Genetic and management approaches to boost UK wheat yields by ameliorating water deficits

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Abstract

Faced with the challenge of increasing global food production, there is the need to exploit all approaches to increasing crop yields. A major obstacle to boosting yields of wheat (an important staple in many parts of the world) is the availability and efficient use of water, since there is increasing stress on water resources used for agriculture globally, and also in parts of the UK. Improved soil and crop management and the development of new genotypes may increase wheat yields when water is limiting. Technical and scientific issues concerning management options such as irrigation and the use of growth-promoting rhizobacteria are explored, since these may allow the more efficient use of irrigation. Fundamental understanding of how crops sense and respond to multiple abiotic stresses can help improve the effective use of irrigation water. Experiments are needed to test the hypothesis that modifying wheat root system architecture (by increasing root proliferation deep in the soil profile) will allow greater soil water extraction thereby benefiting productivity and yield stability. Furthermore, better knowledge of plant and soil interactions and how below-ground and above-ground processes communicate within the plant can help identify traits and ultimately genes (or alleles) that will define genotypes that yield better under dry conditions. Developing new genotypes will take time and, therefore, these challenges need to be addressed now.

Key words: Irrigation, plant breeding, rhizobacteria, wheat.

Introduction

A steadily increasing world population requires that global agriculture doubles food production by 2050 to ensure food security for all (Foresight, 2011). This should be achieved while also decreasing the environmental footprint of agriculture by optimizing efficient use of fertilizers, pesticides, and water (Royal Society, 2009). The challenge is made more difficult because the availability of water has a large effect on crop yields. Furthermore, droughts are common and are predicted to become more frequent and more severe with climate change (Gornall et al., 2010). In some arid areas, crops are often irrigated unsustainably with water drawn from dwindling aquifers (Kang et al., 2008).

On a global scale, this situation may require that greater emphasis is placed on growing crops in environments where competition for water resources between agriculture and other sectors is small. Recently, global mapping of water productivity (defined as yield per unit of water used) has demonstrated that, for wheat (Triticum aestivum L.) production, the UK and regions with similar climates show much greater water productivity than other areas (Zwart et al., 2010). Although the UK produces only 2–3% of the global wheat supply (FAOSTAT, 2008), it is important to understand genetic and management approaches to improve water productivity further since this has implications for every climatic region. It has been highlighted that many products consumed in the UK have a poor ‘water footprint’ because they are produced abroad in regions of low water productivity and shipped to the UK (Lillywhite et al., 2009).

One example is tomatoes imported from Spain where tomato growers compete with domestic and industrial water users for limited water supplies (Chapagain and Orr, 2009). In the future, there may be global changes in where particular crops are grown so that food can be produced with the best use of natural resources. A fundamental understanding of soil, water, and plant interactions is necessary to allow improvements in yield and water productivity. Here we consider the UK wheat crop as a case study.

UK wheat yields are water limited: relationships with soil biophysical properties

First, it is necessary to understand the impact of water deficits on UK wheat yields. An evaluation of 25
experiments in the UK showed that yield responses to irrigation greater than 10% were infrequent (Cannell et al., 1984). However, it is estimated that 30% of the UK wheat acreage is planted on drought-prone land such that annual losses average 1–2 tonnes ha−1, or 10% of potential production is lost annually because the moisture available to the crop is insufficient at some point during growth (Foulkes et al., 2007). The yield response depends on the extent and timing of water deficit of rainfed crops in relation to sensitive stages of crop development, such as early stem extension, flowering, and grain filling and the degree to which water deficits were eliminated on irrigated plots. Further experiments that grew six elite UK winter wheat lines on a shallow, well-drained, sandy soil at the Woburn Experimental Farm demonstrated that irrigation increased grain yield (averaged across varieties) by 68% and 29% in 2009 and 2010, respectively (Fig. 1). Another experiment comparing rainfed and irrigated yields at Broom’s Barn (Suffolk) on a sandy loam soil in 2010 showed a yield increase of 38% (Fig. 1). The lost yield of rainfed crops was due mainly to fewer ears m−2 and fewer fertile secondary tillers.

Other experiments have demonstrated that irrigation increased the yield of winter wheat by 17–55% (see Table 1 in Whalley et al., 2006). In this work, measurements of soil matric potential were used to inform irrigation scheduling, and yield decreased approximately linearly with matric potential when integrated over the period of rapid vegetative growth in spring (April–June). However, since some irrigation water applied was not used by the crop, the amount of irrigation water had a non-linear relationship with yield, even though cumulative abiotic stresses (either matric potential or soil strength) may be linearly related to yield (Whalley et al., 2006; Whitmore et al., 2011). At high irrigation rates, drainage of water from sandy soils may limit the efficiency with which water is used. This raises the issue of the most effective form of irrigation control to minimize water loss, especially by drainage.

