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SELECTING FOR IMPROVED GRAIN YIELDS IN VARIABLE ENVIRONMENTS

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ABSTRACT

For the last two to three decades, direct selection for grain yield has been the primary aim in wheat and barley programmes in southern Australia. Progeny methods have predominated and theoretical attention has been devoted to methods of identification of superior genotypes in this variable environment. The identification of suitable locations and plot techniques for trials, and the recognition of plant characteristics responding to selection are two problems encountered.

The introduction of CIMMYT breeding material has increased genetic diversity in current Australian varieties. It is now possible to identify distinct ecological zones in which particular varieties predominate.

The F_2 progeny method can be reassessed after two decades of work. While this method has allowed selection where pre-existing methods of pedigree and backcross have been ineffectual, it is slow and valuable genetic material may be discarded because a superior trait was not recognised in time. Further improvements in breeding techniques will result from the integration of efficient screening techniques and selective backcrossing into the progeny method.

KEYWORDS

Wheat, southern Australia, F_2 progeny method, boron tolerance, *Septoria tritici.*

INTRODUCTION

The cereal growing areas of southern Australia are characterised by a variable, but generally rather arid, climate and by ancient, highly weathered soils. Production per unit area is low by world standards and there is a long tradition of seeking improved productivity through breeding, whereby changes in technology can be implemented with very low economic outlay.

The agricultural settlers originated mostly from northern Europe, and it soon became clear that the varieties of agricultural crops introduced from that climatic zone were poorly suited to Australian conditions. A strong scientific interest in plant introduction developed and selection within introduced land races was outstandingly successful in the 1850's and 1860's. Frame's selection of the wheat variety Purple Straw (Wrigley & Rathjen, 1981) enabled the major expansion of the wheat belt and the establishment of export markets. Renewed interest in genetic improvement during the 1880's and 1890's culminated in the development of the pedigree method of breeding to exploit the genetic variation released following crossing. Farrer received worldwide recognition for this and for the next 40-50 years the emphasis remained on the selection of agronomically adapted plants on the basis of their phenotype, especially in the F_2.

By the 1940's, Australian wheat cultivars were well adapted in maturity and plant habit to the environment and the more alert of the breeders began to recognise that the pedigree method was not achieving further genetic improvement (Pugsley, 1949). Progress using backcrossing techniques, however, was slow. It depended upon the availability of high yielding lines, and was usually limited to the more spectacular of the leaf and stem diseases, many of which were unimportant in Australia. For instance, stem rust, which is easily the most significant of these, causes an annual reduction in yield of about 1-1.5% in South Australia in the absence of resistant varieties. K.W. Finlay, who succeeded Pugsley at the Waite Institute, saw a need to increase the genetic diversity within the cereal programmes. His efforts in assessing the breeding potential of a large collection of barley varieties led to the rapid development of mechanisation and to the popularisation of analysis of genotype x environment interaction or adaptation analysis (Finlay & Wilkinson, 1963).

THE F_2 PROGENY METHOD OF BREEDING

Lupton & Whitehouse (1957) named and thoroughly described this breeding procedure, but apparently did not adopt it to any significant extent. While Breakwell & Hutton (1939) experimented with a similar system during the 1930's, it was not until mechanisation and computerisation resulted in significant improvements in the growing and analysing of yield trials that it became feasible to adopt this system. When breeding resumed at the Waite Institute in the late 1950's it evolved to a system closely allied to that described by Lupton and Whitehouse with direct selection for grain yield as the primary aim. The F_2 progeny method is now widely adopted in southern Australia, but apparently is not extensively used elsewhere in the world. Whereas Lupton and Whitehouse suggested rejecting at least 90% of F_2 plants, F_2 plots are now grown at normal sowing rates in yield trials. From these plots 40 to 100 heads are collected and individually multiplied as a sample of the F_2 segregation from each cross.

The name derives from the fact that selection is based on the results of the progeny of the F_2, rather than on the phenotype of the F_2. Thus it is analogous to the progeny methods used in animal breeding, except that the F_2-derived line is the basis of further selection and crossing, rather than the F_2 individual itself. The gene frequencies in the F_2 derived lines are those of the F_2, although the genotype frequencies alter, so in effect the replicated trials are being conducted on the generation of maximum heterozygosity. In the event of partial or complete dominance of the desired genotype, the method has substantial advantages over bulk breeding procedures or single seed descent (Whan *et al.*, 1982; Shebeski, 1967).

The system as currently practised at the Waite Institute is outlined in Fig. 1. It is essentially a two-phase selection scheme, the second phase of which was introduced to give reasonable homogeneity to the final progeny.

However, in some instances the second round of selection gives a substantial increase in selection intensity (Rathjen, 1983) which is of considerable significance in a breeding scheme with much lower selection intensity in early generations than that used in pedigree selection. While in earlier years the selection was almost entirely towards increased grain yield, in recent years we have adopted screening of the F_3 and F_6 hill plots for disease resistance as described by Hollamby *et al.* (1983). The system is readily modified to incorporate pedigree selection if characters identifiable in F_2 become an objective.

