

Drought resistance, water-use efficiency, and yield potential—*are they compatible, dissonant, or mutually exclusive?*

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Abstract. This presentation is a concept review paper dealing with a central dilemma in understanding, designing, and acting upon crop plant improvement programs for drought conditions. The association among yield potential (YP), drought resistance (DR), and water-use efficiency (WUE) is often misunderstood, which in turn can lead to conceptual oversight and wrong decisions in implementing breeding programs for drought-prone environments.

Although high YP is the target of most crop breeding programs, it might not be compatible with superior DR. On the other hand, high YP can contribute to yield in moderate stress environments. Plant production in water-limited environments is very often affected by constitutive plant traits that allow maintenance of a high plant water status (dehydration avoidance). Osmotic adjustment (OA) is a major cellular stress adaptive response in certain crop plants that enhances dehydration avoidance and supports yield under stress. Despite past voiced speculations, there is no proof that OA entails a cost in terms of reduced YP.

WUE for yield is often equated in a simplistic manner with DR. The large accumulation of knowledge on crop WUE as derived from research on carbon isotope discrimination allows some conclusions on the relations between WUE on the one hand, and DR and YP on the other, to be made. Briefly, apparent genotypic variations in WUE are normally expressed mainly due to variations in water use (WU; the denominator). Reduced WU, which is reflected in higher WUE, is generally achieved by plant traits and environmental responses that reduce YP. Improved WUE on the basis of reduced WU is expressed in improved yield under water-limited conditions only when there is need to balance crop water use against a limited and known soil moisture reserve. However, under most dryland situations where crops depend on unpredictable seasonal rainfall, the maximisation of soil moisture use is a crucial component of drought resistance (avoidance), which is generally expressed in lower WUE.

It is concluded that the effect of a single ‘drought adaptive’ gene on crop performance in water-limited environments can be assessed only when the whole system is considered in terms of YP, DR, and WUE.

Additional keywords: plant breeding, osmotic adjustment, drought tolerance, phenology.

Introduction

As conventional breeding and biotechnology make headways into the development of drought-resistant cultivars, the conceptual framework of what actually constitutes a viable target for selection in this respect is not always clear. The drought-resistant ideotype is not always well defined. In workshops dealing with breeding for drought-prone environments there is a constant debate of ‘putative’ drought resistance mechanisms, ‘water-use efficiency’, and their interrelationship and associations with yield potential. Water-use efficiency (WUE) is often equated with drought resistance and the improvement of crop yield under stress, which is not necessarily the case. Drought resistance is sometimes considered as a penalty towards yield potential, which is not necessarily the case. Molecular biologists entering this

discipline often report the effect of an exotic gene towards ‘drought tolerance’ and advertise its expected value in breeding, which is rarely the case.

Yield potential is defined here as the maximum yield realised under non-stress conditions. Drought resistance in its physiological context is defined according to Levitt (1972) being determined by ‘dehydration avoidance’ and/or ‘dehydration tolerance’. WUE is mostly discussed in terms of plant production rather than gas exchange. Yield under water-limited conditions can be determined by the genetic factors controlling yield potential, and/or drought resistance, and/or WUE.

This review is therefore offered as a pragmatic concept paper discussing some of the key factors in the relationships among yield potential, drought resistance and water-use

efficiency, which may have an effect on a breeding program designed to release better yielding cultivars for water-limited environments.

Yield potential

The classical plant-breeding axiom that a high-yielding variety will perform well under most environments is still widely accepted by breeders. This is not an untrue axiom. The heart of the matter is the definition of 'most environments' and the delineation of those environments where high yield potential will not suffice for sustained performance. A delineation of such environments can be assessed by the crossover interaction, whereas under a particular pressure of environmental stress, cultivars with high yield potential produce less than certain cultivars that have lower yield potential but seem to be better adapted to stress. For most cereals grown under water-limited conditions the crossover occurs at a yield level of around 2–3 t/ha (e.g. Blum and Pnuel 1990; Ceccarelli and Grandi 1991), which is approximately one-third of the yield potential. The main reason for a crossover under conditions of variable water supply is an inherent difference among the tested cultivars in drought resistance, beyond difference in their yield potential. The lack of a crossover interaction in any set of tested cultivars may have 2 reasons: (a) stress-adapted materials are not present in the test and the tested cultivars differ mainly in their yield potential due to factors that have very little to do with stress adaptation; (b) the range of conditions under which these cultivars are tested does not include stress environments severe enough to reduce yield below the expected point of crossover. This was observed in international wheat variety trials some 15–20 years ago, where often stress environments were represented by mean yields of 4–5 t/ha as compared with a maximum yield of ~8 t/ha.

The prevalence of the crossover interaction is a source of frustration to the breeder in his attempt to select in one environment and achieve good performance also in others. Again, breeders always expected the ideal cultivar to perform well over all environments, a requirement that cannot be reconciled at least with the prevalence of the crossover interaction with respect to the water regime. This has led breeders in drought-prone regions to develop dedicated selection programs towards the development of drought-adapted cultivars, using programmed stress environments and other selection tools. When in such programs selection for yield was performed under low-yielding stress conditions, large differences were seen among different years, locations, and studies in the heritability estimates for yield under stress in a given crop (e.g. Blum 1988). Heritability for yield under stress largely depends on 2 key factors: (a) the existence of genes for drought resistance in the population, which are effective in the stress environments under which selection is performed (Blum *et al.* 2001), and (b) the degree of control over the homogeneity and general stress conditions in the

selection nursery. Selection in stress-managed environments that do not suffer from additional problems (weeds, diseases, nematodes, inherent soil variability, etc.) will provide better heritability estimates for yield under stress than in unmanaged environments. Therefore, with the appropriate genetic materials and minimisation of the error variance, heritability for yield under stress can be high and selection effective. It is obvious from the previous discussion that a water-limited environment for effective selection towards drought resistance is that where mean yield level is below the crossover yield range.

When effective and successful selection for yield under stress is exercised it most likely involves a genetic shift towards a dehydration-avoidant plant type (see further discussion below). Such a dehydration-avoidant phenotype, which is characterised by the maintenance of high plant water status under stress, can present, for example, any of the following features: early flowering, smaller plant, small leaf area, or limited tillering (in cereals) (e.g. Blum 1988), all of which are in contrast to a high yield potential phenotype. Therefore, a crossover interaction for yield is to be expected over a range of environments. By this token, the crossover interaction can *theoretically* be avoided and drought resistance can be recombined with high yield potential if selection is designed to recombine a high yield potential genotype with relevant dehydration-avoidance factors that are not associated with lower yield potential. This depends largely on what would constitute an effective drought-resistance mechanism in the target environment. For example, if stress-induced abscisic acid (ABA) accumulation is an important cause of fertility reduction in wheat under drought stress (Westgate *et al.* 1996), an ABA-insensitive genotype (Blum and Sinmena 1995) might perhaps be an appropriate solution for expressing both drought resistance and high yield potential. Another example might be osmotic adjustment, which has no obligatory association with low yield potential (see below).

