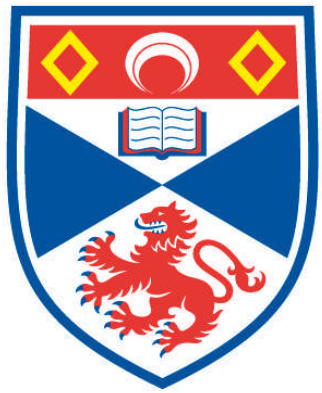
THE EFFICIENCY OF SELECTION IN THE EARLY GENERATIONS OF A POTATO BREEDING PROGRAMME

Jack Brown

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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A thesis presented for the degree of Doctor of Philosophy at the University of St Andrews

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ABSTRACT

The efficiency of selection in the early generations of a potato breeding programme is examined. A number of unselected potato (Solanum tuberosum L.) clones were grown in a glasshouse, from true botanical seed, and thereafter in the field at two locations (a seed site and a ware site) for three consecutive years. At each stage, a number of tuber characteristics were visually assessed and yield plus the yield components were recorded. Four potato breeders visually assessed the produce from each clone after harvesting each years trials and were in good agreement as to which clones would be selected in each environment. Selection for visually assessed characters in both the glasshouse and first clonal year produced a desirable response. However, such selection carried a high cost in terms of losing clones with commercial potential. Selecting clones for yield in the seedling and first clonal year was only marginally more effective than a random reduction in number of genotypes, while selection in the second clonal year appeared to be somewhat more effective as judged by performance in later generations. Comparison of a random sample of clones with ones from the same crosses which had been selected at the seedling and first clonal year stage was at best random, with some suggestion, however, of a negative effect.

The causes behind the inefficiency of selection were found to be complex. The inefficiency was ascribed, at least in part, to (i) the inaccuracy of assessment on single plant plots; (ii) the "carry-over" effect of the mother tubers and (iii) selection under a short growing season.

Although there was a formally significant interaction between progenies and environments, the rank of the mean of a cross remained relatively consistent over different growing conditions. It was found that the mean and square root of the variance obtained from breeders' preference in any of the environments provided a good basis for

prediction of the number of clones in each cross which would exceed (or equal) a given target value. The square root of the variance added increasingly to the accuracy of the prediction as the target value increased but was never a major component in such predictions. When the predictions were used to provide ranking of the crosses, the rank correlations showed good agreement between the different environments and between observed and expected ranks. There was no evidence to suggest that univariate cross prediction for any of the other characters under study would not be effective.

A new cultivar is unlikely to be sucessful simply because of high expression for a single character, but will rather be an all round improvement over cultivars already available. Three methods of multivariate cross prediction were therefore examined namely multivariate probabilities, sum of ranks and the frequency of genotypes in a sample that transgress set target values. The characters total tuber weight, mean tuber weight, number of tubers and regularity of tuber shape were examined. It was found that a sample as small as 25 clones provided good predictions (as judged by the observed frequencies in a larger progeny sample examined in various environments). The best estimates were obtained using multivariate probabilities based on the means, within progeny variances, and the phenotypic correlations between variates. The ranking of crosses according to these multivariate probabilities provided good indications of the number of clones which survived selection in an actual breeding scheme.

Thus it is suggested that an empirical examination of a sub-sample of the progeny from a cross could be used to determine the crosses which would have the highest probability of producing improved, potato cultivars. Selection of crosses rather than individual clones has several advantages which would favour such

techniques being used in the early generations of a potato breeding programme.

Cross prediction based on parental performance also provided an indication of the crosses, and parents, which would give the highest frequency of desirable recombinants. These predictions were not as accurate as those derived from examination of a sub-sample of progeny from each cross. But they would allow an earlier, and hence powerful, method of prediction.

DECLARATION

I, Jack Brown, declare that this thesis is my own work, and that it has not been submitted for any other degree.

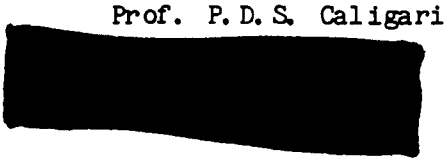
Jack Brown.

St Andrews, March 1988.

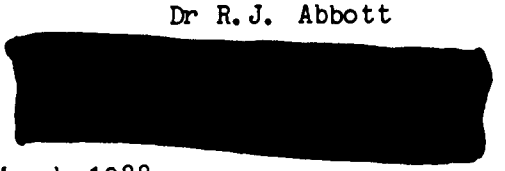
SUPERVISORS CERTIFICATE

We certify that Jack Brown has conducted the appropriate period of research under our direction, that he has fulfilled the conditions of Ordinance General No. 12 and Resolution of the University Court 1967 No. 1, and that he is qualified to submit this thesis for the degree of Doctor of Phylosophy.

Prof. P. D. S. Caligari



Dr R. J. Abbott



St Andrews March 1988

ACKNOWLEDGEMENTS

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Contents

CHAPTER 1

INTRODUCTION

1.1 Introduction to Plant Breeding

The ultimate aim of any plant breeding programme is to increase the quality and production of the crop concerned. This can be achieved in a number of ways, although, three factors are of overriding importance; they are, yield *per se*, quality of product and disease resistance. In most plant breeding programmes these characters are generally subjected to most attention.

The pattern of crosses and the passage of genetic material through a plant breeding programme is largely determined by the breeding system of the crop. Crop plants are generally divided into two broad groups:

(i) Inbreeders;

and (ii) Outbreeders.

Outbreeders tend to carry deleterious recessive genes in the heterozygous state and show inbreeding depression on selfing (Simmonds, 1979). The floral morphology of outbreeding species frequently favours cross pollination between different genotypes; eg. plants produce large showy flowers that may exhibit dichogamy (ie. the anthers and stigmas develop at different times in the same flower). In a number of instances the male and female sex organs are positioned in separate flowers on the same plant (monoecious) or on different plants (dioecious). Many species also exhibit self-incompatibility systems. In contrast, inbreeders, which are almost exclusively self pollinating, lack the deleterious recessive genes and self incompatibility systems that exist in outbreeders, and are tolerant to long term selfing.

When breeding for increased production, four population types may be produced, depending on form of reproduction and breeding system of

the crop:

(i) Inbred pure lines;

(ii) Cross-pollinated populations;

(iii) Hybrid varieties;

(iv) Clonally reproduced species.

For a crop to be grown as a true breeding line, breeders often begin by hybridisation between two homozygous genotypes. A major problem with breeding inbred varieties is that subsequent selection is conducted either on single plants over a number of years (in a pure pedigree breeding scheme) or on heterozygous bulk populations derived from either F_2 or F_3 single plants (a pedigree/bulk breeding system, Lupton & Whitehouse 1957). In both instances phenotypic expression can be masked by dominance effects. Alternative approaches, such as single seed descent or the production of monoploids, can be used to derive populations of inbred lines before making any selection although such methods may be labour intensive and time consuming.

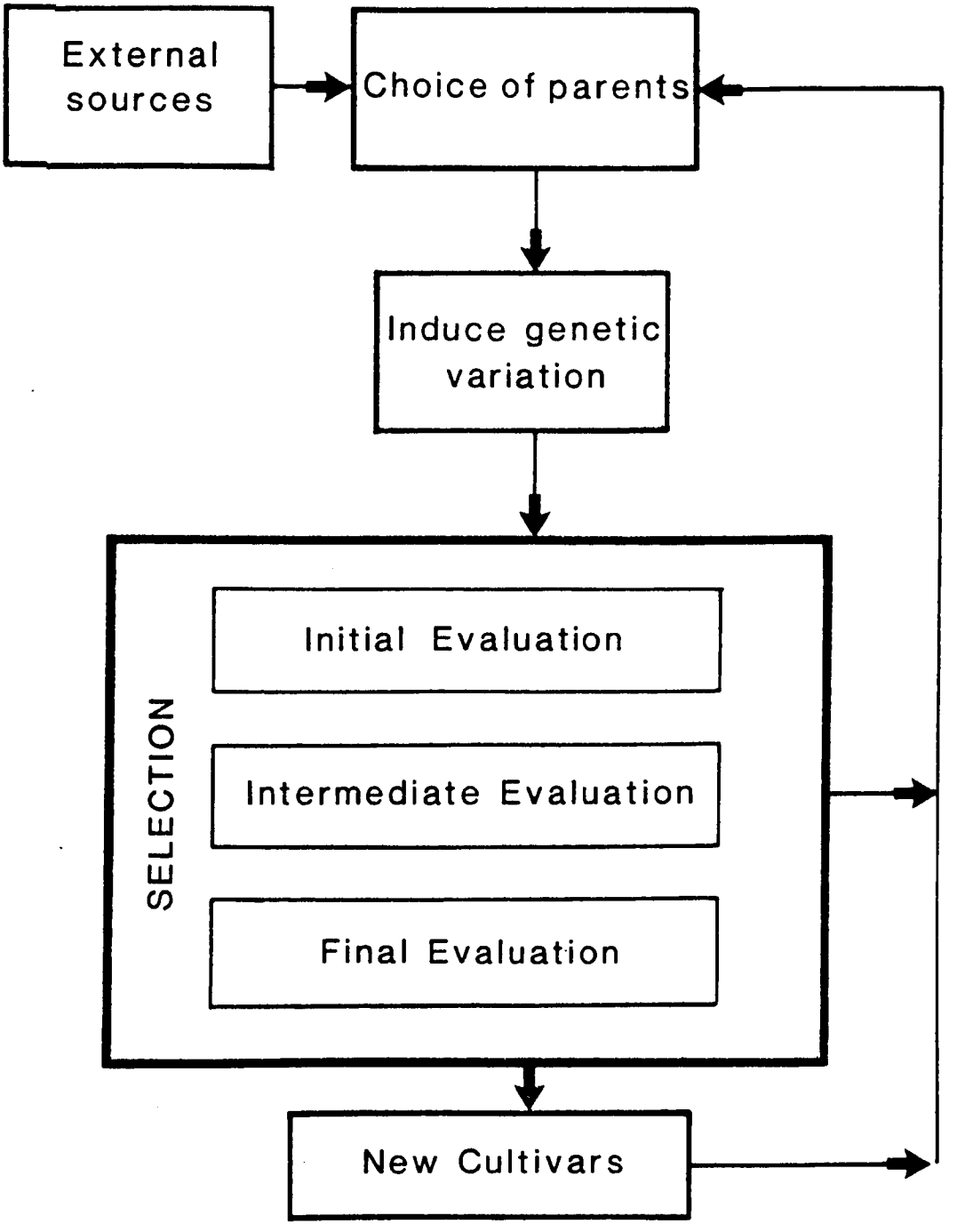
Breeding a cross-pollinating species involves increasing the overall gene frequency of desirable genes into a population of heterozygotes. This is most often achieved by mass selection, backcrossing and recurrent selection (Allard, 1960). To avoid inbreeding depression, heterozygosity must be maintained throughout the breeding scheme or restored as a final step in variety production. Greater control can be achieved through the production of hybrid varieties as is frequently done in Zea mays and some Brassica species. However, the success of hybrid breeding is determined largely by the ease of producing hybrid seed, a process usually involving presence of cytoplasmic male sterility or the availability of suitable chemical treatment. Hybrid production, using cytoplasmic male sterility, can of course have a secondary effect when the harvestable product is in fact the grain of the crop. In these cases it must be ensured that

male fertility is restored if the hybrids are to be grown in agriculture. Finally, in those species where it is possible, clonal reproducion enables the "genetic fixation" of desirable recombinants in one step and the perpetuation of these genotypes thereafter. However, the parental material available to breeders in clonally reproduced crops tends to be highly heterozygous, and many of the undesirable attributes of these parents will be masked by dominance effects.

Irrespective of the breeding system of a crop, plant breeding can in its simplest terms, be considered as a two step operation (Figure 1.1). Genetic variation is produced and selection is imposed on the resulting population in order to identify desirable recombinants. The selection process is often repeated over a number of years and in some of these years, at a number of different locations. At each selection stage desirable genotypes will be retained for re-evaluation and those which do not, on a phenotypic basis, show commercial suitability are discarded from the breeding scheme.

The most common method of producing genetic variation is by artificially hybridising chosen parents. The majority of parents used in a plant breeding programme will be genetically adapted to the area concerned (Simmonds, 1979). Other parents used will include wild, or unadapted genotypes, or lines derived from amongst the breeding lines, i.e. those lines which would not have had all the attributes of a new cultivar, but nevertheless have very good expression for one or more desirable traits hence making them good parents. Genetic variation can also be produced by mutation (Yonazawa & Yamagata, 1977), induced for example by gamma rays, or chemically, or by somatic hybridisation (Shepherd, 1982). Limited transfer of genes has been successful using irradiated pollen (Powell, Caligari & Hayter, 1983), irradiated protoplasts and by gene insertion through Agro-bacterium (Ooms, 1987).

Figure 1.1 Outline of operations involved in a plant breeding programme.



The full implications of these novel technologies (excluding mutation) have, as yet, to be realised and artificial hybridisation continues to be the most favoured method used by plant breeders for producing genetic variation.

The fundamental assumption of plant breeding is that selection practised in breeders' assessment plots is eugenic, in the sense of promoting better adaptation of new varieties to the prevailing agricultural conditions. Selection of desirable recombinants can for convenience be divided into three stages (Figure 1.1). In the first stage, many thousands of genetically different lines require assessment. Limited quantities of material will be available for planting assessment plots, also economic considerations usually dictate that the early selection assessments are carried out on small plots. These plots, which in the first instance often contain only a single plant, are rarely randomised and selection is made by visual appraisal. Highly heritable characters (ie. major gene characters) are affected only slightly by the environment in which the genotypes are grown so these tend to be the characters that are selected for in the earliest stages of a breeding scheme.

By the intermediate stage of selection the majority of obviously unacceptable genotypes should have been discarded. This allows more material to be available for growing assessment trials. In these cases yield trials of larger, replicated, plots are grown. In the first instance these trials may only be grown at a single location. It is usual at this stage that the more weakly heritable characters (such as yield, quality and quantitative disease resistance) are effectively assessed. The third, and final, stage of a selection programme involves the selected genotypes being grown at several different locations to determine general adaptability. An important part of this final stage is the submission of the more desirable lines

into National List Trials (a statutory regulation in many countries) before a new variety is released into agriculture.

Failure of a plant breeding scheme can occur at the stage of producing genetic variation or at one, or all, stages of selection. In general, a plant breeding programme may fail to produce cultivars that are better than those already used in agriculture for two reasons:

(i) There is not sufficient genetic variation within the initial parental material that is used;

or

(ii) The method of selection that is used is not effective in identifing the desirable recombinants.

Before breeding any crop species it is desirable to have a good knowledge of the biology and history of the crop so that clear breeding objectives can be set.

1.2 History of the Potato Crop

European potatoes are derived from species within the genus Solanum. Other cultivated species in the Solanum genus include the egg plant or aubergine (S. melongena) and pepino (S. muricatum). Potatoes were first named as Solanum tuberosum by Caspar Banhin in 1596 (Hawkes, 1966). Within the Solanum genus there are around 170 species belonging to at least 17 different groups or series. In addition to S. tuberosum, there are seven other cultivated species and 154 wild species, generally recognised (Hawkes 1978b). The basic chromosome number of potatoes is n=12, and diploid (2n=24) through to hexaploid (6n=72) types are found amongst wild species. The domesticated potatoes of Europe and North America are almost

exclusively tetrapploid (2n=4x=48). A full and detailed description of the cytology and classification of potato species is given by Hawkes (1978b).

The potato was originally thought to have come from Virginia (now North Carolina) in the United States of America. This now seems to be incorrect and there is little doubt that potatoes originated from the western regions of South America.

In certain areas of South America potatoes have been grown for human consumption for many thousands of years. When the Spanish first arrived in Peru and Bolivia, potatoes were already a well established crop of that region. In certain highland areas of south Peru and north Bolivia the agricultural land is situated at such a high altitude that maize (the most prominent crop in South America) will not grow. In these regions potatoes are believed to have been the major food source of the native Indians (La Barre, 1947). The exact date when potatoes were first grown as an agricultural crop is not known although scanning electron microscope techniques have identified potatoes from the Chilean Valley near Lima (Peru) and radiocarbon dated to be over 8000 years old (Hawkes 1978a).

