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Review paper

Mitigation of plant drought stress in a changing climate

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ABSTRACT: This review paper addresses possible adaptation strategies to mitigate drought effects on plants that will increase under climate change. The focus will be on two approaches: use of water-saving deficit irrigation methods (partial root-zone drying-PRD and regulated deficit irrigation-RDI) and breeding of genotypes with increased drought resistance. Both approaches are based on knowledge of plant stress physiology.

KEY WORDS: drought, deficit irrigation, resistance

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INTRODUCTION

Climate change is one of the most serious problems facing the world today. The Intergovernmental Panel on Climate Change (IPCC) predicts that during the next decades CO_2 concentration and average temperature will increase, the precipitation will increase in high latitudes, and decrease in most subtropical regions, as well as increases in extreme events, including heat waves, storms and floods (IPCC 2007). According to Burke *et al.* (2006), the proportion of the land surface suffering extreme drought could increase to 30% by the end of the twenty-first century. The impact of this change will have serious effects, including reduced crop yield but also change in vegetation in many areas in the world (Jiang *et al.* 2013). The predictions are also that the demand for irrigation will increase considerably in years to come to alleviate the consequences of climate change and more frequent and severe droughts. However, in many countries, as a consequence of global climate changes and environmental pollution, water use in agriculture will be reduced. Water supplies are also under pressure from users other than agricultural and saving of water resources and increasing agricultural productivity per unit of water ("more crop per drop") are becoming of strategic importance for many countries (Luquet *et al.* 2005). Emphasis therefore must be placed on crop physiology and crop management under dry conditions to make plants more efficient water users (Chaves *et al.* 2003; Morison *et al.* 2008; Rouf Mir *et al.* 2012; Lawlor 2013).

The aim of this paper is to provide a short overview of some of the current challenges and opportunities to minimize the problem of agricultural production under water scarcity. The focus will be on the two approaches: use of deficit irrigation methods (partial root-zone drying-PRD and regulated deficit irrigation-RDI) and use and breeding of genotypes with increased drought resistance. Both approaches are based on knowledge of crop stress physiology. The paper also presents some of the current information on application of these approaches to mitigate the effects of drought on tomato (*Lycopersicon esculentum* L.) and potato (*Solanum tuberosum* L.), the two most widely grown vegetables in the world and significant water consumers (FAO 2006).

DEFICIT IRRIGATION METHODS: THE PRACTICAL EXPLOITATION OF PLANT STRESS CHEMICAL SIGNALLING

Drought induces a restriction of water supply which results in a reduction of tissue water content, stomatal conductance, metabolic processes and growth. Numerous studies have shown that plant roots can sense changes in soil water content. As soils become dry, root-sourced

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signals are transported *via* the xylem to leaves and result in reduced water loss and decreased leaf growth (Schachtman & Goodger 2008). Jones (1980) was the first to suggest that this soil drying might involve the transfer of chemical information from the roots to shoots *via* the xylem. Such control has been termed non-hydraulic or chemical signalling. This distinguishes it from hydraulic signalling, which represents the transmission of reduced soil water *via* changes in the xylem sap tension (Dodd *et al.* 1996).

Numerous studies confirmed the contribution of different chemicals to root-to-shoot signalling, and the complexity of constituents and their interactions. The plant hormone abscisic acid (ABA) plays a key role in chemical signalling. Substantial evidence obtained from a large number of experiments has demonstrated that reduced stomatal conductance, reduced leaf area and increased root biomass, are three of the major adaptive processes regulated by ABA (Davies *et al.* 2005). ABA present in xylem sap in conjugated forms, such as abscisic acid-glucose ester (ABA-GE) could serve as a transported form of the hormone and, moreover, as a stress signal (Schachtman & Goodger 2008).

Signalling of ABA could also be regulated by different factors including pH, root growth promoting rhizobacteria, ions and apoplastic β-glucosidases in the leaves (Davies *et al.* 2005). Xylem sap and apoplastic pH are highly dependent upon water availability to the roots. Increases in xylem sap pH have been recorded in many plant species, including tomato, grown in drying soils, and may act as a root signal (Wilkinson & Davies 2008). However, the reaction of stomata on mutual effects of ABA and pH seems to be species or genotype dependent (Prokic *et al.* 2006).