Further explanation is needed regarding the genetic shift in yield potential brought about by selection for yield under drought stress. This is done using the following analogy. Historically (e.g. the 'green revolution'), it is well established that selection for high yield potential in cereals by using yield as a selection criterion provided the desired result by way of a genetic shift towards greater harvest index. Selection for yield generally did not increase total biomass but only the proportion between grain and stover within a given biomass. Harvest index was not part of the selection criteria. If we had known how to select for high yield potential using criteria other than yield, perhaps results could have been achieved by way of enhanced total plant productivity rather than just by changing the production ratio. Hybrid vigour (heterosis) in grain yield of sorghum is expressed by way of greater biomass production in shorter time with no effect on harvest index (Blum 2004), indicating that an increase in yield potential

can be achieved by raising total plant production rather than just by its partitioning. Therefore, by the same token, I propose that selection for yield under drought stress resulted in a dehydration-avoidant phenotype that is rarely compatible with a high yield potential phenotype. If selection will address factors of stress adaptation in addition to yield under stress, perhaps higher yield potential and drought resistance can be recombined.

Another reason for a negative relationship between yield potential and drought resistance (mainly dehydration avoidance) is the fact that at least in cereals, high yield and a large sink constitute a load on the shoot in terms of its water status and turgor maintenance under drought stress (Blum *et al.* 1988; Khanna-Chopra and Sinha 1988). The reason most likely is the strong assimilate export from the leaves into the grain and the increase in stomatal conductance under the effect of a large sink demand. Hormonal signals might be involved. Indeed, the suggested selection for high stomatal conductance as a surrogate for high yield potential under irrigation (e.g. Amani *et al.* 1996) can be regarded as being derived from the association between high stomatal conductance and a large sink.

Drought resistance

Drought resistance and its components are almost constantly being 'redefined', whereas newcomers to this discipline often express outstanding inventive capacity for terminology. For their benefit they are reminded that the original terminology and definitions of Levitt (1972) still hold very well. This is not nostalgia; it is a matter of scientific correctness (see Introduction).

When a genotype yields better than another under a severe (below the 'crossover') strain of drought, it is relatively more drought resistant. The strain of drought is developed when crop demand for water is not met by the supply, and plant water status is reduced. Plants can resist drought by either dehydration avoidance or by dehydration tolerance. Drought resistance in terms of the physiology involved interacts with the magnitude and the timing of the stress. Timing here refers to the stage of plant development when stress occurs. For example, drought resistance in seedlings grown in a pot has nothing to do with drought resistance during grain filling in the field.

Dehydration avoidance

Dehydration avoidance is defined as the plant capacity to sustain high plant water status or cellular hydration under the effect of drought. Hence, by this mechanism the plant avoids being stressed because plant functions are relatively unexposed to tissue dehydration. Crop plants avoid dehydration by enhanced capture of soil moisture, by limited crop water loss, and by retaining cellular hydration despite the reduction in plant water potential.

Enhanced capture of soil moisture

Much has been written and debated about roots and soil moisture uptake. At the end of the day the essence of the matter is that where deep soil moisture is available a *long root* to reach this moisture is simply as effective as a long rope in a deep well.

Genetic variation exists in potential root length (maximum root length measured under non-stress and non-restrictive soil conditions). However, when plants are exposed to a drying soil, root morphology and growth can change to the extent that the potential root length, whether it is short or long, becomes irrelevant. In cereals a drying, hard topsoil resists the penetration and establishment of adventitious (crown) roots while existing roots receive all transient assimilates and grow deeper (Blum and Ritchie 1984; Asseng *et al.* 1998). Shoot/root dry matter ratio increases under drought stress, not because of an increase in root mass but due to a relatively greater decrease in shoot mass. Root mass rarely increases under stress. However, root length and depth may increase in a drying soil even at a reduced total root mass. Hence, total root dry matter or its ratio to shoot dry matter is not helpful information towards selection.

It is not absolutely clear whether the capacity for developing longer roots under stress is compatible with a high yield potential phenotype. When all their requirements are effectively supplied, plants do not need a large root. Root mass under very productive drip irrigation systems is relatively small. In such a system a large potential root is a waste of dry matter. However, under conditions of unsecured soil resources, a potentially large root is required to ensure capture of resources under erratic conditions. This form of insurance may pose a load on yield potential if a large root is expressed in large root mass (see above). In cereal crops that tiller (and most certainly in rice) a deep root is very likely associated with a limited number of adventitious root axes, which is a result of reduced tillering. Therefore, where extensive tillering is an important component of high yield potential, constitutively developed deep roots and high yield potential can be mutually exclusive. However, as indicated above, the inherent developmental plasticity of the cereal plant will often allow a high tillering phenotype to penetrate deep soil when the topsoil is drying for a sufficient length of time during the tillering phase.

Reduced water use

Plants are developmentally and physiologically designed by evolution to reduce water use (WU) under drought stress. Since plant production is a function of WU the issue for the breeder is how to reduce WU under stress while minimising the associated reduction in production. It would seem that this is a question of the genetic scatter around the very firm regression of biomass production on crop water use. However, the regression of biomass on crop water use in itself can

be changed. Water-use efficiency for grain yield (WUE; the slope of the regression) is not a fixed crop entity. The rate of reduction in water use against the rate of reduction in yield as drought develops allows room for manipulations. This does not mean that WUE must be addressed by the breeder but rather by the dynamics of its nominator and denominator under stress.

For example, reduced plant size, leaf area, and leaf area index (LAI) are a major mechanism for moderating water use and reducing injury under drought stress (e.g. Mitchell *et al.* 1998). Often, crop cultivars bred for water-limited environments by selection for yield under stress have a constitutively reduced leaf area. Pathways for constitutive reduction in plant size and leaf area are smaller leaves, reduced tillering, and early flowering. Reduced growth duration is associated with reduced leaf number (Blum 2004). A crop plant designed for constitutive moderation of water use by the above pathways cannot attain high yield potential. The question asked for given drought scenarios is which is the most appropriate avenue for reduction in crop leaf area? Early flowering will also ascribe escape of late-season stress, and reduced tillering may also ascribe deeper roots.

