indicate pronounced changes in xylem loading as the soil dries, although considerable additional work is needed to establish that changes in xylem sap composition can actually regulate leaf growth and gas exchange (Dodd, 2005). Furthermore, multianalyte hormone measurements of xylem sap composition (e.g. Albacete *et al.*, 2008; Alvarez *et al.*, 2008) will doubtless demonstrate other changes in xylem phytohormone composition as the soil dries.

While different soil drying episodes (varying in intensity and duration) induce variable changes in xylem sap composition and Ψ_{leaf}, plants with low Ψ_{leaf} generally show rapid (within hours) recovery of Ψ_{leaf} and leaf growth in response to re-wetting the soil (Loewenstein and Pallardy, 2002; Parent *et al.*, 2009). Recovery of Ψ_{leaf} and leaf elongation upon rehydration paralleled increases in root hydraulic conductivity and were successfully modelled by determining water transfer following rehydration (Parent *et al.*, 2009). Following re-wetting, Ψ_{leaf} and leaf elongation recovered more rapidly in maize lines with higher endogenous ABA concentration due to their higher root hydraulic conductivity.

In contrast, stomatal responses to re-wetting the soil can be significantly delayed. Following prolonged soil drying, there can be long-term (several days) residual suppression of g_s (Fig. 2). These 'after-effects' on stomatal responses (Davies and Kozlowski, 1977; Dörffling *et al.*, 1977) have been associated with elevated xylem ABA concentrations (Correia and Pereira, 1994; Loewenstein and Pallardy, 2002). Even though xylem ABA concentration sometimes recovers to the levels of well-watered plants while stomata remain partially closed (Fig. 2), rapid recovery of Ψ_{leaf} yet slower recovery of g_s may be considered as further evidence for the existence of root to shoot signals regulating stomatal responses. Interestingly, stomatal conductance of rewatered plants appears to be more sensitive to xylem ABA than in droughted plants (Loewenstein and Pallardy, 2002), although it is unknown whether this is related to elevated apoplastic ABA concentrations around the guard cells, as a result of changes in catabolism of xylem-supplied ABA (Gowing *et al.*, 1993) and/or sequestration of ABA into the mesophyll (Wilkinson and Davies, 1997). An alternative explanation is that rewatering also changes root to shoot signalling of other phytohormones, which may alter stomatal sensitivity to ABA (Dodd *et al.*, 1996).

Rewatering bare-rooted mandarin seedlings, that had been transplanted to dry sand for 24 h, caused exponential
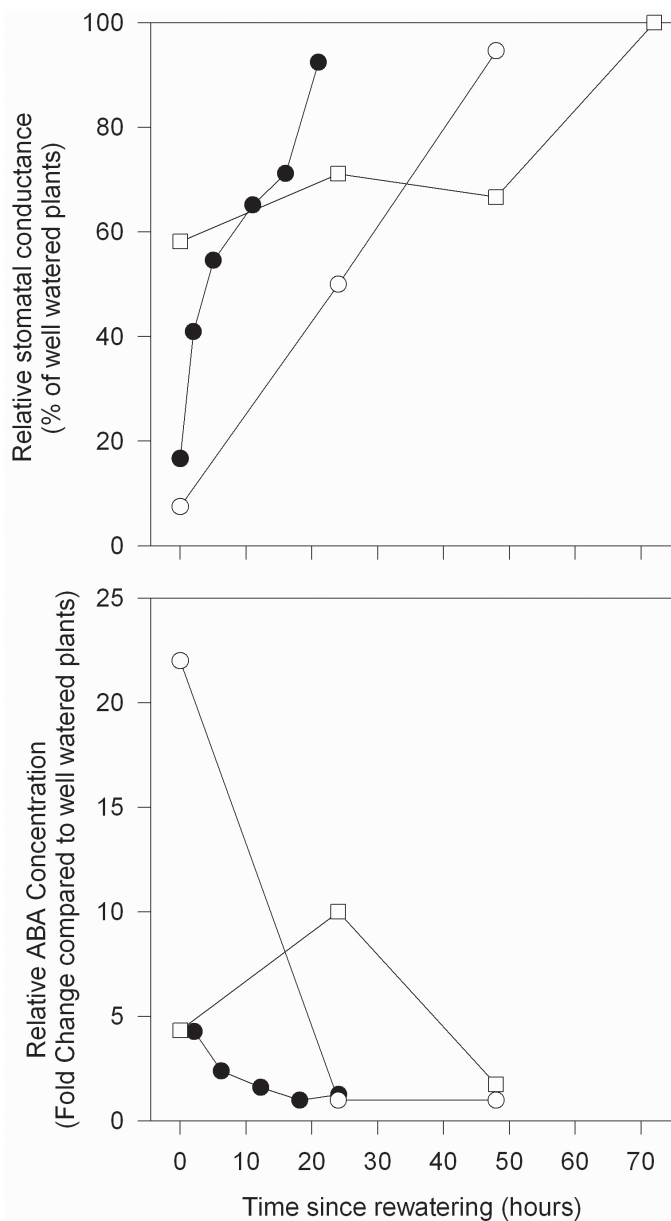
Fig. 2. Relative changes in stomatal conductance (a) and xylem ABA concentration (b) of plants that were exposed to soil drying and then re-watered at time 0h (compared with well-watered plants=100% and 1.0, respectively). Data are re-plotted from Gomez-Cadenas *et al.* (1996) (Mandarin, filled circles) and Loewenstein and Pallardy (2002) (*Populus deltoides*, open circles; and *Quercus alba*, open squares).

decreases in both xylem ABA and 1-aminocyclopropane-1-carboxylic acid (ACC) concentrations (Tudela and Primo-Millo, 1992). Peak ACC concentrations were attributed to ACC export from the root system (after root ACC accumulation during exposure to drying soil) following the resumption of water uptake from the root system. Following rewatering, stomatal re-opening was achieved more rapidly in plants which had been pre-treated with a soil drench of fluridone (an ABA biosynthesis inhibitor) that diminished both root and xylem sap (but not leaf) ABA concentrations (Gomez-Cadenas *et al.*, 1996). However, fluridone also attenuated rehydration-induced changes in root, xylem sap, and leaf ACC concentrations, and leaf ethylene evolution (Gomez-Cadenas

et al., 1996), consistent with evidence that ethylene can inhibit stomatal opening. In contrast, 1-methylcyclopropene treatment (which inhibits ethylene binding to receptors) prevented the stomata of older wheat leaves from opening in response to rehydration (Chen *et al.*, 2013), although the dynamics of xylem and leaf phytohormone responses were not measured. Further work is needed to evaluate the role(s) of both ABA and ethylene in regulating physiological responses to rewatering.

Changes in xylem cytokinin concentrations and delivery may also occur following rewatering. Rewatering sunflower plants (that had reached a Ψ_{leaf} of –1.0 MPa) caused an exponential decline of xylem ABA concentration (reaching a plateau after 4h) while xylem zeatin riboside concentration rapidly increased (~5-fold) within 6h of rewatering (Hansen and Dörffling, 2003). Cytokinin-mediated antagonism of ABA-induced stomatal closure was hypothesized to assist stomatal re-opening. The potential physiological importance of cytokinins was further suggested in experiments with Kentucky bluegrass (*Poa pratensis*) that had dehydrated to 40% leaf relative water content, such that rewatering accompanied by foliar sprays of a synthetic cytokinin (10 µM 6-benzylaminopurine) promoted stomatal re-opening (to a greater extent than rewatering alone), although supplementary cytokinins had no significant effect on photosynthetic recovery (Hu *et al.*, 2013). Interestingly, foliar sprays of 50 mM potassium chloride also significantly enhanced the recovery of g_s. This effect may also be cytokinin mediated, as potassium deficiency decreases plant cytokinin status (Wang *et al.*, 2012a), although a direct relationship between foliar potassium sprays and enhanced foliar cytokinin synthesis remains to be demonstrated. Enhanced xylem cytokinin concentrations following rewatering may occur in response to increased root water potential (Ψ_{root}) (Hansen and Dörffling, 2003) and/or altered nutrient uptake.

While there are multiple phytohormonal mechanisms that may regulate stomatal responses following rewatering, alternative explanations may also apply. Severe dehydration causes membrane injury, and it was postulated that restoration of ion transport across the guard cell plasma membrane may be delayed following rewatering (Loewenstein and Pallardy, 2002). While this theory may be supported by accelerated recovery of g_s if rewatering is accompanied by foliar potassium spraying (Hu *et al.*, 2013), detailed ultrastructural measurements are required to establish the existence of guard cell membrane injury (and recovery).

In general, there have been relatively few studies of changes in xylem sap composition following rewatering of dry soil (in contrast to multiple studies that have considered responses to drying soil). These studies should consider effects of soil and root water status on water, nutrient, and hormone uptake from the soil, hormone synthesis and metabolism in the roots, and xylem loading of both nutrients and hormones. Whether whole-plant responses to rewatering can help interpret responses to rewatering only part of the rootzone (as occurs in alternate PRD) is considered next.

