Chapter 23
Drought

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Abstract Established breeding methods for wheat in dry environments continue to make gains. It will remain the cornerstone for wheat improvement. This Chapter discusses proven methods to make additional gains. It discusses a way to benchmark yield potential in dry environments and how this can be used to determine whether unexpected agronomic or genetic factors are limiting yields. It examines opportunities, advantages and disadvantages of trait-based selection methods for dry environments, and it presents a framework by which important traits can be selected. Both high throughput and marker-based methods of selection are examined for their success and feasibility of use in breeding. It also highlights the importance of agronomic approaches in combination with breeding to continue to improve yield potential in water limited environments. Finally, the elements of success of translation from research to the delivery of new varieties is examined.

Keywords Water use · Water use efficiency (WUE) · Harvest index · Water-limited yield potential · Trait-based selection

23.1 Learning Objectives

- Identify factors responsible for yield gap before improving yield potential under drought.
- Establishing a water-limited framework to improve yield.
- Identification of physiological traits that can improve performance under drought.
- Combining trait-based selection with management practices to improve grain yield.
- Breeding and selection of physiological traits.

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- Translation from pre-breeding to new cultivars – the elements of success.

23.2 Introduction

Drought is a recurring feature in most parts of the world where wheat is grown. Around 75% of the area sown to wheat is rainfed and of this 46% has low to moderate rainfall and 29% high rainfall. The remaining 24% of the land is irrigated. However, the high rainfall and irrigated regions will have either sub-optimal rainfall in some years or insufficient irrigation water to meet the crops water requirement for maximum yield [1]. Accordingly, water limitations are a regular occurrence in almost all wheat growing regions. This will be exacerbated as pressure mounts on water for irrigation to be used for higher value crops than wheat, as well as for cities, industrial use and for the environment. With increasing population growth and increasing demand for food this places greater importance on increased productivity with less water.

Wheat improvement in water-limited environments has always been a challenge. Wheat breeders have struggled to make genetic gain and although they have been successful progress has been slow. This is because every drought is different in terms of intensity, duration and timing and so genotype x year interactions are large, and this slows genetic gain. Agronomists have also struggled to understand the complex underlying limitations of rainfed cropping environments and there is the complex and unpredictable seasonal variability to contend with. This seasonal variability can make management decisions difficult.

Maximising grain yield in dry environments depends on the ability of the crop to use as much of the available soil water as possible in a time frame where other constraints such as heat and more severe drought is avoided as much as possible. Thus, breeders who selected for earlier flowering in an environment where terminal drought was a common feature provided the first successful varieties in dry environments. This was because crops avoided flowering during the more severe dry and hot periods. It also resulted in a higher harvest index.

Important yield improvements have relied on a better understanding of the cropping environment. A startling example of the complexity of dryland cropping environments comes from studies in Australia that examined the on-farm relationship between seasonal rainfall and grain yield [2]. The expectation is that grain yield will be closely related to rainfall. But in semi-arid environments this was often not observed. Instead, to our surprise there was almost no relationship (Fig. 23.1). Although with enough data points an upper boundary line between rainfall and yield emerged. The slope of this boundary line in fact defines the upper limit to water use efficiency (WUE). In the French and Schultz study [2] it was around 20 kg grain per mm of rainfall. It was also found that the intersect on the rainfall axis was about 100 mm. In other words, about 100 mm of rainfall is required before grain is formed, which demonstrates that precious rainfall is squandered through often unavoidable evaporation from the soil surface.

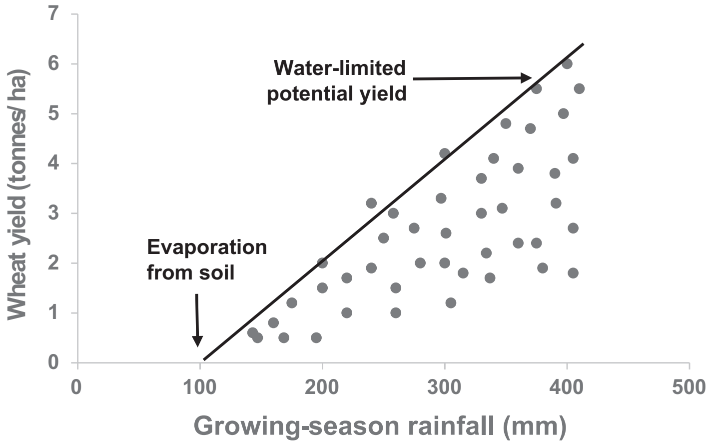

Fig. 23.1 Schematic representation of the relationship between wheat yield and growing season rainfall. Circles represent examples of individual farm paddock yields. (Modified with permission from [3])