If breeding retains a large leaf area that is conducive to greater yield potential, then when stress occurs a large part of this leaf area, which is a dry matter investment, will be irreversibly desiccated and lost. In some drought-adapted crop plants, typically sorghum, older leaves are selectively killed under stress while the remaining young leaves retain turgor, stomatal conductance, and assimilation (Blum and Arkin 1984), as a result of high osmotic adjustment in the younger leaves. This is another demonstration of an opportune window for manipulating WU against plant production under stress.

The radiative energy load on the canopy (net radiation), of which only a fraction is used for photosynthesis, is dissipated mainly by transpiration. A reduction in transpiration can be achieved by reducing net radiation by way of reflection, namely increasing crop albedo. Various plant-surface structures allow an increase in albedo (e.g. Holmes and Keiller 2002). Epicuticular wax or plant glaucousness reduces cuticular conductance and reflects incoming radiation at the UV and 400–700 nm wavelengths to the extent that leaf temperature and transpiration are reduced without a reduction in stomatal conductance. This is expressed in greater WUE for the glaucous genotype (Premachandra *et al.* 1994). Reduced leaf chlorophyll content expressed in yellowish or pallid green shade of colour is indicative of reduced antenna complexes at the Photosystem II reaction centre. This reduces photosynthetically active radiation (PAR) absorption and subsequently water use. Such varieties were found adapted to dry and cold conditions (Watanabe *et al.* 1995). However, at the same time, these reflective properties that are beneficial under drought stress were often associated with reduced

photosynthesis and yield potential (Premachandra *et al.* 1994; Sanchez *et al.* 2001).

Programmed moderated crop water use has become an important agronomic practice in maximising crop production in dryland environments that are largely based on stored soil moisture use. This is the case for Mediterranean-region summer crops, certain Mediterranean climates in eastern Australia, and for some of the rabi (winter) crops in India. The situation is extreme in parts of the southern and eastern Mediterranean region where no effective rain is received after planting dryland summer crops such as sorghum, sunflower, or safflower. In sorghum, for example, the grower determines soil moisture content to a depth of 1.8 m just before planting. He then adapts the variety to be used (mainly its growth duration) and plant density to the available soil moisture so as not to deplete it before maturity. Even planting geometry was found to be effective in reducing water use by increasing plant competition at a given plant density (Blum and Naveh 1976). In the Australian Mediterranean environment, moderated water use was initially thought to be achieved via a genetic reduction in root conductance by the restriction of root xylem diameter in wheat (Richards and Passioura 1989). Although the approach was innovative and biologically sound, it was not adopted as a breeding method. Early flowering was a limited solution due to problems of frost damage in very early-flowering cultivars. More recently, there is success in developing cultivars of moderate water use by selection for high water-use efficiency (low carbon isotope discrimination) (see below).

In conclusion, the design of a dehydration-avoidant genotype based on moderate water use cannot consider only one physiological factor or one gene without understanding the full spectrum of interactions among plant development, phenology, water use, penalty in yield potential, and the specific dryland ecosystem.

Osmotic adjustment and conserved cellular water content

This section is not intended to serve as a comprehensive review of osmotic adjustment but rather as a discussion of osmotic adjustment in relation to the subject matter of this presentation.

An increasing number of reports provides evidence on the association between high rate of osmotic adjustment (OA) and sustained yield or biomass under water-limited conditions across different cultivars of crop plants (Table 1). Since OA helps to maintain higher leaf relative water content (RWC) at low leaf water potential (LWP), it is evident that OA helps to sustain growth while the plant is meeting transpirational demand by reducing its LWP. 'Osmotic adjustment sustained turgor maintenance and hence the yield-forming processes during moderate and severe water stress' (Ali *et al.* 1999). Increased deep-soil moisture extraction has been found to be a major contribution of OA in sorghum (e.g. Wright and Smith 1983). Beyond the effect

on cellular hydration, other putative roles of OA have been recently assembled under the vague term of ‘osmoprotection’ (e.g. Rontein *et al.* 2002). Such a possible role for cell-compatible osmolytes in protecting enzymes against heat inactivation was indicated a while ago (Paleg *et al.* 1981). Associations between OA and cellular membrane stability under drought stress were suggested more recently (e.g. Riga and Vartanian 1999; Chandra Babu *et al.* 2004). However, despite the emerging evidence and the passing of time there has been no quantification of an ‘osmoprotective’ function in terms of plant production under stress. One can only guess that some of the associations listed in Table 1 might be supported by such protective roles of OA (e.g. Chandra Babu *et al.* 2004).

Despite earlier voiced or printed concerns, there is no solid evidence of a cost in yield potential for OA capacity. We do not know of any plant constitutive function or trait that would enhance OA under drought stress while deteriorating yield potential. Only in rice are there some indications (Lilley *et al.* 1996) that there may be a genetic linkage between a high capacity for OA and a small root, as expressed in *indica* rice typical of the lowland high-yield cultivars. Very likely this is a case limited to rice, which relates to its specific culture and evolution.

Dehydration (desiccation) tolerance

Dehydration tolerance is defined as the relative capacity to sustain or conserve plant function in a dehydrated state. This is sometimes seen as the second defence line after dehydration avoidance. A legitimate measure of genetic

Table 1. Documented evidence for the association between osmotic adjustment and crop production (yield and/or biomass) under water-limited conditions

Crop	Reference
Barley	Gonzalez <i>et al.</i> (1999)
Barley and wheat	Teulat <i>et al.</i> (1997)
Birdseed millet	Karyudi and Fletcher (2003)
<i>Brassica</i> sp.	Singh <i>et al.</i> (1985)
<i>Brassica</i> sp.	Wright <i>et al.</i> (1997)
Chickpea	Morgan <i>et al.</i> (1991)
Chickpea	Moinuddin and Khanna-Chopra (2004)
Cotton	Saranga <i>et al.</i> (2001)
Pea	Rodriguezmaribona <i>et al.</i> (1992)
Pigeonpea	Subbarao <i>et al.</i> (2000)
Sorghum	Santamaria <i>et al.</i> (1990)
Sorghum	Tangpremsri <i>et al.</i> (1991)
Sorghum	Tangpremsri <i>et al.</i> (1995)
Sunflower	Chimentti <i>et al.</i> (2002)
Wheat	Fischer and Wood (1979)
Wheat	Johnson <i>et al.</i> (1984)
Wheat	Morgan <i>et al.</i> (1986)
Wheat	Morgan and Condon (1986)
Wheat	Blum and Pnuel (1990)
Wheat	Ali <i>et al.</i> (1999)
Wheat	Blum <i>et al.</i> (1999)
Wheat	Morgan (2000)

variation in desiccation tolerance is the comparative function at low tissue RWC.

