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Physiological traits used in the breeding of new cultivars for water-scarce environments

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Abstract

A physiological understanding of plants' responses to drought has often been sought on the pretext that this understanding will assist plant breeders develop higher yielding varieties for water-scarce environments. However, despite an extensive literature on plants' response to drought there are few documented examples where a physiological understanding of drought has identified traits that limit yield under drought and where these have been used in successful crop improvement programs to enhance crop yields. This paper selects seven examples where a physiological understanding has resulted in more precise targeting of genetic variation and has resulted in higher yielding or more productive germplasm or varieties. The underlying features of these successes are then examined to identify the elements of success that may be used to further enhance yield improvement in dry environments. The conclusions are that all of these traits directly or indirectly transfer their effects to yield over long time scales by increasing either water-use (amount and pattern), water-use efficiency or partitioning of more biomass to grain.
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1. Introduction

Conventional breeding of grain crops continues to deliver improved varieties to farmers with little evidence of a levelling in yield (Brancourt-Hulmel et al., 2003). In general, these

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genetic increases in yield go hand in hand with improved management practices and the relative contribution of management and breeding is usually about equal. In some countries, such as Australia, where grain is sold to discerning international markets, there is evidence of a slower rate of genetic progress in yield. This may be due to increased emphasis on grain quality improvement which has restricted improvements in grain yield. On the other hand, it may be due to the large genotype × environment interactions for yield arising from fluctuating seasonal variation in rainfall. Most of the genetic increases in yield around the world have come from breeders playing 'the numbers game'. In general, breeders rely on effective discriminating environments for diseases and broad scale yield and quality testing to select desirable genotypes. In most breeding programs, there is almost no direct selection for physiological traits, apart from flowering time and plant height. In early generations, breeders rely on their experienced 'eye' to select for what are considered to be appropriate plant types and in later generations rely on yield testing. The most recent advances in genetic progress are probably due to improvements in mechanisation and statistical analysis which have resulted in greater numbers of lines to evaluate and a reduction in errors when discriminating between genotypes. The use of molecular markers is beginning to play an important role in breeding programs for yield maintenance. They are primarily being used to select for resistance to diseases which are difficult to screen, such as nematodes and viruses.

Considering that any improvement in grain yield must be a result of an underlying physiological change it is surprising that direct selection for a physiological trait has not contributed more to yield progress in our grain crops. Physiological changes are interpreted here in the broadest sense as any change to the growth, development, morphology, anatomy or physiology of a crop. Nevertheless, physiological changes, such as flowering time and plant height have been important for yield progress and breeders regularly select for desirable expression of these traits to maintain adaptation and optimal yield. Flowering time has been particularly important for yield improvement in water-limited environments, such as Australia (Siddique et al., 1990; Richards, 1991). In these environments, flowering must not only be early enough to avoid the detrimental effects of declining soil moisture and increasing temperatures, but late enough to avoid frost. Selection for an optimal plant height has been important, particularly in temperate crops to avoid lodging and to maximise harvest index (HI) in favourable environments. HI is the ratio of grain weight to total above-ground weight, and genes for reduced height have contributed to higher yields as they have increased the allocation of assimilates to grain and the reproductive organs rather than to the stem (Richards, 1992).

Other physiological traits increasing crop production in water-scarce environments are more elusive. To be useful in breeding, they must be relatively easy and inexpensive to measure, they should be highly heritable, not result in penalties when conditions are favourable, nor be associated with negative pleiotropic effects on other important agronomic or marketable attributes. Despite substantial physiological research into understanding the response of plants to drought, and genetic variation in these responses, there are few examples where this research has led to improved varieties. There are several reasons for this and I suggest the most important are as follows. Firstly, considerable effort

in the past, and to some extent now, has been directed towards traits that contribute to plant survival in dry conditions. However, any advantages that these traits impart are unlikely to be realised by many farmers as crop yields will be so low that they will be uneconomic and of little benefit to farmers. Secondly, the focus of the research has often been on isolated plants and not on the community of plants that form a crop. Thirdly, physiological traits for water-limited environments are unlikely to be universal and some will be important in one region but detrimental in another. Often there is not the appreciation that there are different types of drought, and traits that may be important when the crop is growing almost exclusively on water stored in the soil are likely to be different from when the crop is solely reliant on current rainfall.

