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## Defining selection criteria to improve yield under drought

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### Abstract

The many selection criteria that have been proposed to increase drought resistance of our crops have had little, if any, impact on improving crop yields in dry environments. There are several likely reasons for this lack of success. Some of these are: (i) criteria proposed have been related more to survival mechanisms under drought than to productivity, (ii) criteria are inappropriate to the target environment, and (iii) criteria are temporal and are therefore likely to have minimal impact on growth and yield over the entire lifecycle. Another important reason is that breeders have not been convinced the proposed criteria will be successful as they are too difficult to measure. On the other hand, empirical breeding programmes to improve yield under drought have been successful. Surprisingly, some of the greatest successes have been achieved by breeding in environments where water is non-limiting. This paper reviews breeding approaches to improve yield under drought. It focuses on critical factors that must be considered to identify likely plant attributes that can be targeted. These factors, their link with yield, the nature of the target environment, the level of organisation where the trait is expressed are discussed. Three quite different examples are given to emphasize the above considerations and which show substantial promise in targeting traits to improve yield under drought. They are drought at flowering, improving transpiration efficiency and improving early leaf area development.

### Introduction

An array of plant species have evolved to both thrive and survive in dry habitats. The wondrous display of plant adaptations to these habitats is testimony to the remarkable evolutionary history of many species. This has resulted in the notion that substantial genetic variation in drought tolerance exists and that it may be possible to use this variation in plant breeding to overcome some of the devastating effects of drought on our important crop species. There are additional factors that have also raised our hopes of being able to breed strains that tolerate the effects of drought. These are firstly, our increased understanding of how plants respond to drought. Secondly, the many ways that are available to quantify a plant's response to drought and the sophistication of some of the instruments used to do this. Thirdly, the large amount of genetic variation for drought response, and the possible amplification of this variation by molecular means or by hybridising crop species with their wild relatives.

In retrospect, our hopes of overcoming the devastating effects of drought and raising the hopes of farmers and others has been naive. It will never be possible to *overcome* the effects of drought, and any progress to improve yield under drought is likely to be slow and gains will only be small. Past efforts to improve drought resistance is evidence for this. Despite our better understanding of the plant characteristics that seem to be important, our ability to source new gene pools, and the increasing precision and sophistication in our ability to manipulate traits genetically, we have not made substantial genetic progress in improving drought tolerance. Trait identification for improving yield under drought has had very little impact. For example, there are no well-documented examples whereby plant breeders have released new germplasm to farmers developed on the basis of a physiological understanding of plant responses to drought. With the exception of flowering time, the only morphological or physiological traits that are touted as being important under drought and that may be used by breeders are: the

presence of awns in cereals (Atkins and Norris 1955; Evans et al. 1972), leaf pubescence (Ghorashy et al. 1971), glaucousness (Richards et al. 1986) and deeper or more extensive rooting depth (Hurd and Townley-Smith 1972; Sloane et al. 1990). Genes for these traits have now been identified in a number of species and can be incorporated into breeding programmes. A greater physiological understanding of them has also resulted in breeders enhancing the expression of these traits in some cultivars, or deliberately incorporating new sources of variation for them into their breeding programmes.

However, breeders have not been convinced that they should pay *even more* attention to specific drought adaptive traits and they will probably remain unconvinced until there is more evidence to suggest that they could make important yield gains by selecting for specific traits. But, to ignore those controlling factors influencing yield under drought may mean that important gains will be prevented as suitable genetic variation for traits will otherwise not be found within existing breeding programmes.

#### Will breeders adopt new criteria for drought resistance?

Breeders have sometimes been criticised for not being more cavalier in their breeding programmes and not selecting some of the many traits that have been proposed as being important under drought. The basic rationale for these criticisms is often quite valid. That is, by not targeting specific traits to improve yield under drought breeders will not have the appropriate genetic variation in their programmes to make gains. However, there are a number of good reasons why breeders are not more adventurous. Hybridising unadapted with adapted parents usually conserves chromosomal regions containing large amounts of 'junk genes'. Their linkage with favourable gene combinations may take a long time to separate and therefore considerable time and effort to recover previous yield levels. Many years of breeding in our highly bred crops has resulted in combinations of genes that act together in great harmony. Many years may be spent in rebuilding the harmonious combinations again after introducing new traits from poorly adapted genetic backgrounds (e.g. Richards and Passioura 1989). The introduction of unadapted parents into breeding programmes are therefore a risk that breeders are reluctant to take unless

they can target a specific trait from the unadapted parent.