The central aim for a successful programme of this type is the maximisation of the correlation between the yields of the lines in plots and their yield in commercial conditions. This correlation tends to be higher when the lines are grown in commercial conditions, than when grown in specialised circumstances, e.g. when water and fertility are unlimited, when there is a dual correlation (Janssens, 1979). Maximising the correlation is here considered in two distinct aspects. Firstly, the conditions under which the

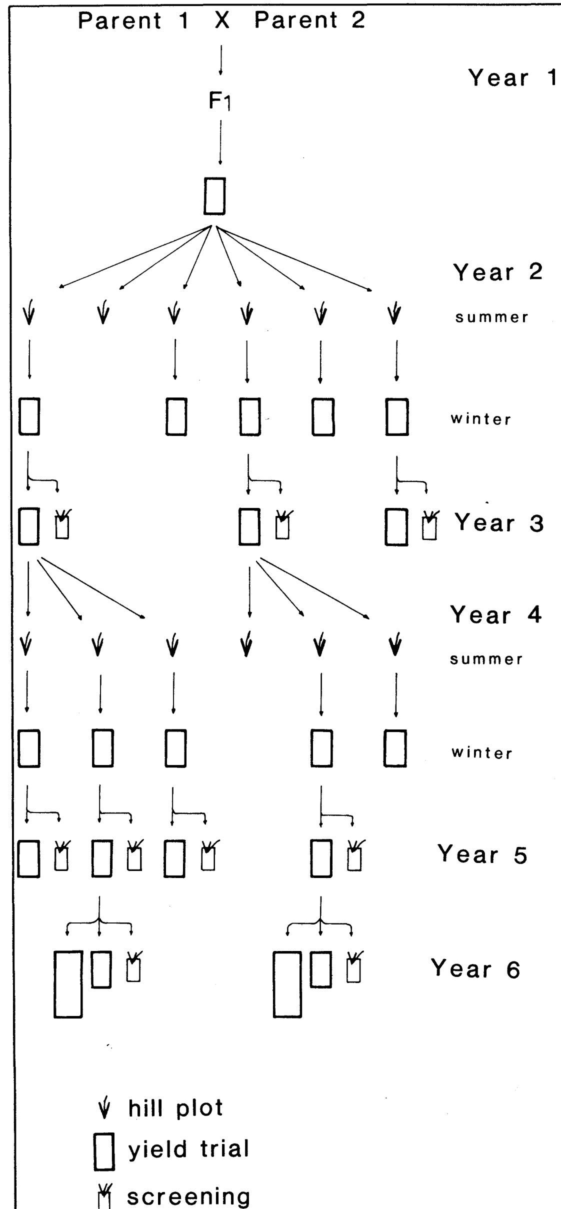


Figure 1. The F_2 progeny method of breeding as practised at the Waite Institute. The hill plots are selected for stem rust and BYDV (barley yellow dwarf virus) resistance. The screening for *Septoria tritici*, boron tolerance, milling extraction, stripe rust and eelworm (*Heterodena avenae*) is conducted in the F_5, F_8 and F_9 generations.

lines are assessed — the plot technique — must resemble the potential commercial conditions as closely as possible, secondly, the choice of selection locations must be representative of the whole cereal zone.

An alternative approach to direct selection for grain yield is possible where there is substantial scientific back-up from other disciplines. When major commercial problems have been accurately identified, when there is a detailed knowledge of their genetics, and the appropriate selection techniques have been developed, it is possible to continue to select for specific characteristics. The breeding programmes in the north-west of the U.S.A. are notable for this approach. Even with this, it remains necessary to ensure that the background genotype is satisfactory, and lines with the newly incorporated characteristic need to be assessed by widespread yield trials. In Australia this approach has not been feasible, due to the lack of scientific resources devoted to identifying problems and to the large areas and diversity of the cereal growing regions.

DESIGN AND ANALYSIS OF FIELD TRIALS

A primary aim of cereal breeding trials must be to maximise the correlation between the grain yields of the lines in trials and their performance as commercial crops in the same location. This involves a compromise between the plot size and the number of lines in trial. Competition between different genotypes in adjacent plots is well understood for the aerial aspects of plant growth, but the nature and importance of below ground reactions are virtually unknown.

Earlier work concentrated upon competition for light, and there are environments where shading has to be taken into account (Fisher, 1976). Furthermore, relationships have been established between plot-size and the development of epidemics of leaf and stem disease (Parlevliet & van Ommeren, 1984). Effective field resistance is difficult to recognise in small plots for a number of diseases, such as *Septoria tritici*. Susceptible material appears more resistant, and moderately resistant material appears somewhat susceptible due to the influx of spores from nearby susceptible lines. Other air-borne diseases, including stem rust, can be selected in much smaller plots, since the influx of spores is less important in the progression of the disease.

Competition for nutrients and water, and the spread of disease below ground have the potential for greater complexity than above ground phenomena and are exceedingly difficult to investigate. The soil, especially below the cultivation layer, is spacially much more heterogeneous than the atmosphere and this accounts for much of the experimental variation within a trial. Knight (pers. comm.) studied year to year variation in soil-based effects and concluded that his uniformity trials did not have predictive value in providing a co-variate for subsequent experiments.

Nearest neighbour analysis (Wilkinson *et al.*, 1983) was proposed as a statistical approach to this problem. Soil heterogeneity is not random, so with small plots relative to this heterogeneity, localised blocks may reduce the experimental error and increase discrimination between lines. This technique is being widely adopted, but it is too early to assess its impact in increasing the accuracy of selection. Experimental error in the field operations of seeding and harvest, and from previous treatments is often systematic, depending upon the direction of travel of machinery. With an appropriate design, the estimate of experimental error may be reduced by taking row and column effects into account and this technique, together with the use of localised blocks, is likely to produce a more satisfactory level of discrimination between lines. With all of these statistical techniques, it is essential that effects attributable to interplot competition are small compared to the genetic effects, otherwise 'ripple' effects in plot yields will invalidate the selection.

