Paper 2

WILD SPECIES AS GENETIC RESOURCES FOR PLANT BREEDING

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ABSTRACT

Increased claims are being made for the role of wild crop-related species as genetic resources for plant improvement. Recently the International Board of Plant Genetic Resources, in looking forward from its first decade, has called for greater emphasis on wild relatives. However, breeders of field crops are not the primary users of wild species — they prefer to use 'prebred' lines containing desirable wild traits in domesticated genetic backgrounds. The major factors hindering the use of wild genetic resources are: the number, extent, and evenness of sampling of the species range; the availability of and knowledge about samples contained in collections; the weak viability or sterility of hybrids; the restriction on, or tedious process of getting recombinants; the discerning of useful traits in wild germplasm; and the expression of such alien traits in the cultivated genetic background. To improve the use of wild germplasm in plant improvement it will be necessary to encourage access to samples, to define marker systems for manipulation, and to make more informed decisions when specifying desirable traits.

KEYWORDS

Gene collections, conservation, wild germplasm, hybrids, gene interactions.

INTRODUCTION

Much has been written and said about the potential of wild species as genetic resources. The recent scientific literature emphasises the significance of the wild relatives of crop plants in plant breeding both with striking case studies e.g. tomatoes (Rick, 1982), or in general reviews (Harlan, 1984; Stalker, 1980; Marshall and Broue, 1981). Indications are that the wild relatives of crop plants will receive even more attention in the near future. For example, the International Board of Plant Genetic Resources has accorded their collection and its use high priority during its next decade (Williams, 1984). Finally, the genetic engineers have foreshadowed new methods which will circumvent the problems of sexual hybridisation and of undesirable linkages — problems which often severely restrict the use of wild relatives in plant breeding.

Wild relatives differ from cultivated crops in a number of important ways which greatly affect strategies for their collection, conservation and utilisation. The effects of the differences between wild and cultivated species upon sampling strategies have been described in detail by Marshall and Brown (1983), and upon conservation by Frankel and Soule (1981). Hence we consider here the implications of these differences for the use of the genetic resources of wild relatives in plant breeding. In particular, we wish to consider realistic expectations for the use of germplasm resources of wild species in breeding, the primary users of such resources, and the major problems hindering the flow of wild germplasm into commercial varieties.

THE PRIMARY USERS

A major difference between wild and cultivated germplasm is the ease of use and hence, likely users. For cultivated species the primary users of genetic resources, whether the resources be landraces, or superseded or current cultivars, will be plant breeders who produce commercial varieties. On the other hand, the primary users of wild germplasm are likely to be research workers who justify their efforts in terms of basic research. The reason is simply that cultivated genotypes can be used directly in crosses to produce varieties while wild species seldom can. Indeed, the use of wild species is rarely a single step process as Hawkes (1977) amongst others has pointed out. Rather, considerable and prolonged 'prebreeding' is usually required. As an example, consider the use of the linked leaf and stem rust resistance genes Lr24 and Sr24 respectively, in Australian wheat varieties. These genes, carried on chromosome 3Ag of *Agropyron elongatum* (2n = 70), were transferred by chromosome translocations to Chinese spring wheat by Dr E.R. Sears (1973). Dr Sears made five translocation lines available to Dr R. McIntosh and the linked genes were transferred to several prominent Australian cultivars for use in the National Rust Control

Programme (NRCP) at Sydney University. Backcross material from the NRCP was supplied to breeders and five varieties (Torres, Skua, Sundor, Sunelg and Vasco) have now been released into commercial cultivation by four different breeders. This example emphasises the multistep nature of the 'domestication' of wild genes, and highlights the fact that while practical plant breeders do not usually have the time, resources, or expertise to go back to the original wild sources for genes, they are keen users of such genes if they are useful and in an adapted genetic background.

The point we wish to stress is that commercial plant breeders will seldom be the primary users of wild germplasm. Rather, this role will be filled by basic researchers who have more ready access to the sophisticated research tools often needed to achieve the initial transfer of 'wild' genes to the crop.

If the above logic is valid, and cultivated and wild germplasm collections cater to different primary users then this has a number of important implications. In particular it means that germplasm collections of wild relatives will be used by few groups. But these groups will generally be operating at a more sophisticated level and require more complete documentation on fewer samples. Hence there must be fewer specialist collections set up and run to meet the needs of their real primary users.

