

Barley domestication – *Hordeum spontaneum*, a source of new genes for crop improvement

R.P. Ellis, J. Russell, L. Ramsay, R. Waugh & W. Powell

The challenge that faces farmers in the future is the sustainable production of crops for an expanding human population. It is possible to envisage a number of pressure points such as the need for improved resistance to pests and diseases, greater fertilizer efficiency and economic water usage. In particular circumstances, it may be necessary to develop farming systems that use brackish water. The breeding of crops for such complex objectives requires the development and use of marker-assisted breeding schemes. But before marker-assisted breeding schemes can be implemented, gene maps are required to locate suitable genes.

To date, our use of molecular markers has focused on their development for use in breeding and for gene isolation for transformation (SCRI Ann. Rep. 1997/98, 64-66). One other important area of research in plant breeding is the discovery of new genes or alleles, particularly in the wild relatives of crop species. Our work with wild barley has appeared

in a number of reports (SCRI Ann. Rep. 1992, 20-23; 1993, 39-40) and a cross between a cultivar and wild barley was particularly useful for gene mapping, as it provided wider contrasts (SCRI Ann. Rep. 1996/7, 82-84) than crosses between cultivars (SCRI Ann. Rep. 1995, 59-62).

Wild barley exists as isolated populations throughout the Eastern Mediterranean, Middle East, and Northern Asia (Fig. 1). Our concept of wild barley and its relationship to cultivars depends on the systems used for collection and assessment. It has not been possible to use markers to genotype material as it is collected, so the main strategy has been to sample populations systemically. This implies that collections that exist in many centres, e.g. John Innes Centre, Norwich and Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany, will contain a wide range of genotypes but are completely uncharacterised. This has hampered the utilisation of the material for breeding, and in the past its main use has



Figure 1 The Middle East, particularly the Fertile Crescent (modern day Israel, Lebanon, Syria and Iraq with Turkey and Iran) has been defined as the Centre of Origin of many cereal crops and is the region in which wild barley (*Hordeum spontaneum*) shows greatest variability.

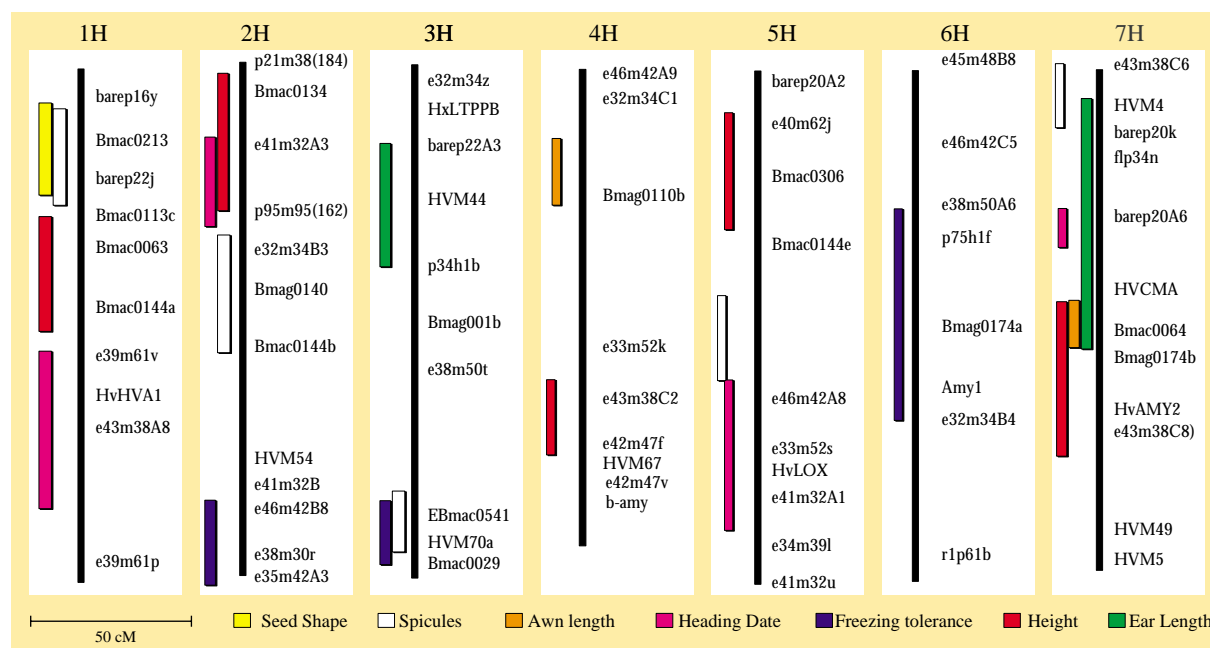
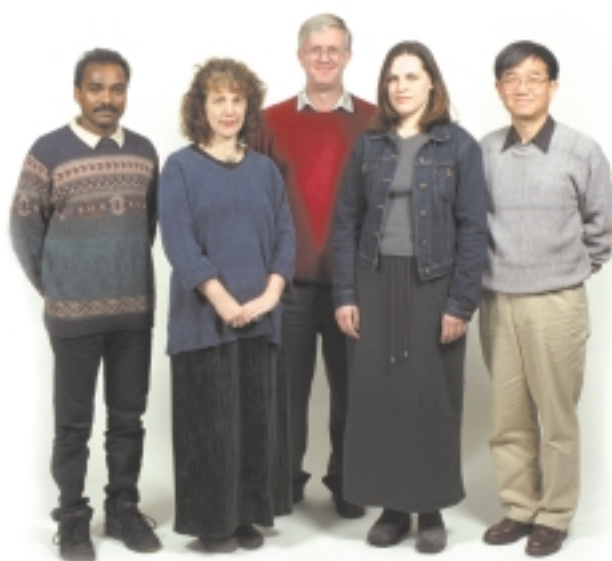