REPRESENTATIVE ENVIRONMENTS

The choice of representative environments for field trials, such that there is a high correlation between the results in the trials and the results over the whole of the cropping area, has proved to be difficult. Correlations and pattern analyses (Byth, 1977) have been used to investigate the similarity of trial sites and have proved to be helpful in deciding the number and location of selection trials. Following a comparison of varietal performance in the Waite Institute selection trials and the state-wide Department of Agriculture trials, one Waite Institute site was abandoned and another down-graded (Pederson & Rathjen, 1981). Both of these were located on Research Stations, whereas the more effective selection sites were located on commercial farms. Fertilizer practice, rotations, cultivation techniques and weed control on research stations can be quite different from those on farms and these may explain the poor results on stations. Frequently, research stations are not even in suitable locations for yield trials.

Crop rotation is particularly important in the build-up of disease. For instance, it appears that with two susceptible crops every three years eelworm will remain a major pest (Fisher, pers. comm.). Take-all, *Gaeumannomyces graminis*, is most damaging in the second to fourth wheat crops, after which take-all decline sets in. Yellow spot is a stubble borne disease with limited spread so that damage is more likely to occur where wheat follows wheat.

The recent decision of the Australian Wheat Board to record wheat receivals according to variety provides a data base of considerable potential for deciding the location of field trials. With a few years' experience, farmers can form a very accurate picture of the relative values of different varieties and grow those which maximise their return (Fig's 2 and 3). Commercial influences, through the returns for different quality, individual idiosyncrasies and continued experimentation by farmers, do alter the varietal distribution to some degree, but rarely cause major departures from the general trend in Australia.

Figure 2. The distribution of commercial varieties in South Australia (data from the Australian Wheat Board) as indicated by deliveries into the silo system. 400 mm rainfall isohyet shown as dashed line.
(A) Festiguay (eelworm resistant) in areas where barley is the major crop.
(B) Halberd

