Barley Crop Development

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Introduction George Mackay described the changes to the SCRI programme since the mid-1970s[1]. These comments apply to barley research so this review can focus on scientific and technical developments in the barley crop. There have been several short reports in the SCRI Annual Report the but the last full report on the barley programme was in the 1978/9 SPBS Annual Report[2]. Since then knowledge of the crop, it origins, breeding methodology, and genetical research have advanced out of all recognition. In particular the development of DNA based technologies have revolutionised biology. However, despite specific examples of the application of marker-assisted selection[3], the full impact of modern genetic technology on barley breeding is yet to be realised. Marker assisted backcross conversion offers a more certain technique for the introduction of novel alleles into cultivars than the simple backcross technique used to move the high amylose character from Glacier to adapted cultivars[2]. The current updating of the International Treaty on Plant Genetic Resources, which emphasises the use of germplasm, highlights the possibility of breeding new cultivars with useful traits from landraces, illustrated below in relation to Scots Bere.

Origin – use of wild barley? Barley, as a crop, originated in the Fertile Crescent and became a successor crop to wheat because of its greater tolerance to the soil salinity, accidentally induced by irrigation[4]. The main uses of barley are for animal feed and beverage production. As the processes of domestication[5] were succeeded in turn by 'involuntary' breeding, to produce landraces, and then by deliberate breeding, to give highly bred cultivars, so characteristic traits of wild barley were lost. A large body of work has developed based on the use of disease resistance[6] and the wider genetic variation in wild barley for cultivar improvement[7]. The SCRI programme explored the use of mildew resistance from wild barley[8] in a backcross programme that produced resistant lines. Even although these genotypes were later tested in Egypt, Morocco and Tunisia in an EU funded project[9] they did not achieve commercially acceptable performance. If a market in pre-bred lines existed in the UK then they could have made an impact after re-crossing to more advanced materials within a commercial programme.

Other examples of work with wild barley at SCRI concerned the improvement of tolerance to physiological stress. A useful discovery was of the stable isotopic changes related to stress reactions through avoidance rather than tolerance[10]. Drought avoidance is enhanced by the development of high levels of post harvest dormancy[11] but this trait can be problematic for *ex situ* collections. The largest collection of wild barley is the BBSRC collection (some 25,000 samples) held at the John Innes Centre (JIC). Professors Hayes (Welsh Plant Breeding Station) and Dinoor (Hebrew University of Jerusalem) jointly organised the collection of 230 Israeli populations in 1977. The original seed material was jointly multiplied, on a single plant basis, in the UK by workers at PBI, Cambridge, SPBS and WPBS and then deposited in a high quality seed store at PBI and later moved to JIC. When samples were tested in 1999, following a recent multiplication cycle at JIC, dormancy was found in all samples and germination ranged from 0% to 80%. This effect relates to the interaction of the genotypes with the glasshouse environment. In Northern Europe the abiotic stresses tend to be at lower levels than those in the Middle East and are less predictable e.g. rainfall does not follow any seasonal pattern. So in this context high post-harvest dormancy does not have any adaptive significance and is antagonistic to good malting quality. The use of wild barley accesses the wide genetic diversity between wild and cultivated barley parents but requires a more rigorous selection programme than cultivar inter-crosses, perhaps providing an opportunity for marker assisted selection in early generations to eliminate the undesirable characters of wild barley.

Landraces – not wild barley! It is however, interesting that perhaps the most important single gene for Northern European barley growers, the *mlo* mildew resistance, was discovered in Ethiopian Landraces rather than wild barley[12]. Landraces are genetically closer to modern cultivars than wild barley but even so extensive breeding was necessary to assemble favourable alleles in appropriate linkage blocks[13]. Landraces existed worldwide and still represent a source of useful alleles closer to cultivars than wild barley. An interesting example is the tolerance of acid soils through limited uptake of heavy metals (Al, Fe, Mn) into the cytoplasm (Fig. 1). Barley is less tolerant of acid soils than wheat or oats so a major trans-

formation of Scottish soils, by the practice of liming, started as barley crops replaced Scots Bere, a Scottish Landrace, particularly in the 19th and early 20th century. It would be possible to reduce the costs of liming if barley were as tolerant as other crops but at the risk of increasing the aluminium content of animal diets.

