Potato Breeding at SCRI during the last quarter of the 20th century

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Introduction In 1977, an historical review of potato breeding at Pentlandfield was published (Holden, SPBS Annual Report 1976-77, 66-97). Twenty-five years on, it seemed opportune to review progress since then. Much has changed, both in terms of the organisation and funding of plant breeding in the UK, as well as the technologies and scientific know-how available to modern plant breeders. There is no mention in the 1977 review, for example, of progeny tests, targeted and accelerated breeding, DNA, marker-assisted selection nor genomics. Moreover, at that time and during the early and mid-1980s, the institute was commissioned by government to produce finished cultivars. In the 1977 review, discussion on breeding procedures focused almost entirely on aspects of selection and the methods employed to identify superior individual clones, by their phenotypes, amongst large segregating populations generated by sexual hybridisation of parental clones or cultivars, also selected on the basis of their phenotypes.

Although it was recognised that the choice of parents was of equal, perhaps greater significance than selection methods, cultivars or clones with complementary phenotypes were crossed "in the hope" that their progeny might contain superior individuals (recombinants) with the best features of both parents. The need for greater scientific input into parental section was recognised and it is interesting to see if and how this has been achieved, and might be further improved by the application of modern technologies.

It is not possible in a short review of this nature to cover in depth all aspects of research into the genetics and breeding of potatoes at SCRI since 1977, so it focuses primarily on those aspects of organisation and research that have had a direct bearing on the production of cultivars.

Organisation and funding sources It would not be possible in a review of this nature not to make some reference to the organisation and funding of the breeding programme, which have obviously had an influence on the objectives and priorities of the breeding team. Up until 1987, all SCRI-bred potato cultivars were promoted and marketed by the National Seed Development Organisation (NSDO), which was the sole agency for all state-bred cultivars. The interaction and relationship between SCRI breeders and NSDO was complex and not entirely satisfactory. The breeders' priorities and objectives were, by and large, determined in-house and in accord with the policies of the (then) Department of Agriculture and Fisheries for Scotland (DAFS) [later the Scottish Office Agriculture and Fisheries Department (SOAFD), soon to become the Scottish Office Agriculture, Environment and Fisheries Department (SOAEFD) and now, since devolution, the Scottish Executive Environment and Rural Affairs Department (SEERAD)]. NSDO only became directly involved at the point where SPBS/SCRI decided to submit a clone to National List Trials (NLT), with the exception of their interest in overseas trialling of pre-NLT clones in the mid-1980s. However, NSDO were also responsible for the promotion and marketing of cultivars bred by the Plant Breeding Institute (PBI) in England and the Department of Agriculture for Northern Ireland (DANI). This meant that NSDO had no direct influence on the choice of products of the SPBS/SCRI programme and were often faced with promoting and marketing similar cultivars aimed at the same markets from all three sister institutes. This was sometimes quite frustrating for the breeders. Although there are over one hundred potato cultivars on the UK National List, the acreage is dominated by fewer than ten major cultivars which account for more than 70% of this acreage.

Promoting and marketing a new cultivar in such circumstances is expensive and involves substantial financial risk in building up seed stocks to satisfy a market demand that may not materialise. Thus, NSDO were sometimes obliged to focus their promotional activities on the product of one institution versus that of another, and the lifetime of latter cultivars was often quite short. In an attempt to rationalise this SPBS, PBI and DANI did attempt to co-ordinate the testing and trialling of their advanced pre-NL clones using common origin seed produced at SPBS's high grade seed site at Blythbank (SPBS Annual Report 1979-80, 67). However, each institute retained the

right to submit their own choice of clones to NLT, so this was not a complete solution. In 1987, everything changed: NSDO (and PBI) were sold to Unilever to become Plant Breeding International Cambridge (PBIC) Ltd. SCRI was then obliged to seek alternative outlets for the products of their potato, brassicas, beans, barley and soft fruit breeding programmes as public sector funding of the production of finished cultivars was withdrawn. An agreement, excluding soft fruit, was struck between a consortium of Dalgety Agriculture Ltd and Nickersons Seeds Ltd (SCRI Annual Report 1988, 74). Under the terms of this agreement, SCRI continued to breed and select potatoes in accordance with their strategic objectives, the consortium became responsible for testing and trialling of clones reaching the stage at which SCRI would historically have initiated their routine regional trials in England and overseas.

The arrangement with the consortium had little influence on the priorities and objectives of the SCRI breeders, which remained strategically driven. The consortium's objectives were much more market led. Yield and skin finish became priorities and, whilst the companies professed to recognise the need for more disease and pest-resistant cultivars, they held to the view that these objectives were in the public good i.e. to facilitate more sustainable agricultural practice and to reduce reliance on agrochemicals, so that they were more properly the responsibility of the public sector. This was most noticeable in the priorities afforded to the disease testing of potential cultivars. Late blight and cyst nematode (PCN) resistance were assigned some importance, but resistance to the common viruses less so. It has been suggested that the latter facilitates may encourage the use of home-saved seed and, therefore, is of disadvantage to specialist seed producers.