There are many reasons for the surprising finding that rainfall had little bearing on crop yield in water-limited environments. The most important ones are as follows:

(i) There are many soil constraints other than rainfall such as soils may be too acid, too salty, or too hard, which limit the growth of the roots and hence water and nutrient uptake.
(ii) Soil-borne diseases are common which also limits the growth of an effective and healthy root system for the uptake of water.
(iii) And as a result of the above farmers may be reluctant to use adequate fertilisers because they are not cost effective. This will further limit yields if other constraints are minor.

Accordingly, improving performance in water-limited environments may not necessarily come from introducing particular physiological traits associated with water uptake and water-use efficiency because water may not be the main limiting factor for yield. Rather, improved yields may come from changing management practices that reduce soil-borne diseases of wheat or lessen soil constraints. It may also come from breeding for tolerance to soil-borne diseases or soil chemical constraints as these limit water uptake from the soil. These may have a greater impact than improving traits more directly involved with water uptake or the efficiency of water use.

This work by French and Shultz has provided a much more objective assessment of how and what changes to cropping systems and breeding are required for increased yield in water-limited conditions. It has been adopted widely by farmers and agronomists as a benchmark for measuring yield potential in rainfed regions in Australia, Argentina, USA and China [4].

Around the time French and Schultz were collecting data for their surprising findings Passioura published a seminal paper in 1977 [5] which simplified our understanding of the critical factors responsible for increasing grain yield in dry environments. He identified three factors that determines crop performance in dry environments. These provided a more precise way to identify factors that form the basis of genetic or agronomic improvement in crop yields when water is limited.

The three factors Passioura proposed to improve crop performance were as follows:

(i) Transpire more of the limited water supply (increase water use),
(ii) Increase the efficiency of this transpired water during the exchange of CO_2 for water to produce biomass (increase transpiration efficiency).
(iii) Convert more of the biomass into grain (increase harvest index)

This is simply stated as:

$$\text{Grain Yield} = \text{Water Use} \times \text{Water Use Efficiency} \times \text{Harvest Index}$$

Passioura suggested that an increase in any one of these three determinants should increase grain yield in water-limited environments. Furthermore, he suggested that unlike the yield components (spike number, grain number, grain size, etc.), each component is likely to be largely independent of the other enabling breeders to focus on selection for one or all determinants.

This framework was a radical departure from earlier thinking on ways to improve the growth and yield of water-limited crops. One of the most important aspects of this identity is that it focuses on crop productivity and not drought tolerance or drought resistance and it also removes the focus away from survival, which for crop plants, has little relevance. This latter point has been important as most candidate transgenes for drought have been identified from selecting for survival in managed conditions yet this bears no relationship to crop performance [6]. The focus on crop productivity also turned our attention to longer term processes associated with crop production and to resource limitations. It drew attention to the importance of practices pre-crop (stubble retention, fallow weed control, crop sequence, sowing time) and in-crop (weed control, fertiliser application) to improve available water use and water use efficiency so as to increase grain yield [7].

This identity provided a very important framework for improving wheat productivity in water-limited environments through genetic improvement.

23.3 Breeding and Selection for Yield in Water-Limited Environments

Wheat breeding is generally empirical – that is guided by experience. It is similar world-wide with selection during early generations for highly heritable traits such as flowering time, plant height, some disease resistances and some grain attributes.

After selection and selfing more homozygous germplasm is available for evaluation in larger field plots. Identification of more elite material is then made with a focus on grain yield, disease resistance and grain quality, if the grain is used for making end products. This elite material is then tested at multi-locations in the target region. Eventually, after consideration of yield performance, disease resistance and grain quality new cultivars are released. Molecular markers are likely to be included in the selection process for traits controlled by few loci. So far there are none that specifically target dry conditions. However, there are markers that can help optimise the time of flowering to avoid drought and markers for acid soil tolerance and nematode resistance that are important to improve the growth of root systems where soil acidity and nematodes are problems.