The ancient South American indian name for potatoes was papa. Although this name is still common amongst South American local dialects, it has never spread to other parts of the world. The name "potato" used in Europe was derived from the Caribbean Aeawak indian word batata which actually refers to the sweet potato. Spanish settlers in South America took this word to refer to any tuber bearing plant and hence it was used for potatoes (S. tuberosum).

Potatoes arrived into Europe towards the end of the sixteenth century. They were reported to have been introduced to Spain in 1570, and independently into England in either 1588 or 1593 (Hawkes 1966).

They were almost certainly introduced as the remains of ships' stores rather than having any significant biological worth (Salaman, 1937 and Burton, 1948).

There is still a certain amount of controversy as to whether the original introductions into Europe were derived from the S. tuberosum spp tuberosum species from Chile (Juzepczuk & Bukasov, 1929) or whether they were derived from the S. tuberosum spp andigena species from the Andes of Peru and Bolivia (Salaman, 1946 and 1954). If the latter hypothesis is true, and the evidence suggests this to be the most likely, the plants which were introduced would not have been suitable for tuberisation under the long day conditions of Europe. Instead they would have been adapted to the 12 hour daylengths of tropical latitudes. Genotypes which would tuberise under European conditions would have needed to have been selected before the potato could have been grown as a commercial crop.

Legend associates the introduction of potatoes with Sir Walter Raleigh and Sir Francis Drake although there is no evidence to substantiate this. In fact there is a great deal of evidence available which would suggest that neither of these travellers were connected with the introduction of potatoes into Europe. The central figure in the spread of potatoes through Germany, France, Switzerland and other eastern European countries in the late sixteenth century was the botanist Charles D'Ecluse, or Clusuis as he was known (Hawkes 1966). After introduction into England the potato was introduced to Ireland, Scotland, Wales and the Scandinavian countries Sweden, Norway and Finland. From Europe the potato was taken to North America in the late seventeenth or early eighteenth century (Kranty, 1923).

After being introduced into Europe, potatoes were grown vegetatively (by planting tubers) and also by sowing true seeds that had been produced from naturally set berries (Hawkes, 1966). Clones

which formed tubers under the long day European conditions were available to farmers by the early seventeenth century. At that time they were already grown commercially in Ireland (Salamon, 1949) and in Burgandy (Bauchin, 1629; in Hawkes, 1966). In Ireland around the 1730's, only a few varieties were known (Davidson, 1934). However, by the mid-eighteenth century, potatoes had become a major food source in England and the number of different varieties that were cultivated had greatly increased. Most of the early European varieties were produced as a result of selection amongst natural selfs. As very few virus diseases (the notable exception being potato spindle tuber viroid) are transmitted through true seeds the early breeders not only selected genotypes which were more productive and adapted to the environmental conditions, but also produced clones that were free from most virus diseases. After a few years of cultivation however, these clones would show deterioration due to potato leaf roll virus, either acting alone, or in combination with potato virus Y.

In the United States of America the initial breeders also selected lines from selfed seed although in time there was a trend to discard this method in favour of clonal selection. A return to sexual breeding occurred around the 1920's after clonal selection had proved unsuccessful.

The rate of breeding new potato varieties was given considerable impetus after the blight epidemic of the 1840's (Davidson, 1934). By the start of the twentieth century, breeding had expanded enormously (Simmonds, 1969) and has since remained relatively constant. The early breeders, although farmers, rather than specialist breeders, made a considerable impact on the potato crop and there remain a number of potato cultivars which were initially bred around the start of this century, that are still grown in Europe and North America (for further details see the next section).

1.3 Description of the Potato Crop

The potato crop grown in the United Kingdom (UK) can be divided into two groups, a seed potato crop and a ware potato crop. Both crops will be grown by planting potato tubers although the produce from a seed crop will be used for planting the following year, while a ware crop will be grown for human or animal consumption, the production of starch or for alcohol production. Potatoes grown in Europe are almost exclusively vegetatively reproduced. They are therefore affected by a number of virus diseases which are transmitted through aphid vectors. Viral, fungal and bacterial diseases in seed potatoes may lower yields by reducing the photosynthetic efficiency and/or by rotting the tubers (Hide & Lapwood, 1978).

The most common use of potatoes throughout the world is for human consumption. Potato production for the starch industry is of some importance in Europe, but only has minor importance in the U.S.A.. In western Europe the Netherlands is the major starch producer (around 70% of the total EEC production). No potatoes are grown in the UK for starch production. Throughout the world, the total amount of potatoes used for starch production is about 1.5 million tons, of which two thirds are produced in Europe. Potatoes can be used to produce alcohol, although no more than a few percent of the world's alcohol is produced in this way. Potatoes that are used for stock feeding in Europe are partly grown for this specific purpose and partly made up from rejects (ie. damaged or mis-shapen tubers) from the grading line. Approximately half of the European production is fed to livestock of which around 40% is grown specifically for this purpose.

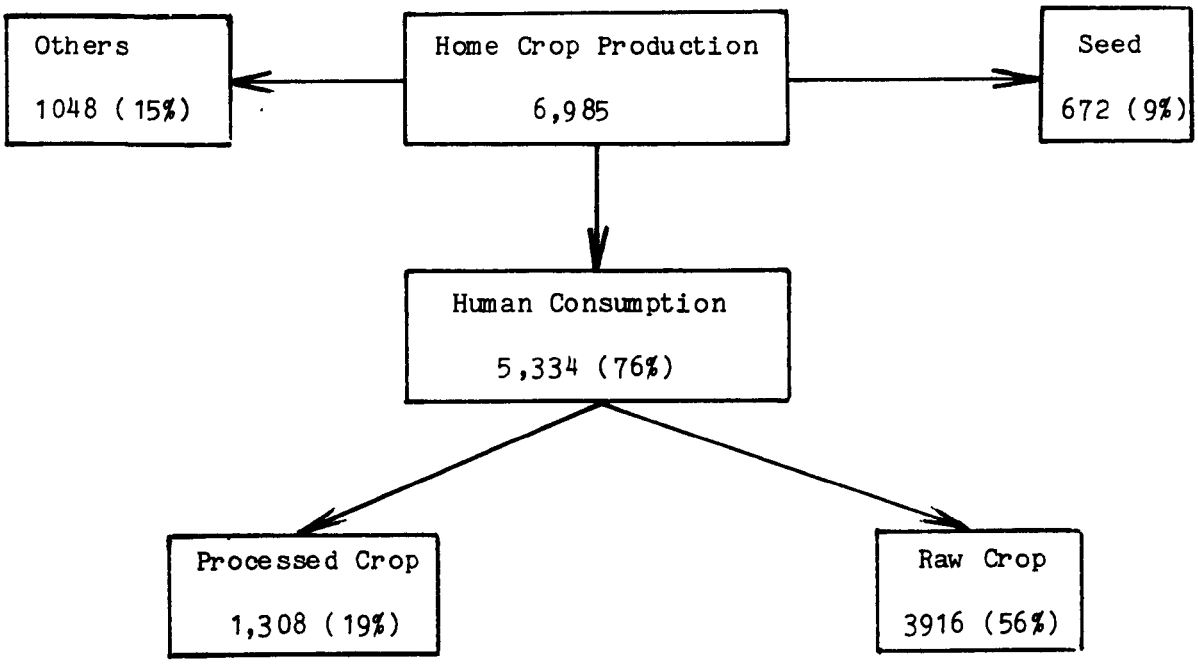
In tropical growing areas, potatoes are grown exclusively for human consumption. In most of these regions only a small proportion of the crop can be refrigerated, and the majority is consumed soon

after harvest. In many tropical regions two potato crops are grown each year. However, despite this, potatoes are not normally available throughout the whole year.

The main uses for the UK home grown potato crop in 1985 are shown in Figure 1.2. The partition of usage shown in this figure was simliar to that in the years between 1970 and 1984. Approximatly 9% of the total UK production is used as seed for the following year's crop. The total tonnage of seed potatoes that are exported from Scotland has increased (by an average of 1663 tonnes per year) over the past 30 years (Figure 1.3). The increase in seed exports has been particularly high over the last ten years and this feature of the potato crop is becoming increasingly important in the UK. A further 15% of the crop goes for animal feed and into the Potato Marketing Board surplus storage although a small proportion of the latter is also exported as ware. None of the UK potato ware crop is used for the production of starch or alcohol. The remaining, and by far the largest proportion of the home grown crop (76%) goes for human consumption. Of this, most is sold as the raw commodity in supermarkets or greengrocers. However, the catering trade also takes a fairly large proportion and the remainder of the raw product is sold in pre-pack lots, mainly from supermarket chains. The rest of the crop for human consumption is processed before selling (19% of total production). Processed products are sold in almost equal proportions to individual households or to caterers. When sold to households the processed crop is almost always sold either as crisps (called chips outside UK) or as frozen potatoes (mainly french fries). Only a small proportion is sold to households canned or dried. In contrast, the catering trade utilises processed potatoes supplied as crisps and frozen products and also dried products.

The potato is an important food source throughout the world,

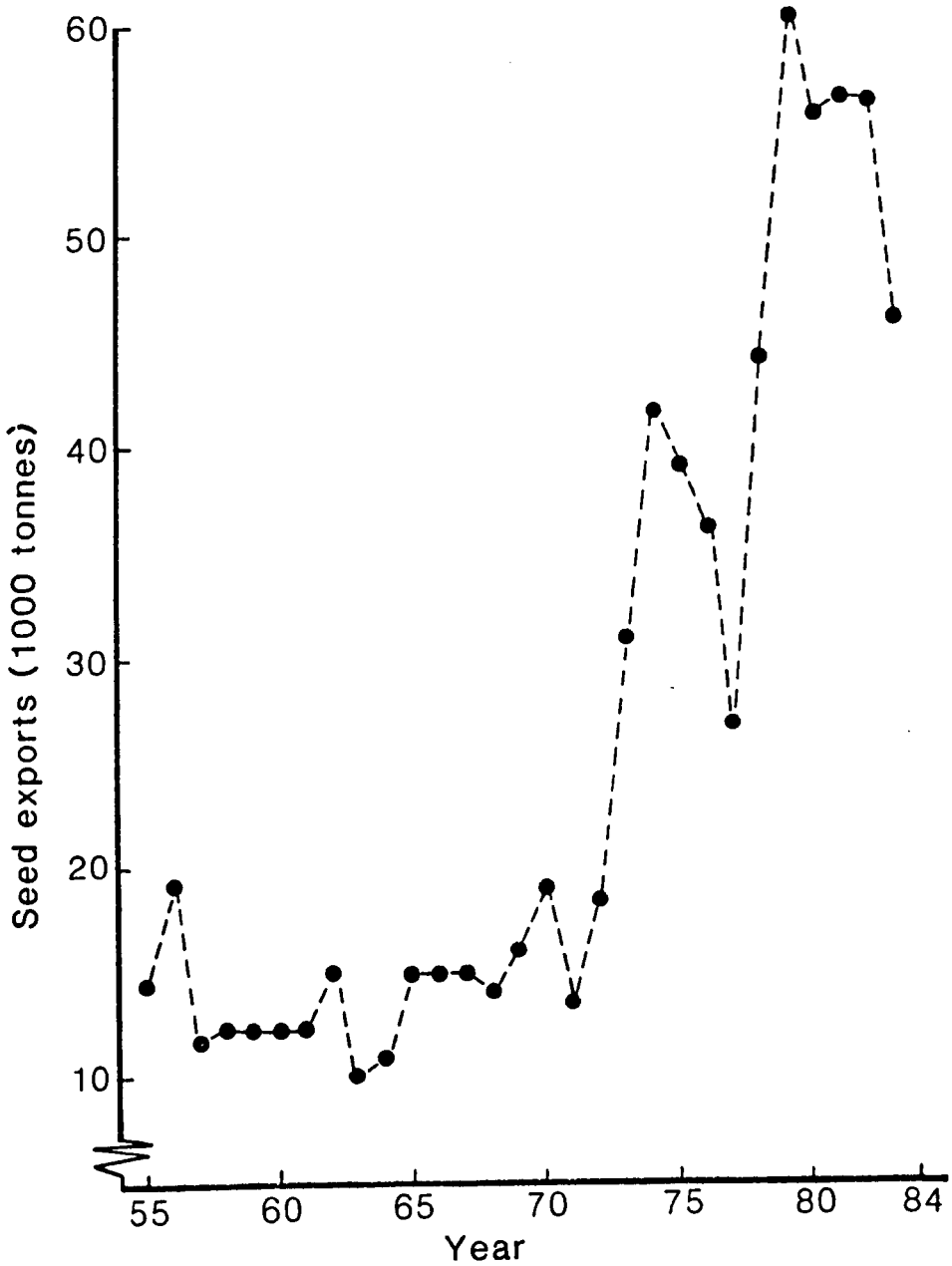
Figure 1.2 A flow chart of the uses for the UK home grown potato crop (,000 tonnes) in 1985 (Anon., 1986b).



Household 549 (8%)	Catering 758 (11%)
Canned 2%	Canned 3%
Crisped 45%	Crisped 30%
Dried 5%	Dried 21%
Frozen 48%	Frozen 46%
Total 100%	Total 100%

Catering	24%
Pre-packed	10%
Loose	63%
Total	100%

Figure 1.3 Yield of potato seed (,000 tonnes) exported from the UK to overseas countries each year between 1955 and 1984 (Anon., 1985 and 1986a).



especially in the northern temperate zones. The nutritional value of potatoes is high, due mainly to the biological value of the protein, the vitamins (especially vitamin C) and the content of minerals (Burton, 1974). Commonly grown potato cultivars contain 6% to 8% of protein, on a dry weight basis, and consequently as much protein per acre can be produced as for cereal grains and other seed crops (Desborough & Weiser, 1974). The average daily consumption of potatoes contributes about 4% of the total energy intake provided in the UK diet. In addition, potatoes provide 4% of the intake of protein, 8% of the intake of iron along with 10% of thiamine, 3% riboflavin, 9% nicotinic acid and around one quarter of our daily intake of vitamin C (Hampson, 1976). The dietary value of the potato does, however, vary depending on how long the product has been stored. Freshly harvested tubers have the best dietary value.

Overall, the potato crop in the UK is important for both human consumption and as an export crop (mainly seed crops). It is, however, a complex crop in that the sale and mobilisation of seed tubers along with the area in which potatoes can legally be grown (without paying a Potato Marketing Board levy) are all highly controlled by statutory regulations.

1.4 Aims of a Potato Breeding Programme

The fact that potatoes are propagated by vegetative reproduction makes their breeding easier than that of crops which are only sexually reproduced, as selections can be kept true to type through clonal reproduction. However, a great disadvantage of propagating potatoes in this way is that care must be taken to keep the breeding stocks free from virus diseases at all stages of the selection and multiplication process. Most potato virus diseases (an exception is potato spindle tuber viroid) are not transmitted through true

botanical potato seeds. To prevent viral infection at the seedling stage, seedlings are raised in aphid proof glasshouses or under aphid proof screens. Thereafter, to avoid infection during the clonal generations, most breeding schemes involve growing stocks under seed production conditions in addition to the ware conditions that are necessary for assessment purposes (Howard, 1978). Because a large number of genotypes require assessment in the early stages of a breeding programme, and also because only a limited number of seed tubers are available for each genotype, screening during the early phase is normally carried out only under seed production conditions (Simmonds, 1969; Maris, 1964a and Tai & Young, 1984)

There are several other disadvantages that are concerned with breeding potatoes, they are: (i) Most parents used for crossing are highly heterozygous, and therefore a large proportion of their genotype may be masked in the phenotype by dominance effects; (ii) Pollen sterility is common amongst potato cultivars and breeding lines so this can limit the number of parent combinations possible. Ovule sterility is less common and the frequency of successful crossing can be increased by "growing on a brick" (Thijn, 1954) or by grafting onto tomatoes. Both techniques allow maximum plant resources to be channelled into the production of flowers and berries; (iii) Breeding material cannot be stored easily and clonal stocks require to be grown each year; (iv) The multiplication rate of potatoes is considerablely lower than for example, a seed crop and it is often difficult to transport tubers from assessment trials purely due to their bulk.

