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Drought effects and water use efficiency: improving crop production in dry environments

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Abstract. There is global concern over our capacity to feed a rapidly growing world population against a background of climate change and a shortage of renewable resources for agriculture. To address this challenge, sustainable intensification of crop production will be required to deliver increased yields with decreased environmental side effects, while maintaining the land area under cultivation. We must exploit new understanding in the science of crop production, in order to achieve both an improvement of crops and more effective agro-ecological management. The focus of this short article and the following papers that make up a research front on drought effects and water use efficiency is on science for the development of crops and cropping systems for water scarce environments. Both increases in drought resistance and efficiency of water use will be required in the major cropping regions of the world where water is already a significant limiting factor.

Additional keywords: crop management, drought resistance, irrigation, partial rootzone drying, plant improvement, screening, soil biology, water use efficiency.

Current projections by the International Panel for Climate Change (IPCC 2007) predict that water scarcity, together with incidence of high temperature, will increase in the near future in many regions of the globe. Although fertilisation by rising CO_2 may partly offset the effects of these changes on plant growth and development, a detrimental effect on food and feed production is predicted to occur in many of the major food-producing regions of the world (see e.g. Lobell *et al*. 2008). It is therefore important to combine expertise from different disciplines to identify and overcome crop genetic and agronomic limitations to yield under unfavourable environments, particularly under drought. This is a conclusion of a recent report on Food Security produced by the Royal Society of London (The Royal Society 2009). Here, there is a call for substantially enhanced attention (and funding!) to be given to the science of food production that might be exploited to enhance world food supply. This is particularly important as climate changes, soil becomes degraded and vital resources such as irrigation water are in increasingly short supply.

Substantial research efforts in recent years have generated major scientific advancements in our comprehension of the mechanisms underlying plant responses to water deficits and co-occurring stresses (Chaves *et al*. 2003, 2009; Lawlor and Tezara 2009), with high potential for this knowledge to be translated into improved crops (Parry *et al*. 2009; Reynolds *et al*. 2009; Xiao *et al*. 2009; Jiang *et al*. 2010). In the absence of any significant biotechnological advance to date in increasing the drought resistance of the major crop plants (sustained yield under water scarcity), plant improvement is dependent upon the screening of a wide range of germplasm for our major crops in order to identify genetic variation in major traits involved in stress resistance (Lopes and Reynolds 2010; Richards *et al*. 2010; Saint Pierre *et al*. 2010). The importance of this strategy was recognised in the recent conference on 'Integrated approaches to improve crops production under drought prone environments' (InterDrought III, http://www.interdrought.org/), that took place in Shanghai in October 2009. Good progress has been made recently in understanding the basis of the sensitivity of reproductive processes of several major crops to drought and this understanding has been successfully exploited in crop improvement (Edmeades *et al*. 1999). In addition, we have recognised the importance of several developmental characters in increasing crop yield under drought stress via an increase in crop establishment. Significant advances have been made in exploiting fundamental understanding of both the basis leaf level water use efficiency and convenient and rapid means of screening for this character. There is now a general recognition that advances in the efficacy of high throughput screening of plant genetic material will speed progress in crop improvement via breeding programs (see e.g. Richards *et al*. 2010).

At the InterDrought meeting, there was also a compelling report from Monsanto of new drought tolerant maize genotypes that are currently in their plant improvement pipeline. These

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crops and others under development show overexpression of bacterial RNA chaperones (Castiglioni *et al*. 2008), and NF-Y class transcriptional regulators (Nelson *et al*. 2007) in which drought tolerance is reported. Tolerance to a whole range of stresses in plants may also be induced by RNA silencing to downregulate poly ADP ribose polymerase (Vanderauwera *et al*. 2007), and overexpression of a cyanobacterial flavodoxin (Tognetti *et al*. 2006). Until comprehensive field trials are conducted with this material, some caution must be exercised. In recent years, there have been several reports of apparently promising biotechnological manipulations that have failed to deliver drought tolerance in yield terms when the novel material is transferred from the growth room to the field. One important development in this field is the work of an international consortium funded to produce 'Water Efficient Maize for Africa' (WEMA), an ambitious and vitally important target.

