

Breeding Wheat Genotypes for Water Deficit Environments

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1 Introduction

Wheat (*Triticum aestivum* L.) is grown world wide and is the most widely adapted cereal. This crop is mainly grown under rainfed areas where rainfall ranges from 250 to 2000 mm annually (Behl, 1994). Thirty seven per cent of the area in developing countries consists of semi-arid environments in which available moisture contributes a primary constraint on wheat production. The productivity in such environments can only be increased by the development of varieties which are well adapted to dry conditions.

Genetic improvement of crops for drought resistance requires a search for possible physiological components of drought resistance and the exploration of their genetic variation (Blum and Pnuel, 1990). In the past decade, the breeding for improved drought resistance has emerged through four basic approaches (Turner, 1986). The first approach was to breed for high yield and to assume that this will provide a yield advantage under suboptimal conditions. The second approach was to breed for maximum yield in the target environment. This approach suffers from the problems that water limited environments are notably variable from year to year and the expression of low variability for yield and its components in this environment make the breeding progress slow. The third approach involves the development of cultivars for water limited environments through selection and incorporation of physiological and morphological mechanisms for drought resistance through traditional breeding programmes. To this end, considerable progress for rapid screening methods has been made. The fourth approach for breeding under water limited conditions does not utilize multiple physiological selection criteria, but aims to establish a single drought resistant character which will benefit yield under water limited conditions and then incorporate it into the existing breeding programme (Sadiq et al., 1994).

The improvement of yield under water stress should, therefore, combine a reasonably high yield potential with a specific plant factor which would buffer yield against a severe reduction under stress (Blum, 1989). The drought resistance in many instances may also vary according to different stages of plant growth viz., early (preanthesis), mid (flowering) and late season (grain fill). This indicates that the genetic mechanisms of drought resistance are independent and process-specific for each stage of development. Therefore, there is a need to identify the specific characters associated with

drought tolerance over different stages of plant development and the genetics thereof which would help to form the basis of crop improvement programmes (Sadiq et al., 1994).

2 Patterns of drought

Drought resistance in many instances needs to be categorized according to the growth stage when it occurs e.g. early (preanthesis), mid season (flowering), late season (grainfill), or intermittent, of which depend on crop season, rainfall pattern and various other agro-ecological factors. A plant resistant in early stage may or may not be resistant at later stages of plant growth (Blum, 1989). Therefore, the drought resistant genotypes must be tailored in consideration with the occurrence of drought and susceptibility of particular plant growth stages in a particular area. On a global basis, following general patterns of moisture stress can be identified for wheat (Edmeads et al., 1989).

1. Mediterranean: This includes areas of western Asia, northern Africa, Chile and southern and western Australia. The small grains sown in the winter experience a moderate moisture stress at anthesis with stress increasing in severity throughout the grain filling.
2. Southern cone of South America: This pattern is common in Argentina, parts of southern Brazil and north eastern Australia. Stress affects the crop during tillering and perhaps up to anthesis but normally during grain filling.
3. Indian Sub-Continent: In this area small grain cereals are sown during the dry winter season and survive on stored moisture, occasional rains and supplemental irrigation. As temperatures rise in spring and summer in India, Pakistan, Bangladesh and Burma, moisture stress becomes increasingly common during anthesis and grain filling.

In addition, throughout the season there can be unpredictable dry periods which vary considerably in intensity and length within and between years and locations. The patterns appear to describe distinct target environments. However, a common characteristic of all dry tropical environments is high variability both in seasonal rainfall totals and rainfall distribution throughout the season. The anthesis and reproductive stages are commonly affected in all the above mentioned areas, whereas the vegetative stage seemed to be equally prone to drought stress in the Indian Sub-Continent.