Under the terms of this agreement, SCRI was able to offer third parties any clones not selected by the consortium. Several of these "discards" were taken up by other companies and are becoming commercially available, the most recent being cultivar Thyme (2000). It was also possible for SCRI to negotiate contracts for fully funded breeding programmes with other companies. Whilst there is a degree of commercial confidentiality associated with such contracts, the first product of such an arrangement, cv. Anya, appeared on a major supermarket's shelves in 1996 under an exclusivity arrangement with the company to whom the clone was sold by SCRI's commercial arm, Mylnefield Research Services Ltd (MRS). The clone that became Anya derived from early attempts by SCRI breeders to produce novel types of potato for niche markets using cultivars such as Pink Fir Apple as parents. Although not a strategic objective of the core-funded research programme, this capacity to exploit SCRI's extensive germplasm collections has also now resulted in the listing of two clones from SCRI's long-day-adapted phureja population, selected in association with and funded by private companies who wish to exploit their unique organoleptic qualities in niche markets (Ann. Report 1995, 34-37). Soon, cvs Mayan Gold and Inca Sun, the former as a flavour enhancer for other potato products, the latter for garden and allotment use, will appear in the seed catalogues.

In addition, SCRI breeders were able to capitalise on their research into, and breeding of, clones with superior storage and processing traits to develop and apply a targeted, accelerated breeding programme for crisp and French fry potatoes, initially jointly funded by Golden Wonder plc and McCain (UK) (Ann. Report 1996-97, 40-45).

However, during the period 1990-1999, both original members of the consortium changed ownership. This, allied to the increasingly more fundamental nature of SCRI core research, led to the early, mutually agreed termination of the agreement in 1999. Greenvale A.P., successors to Dalgety Agriculture, continue to have first option on the products of SCRI's core-funded research into breeding until the end of March 2003, and are currently testing and trialling the final products of the state-funded programme. It is gratifying to record that one of the most recent of these, cv. Lady Balfour (2001), is an extremely high-yielding maincrop with good resistance to late blight and PCN (*Globodera rostochiensis* and *G. pallida).* Lady Balfour has performed extremely well in independent trials under organic farming conditions. The cultivar is, therefore, currently targeted specifically for organic production, and demonstrable justification for the original, strategic objectives of the historic SCRI "commercial" potato breeding programme.

In accord with current government policy, there is now no core funding of cultivar breeding programmes and SCRI is obliged to produce cultivars solely on a contractual basis with private companies.

Breeding objectives For many years, certainly in 1977 and during the 1980s, the main, strategic objectives of the SCRI potato breeding programme were

Yield
Tuber number, tuber size, bulking rate, drought resistance, storagebility (marketable vs. total yield)

Conformity
Tuber shape, regularity and uniformity

Absence of growth defects
Gemmation, hollow heart, growth cracks

Quality
Table and processing - Enzymic browning, after cooking blackening, sloughing, texture, dry matter content, sugars (crisp colour), storage characteristics (dormancy), etc.

Resistance to mechanical damage
External - Shatter cracks, scuffing, etc.
Internal - Bruising (blackspot).

Eye appeal
Consumer prefences - skin colour, flesh colour.

Miscellaneous disorders
Internal rust spot, wind damage, sensitivity to herbicides, etc.

Disease and pest resistance
Late Blight - tuber and foliage, Common viruses (PVX, PVY, PLRV), Cyst nematodes (*rostochiensis* and *pallida*), Common Scab, Gangrene, Wart, Skinspot, Powdery Scab, Spraing (Tobacco Rattle Virus), Soft Rot, Dry Rot.

Figure 1 Some of the characteristics which SCRI breeders considered in selecting new varieties.

resistance to the common viruses (PVX, PVY and Leafroll), late blight and PCN, whilst also attempting to incorporate resistance to one or other or all of these major biotic constraints, in a background of resistance to other significant potato diseases such as gangrene, common and powdery scab, skin spot, dry rot, spraing and wart (SPBS Ann. Report 1977-78, 42-54). It was a fact then and remains so now that, no matter how resistant a clone may be to late blight, PCN and the common viruses, if extremely susceptible to one of the many other pathogens or abiotic stresses that can affect potatoes, or if of low yield and indifferent quality, it is unlikely to become a successful cultivar. The sheer number of traits that a breeder of cultivars has to take cognisance of has undoubtedly been an overriding factor in dictating the pace of advance in potato breeding methods (Fig. 1).