Gains in breeding under water-limited conditions are likely to be slower than under favourable conditions as year-to-year variation is highly unpredictable and can vary substantially. Accordingly, genotype x environment interactions for yield are high making yield progress slow. This raises the question as to whether further gains may be possible by selecting for specific physiological traits which influence water use, water-use efficiency or harvest index as well as grain yield.

23.4 Direct Selection for Grain Yield or Trait-Based Selection to Improve Performance Under Drought?

A discussion which is important is whether trait-based selection for drought is worthwhile or whether direct selection for grain yield is always going to be more effective. It is common to select for obvious defects in early generations such as grain sterility and susceptibility to disease; it is also common to select for appropriate flowering time or plant height and certain grain quality attributes. But it is rare for breeders to select for physiological traits that may be related to yield under drought. This is largely because easily selectable traits have already been selected and fixed in breeding germplasm; it is also because breeders believe they make more gain using direct selection for yield. It is generally assumed that direct selection for the highest yielding lines in water-limited environments will automatically combine the most favourable traits. Furthermore, the efficiency of direct selection for grain yield has improved in recent decades. Machinery for sowing and harvesting has vastly improved, robotics for seed packaging large trials speeds up the process and reduces errors, and improved herbicides has led to large trials where thousands of lines are evaluated in multi-locations. In addition, statistical tools to manage spatial variability and trial analysis have become outstanding. Improved understanding of limiting factors associated with soils or nutrition have also resulted in better agronomy of breeding trials. Overall, the efficiency of breeding and the direct selection for yield, which integrates all physiological processes, has resulted in very efficient breeding programs (see Chap. 2). Thus, one may ask what is the value of trait-based selection?

Trait-based selection does have highly appealing features for breeding. It is designed to complement existing breeding programs and is not dissimilar to approaches taken to improve specific resistances/tolerances to diseases, soil chemical constraint or for components of grain quality. Possible advantages of this trait-based approach to breeding have previously been enunciated [8]. They are briefly listed here with examples or specific comments given in italics.

1. The desirable expression or appropriate genetic variability for important physiological traits may not be present in breeding programs. Thus, genotypes with greater expression of important traits must be identified for use in breeding; this can lead to faster and greater genetic gain for important traits.
   Long coleoptiles for better emergence in dry soils in a semi-dwarf background are generally not found in breeding programs [8] *– as are other proven traits such as early vigour, xylem vessel diameter.*
2. The physiological trait may have a higher heritability than grain yield and so selection for it may lead to faster genetic gain in yield
   E.g. coleoptile length, early vigour, transpiration efficiency
3. Selection for the trait may be more cost-effective than selection for yield
   This must be the case for all traits if they are to be successful. It is worth pointing out that the cost per field plot for yield is not cheap.
4. Out-of-season selection or selection in controlled environments may be possible resulting in multiple cycles of selection per year and faster genetic gain.
   This is the case for most of the traits given in Table 23.1.
5. The trait may be amenable to marker-assisted selection, whereas grain yield is not.
   See also Table 23.1.
6. Multiple yield enhancing traits may be pyramided.
   A good example of this is coleoptile length and early seedling vigour [9].

23.5 Which Physiological Traits?

Flowering time is the most important trait in almost all dry environments. Fortunately, it is also one of the most heritable traits in wheat and it is easy to select visually. Ideally flowering must occur whilst conditions are still favourable and before it gets too dry or too hot. It is all to do with getting timing right. Time of flowering has been the single most important trait in most dry environments as it marks the transition between further growth of leaves, stems and tillers and the growth of grains. In many regions drought commonly occurs during grain-filling at the end of the season (i.e. terminal drought) when temperatures are higher and so evapotranspiration is also higher. In these circumstances the earlier flowering occurs then the more favourable conditions will be for grain filling. It is worth noting that since the beginning of wheat improvement in dryland Australia in the late 1800s breeders were selecting for greater yields but they were achieving this by inadvertently selecting

Table 23.1 Summary of the most important traits, selection environment and selection method for improving yield of temperate cereals in water-limited environments

Trait	Selection environment – favourable or droughted	Markers or genomic regions identified	Most efficient selection method
Time of flowering	Either	Yes	Phenotype and marker
Seedling establishment	Favourable	Yes	Phenotype and marker
Shoot vigour	Favourable	Yes	Phenotype
Root vigour	Favourable	Yes	Phenotype
Root architecture	Favourable	No	Phenotype
Transpiration efficiency (CID)	Favourable	Yes	Phenotype
Stomatal conductance (transpiration)	Favourable	Yes	Phenotype
Stem carbohydrate remobilization (WSC)	Favourable	Yes	Phenotype
Tillering	Favourable	Yes	Phenotype or marker
Glaucousness	Favourable	Yes	Phenotype
Leaf rolling	Favourable	Yes	Phenotype
Floret sterility	Non-droughted	Yes	Phenotype
Canopy architecture	Favourable	Yes	Phenotype

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for earlier maturity; the importance of phenology was probably not evident at the time.