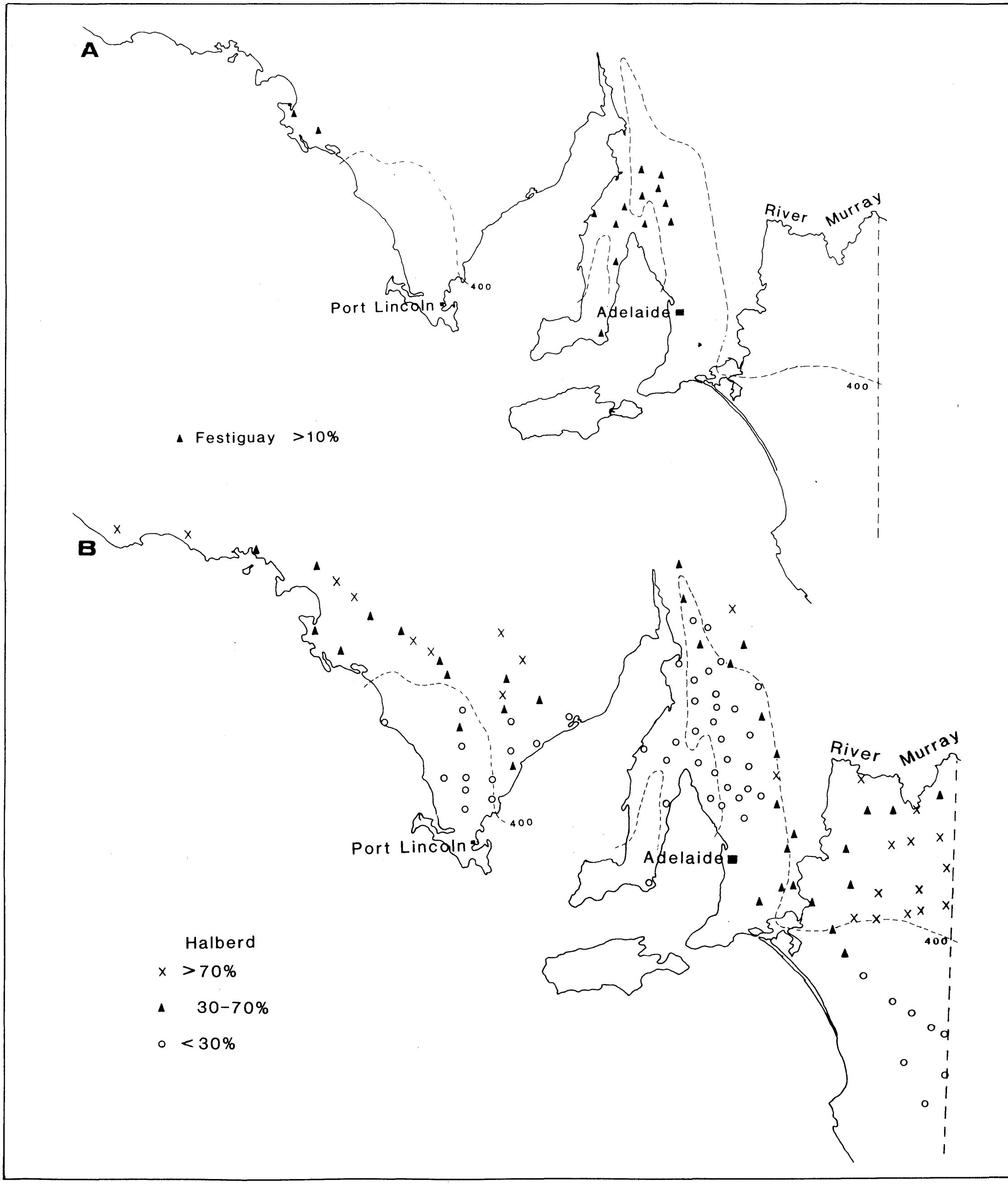
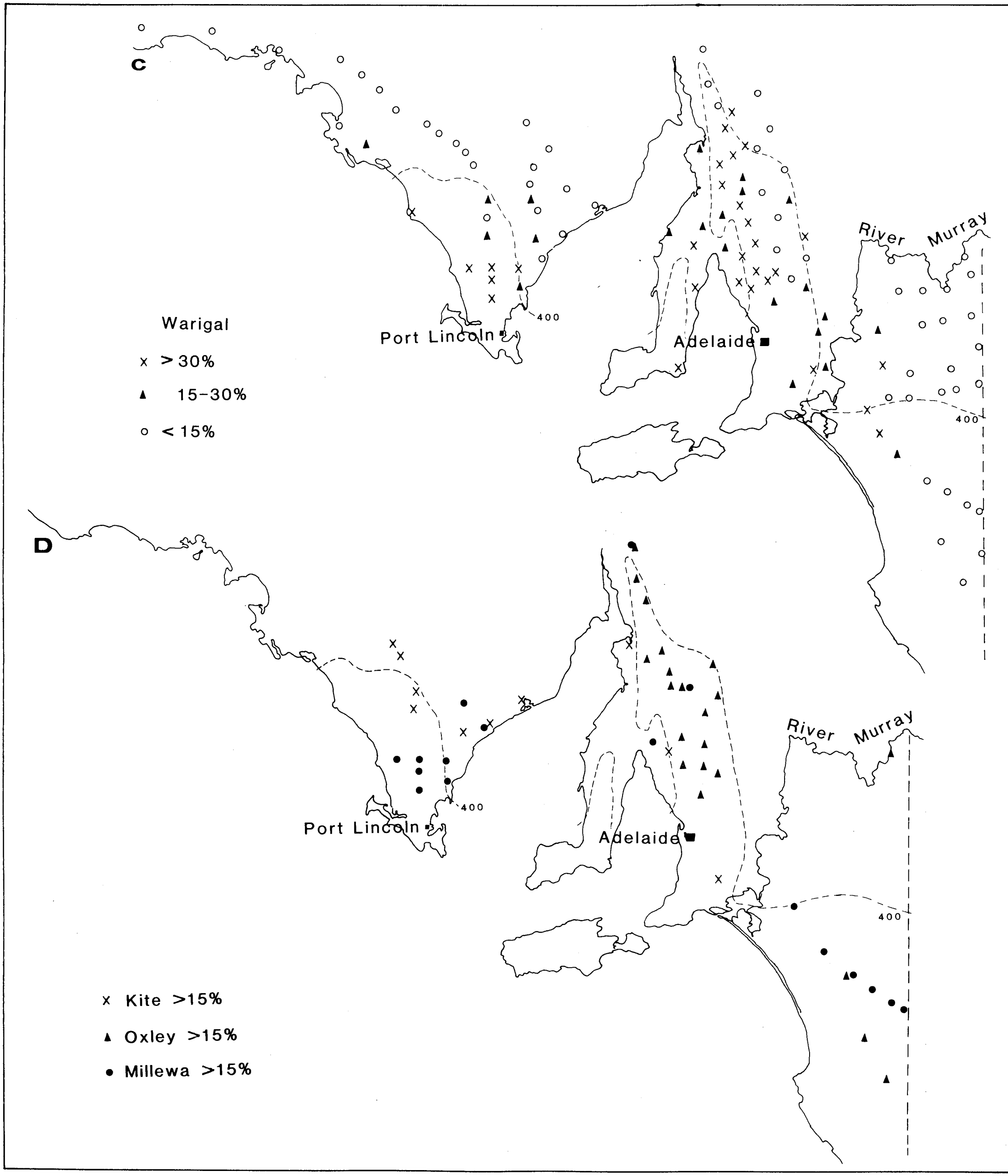


Figure 3. The distribution of commercial varieties in South Australia (data from the Australian Wheat Board) as indicated by deliveries into the silo system. 400 mm rainfall isohyet shown as dashed line.
(C) Warigal
(D) Kite (stem rust resistant), Oxley (stripe rust resistant) and Millewa.



The problem of the selection of representative environments is particularly acute in South Australia. Apart from the climatic range from the margins of arid steppes to waterlogged conditions, the soils vary from deep, fertile clay loams to shallow sandy soils over sheet limestone and windblown calcareous sands. Halberd (35%) and Warigal (20%) are the most common varieties, and their fluctuations in relative yields (Fig. 4) illustrate a further problem. The assessment of new varieties must be conducted over several years as very different conclusions would have been drawn regarding the relative yields of these two varieties if only two or three years, data had been taken into account.

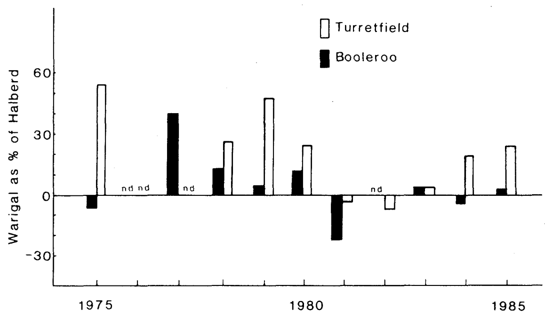


Figure 4. Grain yield of Warigal as a % of Halberd for two locations, Turretfield and Booleroo for an 11 year period. Droughts occurred in 1976, 1977, and 1982. *Septoria tritici* was a major factor at Turretfield in 1975, 1979 and 1985, and was more common before 1980. (Data from T. Heard, South Aust. Dept. of Agric). nd, no data.