Given that direct selection for yield in dry environments is inefficient due to large seasonal variation in weather and generally a large genotype × environment interaction, resulting in low heritability for yield, it would seem that selection for an underlying physiological trait that limits yield could be effective and contribute substantially to yield improvements. Reasons why a physiological approach to yield improvement may contribute to enhanced yields have been outlined before (Richards et al., 2002). In summary, a physiological approach may:

  i. increase genetic variability in traits for further yield progress,
 ii. result in faster response to selection as physiological traits may have a higher heritability than yield,
iii. enable out-of-season selection, i.e. more generations per year,
 iv. be more cost effective in comparison to yield evaluation,
  v. be more amenable to marker-assisted selection,
 vi. lead to pyramiding multiple yield-enhancing traits.

We should not underestimate the difficulties involved in developing new cultivars for water-scarce environments. These environments are highly variable in the timing and amount of rainfall they receive each season. Some crops may experience an end-of-season drought whereas other droughts may occur at any time of the growing season. Water-scarce environments also vary from region to region. For example, some crops rely entirely on stored soil moisture, others on current rainfall alone, and others with a combination of stored soil water and current rainfall. Many factors contribute to high yield and traits that are important for yield potential must be incorporated into new cultivars as well as traits that have a specific advantage under drought to cope with the fluctuating seasonal conditions and to ensure there is little or no penalty when seasonal conditions are favourable. Water-scarce environments are often non-uniform and may vary for soil constraints, such as mineral toxicities, nutrient deficiencies and biotic constraints, such as nematodes. All combine to limit yield progress.

In this paper, I have selected the most successful examples where a physiological understanding of water-limited yield has resulted in a more targeted selection program to increase yield in dry environments. The examples come from wheat, sunflower, soybean, maize and sorghum. In the discussion following the examples, I try to identify common features of the successes that may assist in making further progress to crop yields in water-scarce environments.

2. Extended crop duration in wheat

Temperate crops in Australia are sown in late autumn/early winter (May/June) and harvested in late spring/early summer (November/December). This is not dissimilar to regions in other countries where winter temperatures are not extreme. Varieties sown are usually referred to as spring varieties and are not very responsive to vernalisation or photoperiod. Over recent years, mainly as a result of the recognition of the grazing value of cereal forage (MacIndoe, 1937; Davidson et al., 1990), but also the potential for higher grain yield (Anderson et al., 1996; Penrose et al., 1998) and water-use efficiency (Gomez-Macpherson and Richards, 1995), a deliberate aim has been to breed for an extended duration of the vegetative period. This more effectively matches crop growth with rainfall. This is possible where summer/autumn rainfall is common and it often relies on the inherent drought resistance of cereals during their early vegetative growth. The introduction of vernalisation or photoperiod-responsive genes into wheat germplasm is a simple and effective way to achieve an extended vegetative period and numerous wheat varieties are now available to farmers, particularly in eastern Australia, where some autumn rainfall is common. Some of these varieties have a very flexible sowing window and can be sown from late summer to early autumn to maximise forage value for grazing, through to late autumn. Varieties sown early have a dual purpose and are used for both forage and grain, whereas if sown late the grain is of economic value only.

The advantages of extending crop duration are many. It provides an option for growers to capitalise on price differentials between livestock and grain. In addition, extended crop duration capitalises on a higher intrinsic water-use efficiency as more growth occurs during winter when the exchange of CO_2 for water is highest (high transpiration efficiency). Furthermore, less water is lost by direct evaporation from the soil surface, early growth is fast because soil temperatures are warm, a longer vegetative duration also extends the duration of root growth allowing utilisation of water and nutrients deep in the soil profile. Nutrient-use efficiency is also greater with extended crop duration (Batten and Khan, 1987). A spectacular example of the advantages of extending the duration of crops in dry temperate environments is in chickpea where sowing in autumn rather than the normal spring period doubled yields (Keatinge and Cooper, 1983). A range of wheat cultivars is now available for sowing ranging from those with several vernalisation and photoperiod genes to those with only a brief extension of the vegetative period. Grain quality characteristics of these varieties vary from lower value feed grains to the highest value grains on the international markets.

