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Promising eco-physiological traits for genetic improvement of cereal yields in Mediterranean environments

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Summary

Breeding for improved productivity has been tremendously successful in the last half-century, but needs to be even more efficient in the future. Hope based on contributions from molecular biology for improved yield potential seems to depend upon an improved knowledge of yield physiology. This knowledge may assist breeding either directly, recommending selection criteria, or indirectly identifying simpler traits that could be reliably mapped and selected for through marker-assisted selection. Physiological traits associated with improved performance under water-limited conditions, include phenology (that allows the crop to escape stresses) and those associated with improved water use, water use efficiency and partitioning. Undoubtedly, earliness has been the predominant trait improved for under Mediterranean conditions, and may not be a prospective trait for future breeding. Different traits that may confer the ability to the crop for capturing more water, such as deeper root systems or osmotic adjustment, may be unworkable in terms of their direct use in selection and surrogates would be needed. For instance, canopy temperature depression and discrimination against ^{13}C may be used to assess improved ability to capture water (in these cases yield is positively related to discrimination against ^{13}C in grains). Early vigour, which allows faster ground coverage, also increases the amount of water actually transpired by the canopy by reducing direct evaporation and presents substantial intra-specific variation, and selection for this trait may be successfully carried out either directly or through the use of vegetation indexes. Improved water use efficiency based on transpiration efficiency is largely restricted to conditions where additional water is not available. A constitutively low stomatal conductance or a high stomatal sensitivity may optimise the transpiration efficiency. In this context, discrimination against ^{13}C is also a simple and reliable measure of water use efficiency, and in cases in which no major differences in capturing water is possible discrimination against ^{13}C correlates negatively with yield. Substantial further improvements in partitioning may be limited in most cereals.

Key words: Yield, physiological traits, breeding, Mediterranean, phenology, water use efficiency, wheat, barley

Introduction

Cereal breeding has been extremely successful in the second half of the 20th century, releasing cultivars with a genetic gain in yield of approximately 0.5% year^{-1} (see reviews by Calderini *et al*., 1999 for wheat and Abeledo *et al*., 2002 for barley). Although estimations of breeding contributions to total yield gains (actually observed on-farm) are mostly due to breeding × management interaction (e.g. Evans & Fischer, 1999), in general terms breeding was considered to have been responsible for half of the total gains in yield, as discussed before by Slafer & Andrade (1991) and other sources quoted therein. The other half of the yield gains observed during the last 50 years or so was brought about by management improvements, particularly by increases in N fertilisation (Bell *et al*., 1995; Austin, 1999).

Future breeding needs to be ever more efficient to meet the continuously growing demands of a burgeoning population in a context where, unless we are prepared to pay an enormous cost in terms of environmental degradation, more cropping area seems unlikely to be available. Moreover, the use of agronomic inputs (including water) seems likely to increase at a much slower pace than in the past (and in many areas not at all), while few, if any, opportunities exist for expanding irrigated areas (Cassman, 1999). In addition, and despite the past successes, the rate of increase of food crop production has been noticeably decreasing in recent years (Conway & Toennissen 1999; Slafer & Peltonen-Sainio, 2001).

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This general statement is even reinforced with regard to breeding small grain cereals to improve their productivity in Mediterranean conditions. The expected rate of breeding success is directly related to the environmental background due to the higher heritability of traits in non-limiting environments: that is, the better the environmental conditions where the released cultivars are to be grown the easier it has been to achieve genetic gains in yield (Richards, 1996; Araus *et al*., 2002*b*).

To improve its efficiency, future cereal breeding may exploit physiology and molecular biology to facilitate the identification, characterisation and manipulation of genetic variation to complement the more traditional approaches based on selection for yield *per se* (Sorrells & Wilson, 1997; Slafer *et al*., 1999; Araus *et al*., 2002*b*). In this context, it is relevant to note that in general (with exceptions recognised for targeted environments extremely poor in yield; Ceccarelli & Grando, 1996; Araus *et al*., 2002*b*) improvements in actual yields in Mediterranean conditions (as well as in other, stressful environments) may well depend upon further increases in yield potential, despite the fact that there is a large gap between them. Two facts support this statement: there has been no increase in actual yields obtained by farmers until there was a consistent increase in potential yield of cultivars released by breeders (*c*. by mid-20th century) and trends in actual and potential yields tend to be parallel (see Abeledo *et al*. (2003) for an example in barley; Evans (1993) for examples on soybean and maize and Slafer & Calderini (2005) for examples in wheat, and also see Cassman (1999) for a more general view on the issue). It therefore seems that the contention that selection under favourable conditions usually leads to higher yields in less favourable environments (Richards, 2000; Araus *et al*., 2002*b*) is supported by the empirical evidence. Calderini & Slafer (1999) illustrated this issue showing that modern cultivars have consistently outyielded their older counterparts even in the lowest-yielding conditions in each of the countries analysed, and as pointed out by Richards *et al*. (2001) it may be expected that future genetic progress in favourable environments should continue contributing to yield in less favourable environments.