Breeders may be reluctant to devote more effort to improving drought resistance because this is only one of many criteria that they are attempting to improve. Drought resistance is poorly defined compared to other traits such as those involved in grain quality and disease resistance and, it is not surprising that breeders will target traits where the deficiency is better defined and where selection is known to be effective. Furthermore, improved grain quality and disease resistance are demanded more by farmers and consumers than is improving drought resistance. Breeders have many criteria for which to select and it is not easy for them to take on additional ones, particularly if they are not convinced that they may be useful for their breeding programme, or if it is poorly defined.

Breeders maintain a healthy scepticism for suggestions that if they selected for a particular trait then yield under drought would be improved. A major reason for the scepticism is that the substantial literature on the drought physiology/genetics of plants has not generally resulted in key traits/genes that have improved yield under drought. Another reason is that traits have usually been poorly evaluated for the attributes in which the breeder is most interested and so they are reluctant to adopt them until they are more carefully tested. For example, the growth conditions under which plants were evaluated may have been unrealistic, a recommended trait may be a very difficult one to select and therefore inappropriate for a breeding program, and there may be no indication of the extent of genetic variation. Breeders may also be concerned that genotype  $\times$  environment interactions are high, gene action is unfavourable, heritability is low, and that there may be unfavourable correlated responses in other traits if a trait was selected. They will generally require this information if they are to adopt a new selection criterion. However, if breeders can be convinced that the expression of a particular trait in their programme should be improved and that selection for it is feasible then there is little doubt that they will incorporate it into their programme.

A major factor that has prevented progress for improving yield in water-limited environments is not knowing which are the critical traits to select. A further factor has been in not providing the appropriate information to breeders to show them the importance of particular traits or providing them with feasible ways to select for them. However, before discussing

the main factors appropriate traits able to examine empirical methods environments. progress that is limited environments serves to provide breeding programs selected. The benefits for self-pollination

#### Empirical breeding environments

The first and most important programme is to have the attributes of future cultivars incorporate a number of choosing parents of plant characteristics nor would they their presumed yield because the defined or breed they are highly likely very reluctant material into the required to eliminate also introduced prepared to use precisely select it.

The next step also a vital one. breeders use methods. It is usually the segregating genetic variability the breeder selection of observable, would be selected so as to avoid if they are likely in very dry conditions most important environments. other traits the and that are ea

the main factors to consider in the identification of appropriate traits and giving some examples, it is valuable to examine standard breeding approaches where empirical methods are used to improve yield in dry environments. This will give some appreciation of the progress that is possible in improving yield in water-limited environments and how it is achieved. It also serves to provide some background as to where in a breeding programme new traits may be introduced and selected. The breeding programme outlined is typical for self-pollinated species.

### Empirical breeding programmes for yield in dry environments

The first and most important step in a breeding programme is to identify parents for hybridisation that have the attributes breeders wish to combine into future cultivars. This is the stage when breeders would incorporate a new trait into their programme. When choosing parents, breeders would rarely target specific plant characteristics to improve drought resistance, nor would they be likely to choose parents based on their presumed drought resistance. This is principally because the desirable characteristics are not well defined or breeders are not sufficiently convinced that they are highly desirable. In fact breeders are usually very reluctant to introduce very different parental material into their programmes because of the efforts required to eliminate the undesirable genes that are also introduced. Often the only time when breeders are prepared to use an unadapted parent is when they can precisely select for the characteristic they require from it.

The next step in the breeding programme, which is also a vital one, is usually the first and only time when breeders use morphological and physiological criteria. It is usually very effective and typically occurs in the segregating F<sub>2</sub> generation when the full gamut of genetic variability is first exposed. In this generation the breeder selects plants with the desired expression of observable, highly-heritable traits. Typically plants would be selected that flower at the appropriate time so as to avoid drought and plants would be eliminated if they are likely to be too short to harvest if grown in very dry conditions. These two traits may be the most important factors determining adaptation to dry environments. Breeders are also likely to select for other traits they believe are desirable under drought and that are easy to select for in this generation (e.g.

glauconess). Little selection is likely to be practiced after this for physiological traits other than maintaining the desirable expression of these simple traits and reselecting among segregating lines. In the following generations selection will be for less heritable traits such as yield and characteristics such as grain quality and disease resistance. Selection for yield automatically integrates all the unknown factors that will be important for improving drought resistance. This is a proven path to success providing that plants are grown in conditions which are representative of the target environment and providing that genetic variation is maximised for selection to be effective, and that genotype  $\times$  environment interactions are not too large. Thus, apart from getting phenology right little attention is paid to any other trait that may be related to drought resistance and yield is used as the integrator of everything that may be desirable in water-limited environments.