3. Increased axial resistance in wheat

Most cereals have a dual root system composed of seminal roots that develop from the seed and nodal roots that develop later from nodes above the seed. In wheat, there are typically three seminal axes that grow from each seed. As the seminal roots develop well before the nodal roots they grow deepest into the subsoil. When it is dry, crops are largely reliant on subsoil water and this water must pass through the single xylem vessel in each axis. If plants use this water too fast during the vegetative period then little will be available
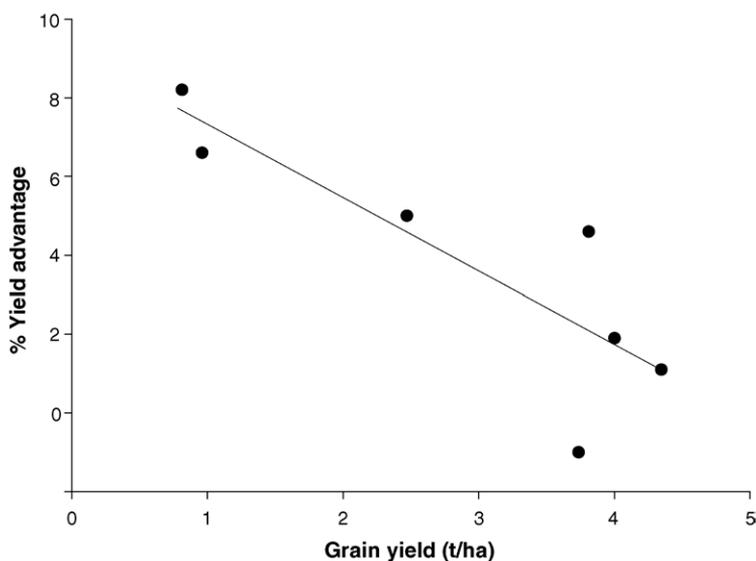
Fig. 1. Yield advantage of lines selected for narrow xylem vessels. Values in each environment are the yield differences between lines selected for narrow xylem vessels and unselected controls averaged over two genetic backgrounds (cultivars Kite and Cook). Data adapted from Richards and Passioura (1989).

for grain filling. Use of subsoil water is slowed if there is a large hydraulic resistance in the seminal roots. Passioura (1972) proposed that breeding for a narrow xylem vessel in the seminal roots of wheat should increase the hydraulic resistance and force plants to use the subsoil water more slowly. An attractive feature of this proposal was that if the soil is wet then there would be no growth penalty as the nodal root system, which is very extensive in the top soil, can adequately supply the crop with water. A breeding program in wheat was initiated after developing a screening protocol for xylem vessel diameter in the seminal roots and after identifying suitable genetic variation. An understanding of the genetic control and of the environmental factors associated with xylem vessel diameter was also investigated to ensure that a breeding program would be successful (Richards and Passioura, 1981a, 1981b). The breeding program reduced the xylem vessel diameter of two Australian commercial wheat varieties from 65 to less than 55 μm. In field trials in eastern Australia narrow vessel selections, averaged over both genetic backgrounds, yielded 8% more than the unselected controls in the driest environments, whereas yield differences in the wetter environments were largely not significant (Richards and Passioura, 1989), and see Fig. 1.

4. Anthesis-silking interval (ASI) in maize

Grain number is a major determinant of yield in maize as well as other crops and factors that contribute to improved grain set, especially under drought, are of great importance to increase crop production. In this crop, it was found that great improvements in yield could