Dehydration tolerance as an effective drought-resistance mechanism in crop plants is rare. It exists in the seed embryo, but once germinated the plant loses its tolerance. Extreme desiccation tolerance is known in resurrection plants and some attempts are made in various laboratories to use this tolerance for improving crop plants. Results are still imminent. Dehydration tolerance, like freezing tolerance, requires that the plant enter a quiescent or a dormant state. The limited studies of dehydration tolerance in crop plants revealed that genotypic variation in plant recovery from dehydration, as a measure of tolerance, was positively correlated with plant water status (e.g. RWC) retained during desiccation (Fig. 1) rather than with a capacity to retain function at a dehydrated state. It is also extremely interesting to note the conclusion made by Chaves *et al.* (2002), who investigated native Mediterranean vegetation, that ‘Differences among species can be traced to different capacities for water acquisition, rather than to differences in metabolism at a given water status’. If all the available literature on crop drought resistance is taken together it can be suggested that both natural selection and selection by man have given preference to dehydration avoidance over dehydration tolerance as the major strategy for coping with drought stress, with the exception of resurrection

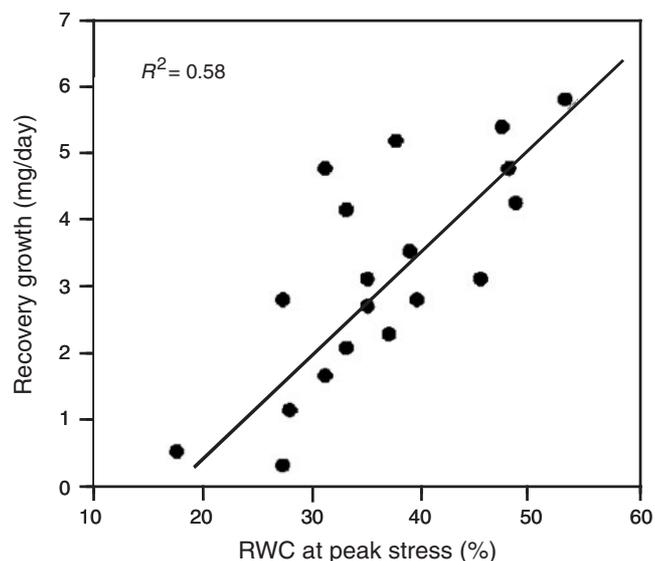


Fig. 1. Seedling growth upon recovery of diverse tef (*Eragrostis tef*) cultivars as a function of their leaf relative water content (RWC) at peak stress when recovery irrigation was applied. Seedlings were grown in fertilised soil/vermiculite potting mixture. Irrigation was stopped at 6 days after emergence. Peak stress was considered when all seedlings appeared severely wilted to different degrees, 16 days after emergence. Recovery irrigation was applied 17 days after emergence. Growth rate was calculated as the rate of dry matter increase per plant from 18 days to 24 days after emergence.

plants. Even exotic genes that are evaluated for function in experimental transgenic plants such as *Arabidopsis* or tobacco are more often expressed in dehydration avoidance and its components rather than in desiccation tolerance (e.g. http://www.plantstress.com/Files/Abiotic-stress_gene.htm).

The only major exception that constitutes a form of an effective dehydration tolerance mechanism in crop plants is stem reserve utilisation for grain filling under drought stress (Blum 1998). This is a harmonised whole-plant process that allows effective grain filling when whole-plant photosynthesis is inhibited by stress during grain filling. It is a tolerance mechanism that allows grain filling in dehydrated or over-heated cereal plants, which can account for up to 90% of total grain weight under stress (Blum *et al.* 1994; Asseng and van Herwaarden 2003). Stem reserve utilisation has been found to be an effective yield-supporting mechanism under drought stress (Hossain *et al.* 1990; Pheloung and Siddique 1991; Gavuzzi *et al.* 1997; Yang *et al.* 2002; Asseng and van Herwaarden 2003; Plaut *et al.* 2004).

The major condition for stem reserves for grain filling is sufficient carbohydrate storage before grain filling. This may be partially linked to plant traits that promote high yield potential, at least during the pre-flowering growth stages.

Although some stem reserve mobilisation may support grain filling under non-stress conditions, reserve mobilisation is noticeably induced by drought stress during grain filling (Blum *et al.* 1994; Palta *et al.* 1994; Yang *et al.* 2001a; Plaut *et al.* 2004). The signal for the induction of reserve mobilisation under drought stress is not clear but likely to involve hormones such as gibberellins and abscisic acid (Yang *et al.* 2001b). Stress that reduces plant water status and photosynthesis during grain filling induces stem storage conversion into soluble sugars and the mobilisation of sugars into the grains. The mobilisation of sugars into the grain can take place in a dehydrated plant and it is apparently a dehydration-tolerance process in the whole plant. The capacity to store stem reserves pre-flowering is most likely supported by a favourable plant water status pre-flowering. However, storage conversion into transportable carbohydrates and the transport of carbohydrates into the inflorescence take place as the whole plant dehydrates. This dehydration-tolerant plant function is sustained even under severe chemical desiccation of the plant (Blum *et al.* 1983; Hossain *et al.* 1990). It is interesting to note that the mobilisation of sugars from older tissues into younger ones during severe dehydration is a feature of the resurrection plant *Craterostigma plantagineum* (Norwood *et al.* 1999).

Non-senescence ('delayed senescence'; 'stay-green'), which has been so well discussed by Thomas and Howarth (2000), is considered an important component for sustaining yield potential and in some cases also for sustaining yield under stress during grain filling (e.g. Tuinstra *et al.* 1998;

Borrell and Hammer 2000; Sanchez *et al.* 2002). Non-senescence is an important factor in sustaining a positive plant nitrogen balance such as in maize (Ma and Dwyer 1998) and sorghum (Borrell and Hammer 2000). Non-senescence is under relatively simple genetic control and can be readily improved by conventional or molecular breeding. However, at the same time, non-senescent genotypes retain more of their photosynthate in the leaves (Borrell and Hammer 2000) and stems, whereas rapid leaf senescence may be indicative of reserve mobilisation to the grain under stress (e.g. Fokar *et al.* 1998; Yang *et al.* 2001a). The delicate balance between stem reserve mobilisation and non-senescence, which involves carbohydrate and nitrogen metabolism, is not quite clear. Other factors, such as protection against stem rot diseases may also be involved in ascribing a yield advantage to non-senescence sorghum (Tenkouano *et al.* 1993). If one considers together all the available information on stem reserve mobilisation and non-senescence it becomes clear that in screening nurseries the 2 traits are mutually exclusive. A decision must be made whether to favour one over the other, when the target environment involves late-season drought or heat stress. It must be quite obvious that when severe stress occurs during grain filling, even a non-senescent leaf cannot function indefinitely and photosynthesis is bound to be drastically reduced. Then, the only possible mechanism that would still allow some grain filling in a standing dehydrated plant is stem reserve mobilisation. On the other hand, there is an obvious advantage to non-senescence in crops or genotypes that are devoid of any effective capacity for stem reserve utilisation for grain filling under stress, such as the normal 3-dwarf sorghum plant (Blum *et al.* 1997) that is in wide use.