The introduction of new traits in a breeding programme and their selection may occur in a variety of ways depending on how difficult the traits are to select and the resources breeders are prepared to devote to them. Breeders may simply use a parent with the desired level of the trait and then make no further selection for it in the following generations. The assumption here is that if the trait is important then the integrating power of yield will ensure that it carries through to later generations. There is great merit in this and it is very simple, although the effort required to identify the most desirable parents should not be underestimated. This approach is appropriate for traits that are difficult to select. However, if the trait is very easy to select and it is highly heritable then selection in the F<sub>2</sub> will guarantee its passage to later generations. Finally, if it has been demonstrated that a trait is very important and it is highly heritable then a backcrossing programme can be used to introduce it into an adapted background. The first selection step for this would normally be the F<sub>2</sub>. The advantages and disadvantages of these approaches have been discussed previously in greater detail (Richards 1989).

Interestingly, selection for yield in the absence of drought has also been a very effective way to improve yield in dry environments. The reason for this is that a high yield potential, expressed in favourable environments, can also have a yield spin-off in less favourable environments. Also, selection for yield in favourable environments is typically more effective than in less favourable environments because genetic variation is maximised (errors are smaller) and geno-

type  $\times$  environment ( $g \times e$ ) interactions are typically lower because the environments are more repeatable. A good example of the value of lines with a high yield potential in dry environments comes from the CIMMYT wheat breeding programme in Mexico. This is conducted under irrigated, high fertility conditions and average yields are about  $7 \text{ t ha}^{-1}$ . CIMMYT bred material has dominated the Australian wheat industry for the last twenty five years and about 95% of current cultivars can be traced to CIMMYT germplasm. Yet, in Australia wheat is grown in water-limited, low nutrient environments with average yields only  $1.7 \text{ t ha}^{-1}$ . This suggests that the characteristics responsible for high yield potential are also important for achieving good yields in low yielding environments. Another example from the CIMMYT program is given in Figure 1 (Sayre et al. 1995). This contrasts the yield of three groups of wheat. One group, comprising 40 lines, was selected in Mexico under irrigated, high fertility conditions, a second group of 20 lines was selected for high yield in Syria under moderate to severe drought conditions and a third group of 15 lines was selected for high yield under drought from other countries. When grown under a line source sprinkler system which generated a gradient in soil water supply the average yield of the wheats selected under irrigated conditions was significantly greater than the wheats selected under droughted conditions at all levels of soil water availability. Similar results in wheat have also been reported by Calhoun et al. (1984). It should be pointed out that the above examples for wheat contrast with those in barley grown in severely stressed environments (Ceccarelli 1994). It is likely that selection under both optimal and droughted conditions represents the ideal environments to select for high yield under drought so as to maintain favourable alleles under drought and at the same time maximising selection response under favourable conditions.

### Trait identification

The previous sections have suggested that plant breeders are making progress in improving yield under drought using standard selection procedures for yield. I have also suggested that breeders do not generally select for specific traits to improve yield under drought principally because drought adaptive traits are usually poorly defined and any advantages have not been adequately demonstrated. Breeders are therefore reluctant to devote resources to these traits. Establishing the importance of a particular trait is very difficult and

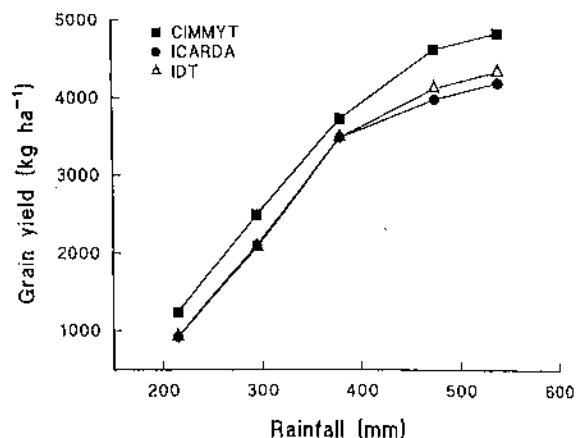


Figure 1. Average yield of three groups of lines, selected in different droughted environments, and grown at one location under a line source sprinkler system. See text for more information (adapted from Sayre et al. 1995).

time consuming. The nature of drought is such that its timing and intensity is unpredictable from year to year and this also means that the physiological responses to drought are also complex and unpredictable. These make breeding for drought resistance particularly slow and difficult whether it be in selection for grain yield or for the evaluation or identification of important traits. Up to the late 1970's defining criteria for improving yield under drought was a haphazard affair. There was not a great deal of attention given to the complex nature of drought or to separating productivity under drought, which was important for agricultural plants, from survival mechanisms, which characterise xerophytes. Yet many adaptations favouring survival tend to reduce economic yield. Tortuous terminologies that were developed for classifying and defining adaptations to drought and survival in natural plant communities were still being used for trait identification in plant breeding in 1980 when it was still a contentious issue (Turner and Kramer 1980).