There is growing interest in soil sensor-based irrigation control (Zotarelli et al., 2011) and improved sensors for soil matric potential have recently been developed (Whalley et al., 2009). However, some key scientific challenges need to be resolved, not least what soil properties should be measured to provide the most effective means to control irrigation. Recent evidence indicates that root water potential (which is not readily measured) is more closely correlated with some physiological variables across a range of soil types, even though, within a single soil type, responses may be more tightly linked to soil matric potential (Dodd et al., 2010a). Typically, an irrigated crop grows in a multiple stress environment and for wheat there is some evidence that increased soil strength due to surface drying may limit yield, rather than there being insufficient water available within the soil profile (Whalley et al., 2008). While the simple use of soil water content sensors may indeed provide effective irrigation control, ultimately soil water content is not a stress but correlated with stresses to crop growth and usually with non-linear functions (Whitmore and Whalley, 2009).

There is some scope for optimism in that sensor developments may allow scientific understanding of plant responses to multiple stresses to be put into practice. The replacement of the neutron probe with time domain reflectometry (TDR; Topp et al., 1980) provided multiplexed sensor systems for measuring soil water content at several depths in the profile. Presently, such systems can record data and transmit it back to a central location (e.g. the farm office) allowing real-time access to data to inform irrigation decisions. An interesting development is the use of heat pulse technology to measure water fluxes in soil as low as 1 cm d−1 (Kamai et al., 2008). TDR and heat pulse technology may be combined to estimate porosity and water-filled pore space (Liu et al., 2008) and, in principle, this would allow irrigation to be stopped to prevent complete saturation of the soil. Currently, soil strength is measured with a penetrometer and this does not lend itself to automation or continuous measurements. However, the velocity of shear and compression waves through soil is one avenue currently being

![Fig. 1. Grain yield of rainfed (filled bars) and irrigated (hollow bars) winter wheat at Woburn and Broom’s Barn (UK). At the Woburn site, data are means ±SE of six cultivars ( cvs Battalion, Consort, Gladiator, Istabraq, Robigus, and Xi-19) grown in three plots per cultivar, while at Broom’s Barn, data are means ±SE of four plots of cv. Solstice. At Woburn, irrigation was applied by drip tape (Access Irrigation 'T tape', TSX506-250, with a typical output of 250 l h−1 per 100 m) laid out between alternate wheat rows grown at 0.2 m inter-row spacing. Soil water content was monitored with water-filled tensiometers and irrigation was controlled manually to keep the matric potential at approximately −10 kPa, although in very dry periods it did fall briefly to approximately −50 kPa. At Broom’s Barn, irrigated plots were supplied with water by boom irrigation to maintain a soil moisture deficit of less than 25 mm throughout the season.](5242_Fig1)
explored as a basis for sensor development (Whalley et al., 2011).

A difficulty of most soil-sensing approaches is that they provide data from a single location whereas the requirement is to irrigate the whole field. There are already emerging solutions to this technical challenge. Electrical resistance tomography is starting to be used to image water-extraction patterns by roots. Such methods can provide electrical resistance images down to a depth of several metres and, when used at shallower depths, can have higher spatial resolution. It seems likely that other measurement approaches that allow image construction, such as measurement of shear wave velocity, will also be used in the future. Measuring soil properties over large parts of the farmer’s holdings are necessary to underpin the development of precision agriculture, allowing rational decisions about which blocks of land might benefit most from supplementary irrigation.

Another approach to this problem is to use plants as indicators of soil water deficit, since their physiological responses are a function of the active root zone, thereby integrating signals from the whole rhizosphere. Stomatal closure (that limits transpirational losses) increases leaf temperature, which can be conveniently detected via thermal imaging (Leinonen and Jones, 2004). While there has been intensive interest in this technique to schedule irrigation, determine areas of the cropping surface where plants are more ‘stressed’, and to identify varieties in breeders’ trials that show contrasting water use strategies (Gutierrez et al., 2010), stable atmospheric conditions (absence of clouds and minimal wind) are required for optimal operation. Such conditions are rare in the UK environment.