Selection for physiological traits to indirectly improve yields started to receive attention around the time of the Green Revolution and the time that the dwarfing genes *Rht-B1b* and *Rht-D1b* were being widely recognised in breeding as a way of increasing grain yield and this drew attention to other possible physiological traits that may be important. For example, what role do awns play in wheat [10]? Are there root system traits, that should be important under drought, available to incorporate into wheats in dry regions and is there genetic variation available [11]? Also, much information was available in the ecological literature on how indigenous plants coped with chronic dry conditions and there was substantial interest in understanding the mechanisms involved as it was proposed that they may also be applied to crops. However, the reality is there are few similarities between plants growing in dry conditions in the wild and crops on farms. Indigenous plants in dry conditions must survive dry conditions whereas crops on farms must be managed so that they produce income for farmers. Survival tactics generally means very slow growth or the cessation of it and this limits the ability of the crop to respond to rainfall.

One of the important features of the Passioura identity was the focus away from survival and towards productivity. Each of the components of the identity are focused on crop growth that results in grain production when water is limited. It has become an important guide to identify traits in breeding as any increase in grain yield must come from an improvement in one of the three components. A corollary of this is that if breeders observe genetic variation for a trait in their populations then it will only be important for yield if it alters one of the three components. Thus, the identity can be used effectively to do a reality check on whether an observed trait will influence yield or not.

Table 23.1 shows a list of the most important traits that have been recommended to improve the grain yield of wheat where water is limited (e.g. [8, 12]). These traits may not be universally important in all rainfed environments as some may have greater impact in specific environments. Indeed, some traits listed may negatively impact on yield in some dry environments. A good example of this is fast early vigour which is considered highly desirable to increase the proportion of transpiration relative to evapotranspiration when the soil surface is exposed and mostly moist during the early vegetative phase as this increases crop water use and increases biomass. However, if the crop is growing on stored soil moisture the extra leaf area growth associated with early vigour is likely to deplete soil water such that little would be available for grain filling and yield would be lower. Further discussion on each of these traits is given in Richards et al. [13].

Several important features are apparent from Table 23.1. Firstly, the most effective environment to select for traits associated with performance under drought is under favourable moisture conditions. Favourable conditions maximise the phenotypic variance and heritability of each trait whereas dry conditions reduce them to slow genetic advance. Secondly, molecular markers or genomic regions (quantitative trait loci – QTL) have been identified for most of the key traits linked to improved performance under drought (Table 23.1). A third notable feature is that, currently, the accurate measurement of the actual phenotype rather than a molecular marker or QTL is the most efficient and fastest method of selection for almost all traits. This is because most traits are controlled by many genes.

There are several drawbacks to using QTL. Firstly, they vary with genetic background and so the identification of QTL is often specific only to the population being studied. QTL x environment interactions are extremely widespread. Finally, all QTL may only account for 30–70% of the total phenotypic variation whereas accurate measurement of the phenotype, even for polygenic traits, may be close to 100% of the phenotypic variation.

For the reasons above a considerable research investment into discovering ways to maximise repeatable phenotypic variation and ways to hasten the time taken for the measurement of the phenotype remains of utmost importance to make effective genetic gain.

It is worth noting that many of these traits will also be important for other abiotic stresses – in particular, adaptation to heat. The best examples here are: (i) time of flowering to adjust phenology, (ii) seedling establishment, (iii) glaucousness, (iv) leaf rolling, (v) canopy erectness. See Hunt et al. [14] for more detailed information on these traits in relation to heat.

Many of the traits shown in Table 23.1 are unlikely to be universally important as was mentioned earlier with the example of early vigour. Thus, some will be critical for some rainfall patterns and not for others. Some physiological traits may also require a particular crop management to obtain maximum benefit. Understanding these interactions will be important to capture the value in new varieties.