Figure 1 Trial plots grown on 'reclaimed' woodland. The rectangles enclose; red Golden Promise, green Scots Bere, blue oats and yellow woodland/arable contrast.

The impact of the historical changes are encapsulated in Fig. 1 where in 1978 trial plots were established on soil that was still highly acidic despite liming after the removal of woodland. Golden Promise was highly susceptible and few seedlings survived; in contrast Scots Bere was more tolerant and produced a grain yield equivalent to 1 t/ha. Oats surrounding the trial grew well and produced a higher yield. The overall impression of the site was that high inputs were necessary to

Figure 2 A small plot trial with Golden Promise (left) grown alongside Scots Bere.

produce economically acceptable grain yield at the expense of overall biodiversity. The trial plots resemble a desert while the mixed woodland (oak, birch, pine) hosted a range of plant and animal species. The 'desert' feel of the site was emphasised by the removal of stones from the soil, a common feature leading to the degradation of Mediterranean soils[14]. Stones protect the soil surface from rain induced erosion and act as 'magnets' for moisture with the consequence that individual plants may escape the effect of soil acidity because their roots encase stones.

Given that modern agriculture is based on high inputs to give high output, Fig. 2 illustrates a more realistic scenario than Fig. 1 as the application of fertilizer, herbicide and fungicide permits higher and more reliable yields from Golden Promise than Scots Bere. Golden Promise with short straw is well suited to combine harvesting and has small grain that germi-

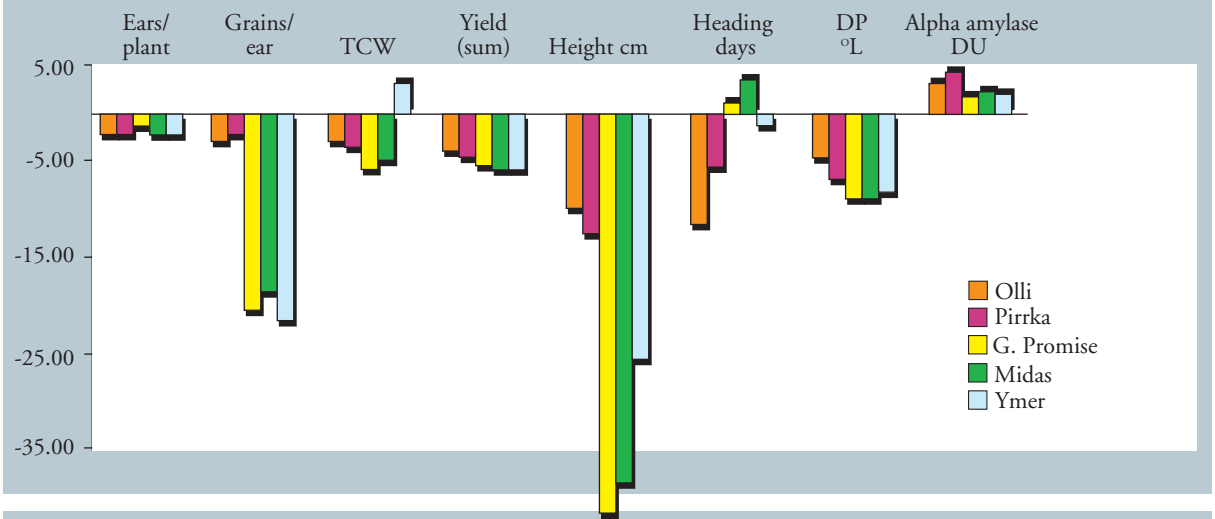

Figure 3 Performance of two six-row (Olli, Pirkka) and three two-row cultivars relative to the base line of Scots Bere's performance [17, 18, 19].