**Soil and root management to improve water availability**

Two key soil management steps can be taken to increase the amount of water available to the crop. In very dry regions and on sandy soils, crop residues can minimize evaporation from the soil surface (Ali and Talukder, 2008; Kirkegaard and Hunt, 2010). Retention of crop residues can decrease surface evaporation by 34–50% (Sauer et al., 1996) but, in the UK environment, evaporation from bare soil usually only affects the surface few centimetres. Evaporation from bare sandy soil over the summer period at Woburn in 2006 only reduced soil matric potential at a depth of 20 cm to –10 kPa (Whalley et al., 2008). This level of soil drying is unlikely to affect the physiological responses of all but the most shallow-rooted crops, even though the distribution of root biomass between the upper (drier) and lower (moister) layers may affect plant responses.

Mechanical cultivation of the subsoil (termed ‘subsoiling’ or ‘deep ripping’) can increase root growth at depth to improve the accessibility of roots to water. When a no tillage system was used on loess soil in northern China, it was only necessary to subsoil once every four years to have the maximum positive effect on crop growth (He et al., 2007). As well as mechanical intervention to create pore structure in the subsoil, roots can exploit existing bio-pores (White and Kirkegaard, 2010). The interaction between roots, soil structure, and deep root penetration merits further investigation. A particularly interesting observation is that nearly all wheat roots in dense subsoil (below 0.6 m) tended to be clumped (White and Kirkegaard, 2010) and hence less effective at extracting water. This emphasizes that, not only are deep roots needed, they must also be distributed for most effective water uptake.

**Genotypes that obtain maximum benefit from soil water**

Soil moisture sensors such as those described above demonstrate that UK winter wheat does not always fully extract moisture stored at depth during the summer (Fig. 2), perhaps due to an inability of the root system to penetrate a comparatively strong subsoil. This results in a soil profile that is comparatively dry at the surface (where the bulk of the roots are located) yet contains considerable moisture at depth. The relatively small proliferation of roots in deep soil layers is a function of soil physical properties and genetic control of root architecture. Recently, it was found that varietal differences in soil water extraction were too small to be detected with soil water content sensors, but measurements of soil strength (which is non-linearly related to water content and allowed greater replication) showed that genotypic differences in water extraction did exist (WR Whalley et al., unpublished data). Other studies have demonstrated genotypic differences in water extraction during drought.
from deep soil layers (Lopes and Reynolds, 2010; ES Ober et al., unpublished data). In experiments at Broom’s Barn, there was a weak negative relationship between water extracted at 80 cm from the soil surface in droughted plots and the irrigated grain yield potential of 21 varieties (data not shown). However, amongst lines that showed the greatest water extraction from depth, there were some lines that also showed good yield potential, suggesting that constitutive costs of deeper root systems may not necessarily be associated with a yield penalty.

Roots in drying soil produce chemical signals such as abscisic acid (ABA) that can be transported to the shoots to restrict leaf growth and limit water loss (reviewed in Dodd, 2005). Minimizing the production of these signals, or attenuating their distribution to the shoot may be a viable way of limiting their negative impacts on crop growth and yield. Genotypic variation in these responses appears to exist in wheat and other species.

When five wheat cultivars were grown in 1 m soil columns and water was only applied at the base of the column (allowing only the surface soil layers to dry), cultivars showing pronounced stomatal closure maintained their leaf water status (indicating effective root-to-shoot signalling) at the expense of total plant production (Blum and Johnson, 1993). However, cultivars with a higher stomatal conductance (and plant production) had lower leaf relative water contents indicating less effective root-to-shoot signalling, probably due to fewer roots being exposed to drying soil (Blum and Johnson, 1993). A rice variety that maintained a higher stomatal conductance (and leaf water potential) but lower foliar ABA concentration as the soil dried had fewer root axes exposed to drying soil (Siopongco et al., 2009). In both studies, separating the effects of root distribution on signal production (and transport to the shoot) from possible genotypic differences in response to the signals was difficult, due to genotypic differences in the relationship between stomatal conductance and foliar ABA concentration (Siopongco et al., 2009) and apparent stomatal (and leaf elongation) sensitivity to exogenous ABA (Blum and Simmena, 1995).

To distinguish the impacts of root distribution on root-to-shoot signalling independently of genotypic variation in other physiological processes, barley plants were grown in split-pots into which different numbers of seminal roots were inserted. All plants were allowed to dry the soil in one pot while the other pot was well watered, thus separating the effects of irrigation volume (the same for all plants) from the number of seminal roots exposed to drying soil. Leaf growth was less and foliar ABA concentrations higher in those plants with more roots in drying soil (Martin-Vertedor and Dodd, 2011), providing evidence that altering root distribution can ameliorate the negative impacts of root signalling on crop growth.

