Breeding for improved drought tolerance and water use efficiency

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Summary

Globally, drought causes more yield losses than any other single biotic or abiotic factor. Even in the UK, a proportion of the wheat yield is lost each year due to insufficient soil moisture. As the wheat area expands onto less suitable land, and as the effects of climate change are increasingly felt, it is likely that more wheat crops will experience drought, particularly in the main wheat growing areas in eastern England. A stressed crop uses resources inefficiently and returns on inputs are poor. Therefore, development of varieties with increased drought tolerance and water use efficiency is crucial to improving the productivity and sustainability of the wheat crop in the UK. Initial results from field trials indicate significant genotypic diversity for drought tolerance within a wide range of UK winter wheat germplasm. To identify superior types, experiments are designed to develop screening techniques based on morphological and physiological traits associated with performance under water-limited conditions.

Drought - and making best use of water resources through breeding

Globally, drought causes more yield losses than any other single biotic or abiotic factor (Boyer, 1982). In the UK, insufficient soil moisture frequently limits crop productivity because rainfall often does not occur when crops need it most. The UK is one of the world's most efficient producers of arable crops, yet approximately 30% of the current wheat area is grown on drought-prone land and drought losses are on average 1-2 t ha^{-1}, which costs >£60M per year (Foulkes *et al*., 2007). There is also evidence that a large component of yield instability (yield variation from site to site and year to year) is due to soil water availability. Furthermore, climate change models predict that summertime droughts will worsen (Jones *et al*., 2003; Richter and Semenov, 2005), which will intensify the competition between agriculture, urban needs and environmentally-sensitive areas for limited water resources.

Sustainable production of food and biofuels on drought-susceptible land depends on the development of varieties with improved water use efficiency (WUE) and drought tolerance. WUE is the yield produced per unit water consumed, and drought tolerance is the proportion of stress-free yield potential maintained when water is limiting. These can be multiple-character traits, and genetic improvements are not easily accomplished; new varieties will not appear over-night. Thus, it is imperative to begin work now. Currently, breeders are not equipped to make these selections because information is lacking on: 1) extent of variation for drought tolerance within elite germplasm; 2) key physiological processes and morphological characters that contribute to drought tolerance and water use efficiency; 3) genetic factors that control these traits; 4) empirical and molecular tools to allow the selection of superior germplasm in breeding programmes. Our current research is aimed at delivering the tools that will enable breeders to develop improved varieties for water-limited conditions.

Recent developments in drought research

Over the last 30 years, plant breeders have improved crop yields for dry conditions, agricultural scientists have improved management techniques for saving water, and plant scientists have furthered understanding of plant responses to water (Parry *et al*., 2005). Recent work in durum wheat shows significant genetic variability and high heritability (additive and dominant control) for WUE (Solomon and Labuschagne, 2004). In bread wheat, an important advance was the release of two new Australian wheat varieties with improved WUE that were bred based on selections for low $^{13}C/^{12}C$ isotope discrimination ratio (Δ) (Condon *et al*., 2004). Currently, there is substantial international effort to address these problems at all levels. Despite the scale of the endeavour, gaps remain in the basic understanding of processes that control WUE and yield, and breeding progress is slow. In addition, many of these research programmes are focused on low-yielding environments in arid and semi-arid areas of the world, characterised by distinct wet and dry seasons and high temperatures. Such programmes are not easily applied to the cropping situation in the UK where rainfall is unpredictable and variable. An important requirement of new UK varieties with enhanced drought tolerance and WUE is that they must not carry a significant yield penalty if they are to be commercially successful.