PERCEIVED LEVEL OF USE OF WILD RELATIVES

It is difficult to gauge the impact of wild species on modern plant breeding. Indeed breeders to not see themselves as relying on wild relatives to a large extent. This view is reinforced by surveys such as that by Duvick (1984) who found only 1% of US plant breeders of major crops turned to wild relatives as sources of stress resistance and 17% for pest resistance. It is therefore generally argued that collections of wild relatives are not being well used and are of limited potential use.

However, this conclusion is open to question. We agree that commercial breeders are generally not the primary users of wild germplasm, but they are enthusiastic secondary users of wild genes once such genes have been transferred to suitable genetic backgrounds. Further, secondary use is not restricted to specific traits. In sugarcane breeding, for example, lines in breeders' collections are of hybrid origin with some wild chromosomes in their makeup. As a result, most of their routine crosses use genes from wild relatives.

Thus, the number of plant breeders personally involved in transferring traits from wild species to commercial cultivars is a very poor indicator of the use of wild relatives in plant breeding. A better index of interest in and use of wild germplasm is the number of papers on this subject in the literature. This index suggests that there is a very widespread and healthy interest, e.g. more than one quarter of the papers in the 1984 issue of the plant breeding journal — Euphytica — dealt with the use of wild relatives

in breeding.

Hence, we believe that the use of wild germplasm is already substantial and growing. However, this does not mean that problems do not exist or that more efficient use could not be made of collections.

LIMITATIONS TO USE OF WILD RELATIVES IN BREEDING

The number of species, and the intensity and eveness of sampling.

For each crop species the first question to arise is: which wild species are relevant. A possible criterion is crossability. Unless the species can be hybridised conventionally it is considered less significant. While this may be a valid factor in apportioning the effort of collecting, conserving, or crossing among several species, it cannot be an absolute criterion. First, this criterion ignores 'non breeding use' (see below). Second, tissue culture and embryo rescue methods have allowed increasingly wider hybridisations. Third, genetic engineering is expected to offer scope for gene transfer from sources unattainable by sexual methods. Congeneric species, and even related genera should be given at least some attention. In the case of wheat, a suggested list of priority might be: wild *Triticum* species, *Aegilops* species with the D or S genomes, other *Aegilops* species, and more distantly related genera e.g. *Elymus, Agropyron*.

Both the limited and uneven sampling of wild species has severely restricted their use. In the past, the accessions of each wild species were often few in number and were obtained on an *ad hoc* basis. Inadequate numbers of accessions or small sample size restricts the extent to which results can be generalised. While desirable sample size is a contentious issue, the plant breeder or geneticist would like at least to have available a larger number from which he may choose a subset for actual use. Unevenness of sampling is yet another problem. Apparently there are about 10000 accessions of *Aegilops* and wild *Triticum* in wheat collections. Of these accessions about 20% are *T. turgidum ssp. dicoccoides* and of these, 1600 are from Israel which is but a small portion of the species range. Priorities of sampling must continually be revised to remove gross imbalances of sampling, using up-to-date knowledge of the ecological, geographic, and taxonomic diversity within species.

Collections — availability of accessions and documentation

Two problems surround the material available from major germplasm collections. First, because wild relatives are generally more difficult to maintain and to regenerate, they have been neglected. Few samples are readily available from working collections, and even fewer in breeders' collections. Rather, the bulk of samples is left to selected specialised collections (e.g. relatives of wheat, soybean). This usually means that accessions must be sought overseas by international seed exchange. This can be slow and

subject to quarantine regulations. The second problem is that basic information to aid the handling and use of accessions is often lacking. Descriptor lists designed for cultivated species may not apply. A thorough biosystematic understanding of the pattern of genetic variation, both nuclear and cytoplasmic, is needed to rationalise the testing and breeding of wild material.

One area where careful study is likely to stimulate greater use is that of analysis of interactions between wild species and the specific pathogens that attack them. For example, Burdon et al. (1983) have analysed the geographic patterns of resistance variation in wild *Avena* species in New South Wales and compared them with virulence variation in coincident isolates of two rust pathogens. More northerly areas with more humid summers, harboured wild oat populations with a greater diversity of resistance genes, and rust isolates with greater diversity of virulence. This kind of evidence bears directly on samping priorities (section a), on likely new sources of resistance, and on strategies for the deployment of resistance genes in crops.