Genotype	Grain yield g/plant		Days to heading (S)	DSI	DRI
	N	S			
WH 147	17.00	6.33	75.00	0.84	1.71
WH 147(U)	18.28	6.87	74.01	0.83	1.98
LoK-1	15.75	4.25	84.10	0.98	0.33
WH 157	16.25	4.29	86.95	0.98	0.46
Kharchia 65	11.38	5.49	88.90	0.69	2.62
HW 2001	11.45	1.62	84.33	1.20	-1.82
CPAN 1992	18.60	3.72	79.98	1.06	-0.72
C 306	12.60	7.00	89.00	0.59	3.93
K 68	13.70	1.03	92.13	1.26	2.11
WH 331	11.20	2.90	84.90	1.08	-0.05
WH 553	16.87	2.62	82.95	1.13	-1.43
Hindi 62	13.93	3.41	92.98	1.01	0.24
PBW 65	17.52	3.82	83.05	0.95	-1.61
WL 410	19.60	3.85	83.33	0.98	0.87
WL 1562	16.70	4.41	82.80	0.98	0.06
Kundan	10.85	3.02	84.67	0.96	0.24
HPW(DL) 30	14.60	3.65	83.00	1.00	0.14
VL 421	9.60	3.22	88.33	0.89	0.65
HD 2329	18.05	3.98	76.00	1.03	-0.82
HD 2329 (U)	20.07	4.83	75.67	1.1	-0.24
HPW 42	19.36	4.53	74.33	0.90	-0.54
HS 295	14.50	2.53	82.33	1.10	-1.07
HPW 56	9.43	3.02	84.03	0.90	0.36
CPAN 3004	12.30	1.90	85.67	1.19	-1.01
HPW 65	18.45	1.55	87.67	1.19	-1.17
RL 6	22.52	5.12	81.67	0.95	-0.24
RL 7	10.20	2.60	85.67	0.99	0.09
RL 68	14.22	2.33	83.97	1.11	-1.00
RL 84	12.35	3.00	83.00	1.00	-0.03
LoK-1 (U)	12.32	4.55	79.05	0.844	0.92

Table 1: Grain yield, days to heading, drought susceptibility index (DSI) and drought resistance index (DRI) of 30 wheat varieties grown under normal (N) and drought stress (S) conditions

3 Parameters of drought resistance

Agronomically a major criterion of breeding for drought resistance is plant productivity. The utilization of various screening techniques in the course of breeding work requires the establishment of significant associations between plant productivity under stress and the various possible physiological and biochemical components of drought resistance. Great progress towards this end has been made in the last three decades (Acevedo et al., 1988). At present, the drought susceptibility index proposed by Fischer and Maurer (1978) is generally used to quantify drought resistance. This index does not consider the time to flowering and is not associated with drought escape and yield potential. Yield under drought conditions is generally negatively related with anthesis date (Acevedo et al., 1988; Behl et al., 1992; Dha nda ,

1993; Fischer and Wood, 1979). In view of this, it may be presumed that DSI is not a suitable indicator of drought resistance on yield level.

Plagella et al. 1992 reported leaf reflectance (IR) at 1940 nm (a water absorption peak) as a suitable method of evaluating water retention capability under drought stress. The IR test showed good capacity when applied at the flowering stage on (a) excised fresh flag leaves, if drought conditions occurred in the field, (b) dehydrated flag leaves at 25 °C for 24 h at 60% relative humidity. Subsequently, Plagella et al. (1994) assessed the predictive value of the IR test in comparison with a yield based DSI. They concluded DSI as a good parameter for the selection of drought tolerant genotypes. Dib et al (1994) explored the possibility of using Proline Accumulation and Fluorescence Inhibition as predictive tests for drought tolerance. Both these parameters showed negative correlation with DSI grain yield, biological yield, 1000 grain weight and tillering index.

Blum (1988) advocated the use of stability analysis (Eberhart and Russel, 1966; Finlay and Wilkinson; 1963) to define stress resistance in terms of yield, provided that the major components of variation in the environmental index could be attributed to water deficit. The drought resistance of a particular variety may be given by the intercept of cultivar yield regressed on the environmental index (mean yield). This approach considers neither the confounding effects of flowering time on yield nor the effect of

yield potential on the slope of the regression and hence on the intercept of drought resistance. Labuschagne and Deventer, (1992) and Cooper et al, (1994) observed significant cultivar and moisture level, and lime and water stress interactions.

Drought resistance index (DRI) defined by Bidinger et al., (1987), based on the residual variation in grain yield adjusted for experimental error, seems to be a better parameter for categorization of drought resistant cultivars. The DRI is capable of removing the influence of confounding factors, e.g. early flowering, yield potential and so on through a multiple regression technique. This index was calculated for 30 varieties of wheat by considering the grain yield at the wetter site as yield potential along with days to heading at the same site (Table 1).