VARIETAL DISTRIBUTION

Since the 1970's when varieties bred from CIMMYT germplasm were first released, there has been considerable genetic diversity in Australian wheats. The varietal composition of the wheat delivered to each of the 116 silos in the South Australian system reveals some major anomalies which are the result of marked ecological differentiation. The most easily identified and illuminating of these has been for the variety Festiguay (Fig. 2).

Heterodera avenae, the cereal eelworm, has probably been in southern Australia since last century (Fisher, pers. comm.), but except by Meagher in Victoria, the economic implications of this pest were almost ignored until 1978. Prior to this, the variety Festiguay had become popular in some areas of South Australia through its moderate resistance to stem rust in the epidemics of 1973 and 1974. When the paddocks, which had been cropped to Festiguay in 1974 and 1975 were re-cropped in 1978, spectacular cleaning effects were recognised through the failure of the eelworm to reproduce on Festiguay during the previous rotation. The fortuitous resistance of Festiguay to eelworm resulted in Festiguay representing 50% of the deliveries in some silo areas in the early 1980's, despite its inherently low yield. It is now recognised that eelworm was responsible for an average loss in production of about 15% in South Australia.

The CIMMYT varieties Pitic 62 and Mexico 120 both have a high degree of tolerance to this pest. However, prior to 1978 this had not been recognised and the data in Table 1. were quoted in undergraduate lectures as a typical example of genotype and environment interaction. By 1978, this tolerance (Fisher *et al.* 1981), introduced unknowingly into the breeding programmes in 1963, had become quite common among advanced lines and is now a feature of a few varieties.

The most spectacular dichotomy is between Halberd, a descendant of the Federation family of wheats which have dominated south eastern Australia for most of this century, and the varieties based on CIMMYT or Australian x CIMMYT parentage. Halberd ranges from over 90% of the deliveries at some sites to being practically non existent at others (Fig. 2), and this pattern is repeated over the whole of southern Australia. As a non-semidwarf, it could be expected that Halberd would have an inherent yield disadvantage of about 10% compared to the newer varieties and it seems reasonable to expect that it has some attribute which compensates for this. In the higher rainfall areas, Warigal and other derivatives of Anza form the bulk of the crop (Fig. 3).

Other varieties, including Kite and Millewa (Fig. 3), show an uneven distribution across the State which reflects a relative advantage in response to unidentified environmental factors.

This method of describing the ecological zones is limited by the genetic variation within the commercial varieties. While it has proved very useful at this stage in the evolution of a breeding programm, it needs to be supported by results from trials where a much greater range of genetic diversity can be encompassed.

Table 1. An example of genotype x environment interaction. Subsequently the line Mexico 120/Koda was recognised as being tolerant to *Heterodera avenae*, a major factor at Winulta.

			Grain yield (t/ha)		
Line	Waite	Saddleworth	Mortlock	Winulta	Mean
Mexico 120/Koda	1.32	3.04	2.52	1.96	2.21
Heron/Mayo	2.80	2.64	2.44	1.36	2.31

IDENTIFICATION OF CHARACTERISTICS RESPONDING TO SELECTION

Recent work has centred around identification of the biological traits which have responded to selection for grain yield. Both selection and choice of parents are facilitated by this identification, especially if the character is simply inherited. The resistance and tolerance to cereal eelworm discussed above are the best documented of these.

Many of the recently released varieties in southern Australia are moderately resistant to *Septoria tritici*. Although several CIMMYT parental cultivars have been successful in breeding, by far the most outstanding has been Anza (WW15) which is rather more resistant than the others to this disease. Moderate levels of resistance have been more effective on a field scale than might have been predicted on the basis of plot information, and in Western Australia and South Australia the disease has been of little consequence since 1979 when Egret, Warigal and Oxley became very common in *Septoria tritici* prone areas. Unfortunately these varieties now have apparently low yields compared to new, more susceptible varieties (Table 2). In the event of susceptible varieties becoming common, we can expect recurrence of the frequent epidemics of *Septoria tritici* which occurred before 1979.

Table 2. Cultivar performance in a region subject to epidemics of *Septoria tritici*. Grain yield at Wanilla measured in a moderately severe epidemic in 1984. Relative yields in the advisory service 'Fact Sheet' are mean for two or three locations in the same zone for four years during which the disease was at a low level. (Data from T. Heard, South Australian Department of Agriculture).

Cultivar	Resistance to *Septoria tritici**	Grain yield (% of mean) Wanilla	Dept. of Agriculture 'Fact Sheet'
Aroona	MR	125	98
Oxley	MR	119	88
Warigal	MR-MS	116	98
Millewa	MS	104	96
Spear	S	101	113
Kite	S	87	88
Halberd	VS	60	100

* MR, moderately resistant; MS, moderately susceptible; S, susceptible, VS, very susceptible.