The same traits are given in Table 23.2 together with an assessment as to whether they are likely to be region specific and the management that may be important to increase their impact or expression. It is evident from Table 23.2 that if any of these traits are incorporated into released varieties then management practices could also be modified to further enhance their value on-farm. This point is particularly important as the greatest successes in breeding have often been associated with a particular management. The best example of this is the Green Revolution where wheats with the dwarfing genes were able to respond to better management and higher inputs because they did not lodge.

Table 23.2 Traits currently being studied or in breeding programs [13] that have been identified to improve yield in dry environments and an assessment of which management practices may influence their impact

Genetically altered trait	Region specific or universal	Agronomic condition or management practice that could influence trait impact
Time of flowering	Universal	Sowing time, prevalence of frost around flowering.
Seedling establishment (long coleoptile)	Universal	Timely sowing, stored soil water, pre-emergent herbicides
Early shoot vigour	Region specific	Late sowing, herbicide resistant weeds, reduced tillage, plant density and row spacing, nitrogen, sowing depth
Root vigour	Universal	Hard soil, nutrient deficient, hostile soil, cultivation, herbicides
Root depth	Region specific	Sowing density, row spacing, cultivation, seed dressings
Reduced tillering	Region specific	Sowing density, early sowing, nitrogen management, sowing depth
Transpiration efficiency/ stomatal conductance	Universal	Stored soil water at sowing, crop duration, sowing date, nitrogen management
Crop duration	Universal	Sowing date, nitrogen management, sowing density, row spacing, availability of grazing animals
Floret sterility	Universal	Sowing date, nitrogen management
Glaucousness	Universal	None identified
Stem carbohydrate storage and remobilisation	Universal	Sowing density, nitrogen management, fungicides
Stay green	Region specific (?)	Nitrogen management, fungicides
Canopy architecture at flowering	Universal	Sowing density, row spacing, nitrogen management

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23.6 Trait Validation and Translation to Breeding Programs

Once traits have been identified the next step is the most important. It is to translate the trait discovery to a product for farmers. It involves the incorporation of the trait into a breeding program and to validate the impact on yield. This can be done at the same time. There are several ways this can be accomplished, and it depends on the trait. If the trait is already in the breeding program and its expression is satisfactory then active selection for the trait is possible as lines progress through the breeding pipeline. If the expression of the trait is known (measured) for each line in a yield trial, then the relationship between trait expression and yield can be assessed. In these trials it is essential to also score height and flowering time on each line to ensure that these factors are equivalent for each trait and that they are not responsible for trait or yield variation.

When the expression of the physiological trait in a breeding population is inadequate and needs to be enhanced then new parental material is required to inject into the breeding program. Under these circumstances a more directed breeding program is required and the nature of it will depend on the inheritance and heritability of the physiological trait. Ideally, a backcrossing program is used to introduce the trait into a desirable background which will be suitable for release to farmers. This will also provide yield information on the high or low expression of the trait in the same genetic background. Conducting a backcrossing program for a complex trait is feasible providing the phenotype can be screened quickly and effectively. More detail on trait validation and incorporation of different traits into breeding programs is also described by Richards et al. [13]. An example of breeding for a complex physiological trait, which is also complex genetically, is given in the case study below.

In general, success in breeding depends upon being able to screen large numbers effectively, it also makes a substantial difference if the selectable trait has a high heritability and that breeders have substantial genetic variation in their breeding population so that selection can occur. But this can still result in slow progress because of large genotype x season interactions.

23.7 A Case Study of Translational Research: Breeding Wheat Varieties with High Transpiration Efficiency Using Carbon Isotope Discrimination

An improvement in transpiration efficiency (TE), i.e. the ratio of the rates of photosynthesis to transpiration, will be important in all water-limited environments provided it is not negatively associated with factors that increase water use or harvest index. During photosynthesis plants discriminate against the rarer $^{13}CO_2$ and prefer the more abundant $^{12}CO_2$. Farquhar and Richards [16] demonstrated that the degree of discrimination against ^{13}C was indeed related to TE in wheat and that there were genetic differences. They proposed that a measure of discrimination denoted as $\Delta^{13}C$ of plant material was a robust measure of TE as it was an integrated measure of photosynthesis and transpiration during the growth of that plant material. Thus, it is not a spot measure like leaf photosynthesis but a time integrated measure over the life of the plant sample measured. It was proposed that selecting for a low $\Delta^{13}C$ could increase TE of crops.