Figure 2 Genome map locating quantitative traits related to domestication in the cross Lina x HS92.

been for the improvement of easily selected characters such as disease resistance.

Wild barley strongly contrasts with cultivars for a number of characteristics. Typically, in wild barley the lemma awns are much more barbed, are tougher and the ear shatters when ripe. These are adaptations to animal dispersal and not suited to cultivation. Relatively high levels of dormancy in wild barley often prevent immediate germination, and time of flowering depends on the satisfaction of a high vernalization requirement and short-day photo-period response. Again, these are not desirable characteristics in cultivars. However, when a simple selection scheme exists, as in the case of mildew resistance, the use of back-crossing often fails to transfer single genes and a whole chromosome segment ends up in the progeny. One common result is the association of disease resistances with characters that impede the fullest development of malting quality (SCRI Ann. Rep. 1993, 24).



The processes of domestication have resulted in similar changes in all cereal species, so that wheat, rye and barley cultivars all have non-shattering ears and flower at a time that is suitable for crop production. Our research has provided an understanding of the contrasts between wild barley and cultivars for characters such as height, time of flowering, ear size and the spiculation or barbing of the grain (Fig. 2). Time of flowering and height are related to genetic mechanisms that control plant development and growth. In turn, these result from genes that control physiological characters, essentially the rate of cell division and cell size. This is clearly seen in analyses of the effects of genes that give semi-dwarf plant stature. There is a contrast between cultivars that possess the *ari-e.GP* gene on chromosome 5H (SCRI Ann. Rep. 1993, 30) and those with the *sdw1* gene on chromosome 3. The former are tolerant to salt while the latter were less tolerant in these tests. The reasons for this contrast in tolerance are not known. The *ari-e.GP* gene was found in the successful Scottish cultivar Golden Promise and was associated with early flower-