be achieved by selection under managed drought environments, within existing elite germplasm, i.e. genetic variation existed that had not been exploited by previous breeding activities for yield potential and disease tolerance (Fischer et al., 1989). In maize, drought that occurs from the mid to late vegetative stage onwards does not affect the timing of tassel anthesis, but delays the process of ear silking. In segregating genotypes under drought (for the same anthesis date), a lengthening of the ASI period is an indicator of poor tolerance to drought, is negatively correlated with grain yield and has a higher heritability than yield (Bolaños and Edmeades, 1996; Chapman and Edmeades, 1999). The reason for the silk delay is that the drought-susceptible genotypes allocate less assimilate to ear growth when the ears are quite small. Even if these silks are pollinated separately, many of the grains will abort, resulting in a low grain number per ear. Recurrent selection for low ASI, high fertile ear number per plant, small tassels and delayed senescence resulted in substantial increases in partitioning to early ear growth and successful grain set. Poor timing of pollen shed itself can be an additional problem (Du Plessis and Dijkhuis, 1967), though in fields of maize, pollen supply is quite high for a long period due to slight variation in plant-to-plant timing of pollen shed. Substantial genetic variation has been found in tropical maize populations and recurrent selection for the ASI has been applied in these populations in Mexico, together with selection for yield and stay-green whilst maintaining gains for yield potential (Edmeades et al., 1999). Significant gains in yield (>10% per S_1 selection cycle in 2 t/ha drought environments) were achieved by recurrent selection when selected populations were grown under drought as well as under low soil nitrogen (Bruce et al., 2002). This germplasm has also performed well under drought in southern and eastern Africa (Banziger et al., 2005) and across most drought prone locations in both tropical and temperate sites (Bruce et al., 2002). More recently, it has been shown that this drought tolerance is largely additive in nature, and so can be passed through to hybrid maize by developing drought tolerance on both sides of a pedigree (Betrán et al., 2003).

5. Nitrogen fixation in soybean

Nitrogen fixation in legumes is very sensitive to soil drying. In dry soils, this results in a reduced supply of N to the plant and lower yields (Sinclair et al., 1987; Purcell and King, 1996). There is substantial genetic variation in N_2 fixation sensitivity to soil drying in soybean (Sall and Sinclair, 1991) and a method to select for sensitivity has been developed. Soil drying results in the accumulation of ureides in the leaves of soybean (Sinclair and Serraj, 1995) and this is thought to inhibit further nodule activity. These products of nitrogen fixation are associated with sensitivity to water deficit. It has been proposed that screening for petiole ureide levels would be an effective initial screen to identify soybean lines whose nitrogen fixation is more tolerant of soil drying (Sinclair et al., 2000). Little is known about the genetic control of N_2 fixation sensitivity. However, the variety Jackson, which is more tolerant of N_2 fixation in drying soils, has been used as a parent in a breeding program and high yielding lines, in the absence of irrigation, have been identified in multi-site trialling (Sinclair et al., 2004). These lines are now being used in breeding programs in the USA for improved tolerance to drought.

6. Transpiration efficiency in wheat

Where water is scarce any improvement in the efficiency of photosynthesis per unit of transpiration, that is, transpiration efficiency (TE), should improve crop yields provided the efficiency of conversion of biomass to grain (harvest index) does not decrease. Farquhar et al. (1982) proposed that the isotopic composition of plant carbon should reflect differences in transpiration efficiency in C_3 species. There are several isotopic forms of carbon that occur naturally in the biosphere. ^{12}C is the most common form and accounts for 98.9% and ^{13}C accounts for almost all of the rest. Plants actively discriminate against ^{13}C during photosynthesis. This discrimination can occur firstly during the diffusion of CO_2 from the air into the sub-stomatal cavities and secondly during the biochemical fixation of CO_2 into simple sugars. The result is that plants have less ^{13}C than the atmosphere. Farquhar and Richards (1984) demonstrated that the degree of discrimination is related to TE in wheat and that there was a genetic component in the extent of this discrimination. Carbon isotope discrimination is negatively correlated with TE. The relationship between carbon isotope discrimination and TE was confirmed in many C_3 crops (see Table 1 in Richards and Condon, 1993). However, it has also been shown that this relationship does not always translate to improved grain yields and it depends on soil water availability (Condon et al., 1987, 2002).