In arid regions, improvements in drought tolerance have been made largely through conventional empirical breeding; that is, selecting varieties that yield well in the target dry environments. However, even though there is substantial genetic variability for WUE and drought tolerance in wheat (Foulkes *et al*., 2001), breeders find it difficult and costly to breed effectively for these traits. Genetic gain is low because yield shows low heritability due to genotype x environment interactions (and drought tolerance is defined on the basis of yield). Marker-assisted selection (MAS) is an attractive option, but this requires the identification of key loci for yield performance under drought. For example, MAS is leading to improvements in drought tolerance of upland rice (Steele *et al*., 2006) and pearl millet (Serraj *et al*., 2005). However, in other species including wheat, quantitative trait loci (QTLs) for drought tolerance *per se* have so far shown limited utility (Blum, 2005). Reasons for the failure of these QTLs to quickly lead to practical markers include: poor quality or insufficient phenotypic data; too many QTLs each with small effect; large QTL by environment interactions; QTLs that are population-specific; use of parental lines too far removed from actual breeding stocks. In barley, many QTLs for yield under drought conditions simply coincided with loci controlling phenology rather than traits conditioning physiological mechanisms of drought tolerance (Forster *et al*., 2004). For example, in UK winter wheat, advantages of drought escape through earliness may be offset by lower yield potential or smaller root system size (Foulkes *et al*., 2004).

Transgenic crops are an alternative approach to improvement in drought tolerance. In the private sector, these products are still in development phases. For instance, both Monsanto and Dupont/Pioneer are field-testing maize lines carrying gene events that appear to improve drought tolerance (Habben, 2005; Nelson *et al*., 2007); a Canadian company has put transgenic rape in field trials (Wang *et al*., 2005); and CIMMYT has tested wheat lines over-expressing the drought-related transcription factor DREB1A (Pelligrineschi *et al*., 2004) . Despite the number of claims that findings in these areas will be useful to breeders, breeders are still waiting for the promises and investments of the genomic era to bear fruit (Blum, 2005). Reasons for these failures include poor communication between biotechnologists, physiologists and breeders, little testing of ideas at the field level (Edmeades *et al*., 2004), and significant penalties in yield potential associated with the constitutive or over-expression of certain genes (Nelson *et al*., 2007). It is now widely recognised that tools for genotyping have outpaced the ability to provide high quality phenotypic information of genetic stocks, particularly under field conditions.

Another approach to improve genetic gain for yield under water-limited conditions is to base selections on secondary traits that are associated with drought tolerance and WUE (Reynolds *et al*., 2005). Many of these traits have been based on studies of the physiological and morphological characters that contribute to yield and WUE, but successful implementation in practice requires a multi-disciplinary team interacting with breeders (Lafitte *et al*., 2006; Richards, 2006). For the 'indirect trait' approach to be successful, the trait must have high genetic correlation with yield, high heritability, and selection methods must be applicable on a large scale (i.e. quick and inexpensive).
In maize, after a period of intense investment by CIMMYT and Pioneer in ‘drought’ QTLs, attention has turned back to physiology-based development of markers using large-scale managed drought conditions for phenotypic evaluation (Bruce *et al*., 2002). One reason for this shift in research emphasis is that component traits are often controlled by a smaller number of major QTLs compared with yield QTLs. Such secondary traits often show high heritability; examples include osmotic adjustment (Moinuddin *et al*., 2005), transpiration efficiency (Malik *et al*., 1999; Solomon and Labuschagne, 2004), relative leaf water content (Schonfeld *et al*., 1988), leaf conductance (Rebetzke *et al*., 2003) and leaf rolling (Price *et al*., 2002). Also, carbon isotope discrimination ratio (Δ), an indirect measure of WUE, is controlled by one major QTL linked to the *ERECTA* gene in the model species *Arabidopsis* (Masle *et al*., 2005). Δ has been used as the selection criterion for the development of two new Australian wheat varieties with significant improvement in WUE (Condon *et al*., 2004).