In addition to attending to these problems, potato breeders probably have to consider more plant characteristics than breeders of most other crop species. Yield of tubers is of course an important character and a new variety is unlikely to be successful unless it can produce at least acceptable yields. Yield is, however, a complex

character in potatoes and can be greatly influenced by the length of growing season before harvest, quality and size of seed tubers (Allen, 1978), degree of sprouting (O'Brien, Bean, Griffith, Jones & Jones, 1983), level of plant spacing (Marshal, 1986) and final number of tubers and tuber size. A breeding line which has a high yield of many very small tubers is unlikely to be successful. Similarly, a variety which produces very few, but large tubers, may have limited market potential.

Breeding new varieties resistant to diseases and pests may often be the easiest way of breeding for high yield (Howard 1978). The potato crop is prone to more than 100 different diseases caused by bacteria, fungi, viruses or mycoplasma (Hide & Lapwood, 1978). Fortunately, relatively few of these reach serious proportions in any one area.

The major virus diseases include virus Y, leaf roll virus, virus X and virus A. Virus X is spread by leaf contact and does not require an aphid vector. The other three virus diseases are transmitted by aphids. Although virus diseases can be controlled by growing seed crops in areas where the risk of aphids is small and by rigorous crop inspection (Jeffries, 1986), there is a need to produce varieties which have resistance to virus diseases so as to reduce the probability that high grade seed stocks become infected and hence down-graded.

Many potato diseases are caused by fungi. The most important fungal diseases in UK agriculture include wart (Synchytrium endobioticum) and potato blight (Phytophthora infestans), both in the tuber and the foliage. The major bacterial disease, especially important to potato seed exporters, is blackleg (Erwinia spp. carotovra or Erwinia spp. atroseptica).

Resistance to pests is another important feature of a new potato cultivar. The major pests in the UK are the two nematode species G.rostochiensis and G.palida (for a detailed description see Evans & Trudgill, 1978). Both of these species can cause large yield reductions in cultivars which are not resistant and/or tolerant to them. Aphids (ie. Merzus persicus) also cause direct damage to a potato crop although this damage is minimal in comparison to the indirect effects caused by aphid transmitted diseases.

When a new variety is targeted for household use the quality characters of greatest importance include flavour and absence from blackening or disintegtarion on cooking. However, if a new variety is aimed at processing crisps or french fries, then fry colour, dry matter content and accumulation of sugars during low temperature storage will be major considerations. Irrespective of the eventual market of a new variety, tuber characteristics such as uniformity of tuber shape, depth of eyes, absence of growth defects and damage susceptibility will greatly affect the success of a variety.

The method of breeding new potato varieties has not changed dramatically since artificial cross pollination between chosen parents was first suggested by Thomas Knight in 1807. The time from crossing to the release of a new cultivar is usually 9-12 years (Ross, 1986). Parental material is chosen and artificial hybridisation is carried out to produce true botanical seeds. A number of seedlings will then be raised depending on the nature of the cross. It used to be common practise to grow seedlings for selection under field conditions although the standard procedure now is to raise them either under aphid-proof glasshouses or in aphid-proof screens. Each seedling will, of course, be unique and if vegetative reproduction is followed, each will be genetically fixed. A number of breeding schemes still involve selection of desirable clones at the seedling stage. However,

as a result of recent research (for a complete review see section 3.1 and Brown 1985) there is now a tendency for breeding programmes to retain all the genotypes at the 'seedling' stage without imposing selection (Table 1.1). Irrespective of whether selection is carried out at the seedling stage, clones are grown in the field the following year from seedling produced tubers. It is usual to plant only a single tuber (the largest tuber) produced by a seedling plant. Between 7% and 15% (see Table 1.1) of the first clonal year genotypes are normally selected for re-evaluation the following year, the remainder is discarded from the breeding scheme. Therefore, after the breeding lines have been grown as seedlings and selected (usually as single plants) in the first clonal year, between 85% and 98% of the initial population of genotypes will have been discarded. Hence selection in the very earliest stages is very intensive. Clones which are selected in the first clonal year are grown in larger plots (between 3 and 10 plants) in the second clonal year.

Selection of seedlings, first clonal year plants and second clonal year plots is usually conducted by visual assessment (breeders' preference). Breeders' preference takes into account a number of tuber characteristics (ie. yield, tuber size, tuber shape, etc.) in an attempt to give an overall impression of commercial acceptability.

Not until the third clonal year is breeding material grown in trials for an accurate assessment of yield, quality or disease resistance. By this stage between 96% and 99% of the initial clones in the scheme will have been discarded.

Inspection of main crop potato yields (Figure 1.4) and early cultivar potato yield (Figure 1.5) between 1955 and 1984 might suggest that plant breeders have been successful in producing higher yielding cultivars for agriculture. However, Howard (1962) found that other crops over the period 1930 to 1960 had a two to three times increase

Table 1.1 The number of genotypes that are screened by seven potato breeding schemes in Europe and North America at the seedling stage, first clonal year (FCY), second clonal year (SCY) and third clonal year (TCY) along with the percentage of breeding lines that are retained (sel) at each stage. The percentage of the initial population of clones that have been discarded after the seedling and first clonal year stage (i) and after the seedling, first clonal year and second clonal year stage (ii) is also shown.

	Seedlings		FCY		SCY		TCY		
Country	Grow	sel	Grow	sel	Grow	sel	Grow	(i)	(ii
1. Scotland	100,000	40%	40,000	10%	4,000	25%	1,000	96%	
2. W. Germany	140,000	71%	100,000	7%	7,000	20%	1,400	95%	
3. Russia	80,000	30%	24,000	13%	3,100	32%	1,000	96%	
4. Holland	1,000,000	65%	650,000	11%	71,500	21%	15,000	93%	
5. U. S. A.	60,000	100%	60,000	4%	2,500	16%	400	96%	
6. Canada	40,000	100%	40,000	15%	6,000	25%	1,500	85%	
7. R. or Ireland	100,000	36%	36,800	7%	2,680	7%	176	98%	

References

1= Mackay, 1982; 2= Fitschen, 1984; 3= Dorozhkin, Reiter & Grabouskaya, 1982; 4= Louwes, 1986 (personal communication); 5= Thornton, 1984 (personal communication); 6= Tai & Young, 1984; 7= Kehoe, 1982.

Figure 1.4 Yield (tonnes/hectare) of main crop ware potatoes in the UK each year between 1955 and 1984 (Anon., 1985 and 1986a).

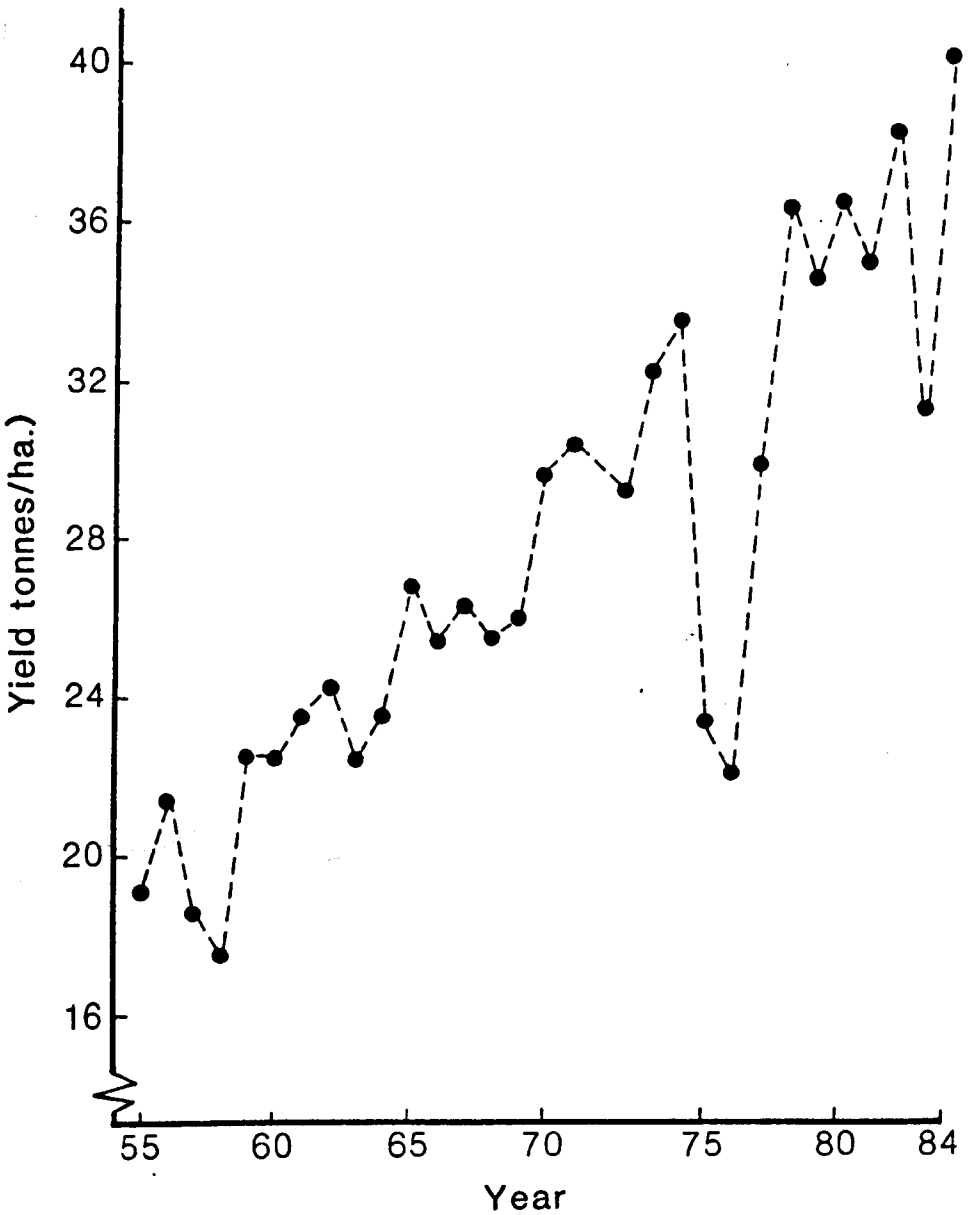
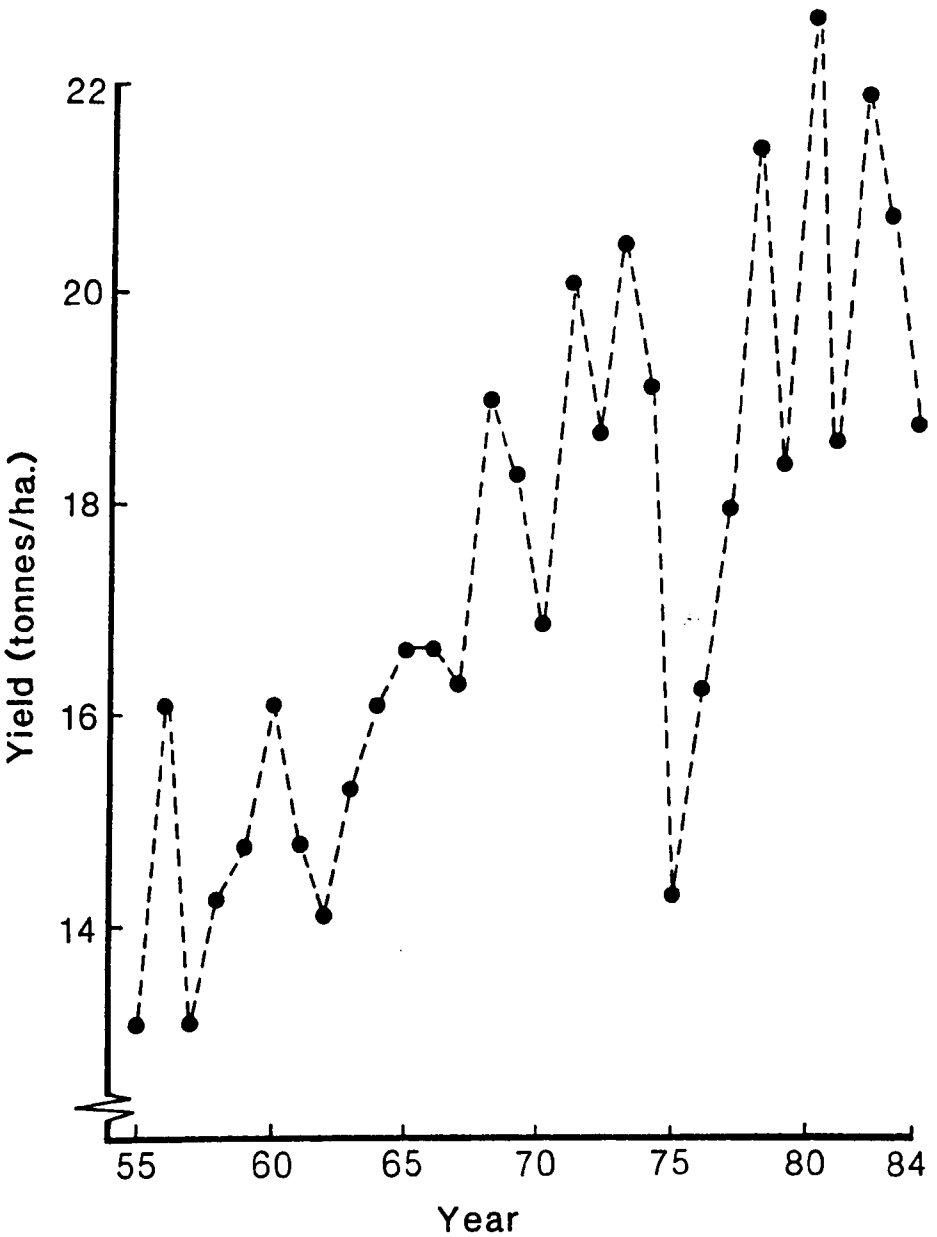


Figure 1.5 Yield (tonnes/hectare) of first early potatoes in the UK each year between 1955 and 1984 (Anon., 1985 and 1986a).



in yield compared with that of potatoes. It is of interest that although there have been a few notable introductions of new varieties this century there are still a number of old varieties which command a high percentage of the UK acreage (Table 1.2). Similarly, the variety Russet Burbank (introduced before 1900) and Bintji (introduced in 1910) are still extensively grown in North America and Europe respectively. This suggests, therefore, that increased potato yields are due largely to improved agronomic practices rather than the release of new higher yielding varieties.

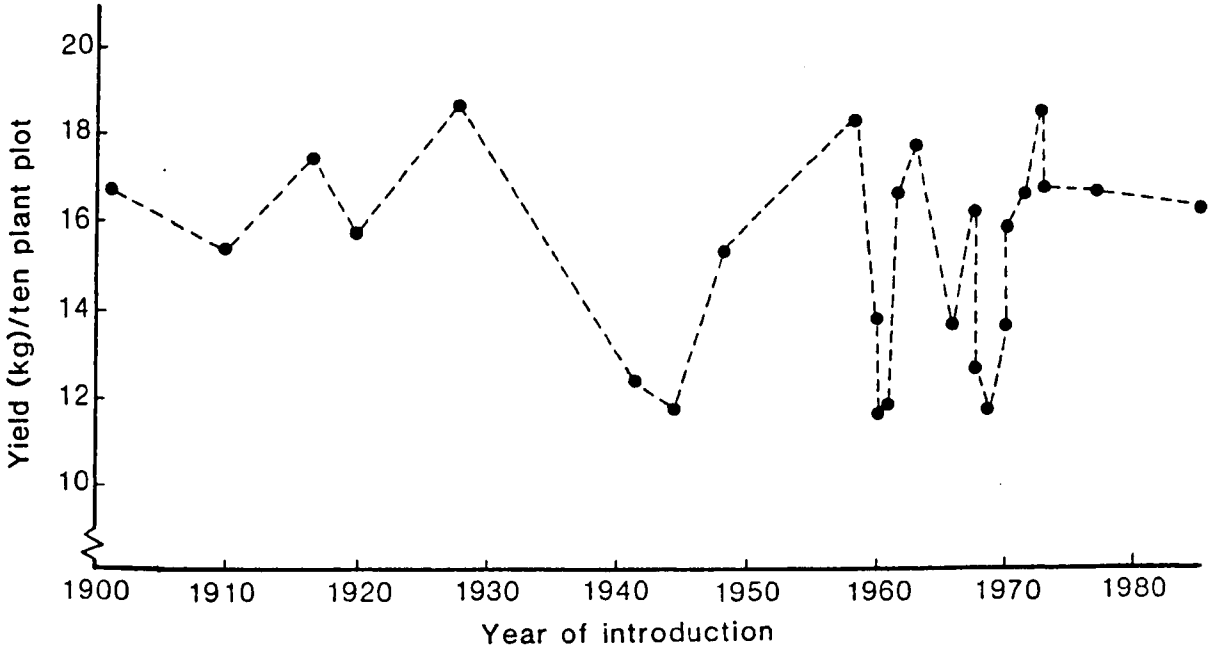
Indeed, from records taken at the SCRI, where a number of commercially grown cultivars are included in breeders yield assessment trials each year, it is clear from mean yield of a variety (based on a five year test period) plotted against the year that the cultivar was introduced (Figure 1.6) that newer varieties have shown no increased yielding ability over older ones. From this, therefore it seems there is no direct evidence that any advances in yield potential have been made in recent years. It must be borne in mind however, that many, lower yielding cultivars which used to be grown in UK, may have subsequently been lost to agriculture and so the old varieties that are still grown represent the very best of those that were around at that time.