Moreover, potatoes are put to numerous end uses, each requiring different characteristics of the tuber, not least in some cases 'cosmetic' features such as flesh and skin colour can determine success or failure. In attempting to select potatoes for all possible end uses, the SCRI 'commercial' breeding programme was of necessity genetically broadly based and designed to screen large numbers of phenotypically different clones for many traits simultaneously, clones deemed unsuitable for one end use would often be retained for further assessment for another and the core breeding scheme was of necessity complex and lengthy (Fig. 2).

Year	Site(s)	No. of clones	Plot sizes
1	Glasshouses	200-300 progenies	
2	Blythbank Murrays	40,000 "	Single plants in progenies, 2-4 replicates per progeny
3	Blythbank	4,000	1 x 4
4	Blythbank Murrays	1,000	1 x 6 2 x 5
5	Blythbank Murrays	500	1 x 20 2 x 10
6	Blythbank Murrays	200	1 x 100 (2 x 10) x 2 lifts
7	Blythbank Murrays UK Regions	60	1 x 300 variable
8	Blythbank Murrays UK Regions Overseas	15 60*	1 x 700 (A/S) Variable
9 to 12 (variable)	Submission to UK National List Trials (2 years); repeated trialling/testing as in year 8 of the selected clones (1-5); stocks increased to 0.04ha; VTSC initiated by DAFS. Named variety UK National List (Common Catalogue) VTSC → 0.4Ha A/S =(AA1) NIAB Rec List Trials COSAC ADAS PMB New varieties, extension service trials etc. Commercialisation by NSDO		

Blythbank = seed site (Peeblesshire); Murrays = ware (E.Lothian)
Years 4-8 most routine disease tests, cooking and quality assessment, etc.
* same clones as year 7 UK.

Figure 2 The historic SCRI potato breeding scheme.

During the last twenty-five years, the UK potato industry has undergone major restructuring and reorganisation, and is now largely dominated by the major supermarkets and their suppliers, and rather few major processors, manufacturers of French fries, crisps and other processed products. The increasing proportion of the crop being processed led to close collaboration between SCRI breeders and the Potato Processors Association (PPA) to whom samples of advanced clones were provided for independent evaluation. By 1982, in recognition of the critical importance of low temperature sweetening, a few advanced clones were stored at low temperature (5°C) as well as at the normal higher temperature (10°C) prior to carrying out fry tests. This soon led to the additional screening of earlier generations, for clones capable of being stored at low temperature without exhibiting low temperature sweetening (Ann. Rep. 1983, 63). Over the next few years, this routine screening consistently identified a small proportion of the segregating population which produced pale fry colours following storage at 4°C. Crosses between clones exhibiting this trait confirmed its heritability and led to the purposive selection of cultivars Brodick and Eden, and eventually the targeted, accelerated breeding of Golden Millennium, Harborough Harvest and Montrose (Ann. Rep. 1996-97, 40-44). Unfortunately, despite very encouraging results from the independent PPA trials and its successful completion of National List Trials in 1980, an earlier potential crisping cultivar, Sheriff, displayed a tendency to growth crack under some conditions and its life as a superior, blight resistant, crisping variety was short lived. Brodick too, despite its excellent qualities, yield potential and general all round disease resistance, also was withdrawn when it exhibited a weakness which resulted in internal problems (spraing and internal rust spot) in commerce; these failures confirming a grim lesson to all potato breeders. No matter how high yielding, disease resistant or superior in quality a clone may be during its 10-15 years of testing and trialling, a single intermittent fault missed by breeders, by the statutory testing authorities and independent trials will quickly result in the demise of a new variety when it occurs in commercial practice.

As the proportion of the crop utilised for processing has increased, so too has the domination of the table sector by the major supermarkets. The pre-pack trade in washed potatoes now demands a standard of 'skin finish' that is extremely hard to achieve. Diseases or opportunistic fungi such as silver scurf and black dot, which have little effect on productivity, and hence were regarded as minor problems, are now of major economic importance. Similarly, there is an increasing demand for speciality potatoes, punnet or salad types for example, which require cultivars that produce numerous small tubers to fit the very tight grading standards of the supermarkets or, at the other end of the scale, larger tubers that can be sold ready to cook, singly or in small numbers as 'bakers'. To an extent, this was anticipated by SCRI breeders, when they retained some flexibility in their choice of objectives, and crosses were made which eventually led to the cv. Anya (1996) selected in collaboration with a major pre-packer. However, these objectives were much lower priority than SCRI's core funded strategic aims, though they are now the target of several market-led, commercially funded contracts.