Candidate genes and traits for UK conditions

Work done specifically on UK wheat with regard to drought tolerance and water use efficiency has provided an important foundation of data. For instance, the relative importance of earliness, stem reserves, flag leaf persistence and dwarfing genes has been studied (Austin, 1987; Foulkes *et al*., 2002; Foulkes *et al*., 2007; Foulkes *et al*., 2004; Innes and Quarrie, 1987), and putative QTLs for drought-related characters have been found (Quarrie *et al*., 2003; Verma *et al*., 2004), which could aid introgression of favourable traits into elite germplasm. However, there may be varieties or breeding lines that already have good drought tolerance and WUE. It is important to breeders to exploit first the range of drought tolerance available within the UK pool because of the considerable time and resources needed to introgress exotic germplasm into elite UK material. Secondly, it is also important to explore sources of drought tolerance that are genetically quite distinct from the UK pool. These materials may harbour alleles conferring drought tolerance that are qualitatively and quantitatively different from the alleles present in largely European germplasm. Some of the traits in foreign material may be appropriate to UK conditions, while others may not be.

One of the obstacles to improved drought tolerance and water use efficiency is the negative association between certain stress-adaptive traits and productivity in ideal environments (Chapin *et al.*, 1993). Many studies (predominantly using transgenic *Arabidopsis* or tobacco) that demonstrate 'drought tolerance' in the laboratory have little relevance to agricultural conditions because growth is affected under unstressed conditions (Vinocur and Altman, 2005). The genes modified in some of these studies merely affect stomatal control, the rate of gas exchange, and hence growth (Passioura, 2006). However, some beneficial traits, such as stem reserves, are correlated with yield under all conditions (Foulkes *et al*., 2007; Shearman *et al*., 2005). In environments characterised by predictable dry periods, growers are willing to sacrifice some yield potential in order to achieve better yield under limiting conditions. In variable environments, the trade-offs have to be balanced more delicately, which requires knowledge of the water-holding capacity of the soil and the relative drought-susceptibility of current varieties.

Other genes that have been proposed to improve drought tolerance include:

1) proteins (e.g. dehydrins) that help protect cellular structures when plant cells become dehydrated (Lopez *et al*., 2003);

2) transcription factors (e.g. the DREB/CBF family) or signal transduction factors (Creelman, 2005; Pelligrineschi *et al*., 2004);

3) proteins that maintain redox balance and/or handle damaging reactive oxygen species that accumulate in stressed plants (Foyer and Noctor, 2005).

4) genes that control osmotic adjustment (Moinuddin *et al*., 2005) or plant morphology, such as root length and thickness, stomatal density, epicuticular wax deposition, etc. Clearly, deeper, more effective root systems are important to avoid or delay the effects of drought. Improved rice cultivars have been developed by introgressing alleles conditioning root depth and penetration ability via markers linked to root trait QTLs. For UK winter wheat, it remains unclear how much, if at all, rooting depth limits water use efficiency, and whether or not dwarfing genes affect root system size.

5) proteins that sense and regulate assimilate flux between source and sink organs. These could be key to determining aspects such as floret abortion, grain size and number, and mobilization of stem reserves. These processes are also the least understood. Genes that respond to ABA and sucrose are probably key players; apoplastic acid invertase is one likely target (Boyer and Westgate, 2004; Koch, 2004; Liu *et al*., 2005; Wardlaw and Willenbrink, 2000). Can alteration in the expression of one gene make a difference? The *ERECTA* gene in *Arabidopsis,* which controls differences in WUE, is a developmental gene that affects leaf thickness, stomatal density, and ultimately, the conductance to CO_2 within the leaf. (Masle *et al*., 2005). This study shows that manipulation of a single gene may have profound effects on WUE without penalising growth.

Current research

Figure 1. Polytunnels used to impose drought in 2007. The polytunnel system, which has only a minor effect on crop microclimate, is also used to screen for drought tolerance and water use efficiency in sugar beet (Ober ES, 2004).