After investigating rainfall patterns throughout the wheat growing regions in Australia we targeted the northern wheat growing region as the region that low $\Delta^{13}C$ should be most effective. This region has less in-season rainfall as a proportion of total rainfall than other parts of Australia and hence relies more on water stored in the soil than other regions. Low $\Delta^{13}C$ can be associated with a lower stomatal conductance and so there may be an extra benefit for low $\Delta^{13}C$ in water-limited environments where there is a terminal drought, such as in Australia's northern region, as a lower conductance may conserve soil moisture for use during grain filling which is likely to increase harvest index [17].

For regions of Australia with a larger proportion of in-season rainfall, particularly during the winter, we believe greater progress in yield could be made by selecting for greater early vigour [8, 18, 19]. Lines with low $\Delta^{13}C$ may be at a disadvantage due to a possible negative association between early growth and low $\Delta^{13}C$ [19]. We undertook a detailed study on how carbon isotope discrimination ($\Delta^{13}C$) varies with season, genotype, growth conditions and the tissue to measure. This is described in Condon et al. [20]. This information was essential to establish the most effective way to screen germplasm for $\Delta^{13}C$. This aspect of the work took several years of research. It established that the $\Delta^{13}C$ was not expressed satisfactorily under controlled conditions and that it had to be measured in the field and that single plants or single rows could be used as they had the same value of $\Delta^{13}C$ as plots. It was also established that the measurement of $\Delta^{13}C$ is ideally done at the early mid-tillering stage of growth and that the soil moisture conditions should be favourable. If conditions are unfavourable, then this can alter stomatal conductance and hence alter the $\Delta^{13}C$ value. These factors established that optimal conditions were important to maximise the genetic component of $\Delta^{13}C$ variation and hence the heritability.

There was substantial risk involved in selecting for $\Delta^{13}C$ in a breeding program as it is a complex trait and, while QTL for $\Delta^{13}C$ have also been identified in several wheat populations, each of these QTL have a small effect and therefore unlikely to be useful in breeding [21]. On the other hand, earlier work established that the measurement of $\Delta^{13}C$ was highly repeatable and heritable and genotype x year interactions were small and it is an integrative measure over time [18].

The research described above was conducted at the same time as an extensive search was made for the most suitable donor of high TE (low $\Delta^{13}C$) to use in the breeding program. An older commercial variety from the southern part of Australia called Quarrion was chosen. It was a winter wheat, but a spring wheat was required for the target region. Despite some limitations Quarrion already had a reasonable 'package' of adaptation, disease resistance and grain quality to the target region and so this variety was unlikely to introduce too many undesirable features into the breeding program. A backcross program was embarked upon and the reason for this is that the recurrent parent from the target region that already possessed highly desirable attributes could be chosen. In this case Hartog was chosen as the recurrent parent. It was already very well adapted to the target region in terms of yield. It was accepted by growers because of its yield and it also had robust disease resistance and very good grain quality and most important it had a relatively low TE (high $\Delta^{13}C$). A breeding program was commenced to backcross low $\Delta^{13}C$ (high TE) from the donor parent Quarrion into the variety Hartog. Another commercial wheat was also chosen to be a recurrent parent that had very high yield but poor grain quality and a low TE. Over time the importance of grain quality in this region increased and so the focus on the Hartog background increased.

Time was clearly important as during the backcrossing disease resistances can break down and further breeding progress in yield can mean the recurrent parent is superceded. The initial generations were speeded up in the glasshouse and we conducted our first screen in the field on F_3 lines. Multiple low $\Delta^{13}C$ lines were selected and immediately crossed several times to Hartog and BC_2F_4 lines were developed in the glasshouse. Large numbers of these lines were grown in the field to select for low $\Delta^{13}C$. A substantial number of $BC_2F_{4.6}$ lines were then yield tested over several years at multiple locations as well as extensive grain quality and disease resistance testing. Limited backcrossing was done to retain as much variation as possible in agronomic and grain quality traits so that selection for these traits could also be carried out.