Late blight and PCN resistance have both remained top priorities for core-funded research into the genetics and breeding of potatoes at SCRI throughout the period of this review, and are recognised as desirable, if not essential, by SCRI's private partners. However, resistance to the common viruses has become a very much reduced priority. Historically, virus resistance was a major objective of the SPBS/SCRI breeding programme (Davidson, SPBS Ann. Rep. 1979-80, 100-108). Indeed, its most successful cultivar, Pentland Crown, was a product of this component of the programme. The resurgence of interest in Pentland Crown following the mild winters and warm summers of the early 1970s, when virus health of the Scottish seed crop was severely affected by early spread of aphid-borne viruses, is indicative of the value of such resistances (to PVY and PLRV) should similar circumstances return (Fig. 3). Industry's current view

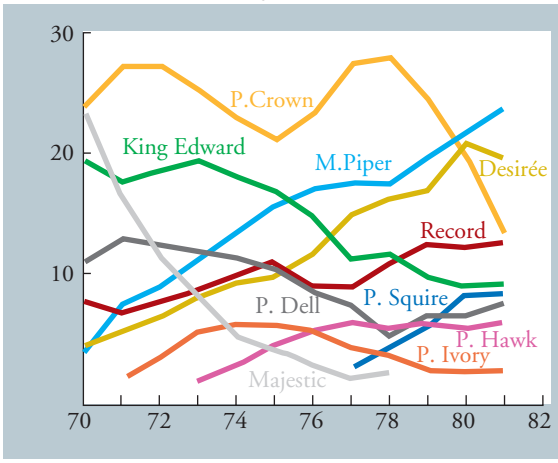

Figure 3 Maincrop potato cultivars percentage area planted (GB).

seems to be that the seed certification scheme and expertise of specialist seed growers are adequate to control the virus health of the crop. One hopes that they are right but questions whether this philosophy is sustainable.

During the mid to late 1980s, SCRI's brief venture into the breeding of cultivars suitable for export also led to a broadening of breeders' objectives to include warm climate diseases such as verticillium and early blight (alternaria) as well as tolerance to abiotic stresses such as heat stress and use of brackish irrigation water.

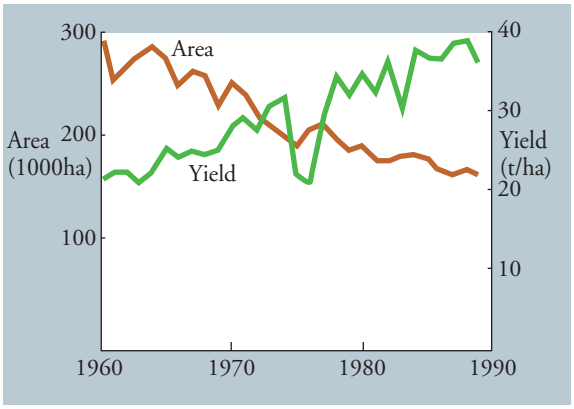

Figure 4 Great Britain potato statistics.

Breeding for overseas It has long been recognised that seed potato production has an extremely important place in the Scottish potato industry. As ware yields have increased and acreages declined, so too has demand for seed within Great Britain (Fig. 4). However, the Scottish seed industry also exports seed, particularly to the Mediterranean region and North Africa. This provides an opportunity for the industry to exploit its climatological and geographic advantage by developing this trade further still. In recognition of the export potential of British-bred potato cultivars, NSDO, in the period up to 1987, appointed various agents for "their" varieties in potential export markets. However, funding was only provided for the trialling and testing of relatively few cultivars once they had been selected as suitable for submission to the UK NLT. With the support of Matutano S.A., an enthusiastic agent for NSDO in Spain and the Balearic Islands, SPBS were able to supply small samples of pre-NLT clones for trial in Spain and Mallorca (Ann. Rep. 1982, p.74). As was anticipated, it soon became obvious that clones with potential as "export" varieties were being discarded on the basis of their performance in the UK. Eventually, an agreement was reached with NSDO to finance the trialling of all clones reaching an advanced, but pre-NLT stage of selection, at four locations in Spain and Mallorca and, by 1984, SPBS was finally commissioned to "Breed potatoes for export and select suitable cultivars by overseas trialling" (Ann. Rep. 1984, pp.68). Primary trialling sites were located in Spain, Mallorca, Cyprus and Israel. Clones which performed well in these trials were also sent for trial in Egypt, Tunisia and Algeria by arrangement with Solanex Ltd., a company set up by NSDO to exploit these markets. The routine testing and trialling in Israel led to substantial collaborative links with the Volcani research centre and led to some limited research and development into breeding for resistance to hot climate diseases such as verticillium and alternaria, as well as tolerance to abiotic stresses such as the use of saline irrigation water (Ann. Rep. 1993, pp. 20-23)(Fig. 5).

Figure 5 Breeders' trial plots in Negev Desert.