This index was positively associated with yield under drought conditions and independent of yield potential and time to flowering (Dhanda, 1993). This index was considered as a good criterion for assessment of drought resistance as the resistance is free from the confounding effects of other factors.

4 Evaluation of traits

The specific plant traits are of value to plant breeders only if they can be used as selection criteria. For this purpose these traits must have a relatively high heritability, also rapid and simple assessment and have a proven effect on final crop yields under drought stress. Compensation of one system for another and interactions with the environment make these even more difficult to correlate with the grain yield (Blum, 1989). Therefore, an integrated approach of testing the material in the field, laboratory and in vitro conditions is required with the emphasis on combining the components of drought resistance with high yield potential. A number of specific plant traits for drought resistance may be categorized as follows:

4.1 Drought escape and developmental plasticity

Short duration cultivars that escape terminal stress can easily be used because the heritability of flowering time is usually high, and character is easily assessed. They can contribute greatly to yield stability in arid regions where terminal drought stress occurs (Behl et al., 1992; Fischer and Wood, 1979; Ludlow and Muchow, 1990).

Earliness is frequently associated with reduced yield potential (Dalton, 1967) but an increase in harvest index can compensate this (Evans, 1981; Evans et al., 1984). Perhaps the major disadvantage of earliness as an escape mechanism is that in a season with early drought stress, short duration varieties are more seriously affected (Mahalakshmi and Bidinger, 1985). Therefore, a farmer interested in stability of yield should grow both normal and short duration cultivars as part of a mixed cropping system.

Photoperiod insensitivity is highly heritable and can be selected easily if environments are available or can be created that differ in day length. But it may not be advantageous because of the large number of pleiotropic effects of photosensitive genes and its association with adaptation (Bidinger and Witcomb, 1989; Blum, 1988).

There are reports of higher yields with an indeterminate tillering habit in dry land environments (Richards, 1987). Mahalakshmi and Bidinger (1985) reported that stable yields can be obtained in asynchronous and high tillering genotypes under drought stress. As tillering and asynchrony are heritable traits and can be selected on a visual basis in spaced plants, plant breeders can use this trait in a breeding programme for drought resistance.

4.2 Drought avoidance

4.2.1 Stomatal and epidermal conductance

The selection can be used to reduce the conductance through stomata and epidermis (cuticle) during periods of

maximum daily evaporative demand, without a significant reduction of total photosynthesis. For selection to be effective, the degree of conductance needs to have a reasonably high heritability. The waxes are under the control of major and minor genes and have high heritability, but for stomatal conductance, the available information is not consistent on these points (Jones, 1980; Jones, 1987).

Stomatal diffusion resistance, rate of evaporation from the flag leaf at the milk stage and water use efficiency (WUE) correlated quite significantly with grain weight per plant, Chai et al (1993). From a practical view point, it would be difficult to use stomatal conductance in a breeding programme because the measurements may vary drastically with the time of the day, and because it is not feasible at present to record stomatal conductance on large populations that plant breeders normally deal with.

Excised leaf water loss as a measure of epidermal conductance and as a suitable technique for screening large numbers of populations indicated low correlations with grain yield under drought stress (Clarke, 1987). Excised leaf water loss was related to drought resistance in wheat (McCaig and Ramagosa, 1991; Winter et al., 1988), but its relationship was not consistent on the various stages of plant growth (Dhanda, 1993). Several other reports on excised leaf water loss are also contradictory (Clarke, 1992; Cedela et al., 1994).

Epidermal conductance can also be estimated through measurements of total wax content (Ebercon, 1977). Blum (1985), however, pointed out that the effects of epicuticular waxes extend beyond the direct effects on cuticular transpiration, as they affect leaf reflectance. Therefore, selecting for increased epicuticular waxes may not be a worthwhile breeding objective because of the direct value of leaf reflectance and the reduction in cuticular transpiration.