Water-use efficiency

WUE is often equated in a simplistic manner with drought resistance without considering the fact that it is a ratio between 2 physiological (transpiration and photosynthesis) or agronomic (yield and crop water use) entities. As a ratio it is often susceptible to misinterpretation, especially when the dynamics of the nominator and the denominator are obscure.

The intrinsic paradox in assuming that a high WUE means better yield under stress is demonstrated in results of a greenhouse experiment (A. Blum and C. Y. Sullivan 1983, unpublished data) briefly presented here (Fig. 2). The experiment compared a high-yielding semi-dwarf cultivar (HYV) with a landrace (LR) of durum wheat (*Triticum durum*) grown under stress and control conditions. Plants were grown in 1.5-m-long, white PVC tubes in aerated hydroponics culture. Control plants were grown with full volume of half-strength Hoagland's nutrient solution. Stressed plants were allowed to draw down the solution in the tube (while the solution was exchanged daily to maintain standard nutrient concentration). When the solution reached

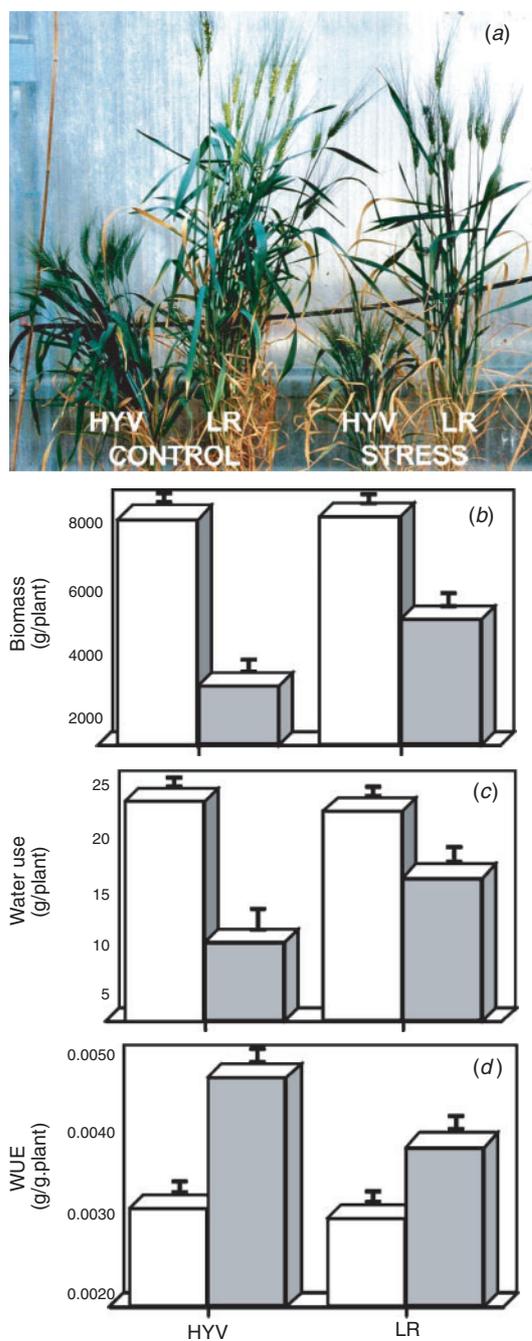


Fig. 2. Results of a greenhouse experiment comparing a semi-dwarf high-yielding cultivar (HYV) and a landrace (LR) of durum wheat (*Triticum durum*) grown under stress and control conditions. Plants were grown in 1.2-m-long PVC tubes in aerated hydroponics culture. Control plants were grown with full volume of nutrient solution. Stress plants were allowed to draw down the solution in the tube (while the solution was exchanged daily to maintain standard nutrient concentration). When the solution reached a level of 15 cm above the bottom it was maintained at that level while only the tips of roots were immersed in the solution. (a) The appearance of cultivars and treatments at the onset of grain filling; (b) above-ground dry biomass; (c) total seasonal water use; (d) water-use efficiency (WUE) for biomass. Vertical bars are s.e. of the mean.

a level of 15 cm above the bottom of the tube it was maintained at that level while only the tips of roots were immersed in the solution. This state was reached at about the end of the stem elongation growth stage. Plants under stress expressed symptoms of water deficit such as advanced drying of lower leaves and reduced growth (Fig. 2a). The 2 cultivars flowered at the same time in the control treatment and 2–3 days earlier under stress. Water use was measured throughout the growing season by recording the daily amounts of water needed to replenish the solutions. Total shoot dry biomass as a measure of above-ground plant production was determined at maturity. WUE for biomass was then calculated.

Water use and biomass were reduced by the stress treatment. Water use was the same for both cultivars in the control but relatively higher in the LR than in the HYV under stress. Biomass under stress was relatively higher in the LR than in the HYV. WUE was the same in both cultivars in the control and it increased under stress. WUE under stress was higher in the HYV than in the LR because of the relative differences in their water use and biomass. Greater biomass production under stress was associated with relatively greater water use and lower WUE as seen in the LR.

Due to the abundant data developed in the last decade for WUE (in terms of carbon isotope discrimination), important conclusions about WUE in plant breeding can now be drawn, as presented by Condon *et al.* (2002) and as further discussed here.

As depicted in Fig. 2 it is now well documented that high yield potential and high yield under water-limited conditions are generally associated with reduced WUE (e.g. Munoz *et al.* 1998) mainly because of high water use. Features linked to low yield potential, such as smaller plants (Martin *et al.* 1999) or short growth duration (Lopezcastaneda and Richards 1994), ascribe high WUE because they reduced water use.