As many modern potato breeding schemes include better disease assessment, which is applied to breeding material earlier in the selection system, it is to be expected that newer varieties should have better disease resistance than older introductions. This is not conclusively substantiated however, by inspection of data collected by the National Institute of Agricultural Botany (NIAB) (Anon., 1987). When cultivars assessed by NIAB are grouped according to year of introduction (ie. 1890 to 1940; 1941 to 1960; 1961 to 1970; 1971 to 1980 and 1980 to 1981) the average disease rating of each group can be

Table 1.2 Area of agricultural land in the UK that is used per variety by registered growers in 1985 along with the year that each variety was introduced (Anon., 1986c).

	Year of introduction	Area planted	Percentage of total
First earlies			
Arran Comet	1956	1,543	8%
Epicure	1897	708	4%
Home Guard	1942	1,939	10%
Maris Bard	1974	4,628	24%
Pentaland Javelin	1968	5,378	28%
Ulster Sceptre	1964	3,132	16%
Vanessa	1968	584	8%
Others	--	1,621	8%
Second earlies			
Estima	1973	8,379	26%
Maris Peer	1962	1,803	6%
Wilja	1972	18,976	59%
Others	--	2,779	9%
Main crops			
Cara	1976	6,678	6%
Desiree	1962	18,934	17%
King Edward	1902	3,402	3%
Maris Piper	1963	24,028	22%
Pentland Crown	1958	10,394	9%
Pentland Dell	1967	4,190	4%
Pentland Squire	1970	10,099	9%
Record	1940	16,555	15%
Romano	1978	4,286	4%
Others	--	4,896	4%

Figure 1.6 Saleable yield (kg of saleable tubers greater than 40mm per ten plant plot) of cultivars grown in SCRI breeders trials between 1984 and 1986 against the year that each variety was introduced (data provided by the Potato Breeding Department at SCRI).



obtained (Table 1.3). Rather surprisingly, the levels of resistance to common scab appear to be greater amongst the older varieties than amongst the most recent introductions. In contrast, there is an increase in resistance to potato leaf roll virus in the newer varieties over the older introductions. However, for other diseases examined the same levels of resistance tend to be shown by all the introduced groups. In regard to yielding ability and general appearance of tubers, the NIAB records do provide evidence of improvement due to breeding new varieties.

In support of potato breeding efforts, there have been improved levels of resistance to potato cyst nematode (Globodera) in newer cultivars. Resistance to the golden cyst (G. rostochiensis) has resulted from the introduction of a single major gene (H_1). However, as more new varieties were produced which contained the H_1 gene, the balance of nematodes changed from almost exclusively G. rostochiensis to the other common species G. palida. Recent breeding efforts have produced clones which are both resistant and tolerant to both nematode species. Breeders have also been successful in producing new varieties that contain comprehensive resistance to wart.

Despite the limited successes, in general, potato breeders have not had a great effect on the yielding potential or disease resistance of the crop, especially when compared to the success achieved in other crops. This could be the result of two factors. First, poor advances could be due to a limited gene-pool (Simmonds, 1969 and Glendinning, 1979 and 1983). There is evidence that very few new genes have been introduced since potatoes were first brought to Europe. Also the variation that was present amongst the genotypes which were first introduced may have been reduced further as a result of the potato blight epidemic of the 1840's (Glendinning, 1979). Against these factors is the fact that out of some 345 cultivars of known origin

Table 1.3 Average rating by the National Institute of Agricultural Botany (Anon., 1987) of potato cultivars for a number of tuber and disease characteristics. Values are meaned over cultivars according to the year that they were introduced.

First early cultivars

Year	No. cult.	Yld	Appe.	Gang.	F. Bl	T. Bl	Scab	LR	Y	TRV
1890-1940	3	4.7	4.7	6.0	4.0	2.3	6.0	4.3	3.7	7.5
1941-1960	4	5.2	6.2	5.7	3.5	3.0	6.0	4.5	4.0	5.3
1961-1970	6	6.7	6.8	4.6	4.3	3.5	5.7	4.8	4.8	3.3
1971-1980	10	7.4	6.1	4.6	3.5	3.3	5.0	4.5	5.8	5.1
1980-1986	3	6.7	6.7	4.0	4.0	3.3	4.0	6.3	6.3	7.3

Second early and main crop varieties

Year	No. cult.	Yld	Appe.	Gang.	F. Bl	T. Bl	Scab	LR	Y	TRV
1890-1940	9	5.0	5.1	4.5	4.2	4.0	5.1	4.8	4.7	5.3
1941-1960	6	6.0	6.3	5.4	4.6	4.6	6.0	4.2	4.4	4.2
1961-1970	10	6.0	6.1	5.4	5.3	5.6	5.2	4.8	4.4	3.8
1971-1980	13	7.1	6.2	4.4	5.4	5.6	4.8	4.4	4.4	4.3
1981-1986	6	7.5	7.3	5.5	4.3	3.7	4.5	5.0	5.2	3.8

No. cult. = number of cultivars in group; Yld = yielding ability; Appe. = visual appearance of tubers; Gang. = resistance to gangrene; F. Bl = resistance to foliage blight; T. Bl = resistance to tuber blight; Scab = resistance to common scab; LR = resistance to leaf roll virus; Y = resistance to virus Y; TRY = resistance to tobacco rattle virus.

grown in Europe, 65% have wild or primitive cultivars in their ancestry (Swiezynski, 1983). A second cause of the poor results achieved by breeders may stem from the employment of poor breeding methodology and ineffective selection procedures. It has been estimated that a successful potato variety will only occur once in every 100,000 genotypes (Howard, 1962). Some estimates have been given as high as once in five million seedlings (Rieman, Hooker, Kranty & Werner, 1956). Each year at least six million potato seedlings are raised in breeding schemes in the northern hemisphere (Simmonds, 1969). It would be expected, therefore, that at least one, and potentially up to sixty successful cultivars should be introduced each year. This does not appear to have happened over the past years. Therefore, either the expected theoretical frequency of a successful new variety has been greatly over-estimated, or the methods of identifing these potential new cultivars are inefficient. It is this latter possibility which will be examined in this thesis.

1.5 Objectives of the thesis

The primary aim of this thesis is to investigate the efficiency of selection in the early generations of a potato breeding programme. To this end, the efficiency of identifing superior genotypes at the seedling, first clonal year, second clonal year and third clonal year stages is examined. Factors important to the efficiency of selection in the early generation stages are also examined and an alternative approach to plant breeding in the early generations is investigated. The overall objective of the thesis, therefore, is to determine how methods of selection might increase the effectiveness of producing new and improved potato cultivars.

CHAPTER 2

MATERIAL AND METHODS

2.1 Introduction

The material and methods are, for convenience, divided into four different groups. These groups will be referred to by the letters 'A' through to 'D'.

All of the field experiments examined in the thesis were grown at either Blythbank farm (BB), the Murrays farm (MURR) or at both BB and MURR. The MURR farm, situated in East Lothian, is used by the Potato Breeding Department of the Scottish Crop Research Institute (SCRI) for yield trials of advanced breeding material (ie. treated generally as a typical ware growing site). BB, on the other hand, is used by SCRI and also the Potato Breeding Department of the Plant Breeding Institute, Cambridge, for the maintenance and multiplication of healthy seed stocks (ie. a typical "seed" potato production site). It should also be noted that BB is the only location used by the potato breeders at SCRI for the routine assessment of breeding material in the first and second clonal generations of the normal breeding scheme. It is not until clones have survived selection at the seedling stage and in the first and second clonal generations that the surviving clones will be assessed at MURR under ware growing conditions. The MURR farm is situated at lower altitude and has a different soil type to BB. Also, to avoid the risk of viral infection through aphids, the BB site is always planted later and harvested earlier than MURR.

One of the variates that was repeatedly assessed on genotypes was the character breeders' preference. In a number of cases more than one breeder was involved in the assessment of this variate. In these instances the breeders were identified by the codes PB1, PB2, etc. Otherwise, all visual assessments, including breeders' preference were made by a single breeder (PB1). The breeders' preference score, on a

1 to 9 scale of increasing desirability, is a visual impression collating a number of tuber characters to indicate the commercial worth of each clone. Before assessing any of the genotypes in this study, the breeders involved had decided that a breeders' preference score of 5, or more, would indicate that, under the normal breeding scheme, the particular plot would have been selected or retained for re-evaluation. Conversely, a breeders' preference score less than 5 would indicate that the plot, under normal selection, would have been discarded. However, in the experiments reported here, genotypes were never actually discarded, other than on a random basis.

All parental genotypes used in artifical hybridisations were tetraploid and from the species S. tuberosum ssp. tuberosum. Plot sizes and plant spacing used in all experiments were generally those used in the appropriate generations of the normal breeding programme at SCRI.

2.2 Description of the 'A' material

The genotypes in the 'A' material were derived from eight potato crosses that were hybridised prior to 1981. These crosses were not specifically carried out to investigate the efficiency of early generation selection. They were, however, chosen to be representative of crosses which are carried out routinely by the Potato Breeding Department at SCRI and they covered the spectrum of breeding objectives in which the Department was interested (Holden, 1977 and Mackay, 1982).

The eight crosses were identified by the codes A1 to A8 inclusively. Individual genotypes from each cross were identified by a cross code followed by a number (1 to 200). For example, the code A3.76 refered to the 76th clone from the cross A3. The immediate parentage of each cross is shown in Table 2.1. Although in theory,

Table 2.1 Progeny codes, parentages and main breeding objective of the eight crosses in the 'A' material.

Progeny Code	Parentage	Breeding Objective
A1	Desiree x Pentland Crown	High yield and quality
A2	SCRI 11215ab16 x SCRI 12380ab2	P. C. N. resistance
A3	SCRI 4086d16 x SCRI 4085D1	P. C. N. resistance
A4	SCRI 6582(12) x SCRI 6240(3)	Virus resistance
A5	Desiree x H1H3(9)	P. C. N. resistance
A6	Desiree x SCRI 3683a2	Tuber & foliage blight
A7	SCRI 3683a2 x Pentland Dell	Tuber & foliage blight
A8	Pentland Dell x SCRI 8204a4	High yield and quality

(P. C. N. = Potato cyst nematode)

each cross should be capable of producing a new and improved potato cultivar, each hybridisation was carried out with a specific breeding objective in mind. These breeding objectives are also shown in the right hand column of Table 2.1. The parents Pentland Crown, Desiree and Pentland Dell are established cultivars which are grown commercially in the United Kingdom. The other parents were selected lines from within the SCRI breeding programme. These clones were not considered suitable as varieties in their own right, although each possessed attributes which made them useful parents (eg. resistance to late blight or nematodes).

The growing conditions in the glasshouse (seedling stage) and at the first clonal year stage have been described in detail by Brown (1985), for clarity the details are repeated here.

2.2.1 The seedling stage.

In 1981, 400 seedlings from each of the eight progenies were raised in seed pans, one seed pan to each cross. For the first three weeks, the seedlings were irrigated by mist propagation. After three weeks of growth, 200 seedlings were pricked out at random and transplanted into 10cm square pots containing a peat based compost. The pots were arranged in unrandomised blocks on a sand bed. Seedlings were watered from below via the sand bed and grown to maturity in an aphid proof glasshouse.

Before harvest, the haulms were removed and the water supply disconnected to allow the compost in the pots to dry. Each of the seedlings was harvested individually by removing the compost and placing the tubers back into the empty pots. At this stage each of the 1600 genotypes were uniquely identified with a cross number (A1 to A8) and a genotype within cross number (1 to 200).

2.2.2 The first clonal year stage.

All the tubers from each of the seedlings were retained and stored in a darkened cold room at 4°C. Each genotype which produced a tuber at the seedling stage was planted in the field in the first clonal year. Clones which produced more than one tuber were planted at two locations, Blythbank Farm (BB) and the Murrays Farm (MURR) The MURR trial was planted on the 17th of April and the BB trial was planted on the 7th of May 1982.

Each trial consisted of two completely randomised blocks, with each plot within a block being a single plant. The tubers were planted into opened drills, which had been drawn 75cm apart. At both sites tubers were planted 47cm apart with a 95cm gap after every tenth plant. From the original 1600 seedlings grown in the glasshouse, 224 genotypes failed to produce any tubers. Genotypes which produced four or more tubers in the glasshouse, (824 clones) were planted in both randomised blocks at BB and MURR. Those which produced three tubers in the glashouse (225 clones) were planted in the first block at BB and in both blocks at MURR. Those genotypes which produced two tubers at the seedling stage (205 clones) were planted in the first block at both sites, while those which produced only a single tuber (122 clones) were planted in the first block at BB.

Tubers were not assigned to blocks at random, but rather were allocated to blocks according to seed tuber weight. The heaviest tuber produced by each seedling was always planted in the first block at BB, the second and third heaviest tubers were planted at MURR, with the second heaviest being in the first block. The lightest tuber from the four was always planted in the second block at BB. The allocation of seed tubers to specific blocks was carried out for two reasons. First, the normal practise in the potato breeding scheme used at SCRI is to plant the largest tuber from each of the selected genotypes at

BB in the first clonal year. Secondly, the second largest tuber was planted at MURR to ensure that as many clones as possible were represented at both locations. From this, the BB trial contained 1376 clones in the first block, while the MURR trial contained 1254 clones in the first block. In each block at both locations, six plots of each of the commercially grown cultivars Pentland Crown, Pentland Dell, Pentland Squire, Maris Piper and Desiree were included in the randomisation.

Before harvest, plants were defoliated by a single dose of sulphuric acid at BB on the 21st of August. At MURR the haulms were mechanically removed 16 days later. After defoliation, it was assumed that tuber bulking was stopped. At both sites each plant was individually harvested by hand and the tubers from each plant were placed in groups on the soil surface. At this stage the tubers from each plant were visually assessed for breeders' preference by four potato breeders. After assessing the plots, all the tubers from each plant were bagged and taken into storage.

2.2.3 The second clonal year.

It was not possible to retain all the genotypes that had been grown in the first clonal year and grow these in the second clonal year in larger plots. A random sample of 70 clones was identified from each of the eight crosses. This random sample (560 clones) was grown at both BB and MURR in the second clonal year. If an adequate number of tubers was produced in the first clonal year at BB (the seed production site) then each clone was replicated twice in completely randomised blocks at each site. From the random sample of 560 clones, 121 produced more than 12 tubers in the first clonal year, these were grown in two randomised blocks at both BB and MURR. Clones which produced more than 9 tubers, but less than 12 tubers in the first

clonal year, (138 clones) were grown in both randomised blocks at MJRR and only one block at BB. Clones which produced fewer than 9 tubers but more than 5 tubers the previous year were grown in a single block at each site (148 clones) and those clones which produced fewer than 6 tubers (164 clones) were only grown in a single randomised block at BB. Each plot contained three tubers in a single drill. Plants within a plot were grown 30cm apart with a 60cm gap between plots.