4.2.2 Leaf characteristics

Richards (1987) reported that glaucous lines in wheat out yielded the non-glaucous lines because of a reduced transpiration during the night (reduced cuticular transpiration) and reduced reflectance during the day time, a lower level of transpiration for a given level of photosynthesis and a cooler photosynthetic surface. Leaf pubescence also reduces the energy load during day time through reduced leaf temperature or transpiration or both (Baldocchi et al., 1983). These characters are under genetic control and influenced by both major and minor genes. These characters can also be visually assessed. In crops that have no epicuticular wax, it would be worthwhile to include leaf pubescence in selection criteria.

An upright leaf habit in wheat reduces the energy load on the leaf during the times of the day when incident radiation is the highest and consequently reduces the leaf temperature and transpiration (Innes and Blackwell, 1983). This character is heritable, easily assessed and can be used as a part of drought resistance breeding programmes (Schulze, 1988).

Leaf rolling is also a common response to drought in annual cereals and results in radiation shedding (Turner and Kramer, 1980). Although there is some evidence for genetic differences for this trait, it is not clear that the field differences in leaf rolling represent differential responses to stress or different degrees of stress (Ludlow and Muchow, 1988). Consequently, it cannot be recommended as a selection criterion.

Reduced leaf area, leaf firing and accelerated senescence are common responses to water deficits. The reduction in leaf area increases plant survival but may reduce further crop growth and yield because of reduction in the photosynthetic capacity. Ludlow and Muchow (1990) concluded that maintenance of leaf area was undesirable under terminal stress and desirable under intermittent stress. This trait is also under genetic control and can serve as a good selection criteria under drought stress conditions.

4.2.3 Root characteristics

The traditional view is that a large vigorous root system, through avoidance of plant water deficits, is a major feature of high yield in water limited environments. However, where the soil is not replenished at a sufficient depth between crops, greater root depth would be of little advantage, and could even be disadvantageous by reducing shoot dry weight or harvest index because biomass is partitioned to root at the expense of shoots (Ludlow and Muchow, 1990; Passioura, 1983). Furthermore, several workers have shown that a greater rooting depth is associated with improved performance under water limited field conditions, e. g. *sorghum* (Wright and Smith, 1983) and wheat (Hurd, 1974; Sharma and Lafaver, 1992). The heritability and gene action studies of this trait are scarce due to the difficulty in measuring this trait, and therefore, more work is required in this direction.

Increased root hydraulic resistance has been proposed as a valuable trait for crops growing mainly on stored water (Passioura, 1977). By restricting water use more water is available for grain filling, thus minimizing the decrease in harvest index. Passioura (1983) presented experimental evidence showing sufficient variability and heritability for this trait in wheat, and the lines with increased hydraulic resistance had a yield advantage in dry experiments. However, further information is required to assess the value of this trait for adopting as a selection criterion for drought resistance. Farshadfar (1993) identified ev. Plainsman as most suitable for breeding drought tolerance due to its better root system, higher yield and lower plant height.

4.3 Dehydration tolerance

4.3.1 Water status of plant

The degree to which plant parts withstand desiccation is expressed as relative water content or water potential at which leaves die. Among the various indications of leaf water status under stress, Schonfeld et al. (1988) and Ritchie et al. (1990) considered relative water content more reliable than the bulk measure of water turgor, water and solute potentials

because of its close relationship with cell volume, which reflect the balance between water supply to the leaf and transpiration rate. There is genetic variability in relative water content in wheat (Makoto et al, 1990) under drought stress conditions which could be used as a selection criterion. Because the water status of plants under drought stress influences survival, it has no direct effect on yield and its component. However, it contributes to dehydration tolerance and to leaf survival during intermittent water stress (Flower and Ludlow, 1986; Ludlow and Muchow, 1990; Sinclair and Ludlow, 1986). Therefore, it has limited scope for selecting for yield improvement under drought stress.

4.3.2 Osmotic adjustment

Osmotic adjustment involves the increase in the number of solute molecules inside the cells in response to a decline in external water potential. This has the effect of reducing the out flow of water from the cell, thereby reducing loss of turgor pressure. This allows the continuation of the turgor driven processes such as stomatal opening and expansion growth, though at reduced rates, to progressively lower water potentials (Ludlow and Muchow, 1990; Morgan, 1989). Genetic variability in osmotic adjustment has been found in wheat (Morgan et al., 1986) and for maintaining harvest index (Ludlow et al., 1990; Santamaria et al., 1990). However, the genetic information on this trait is scarce. Apart from the risk of exhausting soil water supply especially because of terminal stress, lack of rapid screening procedures, and low heritability, this trait can be used in association with components of yield, determinants of survival for increasing yield stability and potential index under drought stress (Ludlow and Muchow, 1990).