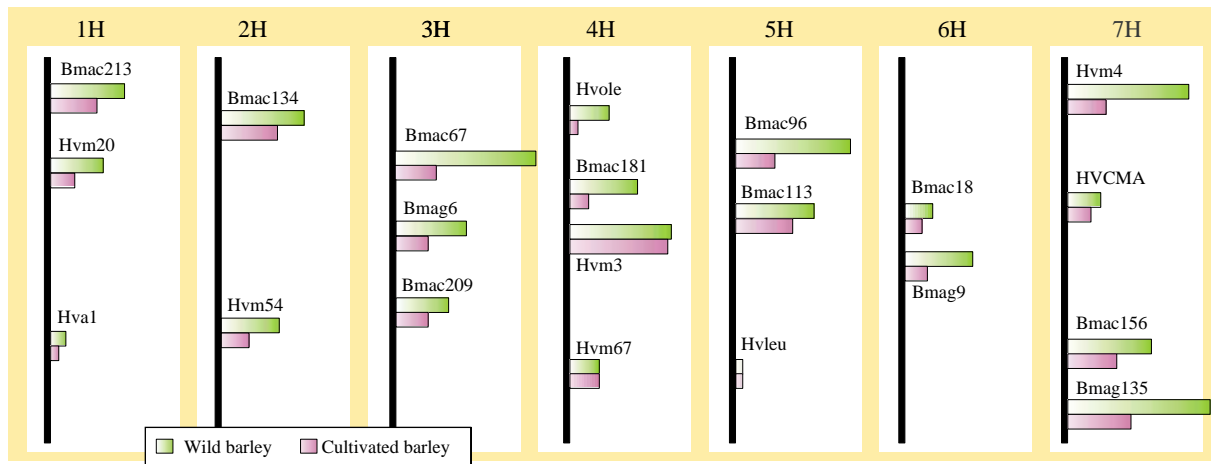


Figure 3 Allelic variability present in wild barley compared to cultivated barley during domestication and selection.

ing and low yield potential. More modern cultivars, such as Cooper, Landlord and Optic, are later and have much higher yield potential, essentially due to larger grain size than the cultivars with *ari-e.GP*. The contrast between cultivars and wild barley is even more extreme with a wide range of flowering dates and very small grain size, i.e. a relatively smaller investment of limited resources into reproduction as numbers of seed matters more than size resulting in greater tolerance of abiotic stresses.

In addition to revealing the current genetic composition of cultivars, our studies have revealed the effects of selection during the process of domestication. Some very obvious differences between wild and cultivated barley, for example the appearance of a tough ear, reduction in awn stiffness and an increase in grain size, must have occurred very rapidly. Other differences, such as increases in grain yield and malting quality, have been accumulated over successive cycles of selection in breeding programmes. While it was expected that height and heading date would show more than one quantitative trait locus, it was more of a surprise to find that lemma spicules were determined by five QTLs. Spicules on the lemma have been used as a diagnostic trait for the identification of cultivars but modern spring barleys have relatively few. In contrast some winter barleys, e.g. Malta and all wild barleys, have highly spiculate lemmas. The origin of smooth skinned barleys is in the hand-evaluation methods used to select malting barley cultivars, prior to the development of micromalting at the Plant Breeding Institute, Cambridge, in the 1960s. The result of hand-evaluation was that malting cultivars of the 1950-1980 period were lower yielding than feed types. At the time, this was attributed to the greater

complexity of selection for malting quality than feeding types. Our new evidence suggests that the root cause of the problem is the simultaneous selection for alleles at a number of loci. This selection may have acted directly or indirectly to reduce plant vigour. In this context, it is interesting to note that silicon, a respiratory irritant in grain dust, is an important plant nutrient that is essential for plant structure and disease resistance. This is very apparent in hydroponic experiments, where the omission of silicon results in an increase in disease susceptibility.

Our experience in mapping genes of economic importance (SCRI Ann. Rep. 1994, 60) shows that very dense genetic marker maps are needed to analyse the complex effects of important genes such as *ari-e.GP* or *sdw1*. It is still difficult to separate the direct effects of these genes from indirect effects, or the effects of distinct but closely linked genes, without obtaining a complete gene sequence and determining gene function. For the present, our work has concentrated on setting the scene by a retrospective analysis of the genetic composition of cultivars since 1880.