However, identifying these genotypes in the field may be more problematic. While foliar ABA accumulation is correlated with stomatal closure in many species including wheat (Ali et al., 1998) and is relatively easily measured, it is not always a reliable indicator of crop water use. Controlled environment experiments indicate that maize xylem ABA concentration can increase in response to drying of the upper soil layers well before any changes in foliar ABA concentration are detected (Zhang and Davies, 1989). Furthermore, pearl millet near isogenic lines with a terminal drought tolerance QTL and differing in foliar ABA concentration apparently did not differ in total water extraction (Kholova et al., 2010). Clearly, further work is needed to understand whether temporal and spatial differences in soil drying and plant water uptake can account for temporal differences in foliar ABA concentration, before this variable can be regarded as a useful indicator of whole plant water use.

**High yield potential can buffer yield losses when water is limiting**

The relationship between yield and water use has been described by Passioura (1977) as:

\[
\text{Grain yield} = \frac{\text{Transpiration}}{\text{Transpiration efficiency}} \times \text{Harvest index}
\]

where transpiration efficiency represents biomass production per unit of water transpired and harvest index is the proportion of the crop biomass partitioned to the grain. Increases in any of these three components will translate into greater yield. For instance, a larger proportion of root biomass located in deep soil layers can maintain greater transpiration rates (Lopes and Reynolds, 2010). There is evidence that mild water deficits can improve harvest index and carbon partitioning to the grain (Yang and Zhang, 2006).

Whole plant transpiration efficiency can be determined accurately by growing crops in weighing lysimeters to account for whole plant transpiration and water losses below the root zone (Liu et al., 2002). However, this can be done only on a limited number of genotypes or treatments. Consequently, researchers have often preferred to measure intrinsic leaf water use efficiency (the ratio of assimilation rate to stomatal conductance) using conventional infrared gas analysis, but even this method cannot be used on a large scale in a breeding programme. Thus surrogate measures such as specific leaf area (Morgan and LeCain, 1991) or carbon isotope discrimination, \(\Delta^{13}C\) (Condon et al., 2004) have been suggested as proxy traits to select for increased water use efficiency.

In wheat, in Australian soils with restricted water storage capacity, selection for low carbon isotope discrimination (thus increased transpiration efficiency) within a breeding programme resulted in the release of new varieties with increased water use efficiency and improved grain yields in low yielding environments (<5 tonnes ha\(^{-1}\)) (Condon et al., 2004). Under conditions relevant to the UK, a positive association has been observed between grain yield and grain \(\Delta^{13}C\) (Ober et al., 2010; Kumar et al., 2011; Cabrera-
moisture from approximately 2 weeks before flowering until polytunnel rainout shelters, such that plants used only stored soil loam soil at Broom’s Barn. Drought was imposed using large
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Bosquet et al., 2011), indicative of greater rates of transpiration but lower water use efficiency. Consequently, under these conditions, ‘effective use of water’ is more relevant than ‘water use efficiency’ (Blum, 2009).
Within 66 UK winter wheat lines, there was a strong correlation between yield under irrigated and rainfed conditions (Fig. 3). This suggests that, under UK conditions, the standard practice of selecting for high-yielding varieties quite often produces varieties that will also do well under water-limited conditions. However, this is no guarantee: some varieties that have high yields under optimum conditions show disappointing performance under stressed conditions (those points that fall below the regression line in Fig. 3). It is important for breeders to be able to identify and cull such susceptible genotypes before they are released as varieties.

Using soil biota to improve wheat yields
Other agronomic techniques such as applying plant growth-promoting rhizobacteria (PGPR) have been proposed to ameliorate water deficits (Dodd, 2009) and other abiotic stresses, thereby boosting crop yields. Although PGPR applications to wheat have increased yields in some parts of the world, considerable research is necessary before such techniques could be considered viable under UK conditions.

One perceived difficulty is establishing sufficient populations of an introduced inoculum to have physiological effects on the plant. Peat-based seed inoculation with rhizobacteria selected for high auxin production stimulated wheat grain yields in field experiments by up to 28% (Khalid et al., 2004). Furthermore, applying an aqueous formulation (10^9 colony forming units ml^-1) of Azospirillum brasilense strain Az-39 to wheat seed prior to sowing increased wheat yield by 8% over a 5-year trial in Argentina (Diaz-Zorita and Fernandez-Canigi, 2009). Improved yield was due to small increases in spikes m^-2, grains spike^-1, and kernel weight, although the specific physiological mechanism(s) responsible have yet to be identified. This particular strain can produce several plant hormones (auxin, gibberellic acid, zeatin) when cultured in vitro (Perrig et al., 2007). Although a recent review highlighted relatively few measurements of phytohormone concentrations in planta in response to rhizobacterial inoculation (Dodd et al., 2010b), phytohormone concentrations of developing grains seem particularly important in determining their growth (Foulkes et al., 2011). Minimizing ethylene production by developing grains seems key to prevent stress-induced yield losses (Hays et al., 2007).