Broom's Barn Research Centre is currently engaged in a Defra Sustainable Arable LINK funded project, in collaboration with British Wheat Breeders and the HGCA, to investigate the relative differences in drought tolerance and WUE within UK winter wheat varieties. This is determined using a combination of field trials and analysis of yield data generated by Recommended List and breeders' multi-location variety trials. In 2007, 120 varieties comprising RL varieties and breeders' advanced lines, were planted at Broom's Barn Research Centre, Suffolk, and subjected to either drought or unstressed rain-fed conditions. Drought was imposed by covering plots on 24 May until maturity with polythene using large polytunnels (Fig. 1; Ober *et al*., 2004). Thus, plants in droughted plots used only stored soil moisture during this period. In the control, the mean grain yield was 8.8 t ha^{-1}, *versus* 7.6 t ha^{-1} under drought, which equates to a mean yield loss of 14%. The response for each genotype was computed using a typical drought tolerance index (DTI):

$$DTI = \frac{Y_D / Y_I}{\overline{Y_D} / \overline{Y_I}}$$

where Y_D is the yield under drought and Y_I is the genotype yield potential (mean yield without stress). The denominator is the drought intensity index for the trial based on the mean droughted and unstressed yields across all genotypes within the trial. There were significant ($P<0.001$) genotypic differences in DTI, which showed a near-normal distribution across the entire set (Fig. 2). The next step is to repeat the experiment to examine the repeatability of the genotypic rankings. An important question to address is what particular traits characterise genotypes with consistently low DTI compared with drought tolerant genotypes with high DTI. During the growth of the crop a suite of measurements were made on physiological and morphological traits that have been associated with drought tolerance. Results from these experiments will be reported when the full analysis has been completed.

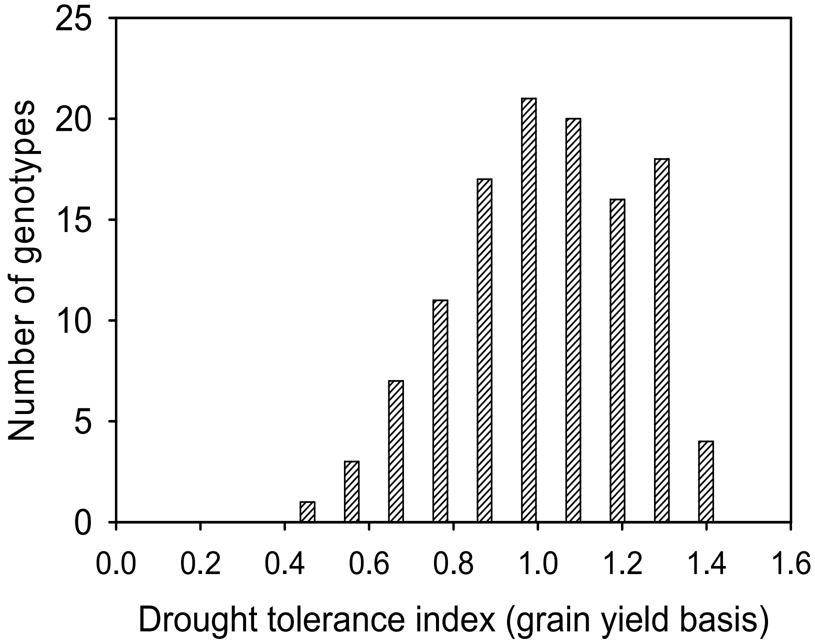

Figure 2. Distribution of responses to drought among 118 winter wheat genotypes tested under managed drought conditions in the field in 2007 at Broom's Barn, Suffolk ($LSD_{0.05}$ = 0.3). Drought tolerance indices greater than 1 indicate relatively greater drought tolerance (Ober ES, 2004).

Untapped value of variety trial data

To quantify the relative drought tolerance of many different wheat varieties, and to locate the few with superior characteristics, large scale yield trials under varying environmental conditions would have to be conducted. Fortunately, this costly exercise is already conducted in the form of the HGCA Recommended List variety trials, which are conducted on a range of soil types across years under differing amounts of rainfall. Thus some sites in nearly every year develop some degree of drought stress. The approach uses the Sirius wheat growth simulation model that is run on the actual weather and soil variables from each trial site and year in order to derive a drought stress index (DSI) for each trial. The relative performances of varieties are then judged across a range of increasing DSI. The accuracy of the computed DSI depends on soil and rainfall data that are specific to each location, and use of a crop growth model that estimates actual water use. This approach has been successful in identifying drought tolerant types in sugar beet (Pidgeon *et al*., 2006), barley (Rizza *et al*., 2004) and sorghum (Chapman *et al*., 2002).