Osmotic adjustment is an important acclimation mechanism which could allow for the maintenance of relatively greater metabolic functions at low leaf water potentials (Gunasekera and Beakowitz 1992). Singh et al (1990) reported that cv.C 306 and Wtzu5 exhibited smaller reduction in leaf water potential and osmotic potential than other susceptible genotypes.

4.3.3 Remobilization of assimilates

Bidinger et al. (1977) observed that 20 % of the preanthesis assimilate can be transferred to the grain in water stressed wheat. In contrast values of up to 80 % have been recorded in sorghum subjected to water stress during grain filling stage (Ludlow and Muchow, 1990). Turner and Nicholes (1988) and Muchow (1989) have also shown that the contribution of preanthesis assimilate can be significant under drought. A high transfer of assimilate to grain yield would maximize harvest index and improve yield stability by acting as a buffer against the effects of water deficits on current assimilation. However, further work is required to assess the consequences of this trait on yield potential and lodging particularly in intermittent stress conditions.

4.3.4 Electrolyte leakage

This method of measuring drought tolerance introduced by Sullivan (1971) is based on in vitro desiccation of leaf tis-

sues and subsequent measurement of electrolyte leakage into an aqueous medium. This technique seems to be efficient as a measure of drought and heat tolerance and correlates well with tolerance of stress in other plant processes (Blum, 1988; Deshmukh et al., 1991; Premchandra et al., 1990; Saddalla et al., 1990; Sullivan and Ross, 1979). Genetic variability and heritability of electrolyte leakage in wheat was sufficiently high enough to use this trait as a selection criterion (Dhanda, 1993). Genotypic differences in cell membrane reaction can be observed using 40 per cent polyethylene glycol (PEG) - 6000. Using this technique, Singh et al. (1992) reported that cell membrane injury measured at 25 days after germination was related to genotypic performance under drought condition.

4.4 Metabolic indicators

In order to provide adaptation to drought, metabolites should be produced in well characterized reactions, accumulate in reproducible fashion, have clear functions in metabolism and a well understood mode of action in stressed tissue. Metabolites presently used as selection criteria do not meet these requirements. Proline for example, does not have well characterized reactions, clear functions or a clear mode of action (Lawlor, 1987). Soluble proteins or activities of enzymes (RuBPC-O) relate only photosynthetic capacity and their relation with drought resistance is unclear. Metabolites from photosynthesis or secondary reactions often correlate with a particular kind of stress threshold (Hsiao, 1973; Jones et al., 1989; Lawlor, 1987). This indicated that the metabolic functions can be correlated with growth and production. The most useful of these are amino acids (ABA, Betaines) and indicators of membrane damage (polyamines esp. putrescine). These are also related with other physiological changes e.g. osmotic adjustment and may be analysed by routine automated chemistry (Blum, 1989). Measurement of metabolic change provides an insight into the mechanisms of plant production under drought, although no one process unequivocally meets the criterion of predicting improved productivity and yield stability. Studies with drought tolerant C306 and drought susceptible HD2428 revealed that under irrigated conditions HD2428 maintained a relatively higher relative water content, membrane stability, chlorophyll stability, photosynthesis activities of nitrate reductase, glutamate dehydrogenase and glutamine synthetase as compared with C306. Under moisture stress C306 showed higher metabolic activity than HD2428 and a better recovery following irrigation for most of the measured traits. C306 is associated with its ability to maintain high relative water content, metabolic activity and membrane stability under conditions of water stress (Sairam, 1994). Water stress alters the equilibrium between free radical production and the enzymatic defence reaction in wheat species and also that hexaploids have less efficient antioxidant system than tetraploid and diploid wheat (Zhang and Kirkham, 1994). Activities of Superoxide dismutase (SOD), Catalase (CAT) and Peroxidase (POD) can be used as a parameter of membrane damage by free radicals.