However, further raising potential yields is not a simple task. Despite breeding having quite successfully achieved this objective in the second half of the 20th century, breeders currently start with a crop that has already undergone an intensive process of selection for increased yields. We believe that further improvements need the integration of new tools/strategies to complement traditional breeding approaches.

Do we Need Physiological Traits?

Promising advancements produced in the last decade or so have occurred through progress in molecular biology. There is little doubt that marker-assisted selection (MAS, selection based on the presence of few genes or quantitative trait loci, QTLs) would increase efficiency in breeding programmes aimed at introgressing particular traits into an adapted genetic background by pyramiding useful genes, which are difficult or expensive to select for directly by phenotypic observation. In addition, selection may be faster and made in early generations. The usefulness of these advancements for simple traits can be acknowledged (i) academically from examples in the literature actually introgressing alien genes, affecting phenotype as predicted in the genome in which it was introgressed, and (ii) empirically by the simple awareness of the number of transgenic crop cultivars commercially used in several agricultural regions of the globe.

As the recent literature offers a wide range of papers reporting on QTLs for yield, we could possibly operate in the same way as for simple traits, with regard to introgressing yield QTLs. In other words, if we do know the QTLs for yield and associated markers we could directly introgress them (for instance by backcrossing and selecting by the presence of the marker associated to the QTL for yield) and eliminating the cumbersome, time-consuming and sometimes difficult phenotyping of physiological traits.

However, application of MAS for complex quantitative traits, such as those related to increased productivity in a particular population of environments, remains challenging (Slafer, 2003). QTLs for complex traits like yield can easily be identified in specific mapping populations, and the identification of QTLs for yield is widespread in the literature. However, expression may be dependent upon the genetic background (Stuber *et al*., 1999); this dependence being one of the reasons to believe that there is an intrinsic complexity in identifying trustworthy QTLs for yield. The approach by Thomas (2003) comparing QTLs for yield in a number of mapping populations serves to illustrate the problem of the strong dependence on the specific mapping population (and QTLs being of no use for other populations such as that of the elite germplasm from where new cultivars would come from). Other major problems with QTLs for yield commonly reported in the literature are that they commonly possess a low resolution; frequently have a small individual effect on yield; and are normally strongly dependent on the G×E interaction (e.g. Kjaer & Jensen, 1996; Romagosa *et al*., 1996; Yin *et al*., 1999).

Consequently, the evidence of reported QTLs for yield to improve performance of a different genetic background to that of the mapping population and also in a wide range of environments (those in which a successful cultivar will be released, including different sites, different managements and different years), has still to be demonstrated. On the other hand, examples of failures have been reported in the literature. For instance, Reyna & Sneller (2001) attempted to evaluate to what degree they might breed for higher yields in their soybean programme by introgressing QTLs for yield, identified in a mapping population, through successive backcrosses. A few years earlier, Orf *et al.* (1999) had identified a number of QTLs for yield in a mapping population in which the soybean cv. Archer contributed the QTLs associated with improved performance in the studies conducted with this mapping population. Reyna & Sneller (2001) decided to build up near-isogenic lines for each QTL for yield identified in Archer; they used four genetic backgrounds for each of the isogenic lines. Later they compared performance of the lines with the "wild" genome with those with the QTL for yield introgressed in that background in field experiments in six different environments. There were no significant interactions between marker genotype and NIL set or between QTL and environment (the effect of the QTL could be averaged across near isogenic lines and environments, Fig. 1). It has been clear from the experience illustrated in Fig. 1 that the value assigned to a QTL for yield in a particular mapping population and set of environments in which these QTLs are identified/quantified may be quite distinct from the value added produced by their introgression in different genetic backgrounds (e.g. that of the elite germplasm of a real breeding programme) and environmental conditions (e.g. those in which the eventually released cultivar has to be grown).