Conclusion

Although some changes in climate may benefit plants, there is little doubt that a huge global challenge is to produce more food with limited supplies of water. This article has reviewed the various ways to approach breeding for improved drought tolerance and water use efficiency. Plants deal with the challenge of growing in the face of water shortage with a myriad of responses and strategies, but we are beginning to understand what is important, and what can be improved in crop varieties. Indeed, we may find that while the entire physiological picture is multifaceted, the practical solutions can be simple. Abraham Blum (Scientist Emeritus, The Volcani Center, Israel), who has considered these issues for more than 30 years, does not like the thinking that drought is an intractably complex problem with little chance for making progress: “Drought tolerance is not complex, but breeding for drought tolerance can be complicated.” (Blum, 2005). It is a challenge, but with good investment and collaboration there will be real accomplishment.

References

Austin R.B. (1987). Some crop characteristics of wheat and their influence on yield and water use. *In, JP Srivastava et al., eds, Drought tolerance in winter cereals. John Wiley,* pp 321-336.

Boyer J.S. (1982). Plant productivity and environment. *Science* ***218,*** *443-8*.

Boyer J.S., Westgate M.E. (2004). Grain yields with limited water. *Journal of Experimental Botany* ***55****, 2385-2394*.

Bruce W.B., Edmeades G.O., Barker T.C. (2002). Molecular and physiological approaches to maize improvement for drought tolerance. *Journal of Experimental Botany* ***53****, 13-25*.

Chapin F.S. III, Autumn K., Pugnaire F. (1993). Evolution of suites of traits in response to environmental stress. *American Naturalist* ***142****, S78-S92*.

Chapman S.C., Cooper M., Hammer G.L. (2002). Using crop simulation to generate genotype by environment interaction effects for sorghum in water-limited environments. *Australian Journal of Agriculture Research* ***53****, 379-89*.

Condon A.G., Richards R.A., Rebetzke G.J., Farquhar G.D. (2004). Breeding for high water-use efficiency. *Journal of Experimental Botany* ***55****, 2447-2460*.

Creelman, R.A., Ratcliffe O.J., Repetti P., Hempel F., Kumimoto R., Krolikowski K., Gutterson N. (2005). Identification of transcription factors regulating water stress responses. *Comp Biochem Physiol part A* ***141****, S299.*

Edmeades G.O., McMaster G.S., White J.W., Campos H. (2004). Genomics and the physiologist: bridging the gap between genes and crop response. *Field Crops Research* ***90****, 5-18*.

Forster B.P., Ellis R.P., Moir J., Talemè V., Sanguinetti M.C., Tuberosa R., This D., Teulat-Merah B., Ahmed I., Mariy S.A.E.E., Bahri H., El Ouahabi M., Zoumarou-Wallis N., El-Fellah M., Ben Salem M. (2004). Genotype and phenotype associations with drought tolerance in barley tested in North Africa. *Annals of Applied Biology* ***144****, 157-168*.

Foulkes M.J., Scott R.K., Sylvester-Bradley R. (2001). The ability of wheat cultivars to withstand drought in UK conditions: resource capture. *Journal of Agricultural Science* ***137,*** *1-16*.

Foulkes M.J., Scott R.K., Sylvester-Bradley R. (2002). The ability of wheat cultivars to withstand drought in UK conditions: formation of grain yield. *Journal of Agricultural Science* ***138****, 153-169*.

Foulkes M.J., Sylvester-Bradley R., Weightman R., Snape J.W. (2007). Identifying physiological traits associated with improved drought resistance in winter wheat. *Field Crops Research* ***103****, 11-24.*

Foulkes M.J., Sylvester-Bradley R., Worland A.J., Snape J.W. (2004). Effects of a photoperiod-response gene Ppd-D1 on yield potential and drought resistance in UK winter wheat. *Euphytica* ***135****, 63-73*.