Halberd has been a major focus of research, with its root disease reaction receiving detailed attention. In 1982, Cartwright *et al.* (1984) identified a common non-pathogenic leaf blotch of barley as being symptomatic of boron toxicity. Field work in 1983 at Two Wells, where subsoil levels of boron are very high, showed spectacular differences in susceptibility of barley to this problem and suggested that there was variation between wheat varieties. This was supported in 1984 (Table 3) — Halberd and its relatives have much lower concentrations of boron in the grain and high relative yields. Paull (1985) has confirmed the tolerance of Halberd to boron and its distribution across South Australia is closely related to the levels of boron measured in barley grain (Fig. 5 from Cartwright & Zarcinas). It is probable that the regional advantage Halberd and its newly released relative Spear have over other semidwarf varieties is mostly attributable to this tolerance.

Three other characteristics are currently of interest. Most of the recently released varieties are somewhat resistant to *Bipolaris sorokiniana*, a common organism in the local soils (Mooen & Harris, 1980). Again some tolerance to BYDV (barley yellow dwarf virus) is very common. Many of the South Australian soils have high levels of calcium carbonate and in these circumstances manganese is often deficient. In barley, major differences between cultivars in tolerance to manganese deficiency have been recorded (Graham *et al.*, 1983), and it is likely that this will be a major feature in future South Australian wheats.

REASSESSMENT OF THE F_2 PROGENY METHOD

The F_2 progeny method has enabled selection for increased grain yield where the pre-existing methods of pedigree or backcross breeding had become ineffectual. However, progress has not been very rapid, and this is a reflection of our poor initial appreciation of the crucial role of site selection and the low selection pressures which are

Table 3. Comparison of tolerance at seedling stage with boron concentration in the grain and grain yield, from Two Wells, 1984.

Variety	Seedling Response	Grain boron p.p.m.	Yield % site mean	Maturity
Halberd	tolerant	3.15	112	mod-early
Olympic	tolerant	3.14	99	late
Insignia	tolerant	3.57	125	early
Gabo	intolerant	8.22	76	early
Kite	intolerant	8.31	85	mod-early
(WI/MMC)	very intolerant	9.07	49	mod-early

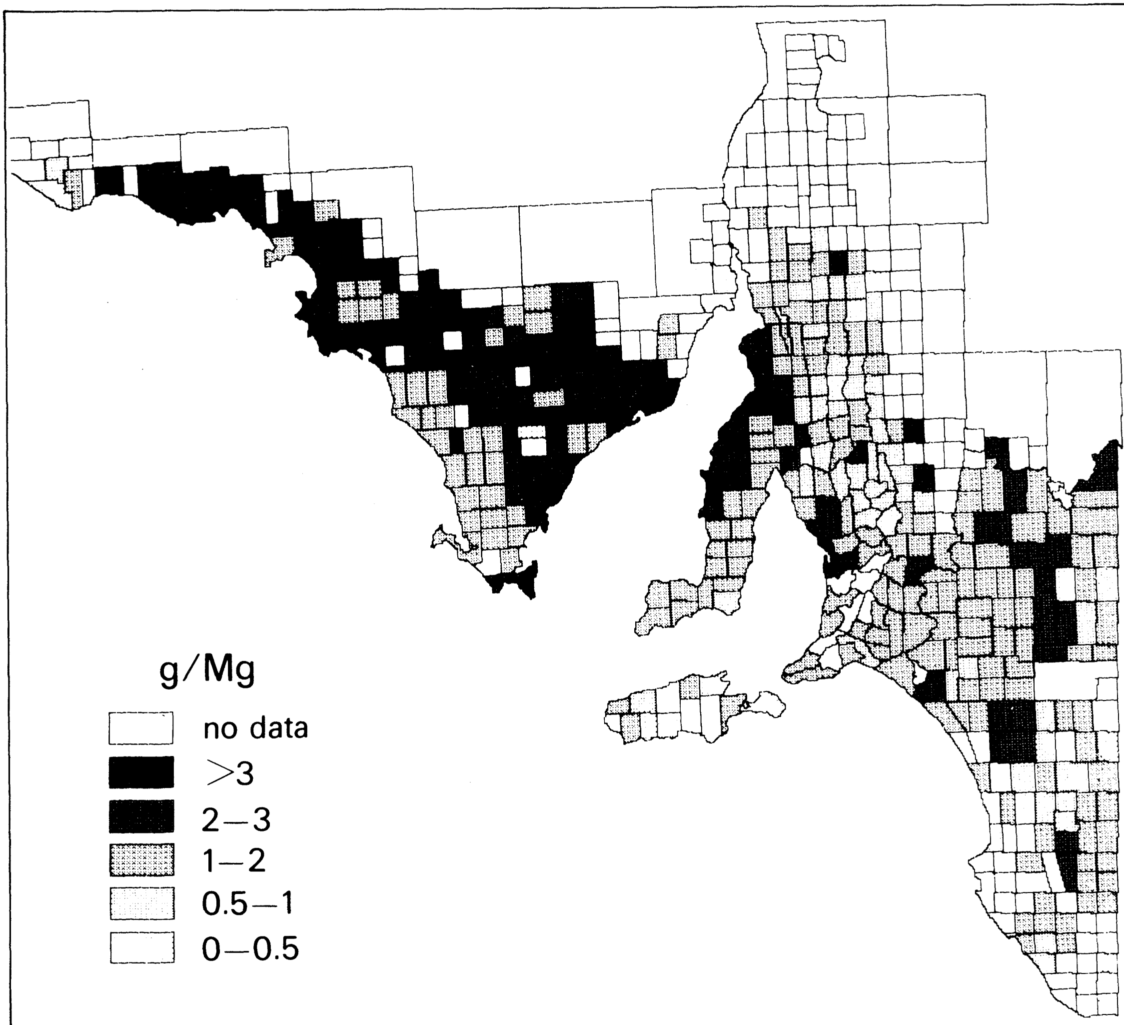


Figure 5. The concentration of boron in barley grain. Grain analysed from pre-delivery samples. (Diagram from B. Cartwright and B. Zarcinas, C.S.I.R.O. Division of Soils.)

inherent in the progeny method. Our early attempts at site selection were simplistic, aiming merely at high and low average rainfall and high (clay loam) and low (sandy loam) fertility. Now the sites are dispersed across the whole state (Fig. 6) to take account of differences in climatic and soil conditions (Table 4). A second series of trial sites has been instituted to allow screening for particular diseases following the approach used in the north west of the U.S.A. Furthermore, the progeny method is more efficient where the characters are of low heritability and multigenic in control, but increasingly it is obvious that there are often several specific characters responding to selection for grain yield. Generally these characters are fairly simply inherited.