Although rhizobacteria can produce and/or metabolize almost all the major groups of phytohormones (Dodd et al., 2010b), there has been much recent interest in a group of organisms containing the enzyme ACC deaminase, that breaks down the precursor of the plant hormone ethylene (Glick et al., 2007). Wheat biomass and grain yield was stimulated (15-45%) in a series of pot experiments and field trials with ACC deaminase-containing strains of Pseudomonas fluorescens (Shaharoona et al., 2007, 2008), although it is difficult to determine whether this response was ethylene-mediated since these strains had additional properties (e.g. antibiotic production) that may stimulate wheat growth by antagonizing the growth of root pathogens. The ACC deaminase-containing rhizobacterium Variovorax paradoxus 5C-2 stimulated early vegetative growth (and ultimately yield) of pea which was absent in an ACC deaminase-deficient mutant (Belimov et al., 2009), prompting additional work (in progress) with wheat. However, rhizobacterial benefits may be highly dependent on crop nutrition since the stimulatory effect of ACC deaminase-containing rhizobacteria on root length depended on external nutrient supply (Belimov et al., 2002) and the stimulatory effect of one strain on wheat yield decreased with fertilizer addition (Shaharoona et al., 2008). Although water and nutrient availability within UK wheat cropping systems may limit rhizobacterial impacts, the move to decreasing fertilizer inputs within UK cropping systems (both due to the costs of chemical fertilizers, and concern over nutrient leaching to watercourses) may stimulate the adoption of rhizobacterial inoculants. Further research on rhizobacterial inoculation of major food crops seems warranted, given the promise of significant yield increments within a relatively short period of time, compared with the time required to develop new crop varieties.

Fig. 3. Relationship between irrigated and droughted grain yield of 63 mainly UK varieties. Each point represents the mean (n=4) yields of an individual variety grown in 1.5×5 m plots on sandy loam soil at Broom’s Barn. Drought was imposed using large polytunnel rainout shelters, such that plants used only stored soil moisture from approximately 2 weeks before flowering until maturity (Rajabi et al., 2009; Ober et al., 2010).
Conclusions

Although irrigation can produce impressive increases in wheat yield over a range of genotypes, sites, and soil types (Fig. 1), wheat is rarely irrigated in the UK (approximately 1% of the acreage in 2000), and few growers are likely to do so (Spink et al., 2009). When water is available and conditions are dry, it is likely that irrigation would be applied to higher value vegetable crops such as potato. It is possible that shifts in market forces (e.g. the escalation in the price of wheat following the drought and heat stress in 2010 that prompted Russia to halt wheat exports) or a larger scale ‘food security crisis’ could make the irrigation of wheat plausible and profitable where abstraction licences permitted the practice. Indeed, limited rainfall in many parts of the UK in spring 2011, together with high grain prices, has stimulated renewed interest in the irrigation of cereal crops (M Kay, UK Irrigation Association, personal communication). If logistically possible and economically justifiable, irrigation to alleviate the estimated 10% annual yield losses due to water deficit could contribute an additional 4.8 Mt of wheat to the market.

Climate change models indicate less summer rainfall and increased soil moisture deficits in many UK cropping regions, particularly in the east of England where much of the wheat crop is grown (Gornall et al., 2010; Knox et al., 2010). For long-term sustainability (in terms of available water resources) and in the absence of significant advances in management practices or genetics to improve water productivity, wheat cropping in the future could shift west and north. Alternatively, if varieties that maintain growth and yield as the soil dries could help avoid half of the yield losses attributed to water deficit (no variety is likely to avoid stress-induced losses altogether), this would boost yields by 5%. Since the same inputs (e.g. fertilizer) are typically applied to fields because the severity and duration of any subsequent soil water deficits are difficult to predict under UK conditions, any yield increases will increase resource use efficiency. Consequently, continued development of new varieties and management techniques to ameliorate the impacts of water deficits on UK wheat crops is warranted, both to boost local production and in the hope that lessons learnt from this research can have a wider impact on global food security.

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