4.5 Water use efficiency (WUE) and carbon assimilation

The amount of growth occurring when rainfall is limited depends on the ratio of assimilation rate to the transpiration rate. The term WUE represents the ratio of carbon gained to water lost by a single plant, it is usually reserved in a crop content for the ratio of carbon accumulated to the total water used, including soil evaporation. The differences for WUE were demonstrated in species and among the cultivars within species very early in this century (Briggs and Shantz, 1914). WUE simply involved measurement of plant dry weight and of the pot weight. Although simple in concept, it is tedious to apply on the large scale that is required for selection by breeders, however, in recent studies on genetic variations seen at single leaf and single plant level this could not be verified at field level (Jarvis and McNoughton, 1986). This may be due to the interaction of several other factors, such as leaf wax, cuticular transpiration, stomatal control influencing transpiration and assimilatory organs e. g. awns which have far better transpiration efficiency than glumes and flag leaves (Blum, 1985).

A recent approach of leaf isotopic carbon ratio ($^{13}C/^{12}C$) can be predictive of the genotype's WUE, which is extremely important (Farquhar and Richards, 1984; Farquhar et al., 1989). The theory predicts that the amount of discrimination is determined by the intercellular partial pressure of CO_2 in C3 plants which is then regulated by variation in both stomatal conductance and assimilatory capacity (Farquhar et al., 1982). Measurement of carbon isotope discrimination to estimate total growth relative to water use has many features attractive to breeders. It can be determined on fresh or stored, immature or mature plants, leaves, stems, or grains providing plant material was grown in the same environment. A particular advantage of this approach is that the plant need not necessarily be water stressed when analysed. On the other hand, the analysis requires an expensive instrument (ratio mass spectrometer) that is not readily available to most breeders.

The potential use of this technique will depend primarily on the criteria such as, it must be correlated with WUE in large field plots, hence, data in this regard is not available (Farquhar et al., 1989). Secondly, there must be variation for this trait, and it must have insignificant pleiotropic effects. Blum (1989) indicated sufficient variability for this trait in wheat but information on its linkage with other traits is lacking. Since the measurement of carbon isotope discrimination integrates the diffusion of CO_2 and H_2O into and out of leaves in relation to assimilatory capacity over an entire growing season, it may have considerable potential in plant breeding but it is too early to understand its significance.

4.6 Tissue and cell culture

Studies on the possibilities of using tissue and cell cultures in selection of drought resistance in wheat are just emerging. The procedure involves the selections of cell cultures or calluses under osmotic stress applied by polyethylene glycol (PEG). Handa et al. (1983), Mohamad and Nabors (1991) and Scott et al. (1992) showed that cells or calluses

tolerant to PEG stress can be obtained. Resistance indicated by PEG stress is largely dependent on osmotic adjustment (Blum, 1988), however, resistance was lost upon passage to a non-stress medium (Hasegawa et al., 1984). Tuchin and D'yachak (1994) described a method for producing resistant forms that involve a single selection cycle on selective medium with 20 per cent PEG.

The adaptive properties of yield traits of 50 somaclones produced by selection for resistance to low water potential in callus cultures of spring bread wheat variety Ershovskaya are being examined. The genetic improvement of osmotic adjustment in cell or tissue culture may be feasible in the future only if the resistance can be recovered and stabilized in the regenerated plant.

5 Field versus laboratory parameters

Plant breeders have long looked to the physiologists for the resolution of drought resistance into major components, and for development of screening techniques enabling selection for these components. There has been no lack of competitive physiological research identifying the many component processes that appear to contribute to survival or productivity and may be seen in the books edited by Mus-sels and Staples (1979), Turner and Kramer (1980), Srivastava et al. (1987), Baker (1989), Jones et al. (1989) and Behl (1994). Although a large number of screening tests have been devised, their effective use in plant breeding programmes is still lacking. It may be due to the fact that (I) genetic analysis has not complemented for most of the physiological techniques, and (II) many crop physiologists and plant breeders are too far in their concept that selection for an individual component of stress resistance, especially closer to a cellular or molecular level is not likely to result in better performance of the crop in the field.

The great need at present is not for the screening techniques but for the evidence that selection for at least some of the characters of potential importance of drought resistance under laboratory conditions will reflect their performance under field conditions, and at least as rapidly as the empirical selection process. Morgan (1983) has shown that selection for high osmoregulatory ability in wheat can result in substantially greater yield under drought conditions than the lines with low osmoregulation, but whether a such relation will lead to better performance than that by existing adapted varieties, or faster improvements than that by empirical selections remains to be seen.