Foyer C.H., Noctor N. (2005). Redox homeostasis and antioxidant signalling: a metabolic interface between stress perception and physiological responses. *The Plant Cell* ***17****, 1866-1875*.

Habben, J. (2005). Improving drought tolerance in maize: an industry perspective. *2nd International Conference on Integrated Approaches to Sustain and Improve Plant Production under Drought Stress, September, 2005, Rome.*

Innes P., Quarrie S.A. (1987). Water relations. *In, FGH Lupton, ed, Wheat Breeding. Chapman Hall*, pp 313-337*.*

Jones P.D., Lister D.H., Jaggard K.W., Pidgeon J.D. (2003). Future climate change impact on the productivity of sugar beet (*Beta vulgaris* L.) in Europe. *Climatic Change* ***58****, 93-108*.

Koch, K. (2004). Sucrose metabolism: regulatory mechanisms and pivotal roles in sugar sensing and plant development. *Current Opinion in Plant Biology* ***7****, 235-246*.

Lafitte H.R., Yongsheng G., Yan S., Li Z-K. (2006). Whole plant responses, key processes, and adaptation to drought stress: the case of rice. *Journal of Experimental Botany* ***58****, 169-175*.

Liu F.L., Jensen C.R., Andersen M.N. (2005). A review of drought adaptation in crop plants: changes in vegetative and reproductive physiology induced by ABA-abased chemical signals. *Australian Journal of Agriculture Research* ***56****, 1245-1252*.

Lopez C.G., Banowetz G.M., Peterson C.J., Kronstad W.E. (2003). Dehydrin expression and drought tolerance in seven wheat cultivars. *Crop Science* ***43****, 577-582*.

Malik T.A., Wright D., Virk D.S. (1999). Inheritance of net photosynthesis and transpiration efficiency in spring wheat *Triticum aestivum* L., under drought. *Plant Breeding* ***118****, 93-95*.

Masle J., Gilmore S.R., Farquhar G.D. (2005). The ERECTA gene regulates plant transpiration efficiency in *Arabidopsis*. *Nature* ***436****, 866-870*.

Moinuddin, Fischer R.A., Sayre K.D., Reynolds M.P. (2005). Osmotic adjustment in wheat in relation to grain yield under water deficit environments. *Agronomy Journal* ***97****, 1062-1071*.

Nelson D.E., Repetti P.P., Adams T.R., Creelman R.A., Wu J., Warner D.C., Amstrom D.C., Bensen R.J., Castiglioni P.P., Donnarummo M.G., Hinchey B.S., Kumimoto R.W., Maszle D.R., Canales R.D., Krolikowski K.A., Dotson S.B., Gutterson N., Ratcliffe O.J., Heard J.E. (2007). Plant nuclear factor Y (NF-Y) B subunits confer drought tolerance and lead to improved corn yields on water-limited acres. *Proceedings of the National Academy of Sciences* ***104****, 16450-16455*.

Ober E.S., Clark C.J.A., Le Bloa M., Royal A., Jaggard K.W., Pidgeon J.D. (2004). Assessing the genetic resources to improve drought tolerance in sugar beet: agronomic traits of diverse genotypes under droughted and irrigated conditions. *Field Crops Research* ***90****, 213-234*.

Parry M.A.J., Flexas J., Medrano H. (2005). Prospects for crop production under drought: research priorities and future directions. *Annals of Applied Biology* ***147****, 211-226*.

Passioura, J.B. (2006). Increasing crop productivity when water is scarce - from breeding to field management. *Agricultural Water Management 80, 176-196*.

Pelligrineschi A., Reynolds M., Pacheco M., Brito R.M., Almeraya R., Yamaguchi-Shinozaki K., Hoisington D. (2004). Stress-induced expression in wheat of *Arabidopsis thaliana* DREB1A gene delays water stress symptoms under greenhouse conditions. *Genome* ***47****, 493-500*.