Studies demonstrated that in south-eastern Australia lines selected for low $\Delta^{13}C$ resulted in a 2 to 15% yield advantage at yield levels between 5 t ha^{-1} and 1 t ha^{-1} when compared with high-$\Delta^{13}C$ sister lines [22]. Subsequently the varieties Drysdale and Rees were released commercially. These varieties combined high TE with broad spectrum disease resistance and with high grain quality suitable for international markets. Unfortunately, soon after their release, a new exotic strain of stripe rust entered Australia that was virulent on Drysdale and Rees and this has limited the adoption of these varieties. Backing up the breeding program a more-recent spring wheat variety, LPB Scout, derived from parents with low $\Delta^{13}C$ was also released in Australia.

Clearly, $\Delta^{13}C$ is a complex trait and, while QTL for $\Delta^{13}C$ have also been identified in several wheat populations, each of these QTL have had a small effect and therefore unlikely to be useful in breeding [21].

23.8 The Elements of Success

Retrospectively it is evident that the approach enunciated by Passioura [5] to increase the yield of water-limited crops has been enlightening and has provided clear guidelines to both breeders and agronomists (see also [3]). It has been successful because it proposed a resource-driven approach linked to crop productivity instead of associating yield with drought resistance. A further extension to these ideas, developed by French and Schultz [2], identified a practical upper limit to the yield of field grown crops in water-limited environments. This upper limit, linearly related to the water supply, was adopted as a benchmark by agronomists and farmers, and has been particularly important to improving the management of water-limited crops worldwide.

The main elements of success have been to identify physiological traits to improve performance under drought and the following points are suggested as essential for success:

1. A clear physiological framework complimented by a rigorous understanding of the target environment.
2. A strong focus on wheat improvement for a target set of environments.
3. An integrated stable team with skills in agronomy, physiology, molecular biology, genetics and breeding that are mainly located together and who have daily dialogue.
4. A focus on precise phenotyping.
5. A commitment to field research and field validation using appropriate populations fixed for height and maturity but varying for the target trait(s).
6. Stability in funding and a long-term commitment to maintaining a broad skills base.
7. A commitment to the application of results and germplasm to commercial plant breeders, combined with a regular dialogue with breeders.
8. An interaction with farmers and knowledge of the broader cereal industry.

However, success in delivering to breeders and then breeders delivering new varieties to farmers is rare. Failure is where the trait is not adopted in breeding programs. There can be many reasons for failure and some are:

1. The hands-on commercial breeder does not have the time or commitment to the trait as does the pre-breeder. The breeder is more committed to his/her own material where they designed the cross and have nurtured the material through the breeding process.
2. There may be more immediate priorities for the breeder such as more robust disease resistance or better grain quality that will be more readily adopted by farmers.
3. The breeder may receive unadapted parental material from the pre-breeder which means that the breeder has to make the initial crosses and make selections in subsequent generations in unadapted material.
4. Where the breeder does receive adapted material such as in a BC_2F_3 material the genetic background may not be suitable to the breeder's target environment.
5. If the breeder has to make selection for the trait then she/he may not have the resources nor the intimate knowledge of the physiological trait to make effective selection.
6. There could be IP issues which may discourage commitment by the breeder.

It is proposed that for delivery of new varieties to farmers the best solution is for the pre-breeder to work side-by-side with the breeder throughout every part of the breeding process. This starts with the breeder having input into the most suitable genetic backgrounds to use in crossing and it may involve pre-release parental material from the breeding program. The breeder and pre-breeder may then guide the germplasm through early generation speed breeding to provide the pre-breeder with germplasm to conduct effective early generation selections for the desired trait. Later generations in the field then require input from both the breeder and pre-breeder.

23.9 Key Concepts

- Trait based selection can complement established breeding methods to improve yield in water-limited environments.
- The presence of limiting factors that impede the growth of an effective root system should first be explored and overcome if present e.g. root diseases and/or soil chemical constraints.
- Identification of important traits must be based on a crop productivity framework of water-use, water-use efficiency and harvest index. This must be in relation to the target environment.
- Management practices must be considered in relation to traits as they can be synergistic to yield.
- Most important traits are polygenic and unsuitable for marker-based selection. However, high throughput selection methods can generally be developed.
- A close working relationship with a commercial breeder is essential for success to develop an integrated varietal package for farmers and to validate traits in the field as quickly as possible.

23.10 Summary

A scientific understanding of factors underpinning adaptation to water-limited environments coupled with good genetics and breeding will deliver potential varieties and/or parents with potential for improved performance under drought in the target environments. Success in the delivery of new varieties with yield enhancing traits will finally depend on forming a strong relationship with a commercial breeder.

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