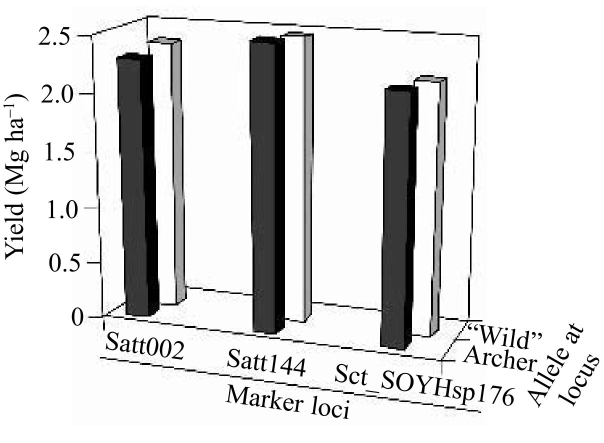

Fig. 1. Yield of soybean near-isogenic lines with the same genetic background (that adapted to the region in which breeding was taking place) but with either the genes corresponding to the adapted germplasm ("wild") or those of the three QTLs for yield (Satt144, Satt002 and Sct_33/SOYHsp176) identified in cv. Archer in a previous study (Orf *et al.*, 1999). Each value is the average of four different NILs and for the six environments in which these NILs were field-trialled (interactions marker genotype × NIL set and QTL × environment were non-significant). Figure was built up with data taken from Reyna & Sneller (2001).

In this context, it seems that the usefulness of the powerful tools provided by the advances in molecular biology to improve complex traits would depend upon prior knowledge about their physiological determinants (see also Araus *et al.*, 2003*a*), and that this improved knowledge may be critical for transforming the idea that biotechnology may be essential to raise yield ceilings (Conway & Toennissen, 1999) from a speculation into a reality (for more details on this issue, see the illustrative review of Sinclair *et al.*, 2004). Then we could either (i) identify such simple traits putatively related to yield, which can be further mapped and transferred from one population to another, or (ii) when a QTL for yield is identified, understand its physiological determinants and the way in which those traits interact with the targeted environments before selecting with MAS for that QTL. In other words, with regard to yield (and other complex traits) molecular biology progress has increased, rather than eliminated, the need to understand better the physiology of yield determination. In addition, this better understanding may help traditional breeding programmes in the identification of appropriate parents and efficient selection of progeny (Austin, 1993; Slafer *et al.*, 1999) either using the traits themselves or identifying cost-effective surrogate traits (e.g. Araus, 1996; Araus *et al.*, 2001). In summary, breeding to improve cereal yields (either by traditional or biotechnological means) could increase its efficiency if based on attributes at the crop level of organization putatively maximising yields (Araus, 1996; Richards, 1996; Slafer & Araus, 1998; Slafer *et al.*, 1999). For this to be realised, knowledge of the crop-physiological attributes determining yield of cereals has to be improved considerably (Araus *et al.*, 2004).

Promising Eco-Physiological Traits

Water deficit is the main environmental constraint limiting cereal yield worldwide, and particularly within the Mediterranean Basin, a problem likely to become even worse in the future. Cereal plants respond to drought through morphological, physiological, and metabolic modifications occurring in all plant organs and therefore traits associated with improved performance under water-limited conditions, or improved survival to extremely low water availability, are diverse. In this paper we will only refer to those associated with improved performance, which are the most useful under field conditions (Passioura, 1996; Slafer & Araus, 1998; Richards, 2000). These traits deal more with the economy of dry matter acquisition and partitioning under water-limited situations than with the mechanisms allowing survival under extremely dry conditions, in which agriculture can be hardly practiced. In addition, these traits must be directly related to crop yield under field conditions rather than focused on levels of organisation much lower than the crop canopy, frequently poorly and inconsistently related to yield in the field (Araus, 1996; Richards, 1996; Slafer *et al.*, 1999; Araus *et al.*, 2001).