The control cultivars, Pentland Crown, Pentland Dell, Pentland Squire, Desiree and Maris Piper were included in the randomisation of each block. Each control cultivar appeared at least four times in each block at both sites. The MJRR trial was planted on the 24th of March and the BB trial was planted on the 27th of April, 1983. Towards the end of the growing season, plots within the MJRR trial were visually assessed for foliage maturity on a 1 to 9 scale. The time of assessment was judged by examination of control cultivars of known maturity class.

Before harvest the BB trial was defoliated by application of sulphuric acid on the 4th of September and the MJRR trial was mechanically defoliated 21 days later. Both trials were harvested mechanically and the tubers from each plot were hand picked and placed into wooden boxes. While the boxes were still in the field, each plot was assessed by four potato breeders for breeders' preference. The produce from each plot was then taken into storage where the remaining characters were assessed.

2.2.4 The third clonal year.

In the third clonal year the number of clones per cross examined was further reduced at random to 25 clones per cross. A number of clones which appeared on the performance of the second clonal year trials to have commercial worth (76 clones in total) were also

retained and planted in the third clonal year. Added to this were four plots from each of the control cultivars Pentland Crown, Pentland Dell, Pentland Squire, Desiree, Maris Piper and Record. The third clonal year trial therefore consisted of 300 entries (200 random clones, 76 selected clones and 24 control cultivars). These were grown at BB and MURR in two completely randomised blocks at each location. Within each randomised block, each entry was represented by a five plant plot. Each plot was planted in a single drill with 30cm between plants and a 180cm gap between plots (for ease of mechanical harvest).

In addition to this trial each of the 300 entries were grown in an adjacent trial with only a single replicate of single plant plots. The single plant plots were also randomised. The single plant plots and five plant plots grown at MURR were planted on the 20th of April and the BB plots were planted on the 7th of May. Towards the end of the growing season the foliage maturity was visually assessed on a 1 to 9 scale (1 = very early maturing to 9 = very late maturity) on the five plant plots at MURR.

The BB trial was harvested on the 28th of September, while the MURR trial was harvested on the 10th of October. Plots were mechanically harvested, tubers from each plot were hand picked into boxes and immediately taken into storage. All variates recorded on the third clonal year trials were assessed and recorded in the store.

2.2.5 Beyond the third clonal year.

Beyond the third clonal year stage clones in this experiment were included into the normal breeding scheme of the potato breeding department at SCRI. Therefore it was only the clones which were considered to have commercial worth that were grown in further generations. The criteria used to select the material was identical

to that used for the normal breeding material (Holden, 1977 and Mackay, 1982). There was however, one small trial grown in the fourth clonal year. This trial contained 18 clones from the cross A1 which had been grown in larger quantities and selected in the normal way along with other crosses in the potato breeding scheme. Also, 18 clones from amongst the random sample of 25 clones from this cross were examined in the experiment. These 36 clones were grown in a common trial in two completely randomised blocks with five-plant plots at MURR only (cf third clonal year trial).

2.2.6 Variates recorded on the 'A' material.

After harvesting trials each year, every plot was visually assessed by four potato breeders (PB1 to PB4) for breeders' preference (see section 2.1). The assessment of the seedlings was carried out in the glasshouse while the first and second clonal year trials were assessed for breeders' preference in the field. In the third clonal year breeders' preference was assessed in the store and only by PB1 and PB3. While the harvested tubers were in storage, the total tuber weight and number of tubers per plot was recorded. From this, mean tuber weight was calculated. The tuber characters, uniformity of tuber shape, distribution of tuber size, absence of growth cracks and tuber dormancy were visually assessed on all plots from each trial. The variates, stolon persistence and depth of eyes were visually assessed on the seedlings, first and second clonal year trials. Only breeders' preference total tuber weight and number of tubers were recorded on the single plant plot trial grown at MURR in the third clonal year.

A summary of the 'A' experiment is given in Table 2.2 and a description of the variates recorded is shown in Table 2.3.

Table 2.2 Summary of the 'A' experiment.

Year	Name	Number of crosses	Number of clones per cross	Plot size	Number reps	Site names
1	GH	8	200	1	1	GH
2	FCY	8	up to 200	1	2	BB & MURR
3	SCY	8	70	3	2	BB & MURR
4	TCY	8	25	6/5	2	BB & MURR

GH, FCY, SCY and TCY = glasshouse, first clonal year, second clonal year and third clonal year, respectively. BB = Blythbank Farm; MURR = Murrays Farm.

Table 2.3 Description of variates recorded on the 'A', 'B', 'C' and 'D' material.

Expt.	Variate Name	Scale	Description
A, B, C, D	- Breeders' preference	1-9	1 = very unattractive
A	- Eye depth	1-9	1 = very deep eyes
A	- Uniformity of tuber shape	1-9	1 = poor shape
A	- Distribution of tuber size	1-9	1 = irregular size
A	- Stolon persistence	1-9	1 = persistent stolons
A	- Absence from growth cracks	1-9	1 = many growth cracks
A	- Tuber dormancy	1-9	1 = poor tuber dormancy
A, B, C, D	- Total tuber weight	recorded	Kgs per 10 plants
A, B, C, D	- Mean tuber weight	recorded	Kgs per 10 tubers
A, B, C, D	- Number of tubers	recorded	Number per plant

2.3 Description of the 'B' material.

The aim of growing the 'B' material genotypes was to examine the effect of seed tuber size used in the first clonal year assessments on the efficiency of selection.

Five crosses were examined in the 'B' experiment. As with the 'A' material, these crosses were representative of those normally screened in the commercial potato breeding programme at SCRI. The crosses are identified by the codes B1 to B5. The immediate parentage of the crosses were Croft x Cara (B1); SCRI 3683 a 2 x Cara (B2); Desiree x Pentland Dell (B3) and Croft x Pentland Squire (B4). The clone SCRI 3683 a 2 was derived from within the breeding programme while the other parents are commercially grown cultivars.

2.3.1 The seedling year.

In the spring of 1983 two hundred seeds from each of the five crosses were sown in seed pans. After three weeks growth, seedlings were pricked out at random and transplanted into individual pots. Three different square pot sizes were used (2.5cm - small, 10cm - medium and 14cm - large). Twenty seedlings from each cross were transplanted into each of the small, medium and large sized pots. With such large differences between pot sizes it was considered unwise to completely randomise all the pots. Each cross and pot size was therefore divided into two groups of 10 clones. These 30 samples (5 crosses x three pot sizes x 2 sample) were completely randomised on a sand bed and the plants were grown to maturity in an aphid proof glasshouse.

At harvest the haulms were removed and the tubers were harvested. The total weight of all tubers, the weight of the largest tuber and the number of tubers that each seedling produced was recorded. The largest tuber from each seedling was stored in a darkened cold room at

4^{0}C. until planting the following year.

The whole experiment was repeated with a later sowing giving a factorial arrangement of five crosses x two sowing dates x three pot sizes x two sample per pot size (each sample consisting of 10 seedlings).

2.3.2 The first clonal year.

In the first clonal year the largest tuber from each of the seedlings grown in the glasshouse was planted at BB. Each clone was grown in a single plant plot. The individual plants were not completely randomised, samples were however randomised throughout the trial. The whole trial consisted of the factorial arrangement grown at the seedling stage (see above).

At harvest each plant was individually harvested and the tubers exposed on the soil surface. At this stage every plot (plant) was assessed by three potato breeders (PB1 to PB3) for breeders' preference (see section 2.1). All tubers from each plant were bagged and taken into storage. While in storage, total tuber weight and the number of tubers per plant were recorded from which the mean tuber weight was calculated.

2.3.3 The second clonal year.

In the second clonal year the first five clones from each sample at the first clonal year stage were grown at BB in three plant plots. The whole trial consisted of 60 clones from each of the five crosses. These clones were made up of five clones from each of the 12 categories (sowing 1, small pots, sample 1; sowing 1, small pots, sample 2; sowing 1, medium size pots, sample 1; ..... ; sowing 2, large pots, sample 2).

The 300 clones were grown in a single completely randomised

block, each plot being three plants, with 45cm between plants and a 120cm gap between plots. At harvest, plots were mechanically dug and the tubers hand picked and placed into wooden boxes. While still in the field the produce from each plot was assessed for breeders' preference by three potato breeders. All plots were taken into the store where total tuber weight and number of tubers were recorded.

2.3.4 The third clonal year.

In the third clonal year only clones from three of the five crosses were grown (B2, B3 and B4). Irrespective of pot size or sowing in the glasshouse, 20 clones were taken at random from each cross and grown at MJRR in two completely randomised blocks. Each of the 60 clones were represented by a five plant plot (45cm between plants and a 120cm gap between plots) in each block.

The plots were mechanically harvested and taken into storage. These plots were not assessed for breeders' preference. Total tuber weight per plot was the only variate recorded. A summary of the experiment is given in Table 2.4 while a description of the variates recorded on this material can be found in Table 2.3.

2.4 Description of the 'C' material.

The main aim of the 'C' experiment was to examine the efficiency of selection where potato seedlings were grown in the field rather than in small pots in the glasshouse.

The progeny from four potato crosses were examined. These crosses were in fact A3, A4, A6 and A8 (for a description see table 2.1). As they are different unique samples from these crosses they will be identified by the codes C3, C4, C6 and C8.

Table 2.4 Summary of the 'B' experiment.

Year	Name	Number of crosses	Number of clones per cross	Plot size	Number reps	Site names
1	GH	5	120'	1	1	GH
2	FCY	5	120'	1	1	BB
3	SCY	5	60''	3	1	BB
4	TCY	3	20'''	5	2	MURR

' = 2 glasshouse sowings x 3 glasshouse pot sizes x 2 samples per sowing x 10 genotypes per sample. '' = 2 glasshouse sowings x 3 glasshouse pot sizes x 2 samples per pot size x 5 genotypes per sample. ''' a random sample of 20 clones per cross irrespective of conditions of seedling growth.

2.4.1 The seedling year.

On the 4th April, 1983, four samples of 50 seeds from each cross were sown into petri dishes containing moistened filter paper. After the seeds had germinated 24 seelings were pricked out from each sample, transplanted into jiffy-7 peat blocks and put into large seed trays containing peat. The 16 plots (4 cross x 4 samples/cross) were arranged into 4 completely randomised sample blocks, each block containing one sample from each cross. The seedlings were then put into a heated glasshouse. After 8 weeks of growth the seedlings were moved to a cold frame for a period of 2 weeks.

The seedlings were transplanted into the field (MURR) on the 20th June. The transplants were hand planted into ridged drills. The experiment consisted of four blocks, each block containing one 24 plant plot from each of the four crosses. The 24 plants in each plot were, of course, genetically different although progeny from the same cross. Immediately after transplanting the seedlings were watered and then hand watered for three consecutive days.

The haulms of the plants were not removed before harvest in order to ensure maximum tuber bulking. At harvest, each plant was harvested individually, the tubers from each plant were bagged and taken into storage. While in store, total tuber weight and number of tubers per plant were recorded, from which mean tuber weight was calculated.

2.4.2 The first clonal year.

A random sample of 40 clones from each of the four crosses were identified for growing in the second clonal year (ten clones from each of the four samples in the seedling year). These 160 clones were grown at MURR in the first clonal year. The trial design was of two completely randomised blocks with each clone being represented in each block by a three plant plot. A 45cm gap was left between plants with

120cm gap between plots to allow mechanical harvest.

At harvest the trial was mechanically dug and the tubers hand picked and put into boxes. The total weight and number of tubers per plot were recorded from which mean tuber weight was calculated. All data were converted to a per plant basis before analysis. After the plots had been weighed all the tubers were discarded. A summary of the 'C' experiment is shown in Table 2.5 while details of the variates recorded are again shown in Table 2.3.

2.5 Description of the 'D' material.

The main reason for examination of the 'D' material was to evaluate the possibility of cross prediction by evaluation of parental clones.

The crossing design used was a half-diallel with selfs. The crosses were carried out and seed obtained in the spring and summer of 1981. Five parents were used in crossing, Pentland Ivory, Baillie, Wilja, Cara and Desiree. All parents are commercially grown cultivars in the UK. Progeny from crosses were identified by the letter D followed by two integer numbers which indicate the two parents used (Table 2.6). Wilja was found to have very poor berry retention and it was not possible to obtain seed from the Wilja self cross. All other crosses yielded sufficient quantities of seed.

2.5.1 The seedling and first clonal years.

The seedling and first clonal years of the experiment were designed to produce seed tubers for the main experiment to be grown in the second clonal year, although, seedlings were assessed in the same way as the 'A' material. The growing conditions at these stages were the same at those used for these years in the 'A' material (see section 2.2.1 and 2.2.2). One hundred seeds from each of the 14

Table 2.5 Summary of the 'C' experiment.

Year	Name	Number of crosses	Number of clones per cross	Plot size	Number reps	Site names
1	SEED	4	96	1	1	MURR
2	FCY	4	40	3	2	MURR

Table 2.6 Cross codes and parentages of the 'D' material.

	P. Ivory				
P. Ivory	D11	Baillie			
Baillie	D12	D22	Wilja		
Wilja	D13	D23	-	Cara	
Cara	D14	D24	D34	D44	Desiree
Desiree	D15	D25	D35	D45	D55

crosses were sown in seed pans and transplanted to 10cm square pots after three weeks of growth. At harvest 50 seedlings were taken at random and the largest tuber produced from each of these were retained for planting in the first clonal year.

The first clonal year plants were grown at BB, planted on the 25th of March, 1983, and defoliated on the 11th of September. The experimental design was a completely randomised block with each cross being represented by 50 genotypes each grown as a single plant. Tubers were planted 45cm apart with a 120cm gap after every tenth plant. At harvest, each plant was individually harvested and all tubers from each plant were bagged and taken into storage.

2.5.2 The second clonal year.

In the second clonal year, 25 clones from each cross (350 genotypes) were taken at random for planting. However, there was the restriction that each of the clones used had at least 6 tubers from the second clonal year stage. This restriction did not have a serious effect on the choice of clones because more that 95% of all second clonal year plants complied to this criterion.

The 350 clones were planted in a single randomised block at BB and also at MURR. Each plot at each site consisted of three plants, planted 45cm apart with a 120cm gap between plots. Five plots of the parental clones, Pentland Ivory, Baillie, Wilja, Cara and Desiree were included in the randomisation at each site.

The MURR trial was planted on the 21st of April, 1984, and the BB trial was planted on the 7th of May. Before harvest the BB plots were defoliated by a double application of sulphuric acid while the MURR plots were mechanically defoliated 21 days later. Both trials were mechanically harvested and the tubers produced by each plot hand-picked and placed into boxes. While the tubers were still in the

field they were assessed for breeders' preference by a single breeder (PB1) on a 1 to 9 scale (see section 2.1). The produce from each plot was taken into storage where the total tuber weight and number of tubers per plot were recorded. Also in store uniformity of tuber shape, stolon persistence, absence from growth cracks, eye depth, distribution of tuber size and tuber dormancy were assessed on a 1 to 9 scale (see Table 2.3).

2.5.3 The third clonal year and beyond.

In the third clonal year a random sample of 155 clones were identified and grown at MURR. No restrictions were imposed on the random sample and it did not contain any predefined number from each of the 14 crosses. The trial had the same format as the 'A' material third clonal year trial (see section 2.2.4). Each clone was represented in two completely randomised blocks, each plot being five plants in a single drill. This trial was treated in exactly the same way as the normal commercial potato breeders third clonal year trials and clones were discarded from this trial unless they complied to the normal selection criteria. If they appeared to have commercial worth they continued in the breeding scheme and if they fell short of the desired adaptability they were discarded from the system. A summary of the 'D' experiment is shown in Table 2.7 while a description of the variates recorded are shown in Table 2.3.

Table 2.7 Summary of the 'D' experiment.

Year	Name	Number of crosses	Number of clones per cross	Plot size	Number reps	Site names
1	GH	14	100	1	1	GH
2	FCY	14	50	1	1	BB'
3	SCY	14	25	3	1	BB & MURR

' = Multiplication only, no data recorded.