Mounting concern over our capacity to feed a world population of seven billion, perhaps rising to nine billion by the middle of the 21st Century, has resulted in a call to double food production over this time period. The most optimistic predictions suggest that a 50% increase in food production will be required (The Royal Society 2009). The 'sustainable intensification' required to deliver increased food production will place enhanced pressure on water resources. At the same time, there is increased global perception of a need to reduce the 'water footprint' for irrigated crops (www.fao.org/nr/water/aquastat/data/query/index.html) (Cominelli *et al.* 2009). At InterDrought III, Peng and colleagues from the Ministry of Agriculture in China highlighted the very significant falls in groundwater levels in both NW China and on the North China Plain, both important food production regions in China. Concern over the capacity of farmers to sustain food production in these conditions, a concern shared by food producers in many water-scarce regions of the world, has led to the development of the discipline of water saving agriculture.

As pointed out by Passioura (2007) and Blum (2009), the effective use by the crop of a limiting water supply is the keystone of 'drought resistance'. This can be achieved by adjusting crop phenology to its environment or by using agronomic practices aiming at an improved water use such as deficit irrigation. A variety of approaches have been particularly successful in the irrigation of top fruit and vineyards (Chaves *et al*. 2007; Fereres and Soriano 2007; Beis and Patakas 2010; Collins *et al.* 2010; Lovisolo *et al.* 2010) but also in annual crops (Kang and Zhang 2004; Dodd *et al*. 2006; Kirda *et al*. 2007; Wang *et al*. 2010). In addition to minimising changes in shoot water status, deficit irrigation enhances the balance between fruit and vegetative growth (Davies *et al.* 2002; Chaves and Oliveira 2004).

Over the last 20 years or so, there has been interest in exploiting novel understanding of plant biology to optimise use of irrigation water in water-scarce environments. One technique that aims to do this by exploiting the science of plant root-to-shoot signalling is partial root zone drying (PRD) (see e.g. Stoll *et al*. 2000). There have been two recent meta-analyses of the agronomic impacts of PRD. In one of these, which focuses exclusively on field-grown, mainly woody perennial crops (Sadras 2009), there is little difference reported in the effects of reduced amounts of water applied in different ways, suggesting that in these systems there may be little 'added value' from PDR irrigation compared with other forms of deficit irrigation. In the other meta analysis (Dodd 2009), where a broader range of annual and perennial crops were grown in both containers and in the field, spatial variation in the supply of reduced amounts of water to the soil generated important differences in crop yield. In 40% of the cases considered, plants irrigated using PRD techniques showed statistically higher agricultural water use efficiencies (yield per unit of water applied). It is important to understand the physiological basis of these responses and to devise reliable ways of delivering these results in commercial crop production.

Dodd (2009) reviews evidence that under partial root drying the cycles of soil drying/rewetting stimulate mineralisation of organic N due to microbial death upon drying. Turner and Haygarth (2001) have reported enhanced mobilisation of phosphorus in response to wetting and drying of soils. Kirda *et al*. (2005) have shown that PRD can increase nitrogen scavenging by root systems, when compared with nutrient uptake by plants irrigated by other deficit irrigation techniques. Changed nutrient relations may be one explanation for superior performance of PRD plants under certain conditions.

Detailed work by Dodd and colleagues (Dodd *et al*. 2006, 2008*a*, 2008*b*; Dodd 2007) has shown how PRD can enhance hormone signalling between roots and shoots and that such signalling can have beneficial effects on the efficiency of water use. However, enhanced signalling does not always occur and this is particularly the case at lower soil water contents, an observation that can explain some of the negligible effects of PRD reported by Sadras. Dodd's analysis suggests that PRD can be an effective means of increasing the production of more 'crop per drop' but that this result depends on the technique used to apply the soil water deficit, the extent of the drying treatment and the crop in question.

Recently, rhizobacteria have been shown to be effective in reducing the yield penalty induced by soil drying (Díaz-Zorita and Fernández-Canigia 2009), apparently acting via effects on root growth, hormone signalling and nodulation (Belimov *et al*. 2009). This work suggests that attention given to manipulation of soil biology as well as to novel plant biology, can allow more sustainable use of water and nutrients in agriculture. There are increasing numbers of reports suggesting microbial activity in soils can be an important regulator of crop development and functioning. These arise, for example, from studies where minimum tillage techniques are assessed (e.g. Pankhurst *et al*. 2002). The studies of Belimov and co-workers and others (e.g. Glick *et al.* 1998) suggest that particular kinds of microbial activity in soils can enhance the drought resistance of crops.

Several biological-based technologies have been developed in the past decades to allow maintenance of crop production and functioning under adverse environments, and in particular drought prone areas. These are fundamental if we are to increase food production at the global scale, while at the same time preserving natural resources. It is recognised (see The Royal Society 2009) that the large improvements needed to attain such a goal require a rapid strengthening of human capital and research funding and human capital to overcome chronic underfunding of plant/agriculture science research.

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