The same holds true for various other techniques, namely, vascular resistance (Richards and Passioura, 1981) resulting in conservation of more water until the later stages of crop growth. Quarrie et al (1994) examined a series of chromosome substitution lines of high abscisic

acid (ABA) genotype ciano 67 in low ABA recipient Chinese spring, results showed that the chromosome 5A carries gene (s) that have a major influence on ABA accumulation in a drought test with detached and partially dehydrated leaves (DLT). Analysis of variance confirmed the location of the gene(s) on the long arm of chromosome 5A. MADMAKER QTL showed that the most likely position for ABA QTL is to be between loci XPSR575 and XPSRU26 about 8cm from XPSRU26. Plants respond to different environmental stress stimuli by rapid synthesis of stress proteins which are hypothesized to have a protective function in cellular metabolism. The nucleotide sequence of a wheat DNA clone (P Tawsp 23) encoding such a protein WSP23 whose transcripts rapidly accumulate during water stress is presented by Joshi et al (1992).

6 Conclusions

Breeding for drought resistance is difficult to achieve by using single criterion of yield performance under stress, therefore, physiological criteria must be used in selection. Since yield potential has no effect on yield performance under drought stress, the ideotype must be drought resistant and of

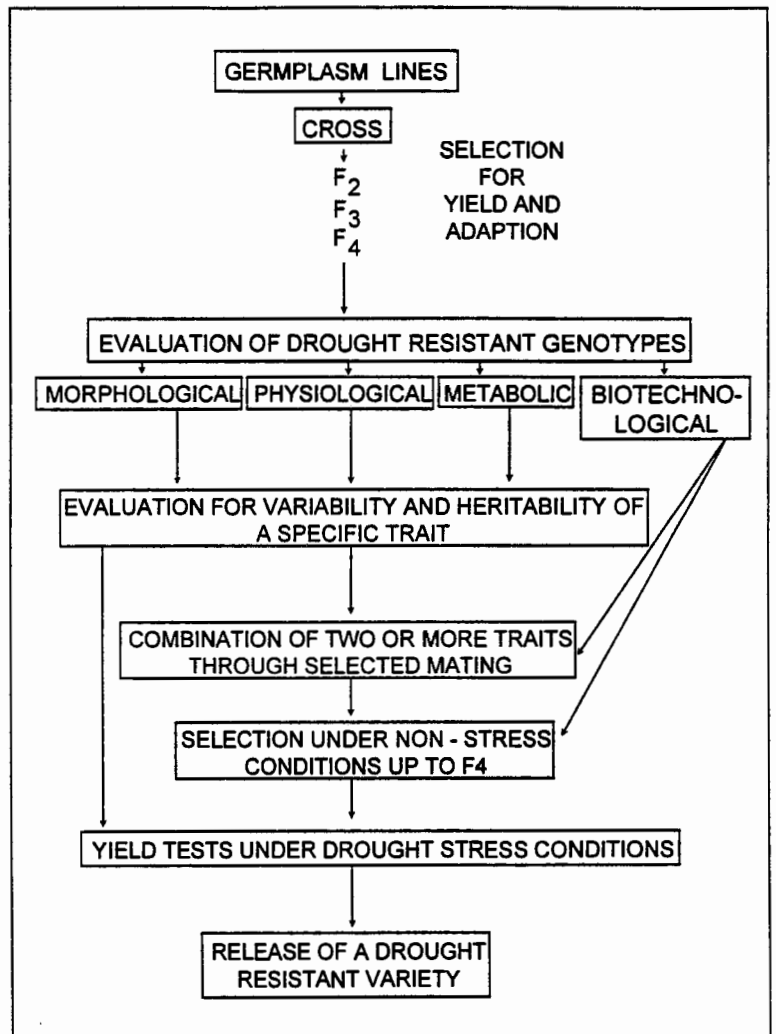


Figure 1: Breeding strategy for drought resistance

a reasonably high yield potential. Therefore, under the environments having unpredictable and/or mild drought stress, potentially high yielding genotypes that carry some elementary properties of drought adaptation (proper phenology, deeper roots, reduced leaf area etc.) may be desirable. But for more dry areas the components of drought resistance must be increased. Although the survival traits are of limited value where production rather than survival of the species is concerned, these can be included in the environments with intermittent water stress as they delay the time of plant death. To be suitable, such traits should have (I) a much greater heritability than yield, (II) an appreciable correlation with yield, and (III) easy and rapid assessability over the range of environments likely to be encountered over seasons and locations.