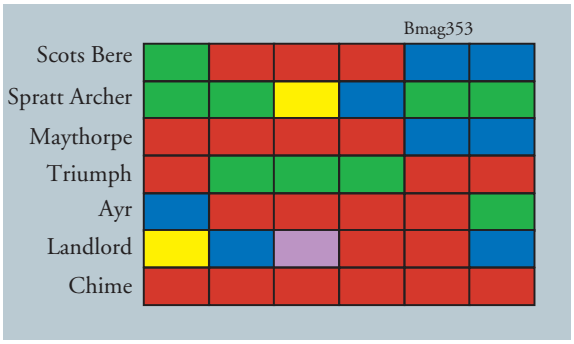

Figure 4 4 SSR alleles at six loci on chromosome 4H. The alleles are colour coded to indicate their frequency (red = high; violet = low) in European germplasm.

nates very evenly in maltings. In particular, the weak straw of Scots Bere (lodging lowers yield) obscures the merits of this landrace. This is well illustrated by the results from a large diallel experiment carried out at the SPBS in the early 1970s (Fig. 3). Scots Bere, Golden Promise and Ymer are adapted to Scotland but are not as excessively early to heading as Olli and Pirkka. Scots Bere was tallest, its straw being 40cm longer than Golden Promise, and was the highest yielding line when the yield components (Ears/m^{-1}, Grains/ear, TCW) were summed. This apparent contradiction of historical experience means that these results should be treated with caution. The results of carefully designed experiments, while accurate, may not be repeatable under normal field conditions.

An additional point of interest is that Scots Bere had the highest level of diastatic power despite having lower alpha-amylase. Diastatic power is the sum of the starch degrading enzyme activity in the malt and is made up of limit dextrinase, alpha-amylase and beta-amylase components. Alpha-amylase is synthesised *de novo* in the aleurone layer in response to a gibberellic acid signal from the embryo at the start of germination. In contrast, beta-amylase is synthesised during grain development and so is a component of the albumin proteins of the grain. Albumins have a higher content of the amino acid lysine than the hordeins, the major storage proteins of the grain. High beta-amylase has the corollary of higher grain lysine content in the endosperm. If re-investigation confirms these results then a major objective, of improving grain nutritional quality, could finally be achieved[15, 16]. It is important to ensure that yield and grain components are compared under carefully controlled conditions, as high grain nitrogen may be simply the corollary of low yield. An appropriate experimental design involves the generation of random inbred lines from a cross between Scots Bere and a modern cultivar and this process has been started.

The development of single sequence repeats (SSRs) in barley[20] sped up the mapping phenotypic traits[21]. In a particularly useful exercise, a range of germplasm (some 900 genotypes) have been scanned for 50 SSRs chosen to give a stratified sample of the genome[22]. The allelic variation (Fig. 4) for the SSRs[23] on chromosome 4H showed a number of unique alleles linked to the genetic factor, mapped to chromosome 4H with morphological markers[24], responsible for acid soil tolerance. Subsequent work[25] in Australia indicated close linkage between *alt,* the gene responsible for acid soil tolerance, and the SSR Bmag353. So, provided that the relative level of tolerance of cross parents is known, selection for Bmag353 can be used in cultivar improvement.

Cultivar breeding Barley cultivars are inbred, although in Scotland levels of out crossing as high as 5% have been observed[26] i.e. the equivalent of or higher than the levels seen in wild barley[27]. Single plant selection was the method used in breeding barley even before the re-discovery of Mendelian genetics by de Vries[28] in 1900. This method was used for example in the development of Chevallier[29], a cultivar that dominated the 19th century English market[30] for malting barley. The intensification of agriculture in the mid-1920s led to the development of breeding programmes to produce varieties bred specifically for malting quality with selection by micromalting[31]. In retrospect the release of Proctor in 1953 by the Plant Breeding Institute, Cambridge was an important prelude to the development of commercial barley breeding in the UK. Commercial breeding became practical after the enactment of the Plant Variety Rights Act in 1964 enabled breeders to earn royalties from certified seed crops. The Plant Variety Rights Act established two hurdles for the breeder; the need to demonstrate the new cultivar was distinct, uniform and stable (DUS) and that it had a useful improvement in performance i.e. value for cultivation and use (VCU). When these tests were satisfied the cultivar could be added to the National List and traded, but in practice little seed was sold unless the cultivar was also added to the UK Recommended List (originally the Recommended Lists of the National Institute of Agricultural Botany (NIAB) and Scottish Agricultural Colleges (SAC)). Relatively few spring barley varieties persisted on Recommended Lists for longer than twelve years (including Proctor, Golden Promise, Midas, Atem, Triumph).