A shift in thinking occurred in the late 1970's which changed the basis for identifying criteria for improving yield under drought. There was a switch away from thinking how plants protect themselves against drought to thinking how to maximise the economic product when water is limited. This thinking was pioneered by Passioura (1977) and may have arisen by thinking about resource limitations rather than about defence mechanisms against dying from too little water. Passioura proposed that when water is limited, the yield of biomass is a function of the amount of water transpired

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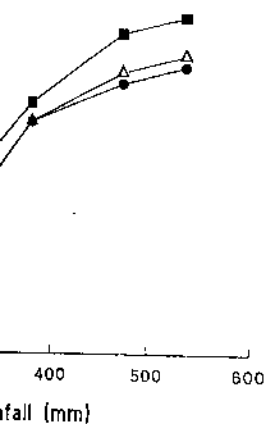
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by the crop ( $T$ ) and how efficiently the crop uses this water ie. the water use efficiency ( $WUE$ ), where:

$$\text{biomass} = T \times WUE \quad (1)$$

If grain is the economic product then biomass is partitioned into grain as the proportion of biomass ie. the harvest index ( $HI$ ), such that:

$$\text{grainyield} = T \times WUE \times HI \quad (2)$$

As this identity is always true, then it was argued that as  $T$ ,  $WUE$  and  $HI$  are likely to be independent of each other then an improvement in any one of them should result in an increase in yield. Using this model it was possible to assess whether a particular trait was likely to increase any one of the components and thereby increase yield under drought. This provided a framework to more critically identify important traits to improve yield under drought.

#### Trait hierarchy and the target environment

To refine the identification of the critical traits that are most likely to improve yield under drought there are several principles that can help. The first is that the degree of influence of a trait on yield depends on the time scale over which it is effective (Passioura 1982, and this volume). For example, a trait that influences the development of leaf area will be more important than a trait that influences stomatal response to the onset of drought. Another principle is that the capacity of a trait to influence yield is related to the level of organisation (molecule – cell – organ – plant – crop) in which the trait is primarily expressed. Thus, a trait like plant height will have a large effect on yield because it is expressed at the level of the crop whereas the doubling in activity of a key enzyme may have little effect because its expression may be greatly modified by other steps in the pathway, by other products, by the growth of other organs and by environmental factors.

Two examples which show the importance of the level of organisation are as follows. Plant breeding since 1900 has been effective in doubling grain yield yet, amazingly, the rate of photosynthesis in many crops has decreased (Gifford and Evans 1981; Cook and Evans 1983). Thus, despite a huge gain in crop productivity, the most fundamental process in plant growth, which is expressed at the cellular-organ level, is of little consequence. The likely reason for this is that leaf area has increased and has easily compensated

for the decline in photosynthesis. The second example is the very small number of genes that have had a significant impact on yields if we do not include disease resistance genes. Of the tens of thousands of genes in wheat, for example, only four have been identified as being largely responsible for yield and adaptation. There is the  $Q$  locus which prevents spikes from shattering and which allowed the domestication of wheat, vernalisation and photoperiod genes that affect flowering time, and the dwarfing genes that effect plant height. Each of these genes are for traits expressed at the crop level. Thus, as a general rule of thumb, the closer a trait is to the level of organisation of the crop the more influence it will have on productivity. If this is generally correct then it is difficult to perceive how altering the level of a biochemical trait will impact on crop performance.

The final general rule which is important for identifying the most likely traits to improve yield is knowing the nature of the target environment. This can sometimes be difficult because dry environments are typically highly variable, although often there is some underlying pattern of rainfall. Environments may range from Mediterranean-like, where rainfall is highest during the winter and then declines to almost zero in summer, to environments where summer rainfall is probable and winter rainfall is rare. There is of course a full spectrum in between. Careful consideration must also be given to how important a specific trait will be in each target environment. For example, there is little point in selecting for a deeper or more extensive root system if all of the available soil water is already used by current varieties. Monitoring crop water use over a number of years in the target environment maybe required to establish this. It may also be important to grow indicator species or cultivars in the target environment. These can establish whether any water remaining in the profile is due to the inability of the roots to extract the water, or to nutrient deficiency, toxicity, or root pathogens. If any of these are important then overcoming them by either breeding or management will result in improved yields under drought.

The economic environment must also be taken into account when defining selection criteria. For example, will the grain produced be sold nationally or internationally, or will it be consumed by the farmer such as in subsistence agriculture. Desirable traits may differ substantially for both forms of agriculture. In the former, economic gains may be averaged over several years and so yield in the good years will dominate, whereas for the subsistence farmer adequate grain *every* year

is essential and high production in good years is not important.