In order to develop a general breeding strategy in segregating generations, selection for yield potential and general agronomic traits should be carried out at initial segregating generations preferably up to F₄ and then for drought resistance (Blum, 1989). This is also consistent with the fact that most practical selection methods for drought resistance do not fit single plant selection and are therefore, appropriate at more advanced generations (Figure 1).

Due to the lack of a single physiological selection criterion for drought resistance, the construction of a multiple selection index should be considered that takes into account the target environment, the physiological issues involved and the available methodology. Recent developments in the direct of probing of plant production processes and further research into the physiology biochemistry and genetics of drought resistance may open the way for upgrading the selection system in the future. By employing optimum bombardment conditions and improved methods for somatic embryogenesis from scutellar tissue of immature zygotic embryos, wheat transformation has now been accomplished in several leading laboratories around the world (Nehra et al., 1995). This breakthrough marks the beginning of a new era for wheat improvement through molecular approaches.

Genuine progress in the direction of an effective use of water and nutrients by plants can only be achieved if plant breeders finally consider criteria related to an improved response of cultivars in their breeding activities (El Bassam, 1995).

Züchtung von Weizengentypen für wasserdefizitäre Gebiete

Das Heranziehen physiologischer Kriterien ist für die Selektion trockenresistenter Genotypen unerlässlich, da die Züchtung auf Dürre-resistenz durch Berücksichtigung von ausschließlich einzelnen Faktoren nicht durchzuführen ist. Der Idealtyp muß neben einer hohen Trockenresistenz ein angemessenes Ertragspotential aufweisen. Aus diesen Gründen sind Genotypen, die ein hohes Ertragspotential sowie einige Eigenschaften für eine Anpassung an wasserdefizitäre Umwelten wie angemessene Phänologie, tiefe Wurzeln, reduzierte Blattfläche etc. besitzen, wünschenswert.

Bei der Entwicklung einer allgemeinen Züchtungsstrategie für die aufspaltenden Generationen, sollte vorzugsweise bis zur F₄-Generation das Schwergewicht auf die Selektion von Ertragspotential und allgemeine agronomische Eigenschaften und dann erst auf die Selektion der Merkmale für eine Trockenresistenz gelegt werden.

Dies stimmt auch mit dem Tatbestand überein, daß die meisten angewendeten Selektionsmethoden für Trockenresistenz sich nicht für Einzelpflanzenselektion einsetzen lassen, sondern nur für fortgeschrittene Generationen geeignet sind.

Aufgrund des Fehlens von einzelnen physiologischen Selektionskriterien für Trockenresistenz sollte die Erarbeitung eines vielfältigen Selektionsindex, der die Umwelt, die beteiligten physiologischen Vorgänge und somit die verfügbaren Methoden berücksichtigt, in Betracht gezogen werden.

Neueste Entwicklungen bei der Prüfung direkter Pflanzenproduktionsprozesse sowie weitere Forschungen im Bereich der Biochemie und Genetik der Trockenresistenz werden den Weg für eine Verbesserung der Selektionssysteme in der Zukunft frei machen.

Durch die Optimierung der Techniken in der Genübertragung und durch die Verbesserung der Herstellung von somatischen Embryonen aus dem Scutellum-Gewebe unreifer zygotischer Embryonen, wird die Transformation des Weizens jetzt schon in einigen führenden Laboratorien der Welt durchgeführt.

Dieser Durchbruch markiert den Beginn eines neuen Zeitabschnittes, der die Verbesserung des Weizens mit Hilfe von molekularen Methoden vorantreibt. Ein entscheidender Fortschritt in der Richtung einer effizienten Wasser- und Nährstoffausnutzung der Pflanze kann aber nur erreicht werden, wenn die Züchter Kriterien für diese Eigenschaften in ihre Züchtungsaktivitäten einbauen können.

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