The cultivars sampled in this study include genotypes from the 1880s through to modern-day cultivars. This affords an opportunity to examine changes in levels and patterns of variability over time and establish, in a quantitative manner, whether the genetic base of barley is being eroded. By representing the distribution of alleles in the form of a two-dimensional graph (Fig. 3), we can begin to highlight specific allele substitution events and examine the effects of selection over time. Each allele is coded with a different colour and loci are ordered linearly into linkage groups. The overall effect is a reduction in colours as we move from the top to the bottom of the graph, suggesting a loss of alleles

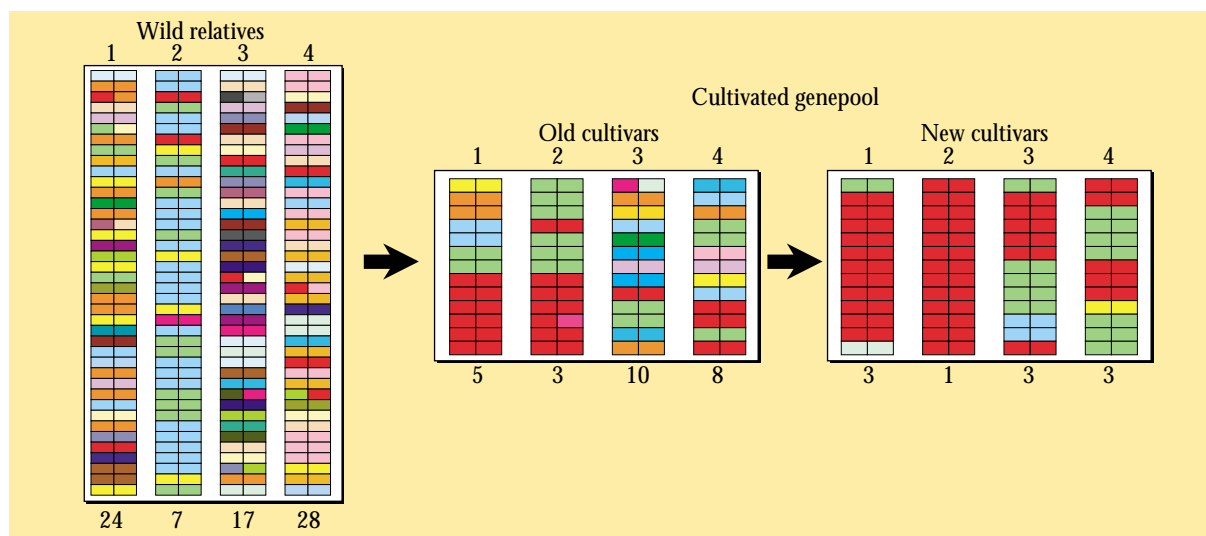


Figure 4 Allelic composition of wild barley compared to cultivated barley on chromosome 7H. The SSRs are coded (1) Hvm4, (2) HvCMA, (3) Bmag135, (4) Bmac156. The numbers of distinct alleles found in wild barley, old cultivars and new cultivars are given at the foot of each column.

over time. These results indicate clearly that the effect of commercial plant breeding, with the need to demonstrate distinctness, uniformity and stability before cultivar registration, was to produce crops that were more genetically uniform.

Partitioning of variation between wild and cultivated barley has re-emphasised the comparatively narrow genetic base of barley, with 54% of the alleles being unique to wild barley and absent in the sample of cultivated genotypes assayed. Only 39% of the alleles in the wild

gene pool have been transmitted into the cultivated gene pool. An examination of the distribution of allele frequencies in *H. spontaneum* and *H. vulgare* confirms

the loss of rare alleles and decrease in genetic diversity during domestication, with a further narrowing of the genetic base by subsequent breeding (Fig. 4).

Comparisons between the gene pools provides evidence of successive genetic bottlenecks in the domestication of barley as well as in the development of the most recent cultivars. The constraints imposed by lack of genetic variation in cultivated barley can be overcome by exploiting molecular markers to access a broader spectrum of genetic variation from wild barley.

In this way, molecular markers, particularly microsatellites, have a significant role in promoting the sustainable use of genetic resources.