Responses to alternate partial rootzone drying (PRD)

PRD was originally conceived in the laboratory, to disentangle the effects of hydraulic and chemical signals on shoot physiology. When maize plants were grown with their roots split between two soil compartments, and only one compartment was watered, g_s declined while Ψ_{leaf} was maintained (Blackman and Davies, 1985), suggesting that g_s was responding to chemical signals generated in the roots in the dry compartment. This concept was subsequently applied to grapevine in the field by placing drip-emitters on separate feeder lines either side of the vine row (Dry *et al.*, 1996) or watering every other furrow of maize plants (Kang *et al.*, 1997) to exploit chemical signalling to limit excessive vegetative vigour (grape) and luxury transpiration (maize), thereby improving crop WUE.

One of the difficulties of applying PRD is that although soil drying is needed to alter root metabolism to produce chemical signals in the roots, water uptake from those roots is also diminished. Thus chemical signal production is increased while signal transport (from those roots) is decreased, and the relative sensitivity of those two processes to soil drying will determine whether root to shoot chemical signalling is actually enhanced by PRD. While both processes can be measured (e.g. Dodd *et al.*, 2010), ultimately sap flux from roots in drying soil may cease entirely, thus allowing stomatal re-opening as the duration of PRD increases (Khalil and Grace, 1993; Stoll *et al.*, 2000). A practical solution to this problem has been to alternate the wet and dry parts of the rootzone regularly, to ensure that some roots remain in drying (not completely dry) soil, allowing continued signal production and transport to the shoot.

Given this conceptual basis, it is surprising that few studies have attempted to measure xylem sap composition during alternating PRD cycles, even in containerized plants. When tomato plants were grown in split pots, alternating the wet and dry soil compartments had no effect on Ψ_{leaf} compared with plants supplied with the same irrigation volume but with the wet and dry soil compartments remaining fixed (Dodd *et al.*, 2006). However, within 1 h of alternating the irrigation, leaf xylem ABA concentration ([X-ABA]$_{leaf}$) significantly increased and g_s further declined, effects which persisted throughout the entire photoperiod but not beyond. Enhanced [X-ABA]$_{leaf}$ following re-watering the originally dry soil compartment probably mobilized root-sourced ABA to the transpiration stream. It was suggested that soil drying caused root ABA accumulation by enhancing root ABA biosynthesis, but then reduced water uptake (and sap flow) limited transport of this additional ABA to the shoots. Nevertheless, increased [X-ABA]$_{leaf}$ following rewatering (irrigation alternation) of PRD plants is not universal (Wang *et al.*, 2012c; Pérez-Pérez and Dodd, 2015). Hydraulic redistribution of water from irrigated to drying roots during a drying cycle (Caldwell and Richards, 1989; Burgess *et al.*, 1998) may limit root ABA accumulation by mitigating decreases in Ψ_{root} (Puertolas *et al.*, 2013). The magnitude and duration of any ABA pulse following rewatering probably depends on the dynamics of water uptake by the previously dried roots,

the size of the ABA pool accumulated within these roots, and possible losses of ABA from the root system via metabolism and ABA efflux to the soil after rewatering. Should rewatering occur during the photoperiod, Ψ_{root} will be lower than soil water potential (Ψ_{soil}), thus any root exudation into the rhizosphere must occur in opposition to massive plant water uptake from the soil. Theoretically, an efflux of ABA-loaded water to the soil can only happen when soil water is redistributed from wet to dry soil during the night via the plant (Fig. 3).

Increased [X-ABA]$_{leaf}$ following alternation of the wet and dry parts of the root system may depend on the severity of soil drying. Alternating wet and dry sides after 3 d of PRD had no effect on [X-ABA]$_{leaf}$ or g_s, and further drying of part of the soil was needed to liberate an ABA pulse following rewatering (Dodd *et al.*, 2006). More recent experiments in the same soil type failed to demonstrate this ABA pulse, and maintaining or alternating the wet and dry parts of the rootzone resulted in similar relationships between [X-ABA]$_{leaf}$, Ψ_{leaf}, and whole-pot soil water availability (Pérez-Pérez and Dodd, 2015), even though a similar degree of soil drying occurred to that in the previous study (Dodd *et al.*, 2006). The chief difference between the two studies was the depth of the soil profile (13 cm versus 30 cm in Pérez-Pérez and Dodd, 2015 versus Dodd *et al.*, 2006) but, paradoxically, root ABA accumulation was attenuated when there were more pronounced vertical gradients in soil moisture than a more homogenous soil moisture distribution (Puertolas et al., 2013). Furthermore, roots apparently accumulate more ABA (at the same soil water content) when PRD is imposed laterally rather than vertically (Puertolas et al., 2015), perhaps due to differences in ages of the roots sampled. Both these observations suggest that growing PRD plants in long columns (rather than shorter pots) should have prevented a stimulation of [X-ABA]$_{leaf}$ following irrigation alternation. A potential explanation is that when root systems are constrained within pots, those growing at the pot's edge will be exposed to different environmental conditions from those embedded in the substrate; thus, differences in surface area to volume ratio between container sizes may result in different root system ABA accumulation at the same bulk soil water content (Pérez-Pérez and Dodd, 2015). Clearly, further studies are needed to understand the factors affecting root ABA accumulation and export of ABA to the shoot during PRD, to identify conditions under which alternating the wet and dry parts of the root system stimulates ABA transport to the shoot.

Changes in ABA export following alternation of wet and dry parts of the root system are probably of physiological significance in field-grown plants. On the day following re-irrigation, whole-plant water use of grapevines was much more conservative when plants were grown with PRD than conventional irrigation (Collins *et al.*, 2010). Nevertheless, relatively few studies have measured changes in xylem sap composition in response to alternate PRD in the field. Diurnal measurements revealed that mid-morning (09:00–12:00 h) xylem ABA concentration of PRD grapevine was approximately double that of well-watered plants (Stoll *et al.*, 2000), although the timing of these measurements relative to the alternation of
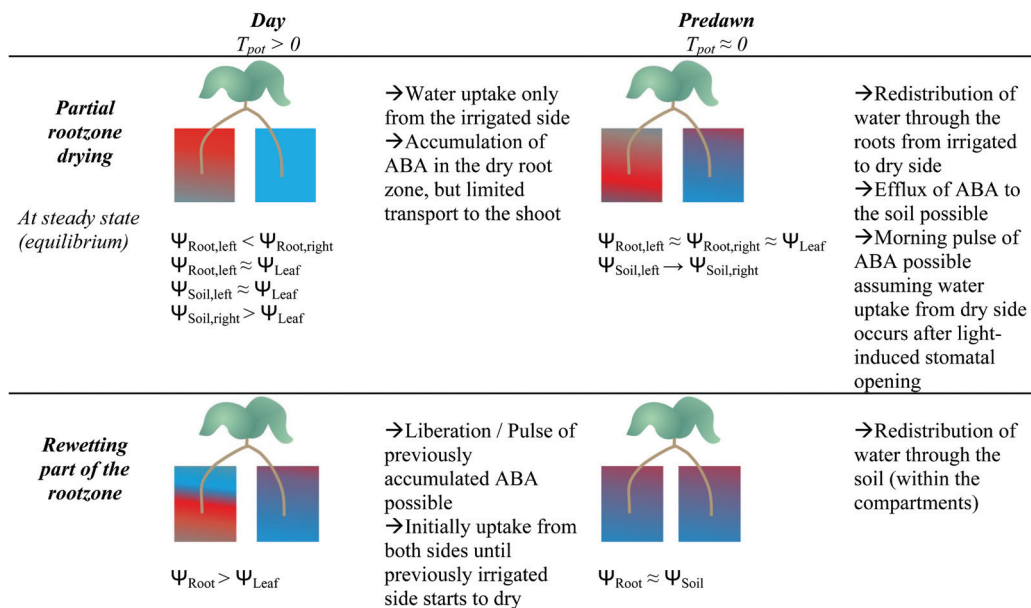
Fig. 3. Simplified representation of water and ABA relations upon rewetting partially dried split-root systems during the day (when transpiration, Tpot, is measurable) and pre-dawn (when transpiration is negligible). Dry and wet soil are indicated by red and blue colours respectively.

wet and dry parts of the rootzone was not specified. Prior to irrigation, field-grown tomato plants exposed to PRD and DI had similar [X-ABA]$_{leaf}$ throughout a diurnal cycle (Topcu *et al.*, 2007). Following re-watering, PRD and DI plants only had a similar [X-ABA]$_{leaf}$ during the early morning (before 10:00 h), with higher [X-ABA]$_{leaf}$ detected in PRD plants during the afternoon. Similar diurnal measurements in grapevine following alternation of wet and dry sides revealed some significant differences in [X-ABA]$_{leaf}$ between PRD and DI plants, but there was no consistent response throughout the day (Romero *et al.*, 2012). In lemon trees grown in the same geographical region, [X-ABA]$_{leaf}$ did not differ between PRD and DI treatments either before or immediately after (<12 h) rewatering the dry side of PRD trees, yet crop WUE was still greater in PRD trees (Pérez-Pérez *et al.*, 2012). Paired measurements of [X-ABA]$_{leaf}$ and soil moisture availability are necessary to determine whether different irrigation techniques induce genuine differences in chemical signalling.