Traits putatively related to yield must positively affect water use, water use efficiency (WUE) or biomass partitioning towards reproductive organs (Passioura, 1977, 1996; Richards, 1996, 2000; Araus *et al.*, 2002*b*). Doubtless the single most important attribute of the crop conferring the ability to perform better under stressful conditions is its phenological development (Passioura, 1996, 2002; Richards, 1996; González *et al.*, 1999; Villegas *et al.*, 2000; Araus *et al.*, 2002*b*). Changes in phenological development allow the crop to escape stresses, either actually avoiding stress during the crop cycle or, most frequently, by avoiding the coincidence of the most sensitive phases with the most likely occurrence of the stress. Once developmental pattern is fitted, traits associated with improved water use are relevant when crops do not completely use the water potentially available for growth, while traits related to WUE and partitioning become more important when available water is already depleted. This issue may result in some differences between strategies being suggested (e.g. selecting either for a higher or lower WUE) for regions with Mediterranean climate (Richards *et al.*, 2002; Araus *et al.*, 2003*a*).

Phenology

As stressed above, the single most important attribute determining performance under water stress is that related to the rate of crop development determining the phenology of the genoptype in a particular population of environments. The most largely recognised impact of phenological development on performance under Mediterranean conditions is related to the escape from water stress, due to the benefits of tailoring a developmental pattern that matches the pattern of rainfall. As Mediterranean conditions are characterised by exposing cereal growth to drought developing increasingly throughout the late reproductive and grain-filling phases (Loss & Siddique, 1994), the natural outcome of breeding for adaptation has been the selection for earliness. For example, comparing the outcome of breeding for yield *per se* during the last century or so, in terms of developmental patterns in regions characterised by wheat being grown under stressful environments but with different timings of this stress, illustrates this point. Whereas, in regions with stresses not necessarily occurring late in the season (like in Canada or Argentina) breeding has not tended to consistently change the timing of anthesis (e.g. Hucl & Baker, 1987; Slafer & Andrade, 1989), in Mediterranean regions (like in Western Australia or Spain) time to anthesis has tended to be reduced systematically as new cultivars have been released (e.g. Siddique *et al.*, 1989*a*; Ramdani, 2004). Selection for earliness has two important consequences on the physiology of cereal yields: firstly it increases the likelihood to escape droughts that are expected to be terminal, and secondly it improves the partitioning of the total water used by the crop actually absorbed and transpired after anthesis. There is a curvilinear, hyperbolic relationship between harvest index (and yield) and the amount of post-anthesis transpiration as a percentage of the total amount of water used (Siddique *et al.*, 1990; Sadras & Connor, 1991; Slafer *et al.*, 1994).

Breeding for earliness of flowering is relatively simple, as major genes responsible for sensitivity/insensitivity to photoperiod and vernalisation are well known and relatively easily manipulated, enabling crop duration to flowering to be manipulated (e.g. Hay & Ellis, 1998; Snape, 1996; Slafer & Whitechurch, 2001) (although genes for intrinsic earliness (or earliness *per se*; Slafer, 1996), may allow fine-tuning developmental rates for small changes in phenology exist, they are not as well known (Snape *et al.*, 2001) and may also interact with temperature (Slafer and Rawson, 1995; Appendino and Slafer, 2003) making them impractical for traditional breeding). However, in most Mediterranean regions where cereal breeding has been carried out for decades, selection for earliness has already taken place and there may be only marginal scope for further raising yield due to selecting for even earlier flowering crops (still avoiding frost risks and yield penalty). Thus earliness may not be very relevant as a major prospective trait for future breeding.

Another indirect effect of developmental patterns influencing performance, more recently proposed and consequently less discussed than earliness, relates to the partitioning of a particular crop cycle into different proportions of vegetative and reproductive phases (Fig. 2). As recently hypothesised (e.g. Slafer *et al.*, 2001), extending the duration of stem elongation would raise the number of grains per spike and the harvest index (Miralles *et al.*, 2000; González *et al.*, 2003), without altering the amount of water used by the crop. This may be particularly relevant in cases when the crop actually