Other hormones, especially cytokinins and ethylene, are important for signalling. Cytokinins are considered as negative root-to-shoot stress signals whose production and transport decrease as the soil dries. However, there is a lot of uncertainty of the intensity of the cytokinin signal in the xylem and universality of stomatal reaction to their decreased concentration in xylem in different plant species (Kudoyarova *et al.* 2007). Several studies have also pointed out the importance of the interaction between ABA and ethylene in plant development (Sharp 2002). Although the role of ABA and other chemical signals is supported by many experiments, their contribution to root-to-shoot signalling remains controversial. This controversy may be due to differing responses between species, the different intensities of stress treatments applied, the time at which samples were collected during the imposition of drought, and/or the different methods used for xylem sap extraction (Schachtman & Goodger 2008).

In recent years, significant attention has been given to the practical exploitation of signalling mechanisms by deficit irrigation strategies. The term *deficit irrigation* describes an irrigation scheduling strategy that allows a plant's water status to decrease to the certain point of drought stress. Currently, two deficit irrigation methods are in use: regulated deficit irrigation and partial root-zone drying (FAO 2002).

Regulated deficit irrigation. In regulated deficit irrigation (RDI) the entire root zone is irrigated with an amount of water less than the potential evapotranspiration during specific periods of the crop cycle (English & Raja 1996). The principle of the RDI technique is that plant sensitivity to drought is not constant during the growing season and that intermittent water deficit during specific periods of ontogenesis may increase water savings and improve yield quality (Loveys *et al.* 2004).

Implementing RDI could also be difficult where there is a high water table or deep soil with a high water holding capacity. However, if RDI is managed carefully, the negative impact on yield could be avoided. Results for numerous field crops (maize, wheat, soybean, sunflower), tree crops and grapevine showed that optimal managing of RDI might increase water productivity or yield quality (Jovanovic & Stikic 2012; Savic *et al.* 2011).

Partial root-zone drying. Regulated deficit irrigation is a method where water application is manipulated over time, while partial root-zone drying (PRD) is a method where water is manipulated over space. PRD is designed to maintain half of the root system in a dry or drying state, while the other half is irrigated. The treatment is then reversed, allowing the previously well-watered side of the root system to dry down while fully irrigating the previously dry side (FAO 2002).

The principle behind PRD is that irrigating part of the root system keeps the leaves hydrated and in a favorable plant water status, while drying on the other part of the root system promotes the synthesis and transport of chemical signals from roots to the shoot *via* the xylem to induce a physiological response (Dodd *et al.* 2006). Triggering partial stomatal closure under PRD irrigation prevents excessive water loss and also the metabolic inhibition of CO_2 assimilation, that otherwise would occur in extensive development of drought stress (Chaves *et al.* 2003; Costa *et al.* 2007). The frequency of the switch depends on soil type, genotype, rainfall and temperature. Most often the PRD cycle is 10-15 days (Davies *et al.* 2000).

Compared to RDI, implementing the PRD technique is simpler, requiring only the adaptation of irrigation systems to allow alternate wetting and drying of part of the rootzone. PRD may be applied by different techniques in the field depending on the cultivated crops or soil condition. PRD irrigation (alternate or fixed) could be done by subsurface or surface drip lines, furrow, micro-sprinkler or vertical soil profile methods (Jensen *et al.* 2010; Jovanovic *et al.*, 2010, 2012; Stikic *et al.* 2010)

The partial root drying method is applied in a wide range of crops and experimental systems. Comprehensive data sets from both field and glasshouse studies have shown that under PRD irrigation water may be reduced by approximately 30-50% without significant yield reduction and in some cases with an improved yield quality (Jovanovic & Stikic 2012).

An important mechanism of plant response to PRD may be the promotion of root growth (Prokic & Stikic 2012) and increase of root biomass (Mingo *et al.* 2004). Enhanced root growth will increase the plant's ability to explore a greater soil volume potentially increasing soil water and nutrient acquisition.

Most of the results also demonstrated that the effect of PRD is smaller in fruits compared to vegetative parts of plants. According to the theory of shoot-to-root signalling, the PRD effect on plant growth could be explained by smaller accumulation of ABA in the fruits compared with the shoots (Davies *et al.* 2000). Results from several experiments demonstrated that tomato fruit growth was reduced more by RDI than by PRD treatments (Davies *et al.* 2000). Our results showed that different effects of PRD and RDI on fruit growth might be explained by differences in the activities of cell wall enzymes in the exocarp of fruits (Savić *et al.* 2008). However, few studies have provided comprehensive information about the genetic and molecular basis of PRD and RDI effects. Our recent PRD and RDI experiments were done with the wild type (WT) and *flacca* mutant of tomato (deficient in ABA content). Similar expression patterns of ABA biosynthetic genes (*TAO1* and *NCED*) and ethylene transcription factors (*EIL1*) indicated synergistic signalling pathways for ABA and ethylene in WT tomato plants under PRD (Milosavljević *et al.* 2012). Proteomic analyses and up-regulation of some of the antioxidative enzymes during the cell expansion phase of PRD fruits of tomato WT plants appears to be related to their role in protecting fruits against the mild stress induced by PRD (Marjanovic *et al.* 2012).