Dehydration avoidance as achieved by enhanced capture of soil moisture by roots has been found to be associated with low WUE in such diverse species as rice (Kobata *et al.* 1996) and Ponderosa pine (Zhang *et al.* 1997). On the other hand, reduced transpiration in rice (Kobata *et al.* 1996) and reduced evapotranspiration in sorghum (Tolk and Howell 2003) were associated with higher WUE. Taken together, these and other reviews (e.g. Condon *et al.* 2002) most clearly indicate that *genotypic variations in WUE were driven mainly by variations in water use rather than by variations in plant production or assimilation per given amount of water use*. It is therefore not surprising that selection for high WUE by using carbon isotope discrimination resulted in smaller or earlier flowering plants that use less water over the growing season. These plants were found to be very suitable mainly for conditions of stored soil moisture (see above) where moderated use of the given amount of stored soil moisture is crucial (Condon *et al.* 2002). Therefore, if there is any relationship at all between WUE

and the maintenance of plant production under water limited conditions, it exists for dryland conditions of stored soil moisture (e.g. eastern Australia) (see fig. 6 in Condon *et al.* 2002) that ascribe an advantage to small plants, moderated growth, and short growth duration. In other drought environments where stress may develop at any time during the season (e.g. Western Australia; see fig. 6 in Condon *et al.* 2002), there is no consistent relationship between plant production and WUE. It may therefore be further concluded that for conditions where high WUE is an advantage because it is a marker for low water use, selection for the preferred plant type can be done by directly selecting for small plant size, small leaf area, or reduced growth duration rather than by using the more expensive selection criterion of WUE by way of carbon isotope discrimination.

Conclusions

Constitutive whole-plant traits have a major role in affecting plant water use and plant dehydration avoidance under stress. These largely determine some of the negative relations between yield potential and the ability to sustain yield under severe water shortage.

Crops and native vegetation that are adapted to water-limited conditions in terms of growth and productivity achieve adaptation mainly by dehydration avoidance and escape rather than by desiccation tolerance and the ability to function in a dehydrated state. Besides various developmental and phenological attributes that affect crop performance under drought, osmotic adjustment is a major cellular drought-responsive trait that contributes to cellular dehydration avoidance and yield under stress. Despite past voiced speculations, there is no definitive proof that the capacity for OA entails a cost in terms of reduced yield potential.

Desiccation tolerance might be important in certain drought scenarios or in drought-prone subsistence farming. An exceptional case for a very effective desiccation-tolerance mechanism in crop plants is the sustained or even up-regulated stem reserve mobilisation under stress, which is the only option for grain filling in a standing dehydrated crop. This capacity is mutually exclusive with non-senescence.

Indiscriminant selection for higher WUE with the assumption that it equates with improved drought resistance or improved yield under stress might bring about serious negative consequences. High WUE is largely a function of reduced water use rather than a net improvement in plant production or biochemistry of assimilation. Therefore, in selection programs it may constitute a marker for reduced water use commonly achieved via moderated growth, reduced leaf area, and short growth duration. If low water use is the breeder's target it is highly probable that selection for low water use can be achieved by directly selecting for these simple plant traits, without measuring WUE.

References

- Ali M, Jensen CR, Mogensen VO, Andersen MN, Henson IE (1999) Root signalling and osmotic adjustment during intermittent soil drying sustain grain yield of field grown wheat. *Field Crops Research* **62**, 35–52. doi: 10.1016/S0378-4290(99)00003-9
- Amani I, Fischer RA, Reynolds MP (1996) Canopy temperature depression association with yield of irrigated spring wheat cultivars in a hot climate. *Journal Agronomy and Crop Science* **176**, 119–129.
- Asseng S, van Herwaarden AF (2003) Analysis of the benefits to wheat yield from assimilates stored prior to grain filling in a range of environments. *Plant and Soil* **256**, 217–229. doi: 10.1023/A:1026231904221
- Asseng S, Ritchie JT, Smucker AJM, Robertson MJ (1998) Root growth and water uptake during water deficit and recovering in wheat. *Plant and Soil* **201**, 265–273. doi: 10.1023/A:1004317523264
- Blum A (1988) 'Plant breeding for stress environments.' (CRC Press: Boca Raton, FL)
- Blum A (1998) Improving wheat grain filling under stress by stem reserve mobilization. *Euphytica* **100**, 77–83. doi: 10.1023/A:1018303922482
- Blum A (2004) Sorghum physiology. In 'Physiology and biotechnology integration for plant breeding'. (Eds HT Nguyen, A Blum) pp. 141–223. (Marcel Dekker: New York)
- Blum A, Arkin GF (1984) Sorghum root growth and water-use as affected by water supply and growth duration. *Field Crops Research* **9**, 131–142. doi: 10.1016/0378-4290(84)90019-4
- Blum A, Golan G, Mayer J, Sinmena B (1997) The effect of dwarfing genes on sorghum grain filling from remobilized stem reserves under stress. *Field Crops Research* **52**, 43–54. doi: 10.1016/S0378-4290(96)03462-4
- Blum A, Klueva N, Nguyen HT (2001) Wheat cellular thermotolerance is related to yield under heat stress. *Euphytica* **117**, 117–123. doi: 10.1023/A:1004083305905
- Blum A, Mayer J, Golan G (1988) The effect of grain number (sink size) on source activity and its water-relations in wheat. *Journal of Experimental Botany* **39**, 106–114.
- Blum A, Naveh M (1976) Improved water-use efficiency by promoted plant competition in dryland sorghum. *Agronomy Journal* **68**, 111–116.
- Blum A, Pnuel Y (1990) Physiological attributes associated with drought resistance of wheat cultivars in a Mediterranean environment. *Australian Journal of Agricultural Research* **41**, 799–810.
- Blum A, Poyarkova H, Golan G, Mayer J (1983) Chemical desiccation of wheat plants as a simulator of post-anthesis stress. I. Effects on translocation and kernel growth. *Field Crops Research* **6**, 51–58. doi: 10.1016/0378-4290(83)90047-3
- Blum A, Ritchie JT (1984) Effect of soil surface water content on sorghum root distribution in the soil. *Field Crops Research* **8**, 169–176. doi: 10.1016/0378-4290(84)90060-1
- Blum A, Sinmena B (1995) Isolation and characterization of variant wheat cultivars for ABA sensitivity. *Plant, Cell and Environment* **18**, 77–83.
- Blum A, Sinmena B, Mayer J, Golan G, Shpiler L (1994) Stem reserve mobilization supports wheat grain filling under heat stress. *Australian Journal of Agricultural Research* **45**, 771–781.
- Blum A, Zhang JX, Nguyen HT (1999) Consistent differences among wheat cultivars in osmotic adjustment and their relationship to plant production. *Field Crops Research* **64**, 287–291. doi: 10.1016/S0378-4290(99)00064-7
- Borrell AK, Hammer GL (2000) Nitrogen dynamics and the physiological basis of stay-green in sorghum. *Crop Science* **40**, 1295–1307.