CHAPTER 3

THE EFFICIENCY OF SELECTING INDIVIDUAL GENOTYPES IN THE EARLY GENERATIONS OF A POTATO BREEDING PROGRAMME

3.1 Introduction.

Early generation selection should be employed when promising genotypes have a greater chance of being selected than less promising ones (Yaneyawa & Yamagata, 1981). The response to selection (R) is given by the equation:

$$R = i\sigma_p h^2 \qquad \text{(Falconer 1964)}$$

where i is the intensity of selection, σ_p is the phenotypic standard deviation of the material under selection and h^2 is the heritability of the character being selected. The selection intensity (i) can be arbitrarily set according to the resources of the breeding scheme with greater intensity resulting possibly, in a higher response. However, irrespective of the selection intensity, little gain will be achieved by selection where there is insufficient genetic variation between genotypes and/or the heritability of the character being selected is low or zero.

3.1.1 Selection efficiency of crops other than potatoes.

The efficiency of selection has been examined in a number of different crop species. When breeding an autogamous species, for example barley or wheat, selection will be influenced by the segregating nature of the breeding lines in the early generations. The highest yielding progeny bulks, derived from F_2 and F_3 single plants, do not necessarily produce the highest yielding segregants (Atkins & Murphy, 1949). Selection for actual yield amongst inbreeding cereal F_2 families gave only a small increase in yield over a random sample (Boyce, Copp & Frankel, 1946; Sprague & Millar, 1952; Grafius, Nelson & Dirks, 1952, Briggs & Shebeski, 1970 and Knott, 1972). Even where the actual yield of early generations of a cereal pedigree bulk breeding scheme, say F_2 or F_3, was found to be

significantly correlated with yield in later generations, say F_5 or F_6, (Lupton & Whitehouse, 1957; McKenzie & Lambert, 1961; Shebeski, 1967; Briggs & Shebeski, 1971 and DePauw & Shebeski, 1973) the associations found between segregating generations were usually so poor that it was questionable whether selection at these early stages (and the expense that this incurred) would be justified (Knott, 1972 and Knott & Kurmar, 1975).

Selection for yield per se in the early segregating generations of other inbreeding species has also been shown to produce an effect which is no better than random (see Dahrya, Walden, Kaushik & Solanki, 1984 - chickpea; Meredith & Bridge, 1973 - cotton; Boerma & Cooper, 1975a, 1975b and Cowley, 1978 - soyabean; Dwivedi, Nanda & Chaudhary, 1978 - rice). However, Luedders, Duclos & Matson, 1973 have reported that selection in soyabeans at the F_3 stage results in higher yielding genotypes at the F_6 stage.

As expected, selection for qualitative disease resistance in the early generations has been found to be more effective than selection for quantitatively inherited characters such as yield (Valentine, 1979). In addition, selection for yield components such as seed size in chickpea (Bisen, Singh & Rao, 1985), and grains per ear in spring barley (Valentine, 1979), was shown to be more effective than selection for yield itself.

The efficiency of selection in a pedigree bulk breeding scheme has been related to the heterozygosity of the bulks selected (Brim & Cockerham, 1961). As homozygosity increases selection becomes more effective. Homozygosity can be accelerated by single seed descent, as first suggested by Goulden (1939) and later modified by Grafius (1965). However, single seed descent in barley may produce a 20% non-random loss of genetic material (Riggs & Hayter, 1976). Homozygosity can also be accelerated by various doubled haploid

techniques (Choo, Reinbergs & Kasha, 1985). Again however, care must be taken in the use of these procedures as there is evidence of non-random success (Powell, Caligari & Thomas, 1986). In time, it is likely that these methods will be refined and non-random loss of material will be significantly reduced.

Most research into the efficiency of selection on clonally reproduced crops (other than potatoes) has been conducted on sugar cane. Millar and James (1975) reported significant correlations between sugar cane seedlings and later clonal generations for stalk number and stalk diameter although it was concluded (James & Millar, 1975) that not more than 60% of the seedling and first clonal year breeding lines should be discarded when selecting for these characters. This prescribed selection intensity was lower than that which had been previously suggested by Skinner (1961).

The large number of genotypes which needs to be assessed in the early generations of a breeding programme usually dictates that most selection is by visual assessment (Simmonds, 1979). Visual assessment of yield and yield components is known to provide a good indication of actual yield and yield components of single plants in spring barley (Valentine, 1979) and also for rows of winter oats (Valentine & Ismail, 1983). It has been suggested that visual selection for yield should begin at the F_2 stage of a pedigree bulk breeding scheme, although the risk of discarding good genotypes will be higher than if actual yield were recorded (Yonezowa & Yomazata, 1981 and Ismail & Valentine, 1983).

Visual assessment of genotype performance is based on a mental image of the desirable attributes that will constitute a successful variety. Such assessments are therefore similar to selection indices (Fry, 1962). The efficiency of visual selection can be influenced by breeders' experience and also the time taken over assessments (Ismail

& Valentine, 1984). Visual assessment was found to be more effective when more than a single breeder scores each plot (Boyce, Copp & Frankel, 1946), although others have reported cases where visual selection by a single breeder was more effective than selection by two or more breeders acting simultaneously (Mariotti, Gimeney-Loscano, Mendoza, Osa & Oyevzabel, 1976).

In sexually reproducing crops selection amongst homozygous lines is more effective than selecting within segergating populations as in the latter case, genotypic expression can be masked by dominance effects. In a clonally reproduced crop, however, the problem of segregation is not considered to be as important. Although individual clones within a breeding programme tend to be highly heterozygous, clonal reproduction ensures the fixation of genotypes.

3.1.2 Selection efficiency in potatoes.

The most common method of selection in the early generations (seedling year, first and second clonal years) of a potato breeding programme is by visual appraisal (breeders' preference) (Kehoe, 1982; Mackay, 1982; Tai & Young, 1984 and Fitschen, 1984). When more than one breeder visually assesses potato seedlings or first clonal year plants, breeders tend to select varying proportions of genotypes (Anderson & Howard, 1981 and Brown, Caligari, Mackay & Swan, 1984). Davies & Johnston (1968) reported that different selectors tended to re-select clones in later generations which they had previously selected themselves rather than to re-select clones which were selected by a different breeder. This result, however, was not found by either Anderson & Howard (1981) or Brown *et al.* (1984). There was good agreement between the scores of different breeders when assessing seedlings and first clonal year plants (Anderson & Howard, 1981 and Brown *et al.*, 1984), although Brown (1985) pointed out that the

agreement between breeders at the first clonal year stage was greater than on seedlings. In contrast, Davis & Johnston (1965) and Tai (1975) did not find a good relationship between visual preference scores of different breeders. They concluded that this was due to breeders setting different selection criteria and the inherent difficulties of single plant selection (see section 4.3). In general, visual assessment of seedlings and first clonal year plants appears to be greatly influenced by total tuber weight, tuber size and number of tubers per plant (Maris, 1969 and Tai, 1975) and also to a lesser extent by uniformity of tuber shape (Brown, 1985).

Howard (1962) reported that seedlings which produced a large number of tubers which were very long in shape and, in addition, had long stolons and very low yields, could effectively be selected against. He found, however, that selection for uniformity of tuber shape and distribution of tuber size was ineffective at the seedling stage. Seedling selection was reported by Lynch (1982) to produce a small, but significant improvement in yield and maturity in the first clonal year. Moreover, it was also highly effective for selecting genotypes with low levels of growth cracking (Kichefski, Quinn & Peloquin, 1976). Kranty (1938) was able to divide clones according to different maturity classes on seedling performance. Small seedlings tended to be early maturing while tall seedlings matured later (Maris, 1964). Stuart (1923) concluded that selection could begin at the seedling stage against irregular tubers, deep eyes and too many tubers while Tellheim (1975) found that selection for foliage maturity and tuber yield was also effective at the seedling stage.

Significant correlation coefficients have been obtained between seedling performance and first clonal year performance based on breeders' preference (Pfeffer, 1963; Tai, 1975; Tai & Young, 1984, Brown et al., 1984 and Brown, 1985), and also total yield and yield

components (Tai, 1975; Brown, 1985 and Brown & Caligari, 1986). However, despite these significant correlations most recent studies have shown that a high proportion of potentially useful clones will be discarded if selection is carried out at the seedling stage (see Anderson & Howard, 1981 and Brown, 1985). Seedling selection has, of course, been found effective for major gene inherited traits (Plaisted, Thurston, Brodie & Hoopes, 1984 and Swiezynski, 1984). Nevertheless, it has been suggested that only negative selection should be made at the seedling stage (Pfeffer, 1963; Maris, 1964 and Tai & Young, 1984) although some have concluded that no selection at all would be best (Brown et al., 1984 and Brown & Caligari, 1986).

There is, therefore, still some controversy as to the efficiency of selection at the seedling stage although many breeders now agree that the seedling year should only provide tubers for field trials. Despite this, a large proportion of breeding schemes (see Table 1.3) still discard a high proportion of seedlings on their performance when grown in pots under glass!

Although seedling selection is not always practised, selection of individual genotypes at the first clonal year stage is common to all potato breeding schemes. In fact, it is usually at the first clonal year stage that the highest proportion of genotypes in the breeding scheme is discarded. Because most past research has focused on the efficiency of seedling selection there are only a few reports concerned with the efficiency of selection imposed on other early generations of a potato breeding scheme. One report, by Anderson & Howard (1981), showed that selection in the first clonal year was no more efficient than seedling selection. Maris (1969) examined phenotypic performance in the first and second clonal generations and obtained highly significant correlations for yield (r=0.68-0.86), breeders' preference (r=0.49-0.75), number of tubers per plant

(r=0.62-0.76) and mean tuber weight (r=0.83-0.87). He concluded, however, that these coefficients were not sufficiently large to justify positive selection for these traits in the first clonal generation. Similar correlation coefficients were obtained between different clonal generations by Swiezynski (1984). In contrast to Maris, he concluded that it would be worthwhile to select in the early generations by bulking all the produce from seedlings or first clonal year plants, and subsequently selecting individual tubers on their desirability.

In almost all previous studies the efficiency of seedling selection has been estimated by comparing the assessments of genotypes grown as seedlings and as first (or occasionally, second) clonal year plots. Likewise, the few examples investigating the efficiency of selection in the first clonal year, compare first clonal year performance with second clonal year performance. In this chapter the efficiency of selecting individual genotypes grown as seedlings, first clonal year and second clonal year plots, is examined by comparision with performance in the third clonal year. The material which was investigated is the 'A' material described in section 2.2 of Material and Methods. Details of the growing conditions, experimental design and variates recorded are also given in that section.

3.2 Variation within seasons.

In this section phenotypic performance between BB and MURR in each of three seasons is considered along with the relationship between variates in each environment.

3.2.1 Breeders' preference.

The four potato breeders selected differing proportions of the 'A' material as seedlings in the glasshouse and as clonal plots at BB

and MURR in the first, second and third clonal years (Table 3.1). Only genotypes with a breeders' preference score of greater than, or equal to, 5 were deemed worthy of selection. PB1 almost always selected a higher percentage (25.9%, on average) of clones than the other three breeders who tended to select similar proportions (averaging between 12.6% and 16.7%). Over all breeders, the percentage of total genotypes selected in each generation was 37.2% of seedlings, 17.1% of first clonal plants, 13.3% of second clonal year plots and 13.4% of third clonal year plots. Despite clone numbers only being reduced on a random basis, the proportion of clones which were considered to be "acceptable" at each generation were similar to the percentages selected in the normal breeding scheme at the SCRI (see Holden, 1977 and Mackay, 1982).

Breeders' preference scores were significantly higher ($p<0.001$) at MURR than at BB in the first clonal year (Table 3.2), however, in the second clonal year the situation was reversed. No significant difference between the scores at BB and MURR were detected in the third clonal year. Over all three analyses (Table 3.2) the interaction breeders x clones within progenies, was relatively small in magnitude, suggesting that the breeders were in agreement as to the desirability of clones in each environment.

The agreement between different breeders' assessments in the same environment was further examined by a correlation analysis between the scores of breeders taken in pairs (Table 3.3). It should be noted that these correlations are not independent of each other. All correlations between different pairs of breeders assessments were highly significant ($p<0.001$). Averaged over all pairwise comparisons in a single environment, the lowest coefficients were obtained in the glasshouse ($r=0.64$). There was a slight increase in the magnitude of correlation coefficient with increasing plot size (e.g. average

Table 3.1 Percentage of clones which were selected (breeders' preference $\geq$ 5.0) by each of four potato breeders (PB1 to PB4) in the glasshouse (GH) and at BB and MURR in the first (FCY), second (SCY) and third clonal years (TCY).

Location	PB1	PB2	PB3	PB4	Mean
GH	48.0	33.0	40.8	26.9	37.2
BB - FCY	21.6	11.4	12.1	15.4	15.1
MURR - FCY	33.0	10.5	13.2	19.6	19.1
BB - SCY	17.3	14.8	14.6	21.6	17.1
MURR - SCY	11.4	7.5	8.4	10.9	9.6
BB - TCY	24.5	5.5	8.0	3.5	10.4
MURR - TCY	25.5	5.5	19.5	15.5	16.4
Mean	25.9	12.6	16.7	16.1	

Table 3.2 Mean squares from the analysis of variance of four potato breeders preference scores at two locations (BB and MURR) in the first clonal year (FCY), second clonal year (SCY) and third clonal year (TCY), 1982 1983 and 1984 respectively.

Source	df	FCY	SCY	TCY
Sites (S)	1	85.01'''	128.72'''	6.15 ns
Progenies (P)	7	108.80'''	112.12'''	57.22'''
Clones W Progs (C)	552(192[1])	5.56''	5.15'	5.20'''
Breeders (B)	3	98.80'''	11.03 ns	7.95 ns
S x P	7	12.75'''	5.31'''	3.16'''
B x P	21	1.877'	1.77''	2.62'''
S x C W P	552(192[1])	2.52'''	3.71'''	0.91'''
B x C W P	1656(576[1])	0.54 ns	0.37 ns	0.65'
B x S	3	18.22'''	6.55'''	0.34 ns
P x B x S	21	0.71 ns	0.63'''	0.93'''
Residual	1656(576[1])	0.43	0.29	0.35

ns = not significant; ' = 0.05>p>0.01; '' = 0.01>p>0.001; ''' p<0.001

[1] degrees of freedom for the TCY analysis.

Table 3.3 Coefficients obtained by correlation between the preference scores of four potato breeders (PB1 to PB4), of seedlings (GH) and of first (FCY), second (SCY) and third (TCY) clonal year plants grown at two locations (BB and MURR).

		FCY		SCY		TCY[1]	
Combination	GH	BB	MURR	BB	MURR	BB	MURR
PB1 v PB2	0.57	0.69	0.80	0.77	0.75	-	0.82
PB1 v PB3	0.53	0.73	0.80	0.81	0.78	0.94	0.84
PB1 v PB4	0.50	0.67	0.72	0.68	0.80	-	0.88
PB2 v PB3	0.76	0.74	0.78	0.78	0.77	-	0.74
PB2 v PB4	0.73	0.68	0.69	0.63	0.75	-	0.76
PB3 v PB4	0.76	0.72	0.80	0.68	0.77	-	0.87
Mean	0.64	0.70	0.76	0.72	0.77	0.82	0.94

[1] Correlations based on the assessment of 200 genotypes, all other correlations were based on assessments of 560 genotypes. All correlations were highly significant ($p<0.001$).

correlation between breeders in the first clonal year was 0.73, in the second clonal year 0.75 and in the third clonal year 0.84). There was also slightly greater agreement between breeders scoring at MURR (r=0.78) than when scoring at BB (r=0.73).

Both the analysis of variance (Table 3.2) and correlation coefficients between pairs of breeders assessments (Table 3.3) show that the four breeders who assessed breeders' preference were in good agreement. Therefore, to avoid repetition throughout this chapter further analysis will, in most cases, be based on "overall preference", the mean preference score of each clone in each plot averaged over the four breeders (only two breeders at BB in the third clonal year).

Significant interactions ($p<0.001$) were detected between progenies and sites and sites by clones within progenies in all three years (Table 3.2). All correlation coefficients between sites were, however, significantly greater than zero ($p<0.001$) (Table 3.4). As expected, the coefficients based on 200 clones were generally slightly larger in magnitude than those based on 560. Considering only the correlations based on 200 observations, coefficients obtained between sites in the first and second clonal years were of similar magnitude, although there appeared to be better agreement between scores at the two sites in the third clonal year. Overall preference (average preference of four breeders) gave higher correlation coefficients between BB and MURR than indivudual breeders' scores. This suggests greater accuracy of estimation by averaging breeders' preference over four breeders.