The vast range of environments where crops are grown and the large range of genetic variation available in our crops provides many opportunities to make genetic gain in yield under drought providing there is a thorough understanding of the crop and the environmental limitations. It is not my intention to give a shopping list of traits that may be important in dry environments. Descriptions of traits that are likely to be important have been given before both globally (Ludlow and Muchow 1990) and more specifically (Richards 1991). I have chosen to give examples of three very different traits that show substantial potential to improve yield under drought, or in the case of maize, substantial success in increasing yields. Each relate to a different component of the Passioura identity. The first example shows how an adjustment in phenology in maize substantially increased yield by improving harvest index. This example is not only interesting because of its success but also because it represents a different approach to yield improvement under drought compared to the later examples. It was an 'ad hoc' approach whereby selection was made for a number of different traits that were thought to contribute to yield under drought. In the final evaluation it was found to be successful because harvest index increased which in turn increased yield. The second example is directly involved in improving the efficiency of water use through increased transpiration efficiency. Whereas the third example may seem unrelated to drought initially as it is to do with improving early growth under favourable conditions. Early growth should increase yield as it effects T, the amount of water used for transpiration, as well as increasing transpiration efficiency in some environments.

### Drought at flowering in maize

Tropical maize crops are typically grown after a well-defined dry season at a time when rainfall is very unpredictable. Grain yield is related more to grain number than to grain weight and so genetic improvement in maize under drought at CIMMYT has focused on the events during the flowering period when grain number is established (Fischer et al. 1983). Maize is particularly sensitive to drought at flowering. A maize population with high and stable yield was chosen for selection of traits involved in drought tolerance. The population underwent eight cycles of recurrent full-

sib selection in virtually rain-free seasons where water supply was managed with irrigation. Families were grown in three drought regimes – well-watered, intermittent stress and severe stress. Grain yield, leaf and stem extension, the interval between anthesis and silking, canopy temperature and leaf senescence were all measured. An ideotype using the above traits in the different environments was used to define an index for the selection of high yielding, drought tolerant types.

The final selections were evaluated in large plots at a range of different water supplies. Grain yield of the selections increased by  $108 \text{ kg ha}^{-1} \text{ cycle}^{-1}$  at all yield levels (Bolanos and Edmeades 1993a). Surprisingly, the rate of gain was independent of yield level. The increase in yield came about by an increase in harvest index at all yield levels. No change in biomass was found. It is interesting to see how the increase in HI occurred. Flowering was substantially modified. Although the time to flowering was kept constant the interval between anthesis and silking was reduced and this accounted for about 76% of the variation in grain yield (Bolanos and Edmeades 1993b). The reduction in the anthesis-silking interval resulted in an increased ear biomass and increased kernel number. Kernel weight remained unchanged (Bolanos et al. 1993). It is interesting that plant water status was unchanged, suggesting that the increase in yield was due solely to increased partitioning of assimilate to the ear.

It is worth noting that the yield increases in wheat in both wet and dry environments referred to earlier arose in a similar way to those described here for maize. In both crops increased yield was due to an increase in HI rather than to an increase in biomass, and kernel number increased rather than kernel weight.

### Carbon isotope discrimination and transpiration efficiency

Generations of breeders have failed to improve the water-use efficiency of dryland crops by empirical means. In water-limited environments the yield of biomass of current cultivars is about the same as cultivars grown over a century ago (Siddique et al. 1989). With a better understanding of the factors that influence water-use efficiency the opportunity now exists to target the improvement of WUE more precisely.

The ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  in plants varies from that in the air from which it is derived. Differences in the properties of the isotopes of carbon cause different fractionation's during the incorporation of  $\text{CO}_2$  into dry matter.

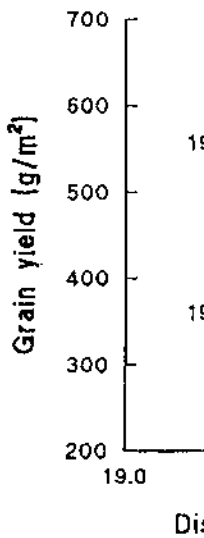


Figure 2. Relationship between grain yield among lines in years differing in soil... (from Richards and Co...)

Variation in the ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  in plants has been used recently, it has been found that the ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  is related to the partial pressure of  $\text{CO}_2$  at the site of transpiration efficiency (Farquhar et al. 1982; Farquhar et al. 1983). The ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  has been related to water-use efficiency and can be precisely measured. There is large genetic variation in this trait and it has been used in plant breeding (Farquhar et al. 1993). The negative correlation has also been confirmed in field studies where water-use efficiency (Farquhar et al. 1988; Condon et al. 1990). In water-limited environments, different species have been used (Richards 1994c). The ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  has also been mainly used in field studies where each been grown in different environments. Scale effects may not be significant (Richards 1993). In water-limited environments, different types use the same amount of water, then the relationship between grain yield and biomass should translate to biomass and hence yield.