Hybrid inviability and sterility

A difficulty often discussed in reviews (e.g. Stalker, 1980) is the failure to get progeny or subsequent generations from attempted crosses. Techniques such as embryo culture have made possible, crosses previously thought impossible. In *Glycine*, hybrids between soybean and perennial Australian *Glycine* previously frustrated by inviability (Ladizinsky et al., 1979), were eventually obtained first at the tetraploid level (Broue et al., 1982; Newell and Hymowitz, 1982) and second, at the diploid level (Grant et al., 1986) by embryo culture. These hybrid plants are perennial and sterile. Colchicine doubling of the chromosome number has so far failed to restore their fertility. The hexaploid hybrid (2n = 118) exhibits multivalents at meiosis, whereas meiosis appears normal in the doubled diploid hybrid (2n = 80), but genic interactions yield male and female sterility.

The considerable effort required to make such crosses generally falls outside the resources available to breeders. The burden will fall on research institutions and universities. Private efforts are being made when the potential payoff justifies the risk; however, it is unlikely that the bridging stocks achieved in private programmes will be made generally available.

Interspecies recombination

The introgression of desirable genes from an alien source into a crop may have the problem of unfavourable characters which are linked on the same chromosome. Sometimes the problem is to overcome restriction on recombination due to a lack of meiotic pairing between genomes. This problem may be partially solved by x-ray-induced translocation, resulting in chromosomes carrying alien segments in which the desired gene is embedded. Even so, there may still be yield-depressing genes, closely linked and inseparable without intergenomic pairing. The valued segment from *Agropyron elongatum* carrying the stem rust

resistance Sr26 and translocated onto Chromosome 6 in wheat is apparently linked to a yield penalty. In meiosis, this segment does not pair with the homoeologous wheat segment, so recombination to reduce this yield penalty is impossible. The introduction of the ph mutant might overcome this problem (Sears, 1973).

Backcrossing is the common, established approach to transferring the desired genes selectively. The rate of replacement of unwanted background genes on other chromosomes is exponential and quite rapid. However, chromosomal linkage of undesirable genes with the selected set decays much less rapidly (Stam and Zeven, 1981). It is therefore desirable to improve the efficiency of backcrossing.

One approach is to use genetic markers to select for or against specific segments. This approach uses protein markers such as isozymes in tomato (Tanksley et al., 1981), pepper (Tanksley and Iglesias-Olivas, 1984) and barley (Brown and Munday, 1983). Unfortunately the number of polymorphic isozyme loci is restricted to about 20. However, the principles should be extendible to markers at the DNA level using restriction fragment length polymorphisms. Apparently such markers will provide high density mapping.

In barley, over 70 third-backcross lines have been developed using various lines of its nearest wild relative *Hordeum spontaneum* as the nonrecurrent parent. The recurrent parent was the standard barley cultivar Clipper. In the segregating generations, each line was selected to carry a segment of *H. spontaneum*-derived chromosome, marked by a distinctive isozyme allele (an isozyme-marked-segment or IMS). Alleles at 20 different loci, scattered through the barley genome, are covered by the 70 BC-lines. The original wild parents span the ecological range of the species in Israel. The BC_3F_2 lines, each homozygous for a wild IMS, were tested in field trials, and as single plants in the glasshouse for yield and yield components (Table 1).

In trials, the lines differed for several characters, with several lines being potential positive donors for these characters. Our next step is to test whether the isozyme genotype is correlated with a particular character. As well, crosses transferring proven IMS's to the latest barley cultivars, and crosses combining two different IMS's are planned.

Alien traits and their expression

We have so far considered each step in the process of using wild relatives as genetic resources: original collecting, the collections themselves, obtaining hybrid derivatives, and separating desirable alien genes from unfavourable linked genes. Finally, useful alien traits and their expression in the cultivated background must be considered. Useful traits may range from disease and pest resistance, stress tolerances, and quality characters through to yield. The genetic basis of these traits may be single genes, or multigenic but strongly inherited.

A major limiting factor in the use of wild relatives is the accurate delineation of attributes which are present in

Table 1. Field and laboratory performance of third-backcross lines of *Hordeum spontaneum* (x *H. vulgare* cv. Clipper). (Unpub. data A. Brown, R. Henry, B Read, S. Ellis).