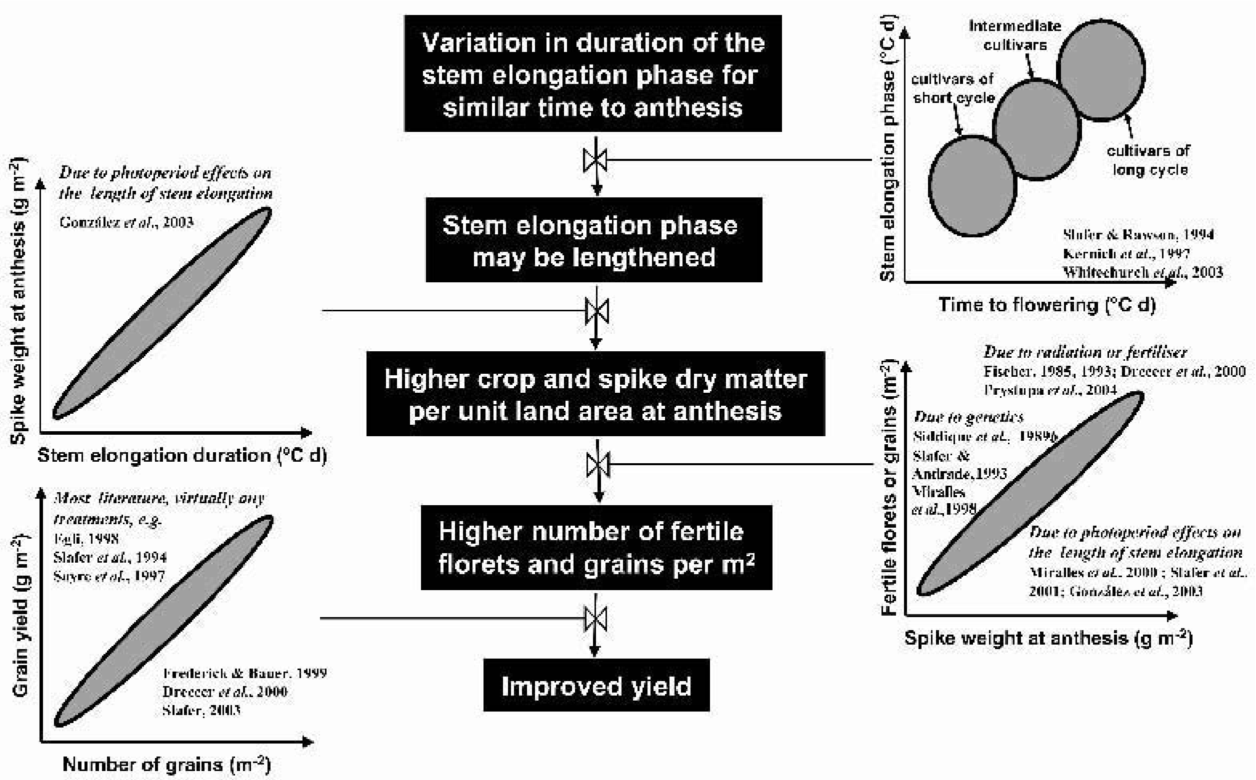

Fig. 2. Schematic diagram of a hypothesised avenue for cereal yield improvement through manipulating the proportion of developmental time allocated to the stem elongation phase, describing some reported relationships supporting the hypothesis.

uses all the water available in the soil, and therefore crop improvements would not be expected from a higher root:shoot ratio, associated with a longer vegetative phase. However, this developmental pattern may be only achieved if deliberately selected for as empirical breeding has not tended to produce these sort of changes when directly selecting for yield *per se* (e.g. Slafer *et al.*, 1994), though exceptional cases may be found (Abeledo *et al.*, 2003).

An extended stem elongation period can be achieved by selecting either for higher sensitivity to photoperiod or for differences in intrinsic earliness during the stem elongation phase. It has been reported that the stem elongation phase of cereals is sensitive to photoperiod and that extending this phase (by exposure to short photoperiod) does result in an increased number of fertile florets and grains produced by the crop (Slafer *et al.*, 2001), and therefore a higher yield. This sensitivity of stem elongation to photoperiod seems to be independent of that of previous phases (Slafer & Rawson, 1994; González *et al.*, 2002), though we must learn much more on the genetic bases determining sensitivity to photoperiod during stem elongation before this information may be useful for practical breeding. So far we have only a partial understanding of the important genes (Whitechurch & Slafer, 2001, 2002), since we only know (and have worked with) a few major genes for photoperiod sensitivity, whilst many others are expected to exist (Snape *et al.*, 2001). Alternative approaches, that have just started to be analysed, include (i) determining what genes are down- or up-regulated when responses to photoperiod take place during different phases (before and after the onset of stem elongation), and (ii) identifying genes/QTLs for differences in length of different phases (and/or for responsiveness to photoperiod in these phases) within mapping populations.

Water use

There are different traits that may confer the ability to the crop canopy for capturing more water. Some of the most widely recognised are deeper root systems, osmotic adjustment and early vigour. The former two would actually increase the amount of water evapotranspired by the crop, while the latter increases the proportion of the total evapotranspiration that is actually transpired by the canopy and then directly linked to crop productivity.