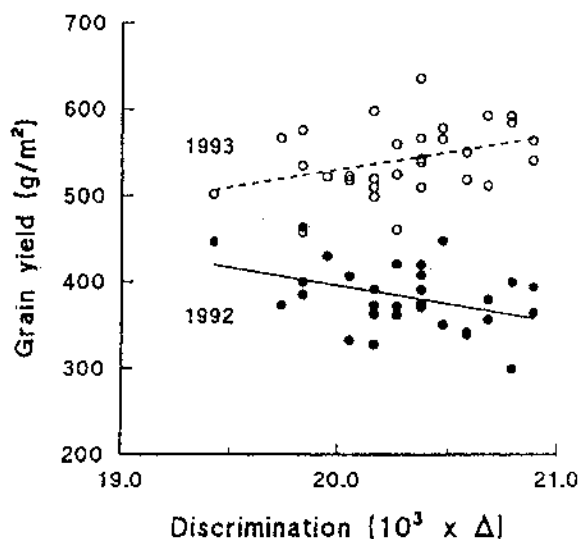


Figure 2. Relationship between carbon isotope discrimination and grain yield among lines derived from a single cross and grown in two years differing in soil water availability and rainfall at Condobolin (from Richards and Condon 1994).

Variation in the ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  between  $\text{C}_3$  and  $\text{C}_4$  species has been used in ecological studies, but more recently, it has been established that the ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  is related to the ratio of the internal to external partial pressure of  $\text{CO}_2$ . This in turn has been related to transpiration efficiency (TE) in  $\text{C}_3$  species (Farquhar et al. 1982; Farquhar and Richards 1984). We call the ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$ ,  $\Delta$  ('delta'). Genetic variation in  $\Delta$  has been related to TE in all pot studies where water-use can be precisely measured. These have shown that there is large genetic variation in  $\Delta$ , that it has a high repeatability and low genotype  $\times$  environment interactions, all of which indicate  $\Delta$  to be very attractive in plant breeding for high TE (Richards and Condon 1993). The negative relationship between  $\Delta$  and TE has also been confirmed within several species in all field studies where TE has been determined (Wright et al. 1988; Condon et al. 1993) but not when several species have been compared (Lopez-Castañeda and Richards 1994c). The relationship between  $\Delta$  and TE has also been maintained where several genotypes have each been grown in fields greater than 1.5 ha and where scale effects may negate any advantage in TE (Condon and Richards 1993).

In water-limited environments, providing all genotypes use the same amount of water for transpiration, then the relationship between  $\Delta$  and TE in the field should translate to low  $\Delta$  genotypes having greater biomass and hence the potential for higher yields.

However, this has not always been found as both +ve and -ve relationships have been reported between  $\Delta$  and biomass or yield (Figure 2). The example in Figure 2, derived from Richards and Condon (1994), are from lines derived from single F2 plants of one cross. Results presented are from lines grown in two consecutive years at Condobolin, Australia. The yields in both years were very favourable and well above the long term average. The expected negative relationship was found in the drier of the two years whereas a positive relationship was found in the wetter year.

There are a number of explanations for the positive relationship observed in Figure 2 and in other studies. They may be due, in part, to a negative trade off between TE and the amount of water used. Thus, if low  $\Delta$  genotypes use less water than high  $\Delta$  genotypes then a positive relationship could result (e.g. White et al. 1990). It could also arise if low  $\Delta$  genotypes are slower growing which results in less water for transpiration as more water is evaporated from the soil surface and also if the slower growth is at a time when vapour pressure deficit of the air is low (e.g. Condon et al. 1993). Another explanation is that if there is genetic variation in grain number to generate a larger 'sink strength' then a positive relationship may also result as lines with a high grain number may maintain a higher stomatal conductance which in turn would result in a higher  $\Delta$ . The latter two explanations are favoured to explain the positive relationship in Figure 2. These explanations are favoured in the cereal studies in wheat by Condon et al. (1987) and Sayre et al. (1995), and in the case of irrigated cotton (Radin et al. 1994). Positive relationships between  $\Delta$  and grain yield can also arise due to the plant part used in the determination of  $\Delta$ . This may be the case for Condon et al. (1987) for wheat and also for barley growing in severely stressed environments in Syria (Acevedo 1993). In these studies the peduncle was used to determine  $\Delta$ . The peduncle is the top part of the stem immediately below the ear in cereals. It forms just before anthesis at a time when water stress is common and small differences in prior water use or in anthesis time can have a large effect on  $\Delta$ . Therefore any variation for  $\Delta$  in the peduncle may reflect environmental effects rather than true genotypic differences. In barley variation in yield was also positively correlated with early flowering. The early flowering lines are likely to have a higher  $\Delta$  than later flowering lines both because of the lower vapour pressure deficit at stem elongation in the early flowering lines and because of the more open stomata expected in the early flowering lines due to drought escape.