Character	N[1]	cv. Clipper (S.E.)	Backcross range	P[2] (%)
Field trials				
Canberra — yield (kg per plot)	28	0.88 (0.22)	0.17-1.30	32
— 1000 grain wt (g)	28	48 (1)	42-51	36
— malt extract (% O.D.)	39	70 (-)	61-77	46
Wagga Wagga — yield	17	3.5 (0.29)	2.3-3.8	6
Horsham — yield	17	3.0 (0.12)	2.6—3.7	41
Glasshouse trial				
Seed wt/per plant (g)	48	2.0 (0.2)	1.5-2.8	53
1000 grain wt (g)	48	47 (1)	42-56	61
Flowering data	49	10 (0.6)	1-21	12
Height (cm)	49	65 (1.7)	51-72	48

[1] Number of third backcross-lines tested; cv. Clipper is the recurrent parent.
[2] Percentage of the lines with values numerically superior to Clipper.

wild species and which it would be beneficial to transfer. Recognition of desirable characters comes from familiarity with the current breeding objectives, a knowledge of what is already available in the cultivated species, and what attributes the wild relatives possess, as well as the imagination to perceive new options. Several quality and fruiting characters in tomato are good examples (Rick, 1982). In the wild *Gossypium* species, the tissue-specific production of the natural insecticide gossypol in the leaves and not in the seed would be a useful trait to transfer to cotton (Marshall and Broue, 1981). This is a good reason why breeders could be encouraged to grow representative samples of the wild relatives of their crop. Such samples can be readily studied at first hand, and reports of potentially useful characters published.

A final problem to consider is that of pleiotropy and epistasis. The former occurs when genes for the desirable wild character, when transferred to the cultivated background, have an unwanted effect on a separate character. The latter refers to the unfavourable interaction of wild derived genes with crop genes and the desired character is not expressed. These are two aspects of the same problem, especially difficult in wide crosses: introgressing genes into what is already for highly bred crops, an integrated, selected system or a co-adapted gene pool virtually of a separate biological species.

The problematic issues of alien traits and their expression are important in the evaluation of wild species collections for use in breeding. For single gene characters, such as disease resistance, evaluation is straightforward. However results are only relevant when account is taken of the virulence races of the pathogen used. The evaluation of characters such as single plant biomass and seed yield (e.g. Nevo et al., 1984) which are of unknown inheritance, and whose expression is environment dependent, is of little value to breeders. For these characters, it is more useful to evaluate the derivatives of a hybridisation and backcrossing programme (Frey, 1976). Without some crossing, there is

no way of interpolating the spectrum of expression in wild germplasm to that already available in breeders' populations. We conclude that phenotypic evaluations of wild relatives should be critically considered to determine whether sources of the trait are already plentiful in the cultivated gene pool, and whether the trait is likely to show marked pleiotropy or epistasis when transferred.

WILD RELATIVES AS MODEL SYSTEMS

Wild relatives have an important, increasing role in research on genetic resources.

Species of *Linum* were surveyed as wild relatives of linseed for variation in the fatty acid composition of their oil (Green, 1984). The question at issue was whether related species could serve as a genetic resource to lower the linolenic acid content of linseed oil from 50 to 3% and thereby convert it to an edible oil. Several species in the section *Linastrum* were found to have high linoleic and low linolenic acid; *Linum tenuifolium* averaged 81% and 4% respectively. However, these species cannot be used directly as a genetic resource because of strong reproductive barriers preventing interspecific hybridisation. Nevertheless they demonstrated that edible oil composition could be achieved in the genus. This finding gave added impetus to a mutation breeding programme, which was ultimately successful (Green, 1985).

Soybean leaf rust is a serious disease of soybean in S.E. Asia and is sporadically serious in Australia. Sources of resistance to the disease are scarce in *Glycine max*. In the perennial wild *Glycine* species from Australia, however, sources are frequent and diverse (Burdon and Marshall, 1981). The resistance is yet to be used in a breeding programme. However, variation in response to infection by different isolates of the pathogen has allowed the recognition of at least six virulence races. In turn this has led to the definition of a set of differential hoses, i.e. lines of *Glycine* which discriminate among the races (Burdon and

Speer, 1984). Such a set of differential lines was not available from the soybean gene pool. Studies of the genetics of resistance, and the structure of natural populations of hosts and isolates can proceed to determining the best strategies of resistance gene deployment.

Soybean is among the more recalcitrant of species in developing tissue culture regimes, particularly in defining techniques for protoplasm culture and differentiation. The wild relatives offer a greater diversity of experimental materials for the preliminary refinement of such techniques. For example Grant (1984) identified an accession of *Glycine canescens* in which it is possible to obtain multiple regenerated plantlets from callus culture.

These three recent examples illustrate that the related wild species of crops are likely to contribute to crop improvement by indirect non breeding means. Such potential contributions should be kept in mind when collecting and conservation priorities are being determined.

CONCLUSION

Wild relatives support the genetic improvement of our crops in a diversity of ways. Basic research scientists rather than commercial plant breeders will generally be the primary users of germplasm resources of wild species. Collection of such species should be developed and maintained with their users clearly in focus.