Table 1 presents some of our recent results in an experiment with tomato cultivar *Amati* grown under PRD and full irrigation in commercial polytunnel conditions (Jovanovic & Stikic 2012). These results also showed that with the PRD method it is possible to increase water-use efficiency (WUE) and save water for irrigation, without statistically significantly reducing tomato yield. Furthermore, in our experiment the antioxidative activity was significantly increased in tomato fruits under PRD compared with the fruits of control plants. This improvement of PRD fruit quality could also be beneficial from the aspect of the health-promoting value of tomato fruits.

The PRD irrigation method has also been successfully trialled with potato (Jovanovic *et al.* 2012). Our results

Table 1. Treatment means of yield, water use efficiency (WUE), fruit quality (total soluble solids - TSS, titrable acidity - TA and antioxidant activities - AA) in fully-irrigated tomato (FI) and tomato under partial root-zone drying (PRD).

Water treatment	Yield (t ha^{-1})	WUE (kg FW m^{-3})	TSS (°Brix)	TA (citric acid µmol g^{-1} FW)	AA (µmol TEAC 100g^{-1} FW)
FI	48.71	34.90^{A}	5.10	19.60	33.33^{A}
PRD	43.41	56.02^{B}	5.10	19.90	50.87^{B}

Different letters show significant differences at 95% level for comparison between irrigation treatments.

Table 2. Treatment means of yield, irrigation water use efficiency (IWUE), tuber quality (%N, starch content and antioxidant activity) of fully-irrigated potato (FI) and potato under partial root-zone drying (PRD) during 2008. Different letters show significant differences at 95%

Water treatment	Yield (t ha^{-1})	IWUE (kg ha^{-1} mm^{-1})	N (%)	Starch (% FW)	Antioxidant activity (µmol TE 100 g^{-1} FW)
FI	53.19	236.40^{A}	2.25^{A}	13.45^{A}	19.13^{A}
PRD	50.46	380.14^{B}	2.68^{B}	15.76^{B}	22.81^{B}

Different letters show significant differences at 95%.

support other published data (Shahnazari *et al.* 2008) in showing an increase in WUE, significant increase in N and starch content and antioxidant activity in potato tuber (Table 2). Furthermore, these results indicated that PRD treatment could improve the allocation of N from the shoot to tubers at final harvest and increase the N-use efficiency (Jovanovic *et al.* 2010). Similarly, results of Shahnazari *et al.* (2008) also showed that PRD treatment may improve soil nitrogen availability during the late phases of the potato growing season indicating a higher N mineralization.

A key factor of PRD irrigation scheduling is re-watering of the dry side. During PRD irrigation, water must be switched regularly from one side of the root to the other to keep roots in dry soil alive and fully functional and sustain the supply of root signals (mainly ABA). The timing of this switch from one side to the other could present a significant difficulty in operating PRD irrigation.

Although RDI and PRD methods function differently, some of their main effects are similar. Both methods limit vegetative growth and improve water use efficiency or water productivity. Excessive vegetative growth is a major problem for many fruit crops, as the use of assimilates in leaf growth restricts fruit set and development, and may cause shading and more fungal diseases (Morison *et al.* 2008). Reduction of vegetative growth may also induce a change of assimilate partitioning and source/sink relationships. The photosynthetically active tissue of mature leaves is an active source of assimilate for sink tissues, such as flowers, fruits, or roots. Among sink organs, fruits or tubers are defined as high priority in the context of competition for assimilates between alternative sinks. Davies *et al.* (2000) showed that reduction of carbohydrate strength (side shoots) in PRD-treated tomato plants resulted in a relative increase in the sink strength of tomato fruit, such that carbohydrate previously partitioned towards the side shoots is redirected towards the fruit.

The literature also demonstrated that in most studies PRD is superior to RDI as a strategy for irrigation of vegetables (Jovanovic & Stikic 2012). In addition to increasing WUE, the benefits of PRD technology are an increase in quality of fruits or tubers, increased root growth and in precise control of vegetative growth. Increased yield quality in many crops could minimize the negative effects of PRD on the yield quantity in some experiments (Kang & Zhang 2004).