Deeper root systems allow the crop access to water in deeper soil layers that might otherwise be unavailable. An option to improve this trait may be to identify genotypes with faster-growing crop roots; a trait presenting large genetic variation (Watt *et al.*, 2001). Cereals with fast-growing roots may also reduce the accumulation of bacteria that can limit shoot growth (Watt *et al*., 2003), and then they may have an improved access to resources down the soil profile later in the growing season. Besides absorbing more water, deeper root systems may help prevent groundwater contamination from nitrate leaching. A major problem with rooting depth as candidate trait is that it is intrinsically difficult to measure and therefore surrogates must be identified.

Osmotic adjustment (accumulation of solutes during water stress decreasing osmotic potential and maintaining water absorption) is an important adaptive mechanism of drought tolerance in major crops (e.g. Morgan, 1983; Ludlow & Muchow, 1990; Chimenti & Hall, 2002). In turn, greater osmotic adjustment may result in more root growth and then an increased ability to extract additional soil water under drought if water is available at deeper layers. Although the genetic basis of this mechanism has been identified in wheat and barley (e.g. Morgan, 1991; Morgan & Tan, 1996; Teulat *et al.*, 1998, 2001), its direct use in selection seems unworkable. Although some methods of selection for this trait have been reported (e.g. Morgan, 2000), there is not conclusive evidence that crop yields benefit by increased osmolyte accumulation (Serraj & Sinclair, 2002).

Two surrogates that offer promise for estimating which genotypes extract more water than others are canopy temperature depression and discrimination against the heaviest stable isotope of carbon (^{13}C).

Canopy temperature depression (the magnitude of the difference between the temperature of the canopy and that of the air surrounding it) is a candidate surrogate, as genotypes having lower canopy temperature at midday have relatively better water status (Blum *et al*., 1982; Garrity & O'Toole, 1995). A positive relationship has been generally found between canopy temperature depression and yield for different genotypes (Blum, 1988; Blum *et al*., 1990; Reynolds *et al*., 1994, 1998; Amani *et al*., 1996; Fischer *et al*., 1998; Reynolds & Pfeiffer, 2000), though sometimes it did not work well (e.g. Villegas *et al*., 2000; Royo *et al.,* 2002). Infrared thermal sensing of canopy temperatures has been proposed as a tool for easy and rapid screening (Blum *et al*., 1982; Reynolds *et al*., 1998; Araus *et al*., 2001), as it can determine the surface temperature of a field plot within a few seconds (Royo *et al*., 2003).

Carbon isotope discrimination ($\delta^{13}C$) is a promising trait for assessing genetic variation in water extracted by different genotypes. It measures the ratio of stable carbon isotopes ($^{13}C/^{12}C$) in the plant dry matter compared to the value of the same ratio in the atmosphere (Farquhar & Richards, 1984). $\delta^{13}C$ is associated with different attributes of the soil-plant-atmosphere system, but it is dominated by the discrimination of Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) against the heavier isotope, in turn related to the intracellular concentration of CO_2 (C_i) relative to that in air (C_a) (Farquhar *et al*., 1982, 1989). This indicates that the level of ^{13}C discrimination by Rubisco would decrease as leaf internal CO_2 concentration decreases, then the value of Δ correlates negatively with transpiration efficiency (here considered as the ratio of net assimilation to transpiration). However as $\delta^{13}C$ usually also correlates positively with stomatal conductance associated with transpiration, $\delta^{13}C$ also reflects the water status of the plant. Therefore a stronger $\delta^{13}C$ becomes an indirect indicator of better water status (Araus *et al.*, 2002*a*, 2003*b*) and then, under restricted water availability, of improved ability to access water unreachable for other genotypes.

Early vigour is a complex trait related to a number of seedling characteristics (Liang & Richards, 1994; López-Castañeda & Richards, 1994*a*; López-Castañeda *et al.*, 1995) which allows faster ground coverage, thus increasing the amount of water actually transpired by the canopy by reducing direct evaporation. This may be especially relevant in Mediterranean regions, where rainfall occurs during early growth stages and evaporation from the uncovered soil may be important, with vigorous genotypes yielding more than less vigorous types (Richards *et al*., 2002). There is substantial intra-specific variation in characteristics conferring early vigour and breeding for them may be successfully carried out (Rebetzke *et al.,* 1996). Early vigour may be directly selected for through visual scores of early differences in ground coverage or through the use of vegetation indexes that may be calibrated to estimate the proportion of soil actually covered by green tissues in a plot (Araus *et al*., 2001).