It is evident from the above that low  $\Delta$ , and hence high TE at the leaf level, may not always translate into greater yields and that we still need to understand the trade-offs between  $\Delta$  and growth in specific environments. However, where crops rely mainly on stored soil water and hence where evaporation of water from the soil surface is low, selecting for low  $\Delta$  shows considerable promise (Richards and Condon 1993). The advantages of selecting for  $\Delta$  are numerous. It is highly heritable, there is substantial genetic variation, genotype  $\times$  environment interactions are small, its measurement is non-destructive and must be measured early in the plants life. Thus selected plants can be used for hybridisation. A drawback in its use has been the cost of measurement, although when this is compared to the cost of running field plots, the assessment of grain quality, or the use of DNA markers, the cost is not exorbitant. Several surrogates for the measurement of  $\Delta$  have emerged such as specific leaf weight in legumes (Wright et al. 1993), ash content (Masle et al. 1992; Maryland et al. 1993) and near-infrared reflectance (Clark et al. 1995). These may be used in early generations to cull segregating populations down to a smaller number for the final selection of lines using  $\Delta$ . This could substantially reduce the cost of using  $\Delta$  in breeding.

### Early vigour

Maximising the early growth of leaf area and biomass (early vigour) has been predicted to result in a greater yield of grain and biomass in environments where rain events are frequent immediately after sowing (Fischer 1980). More vigorous cultivars shade the soil surface thereby increasing crop transpiration at the expense of soil evaporation if the soil surface is moist. It should also result in a greater TE in crops sown during the winter as there will be more growth when vapour pressure deficit is low. There may also be less weeds because a more vigorous crop should prove more competitive. The best evidence for the greater yield and biomass of vigorous crops comes from the comparison of different species differing in early vigour and grown side by side (e.g. in oilseeds – Richards and Thurling 1978 and winter cereals – López-Castañeda and Richards 1994a). Of the winter cereals, barley is the most vigorous (López-Castañeda and Richards 1994b; López-Castañeda et al. 1995), yielding on average 25% more grain than wheat. Most of this yield advantage is because of the greater biomass of barley than in wheat (Siddique et

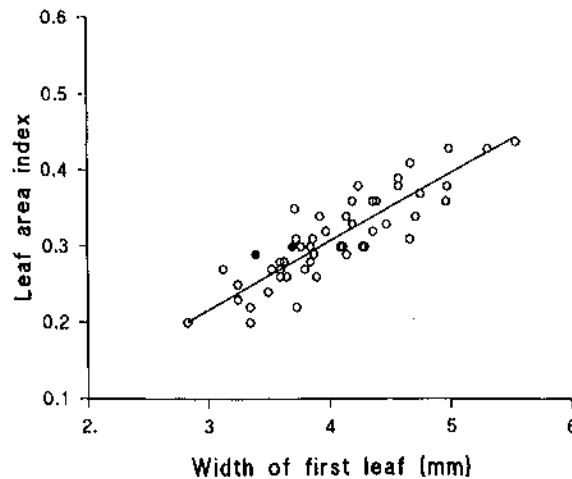


Figure 3. Relationship between leaf area index and the width of the first seedling leaf among lines from a composite cross population. Lines were grown in field plots 10m<sup>2</sup> with two commercial checks (solid circles). (Unpublished data of Rebetzke, Richards and Fischer).

al. 1989; Gregory et al. 1992; López-Castañeda and Richards 1994a).

Barley is more vigorous than wheat from the time of emergence. Leaf area just after emergence is twice that of wheat whereas dry weight is about 40% greater (López-Castañeda et al. 1995). The relative growth rates for barley and wheat are the same, hence barley maintains the leaf area and dry weight advantage over wheat. The early growth advantage in barley arises for several reasons. Barley germinates marginally earlier than wheat, it has a higher leaf area to leaf weight ratio during the early stages of growth thereby spreading its leaf mass over a larger area, and for the same seed weight the embryo of barley is about double that of wheat (López-Castañeda et al. 1995; 1996). The larger embryo in barley results in more expanding cells after imbibition and a more vigorous early root and shoot growth. Additional factors that contribute to early vigour in wheat are the development of coleoptile tillers (Liang and Richards 1994) and the absence of the major dwarfing genes (Richards 1992). With our understanding of the factors responsible for early vigour we are now in a position to pyramid the above traits and incorporate greater vigour into commercially grown cultivars.