Variability in the responses of [X-ABA]$_{leaf}$ to drying and rewetting cycles during PRD implies that it may be possible to develop models as a conceptual framework to determine circumstances in which alternation of PRD irrigation enhances chemical signalling *in planta*. ABA is produced throughout the plant as a function of local water potential (Simonneau *et al.*, 1998). To model a root-induced hormonal signal it is important to know Ψ_{root}, which is in turn a function of the distribution of Ψ_{soil}, the transpiration demand, and the hydraulic conductivity of the plant (Javaux *et al.*, 2013). When soil moisture is non-uniformly distributed (as in PRD experiments), different gradients in Ψ_{soil} will develop and this will redistribute water within the soil or, during the night, through the root system that acts as hydraulic bridges between wet and dry parts in the soil (Stoll *et al.*, 2000). Further, root water uptake from the dry part of the soil may be compensated by uptake from the wetter parts of the rootzone if Ψ_{soil} is non-limiting, thereby preventing local

(rhizosphere) soil moisture depletion (Javaux *et al.*, 2013). Nevertheless, even if the soil water is ample, non-uniform soil moisture distribution decreases xylem water potential (if not bulk Ψ_{leaf}; Blackman and Davies, 1985; Sobeih *et al.*, 2004) more than when soil moisture is uniform (Huber *et al.*, 2014). This can impact on ABA dynamics during PRD.

One method to discriminate between hydraulic and hormonal responses can be simulation studies. Integrating root-induced hormonal signals and stomatal regulation as a function of signal concentration and Ψ_{leaf} (Tardieu and Davies, 1993) within a functional–structural plant model showed that an isohydric response, as observed in maize, could not be adequately described with a root-induced ABA signal (Lobet *et al.*, 2013). Another simulation study (Huber *et al.*, 2014), where the same relationship for a hormonal signal was used, but implemented in a 3D coupled soil and root water flow model (Javaux *et al.*, 2008), illustrated the impact of non-uniformly distributed soil water on Ψ_{root}, resulting hormone concentrations, and subsequent stomatal regulation. Although this study simulated realistic hormone concentrations in the shoot, generally the stomatal reaction to non-uniform soil drying was adequately described by plant hydraulics alone. However, this study did reproduce effects such as the previously described 'pulse' of xylem ABA following rewetting of a previously dry soil (Dodd *et al.*, 2006). This was attributed to the cessation of water uptake when soil became too dry, which trapped hormones in the roots, which were only transported when this part of the soil was rewetted.

These simulation studies only consider the impact of ABA on g_s; however, ABA's influence on root hydraulic conductivity (Parent *et al.*, 2009) will directly affect the production of ABA due to changes in Ψ_{root}. Root water potential will also be affected by hysteretic hydraulic properties of the rhizosphere, which can turn hydrophobic upon drying and can remain in that state for >1.5 h after rewetting (Carminati *et al.*, 2010; Zarebanadkouki and Carminati, 2014). This

leads to a simultaneous reduction in root water uptake and could prolong both the production and transport limitation of root-sourced ABA. Thus rhizosphere properties could directly affect the arrival time and intensity of an ABA pulse following rewatering part of the rootzone.

Since changes in root to shoot chemical signalling following alternation of wet and dry soil compartments during PRD may be transient, they may have limited physiological effects on plant performance when integrated over its life cycle. Furthermore, the logistical challenges of investigating root to shoot signalling in the field mean that it may be more illuminating to determine integrative responses such as cumulative whole-plant water use. At the single-leaf scale, measurements of carbon isotope discrimination (Δ^{13}C) in C$_3$ species can indicate the degree of stomatal closure throughout the leaf lifespan, with greater stomatal closure and WUE indicated by greater (less negative) Δ^{13}C (Condon et al., 2004). Although alternate PRD and DI had statistically similar effects on foliar Δ^{13}C of field-grown grape (de Souza et al., 2003) and glasshouse-grown tomato (Wang et al., 2010a), the latter study indicated consistently greater Δ^{13}C of shoot material of PRD plants. While these measurements were correlated with increased whole-plant WUE of PRD-grown tomato, it is less certain whether these effects can be attributed to phytohormonal or nutritional effects, as foliar Δ^{13}C increased with increased specific leaf N content (Wang et al., 2010a). Further studies in tomato and potato indicated variable effects of PRD (relative to DI) on foliar Δ^{13}C according to N fertilization rates, with higher foliar Δ^{13}C of PRD plants at low (70 mg N kg^{-1} soil) N fertilizer rates but lower foliar Δ^{13}C at high (200 mg N kg^{-1} soil) fertilizer rates (Yan et al., 2012; Sun et al., 2013). These differences reflected variation in xylem ABA concentration in tomato which probably effected stomatal closure (Yan et al., 2012). While such isotopic measurements have repeatedly demonstrated good correlations with agronomic measurements of WUE, the importance of soil DRW cycles has yet to be illustrated by specific comparisons of Δ^{13}C in plants exposed to alternate and fixed PRD. Although such measurements usefully demonstrate seasonal responses, they cannot inform the management of PRD irrigation to determine the optimum time to alternate wet and dry parts of the root system.

Despite these experimental and (more recently) simulation studies of ABA dynamics during alternate PRD, and meta-analyses showing the agronomic benefits of the technique compared with conventional DI (Dodd, 2009) and fixed PRD (Fig. 1), no studies have satisfactorily demonstrated how altered phytohormone signalling during PRD alters crop yields. ABA-induced stomatal closure may limit photosynthetic carbon gain even while improving instantaneous leaf WUE, although improved leaf water relations of ABA-overexpressing transgenics allowed greater leaf extension (Thompson et al., 2007). Paradoxically, the limitation of ABA transport from roots during prolonged drying cycles in PRD (Dodd et al., 2010) and the consequent decline in xylem ABA concentration (which potentially allows higher photosynthesis), rather than any transient pulse in xylem ABA concentration following alternation of wet and dry parts of

the root system (Dodd et al., 2006), may be responsible for the enhanced yield of PRD plants compared with DI plants. Simulations that model the impacts of ABA signalling on whole-plant carbon gain are likely to resolve this uncertainty.

Alternate wetting and drying (AWD)

While the effects of soil DRW during PRD are visualized by comparing plants exposed to alternate and fixed PRD (Fig. 1), the effects of DRW during AWD are compared against continuous inundation of rice paddies. The agronomic effects of AWD seem less predictable (reviewed in Price et al., 2013), possibly due to considerable variation in the phenological phases in the crop life cycle when AWD is applied, which may be related to the onset of the monsoon in some geographical areas. Thus AWD is applied post-transplanting to the onset of flowering in Bangladesh (Price et al., 2013), while in China it is maintained throughout the cropping cycle (Yang and Zhang, 2010). However, another key factor is the extent to which the soil is allowed to dry during AWD.

Compared with plants maintained under continuous flooding, during soil drying cycles AWD decreased photosynthesis linearly with soil water potential (Fig. 4), with even mild soil drying (soil water potential, Ψ_{soil}, of –15 kPa measured with a tensiometer at 15–20 cm depth) decreasing photosynthesis. Photosynthesis increased following rewatering (compared with continuously flooded plants), but only if soil drying was not too severe.

These photosynthetic changes were closely associated with foliar levels of both zeatin-type and isopentenyl-type
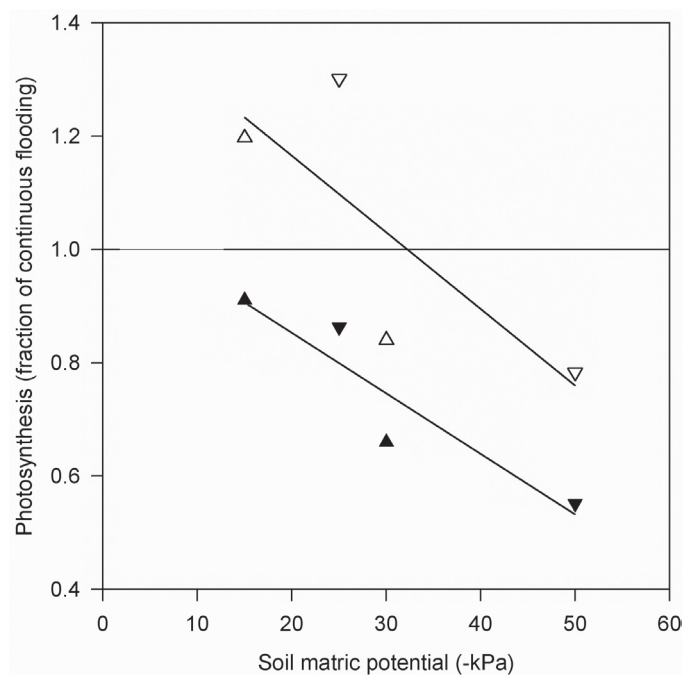
Fig. 4. Relative photosynthesis of rice plants exposed to AWD (compared with plants maintained under continuous flooding=1.0) measured immediately before (filled symbols) and after (open symbols) re-flooding the field plotted against maximum level of soil drying. Data are re-plotted from Zhang et al. (2009; upright triangle) and Zhang et al. (2010; inverted triangles) with linear regressions fitted.

cytokinins, with more severe soil drying (Ψ_{soil} of –50 kPa measured with a tensiometer at 15–20 cm depth) decreasing leaf cytokinin levels and rewatering of plants exposed to mild soil drying increasing leaf cytokinin levels (Zhang *et al.*, 2010). It is less certain whether changes in root cytokinin biosynthesis (and subsequent export to the shoot) are involved. While mild soil drying had no effect on root cytokinin levels, severe soil drying increased concentrations of zeatin-type cytokinins and decreased concentrations of isopentenyl-type cytokinins: changes that were completely immune to rewetting the soil (Zhang *et al.*, 2010). Likewise, root indole acetic acid levels (which were increased ~25% by severe soil drying) showed no change the day after the soil was rewatered. This relative stability of root hormone concentrations contrasts with the relatively rapid changes in xylem hormone concentrations following re-wetting of drying soil (e.g. Fig. 2) and may reflect the relatively mild soil water deficits applied during AWD. However, further investigation of the relationship between root and xylem hormone concentrations is needed to determine possible regulation of xylem fluxes by root hormone biosynthesis during AWD.