DROUGHT RESISTANCE STRATEGIES

Adaptation measures to mitigate the reduction of yield or plant growth induced by drought besides the increase in crop water productivity, include the production and use of more drought resistant genotypes. The prerequisite to produce resistant genotypes is a better understanding of the plant response and adaptation to drought stress, improvement of phenotyping, selection of key-genes involved in resistance to drought and evaluation of the impact of resistance on crop yield and quality. These are very difficult tasks because plant reaction to drought is a complex phenomenon where the response depends on species or genotypes, the type, duration or intensity of drought and on the phenological stage in which drought stress is experienced (Chaves *et al.* 2003).

Plants use various mechanisms to cope with drought stress. These may be classified into three groups: drought escape, drought avoidance and drought tolerance (Levitt 1972). Plants that escape drought due to a rapid phenological development are able to complete their life cycle before the water deficit occurs. This is associated with the plant's ability to store reserves in some organs and to mobilize them for yield production The second mechanism, drought avoidance, involves strategies which help the plant maintain high water status during periods of stress, either by efficient water absorption from roots (by increasing root growth, root thickness, root depth and mass) or by reducing evapotranspiration from aerial parts (by closing stomata, leaf rolling, decreasing canopy area by reducing growth and shedding of older leaves). The drought tolerance response is defined as the capacity of plants to maintain functional growth under low resources (water and minerals). Some plants have the ability to tolerate dehydration or maintain turgor pressure through an osmotic adjustment *via* the active accumulation of solutes called osmoprotectants (amino acids, sugar alcohols, polyols and quaternary ammonium and tertiary sulfonium compounds), ABA content or by an increase of antioxidative and/or other defence mechanisms (Chaves *et al.* 2003; Reddy *et al.* 2004). These mechanisms involve different pathways within the cell, but the end result is the expression of stress-response genes.

These drought resistance strategies are not mutually exclusive and plants may combine a range of different response types for optimal reaction to drought. Therefore, the adaptation of plants to drought and maintenance of productivity would result from the balance between all three strategies. Another challenge for plants in natural or agricultural conditions is that they are exposed to a combination of different abiotic and biotic stresses. Therefore, the reactions are more complex than in the case of one stress factor and different stress pathways overlap (Fujita *et al.* 2006).

Breeding plants for drought resistance. Drought resistance is a quantitative trait, with complex phenotype and genetic control. Therefore, molecular approaches in crop selection must be linked with suitable phenotyping protocols at all stages, such as the screening of germplasm collections, mutant libraries, mapping populations, transgenic lines and breeding materials and the design of OMICS and quantitative trait loci (QTLs) experiments (Salekdeh *et al.* 2009). However, despite the increasing knowledge on the mechanisms involved in plant responses to stress and the advancement of high-throughput OMICS technologies (which refers to the comprehensive analyses of plants using techniques ending in the suffix-omics such as genomics, phenomics, proteomics and metabolomics) to screen large numbers of genes induced by drought mechanisms to regulate plant traits, the improvement of breeding for drought resistance has been relatively modest.

Physiological traits for drought resistance. Although there is evidence for many physiological traits associated with resistance to drought (Table 3), the success in trait-based approaches considering drought avoidance and drought tolerance mechanisms is not big. Table 3 presents some of these traits used in crop plants.

Most of the physiological traits that impact on responses to environmental stress require detailed, sophisticated and usually expensive techniques to phenotype plants, and can be applied only to a very limited number of genotypes (Sinclair 2011). Plant resistance is usually assessed in short-term experiments in controlled conditions and many of the investigated traits are more appropriate for plant survival rather than maintaining plant productivity. According to Tardieu (2011), most traits associated with drought tolerance have a dual effect, positive in very severe drought scenarios and negative in milder scenarios, or the opposite trend. Their effects also depend on other climatic conditions such as evaporative demand or light, and on management practices. Therefore, spectacular results obtained in one drought scenario may have a limited interest for improving food security in other geographical areas with water scarcity.

There is a need to develop new phenotyping methods and platforms that will allow available genetic resources to be screened and plant responses to drought to be monitored *in situ* in the field. Very efficient and promising new non-imaging technologies such as thermal infrared, near infrared, RGB visible or fluorescence enable the dissection of plant responses to drought into a series of component traits (Berger *et al.* 2010).

Quantitative trait locus mapping. Quantitative trait locus (QTL) mapping provides a means to dissect complex traits, such as drought tolerance, into their components, each of which is controlled by QTLs. Molecular marker-supported genotypic information at the identified QTLs potentially enables relatively quick and accurate accumulation of desirable alleles in plant breeding programmes. Plant tolerance to abiotic stress is mediated by complex traits that are sustained by multiple genetic factors with large QTL-by-environment interactions. Due to these interactions, the practical application of marker-assisted selection for stress-related QTLs has proven difficult (Francia *et al.* 2005). Molecular marker technologies help to identify a particular chromosomal location for genes regulating specific traits, and the coincidence of loci for yield with loci for the investigated trait will help in identifying whether the investigated trait is significant for drought resistance.