Based on an understanding of how carbon isotope discrimination varies with growth conditions, season and organ selected (Condon et al., 1992), a breeding program was initiated at CSIRO in Canberra, Australia, to backcross low carbon isotope discrimination (high TE) from the old Australian wheat cultivar Quarrion, into the variety Hartog. Hartog was chosen for its intermediate to high carbon isotope discrimination value, suggesting
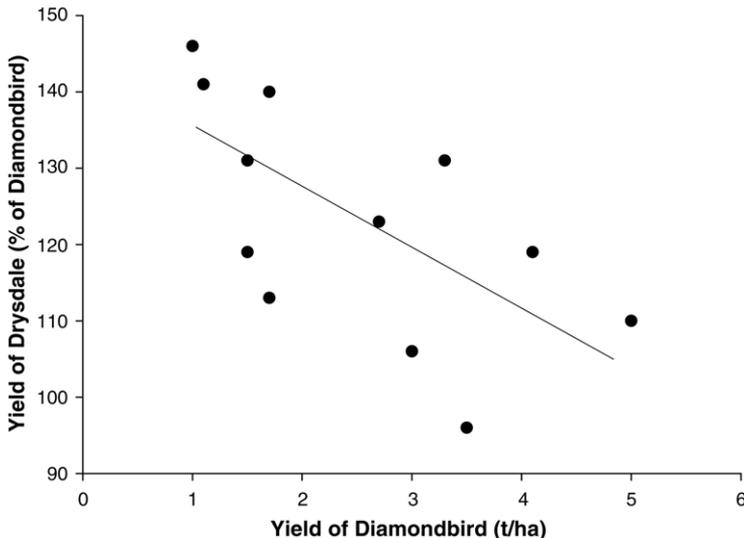

Fig. 2. Yield advantage of high TE Drysdale wheat compared with low TE Diamondbird in 12 environments in southern New South Wales in 2003. Diamondbird is the current recommended wheat variety in the region where trials were sown. Data from Agritech Services.

lowish transpiration efficiency, and for its robust adaptation and good disease resistance and excellent grain quality. Two backcrosses were made to Hartog following selection for carbon isotope discrimination in the field. Limited backcrossing was used so as to retain variation in other traits and to allow selection for agronomic, disease and grain quality characteristics in different target environments in Australia.

A set of $BC_2F_{4:6}$ lines was tested in multiple environments for yield, disease and grain quality and the variety Drysdale was released for southern New South Wales (NSW), Australia, in 2002 and Rees for the northern Australian cropping region in 2003. Studies have demonstrated a yield advantage between 2 and 15% for lines with low carbon isotope discrimination at yield levels from 5 to 1 t ha^{-1} (Rebetzke et al., 2002) when compared with high discrimination sister lines. Trials in southern NSW in 2003 demonstrated significant yield benefits of Drysdale compared with Diamondbird, the current recommended variety for this region (Fig. 2). Averaged over all 12 trial sites, the yield of Drysdale was 23% greater than Diamondbird.

Significant genetic variation in carbon isotope discrimination is also evident in sunflower and like wheat this has been strongly associated with transpiration efficiency (Lambrides et al., 2004). Parents chosen for their low carbon isotope discrimination have been used to produce hybrids. These hybrids were the highest yielding lines in droughted environments (Lambrides, pers. comm.) and are now being incorporated into commercial breeding programs in Australia.

7. Osmotic adjustment in wheat

As a soil dries or evapotranspiration increases, leaf water potential declines. To minimise water loss from cells and to maintain cellular function, cells accumulate solutes. This process is called osmotic adjustment or osmoregulation. It is an active process where solutes increase in plant cells so as to maintain leaf hydration and turgidity. There has been some conjecture as to whether osmoregulation is important in crops as its benefit is most evident at yield levels that some consider uneconomic (Serraj and Sinclair, 2002). However, in the best studied case, Morgan (1991, 2000) identified an osmoregulation (*or*) gene in wheat which was associated with increased grain yield particularly under conditions of high evaporative demand. The recessive *or* gene, associated with potassium accumulation (Morgan, 1999a), is common in Australian wheat breeding programs and trials conducted using backcross lines with and without the *or* gene and more random fixed lines with and without the *or* gene shows that higher yields are associated with the gene in the most stressed environments (Fig. 3).