In a series of papers, Yang and colleagues compared the effects of AWD and continuous flooding on the phytohormone profile of developing rice grains, in attempting to establish whether specific hormonal messages from the root system cause specific physiological responses. Although phytohormone concentrations and grain-filling rates of superior (early flowering) spikelets were similar in plants exposed to AWD and continuous flooding, inferior (late flowering) spikelets showed pronounced differences in grain hormone concentrations. Plants exposed to AWD (Ψ_{soil} of –25 kPa measured with a tensiometer at 15–20 cm depth) had higher grain ABA concentrations throughout growth (Zhang *et al.*, 2012) while grain cytokinin concentrations fluctuated with AWD cycles and the severity of soil drying (Zhang *et al.*, 2010). Rewatering enhanced grain cytokinin concentrations following moderate soil drying (–25 kPa) but had no effect following severe soil drying (–50 kPa) which generally decreased cytokinin concentrations by ~25%. Nevertheless, it remains to be demonstrated whether xylem sap phytohormones can regulate the concentrations detected in developing grains, and exogenous ABA and cytokinin treatments had similar effects to AWD on grain-filling rate (Zhang et al., 2010, 2012), implying that grain hormone concentrations can act independently of root-supplied chemical signals.

These changes in phytohormone signalling during AWD will not only affect leaf gas exchange, but will also modulate grain filling and tiller dynamics. Later flowering inferior spikelets accumulated more ABA under AWD than continuous flooding, which was correlated with increased activities of enzymes involved in sucrose to starch conversion (higher sink strength) and grain-filling rate (Zhang *et al.*, 2012). Phytohormonal changes induced by AWD may also regulate sink strength of tillers, as AWD sometimes increases the percentage of productive tillers (Xue *et al.*, 2013). Establishing a role for root to shoot signalling in regulating such developmental responses requires further attention.

## Soil nutrient availability responses to soil drying and re-wetting

The 'Birch effect'

The contribution of soil DRW cycles to increased mineral nutrient availability, first reported by Birch (1958), is well documented. The effect describes a pulse of organic matter decomposition and mineralization upon rewetting a dried soil, with a decline in rate over time. Different interacting soil processes regulate the occurrence and magnitude of the 'Birch effect' in determining nutrient availability. Briefly, more intense drying (such as that occurring at high temperatures or for long durations) induces more mineralization upon rewetting, and recurrent DRW cycles increase mineralization overall, compared with continuously moist soils (Jarvis *et al.*, 2007), emphasizing the importance of soil moisture fluctuations in driving the underlying nutrient cycling processes. However, whether these fluctuations can be actively managed to enhance soil nutrient provision to plants has received little attention.

Both physical and biological processes cause and regulate the 'Birch effect' (Fig. 5). Physical processes during DRW events disrupt soil aggregates, which can be important causes of nutrient release. Slaking (physical breakdown) caused by DRW can release molybdate-reactive (inorganic) and -unreactive (organic) phosphorus (P) (MRP and MUP, respectively) (Haygarth *et al.*, 1998). Reactive P is readily available to plants. Following rewetting, the extractable reactive P concentration was significantly higher (by up to 44%) in a sterilized, dried soil than a constantly moist soil (Bünemann *et al.*, 2013), indicating the importance of physical processes. Furthermore, DRW can detach soil colloids thereby increasing MRP and MUP in leachate due to shrinkage and swelling of soil aggregates (Chepkwony *et al.*, 2001; Blackwell *et al.*, 2009). However, DRW can also stimulate the P adsorption capacity of some soils, temporarily reducing P availability, which recovers to initial levels following rewetting (Haynes and Swift, 1985).

Biological processes contributing to the 'Birch effect' include the death of soil microbes due to desiccation upon drying and lysis upon rapid rewetting (caused by osmotic shock), releasing their nutrient constituents into the soil solution. This effect contributed the majority (88–95%) of the increased water-extractable MUP from two fertilized pasture soils following DRW (Turner *et al.*, 2003). In many studies, the quantities of organic P released into solution after drying were greater than those of inorganic P (Turner and Haygarth, 2001, 2003; Blackwell *et al.*, 2009; but see Butterly *et al.*, 2011a), due largely to the contributions from the microbial biomass and soil organic matter (SOM) (Blackwell *et al.*, 2009; Butterly *et al.*, 2009). Microbial cell walls also become incorporated into the SOM, and mineralization of labile forms releases inorganic P, which is available for plant uptake and immobilization by both surviving and new microbes (Blackwell *et al.*, 2010). Following rapid rewetting of dry soil, microbial biomass can recover over short time scales (e.g. within 6 h, based on measuring ATP synthesis) (De Nobili
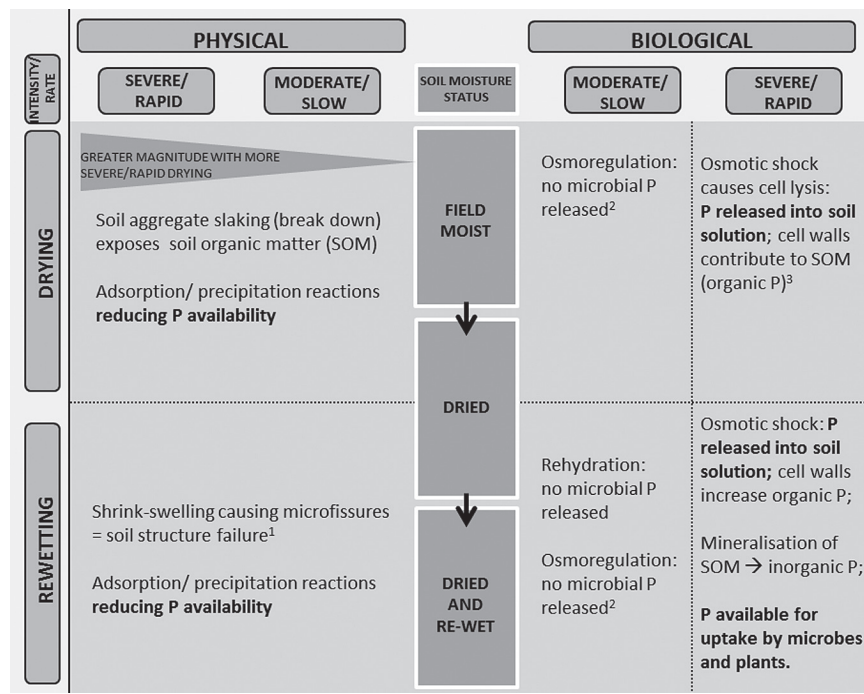
Fig. 5. Effects of soil drying and rewetting on nutrient availability, driven by physical and biological processes across different intensities and rates. Processes can be highly variable according to soil type. Sources are (1) Cosentino et al. (2006); (2) Fierer and Schimel (2003); (3) Gordon et al. (2008).

et al., 2006). Enhanced microbial assimilation of P suggests that any benefits to plants from increased availability of P following DRW events may be short-lived.

Physical and biological processes causing and regulating the 'Birch effect' are coupled. Soil DRW induces structural changes which release SOM from microaggregates. No longer protected, this SOM is more readily mineralized by soil microbes (Chepkwony et al., 2001; Navarro-Garcia et al., 2012). After drying clay soils, fractions of plant-available P (both MRP and sodium bicarbonate-extractable P) increased (as a proportion of total P), a result of structural changes in SOM and physical disturbance of microbial cells (Soinne et al., 2010).

Initial nutrient availability can affect the outcome of soil DRW events on nutrient release, and the important role of the soil microbial biomass in driving observed increases in nutrient availability following DRW has been substantiated by isotope studies. Following application of ^{32}P to a silt loam as an inorganic P source, DRW decreased the specific activity of ^{32}P in soil extracts due to dilution by mineralized ^{31}P, yet soil-extractable P concentration and wheat P uptake and yields increased (Chepkwony et al., 2001). Mineralized P following DRW makes a greater contribution to total extractable P at higher inorganic fertilizer rates (supplied as monocalcium phosphate), since increased soil P adsorption during soil drying results in less adsorption of the mineralized P after rewetting (Chepkwony et al., 2001). Thus initial soil P status affects the impacts of DRW on P availability.