The observed and expected number of clones which were selected and rejected at BB and MURR in the first, second and third clonal year is shown in Table 3.5. The expected number assumes that there is no association between selections made at the two sites. In all three

Table 3.4 Coefficients obtained by correlation of breeders' preference scores between BB and MURR in the first (FCY), second (SCY) and third (TCY) clonal years. Coefficients based on 560 (a) and 200 (b) clones are presented although it should be noted that the two samples are not independent.

	FCY		SCY		TCY
Breeder	(a)	(b)	(a)	(b)	(b)
PB1	0.22	0.28	0.37	0.35	0.57
PB2	0.27	0.26	0.23	0.22	-
PB3	0.34	0.34	0.34	0.37	0.61
PB4	0.35	0.35	0.29	0.33	-
Overall preference	0.44	0.36	0.48	0.38	0.56

All correlations are highly significant ($p<0.001$).

Table 3.5 Observed (Obs.) and expected (Exp.) number of clones that were selected (+) and rejected (-) according to overall breeders' preference score (+ = $\geq$ 4.1) at BB and MURR in the first (FCY), second (SCY) and third (TCY) clonal years.

FCY

BB	MURR	Obs.	Exp.
+	+	61	31.4
+	-	54	83.6
-	+	92	121.6
-	-	353	323.4

$\chi^2_1 = 60.91'''$

% selected mis-classified = 70.5%

SCY

BB	MURR	Obs.	Exp.
+	+	54	29.7
+	-	106	130.3
-	+	50	74.3
-	-	350	325.7

$\chi^2_1 = 34.17'''$

% selected mis-classified = 74.3%

TCY

BB	MURR	Obs.	Exp.
+	+	40	22.8
+	-	26	43.2
-	+	29	46.2
-	-	105	87.8

$\chi^2_1 = 29.60'''$

% selected mis-classified = 57.9%

''' = $0.01<P<0.001$; %selected mis-classified = the percentage of clones selected at either site (ie. ignoring those discarded at both sites) that were discarded at the other site.

generations there was a higher proportion of clones selected at both locations and rejected at both locations than would have been expected, therefore, there is obviously some agreement with regard to clonal performance at BB and MURR. However, despite significant χ^2 values in each generation ($p<0.001$) a large number of clones would have been selected at one of the locations and discarded at the other. The proportion of misclassified clones did not decline with increasing generations (ie. increasing plot sizes), hence suggesting a genotypic response to the different environmental conditions with some clones performing better in one environment than in the other.

To determine which variates the breeders were taking into account when assessing preference, average breeders scores were correlated with other tuber characters (Table 3.6). Breeders' preference was always significantly correlated ($p<0.001$) with total tuber weight, mean tuber weight and uniformity of tuber shape. The correlations between overall preference and tuber weights gave coefficients greater than zero in all environments except at MURR in the third clonal year. Overall preference was significantly correlated with stolon persistence in over half of the environments, absence from growth cracks in all environments except in the glasshouse, and depth of eyes in all environments except at MURR in the first clonal year. Tuber dormancy always resulted in very low correlation coefficients which is not surprising as preference was scored immediately, or soon after, harvest when all tubers would still have been in a dormant state.

The contribution of tuber characters to overall preference was examined in more detail using multiple regression. Results from forward step-wise multiple regression analyses of overall breeders' preference on to the other recorded characters are presented in Table 3.7. Data presented in the table relate to (i) the order that the variables were entered into the forward step-wise multiple regression

Table 3.6 Coefficients obtained by correlating average breeders' preference scores with total tuber weight (TTW), mean tuber weight (MTW), number of tubers (NTU), uniformity of tuber shape (Shape), stolon persistence (Stolon), absence of growth cracks (Growth), tuber dormancy (Dorm), distribution of tuber size (Dist) and depth of eyes (Eyes) that were recorded in the glasshouse (GH) and at BB or MURR in the first (FCY), second (SCY) and third (TCY) clonal year.

		FCY		SCY		TCY[1]	
Variate	GH	BB	MURR	BB	MURR	BB	MURR
TWT	0.71'''	0.60'''	0.56'''	0.66'''	0.72'''	0.67'''	0.62'''
MWT	0.57'''	0.27'''	0.42'''	0.44'''	0.44'''	0.46'''	0.54'''
TNU	0.13''	0.13''	0.36'''	0.43'''	0.46'''	0.22'''	0.00
Shape	0.52'''	0.44'''	0.38'''	0.56'''	0.35'''	0.70'''	0.63'''
Stolon	0.28'''	0.16''	0.08	0.24'''	0.07	-	-
Growth	0.00	0.20'''	0.21'''	0.28'''	0.11'	0.19'''	0.30'''
Dorm	0.01	0.00	0.10	0.09	0.03	0.16'	0.05
Dist	0.13''	0.25'''	0.05	0.38'''-0.08		0.38'''	0.43'''
Eyes	0.16''	0.17''	0.03	0.37'''	0.23'''	-	-

[1] correlation coefficient based on 200 observations, all other correlations were based on 560 observations. ' = 0.05>p>0.01; '' = 0.01>p>0.001; ''' = p<0.001, all other coefficients are not significantly greater than zero.

Table 3.7 Order that variates were entered by forward stepwise multiple regression of average breeders' preference scores against total tuber weight (TTW), mean tuber weight (MTW), number of tubers (TNU), uniformity of tuber shape (Shape), stolon persistence (Stolon), absence from growth cracks (Growth), tuber dormancy (Dorm), distribution of tuber size (Dist) and depth of eyes (Eyes). The increase in percentage of total variation accounted for by the addition of each variate into the regression equation is also shown if the percentage increases by more than 1%.

	FCY			SCY		TCY[1]	
	GH	BB	MURR	BB	MURR	BB	MURR
TTW	1(50%)	1(36%)	1(31%)	1(44%)	1(52%)	2(28%)	2(24%)
MWT	3 (3%)	6	7	4 (3%)	7	6	3 (7%)
TNU	5	5	5 (1%)	6	4 (1%)	7	5 (2%)
Shape	2(22%)	2(18%)	2 (8%)	2(19%)	2 (4%)	1(49%)	1(40%)
Stolon	6	7	8	8	8	-	-
Growth	7	4	6	3 (7%)	3 (3%)	5 (1%)	4 (5%)
Dorm	8	9	9	9	9	4 (1%)	6
Dist	6	3	4 (2%)	5 (2%)	8	3 (1%)	7
Eyes	4	8	3 (5%)	7	6	-	-
Total variation accounted for by All vars.	76%	53%	47%	73%	59%	82%	79%

[1] Multiple regression based on 200 genotypes, all other regressions were based on 560 genotypes.

equation and (ii) the additional percentage of the total variation in overall preference which was accounted for by the regression equation (if greater, or equal, to 1%). As expected from the correlations in Table 3.6, total tuber weight was the variate most often entered first into the regression equation and uniformity of tuber shape was generally entered as the second variate. Multiple regression onto these two variates accounted for, on average, 61% of the total variation in preference scores. The goodness of fit in the regression model was not greatly enhanced by the introduction of other variates although mean tuber weight and tuber number added slightly to the regression equation in some of the environments.

3.2.2 Yield and yield components.

Mean squares from the analyses of variance of total tuber weight, mean tuber weight and number of tubers per plant in the first, second and third clonal years are shown in Table 3.8. The error term used in the analysis of the first clonal year was derived from the control cultivars which were grown in each block because in this year, blocks were confounded with seed tuber size (for a detailed description see Brown, 1985). The shorter growing season at BB resulted in significantly lower total tuber weights with smaller and fewer tubers than at MJRR. The interaction, sites x progenies, was significant for total tuber weight and number of tubers in the first and second clonal year and for total tuber weight in the third clonal year ($p<0.001$). This interaction was also significant at the 5% level for mean tuber weight in the third clonal year. The interaction sites x clones within progenies was significant ($p<0.001$) in the third clonal year and only just significant ($p<0.05$) in the second clonal year. In the first clonal year this interaction was not significant for other variates, suggesting that there was good agreement between sites in terms of the yield components.

Table 3.8 Mean squares from the analysis of variance of total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (TNU) at two locations, BB and MURR in the first (FCY), second (SCY) and third (TCY) clonal years.

FCY

Source	df	TWT	MWT	TNU
Sites (S)	1	4806.3'''	62.77'''	13.77 ns
Progenies (P)	7	590.4'''	6.15'''	485.38'''
Clones W Progs (C)	552	32.9'	0.42 ns	27.10'
S x P	7	135.1'''	0.79 ns	32.86'''
S x C W P	552	17.6 ns	0.39 ns	14.11 ns
Replicate error[1]	100	34.8	1.14	10.62

SCY

Source	df	TWT	MWT	TNU
Sites (S)	1	5966.4'''	12.29'''	4838.71'''
Progenies (P)	7	151.1'''	1.05'''	322.13'''
Clones W Progs (C)	552	9.9 ns	0.09 ns	25.01'
S x P	7	34.7'''	0.11 ns	20.46'''
S x C W P	552	5.5'	0.05 ns	10.43 ns
Replicate error[2]	441	2.6	0.40	6.32

TCY

Source	df	TWT	MWT	TNU
Sites (S)	1	97.05'''	2.714'''	2463.7'''
Progenies (P)	7	26.42'''	0.288'''	140.6'''
Clones W Progs (C)	192	1.54 ns	0.054 ns	18.2 ns
S x P	7	10.75'''	0.090'	21.6 ns
S x C W P	192	1.51'''	0.054 ns	18.2 ns
Replicate error	598	0.68	0.032	19.41

ns = not significant; ' = 0.05>p>0.01; '' = 0.01>p>0.001; ''' = p<0.001

[1]Replicate error estimated from controls within the trial (see Brown, 1985). [2]Replicate error is the harmonic mean of individual trials at the two locations.

Correlation coefficients obtained by correlating total tuber weight and the yield components recorded at BB with those recorded at MURR were all significantly ($p<0.001$) greater than zero (Table 3.9). Correlation coefficients between BB and MURR for total tuber weight were of similar magnitude in all clonal generations. The correlation between sites in the third clonal year resulted in larger coefficients for mean tuber weight and number of tubers. This was perhaps a result of increased plot size. Plot size will be discussed in detail in section 4.2.

If the highest yielding clones (top 20% according to total tuber weight) at each site are considered to be selected (with the remainder being rejected), the pattern of selected and rejected clones at both sites in the three clonal years can be examined. When this was done (Table 3.10), there was always a higher than expected (on a random basis) number of clones which were either selected or rejected at both sites. However, a high proportion (77.7%, 76.1% and 78.1% in the first, second and third clonal years respectively) of clones amongst the top 20% highest yielding at either site, would have been rejected in the other environment. Overall therefore, it appears that there would be a number of differences which would arise between clones selected for high yield or yield components at BB compared to those selected at MURR.

3.2.3 Other tuber characters.

In contrast to the analysis of breeders' preference (Table 3.2) and the yield characters (Table 3.8) there was no difference between BB and MURR for most of the other characters recorded (Table 3.11). In the first and second clonal year, however, clones were given higher scores for uniformity of shape at BB than at MURR. This difference was probably related to smaller tubers produced at BB as a result of

Table 3.9 Coefficients obtained by correlating total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (TNU) recorded at BB and MURR in the first (FCY), second (SCY) and third (TCY) clonal year. Coefficients are presented based on 560 clones (a) and 200 clones (b), although it should be noted that the 560 and 200 clone samples were not independent.

	FCY		SCY		TCY
Variate	(a)	(b)	(a)	(b)	(b)
TTW	0.38	0.41	0.32	0.44	0.38
MWT	0.33	0.47	0.34	0.47	0.55
TNU	0.32	0.26	0.29	0.46	0.63

All correlation coefficients are significantly ($p<0.001$) greater than zero.

Table 3.10 Observed (Obs.) and expected (Exp.), assuming no association between BB and MURR, number of clones which were selected (+) and rejected (-) at BB and MURR according to total tuber weight in the first (FCY), second (SCY) and third (TCY) clonal year. Clones within the top 20% of total tuber weight were selected (+) at each location.

FCY

BB	MURR	Obs.	Exp.
+	+	41	22.4
+	-	74	89.6
-	+	70	89.6
-	-	375	358.4

$\chi^2_1 = 23.22$ '''

% selected mis-classified = 77.8%

SCY

BB	MURR	Obs.	Exp.
+	+	43	22.4
+	-	68	89.6
-	+	69	89.6
-	-	380	358.4

$\chi^2_1 = 30.19$ '''

% selected mis-classified = 76.1%

TCY

BB	MURR	Obs.	Exp.
+	+	14	8.0
+	-	25	32.0
-	+	25	32.0
-	-	136	128.0

$\chi^2_1 = 8.06$ ns

% selected mis-classified = 78.1%

ns = not significant; ''' = $p<0.001$; % selected mis-classified = the percentage of clones selected at either site (ignoring those discarded at both sites) that were discarded at the other site.

Table 3.11 Mean squares from the analysis of variance of uniformity of tuber shape (Shape), stolon persistence (Stol), absence of growth cracks (Grow), tuber dormancy (Dorm), distribution of tuber size (Dist) and depth of eyes (Eyes) between BB and MURR in the first (FCY), second (SCY) and third (TCY) clonal year.

FCY

Source	df	Shape	Stol	Grow	Dorm	Dist	Eyes
Sites (S)	1	32.66'''	1.26	6.49'	257.6'''	0.37	6.11'
Progenies (P)	7	67.68'''	24.80'''	34.49'''	6.5	22.33'''	107.84'''
Clones W Prog	552	2.90	3.90	1.72	1.0	3.82	3.75
S x P	7	3.88	4.76	6.89	2.5	4.87	11.82
S x C W P	552	1.59	2.28	1.35	3.2	3.07	1.71
Replicate error[1]	100	2.04	1.26	0.42	0.75	2.65	1.72

SCY

Source	df	Shape	Stol	Grow	Dorm	Dist	Eyes
Sites (S)	1	46.60'''	23.45'''	0.03	432.43'''	43.57'''	1.45'
Progenies (P)	7	17.81'''	9.62'''	34.92'''	63.71'''	7.10	64.71'''
Clones W Prog	552	2.72	3.11'	1.94'	0.96	2.86	3.61'''
S x P	7	1.62	1.25	2.34	3.59	8.11	1.51
S x C W P	552	1.06	0.78	0.86	2.74	1.86	1.28
Replicate error[2]	441	1.51	1.41	0.82	1.47	2.92	1.62

TCY

Source	df	Shape	Stol	Grow	Dorm	Dist	Eyes
Sites (S)	1	0.49	-	1.82'	370.56'''	16.40'''	-
Progenies (P)	7	24.15'''	-	5.47'''	41.28'''	23.14'''	-
Clones W Prog	192	2.67	-	2.17'''	6.65	2.60	-
S x P	7	1.51	-	1.07	6.30	4.32	-
S x C W P	192	0.87	-	0.80	1.59	2.00	-
Replicate error	598	1.28	-	0.95	1.52	2.43	-

' = 0.05>p>0.01; '' = 0.01>p>0.001; ''' = p<0.001; all other mean squares are not significant. [1] Replicate error estimated from controls within the trial (see Brown, 1985). [2] Replicate error is the harmonic mean of individual trials at the two locations.

the shorter growing season at this site. Similarly, clones from the BB plots appeared to be significantly less dormant than those from the MURR plots, however, this is simply due to the BB trials being assessed at a later date to those at MURR. The interaction of sites by progenies was significant for stolon persistence, growth cracks, and eye depth in the first clonal year, and for uniformity of tuber shape, growth cracks, dormancy and distribution in the second clonal year. In the third clonal year the site x progeny interaction was significant for tuber dormancy and only just significant for distribution. The interaction, sites x clones within progenies, was only significant for absence from growth cracks in the first clonal year.