- Ceccarelli S, Grando S (1991) Selection environment and environmental sensitivity in barley. *Euphytica* **57**, 157–167. doi: 10.1007/BF00023074
- Chandra Babu R, Zhang JX, Blum A, Ho DT-H, Wu R, Nguyen HT (2004) HVA1, a LEA gene from barley confers dehydration tolerance in transgenic rice (*Oryza sativa* L.) via cell membrane protection. *Plant Science* **166**, 855–862. doi: 10.1016/j.plantsci.2003.11.023
- Chaves MM, Pereira JS, Maroco J, Rodrigues ML, Ricardo CPP, Oserio ML, Carvalho I, Faria T, Pinheiro C (2002) How do plants cope with water stress in the field? Photosynthesis and growth. *Annals of Botany* **89**, 907–916. doi: 10.1093/aob/mcf105
- Chimenti CA, Pearson J, Hall AJ (2002) Osmotic adjustment and yield maintenance under drought in sunflower. *Field Crops Research* **75**, 235–246. doi: 10.1016/S0378-4290(02)00029-1
- Condon AG, Richards RA, Rebetzke GJ, Farquhar GD (2002) Improving intrinsic water-use efficiency and crop yield. *Crop Science* **42**, 122–131.
- Fischer RA, Wood JT (1979) Drought resistance in spring wheat cultivars. III. Yield associations with morpho-physiological traits. *Australian Journal of Agricultural Research* **30**, 1001–1011. doi: 10.1071/AR9791001
- Fokar M, Blum A, Nguyen HT (1998) Heat tolerance in spring wheat. II. Grain filling. *Euphytica* **104**, 9–15. doi: 10.1023/A:1018322502271
- Gavuzzi P, Rizza F, Palumbo M, Campanile RG, Ricciardi GL, Borghi B (1997) Evaluation of field and laboratory predictors of drought and heat tolerance in winter cereals. *Canadian Journal of Plant Science* **77**, 523–531.
- Gonzalez A, Martin I, Ayerbe L (1999) Barley yield in water-stress conditions. The influence of precocity, osmotic adjustment and stomatal conductance. *Field Crops Research* **62**, 23–34. doi: 10.1016/S0378-4290(99)00002-7
- Holmes MG, Keiller DR (2002) Effects of pubescence and waxes on the reflectance of leaves in the ultraviolet and photosynthetic wavebands: a comparison of a range of species. *Plant, Cell and Environment* **25**, 85–93. doi: 10.1046/j.1365-3040.2002.00779.x
- Hossain ABS, Sears RG, Cox TS, Paulsen GM (1990) Desiccation tolerance and its relationship to assimilate partitioning in winter wheat. *Crop Science* **30**, 622–627.
- Johnson RC, Nguyen HT, Croy LI (1984) Osmotic adjustment and solute accumulation in two wheat genotypes differing in drought resistance. *Crop Science* **24**, 957–962.
- Karyudi, Fletcher RJ (2003) Osmoregulation in birdseed millet under conditions of water stress II. Variation in F3 lines of *Setaria italica* and its relationship to plant morphology and yield. *Euphytica* **132**, 191–197. doi: 10.1023/A:1024620413781
- Khanna-Chopra R, Sinha SK (1988) Enhancement of drought induced senescence by the reproductive sink in fertile lines of wheat and sorghum. *Annals of Botany* **61**, 649–653.
- Kobata T, Okuno T, Yamamoto T (1996) Contributions of capacity for soil water extraction and water use efficiency to maintenance of dry matter production in rice subjected to drought. *Nihon Sakumotsu Gakkai Kiji* **65**, 652–662.
- Levitt J (1972) 'Responses of plants to environmental stresses.' (Academic Press: New York)
- Lilley JM, Ludlow MM, McCouch SR, O'Toole JC (1996) Locating QTL for osmotic adjustment and dehydration tolerance in rice. *Journal of Experimental Botany* **47**, 1427–1436.
- Lopezcastaneda C, Richards RA (1994) Variation in temperate cereals in rainfed environments. 3. Water use and water-use efficiency. *Field Crops Research* **39**, 85–98. doi: 10.1016/0378-4290(94)90011-6
- Ma BL, Dwyer LM (1998) Nitrogen uptake and use of two contrasting maize hybrids differing in leaf senescence. *Plant and Soil* **199**, 283–291. doi: 10.1023/A:1004397219723
- Martin B, Tauer CG, Lin RK (1999) Carbon isotope discrimination as a tool to improve water-use efficiency in tomato. *Crop Science* **39**, 1775–1783.
- Mitchell JH, Siamhan D, Wamala MH, Risimeri JB, Chinyamakobvu E, Henderson SA, Fukai S (1998) The use of seedling leaf death score for evaluation of drought resistance of rice. *Field Crops Research* **55**, 129–139. doi: 10.1016/S0378-4290(97)00074-9
- Moinuddin, Khanna-Chopra Renu (2004) Osmotic adjustment in chickpea in relation to seed yield and yield parameters. *Crop Science* **44**, 449–455.
- Morgan JM (2000) Increases in grain yield of wheat by breeding for an osmoregulation gene: relationship to water supply and evaporative demand. *Australian Journal of Agricultural Research* **51**, 971–978. doi: 10.1071/AR00062
- Morgan JM, Condon AG (1986) Water use, grain yield and osmoregulation in wheat. *Australian Journal of Plant Physiology* **13**, 523–532.
- Morgan JM, Hare RA, Fletcher RJ (1986) Genetic variation in osmoregulation in bread and durum wheats and its relationship to grain yield in a range of field environments. *Australian Journal of Agricultural Research* **37**, 449–457. doi: 10.1071/AR9860449
- Morgan JM, Rodriguezmaribona B, Knights EJ (1991) Adaptation to water-deficit in chickpea breeding lines by osmoregulation—relationship to grain yields in the field. *Field Crops Research* **27**, 61–70. doi: 10.1016/0378-4290(91)90022-N
- Munoz P, Voltas J, Araus JL, Igartua E, Romagosa I (1998) Changes over time in the adaptation of barley releases in North-eastern Spain. *Plant Breeding* **117**, 531–535.
- Norwood M, Truesdale MR, Richter A, Scott P (1999) Metabolic changes in leaves and roots during dehydration of the resurrection plant *Craterostigma plantagineum* (Hochst). *South African Journal of Botany* **65**, 421–427.
- Paleg LG, Douglas TJ, Van Daal A, Keech DB (1981) Proline and betaine protect enzymes against heat inactivation. *Australian Journal of Plant Physiology* **8**, 107–114.
- Palta JA, Kobata T, Turner NC, Fillery IR (1994) Remobilization of carbon and nitrogen in wheat as influenced by postanthesis water deficits. *Crop Science* **34**, 118–124.
- Pheloung PC, Siddique KHM (1991) Contribution of stem dry matter to grain yield in wheat cultivars. *Australian Journal of Plant Physiology* **18**, 53–64.
- Plaut Z, Butow BJ, Blumenthal CS, Wrigley CW (2004) Transport of dry matter into developing wheat kernels and its contribution to grain yield under post-anthesis water deficit and elevated temperature. *Field Crops Research* **86**, 185–198. doi: 10.1016/j.fcr.2003.08.005
- Premachandra GS, Hahn DT, Axtell JD, Joly RJ (1994) Epicuticular wax load and water use efficiency in bloomless and sparse bloom mutants of *Sorghum bicolor* L. *Environmental and Experimental Botany* **34**, 293–301. doi: 10.1016/0098-8472(94)90050-7
- Richards RA, Passioura JB (1989) A breeding program to reduce the diameter of the major xylem vessel in the seminal roots of wheat and its effect on grain yield in rain-fed environments. *Australian Journal of Agricultural Research* **40**, 943–950. doi: 10.1071/AR9890943
- Riga P, Vartanian N (1999) Sequential expression of adaptive mechanisms is responsible for drought resistance in tobacco. *Australian Journal of Plant Physiology* **26**, 211–220.
- Rodriguezmaribona B, Tenorio JL, Conde JR, Ayerbe L (1992) Correlation between yield and osmotic adjustment of peas (*Pisum sativum* L.) under drought stress. *Field Crops Research* **29**, 15–22. doi: 10.1016/0378-4290(92)90072-H
- Rontein D, Basset G, Hanson AD (2002) Metabolic engineering of osmoprotectant accumulation in plants. *Metabolic Engineering* **4**, 49–56. doi: 10.1006/mben.2001.0208