Drought responsive genes. Many genes related to drought have been isolated and characterized in the last two decades in a variety of crop species. In general, there are two classes of genes responsive to drought. The first category comprises functional proteins involved in direct protection activities; the second category comprises regulatory proteins involved in stress signal transduction pathways and control of the expression of stress-tolerant genes (Shinozaki & Yamaguchi-Shinozaki 1997, 2000).

Table 3. Physiological traits associated with resistance to drought in agricultural plants (source www.plantstress.com).

Traits	Plants
Plant growth and phenological phases (early or late flowering, extended crop duration, anthesis-silking interval, grain number, leaf growth, stay-green)	wheat, maize, sorghum, barley
Photosynthesis (gas exchange, activities of key-enzymes, chlorophyll fluorescence)	grapevine, durum wheat
Assimilate partitioning and stem carbohydrates utilization	wheat, rice
Root growth and hydraulic properties	wheat, barley, oat
Water status, osmotic adjustment, stomatal opening and related traits (leaf and canopy temperature, different spectral indices)	wheat, barley, maize, soybean
Water use efficiency (WUE), carbon isotope discrimination	wheat, sunflower

The first category of stress gene is represented by those that encode proteins involved in plant abiotic stress-tolerance, such as water channel proteins, enzymes for biosynthesis of osmoprotectant metabolites, chaperones, late embryogenesis abundant (LEA) proteins, proteinases and enzymes involved in detoxification. In this category several enzymes have also been identified that relate to sugar metabolism, such as sucrose synthases and invertases, as well as to proline biosynthesis, and fatty acid metabolism. Genes encoding oxidative stress mitigating enzymes or proteins with putative cell protective functions, such as late embryogenesis abundant proteins (LEA) or dehydrins, are also induced by drought (Shinozaki & Yamaguchi-Shinozaki 2007).

The second category of stress genes comprises regulatory genes involved in plant tolerance to abiotic stresses, which include transcription factors, protein kinases, phospholipase C and 14-3-3 protein (Shinozaki & Yamaguchi-Shinozaki 1997). Several protein phosphatases 2C (PP2C) have been found to be induced strongly by drought, and studies in *Arabidopsis thaliana* revealed that specific PP2Cs are key in signal transduction of drought responses (Shinozaki & Yamaguchi-Shinozaki 2007).

However, many genes responsive to drought have been investigated in controlled conditions and have not often proved to be useful in field conditions. Therefore, it is difficult to exploit their expression and function for breeding processes. According to Cattivelli *et al.* (2008), isolation of the *ERECTA* gene that regulates transpiration efficiency in *Arabidopsis* and the transcriptional analysis of wheat genotypes with contrasting transpiration efficiency, is an example that demonstrated a future approach for successful breeding. Significant progress in breeding for drought resistance will be achieved by integration of traditional breeding with physiology and genomics (Rouf Mir *et al.* 2012). Very recently another approach was demonstrated of using knowledge of desiccation tolerance in resurrection plants as a biological engineering strategy for improving plant drought tolerance in important crop species (Mitra *et al.* 2013).

CONCLUSION

To mitigate drought effects on those crops normally grown under irrigation and to ensure a sustainable use of available water resources there is an urgent need to implement PRD and RDI as novel water-saving irrigation techniques. The application of PRD and RDI will be easier to use once we understand better the perception and transduction of root-to-shoot signals in different soils, climatic conditions and different genotypes. However, the more efficient use of available water resources alone without improving the drought resistance of crops could not have a significant long-term impact on reducing the impact of drought on agricultural production. Therefore, more effort must be made in the future to produce crops able to deliver increased yields under drought conditions. To achieve this goal the approach should be multidisciplinary to integrate knowledge and research in the areas of crop physiology, genetics and molecular biology with state-of-the-art breeding technologies.

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REZIME

Ublažavanje stresa suše kod biljaka u uslovima promene klime

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Ovaj revijalni rad se odnosi na adaptivne strategije kojima bi se umanjio efekat suše kod biljaka, a koji će se povećati pod dejstvom klimatskih promena. Fokus je na dva pristupa: korišćenje metoda deficita navodnjavanja pomoću kojih se može smanjiti utrošak vode (regulisani deficit navodnjavanja-RDI i delimično sušenje korenova-PRD) i selekciju genotipova sa povećanom otpornošću na sušu. Oba pristupa su zasnovana na poznavanju fizioloških reakcija biljaka u stresnim uslovima.

Ključne reči: suša, deficit navodnjavanja, otpornost