Water use efficiency

Where additional water is not available, higher WUE based on transpiration efficiency (increasing the efficiency for producing dry matter per unit of transpired water) appears to be an alternative strategy to improve crop yield (Condon *et al.,* 2002; Richards *et al.,* 2002). This strategy, we think, would only be preferred over improving water use in regions where virtually all water attainable by a crop canopy is actually being used by modern cultivars. To define this situation may be important as for some attributes water-saving plants may be those more efficient but less productive.

High stomata sensitivity is a trait that optimises the balance between carbon gains and water losses, by minimising the latter through only allowing gas interchange under low water vapour deficits. Alternatively a constitutively (i.e. already expressed in absence of stress) low stomatal conductance may also optimise the transpiration efficiency. In this context, $\delta^{13}C$ is again a reasonably simple and reliable measure of WUE for cereals and other C3 plants, but in contrast to the situation with improved water use, the relationship between yield and $\delta^{13}C$ is negative (lines producing higher yields due to superior WUE tend to have lower $\delta^{13}C$; Farquhar & Richards, 1984; Hubick & Farquhar, 1989; Condon *et al*., 1990). Therefore, screening for low $\delta^{13}C$ could be instrumental in breeding for higher WUE (Farquhar & Richards, 1984; Farquhar *et al*., 1989; Hall *et al*., 1994) and this has been the criterion used for producing the first two commercial cereal (wheat) cvs –Drysdale and Rees– with $\delta^{13}C$ as an indirect breeding trait (Rebetzke *et al.,* 2002; Richards *et al.,* 2002; http://www.csiro.au/rees). However, it remains critical to guarantee that there are no major genotypic differences in the ability to use more water in the targeted environments where selection for lower $\delta^{13}C$ is going to be made. In the case illustrated for Australia (Rebetzke *et al.,* 2002) it has been clear that the advantage of selecting for lower $\delta^{13}C$ is only expected to take place for the lowest range of rainfall in their environments, with no apparent advantages for regions with more than 350 mm of rainfall during the whole season.

Partitioning

Harvest index is the final level of dry matter partitioning to grains among crop organs. Breeding has been effective in improving harvest index in bread wheat (Calderini *et al*., 1999), barley (Abeledo *et al*., 2002) and other cereals (e.g. Peltonen-Sainio, 1994; Ramdani *et al*., 2003; García del Moral *et al*., 2005). Thus, this trait has already been subjected to an intense breeding effort in the past, and scope for further improvement may be more limited. One of the main attributes modified to increase harvest index has been plant height, which has been systematically reduced. In wheat (Slafer *et al*., 1994; Calderini *et al.*, 1999), barley and other small-grained cereals (Abeledo *et al*., 2002) breeding has always resulted in shorted-stature culms, at least until the cultivars reached a plant height optimising yield. As the relationship between height and yield is parabolic, reducing height beyond the value maximising yields will be disadvantageous and most modern cultivars possess plant heights within the optimum range (of between 70 and 100 cm; Fischer & Quail, 1990; Richards, 1992; Miralles & Slafer, 1995; Flintham *et al*., 1997). It is therefore unlikely that further increases will be achieved by altering plant height.

Therefore, although opportunities to improve harvest index in Mediterranean conditions still remain, they are not extremely promising. Yield in these conditions is strongly reduced by the terminal drought typical of the Mediterranean environments (drought evolves during crop growth and becomes severe during grain filling). Thus, phenological traits increasing the relative amount of water used during grain filling, or adjusting the crop cycle to the seasonal pattern of rainfall, may be useful, providing the advancement of flowering does not increase the risk of frost damages substantially.

An alternative may be increasing the contribution of vegetative stem reserves to grain filling to raise yields under terminal stresses that severely inhibit actual photosynthesis (otherwise source limitation is unlikely; Slafer & Savin, 1994; Richards, 1996; Borras *et al*., 2004). In these cases, augmenting the contribution of carbohydrate reserves accumulated during vegetative growth to grain filling may be worthwhile for improving harvest index (Loss & Siddique, 1994). Genetic variation seems large in both capacity to accumulate reserves in vegetative organs and in remobilization efficiency (e.g. López-Castañeda & Richards, 1994*b*; Richards *et al*., 2002).

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