The intensity and rate of DRW also affect the magnitude of the 'Birch effect'. Dissolved organic C and N concentrations in leachates following DRW increased from fertilized but not unfertilized grassland soils, and the increase in dissolved inorganic N in leachate caused by DRW was most pronounced from the fertilized soil (Gordon et al., 2008).

Decreased microbial biomass N, particularly in the fertilized grassland soils, further suggests nutrient release from microbial cell lysis. Although the fertilized soil reached a lower Ψ_{soil} (–5.74 MPa) than the unfertilized soil (–4.77 MPa) at the same soil water content, greater nutrient release from the fertilized soil was attributed to its lower fungi to bacteria ratio and lower nutrient retention capability. In both soils, it was expected that bacteria were inactive (previously reported at Ψ_{soil} less than –1.0 MPa to –1.5 MPa; Swift et al., 1979) while fungi remained active (previously reported at Ψ_{soil} of –15 MPa or even below –40 MPa, according to species; Swift et al., 1979) (Fischer, 2009). In another study, upon drying to –1.5 MPa (widely recognized as the permanent wilting point for plants), microbial respiration was only 5–8% of the maximum respiration (Fischer, 2009), suggesting that microbial biomass was also adversely affected by the low Ψ_{soil}. This supports the importance of the role of microbial community composition, structure, and function in nutrient dynamics under soil DRW cycles.

Soil carbon status largely determines the energy supply to microbes, regulating mineralization and the extent of the nutrient pulse. Microbial biomass size and composition also has a major regulatory role in determining the significance of the 'Birch effect' to nutrient availability in different soils (Jarvis, 2007; Gordon et al., 2008; Blackwell et al., 2010). Nevertheless, microbial immobilization of P released by DRW, indicated by the strongly reduced C:P ratio of the microbial biomass in the DRW soils compared with control soils, can result in some soils showing no change in reactive P concentrations following DRW (Butterly et al., 2011b). Understanding these transformations upon DRW and the competition between soil microbes and plants is necessary to determine the fate of released nutrients in different soils and management systems.

Interacting physical and biological soil dynamics under DRW pose a challenge to determining the effects of irrigation management on nutrient availability, which is further complicated by the large variability in soil type and DRW methodologies but also nutrient analyses across different studies. To compare nutrient dynamics under different DRW cycles in different studies, it is necessary to relate soil water contents and Ψ_{soil} via a moisture release curve, yet this characterization is often omitted from studies. Further work should prioritize determining thresholds of drying and rewetting intensities and rates at which soil nutrient availability increases, and quantifying the contributions of physiochemical processes and the microbial biomass in different soils and management conditions.

Deficit irrigation techniques and plant nutrient acquisition

Despite the frequently reported increase in N and P availability upon soil DRW, effects of fluctuating water regimes (implied in the DI techniques described above) on plant nutrient acquisition has received limited attention, particularly for P. However, some understanding of the nutritional effects of DI has been achieved.

Partial rootzone drying increased soil N availability (compared with DI) in several studies, with increased plant N concentration attributed to PRD stimulating the microbial biomass and mineralization of soil organic N, enhancing its availability (Wang *et al.*, 2009, 2010*b*, 2012*b*). For containerized potato grown in peat (Wang *et al.*, 2009), PRD increased leaf, stem, and tuber total N concentrations by 17, 35, and 24%, respectively, compared with plants exposed to standard DI. When tomato was grown in a sandy loam (Wang *et al.*, 2010*b*), PRD increased plant N accumulation by 16% compared with plants under standard DI. Mineralization of ^{15}N-labelled straw was 25% greater in the PRD treatment, providing an enhanced pool of inorganic N available for uptake. These results were conserved across contrasting soil types and different crop species, probably due to the more intense soil drying of part of the pot during PRD (even though the same irrigation volumes were supplied in both PRD and DI), which affects microbial processes and nutrient availability.

Determining the relative contributions of plant and microbial processes to N acquisition during DRW remains an important challenge to address. Benefits of PRD on crop N uptake may not always be immediate, but rather may become apparent after several DRW cycles (Wang *et al.*, 2012*b*). Higher shoot N concentrations following PRD may be due to DRW cycles stimulating mineralization of SOM, but additional data on soil N availability would be valuable. Future research could achieve this by labelling soil amendments with both N and P isotopes to trace nutrient movement in different soil pools, with repeated xylem sap sampling from an intact plant (Netting *et al.*, 2012) determining nutrient uptake dynamics.

Measurements of xylem nutrient fluxes may provide a more sensitive indicator of momentary plant sensing of soil nutrient availability than bulk leaf nutrient concentrations. Root

to shoot transfer of nutrients via the transpiration stream may be particularly valuable to detect how the intensity and rate of DRW regulates plant nutrient uptake. Root xylem phosphate concentration and Ψ_{root} were significantly higher in tomato plants after 13 d of PRD (compared with DI) but did not differ thereafter (Wang *et al.*, 2012*c*), suggesting that the lower Ψ_{root} of DI plants may have inhibited P acquisition (Wang *et al.*, 2012*c*). However, xylem sap was not collected at an appropriate flow rate (matching whole-plant transpiration to avoid concentration of xylem sap constituents) despite being critical to comparing xylem sap composition of plants grown at different Ψ_{root} (Dodd *et al.*, 2008). It is uncertain whether these differences in xylem phosphate concentration result from changes in nutrient availability within the soil or variation in plant nutrient uptake ability (as affected by Ψ_{root}).

Possible explanations for the inhibited nutrient uptake include reduced ion diffusion in the soil solution, decreased root nutrient uptake capacity mediated by low Ψ_{root}, and the increased mechanical impedance of dry soil limiting root growth and thus the soil volume explored for nutrient acquisition (Misra and Tyler, 2000). Nevertheless, enhanced root growth has frequently been reported in plants following DRW (e.g. Engels *et al.*, 1994) and specifically under PRD (e.g. Mingo *et al.*, 2004; Wang *et al.*, 2012*b*), which probably enhances root nutrient acquisition.

Nutritional benefits of PRD may not be restricted to nutrient uptake, but also may affect intraplant nutrient allocation. Although PRD and DI had similar N uptake, PRD plants allocated more N to fruits relative to total biomass N (Topcu *et al.*, 2007). This higher N harvest index has great agronomic and economic importance, and it is likely that phythormone signalling within the plant will regulate intraplant N distribution (Pons *et al.*, 2001).

Conclusions

While this review has emphasized phytohormonal and nutritional responses as being largely independent mechanisms contributing to crop yields under different deficit irrigation treatments (eg. Fig. 1), an abundant literature shows that variation in crop nutrient status affects phytohormonal signalling (Kudoyarova *et al.*, 2015). For example, low P supply increases not only xylem ABA concentrations but also stomatal sensitivity to ABA (Radin, 1984). Quantifying xylem sap ionic and phytohormone composition in response to factorial combinations of irrigation (e.g. PRD versus DI) and fertilizer applications may account for physiological responses such as stomatal closure, and greater attention should be given to understanding the sensitivity of leaf tissues to these changes in root to shoot signalling.

While much of the deficit irrigation literature (especially PRD studies) has emphasized that elevated ABA status can increase crop WUE, decoupling of stomatal and xylem ABA responses to the re-wetting of dry soil (Fig. 2) suggests it is necessary to understand the temporal dynamics of other long-distance phytohormonal signals. While single-leaf

measurements may be relatively straightforward, gradients of both stomatal conductance (Soar *et al.*, 2004) and phytohormone concentrations (Havlova *et al.*, 2008) within the canopy suggest that paired measurements of whole-plant gas exchange, and root system ionic and phytohormone export, are necessary to further our understanding of physiological and agronomic responses to different irrigation treatments. These measurements are particularly challenging in field environments due to the difficulties in collecting xylem sap (at flow rates approximating whole-plant transpiration) following whole-plant gas exchange measurements (Steduto *et al.*, 2002), but they are technically feasible for whole plants grown in a pressure chamber and exposed to a single drying cycle in the laboratory (Jarvis and Davies, 1997).

Active management of DRW cycles may not only provide an opportunity to enhance carbon gain (Fig. 4) and yield (Price *et al.*, 2013) relative to conventional management systems, but may also increase soil nutrient availability and crop uptake. More work is required for understanding the fundamental soil properties and mechanisms affecting changes in soil nutrient availability in diverse soils under different patterns of DRW. Gains in crop water and nutrient use efficiency achieved by exploiting these different deficit irrigation treatments will ensure continued research efforts in this area, but our improved understanding of fundamental plant and soil science processes must be better integrated with management decisions made by irrigation practitioners.

Acknowledgements

References

Albacete A, Ghanem ME, Martínez-Andújar C, Acosta M, Sanchez-Bravo J, Martinez V, Lutts S, Dodd IC, Pérez-Alfocea F. 2008. Hormonal changes in relation to biomass partitioning and shoot growth impairment in salinised tomato (*Solanum lycopersicum* L.) plants. *Journal of Experimental Botany* **59,** 4119–4131.