- Sanchez AC, Subudhi PK, Rosenow DT, Nguyen HT (2002) Mapping QTLs associated with drought resistance in sorghum (*Sorghum bicolor* L. Moench). *Plant Molecular Biology* **48**, 713–726. doi: 10.1023/A:1014894130270
- Sanchez FJ, Manzanares M, de Andres EF, Tenorio JL, Ayerbe L (2001) Residual transpiration rate, epicuticular wax load and leaf colour of pea plants in drought conditions. Influence on harvest index and canopy temperature. *European Journal of Agronomy* **15**, 57–70. doi: 10.1016/S1161-0301(01)00094-6
- Santamaria JM, Ludlow MM, Fukai S (1990) Contribution of osmotic adjustment to grain yield in *Sorghum bicolor* (L.) Moench under water-limited conditions. 1. Water stress before anthesis. *Australian Journal of Agricultural Research* **41**, 51–65. doi: 10.1071/AR9900051
- Saranga Y, Menz M, Jiang CX, Wright RJ, Yakir D, Paterson AH (2001) Genomic dissection of genotype × environment interactions conferring adaptation of cotton to arid conditions. *Genome Research* **11**, 1988–1995. doi: 10.1101/gr.157201
- Singh DP, Singh P, Kumar A, Sharma HC (1985) Transpirational cooling as a screening technique for drought tolerance in oil seed brassicas. *Annals of Botany* **56**, 815–820.
- Subbarao GV, Chauhan YS, Johansen C (2000) Patterns of osmotic adjustment in pigeonpea—its importance as a mechanism of drought resistance. *European Journal of Agronomy* **12**, 239–249. doi: 10.1016/S1161-0301(00)00050-2
- Tangpremsri T, Fukai S, Fischer KS (1995) Growth and yield of sorghum lines extracted from a population for differences in osmotic adjustment. *Australian Journal of Agricultural Research* **46**, 61–74. doi: 10.1071/AR9950061
- Tangpremsri T, Fukai S, Fischer KS, Henzell RG (1991) Genotypic variation in osmotic adjustment in grain sorghum. 2. Relation with some growth attributes. *Australian Journal of Agricultural Research* **42**, 759–767. doi: 10.1071/AR9910759
- Tenkouano A, Miller FR, Frederiksen RA, Rosenow DT (1993) Genetics of nonsenescence and charcoal rot resistance in sorghum. *Theoretical and Applied Genetics* **85**, 644–648. doi: 10.1007/BF00220925
- Teulat B, Rekika D, Nachit MM, Monneveux P (1997) Comparative osmotic adjustments in barley and tetraploid wheats. *Plant Breeding* **116**, 519–523.
- Thomas H, Howarth CJ (2000) Five ways to stay green. *Journal of Experimental Botany* **51**, 329–337. doi: 10.1093/jexbot/51.suppl.1.329
- Tolk JA, Howell TA (2003) Water use efficiencies of grain sorghum grown in three USA southern Great Plains soils. *Agricultural Water Management* **59**, 97–111. doi: 10.1016/S0378-3774(02)00157-9
- Tuinstra MR, Ejeta G, Goldsbrough P (1998) Evaluation of near-isogenic sorghum lines contrasting for QTL markers associated with drought tolerance. *Crop Science* **38**, 835–842.
- Watanabe N, Naruse J, Austin RB, Morgan CL (1995) Variation in thylakoid proteins and photosynthesis in Syrian landraces of barley. *Euphytica* **82**, 213–220. doi: 10.1007/BF00029563
- Westgate ME, Passioura JB, Munns R (1996) Water status and abscisic acid content of floral organs in drought-stressed wheat. *Australian Journal of Plant Physiology* **23**, 763–772.
- Wright GC, Smith RCG (1983) Differences between two sorghum genotypes in adaptation to drought stress. II. Root water uptake and water use. *Australian Journal of Agricultural Research* **34**, 627–636. doi: 10.1071/AR9830627
- Wright PR, Morgan JM, Jessop RS (1997) Turgor maintenance by osmoregulation in *Brassica napus* and *B. juncea* under field conditions. *Annals of Botany* **80**, 313–319. doi: 10.1006/anbo.1997.0444
- Yang JC, Zhang JH, Liu LJ, Wang ZQ, Zhu QS (2002) Carbon remobilization and grain filling in Japonica/Indica hybrid rice subjected to postanthesis water deficits. *Agronomy Journal* **94**, 102–109.
- Yang JC, Zhang JH, Wang ZQ, Zhu QS, Wang W (2001a) Remobilization of carbon reserves in response to water deficit during grain filling of rice. *Field Crops Research* **71**, 47–55. doi: 10.1016/S0378-4290(01)00147-2
- Yang JC, Zhang JH, Wang ZQ, Zhu QS, Wang W (2001b) Hormonal changes in the grains of rice subjected to water stress during grain filling. *Plant Physiology* **127**, 315–323. doi: 10.1104/pp.127.1.315
- Zhang JW, Feng Z, Cregg BM, Schumann CM (1997) Carbon isotopic composition, gas exchange, and growth of three populations of ponderosa pine differing in drought tolerance. *Tree Physiology* **17**, 461–466.

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