The most important outcome is that the method has contributed to our understanding of the important environmental factors affecting grain yield. Halberd became an enigma because of its dominance on South Australian farms, despite the advent of *Septoria tritici* resistant, high yielding, semi-dwarf varieties. When these characters are elucidated, there has usually been within the advanced lines, a pool of genetic variability upon which selection can be practised.

In retrospect, it can be seen that valuable genetic material has almost certainly been discarded because its

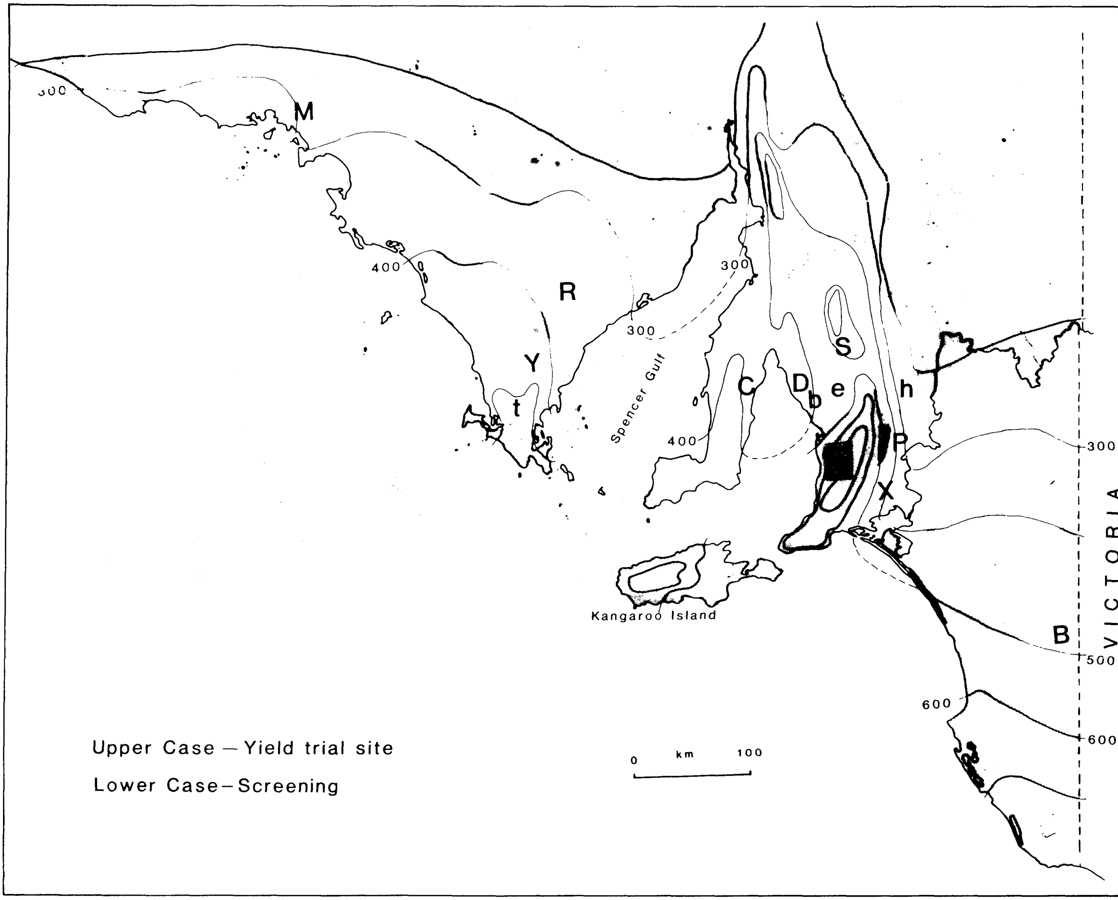


Figure 6. Yield trials and screening sites used in the Waite Institute wheat breeding programme. (See Table 4 for information on sites).

superiority was not recognised at the time. For example, during the 1960's we discarded advanced lines originating from crosses involving Portugese varieties later shown to be resistant to eelworm.

The major improvements to the progeny method will come from the incorporation of specific screening at crucial stages in the programme especially at the F_5 and F_9 stages. Together with backcrossing for specific defects, this will enable continued progress in grain yield and the flexibility to select for other major factors in the environment.

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Table 4. Soil and site characteristics of the locations used in the Waite Institute wheat breeding programme.