Alvarez S, Marsh EL, Schroeder SG, Schachtman DP. 2008. Metabolomic and proteomic changes in the xylem sap of maize under drought. *Plant, Cell and Environment* **31,** 325–340.

Birch HF. 1958. The effect of soil drying on humus decomposition and nitrogen availability. *Plant and Soil* **10,** 9–31.

Blackman P, Davies WJ. 1985. Root to shoot communication in maize plants of the effects of soil drying. *Journal of Experimental Botany* **36,** 39–48.

Blackwell MSA, Brookes PC, de la Fuente-Martinez N, Gordon H, Murray PJ, Snars KE, Williams JK, Bol R, Haygarth PM. 2010. Phosphorus solubilization and potential transfer to surface waters from the soil microbial biomassfollowing drying–rewetting and freezing–thawing. *Advances in Agronomy* **106,** 1–35.

Blackwell MSA, Brookes PC, de la Fuente-Martinez N, Murray PJ, Snars KE, Williams JK, Haygarth PM. 2009. Effects of soil drying and rate of re-wetting on concentrations and forms of phosphorus in leachate. *Biology and Fertility of Soils* **45,** 635–643.

Bünemann EK, Keller B, Hoop D, Jud K, Boivin P, Frossard E. 2013. Increased availability of phosphorus after drying and rewetting of a grassland soil: processes and plant use. *Plant and Soil* **370,** 511–526.

Burgess SSO, Adams MA, Turner NC, Ong CK. 1998. The redistribution of soil water by tree root systems. *Oecologia* **115,** 306–311.

Butterly CR, McNeill AM, Baldock JA, Marschner P. 2011*b*. Changes in water content of two agricultural soils does not alter labile P and C pools. *Plant and Soil* **348,** 185–201.

Butterly CR, Bünemann EK, McNeill AM, Baldock JA, Marschner P. 2009. Carbon pulses but not phosphorus pulses are related to decreases in microbial biomass during repeated drying and rewetting of soils. *Soil Biology and Biochemistry* **41,** 1406–1416.

Butterly CR, McNeill AM, Baldock JA, Marschner P. 2011*a*. Rapid changes in carbon and phosphorus after rewetting of dry soil. *Biology and Fertility of Soils* **47,** 41–50.

Caldwell MM, Richards JH. 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia* **79,** 1–5.

Carminati A, Moradi AB, Vetterlein D, Vontobel P, Lehmann E, Weller U, Vogel HJ, Oswald SE. 2010. Dynamics of soil water content in the rhizosphere. *Plant and Soil* **332,** 163–176.

Chen L, Dodd IC, Davies WJ, Wilkinson S. 2013. Ethylene limits abscisic acid and soil-drying induced stomatal closure in aged wheat leaves. *Plant, Cell and Environment* **36,** 1850–1859.

Chepkwony CK, Haynes RJ, Swift RS, Harrison R. 2001. Mineralization of soil organic P induced by drying and rewetting as a source of plant-available P in limed and unlimed samples of an acid soil. *Plant and Soil* **234,** 83–90.

Christmann A, Weiler EW, Steudle E, Grill E. 2007. A hydraulic signal in root-to-shoot signalling of water shortage. *The Plant Journal* **52,** 167–174.

Collins MJ, Fuentes S, Barlow EWR. 2010. Partial rootzone drying and deficit irrigation increase stomatal sensitivity to vapour pressure deficit in anisohydric grapevines. *Functional Plant Biology* **37,** 128–138.

Condon AG, Richards RA, Rebetzke GJ, Farquhar GD. 2004. Breeding for high water-use efficiency. *Journal of Experimental Botany* **55,** 2447–2460.

Cordell D, Drangert J, White S. 2009. The story of phosphorus: global food security and food for thought. *Global Environmental Change* **19,** 292–305.

Correia MJ, Pereira JS. 1994. Abscisic acid in apoplastic sap can account for the restriction in leaf conductance of white lupins during moderate soil drying and rewatering. *Plant, Cell and Environment* **17,** 845–852.

Cosentino D, Chenu C, Le Bissonnais Y. 2006. Aggregate stability and microbial community dynamics under drying–wetting cycles in a silt loam soil. *Soil Biology and Biochemistry* **38,** 2053–2062.

Davies WJ, Kozlowski TT. 1977. Variations among woody plants in stomatal conductance and photosynthesis during and after drought. *Plant and Soil* **46,** 435–444.

Davies WJ, Zhang J. 1991. Root signals and the regulation of growth and development of plants in drying soil. *Annual Review of Plant Physiology and Plant Molecular Biology* **42,** 55–76.

Davies WJ, Zhang J, Yang J, Dodd IC. 2011. Novel crop science to improve yield and resource use efficiency in water-limited agriculture. *Journal of Agricultural Science* **149,** 123–131.

De Nobili M, Contin M, Brookes PC. 2006. Microbial biomass dynamics in recently air-dried and rewetted soils compared to others stored air-dry for up to 103 years. *Soil Biology and Biochemistry* **38,** 2871–2881.

de Souza CR, Maroco JP, dos Santos TP, Rodrigues ML, Lopes CM, Pereira JS, Chaves MM. 2003. Partial rootzone drying: regulation of stomatal aperture and carbon assimilation in field-grown grapevines (*Vitis vinifera* cv. Moscatel). *Functional Plant Biology* **30,** 653–662.

Dodd IC. 2005. Root-to-shoot signalling: assessing the roles of 'up' in the up and down world of long-distance signalling *in planta*. *Plant and Soil* **274,** 251–270.

Dodd IC. 2009, Rhizosphere manipulations to maximise 'crop per drop' during deficit irrigation. *Journal of Experimental Botany* **60,** 2454–2459.

Dodd IC, Egea G, Davies WJ. 2008. Accounting for sap flow from different parts of the root system improves the prediction of xylem ABA

concentration in plants grown with heterogeneous soil moisture. *Journal of Experimental Botany* **59,** 4083–4093.

Dodd IC, Egea G, Watts C, Whalley WR. 2010. Root water potential integrates discrete soil physical properties to influence ABA signalling during partial rootzone drying. *Journal of Experimental Botany* **61,** 3543–3551.

Dodd IC, Stikic R, Davies WJ. 1996. Chemical regulation of gas exchange and growth of plants in drying soil in the field. *Journal of Experimental Botany* **47,** 1475–1490.

Dodd IC, Theobald JC, Bacon MA, Davies WJ. 2006. Alternation of wet and dry sides during partial rootzone drying irrigation alters root-to-shoot signalling of abscisic acid. *Functional Plant Biology* **33,** 1081–1089.

Dörffling K, Streich J, Kruse W. 1977. Abscisic acid and the after-effect of water stress on stomatal opening potential. *Zeitschrift fur Pflanzephysiologie* **81,** 43–56.

Dry PR, Loveys BR, Botting D, Duering H. 1996. Effects of partial rootzone drying on grapevine vigour, yield, composition of fruit and use of water. In: Stockley CS, Sas AN, Johnstone RS, Lee TH, eds. *Proceedings of the 9th Australian Wine Industry Technical Conference* . Adelaide: Winetitles, 126–131.

Du TS, Kang SZ, Zhang JH, Li FS, Hu XT. 2006. Yield and physiological responses of cotton to partial root-zone irrigation in the oasis field of northwest China. *Agricultural Water Management* **84,** 41–52.

Ernst L, Goodger JQD, Alvarez S, Marsh EL, Berla B, Lockhart E, Jung J, Li P, Bohnert HJ, Schactman DP. 2010. Sulphate as a xylem-borne chemical signal precedes the expression of ABA biosynthetic genes in maize roots. *Journal of Experimental Botany* **61,** 3395–3405.

Elliot J, Deryng D, Mueller C, *et al*. 2014. Constraints and potentials of future irrigation water availability on agricultural production under climate change. *Proceedings of the National Academy of Sciences, USA* **111,** 3239–3244.

Engels C, Mollenkopf M, Marschner H. 1994. Effect of drying and rewetting the topsoil on root growth of maize and rape in different soil depths. *Zeitschrift fürPflanzenernährung und Bodenkunde* **157,** 139–144.

Fereres E, Soriano MA. 2007. Deficit irrigation for reducing agricultural water use. *Journal of Experimental Botany* **58,** 147–159.

Fierer N, Schimel, JP. 2003. A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. *Soil Science Society of America Journal* **67,** 798–805.

Fischer T. 2009. Substantial rewetting phenomena on soil respiration can be observed at low water availability. *Soil Biology and Biochemistry* **41,** 1577–1579.

Fuchs EE, Livingston NJ. 1996. Hydraulic control of stomatal conductance in Douglas fir (Psuedotsuga menziesii (Mirb.) Franco) and alder (Alnus rubra (Bong.)) seedlings. *Plant, Cell and Environment* **19,** 1091–1098.

Gollan T, Passioura JB, Munns R. 1986. Soil water status affects the stomatal conductance of fully turgid wheat and sunflower leaves. *Australian Journal of Plant Physiology* **13,** 459–464.