Pidgeon J.D., Ober E.S., Qi A., Clark C.J.A., Royal A., Jaggard, K.W. (2006). Using multi-environment sugar beet variety trials to screen for drought tolerance. *Field Crops Research* ***95****, 268-279*.

Price A.H., Townend J., Jones M.P., Audebert A., Courtois B. (2002). Mapping QTLs associated with drought avoidance in upland rice grown in the Philippines and West Africa. *Plant Molecular Biology* ***48****, 683-695*.

Quarrie S.A., Dodig D., Pekic S., Kirby J., Kobiljski B. (2003). Prospects for marker-assisted selection of improved drought responses in wheat. *Bulgarian Journal of Plant Physiology, Special Issue,* pp 83-95.

Rebetzke G.J., Condon A.G., Richards R.A., Farquhar G.D. (2003). Gene action for leaf conductance in three wheat crosses. *Australian Journal of Agriculture Research **54**, 381-387*.
Reynolds M.P., Mujeeb-Kazi A., Sawkins M. (2005). Prospects for utilising plant-adaptive mechanisms to improve wheat and other crops in drought- and salinity-prone environments. *Annals of Applied Biology **146**, 239-259*.
Richards R.A. (2006). Physiological traits used in the breeding of new cultivars for water-scarce environments. *Agricultural Water Management 80, 197-211*.
Richter G.M., Semenov M.A. (2005). Modelling impacts of climate change on wheat yields in England and Wales: assessing drought risks. *Agricultural Systems **84**, 77-97*.
Rizza F., Badeck F.W., Cattivelli L., Lidestri O., Di Fonzo N., Stanca A.M. (2004). Use of a water stress index to identify barley genotypes adapted to rainfed and irrigated conditions. *Crop Science **44**, 2127-2137*.
Schonfeld M.A., Johnson R.C., Carver B.F., Mornhinweg D.W. (1988). Water relations in winter wheat as drought resistance indicators. *Crop Science **28**, 526-531*.
Serraj R., Hash C.T., Rizvi S.M.H., Sharma A., Yadav R.S., Bidinger F.R. (2005). Recent advances in marker-assisted selection for drought tolerance in pearl millet. *Plant Production Science **8**, 334-337*.
Shearman V.J., Sylvester-Bradley R., Scot R.K., Foulkes M.J. (2005). Physiological processes associated with wheat yield progress in the UK. *Crop Science **45**, 175-185*.
Solomon K.F., Labuschagne M.T. (2004). Inheritance of evapotranspiration and transpiration efficiencies in the diallel F_1 hybrids of durum wheat (*Triticum turgidum* L. var. *durum*). *Euphytica **136**, 69-79*.
Steele K.A., Price A.H., Shashidhar H.E., Witcombe J.R. (2006). Marker-assisted selection to introgress rice QTLs controlling root traits into and Indian upland rice variety. *Theoretical and Applied Genetics **112**, 208-221*.
Verma V., Foulkes M.J., Worland A.J., Sylvester-Bradley R., Caligari P.D.S., Snape J.W. (2004). Mapping quantitative trait loci for flag leaf senescence as a yield determinant in winter wheat under optimal and drought-stressed environments. *Euphytica **135**, 255-263*.
Vinocur B., Altman A. (2005). Recent advances in engineering plant tolerance to abiotic stress: achievements and limitations. *Current Opinion in Plant Biology **16**, 123-132*.
Wang Y., Ying J., Kuzma M., Chalifoux M., Sample A., McArthur C., Uchacz T., Sarvas C., Wan J., Dennis D.T., McCourt P., Huang Y. (2005). Molecular tailoring of farnesylation for plant drought tolerance and yield protection. *The Plant Journal **43**, 413-424*.
Wardlaw I.F., Willenbrink J. (2000). Mobilization of fructan reserves and changes in enzyme activities in wheat stems correlate with water stress during kernel filling. *New Phytologist **148**, 413-422*.