Code (Fig. 5)	Location	Soil	Diseases & climate
M (farm)	Mudamuckla	calcareous sand	B toxicity, very short growing season
R (farm)	Rudall	siliceous sand over clay	B toxicity, Mn & Zn def., unidentified root rots
Y (farm)	Yeelanna	shallow soil over poorly draining clay	Cu def, waterlogging eelworm, *Septoria tritici*
C (farm)	Winulta	fertile clay-loam	B toxicity, *Septoria tritici*
D (farm)	Windsor	sandy loam	eelworm, *Septoria tritici* & other leaf diseases & root diseases
S (farm)	Saddleworth	grey soil of heavy texture deep profile	stripe rust, Zn def.
W (research stn)	Waite	deep clay-loam	BYDV, mildew and other leaf diseases
X (research stn)	Strathalbyn	loam	eelworm, *Septoria tritici*, stripe rust & root rots following grassy pasture
P (farm)	Palmer	sandy loam	B toxicity, Mo def?, *Bipolaris, Fusarium* & *Gaeumannomyces gramminis*
B (farm)	Bordertown	grey soil of heavy texture deep profile	Mn, Cu & Zn def?, stripe rust
Screening			
t	Wanilla		*Septoria tritici*
b	Two Wells & Redbanks		boron toxicity
e	Roseworthy Agric. College		eelworm
h	Sedan		*Bipolaris sorokiniana*

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SYMPOSIUM DISCUSSION

Dr D.S.C. Wright, Crop Research Division, DSIR

Are there any agronomic practices you can use to overcome your boron problem?

Rathjen

No, it's in the subsoil. If forms a mosaic right across the landscape at least well up towards the 1200 mm rainfall range and you find the symptoms in barley. It is between 30 cm and 100 cm deep in the soil

Dr. W. Bushuk, University of Manitoba

At what stage in your selection programme do you start testing for quality?

Rathjen

We use a bulk method for quality, and we start quite late. Mainly at F7 or F8.

Dr E.J. Walsh, University College, Dublin

In the diagram on your breeding method, you're going back through the second cycle of pulling out plants. Why not use single seed descent?

Rathjen

The problem with single seed descent in wheat is that you go straight to homozygosity and with 21 chromosomes you are looking at extremely large numbers. Whereas if you go through the F2 progeny methods, you're dealing with workable numbers. With barley it's not quite so severe. Any haploid system or single seed descent method of breeding runs into this particular criticism. What it amounts to is that the generation of maximum heterozygosity is the F2, and that is the one that is best to work on, although if you have got very few chromosomes it is perhaps not quite so serious.

Dr F.R. Sanderson, Crop Research Division, DSIR

In screening for *Septoria tritici,* you comment that you developed resistance without consciously selecting for it. You can only do this where the main cultivars in the field are susceptible. Once resistant cultivars become dominant it is no longer possible to screen for resistance in this way.

Rathjen

Yes, that is a very serious matter because we have not had a decent screen for *Septoria* since 1979 — about the time the CIMMYT derived lines became predominant in the areas where *Septoria* was prevalent. The same applies in western Australia, and probably applies in the other eastern states.

Mr L.W.M. Suijs, Geertsema Zaden B.V.

Why do you have so many barriers in your growing conditions in Victoria? Why can you not breed for more adapted varieties to these conditions?

Rathjen

We have rather arid climatic conditions so that there is not a lot of leaf disease, and ancient soils. A lot of our problems are soil problems, and selecting for these is very much more difficult because you cannot see the problem and you cannot replicate. So there is an important difference between the middle-range climate and our climate, just in that geographical aspect.

Suijs

You seem to have limited varieties growing in your regions.

Rathjen

There have been over a thousand varieties released in Australia, maybe over two thousand. We probably have the biggest investment in wheat breeding, per tonne of wheat produced, in the world. Australia was initially an agricultural colony, and it was very important in the early days to get adapted wheats. The interest in plant breeding has been high ever since. In Europe you had adapted wheat, and breeding began quite late in the piece.

Wright

What is the ultimate use of the grain — there seem to be two contrasting types.

Rathjen

Yes, the Warigal type is potentially a higher quality but it only grows in a higher rainfall area, where the protein is rather less. Halberd, which is ASW quality, grows in low rainfall areas where the protein content is such that it should be able to get hard quality. We have a straight conflict. If we could swap those two over it would be worth a few dollars to us.

Sir Otto Frankel, CSIRO

I agree with Mr Suijs that there is a good case for greater specialisation of superior wheat in Australia. We grow few varieties — I cannot understand your two thousand — of considerable adaptability, yet, the adaptability is to a degree a figment of our own ideas. In many parts of the world where there are considerable differences in environment, as there are in Australia, it has paid to have more locally defined varieties.

Rathjen

Ideally, that is true. For instance, if we had boron tolerance and *Septoria* resistance in the same variety, it would be more widely adapted than any of our current varieties. One thing which is not often said, is that breeding advances are rather slow. For instance, in Australia we've been fighting stem rust since 1967, and we are now only marginally ahead in Southern Australia to what we were then. I don't think we want to overestimate breeding progress. There is also a fundamental problem with some soil-borne problems, for example, the response to boron shows a narrow range between toxicity and deficiency, compared to the other minor elements. So varieties which are tolerant to high levels in some soils, will probably show deficiency symptoms in other parts of our wheat belt. So there is no way that we will get a single variety to go across that whole range.

Dr G.W. Burton, USDA, Georgia

Could you screen for boron tolerance in the seedling stage?

Rathjen

Yes.

Burton

If you can do that, could you not eliminate boron as one of your environmental problems?

Rathjen

Yes — the important thing is to have some sort of probe to determine what the environmental variables are. One of the most important messages I'm trying to get over in this paper is that while the F2 progeny method is not very intense in its selection, it has led us in two or three directions which have been very productive. Without the breeding method we would not have found the characters.