Gomez-Cadenas A, Tadeo FR, Talon M, Primo-Millo E. 1996. Leaf abscission induced by ethylene in water-stressed intact seedlings of cleopatra mandarin requires previous abscisic acid accumulation in roots. *Plant Physiology* **112,** 401–408.

Goodger JQD, Sharp RE, Marsh EL, Schactman DP. 2005. Relationships between xylem sap constituents and leaf conductance of well-watered and water-stressed maize across three xylem sap sampling techniques. *Journal of Experimental Botany* **56,** 2389–2400.

Gordon H, Haygarth PM, Bardgett RD. 2008. Drying and rewetting effects on soil microbial community composition and nutrient leaching. *Soil Biology and Biochemistry* **40,** 302–311.

Gowing DJG, Davies WJ, Jones HG. 1993. Xylem-transported abscisic acid: the relative importance of its mass and its concentration in the control of stomatal aperture. *Plant, Cell and Environment* **16,** 453–459.

Grant OM, Stoll M, Jones HG. 2004. Partial rootzone drying does not affect fruit yield of raspberries. *Journal of Horticultural Science and Biotechnology* **79,** 125–130.

Hansen H, Dörffling K. 2003. Root-derived trans-zeatin riboside and abscisic acid in drought-stressed and rewatered sunflower plants:

interaction in the control of leaf diffusive resistance? *Functional Plant Biology* **30,** 365–375.

Havlova M, Dobrev PI, Motyka V, Storchova H, Libus J, Dobra J, Malbeck J, Gaudinova A, Vankova R. 2008. The role of cytokinins in responses to water deficit in tobacco plants over-expressing *trans*-zeatin O-glucosyltransferase gene under *35S* or *SAG12* promoters. *Plant, Cell and Environment* **31,** 341–353.

Haygarth PM, Hepworth L, Jarvis SC. 1998. Forms of phosphorus transfer in hydrological pathways from soil under grazed grassland. *European Journal of Soil Science* **49,** 65–72.

Haynes RJ, Swift RS. 1985. Effects of air-drying on the adsorption and desorption of phosphate and levels of extractable phosphate in a group of acid soils, New Zealand. *Geoderma* **35,** 145–157.

Henson IE, Jensen CR, Turner NC. 1989. Leaf gas exchange and water relations of lupins and wheat. III. Abcisic acid and drought-induced stomatal closure. *Australian Journal of Plant Physiology* **16,** 429–442.

Hu L, Wang Z, Huang B. 2013. Effects of cytokinin and potassium on stomatal and photosynthetic recovery of Kentucky bluegrass from drought stress. *Crop Science* **53,** 221–231.

Huber K, Vanderborght J, Javaux M, Schroeder N, Dodd IC, Vereecken H. 2014. Modelling the impact of heterogeneous rootzone water distribution on the regulation of transpiration by hormone transport and/or hydraulic pressures. *Plant and Soil* **384,** 93–112.

Jackson MB. 1993. Are plant hormones involved in root-to-shoot communication? *Advances in Botanical Research* **19,** 103–187.

Jarvis AJ, Davies WJ. 1997. Whole plant ABA flux and the regulation of water loss in *Cedrella odorata*. *Plant, Cell and Environment* **20,** 521–527.

Jarvis P, Rey A, Petsikos C, *et al*. 2007. Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the 'Birch effect'. *Tree Physiology* **27,** 929–940.

Javaux M, Couvreur V, Vanderborght J, Vereecken H. 2013. Root water uptake: from three-dimensional biophysical processes to macroscopic modeling approaches. *Vadose Zone Journal* **12,** 4.

Javaux M, Schröder T, Vanderborght J, Vereecken H. 2008. Use of a three-dimensional detailed modeling approach for predicting root water uptake. *Vadose Zone Journal* **7,** 1079–1088.

Kang S, Liang Z, Pan Y, Shi P, Zhang J. 2000. Alternate furrow irrigation for maize production in an arid area. *Agricultural Water Management* **45,** 267–274.

Kang S, Zhang L, Hu X, Li Z, Jerie P. 2001. An improved water use efficiency for hot pepper grown under controlled alternate drip irrigation on partial roots. *Scientia Horticulturae* **89,** 257–267.

Kang S, Zhang J, Liang Z, Hu X, Cai H. 1997. The controlled alternative irrigation: a new approach for water saving regulation in farmland. *Agricultural Research in Arid and Semiarid Areas* **15,** 1–6 (in Chinese).

Khalil AAM, Grace J. 1993. Does xylem sap ABA control the stomatal behaviour of water-stressed sycamore (*Acer pseudoplatanus* L.) seedlings? *Journal of Experimental Botany* **44,** 1127–1134.

Kramer PJ. 1988. Changing concepts regarding plant water relations. *Plant, Cell and Environment* **11,** 565–567.

Kudoyarova GR, Vysotskaya LB, Cherkozyanova A, Dodd IC. 2007. Effect of partial rootzone drying on the concentration of zeatin-type cytokinins in tomato (*Solanum lycopersicum* L.) xylem sap and leaves. *Journal of Experimental Botany* **58,** 161–168.

Kudoyarova GR, Dodd IC, Rothwell SA, Veselov D, Veselov S. 2015. Common and specific responses to availability of mineral nutrients and water. *Journal of Experimental Botany* **66,** 2143–2154.

Lobet G, Pages L, Draye X. 2013. First steps towards an explicit modelling of ABA production and translocation in relation with the water uptake dynamics *Acta Horticulturae* **991,** 373–381.

Loewenstein NJ, Pallardy SG. 2002. Influence of a drying cycle on post-drought xylem sap abscisic acid and stomatal responses in young temperate deciduous angiosperms. *New Phytologist* **156,** 351–361.

Masia A, Pitacco A, Braggio L, Giulivo C. 1994. Hormonal responses to partial drying of the root system of *Helianthus annuus*. *Journal of Experimental Botany* **45,** 69–76.

Megat Wahab, PE. 2007. Soil drying effects on two tomato cultivars. PhD thesis, University of Lancaster.

Mencuccini M, Mambelli S, Comstock J. 2000. Stomatal responsiveness to leaf water status (*Phaseolus vulgaris* L.) is a function of time of day. *Plant, Cell and Environment* **23,** 1109–1118.

Mingo DM, Theobald JC, Bacon MA, Davies WJ, Dodd IC. 2004. Biomass allocation in tomato (*Lycopersicon esculentum*) plants grown under partial rootzone drying: enhancement of root growth. *Functional Plant Biology* **31,** 971–978.

Misra A, Tyler G. 2000. Effect of wet and dry cycles in calcareous soil on mineral nutrient uptake of two grasses, *Agrostis stolonifera* L. and *Festuca ovina* L. *Plant and Soil* **224,** 297–303.

Munns R, King RW. 1988. Abscisic acid is not the only inhibitor of transpiration in xylem sap of wheat plants. *Plant Physiology* **88,** 703–708.

Navarro-García F, Casermeiro MA, Schimel JP. 2012. When structure means conservation: effect of aggregate structure in controlling microbial responses to rewetting events. *Soil Biology and Biochemistry* **44,** 1–8.

Netting AG, Theobald JC, Dodd IC. 2012. Xylem sap collection and extraction methodologies to determine *in vivo* concentrations of ABA and its bound forms. *Plant Methods* **8,** 11.

Pantin F, Monnet F, Jannaud D, Costa J, Renaud J, Muller B, Simonneau T, Genty B. 2013. The dual effect of abscisic acid on stomata. *New Phytologist* **197,** 65–72.

Parent B, Hachez C, Redondo E, Simonneau T, Chaumont F, Tardieu F. 2009. Drought and abscisic acid effects on aquaporin content translate into changes in hydraulic conductivity and leaf growth rate: a trans-scale approach. *Plant Physiology* **149,** 2000–2012.

Passioura JB. 1988*a*. Response to Dr P.J. Kramer's article 'Changing concepts regarding plant water relations'. *Plant, Cell and Environment* **11,** 569–571.

Passioura JB. 1988*b*. Root signals control leaf expansion in wheat seedlings growing in drying soil. *Australian Journal of Plant Physiology* **15,** 687–693.

Pérez-Alfocea F, Ghanem ME, Gomez-Cadenas A, Dodd IC. 2011. Omics of root-to-shoot signalling under salt stress and water deficit. *Omics: a Journal of Integrative Biology* **15,** 893–901.

Pérez-Pérez JG, Dodd IC. 2015. Sap fluxes from different parts of the rootzone modulate xylem ABA concentration during partial rootzone drying and re-wetting. *Journal of Experimental Botany* **66,** 2279–2288.

Pérez-Pérez JG, Dodd IC, Botía P. 2012. Partial root-zone drying increases water use efficiency of lemon 'Fino 49' trees independently of root-to-shoot ABA signalling. *Functional Plant Biology* **39,** 366–378.

Pons TL, Jordi W, Kuiper D. 2001. Acclimation of plants to light gradients in leaf canopies: evidence for a possible role for cytokinins transported in the transpiration stream. *Journal of Experimental Botany* **52,** 1563–1574.