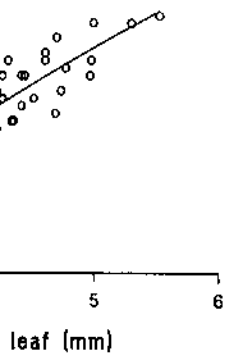
We have found substantial variation for early vigour in wheat. Figure 3 shows leaf area of lines from a composite population selected for a number of traits associated with vigour. Single plant selections from

the composite population showed a wide range of dry weight per plant. The average dry weight of a large coleoptile was 0.15 g. Note in this figure that there is a 2-fold variation in leaf area index of the composite cross. This is a very successful commercial cross (the closed circles) with early vigour. Thirdly, there is a wide range of leaf area index, which we suggest is a result of the ratio of leaf area to dry weight with leaf area index being the more important. Using a backcross strategy to convert early vigour into a stable population of cultivars (including

The expected early vigour is the greater leaf area to increased transpiration, which is likely to be particularly important in environments where soil moisture is low. In these environments, the development of leaf area must be combined with early vigour.

### Concluding remarks

The promise for new wheat varieties under drought is very large and exciting. We have identified how to target the early vigour just beginning to emerge and select for them. The new insights allow us to think about thought that embryo size is an important trait to select for. The measurement of leaf area index given us new insights into the favourable and unfavourable conditions between  $\Delta$  and early vigour. The importance for crop yield will emerge as our understanding of partitioning development and early vigour they are.



leaf area index and the width of a composite cross population of 10m<sup>2</sup> with two commercial cultivars of Rebeizke, Richards and

López-Castañeda and

wheat from the time of emergence is twice that of barley and is about 40% greater than that of wheat.

The relative growth rate of wheat is the same, hence barley has a relative dry weight advantage over wheat. The advantage in barley arises from its earlier emergence marginally larger leaf area to leaf area ratio. The stages of growth thereby result in a larger area, and for the same leaf area of barley is about double that of wheat (López-Castañeda et al. 1995; 1996). The result is more expanding leaves and more vigorous early root growth. Factors that contribute to the development of coleoptile and the absence of coleoptile (Richards 1992). With the relative growth rate responsible for early emergence to pyramid the above into commercially available

selection for early vigour and leaf area of lines from a composite cross population for a number of traits and plant selections from

the composite population were made for leaf area and dry weight per plant, early emergence and the presence of a large coleoptile tiller. There are several things to note in this figure. Firstly, there is more than a two fold variation in leaf area index (early vigour) in the composite cross population. Secondly, the most successful commercially grown cultivars for this region (the closed circles in Figure 3) are generally low in vigour. Thirdly, the width of the first leaf, the trait which we suggest integrates both embryo size and the ratio of leaf area to leaf weight, is highly correlated with leaf area index of plants at a later stage of growth. Using a backcrossing approach we are incorporating early vigour into a number of important commercial cultivars (including those shown in Figure 3).

The expected consequence of increasing early vigour is the greater yield of biomass and grain due to increased transpiration and increased TE. This is likely to be particularly important in Mediterranean environments. However, caution may be required in environments where the crop is relying on water stored in the soil from a previous season because the faster development of leaf area may result in the premature exhaustion of soil water giving rise to reduced yields. In these environments it may be that greater vigour must be combined with earlier flowering.

### Concluding remarks

The promise for making important gains in yield under drought is very large and the future is therefore very exciting. We have finally come of age in understanding how to target the important traits and we are now only just beginning to identify what they are and how to select for them. There are bound to be surprises and new insights along the way. For example, we had not thought that embryo size in cereals was going to be an important trait to improve yield under drought. Also, the measurement of carbon isotope discrimination has given us new insights into plant performance in both favourable and unfavourable conditions. The associations between  $\Delta$  and growth in different species and at different crop stages are still being unravelled as is its importance for crop improvement. Other exciting areas will emerge as our ability to alter key steps in carbon partitioning develop and we find out how important they are.

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## New molecular drought resistance

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### Abstract

The advent of molecular biology has revolutionized the work of agronomists and breeders under stresses. For the first time to be carried out much more rapidly, technology that are being put into improved varieties. QTL analysis takes out much of the guesswork and DNA fragments are used to visualize genes that species among themselves and salt tolerance donor and recipient lines into the recipient. Expression of a particular trait to be identified by comparing the DNA. The likelihood that a gene under droughted conditions programmes to improve

### 1. Introduction

The development of modern agriculture during the last ten years. The analysis of crop genomes from Mendel until the modern era. The numbers had been the numbers. It was able for genetic mapping. The extensive test-crossing. They were restricted. The longest linkage group was of only six megabases on chromosome 5A.