The early results were encouraging, as clones exhibiting resistance or tolerance to these non-indigenous biotic and abiotic constraints were identified. By 1988, specific crosses between such clones were made to produce segregating progenies for research and breeding purposes. However, with the privatisation of NSDO in 1987 and the withdrawal of government support for what was perceived to be "near market"

research soon thereafter, this effort, in common with the regional trialling of advanced selections in the UK, was discontinued as a core activity in 1989.

Nevertheless, three cultivars were identified and National Listed during this brief interlude, largely on the basis of their superior performance in the Mediterranean region and thus of export potential: cvs Rhona (1985), Torridon (1989) and Stirling (1991). More recently, cvs Othello (1991), Amour (1998) and Sebastian (2000) have been selected by our commercial partners on the basis of their performances in the Mediterranean region.

Cultivar breeding procedures Twenty-five years ago, the then 'Commercial Breeding Programme' was basically similar to other public and private sector potato breeding programmes, worldwide, perhaps differing only from those of private companies in its more strategic emphasis on disease and pest resistances.

Figure 6 Glasshouse seedlings and seedling tubers.

Figure 7 Visual appraisal and selection of second clonal generation tubers in the field at Blythbank.

Moreover, SCRI breeders were also, of course, obliged to conduct basic research into genetics and breeding methods in order to further the science and technologies associated with breeding *per se*.

Each year, several hundred pair crosses were made between cultivars and parental clones. These crosses were usually made in a series of independent crossing schedules aimed at achieving one or other of the principal objectives being: cultivars with enhanced resistance to late blight or to PCN or to the common viruses PVY, PVY and Leafroll (PLRV). However, in selecting parental clones, due regard was also paid to resistances to other minor, but nonetheless important diseases and, of course, to yield potential and quality (for both table use and processing). Approximately 100,000 seedlings were sown in the glasshouses to produce tubers (clones) upon which to practise selection (Fig. 6). This population would usually comprise first time sowings of samples of speculative crosses made the previous year of family size *c.* 200, and resowings of crosses from earlier years, selected on the basis of the survival rate of clones from these crosses during the routine testing and trialling procedures. In parallel with this population, approximately 15,000 seedlings bred specifically for resistance to PVX, PVY and PLRV would also be sown. These would be screened for resistance to PVX and PVY by sap inoculation in the glasshouse, then surviving, putatively resistant, clones would be retained and, after screening in the field for resistance to PLRV and PVY, the resistant selections would enter the main, routine clonal trialling system.

Of the 100,000 seedlings sown, approximately 40,000 clones would be selected by visual appraisal of the seedling tubers in their pots, and a single tuber of each

planted in family blocks the following year at the Institute's seed site. At harvest, these 'singles' would be selected, also by visual inspection of their tubers in the field. If selected, originally three but, in later years, four tubers of each selected single would be planted back again at the seed site the next year. These plots were also visually selected at harvest when some attempt to visually compare them with controls (named cultivars) was made (Fig. 7). In subsequent years, selected clones would be grown under ware conditions on the Institute farm, whilst seed stocks were reproduced solely for seed. By this, the fourth year stage, the original population of 100,000 seedlings will have been reduced to fewer than 1,000 clones. Ninety-nine percent of the original genetic variation was thus eliminated on the basis of visual appraisal of tubers produced under the rather atypical growing conditions of a seedling in a pot, a single plant, and then a small unreplicated plot grown under a seed potato regime. Only in the fourth year were selected clones grown under more typical ware conditions and data such as yield, cooking quality and disease resistances collected. Two further clonal years of trialling and selection at the local ware site followed before the remaining clones, *c.* 40 per annum, were also trialled at regional centres, courtesy of ADAS, in ware growing districts of England. Despite the obvious deficiencies of this system, it was the means by which the very successful Pentland series of cultivars was produced and, in 1977, these occupied approximately 40% of the British potato acreage. In 1977, the latest product of this regime, cv. Croft, received the accolade of a recommendation from NIAB as a high yielding, good quality, blight-resistant maincrop.

By 1981, advances in computing hardware and the in-house development of suitable software, dramatically facilitated the planning, management, acquisition, analyses and interpretation of data, such that it became possible to introduce randomisation and, where seed stocks permitted, replication of all trials of all clones undergoing selection (Ann. Rep. 1981, 175). This single development was probably the most significant contribution to placing the potato breeding programme at SCRI on more sound scientific grounds. It dramatically increased both the quantity and quality of data and enhanced selection procedures as well as freeing manpower resources from many time-consuming and tedious aspects of label writing and manual record keeping, to focus on research.

In parallel with, and aided by, these developments in logistics, research into the efficiency of early generation selection continued apace throughout the 1980s. This research and development advanced on two broad but complementary fronts, which not only increased the efficiency with which potential new cultivars can be bred, but also provided the means to estimate breeding value of parental clones and to investigate the genetic architecture of agriculturally important traits. It permitted SCRI breeders to move from phenotypic to genotypic selection.