It is important to remove current limitations to the use of collections. Several steps which could be taken to achieve this objective are:
- Collecting should cover the taxonomic and ecological range and be in sufficient numbers to allow for reliable conclusions on use to be made.
- Collections should give top priority to immediate availability of samples, with supporting documentation.
- Intense prebreeding should be encouraged both as research projects, and where possible, as exploratory crosses by plant breeders.
- Marker systems should be developed to identify desirable chromosomal segments, or nonspecific yield improvement in backcrosses.
- Priority in evaluation should be given to major genes, or the search for defined characters which are essentially unavailable in the cultivated gene pool.
- Significant non-breeding use of related species should be anticipated in the development of collections.

ACKNOWLEDGEMENTS

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SYMPOSIUM DISCUSSION

Dr W. Bushuk, University of Manitoba

In the work on barley that you describe, what were the enzyme markers that you used?

Brown

I used several, at about 20 loci scattered about the genome — whether or not there is a relationship between the enzyme locus and the trait is irrelevant really. In the case of storage protein loci the philosophy is the same, if anyone is really interested in the fact that the gene being followed could not improve quality of product. But here I am using them purely as marker genes.

Bushuk

Could you name the enzymes?

Brown

Alcohol dehydrogenase, esterases, acid phosphotase, PGM, etc. Wild barley gives several differences — it is quite polymorphic, and different from cultivated barley for many of these genes.

Dr R. Burdon, Forest Research Institute

You mentioned an apparently broad spectrum resistance gene in the case of soybean and the question of whether that is a supergene complex or a straight forward single locus.

Brown

We are not looking at that question. We are just starting on the genetic analysis of the kind of resistance found in natural populations. The preliminary work shows that you get what breeders would call quantitative or broad spectrum resistance. Sometimes crosses between resistant and susceptible against one race may be 2 genes of duplicate effect. It is quite a complicated picture — the molecular biologists may be able to help understand that resistance. It would be useful to clone it out, to get it to the soybean but also to understand the structure of that gene. It is remarkable that one simple gene, segregating 3:1 could product resistance to all races, but not unknown.

Dr E. Walsh, University College Dublin

How do you define wild species?

Brown

In our situation we consider a wild species as something that grows on its own, has not been deliberately planted by man, is adventive. With that operational definition you can have races of the same biological species.

Dr H. Eagles, Plant Physiology Division, DSIR

When looking for genes for stress related complexes, could it be worth knowning where they are and then using isozymes to move them? For example in *Zea*, genes for cold tolerance may be mainly on chromosomes 9 and 10 — could isozymes be used to move such genes from wild species to their cultivated relatives.

Brown

It is a possibility where there is sufficient genetic information, for example with wheat. Generally, however we're not in that favourable situation. The corn map is well known so you're in a better position; the barley maps are still behind.

Eagles

Should more effort be put into finding out where these are on the chromosomes?

Brown

Yes, although our approach has been to set up the lines and find the character, and then try sophisticated techniques. In other words hope that you can manipulate it in other crosses. I feel that is less restrictive, even though in setting up backcross lines I am losing a lot of the *spontaneum* genes, I do not see any other way. Instead of evaluating wild barley from a backcrossing programme, factors such as yield and agronomic traits which are of interest to breeders can be assessed in something like a domestic gene pool. This is more relevant to the breeder than saying this plant has yielded ten grams and this five, which may mean nothing at all.

Dr P. Garnock-Jones, Botany Division, DSIR

I was pleased to hear you mention taxonomists in relation to this work. Could you expand a little on the role of taxonomist and perhaps indicate whether breeders are getting the services they require from taxonomists?

Brown

To comment in relation to our *Glycine* programme — with the development of collecting expeditions throughout Australia and the growth of a germplasm bank, we are finding new undescribed species. It would be useful to have the taxonomy straightened out, not just to know what we are dealing with but also to know the affinities between various accessions. Biosystematics rather than just pure naming is useful. Such information is necessary to make more efficient use of limited time in manipulating material — it is useful to know how closely related material is before starting other work on it. It is very important, that is part of the rationale of why we are tied up with the herbarium in our breeding programme.

Dr M.B. Forde, Grasslands Division, DSIR

You have mentioned soybean, linseed, wheat and cotton. Are there other crops where wild relatives have not yet been used but could be?

Brown

Because of the difficulties of incorporating wild material into cultivated lines, breeders tend to use this as a last resort. If a crop has been largely unexplored it may be a function of the breeders not feeling any need for new sources.