Year	Total cultivars on RL	Cultivar	Yield (Untreated)	Malting Quality	Mildew resistance	Maturity
1983	12	Tweed	2	*	1	4
1984	12	Tweed	3	Good	1	7
1985	14	Tweed	5	Good	1	5
		Heriot	5	Good	4	8
1986	14	Tweed	9	Good	5	6
		Heriot	8	Good	9	9
1987	14	Tweed	10	Good	3	4
		Heriot	9	Good	8	10
1988	12	Tyne	2	*	1	1
1989	11	Tyne	1	Medium	1	1
1990	9	Tyne	1	Medium	1	1
1991	9	Tyne	2	Medium	1	1
1992	9	Tyne	4	Medium	3	1
1993	10	Tyne	7	Medium	6	1
1994	14	Tyne	11	Medium	8	1
1995	14	Tyne	12	Poor	6	1
1996	12	Tyne	12	Poor	5	1
1997	9	Tyne	8	Poor	6	1
		Optic	2	Good	6	9

Table 1 Ranks for selected traits reported on SAC Recommended Lists for Heriot, Tweed and Tyne. Optic figures from the 1997 SAC Recommended Lists are included for comparison.

The early history of commercial barley breeding in the UK involved the formation of agency relationships with established seed houses in Continental Europe. This provided a revenue stream to finance the development of in-house varieties. Among the first 'commercially bred' varieties to be marketed in the UK were; Deba Abed (NIAB RL 1965-74, bred by Abed in Denmark), Zephyr (NIAB RL 1966-76, bred by MGH in the Netherlands) and Julia (NIAB RL 1969-78, bred by Cebeco in the Netherlands). These were all general purpose or feed varieties in contrast to the UK bred malting varieties Golden Promise (SAC RL 1968-1990, bred by Milns Masters, Chester) and Ark Royal (NIAB RL 1976-82, bred by Rothwell Plant Breeders in Lincolnshire). In turn, these malting barleys were outclassed by Triumph (Trumpf) (SAC RL 1980-1991, bred by VEB in the German Democratic Republic). Retrospective genetic analysis[32] showed how UK breeding programmes developed around core varieties in succession resulting in cohorts derived from Vada, Proctor, and Triumph.

In this background barley breeding started at the Scottish Plant Breeding Station in 1968[33]. Within ten years a general malting quality remit replaced the more specialist high diastase and high amylose programmes[2] that were aimed at the whisky industry. A number of cultivars[34] were added to the National List and Tweed (1983), Heriot (1985) and Tyne (1988) were added to the SAC Recommended List. The SCRI programmes aimed to select lines that had good expression of traits suited to both the farmer and grain processors. All were semi-dwarf (Tweed and Heriot with the semi-prostrate *sdw1* gene and Tyne with the erectoid *ari-e*.GP gene), had stiff straw, high yield, good disease resistance and good level of malting potential (Table 1). Tyne received a Medium rating for malting quality, the same rating as Golden Promise, until 1995 when more attention was paid to levels of germinal nitriles. Epiheterodendrin[35] occurs naturally in barley and acts as an anti-feeding defence because cyanide is created when it is digested by grazers such as slugs and rabbits. In whisky distillation epiheterodendrin can be converted into ethyl carbamate, a highly carcinogenic compound. The most practical control is to malt only varieties with low epiheterodendrin and this has been the practise of the Scottish Whisky Industry since the problem was defined[36]. Despite these faults Tyne provided a unique combination of yield, earliness and disease resistance that made it one of the most successful cultivars produced by UK publicly funded barley breeding programmes since the introduction of Proctor.