The *or* gene can be selected using a pollen grain technique (Morgan, 1999a) or through the use of linked molecular markers (Morgan and Tan, 1996). A negative feature of the *or* gene is that it is linked to an endosperm peroxidase gene which reduces dough strength and is likely to limit its use in breeding high grain quality wheats (Morgan, 1999b). This may also explain why the *or* gene has not been found extensively in wheats grown in Australia where wheat-growing regions are typically dry and experience very high evaporative demand during grain filling and where a very significant emphasis is placed on producing grain of high quality to compete in international markets. The wheat variety, Mulgara,
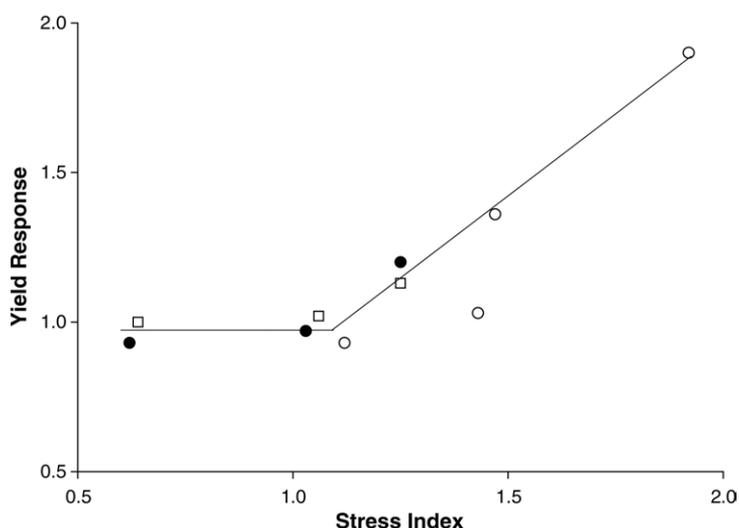
Fig. 3. Relationship between yield response attributed to osmoregulation and a stress index. Data from field experiments conducted using backcross lines (square) and random fixed lines in droughted (open circle) and irrigated (closed circles) trials. The stress index is the ratio of evaporative demand to soil water supply over the active crop growth period. Adapted from Morgan (2000). Yield response is the ratio of the yield of lines with high osmotic adjustment to yield of lines with low osmotic adjustment.

which is a backcross derivative of Sunco and was selected for osmoregulation, was released in Australia in 2000.

8. Stay-green in sorghum

Post-anthesis drought is a common feature of sorghum crops. In Australia, sorghum crops gradually deplete soil water, resulting in leaf senescence and low yields. Stay-green lines have been identified which retain more green leaves under terminal drought compared with lines and hybrids without the stay-green trait and the stay-green lines have a higher yield of grain and biomass (Rosenow et al., 1983; Borrell et al., 2000). Several different sources of genetic variation for stay-green have been found in sorghum native to Africa. In these lines, and hybrids derived from them, more nitrogen is allocated to leaves from early growth stages resulting in a higher specific leaf nitrogen (SLN) (Borrell and Hammer, 2000). It is proposed that the higher SLN results in a cascade of advantages. After anthesis, it is proposed that the higher SLN delays leaf senescence and allows further uptake of soil water and nitrogen (Borrell and Hammer, 2000). Leaf senescence is delayed and this enhances both radiation use efficiency and transpiration efficiency resulting in higher yields. In a rain-out shelter experiment a stay-green hybrid retained some photosynthesis for an additional 15 days longer than a senescent hybrid counterpart (Borrell et al., 2001).

Different types of stay-green have been recognised (Thomas and Howarth, 2000). Some are cosmetic and are not photosynthetically active, whereas others are associated with greater biomass accumulation. The genetic control of stay-green in sorghum is not well

understood. However, up to 11 genomic regions have been reported as being important (Tao et al., 2000; Xu et al., 2000).