Early generation selection and parental breeding

There are a number of important resistances to potato pathogens governed by major dominant genes. The most well documented example is probably the H1 gene ex. CPC 1673(1), which provides qualitative resistance to pathotype RO1 of PCN (*Globodera rostochiensis*, the golden cyst nematode), now present in most modern cultivars. There are also genes such as Ry_{sto} and Rx_{adj} which convey extreme resistances to viruses PVY and PVX respectively. However, the complexity of tetraploid tuberosum complicates the use of such valuable sources of resistance. A parental clone simplex for one such gene will only ensure that 50% of its progeny inherit the resistance in crosses with susceptible clones, thus half the populations so produced will lack the desired phenotype. However, a parent duplex for such a gene raises this probability to more than 80% and a triplex or quadruplex parent guarantees resistance in all its progeny. By deliberately intercrossing clones with these genes then test crossing their progeny, it was possible to selectively breed parental clones duplex at their resistance gene loci. The fact that the recently released cv. Spey (1994) is triplex for H1 provides demonstrable evi-

Rrrr x Rrrr	Simplex genotype x simplex genotype
↓	
$^1/_4$rrrr $^1/_2$Rrrr $^1/_4$RRrr	Duplex genotype recognized in test cross to rrrr by 5 to 1 (11 to 3 with chromatid segregation) ratio of resistant to susceptible progeny compared with 1 to 1 (13:15) ratio if simplex genotype
RRrr x RRrr	Duplex genotype x Duplex genotype
↓	
$^1/_{36}$rrrr $^8/_{36}$Rrrr $^{18}/_{36}$RRrr $^8/_{36}$RRRr $^1/_{36}$RRRR	Triplex or quadruplex genotype recognized in test cross to rrrr as gives all resistant progeny (or 27 to 1 susceptible with chromatid segregation in triplex)

Figure 8 Production of parents multiplex for a major dominant resistance gene R with chromosomal segregation.

dence that this approach need not be at the expense of yield or quality (Fig.8). Such useful qualitatively inherited resistances are rare, nevertheless the principle of breeding and selecting parents by the development and application of progeny tests remains the same. During the 1980s, much research effort was devoted to this end (Ann. rep. 1985, p. 63) and the application of such tests became an integral component of the programme (Ann. Rep. 1991, pp. 13-16). By 1985, SCRI potato breeders were sufficiently confident to abandon the philosophy of raising many thousands of individual seedlings upon which to practise selection and to use the power of progeny testing first to identify superior progenies, then to focus attention on selecting the best clones from amongst those best progenies Mackay *et al.*, (Ann. Rep. 19976/97 pp. 40-45). In 1989, transfer to the Mylnefield site provided a unique opportunity which confirmed the robustness of this concept by re-evaluating progeny testing for agronomic potential in an entirely new environment under different growing conditions (J.E.Bradshaw *et al.* 1998. Early-generation selection between and within pair crosses in a potato (Solanum tuberosum subsp. tuberosum) breeding programme. Theoretical and Applied Genetics 97: 1331-1339.). Finding the best clones from amongst the best progenies does, however, remain a logistical problem in multistage selection for many traits

Initially, progeny tests were applied independently with appropriate sub-populations of the main population being progeny tested for resistance to late blight or PCN or the common viruses etc. In 1990, it was decided to pursue the possibility of combining them in what has become described as the multi-trait selection scheme (Ann. Rep. 1998/99, pp.92-96). An additional major benefit of the progeny-based selection approach is that by using mating designs such as diallel crosses, the data from the progeny tests also provides the means to estimate the breeding value of parents and to partition the genetic variation into its various components, thus, providing insights into the genetic architecture of important traits, and to formulate more scientifically sound breeding strategies.

Moreover, these improvements in the techniques for screening large populations repeatably and efficiently for a range of agronomic, quality and resistance traits are also providing the means to phenotype segregating populations so essential to identifying allelic variation at the underlying Quantitative Trait Loci (QTL) through the associations of traits with mapped molecular markers. Such work is a pre-requisite to marker-assisted selection, which would have its greatest impact in selecting between clones of the best progenies, perhaps as early as at the seedling stage in the glasshouse (Ann. Rep. 1997-98, 86-88).

These techniques have also proved invaluable in screening the CPC and identifying putatively novel sources of resistance to PCN and late blight.