Price AH, Norton GJ, Salt DE et al. 2013. Alternate wetting and drying irrigation for rice in Bangladesh: is it sustainable and has plant breeding something to offer? *Food and Energy Security* **2,** 120–129.

Puértolas J, Alcobendas R, Alarcón JJ, Dodd IC. 2013. Long-distance abscisic acid signalling under different vertical soil moisture gradients depends on bulk root water potential and average soil water content in the root zone. *Plant, Cell and Environment* **36,** 1465–1475.

Puértolas J, Conesa MC, Ballester C, Dodd IC. 2015. Local root abscisic acid (ABA) accumulation depends on the spatial distribution of soil moisture in potato: implications for ABA signalling under heterogeneous soil drying. *Journal of Experimental Botany* **66,** 2289–2298.

Qin H, Cao G, Kristensen M, Refsgaard JC, Rasmussen MO, He X, Liu J, Shu Y, Zheng C. 2013. Integrated hydrological modeling of the North China Plain and implications for sustainable water management. *Hydrology and Earth System Sciences* **17,** 3759–3778.

Radin JW. 1984. Stomatal responses to water stress and to abscisic acid in phosphorus-deficient cotton plants. *Plant Physiology* **76,** 392–394.

Romero R, Dodd IC, Martinez-Cutillas A. 2012. Contrasting physiological effects of partial root-zone drying in field-grown grapevine (*Vitis vinifera* L. cv. Monastrell) according to total soil water availability. *Journal of Experimental Botany* **63,** 4071–4083.

Saliendra NZ, Sperry JS, Comstock J. 1995. Influence of leaf water status on stomatal responses to humidity, hydraulic conductance and soil drought in *Betula occidentalis. Planta* **196,** 357–366.

Simonneau T, Barrieu P, Tardieu F. 1998. Accumulation rate of ABA in detached maize roots correlates with root water potential regardless of age and branching order. *Plant, Cell and Environment* **21,** 1113–1122.

Soar CJ, Speirs J, Maffei SM, Loveys BR. 2004. Gradients in stomatal conductance, xylem sap ABA and bulk leaf ABA along canes of *Vitis vinifera* cv. Shiraz: molecular and physiological studies investigating their source. *Functional Plant Biology* **31,** 659–669.

Sobeih WY, Dodd IC, Bacon MA, Grierson D, Davies WJ. 2004. Long-distance signals regulating stomatal conductance and leaf growth in tomato (*Lycopersicon esculentum*) plants subjected to partial rootzone drying. *Journal of Experimental Botany* **55,** 2353–2363

Soinne H, Raty M, Hartikainen H. 2010. Effect of air-drying on phosphorus fractions in clay soil. *Journal of Plant Nutrition and Soil Science* **173,** 332–336.

Steduto P, Cetinkoku O, Albrizio R, Kanber R. 2002. Automated closed-system canopy-chamber for continuous field-crop monitoring of CO_2 and H_2O fluxes. *Agricultural and Forest Meteorology* **111,** 171–186.

Stoll M, Loveys BR, Dry PR. 2000. Hormonal changes induced by partial rootzone drying of irrigated grapevine. *Journal of Experimental Botany* **51,** 1627–1634.

Sun Y, Yan F, Liu F. 2013. Drying/rewetting cycles of the soil under alternate partial root-zone drying irrigation reduce carbon and nitrogen retention in the soil–plant systems of potato. *Agricultural Water Management* **128,** 85–91.

Swift MJ, Heal OW, Anderson JM. 1979. *Decomposition in terrestrial ecosystems.* Berkeley, CA: University of California Press.

Tang LS, Li Y, Zhang J. 2005. Physiological and yield responses of cotton under partial rootzone irrigation. *Field Crops Research* **94,** 214–223.

Tardieu F, Davies WJ. 1992. Stomatal response to abscisic acid is a function of current plant water status. *Plant Physiology* **98,** 540–545.

Tardieu F, Davies WJ. 1993. Integration of hydraulic and chemical signaling in the control of stomatal conductance and water status of droughted plants. *Plant, Cell and Environment* **16,** 341–349.

Tardieu F, Simonneau T. 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *Journal of Experimental Botany* **49,** 419–432.

Thompson AJ, Andrews J. Mulholland BJ, et al. 2007. Overproduction of abscisic acid in tomato increases transpiration efficiency and root hydraulic conductivity and influences leaf expansion. *Plant Physiology* **143,** 1905–1917.

Topcu S, Kirda C, Dasgan Y, Kaman H, Cetin M, Yazici A, Bacon MA. 2007. Yield response and N-fertiliser recovery of tomato grown under deficit irrigation. *European Journal of Agronomy* **26,** 64–70.

Trejo CL. 1994. Involvement of abscisic acid in the regulation of stomatal aperture during soil drying. PhD thesis. University of Lancaster.

Tudela D, Primo-Millo E. 1992. 1-Aminocyclopropane-1-carboxylic acid transported from roots to shoots promotes leaf abscission in cleopatra mandarine (Citrus reshni Hort ex Tan) seedlings rehydrated after water-stress. *Plant Physiology* **100,** 131–137.

Turner BL, Driessen JP, Haygarth PM, Mckelvie ID. 2003. Potential contribution of lysed bacterial cells to phosphorus solubilisation in two rewetted Australian pasture soils. *Soil Biology and Biochemistry* **35,** 187–189.

Turner BL, Haygarth PM. 2001. Phosphorus solubilisation in rewetted soils. *Nature* **411,** 258.

Turner BL, Haygarth PM. 2003. Changes in bicarbonate-extractable inorganic and organic phosphorus by drying pasture soils. *Soil Science Society of America Journal* **67,** 344–350.

Wang Y, Li B, Du MW, Eneji AE, Wang BM, Duan LS, Li ZH, Tian XL. 2012*a*. Mechanism of phytohormone involvement in feedback regulation of cotton leaf senescence induced by potassium deficiency. *Journal of Experimental Botany* **63,** 5887–5901.

Wang Y, Liu F, Andersen MN, Jensen CR. 2010*a*. Improved plant nitrogen nutrition contributes to higher water use efficiency in tomatoes under alternate partial root-zone irrigation. *Functional Plant Biology* **37,** 175–182.

Wang Y, Liu F, Jensen CR. 2012*c*. Comparative effects of deficit irrigation and alternate partial root-zone irrigation on xylem pH, ABA and ionic concentrations in tomatoes. *Journal of Experimental Botany* **63,** 1907–1917.

Wang Y, Liu F, Kang S, Jensen CR. 2012*b*. Alternate partial root-zone drying irrigation improves nitrogen nutrition in maize (*Zea mays* L.) leaves. *Environmental and Experimental Botany* **75,** 36–40.

Wang Y, Liu F, Neergaard AD, Jensen LS, Luxhøi J, Jensen CR. 2010*b*. Alternate partial root-zone irrigation induced dry/wet cycles of soils stimulate N mineralization and improve N nutrition in tomatoes. *Plant and Soil* **337,** 167–177.

Wang H, Liu F, Andersen MN, Jensen CR. 2009. Comparative effects of partial root-zone drying and deficit irrigation on nitrogen uptake in potatoes (*Solanum tuberosum* L.). *Irrigation Science* **27,** 443–448.

Wilkinson S, Davies WJ. 1997. Xylem sap pH increase: a drought signal received at the apoplastic face of the guard cell which involves the suppression of saturable ABA uptake by the epidermal symplast. *Plant Physiology* **113,** 559–573.

Xue YG, Duan H, Liu LJ, Wang ZQ, Yang JC, Zhang JH. 2013. An improved crop management system increases grain yield and nitrogen and water use efficiency in rice. *Crop Science* **53,** 271–284.

Yan F, Sun Y, Song F, Liu F. 2012. Differential responses of stomatal morphology to partial root-zone drying and deficit irrigation in potato leaves under varied nitrogen rates, *Scientia Horticulturae* **145,** 76–83.

Yang J, Zhang J. 2010. Crop management techniques to enhance harvest index in rice. *Journal of Experimental Botany* **61,** 3177–3189.

Yao C, Moreshet S, Aloni B. 2001. Water relations and hydraulic control of stomatal behaviour in bell pepper plant in partial soil drying. *Plant, Cell and Environment* **24,** 227–235.

Zarebanadkouki M, Carminati A. 2014. Reduced root water uptake after drying and rewetting. *Journal of Plant Nutrition and Soil Science* **177,** 227–236.

Zhang H, Chen T, Wang Z, Yang J, Zhang J. 2010. Involvement of cytokinins in the grain filling of rice under alternate wetting and drying irrigation. *Journal of Experimental Botany* **61,** 3719–3733.

Zhang H, Li H, Yuan L, Wang Z, Yang J, Zhang J. 2012. Post-anthesis alternate wetting and moderate soil drying enhances activities of key enzymes in sucrose-to-starch conversion in inferior spikelets of rice. *Journal of Experimental Botany* **63,** 215–227.

Zhang H, Xue Y, Wang Z, Yang J, Zhang J. 2009. Alternate wetting and moderate soil drying improves root and shoot growth in rice. *Crop Science* **49,** 2246–2260.