9. Discussion

9.1. Do these examples share common features?

A cursory glance at each of the examples would suggest that they share few features and that enhanced yields in dry environments can be achieved through very different mechanisms. In part, this reflects the different timing and intensity of drought and the different biology of the species. However, some common underlying characteristics do emerge when examining the examples more broadly. One stand-out feature is that, although all traits have contributed to increased grain yield in dry environments, the measurement of plant–water relations, or a direct relationship with it, does not feature prominently. The exception is osmotic adjustment. Another is that in general traits are of complex inheritance and probably controlled by a number of genes. Again, the exception here may be osmoregulation in wheat, although even though a single gene has been identified, it does not account for most of the genetic variation observed (Morgan, pers. comm.). Where attempts have been made to understand the underlying genetics of each of the traits, quantitative methods using either linked molecular markers (QTLs) or statistics have been used to understand their genetic control. Extended crop duration in wheat is the most extensively studied trait described here and numerous genes responsible for response to vernalisation, photoperiod and intrinsic development have been found to be important. Nevertheless, a single major gene, such as that for vernalisation response, can be very influential. A third feature is that the timing of drought is important for some traits to be effective. This infers that the traits described are unlikely to be important under all water-scarce conditions. Thus, early to mid-season drought is essential for the ASI and N_2 fixation traits to increase yield, whereas $^{13}C/^{12}C$ discrimination, stay-green in sorghum and root axial resistance in wheat require a terminal drought to realise a yield benefit. These latter traits are unlikely to impact on crop performance if a pre-anthesis drought were relieved. It is significant that none of the traits has a depressing effect on yield under more favourable conditions, although this may be expected with some of them. Carbon isotope discrimination has been positively associated with biomass and grain yield of wheat under favourable conditions (e.g. Condon et al., 1987; Fischer et al., 1998). However, even at yield levels up to about 6 t ha^{-1} this was not evident in Rebetzke et al. (2002) or in Fig. 2. It is also notable that adverse pleiotropic effects have not been detected. The only trait found to have a negative association is osmotic adjustment, where the high lines were associated with lower dough strength which may be important for premium flour markets (Morgan, 1999b).

A common feature to these traits is also the time scale in which they operate. Passioura (2005) has highlighted the significance of traits that operate over long time scales and their likely influence on yield. In the examples given here of successful traits leading to improved cultivars or germplasm, all traits are effective over the life of the crop, except ASI which is effective during the vegetative and early reproductive period, and possibly

osmoregulation which is important during the very sensitive stages of fertilization and early grain formation.

One of the surprises in this analysis was that nitrogen acquisition and utilisation figured prominently to increase water-limited yields in soybean and sorghum. In both cases, this was associated with maximising nitrogen uptake early in crop development so as to drive and sustain further growth. The importance of nitrogen has also been evident in raising yields in water-limited environments by management practices in Australia (Angus, 2001); once some of the soil-borne disease risks were reduced by rotation practices, farmers were able to aim for, and achieve, higher yields through greater water-use.

It is of interest to analyse each of the examples in terms of Passioura (1977) who stated that water-limited grain yield is a function of water transpired, transpiration efficiency (biomass/water transpired) and harvest index. This concept has changed our approach to improving crop yields in water-limited environments by relating crop yield to resource limitations. It has diverted our thinking away from mechanisms associated with drought resistance and survival to longer-term processes associated with crop production. In the soybean and sorghum examples, a greater total water-use is likely to be the reason for enhanced yields. The maintenance of N_2 fixation in soybean when the soil is drying and higher N concentration in early formed sorghum leaves associated with stay-green were associated with an enhanced biomass after flowering. The greater water-use may be attributed to further root growth, leading to an extended crop duration and thereby more growth during grain filling. The additional nitrogen would be available to maintain photosynthetic processes longer, grow deeper roots and divert some N to grain growth and N storage (Borrell et al., 2001). It is likely that harvest index is also improved in both sorghum and soybean as much of the additional growth is of grains. Greater yield as a result of lower carbon isotope discrimination is likely to be directly related to transpiration efficiency. The association between transpiration efficiency and $^{13}C/^{12}C$ discrimination has been confirmed in numerous pot trials in a broad range of crop species (e.g. see Richards and Condon, 1993) and in field studies (Condon et al., 1993). Differences in transpiration efficiency are more difficult to demonstrate in the field as both soil water-use and transpiration are difficult to measure accurately. Differences in transpiration efficiency due to selection for low $^{13}C/^{12}C$ are implicit in the release of the wheat cultivars Drysdale and Rees as well as the greater yields of lines selected for low $^{13}C/^{12}C$ discrimination (Rebetzke et al., 2002). There is some evidence in wheat that low $^{13}C/^{12}C$ discrimination and an associated component, low stomatal conductance, may slow water-use so that HI is also increased (Rebetzke et al., 2002). Yield advantages attributed to osmoregulation (Morgan and Condon, 1986), ASI (Bolaños and Edmeades, 1993) and seminal root axial resistance (Richards and Passioura, 1989) are largely associated with an improved HI. In each case, grain set is protected either because of better water relations (osmoregulation) drought avoidance (root axial resistance), or an enhanced opportunity for successful fertilization (ASI). An extended crop duration improves water-use efficiency and total water-use to increase total biomass. However, harvest index is generally lower (Gomez-Macpherson and Richards, 1995). Further research is required to determine whether harvest index of crops with an extended vegetative period can be improved either by nitrogen management or breeding for reduced height or reduced tillering so as to limit growth of non-reproductive organs.