The significance of public sector involvement in barley breeding was not just development of distinctive cultivars but also an examination the problems of plant breeding from a scientific viewpoint. The use of flexible trial designs[37], obviating the high level of replication inherent in lattice square designs, and the practicality of row and column analysis[38] were both investigated in the SCRI barley programme. The results were published so the implementation of these innovations vastly improved the efficiency of UK barley breeding. Work at SCRI and BioSS indicated how well breeders' trials and National List results could be reconciled[34]. In turn, at the top end of a breeding programme, at the point of entry into National List Trials, it was established that the most serious problem is ensuring DUS criteria are met within a breeder's own programme[33]. The combined effect of the industry wide implementation of technical improvements, the development of new germplasm and the efficiency of National List Trials[40] was the sustained improvement of crop performance (Figure 5.).

Research in genetics[41, 42, 43] and plant physiology[44, 45, 46] at SCRI informed the choice of parents and selection strategies. Visits by and to colleagues in Europe, Australasia and North America were particularly informative. For example the crossing strategy used in the production of Tyne was similar to that

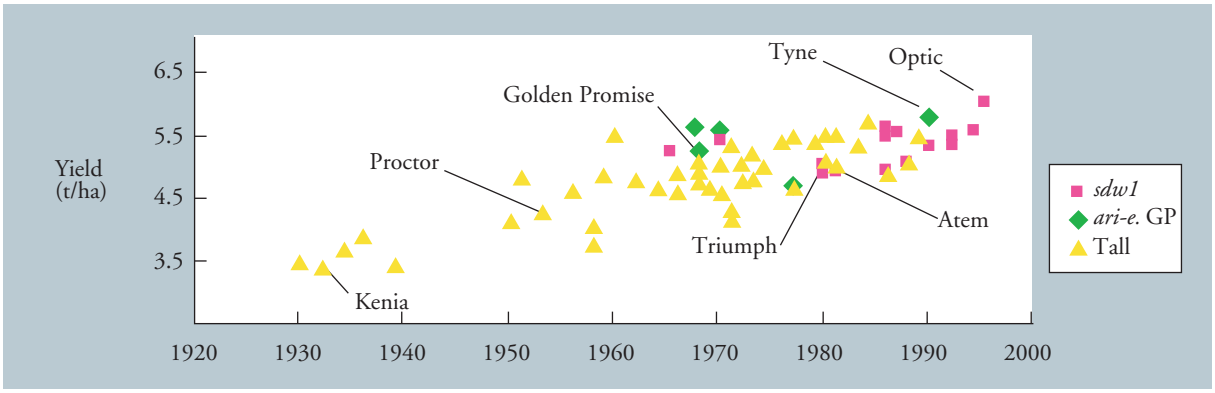

Figure 5 Progress in yield potential related to date of cultivar Recommendation. Estimated from trials grown at SCRI. Note the continued improvement of yield potential despite the use of dwarfing genes.

used in New Zealand to ensure limited recombination within an adapted gene pool. Contrasting parents containing desirable alleles for early maturity (Goldmarker), stiff straw and large grain size (Athos) and good disease resistance (Magnum) were crossed pair wise and then the F_1 re-crossed to give a four-way F_1 (Goldmarker x Athos) x (Goldmarker x Magnum). A particularly large F_3 was raised so that recombinants of parallel ear type could be selected.