Strategic breeding and the Commonwealth Potato Collection Strategic breeding during the period of the 1977 review and during the 1980s primarily focused on broadening the genetic base of tuberosum *sensu lato* by developing long-day-adapted populations of andigena (neo-tuberosum) and of the diploid groups phureja and stenotomum. The Commonwealth Potato Collection (CPC) of wild species and primitive forms was, in 1977, just emerging from the hiatus caused by its screening for Potato Spindle Tuber viroid (PSTV). Discussions were taking place at that time between SPBS, the German-Dutch Potato Collection (at Braunsweig) and the relatively newly-founded International Potato Centre (CIP) in Peru, as to the future of such collections. In the early 1980s, it was mooted that the CPC might be merged with the Dutch-German collection as a precursor to a European gene bank, but difficulties posed by international exchange of potato germplasm due to strict quarantine regulations, eventually negated this possibility. Sources of resistances to late blight, PCN and the common viruses tracing to the CPC were being exploited in the commercial breeding programme, but the CPC itself was by and large held on a care and maintenance basis throughout the 1980s and early 1990s, its immediate exploitation for breeding purposes in abeyance.

However, by 1983, use of neo-tuberosum parents in the commercial crossing programmes re-commenced, after a hiatus also caused by the need to screen all SPBS parental stocks for PSTV (SPBS Ann. Rep. 1983, 69). The diploid populations of phureja/stenotomum also began to be used speculatively as parents in tetraploid breeding programmes (SPBS Ann. Rep. 1985, 68).

The history of the neo-tuberosum programme is a lengthy one, having been initiated at the former John Innes Institute in 1960. By 1981, following a Visiting Group recommendation, a substantial effort was initiated to evaluate this population as parental material for use in breeding cultivars (SPBS Ann. Rep. 1981, 181). In one respect, the admission on to the National List of cv. Shelagh (1986), an F1 hybrid

between a neo-tuberosum clone and an unnamed tuberosum parent, provided tangible evidence that it was possible by phenotypic recurrent selection to upgrade the short-day-adapted primitive form andigena to a point at which it could be used directly in breeding cultivars for the UK, without the usual need to carry out several backcrosses to tuberosum to restore the maturity and yield required in a modern cultivar. However, routine screening of the SCRI neo-tuberosum population did not identify any unique or enhanced resistances to the major pests and pathogens that were, by the late 1980s, not already available in the tuberosum parental stocks available to the breeders. This was probably a reflection of the earlier endeavours by SPBS breeders in incorporating such resistances by conventional introgression and selection directly from wild species and primitive forms (Ann. Rep. 1994, 36-39). In 1987, further work on direct improvement of SCRI neotuberosum was terminated and, in 1996, the elite clones of this population were eventually converted to true botanic seed for long-term storage as a potential genetic resource if required in the future. Similarly, the population improvement of the long-day adapted phureja/stenotomum material was halted as resources began to be redirected at more fundamental genetic research. Nevertheless, SCRI has, by obtaining collaboration and funding from the private sector, recently been able to National List two long-day-adapted phureja clones as named cultivars: Mayan Gold and Inca Sun (2001), whose unique organoleptic properties may compensate for their moderate yields in a more discerning market place where flavour, taste and novelty will add value to these cultivars (Ann. Rep. 1995, 34-37).

In 1986, the future of the CPC at SCRI was secured when the decision to retain it was made and arrangements set in place to augment it by incorporating the University of Birmingham's true seed collection of wild species, after passage through quarantine at the S.A.S.A. (Ann. Rep. 1986, 65). A brief hiatus caused by the closure of Pentlandfield and transfer of staff to the Dundee site (1989) followed, but by 1992 the CPC had become reactivated as a valuable genetic resource at SCRI and was being rapidly augmented by pathogen-free stocks of additional species from the Birmingham Potato Collection (BPC) (Ann. Rep. 1992, 13-17). Recent research has identified numerous potentially novel sources of late blight and PCN resistance in the augmented collection and work has been initiated to explore and exploit these valuable traits using modern molecular technologies to identify the genes controlling them, as well as utilising the elite long-day adapted phurejas to more rapidly introgress these traits into agronomically adapted germplasm more efficiently and rapidly than hitherto. Moreover, the successful acquisition of additional funding in 2001 (FF834) is enabling high-throughput screening of the CPC, in collaboration with Strathclyde University, for biologically active, potentially pharmacologically valuable chemicals, thus raising the possibility of breeding potato cultivars for a range of industrial/pharmaceutical uses as well as consumption as a highly nutritional food source.

State of the art and the way ahead The last 25 years has seen major changes in government policy and restructuring of the potato industry into fewer and larger companies and groups of companies representing the different sectors of producers, processors and retailers. Potato breeding at SCRI has also evolved to meet the challenges of the modern world and to maintain its international reputation as a lead centre for research into genetics and breeding of this extremely important commodity.