In dry wheat-growing regions of Australia, harvest index is the main component of Passioura's (1977) identity that has improved yield as a result of conventional wheat breeding. The two factors that feature most prominently to achieve this yield improvement are earlier flowering in spring wheats (Siddique et al., 1990; Richards, 1991) and plant height, following the introduction of the major semidwarfing genes (*Rht-B1b and Rht-D1b*). Earlier flowering has been important in the drier areas as it provides a better balance between pre-anthesis and post-anthesis water-use so that conditions during grain filling are more favourable. This may have come about with the acceptance of greater frost risk. The semidwarfing genes have conferred benefits in both favourable and unfavourable environments. The principal reason for their advantage is that more assimilate is available for growing ears (as less is used for stem growth) and hence leads to greater floret fertility and more grain set (Fischer and Stockman, 1986; Richards, 1992).

9.2. Future improvements

The ideas developed by Passioura (1977) in relation to physiological determinants of grain yield in water-scarce environments have been readily adopted in the scientific literature and are now contributing to improved varieties for farmers. Other physiological traits in wheat that are in advanced stages of validation or breeding for water-limited environments in Australia are new dwarfing genes that improve crop establishment and early growth, enhanced shoot and root vigour, reduced tillering and greater stem carbohydrate storage (Richards et al., 2002). For each of these traits there is compelling evidence that they would change the physiology of wheat growth and result in improved yields (Richards et al., 2002). Each of these traits has similar features to those discussed earlier. That is, they are not directly related to plant–water relations, they are often quantitative traits, and they influence growth and development over a long time scale.

Below-ground characteristics have been neglected in crop improvement programs due to difficulties in their measurement and a lack of understanding of the rhizosphere. An exception to this in Australia is the genes in wheat contributing to tolerance to acid soils (Aniol, 1990) and to toxic levels of boron (Paull et al., 1992) or genes conferring tolerance/resistance to nematodes (Ogbonnaya et al., 2001). These genes are now common in breeding populations and should contribute to greater water-use where these soil factors are problematic and hence greater yields in both favourable and unfavourable environments. For environments where water remains in the profile, but is not used by crops, little is known about which root traits should be targeted in a breeding program. However, it is known that if deep water is captured it is used with exceptional efficiency and can greatly boost grain yield (Angus and van Herwaarden, 2001). Whilst research into important variation in root growth will be a major challenge for physiologists and breeders, we should not neglect simpler opportunities to extract deep soil water. The analysis of physiological traits here suggests that an extended vegetative period and greater N capture during the vegetative period may be important to maximise water-use.

This review has identified several success stories where a physiological understanding of crop growth and development has resulted in improved cultivars for farmers. The examples are rare. Each of them are characterised by a long period of sustained research involving crop physiologists and breeders that are connected to farming systems and

research conducted in the field. Further advances are likely to be assisted by molecular markers to select genes or chromosomal regions more precisely in segregating breeding populations.

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