The history of barley breeding can be viewed as a contrast between the relative ease in the production of high yielding but poorer quality lines and the additional complication of malting quality selection that reduces the rate of progress for yield. Proctor was out yielded by feed types such as Deba Abed, Julia, Vada, Armelle and Georgie but was the only contemporary choice for a malting quality crop. Maltsters paid a higher price to farmers to compensate for this lower yield potential. The introduction of Triumph overcame the yield differential within spring barley but by the 1970s the high yielding feed crop was actually winter barley, opening a 20% yield differential between the best malting and feed cultivars[48]. Hence the target of breeding a high yielding, good malting quality winter barley is very attractive and could be achieved by converting a spring barley to winter habit or by improving the malting quality of winter types. A crossing programme at Mylnefield attempted to meet these objectives but crosses between spring malting quality and winter cultivars resulted in too high a proportion of lines with a high susceptibility to *Rhynchosporium secalis*. Crosses aimed at converting winter barley to the highest level of malting quality resulted in lines that had high grain nitrogen, resulting from rapid uptake during seedling growth, and so lower hot water extract. Several cycles of crossing resulted in lines with that showed promise but the then available route to commercialisation was suboptimal. There were major handicaps in running a Scottish based winter barley programme, for example the short time between harvest and sowing limited the size of the programme while the absence of regional trialling limited the efficiency of selection. A possible 'technical fix' through the implementation of doubled haploids via anther culture[49] was unsuccessful because the response varied too widely between crosses. The challenge of high malting quality winter barley for Scotland remains to be resolved, especially in the light of changing views on the environmental impact of autumn sown versus spring sown crops.

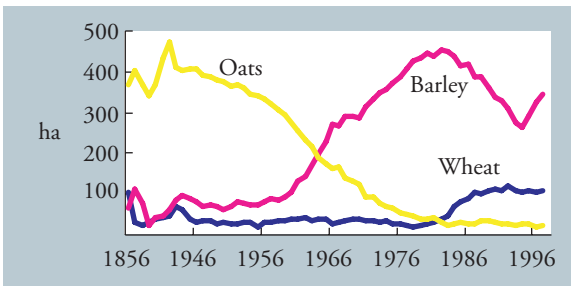

Figure 6 Trends in Scottish cereal crop areas since 1856.

Importance and Future of the Barley Crop

Internationally, barley is still a major small grain crop, albeit less profitable than wheat or maize, that has a particular niche in Scotland. This niche aspect of the crop has an inherent danger as commercial companies need to maximise their return on capital by breeding and marketing over a wide range of environments. In the United Kingdom oats are another example of a niche market. As profitability for breeders and farmers has fallen so the number of entries into NLT has fallen. Long term trends are often difficult to perceive

on a year to year basis and so it is difficult to identify the need for appropriate scientific, technical and economic support. The trends for Scottish Crops (Fig. 6.) over the last 150 years indicate that steady decline over a long period can result in the virtual extinction of even the major regional crop such as oats. The best time to seek alternative crop uses for barley, even for outlandish possibilities such as alcohol production for transport, is now, while there is time to consider the complexity of changes to highly developed systems. If barley growing in Scotland were to be restricted, for example by environmental restraints, then it may not be possible for farming to recover sufficiently when greater production is required.

The history of the barley crop indicates how farmers, breeders and processors have been able to respond to contemporary challenges. New genetical methods, including transformation with genes from other species and cross species genomic comparisons will allow precise analysis of the barley genome and enhance the capability of barley for a wider range of end users. The controversy and public disquiet over genetically manipulated crops has obscured the steady progress made by conventional breeding programmes in response to new challenges such as Ramularia/physiological spotting. Improved genetic mapping will enable marker assisted selection[50] to provide a rapid route to the continued improvement of quality and yield performance. The development of a Product Improvement Centre at SCRI will ensure that research effort if focussed into market deliverable products. Collaboration between publicly funded researchers and private industry, a long term theme of SCRI barley research, is a particular UK strength with the potential to ensure appropriate cultivars are available to farmers and the malting industry. It is particularly timely to seek out and conserve the remnants of landraces before they finally disappear from cultivation. A comprehensive genetic analysis of these landraces will resolve the novel allelic content and value of these genetic resources. Investigations of this type will be promoted under the auspices of the Global Conservation Trust envisaged by the International Plant Genetic Resources Institute, Rome[51]. In the UK the current situation where the main research programme on barley and the gene bank are 'divorced' must be resolved.

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