The Commercial Breeding Department of the Potato Division, as was in 1977, eventually merged with the Brassica breeding department at the time of transfer to the Dundee site, to form the Potato and Brassica Genetics Department in 1988 (Ann. Rep. 1989, 26), shortly after to merge with the other commodity breeding groups, cereals and faba beans, to form the Crop Genetics Department in 1989. In 1999, potato breeding and associated research became part of the Applied Genetics Unit of the Genetics Division and, in 2001, joined the Genome Dynamics Programme in the Genes to Products Theme. In some respects, these organisational changes reflect the move from commodity-led research to more fundamental disciplinary-driven research. However, as a consequence of the research into breeding methods of the 1980s and 1990s, SCRI is now well equipped to explore and exploit the genetic architecture of economically important traits of the potato, armed with the most modern technologies that molecular biology and genomics can bring to bear (Ann. Rep. 1997, 76-80; Ann. Rep. 1997, 86-88; Ann. Rep. 1998, 101-104; Ann. Rep. 2000/01, 75-78). Moreover, it has been possible to capitalise on the wealth of expertise and accumulation of unique enhanced germplasm of the hitherto core-funded breeding programme by attracting investment from private companies to continue to breed and select new improved cultivars.

Listed			
1977	Croft	1993	Buchan
1981	Sheriff	1993	Brodie
1981	Baillie	1996	Othello
1981	Provost	1996	Derek
1982	Kirsty	1996	Claret
1984	Ailsa	1996	Spey
1984	Moira	1996	Kirrie
1985	Morag	1996	Anya
1985	Rhona	1998	Amour
1986	Shula	1998	Blush
1986	Teena	1999	Golden Millennium
1986	Shelagh	1999	Harborough Harvest
1986	Morna	1999	Montrose
1987	Glenna	2000	Sebastian
1989	Torridon	2000	Thyme
1990	Brodick	2001	Scarborough
1991	Stirling	2001	Tay
1991	Eden	2001	LadyBalfour
1991	Glamis	2001	Mayan Gold
1991	Provan	2001	Inca Sun
1992	Cramond		

Commercially available in 2002

Figure 9 SCRI-bred potato cultivars National Listed in the UK since 1977.

There is no doubt that the objectives of these commercially funded breeding programmes are much more market-led than were the hitherto strategic aims of the core funded programme. Nevertheless, as and when the fundamental researches now directed towards exploitation of the CPC; the use of molecular-marker-aided selection is developed to a point of application; genes are mapped and cloned; the genetics of host-pathogen interactions unravelled; the nutritional value of the potato tuber enhanced; it will become possible to use this technology and know-how to continue to breed high-quality, disease- and pest-resistant cultivars required for more sustainable agricultural systems, either in association with and funded by the private sector or to provide industry with the means to achieve these objectives itself. The potato is the fourth most important food crop in the world after rice, wheat and maize. In the absence of disease and abiotic stresses, it is capable of producing a higher yield of highly nutritious food per unit area, more quickly than these grain crops. Moreover, apart from needing to be cooked, potato tubers are immediately ready to consume. Except for a deficiency in the sulphur-bearing amino acids methionine and cysteine, potatoes represent an excellent balance of carbohydrate, minerals, vitamins, protein and fibre – capable, if ever needed, of sustaining human nutritional needs with little need for supplements.

Consumption of potatoes in the developed world is more or less static with an increasing proportion manufactured into processed products. However, the proportion of the world crop grown in the developing cuntries has risen from about 11 percent in the 1960s to 30 percent in the 1990s and continues to rise. Potatoes have a key role in feeding a hungry world but yields are low in the absence of prophylactic chemicals and lack of access to healthy seed. Disease and pest resistances are essential pre-requisites to increasing productivity in less developed countries. Indeed, in developed countries where demands for reduced pesticide use are increasing and the popularity of organic production seems to be gaining ground, intrinsic, genetically-based disease and pest resistances are becoming ever more desirable or perhaps in the case of PCN in the UK, essential. Conventional breeding at SCRI has done much to achieve this objective, but is unlikely to produce cultivars with resistance to all important diseases with the yield, quality (and skin finish) demanded of a modern cultivar. However, in concert with the biotechnologist, the breeder has a much greater opportunity to achieve this aim. SCRI's most important objective in the way ahead is to weld the skills, knowledge and experience of the traditional breeders with those of the molecular biologist. In the 1977 review, it was reported that SPBS had bred and released 24 potato varieties from the UK in the 56 years of its existence. Since 1977, SPBS/SCRI have satisfied the UK National List 'Value for Cultivation and Use' criteria and placed 41 new cultivars on the National List (Fig. 9). A number of these have been withdrawn and no doubt others will be if they do not meet the demanding needs of what is, in terms of varietal choice, a very conservative industry, but only time will tell if the last 25 years of SCRI breeders' efforts can emulate the successes of their predecessors in terms of acreage versus numbers of named cultivars.