The correlation between BB and MURR in the first clonal year for growth cracking and distribution of tuber size was not significantly greater than zero (Table 3.12). The correlations between sites for the other variates in the first clonal year were significant at least at the 5% level. In the second clonal year the correlation between BB and MURR were significantly greater than zero ($p<0.001$) for all variates except distribution of tuber size. For all variates examined, however, correlations between BB and MURR were significantly larger in the third clonal year than between sites in the first or second clonal year.

The association between variates recorded, excluding breeders' preference, was examined by correlating the characters in the different environments. The association between most of these characters in the glasshouse (Table 3.13) and the first clonal year (Table 3.14) was examined by Brown (1985) and re-examination here resulted in similar coefficients. Correlations between variates in the second (Table 3.15) and third clonal year (Table 3.16) showed the same relationships found in earlier generations. In summary, high

Table 3.12 Coefficients obtained by correlating uniformity of tuber shape (Shape), stolon persistence (Stolon), absence from growth cracks (Growth), tuber dormancy (Dorm), distribution of tuber size (Dist) and depth of eyes (Eyes) between BB and MURR in the first (FCY), second (SCY) and third (TCY) clonal year. Coefficients are based on 560 clones and 200 clones, although the two samples were not independant.

	FCY		SCY		TCY
Variate	560	200	560	200	200
Shape	0.27'''	0.25'''	0.32'''	0.34'''	0.67'''
Stolon	0.16''	0.10ns	0.26'''	0.24''	-
Growth	0.05ns	0.13'	0.23'''	0.24''	0.48'''
Dorm	0.24'''	0.26'''	0.26'''	0.35'''	0.62'''
Dist	0.06ns	0.05ns	0.03ns	0.07ns	0.26''
Eyes	0.36'''	0.39'''	0.33'''	0.27'''	-

ns = not significant; ' = 0.05>p>0.01; '' = 0.01>p>0.001; ''' = p<0.001

Table 3.13 Association between variates (correlation coefficients) recorded on 560 genotypes grown as seedlings in the glasshouse.

	TWT	MWT	TNU	Shape	Stol	Grow	Dorm	Dist	Eyes
TWT	-								
MWT	0.58	-							
TNU	0.40	-0.32	-						
Shape	0.07	0.09	-0.02	-					
Stol	0.00	0.09	-0.04	0.51	-				
Grow	0.20	-0.15	0.05	-0.01	0.00	-			
Dorm	0.01	0.14	0.02	0.01	0.00	0.07	-		
Dist	0.10	0.04	0.05	0.17	0.10	0.06	0.10	-	
Eyes	-0.09	-0.13	0.04	0.45	0.45	0.03	0.14	0.17	-

Correlations greater than, or equal to, 0.10 are significant ($p<0.5$) those greater than, or equal to, 0.13 are significant ($p<0.01$) and those greater than, or equal to, 0.19 are significant ($p<0.001$). Correlation coefficients less than 0.10 were not significantly different from zero.

Table 3.14 Association between variates (correlation coefficients) recorded on 560 genotypes grown at BB in the first clonal year (lower triangular) and at MURR in the first clonal year (upper triangular).

TWT	-	0.70	0.71	0.20	0.06	0.31	0.13	0.12	0.04
MWT	0.53	-	0.18	0.27	0.11	0.33	0.01	0.33	0.12
TNU	0.41	-0.12	-	0.17	0.18	0.36	0.00	-0.03	0.11
Shape	0.03	-0.13	-0.11	-	0.62	0.49	0.02	0.54	0.65
Stol	-0.04	-0.03	-0.06	0.36	-	0.57	0.00	0.51	0.69
Grow	0.17	0.15	0.12	0.06	0.03	-	0.05	0.56	0.49
Dorm	0.09	-0.11	0.16	0.10	0.02	0.00	-	0.02	0.23
Dist	0.12	0.09	-0.20	0.24	0.11	0.06	0.00	-	0.45
Eyes	-0.09	-0.12	-0.12	0.59	0.45	-0.06	0.16	0.05	-
	TWT	MWT	TNU	Shape	Stol	Grow	Dorm	Dist	Eyes

Correlations greater than, or equal to, 0.10 are significant ($p<0.5$) those greater than, or equal to, 0.13 are significant ($p<0.01$) and those greater than, or equal to, 0.19 are significant ($p<0.001$). Correlation coefficients less than 0.10 were not significantly different from zero.

Table 3.15 Association between variates (correlation coefficients) recorded on 560 genotypes grown at BB in the second clonal year (lower triangular) and at MURR in the second clonal year (upper triangular).

TWT	-	0.50	0.74	0.19	-0.06	0.00	0.00	-0.21	0.15
MWT	0.54	-	-0.03	0.17	-0.20	-0.04	-0.14	0.15	0.17
TNU	0.74	-0.06	-	0.09	0.06	0.10	0.03	-0.28	0.04
Shape	0.18	0.11	0.08	-	0.43	0.05	-0.10	0.11	0.67
Stol	-0.01	-0.13	0.07	0.58	-	0.14	0.00	0.14	0.51
Grow	0.04	-0.03	0.10	-0.04	0.04	-	0.02	0.06	0.00
Dorm	0.10	0.15	-0.03	0.04	-0.07	-0.10	-	0.06	0.00
Dist	0.34	0.52	-0.07	0.21	0.05	-0.03	0.10	-	0.13
Eyes	0.11	0.09	0.04	0.76	0.60	-0.08	0.02	0.11	-
	TWT	MWT	TNU	Shape	Stol	Grow	Dorm	Dist	Eyes

Correlations greater than, or equal to, 0.10 are significant ($p<0.5$) those greater than, or equal to, 0.13 are significant ($p<0.01$) and those greater than, or equal to, 0.19 are significant ($p<0.001$). Correlation coefficients less than 0.10 were not significantly different from zero.

Table 3.16 Association between variates (correlation coefficients) recorded on 200 genotypes grown at BB in the third clonal year (lower triangular) and at MURR in the third clonal year (upper triangular).

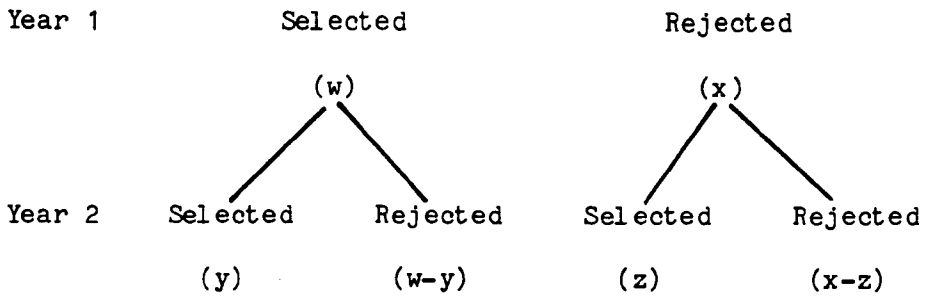
TWT	-	0.44	0.47	0.21	0.04	-0.29	-0.00
MWT	0.39	-	-0.49	0.17	-0.04	0.12	0.41
TNU	0.42	-0.23	-	-0.03	0.10	-0.41	-0.42
Shape	0.25	-0.11	0.03	-	0.12	0.04	0.46
Grow	0.11	0.20	0.12	0.10	-	-0.05	0.10
Dorm	-0.00	0.00	-0.30	0.06	-0.13	-	0.36
Dist	0.11	0.36	-0.29	0.33	0.07	0.24	-
	TWT	MWT	TNU	Shape	Grow	Dorm	Dist

Correlations greater than, or equal to, 0.16 are significant ($p<0.5$) those greater than, or equal to, 0.20 are significant ($p<0.01$) and those greater than, or equal to, 0.25 are significant ($p<0.001$). Correlation coefficients less than 0.16 were not significantly different from zero.

total tuber weights were related to high mean tuber weight and also with numerous, good shaped tubers. Clones with large tubers tended to have fewer tubers than clones with lower mean tuber weights, clones with good distribution of tuber size had fewer larger tubers and clones with uniform tuber shapes tended to have shallow eyes. In general, the associations were therefore those which would have been expected given some knowledge of the potato crop.

3.3 Variation between seasons.

The 'A' clones under investigation were grown in four consecutive seasons, i.e. as seedlings and in the first, second and third clonal years. No selection was carried out at each of these stages (although there was a random reduction in number of clones) so it is possible to simulate selection at various selection intensities. In a normal breeding scheme, selection would have been carried out after each year's assessment. To examine the efficiency of selection at each stage, the relationship between the number of selected and rejected clones was studied taking the years in pairs. For example, the material grown as seedlings can be divided into two categories: those which would have been selected and those which would have been discarded, depending on set criteria. The clones can also be divided into selected and discarded according to their performance in the first clonal year. From this the question can be raised as to what proportion of clones selected in the first clonal year would have been: (a) selected as seedlings; and (b) discarded as seedlings. The ratio of these two proportions will be termed the selection ratio (Brown, 1985) and is:



Selection ratio = (y/w)/(z/x)

If the selection ratio is equal to zero, then either there were no repeat selections made in the second year, or there were no clones selected in the second year which had been discarded in the first. A selection ratio less than 1.0 indicates that a higher proportion of clones were selected from the clones which were discarded in the first year than for those which were selected in that year. A selection ratio of less than 1.0 therefore indicates negative selection; selection ratios equal to 1.0 indicate that there is no association between selections made in the two years (ie selection is at random); and selection ratios greater than 1.0 show that selection was effective, with increasing values of the selection ratio indicating greater correspondence. If the selection ratio between year 1 and year 2 is equal to 2.0 then clones which were selected in year 1 would be twice as likely to be selected in year 2 than clones which were discarded in the first year.

3.3.1 Breeders' preference.

Mean squares from the analysis of variance of four potato breeders' assessments on 200 clones (those which were grown in four years) grown over four seasons are shown in Table 3.17. In the analysis the three-way interactions were tested against the pooled residual terms in Table 3.2. Other terms were tested for significance against the appropriate interaction. In cases where there was doubt as to which interaction to use, the largest mean square was used as

Table 3.17 Mean squares from the analysis of variance of four potato breeders preference scores on 200 clones grown in four consecutive years.

Source	df	M. Sq.
Years (Y)	3	51.67 '''
Progenies (P)	7	88.99 '''
Clones w Prog (C)	192	9.38 '''
Breeders (B)	3	37.15 '''
Y x P	21	5.80 '''
Y x B	9	12.47 '''
P x B	21	1.91 ns
Y x C w P	576	1.25 '''
B x C w P	576	0.64 ns
Y x P x B	63	1.11 '''
Y x B x C w P	1728	0.37 ns
Pooled error	3888	0.36

ns = not significant; ' = 0.05>p>0.01; '' = 0.01>p>0.001; ''' = p<0.001

Pooled error is the pooled breeders x sites x clones within progenies terms in Table 3.2.

the divisor in the F test. Differences between years, breeders, progenies and clones within progenies were all highly significant ($p<0.001$). The interaction terms, progenies x breeders, breeders x clones within progenies and the three-way interaction, were not significant indicating that the breeders were in good agreement as to which progenies and which clones looked attractive in the different years. There were, however, significant ($p<0.001$) genotype by season interactions.

The efficiency of selection by breeders' preference was examined by correlating scores for overall preference (the mean of the four breeders) recorded in the different seasons (Table 3.18). All correlations were significantly ($p<0.001$) greater than zero. Correlation coefficients based on 560 observations were not significantly different from those based on the 200 clones which were grown in all years. Consider first the correlations between scores as seedlings with scores in the three clonal generations. Regression of seedling scores on first clonal year scores accounted for 24% of the total variation in the first clonal year scores. Similar regression of seedlings onto second and third clonal years accounted for 13% and 8% respectively. There was, therefore, a trend of decreasing coefficient of determination with increasing years after seedlings. The correlation between the first clonal year and second clonal year was similarly larger than between the first clonal year and the third clonal year. The largest correlation coefficient was obtained between the second and third clonal years.

The trend of decreasing coefficient with increasing years (ie. GHvFCY > GH$\underline{v}$SCY > GH$\underline{v}$TCY and FCY$\underline{v}$SCY > FCY$\underline{v}$TCY) could be a reflection of increasing numbers of clonal generations after growth from true botanical seed or of increasing 'plot' size. If, however, it was simply due to increasing plot size the correlation between the

Table 3.18 Coefficients obtained by correlating overall breeders' preference scores recorded on seedlings (GH), first (FCY), second (SCY) and third (TCY) clonal years. a) correlations based on 560 observations, b) correlations based on 200 observations.

Comparison	(a)	(b)
GH v FCY	0.48	0.49
GH v SCY	0.37	0.36
GH v TCY	-	0.29
FCY v SCY	0.64	0.58
FCY v TCY	-	0.44
SCY v TCY	-	0.76

All correlation coefficients are significantly ($p<0.001$) greater than zero.

glasshouse and the third clonal year would have been expected to be greater than between the glasshouse and the first clonal year whereas in fact the reverse was true. This reduction in association between increasing years would therefore suggest that a carry-over effect between successive generations was exaggerating the efficiency of selection.

The 560 clones grown as seedlings, and also in the first and second clonal years, can be divided into eight categories, using the previously described criteria, depending on whether each clone was selected or rejected in each of the three seasons (Table 3.19a). The expected numbers were calculated from the proportion of clones selected in each year, assuming independence between seasons. The observed and expected numbers were significantly different. The observed numbers were greater than expected for those selected in all three years, rejected in all years and selected in two of the three years, while they were less for the other categories. From this, one could postulate that selection was effective in each generation. However, it is obvious that a high proportion of mis-classification occurred.

If it is now assumed that the most accurate assessment of the 560 clones was data from the second clonal year (because of increased plot size) then 115 clones were shown to have potential. These were the clones that would have been selected in the second clonal year. Of these 115 clones, it was found that only 31 (27%) of them would have survived to the second clonal year of a normal breeding scheme (Table 3.19b). The remaining 84 clones would have been discarded either as seedlings, as first year clones or in both these previous generations. Even if no selection had been made in the glasshouse then almost half (44%) of the selections in the second clonal year would have been discarded in the first clonal year.

Table 3.19a Observed (Obs.) and expected (Exp.) number of clones which were selected (+) and rejected (-) in the glasshouse (GH), first (FCY) and second (SCY) clonal years according to overall breeders' preference. Observed and expected numbers were based on 560 clones.

GH	FCY	SCY	Obs.	Exp.
+	+	+	31	6.19
+	+	-	30	24.55
+	-	+	19	21.00
-	+	+	33	19.99
+	-	-	55	83.27
-	+	-	36	79.27
-	-	+	32	67.82
-	-	-	335	268.92

$\chi^2_7 = 177.69$ ($p<0.001$)

Table 3.19b Observed number of clones which were selected (+) and rejected (-) in the glasshouse (GH) and first clonal year (FCY) from amongst only those clones which were selected in the second clonal year according to overall breeders' preference (based on 560 clones).

GH	FCY	Number
+	+	31 (=27%)
+	-	19 (=16%)
-	+	33 (=29%)
-	-	32 (=28%)

52 (=45%)

84 (=73%)

A similar examination can be made, including the selection in the third clonal year (Table 3.20a). In this case the observed and expected numbers are based on only the 200 clones grown in all four seasons. The observed number of clones in the categories selected in all years(+ + + +) and rejected in all years (- - - -) were considerably larger than expected, suggesting again that on the surface selection was efficient. There were, however, many clones which would have been selected in one season and discarded in another. From the 75 clones that were selected in the third clonal year, only 20% would have been retained in each of the three previous seasons, while almost one third (29%) would not have been previously selected in any generation (Table 3.20b). Even if no selections are made in either the glasshouse or first clonal year, then just under half of the clones which showed potential in the third clonal year would have been discarded in the previous season. It is concluded therefore, that a large proportion of potentially valuable genotypes will be discarded if selection for breeders' preference is carried out in the early generations.

The efficiency of selection by breeders' preference with varying intensities at the seedling stage was examined by selection ratios (see section 3.3). Selection ratios between seedlings and second clonal year plots (Table 3.21a) were all greater than zero. There was, however, a reduction in selection ratio associated with increased selection intensities on seedlings, whereas increased intensity in the second clonal year resulted in increased ratios. For example, if 91% of seedlings were retained the average selection ratio was 4.7, but when only 10% of seedlings were selected, this value fell to 2.3. Selection ratios between the seedling stage and the third clonal year were generally lower than between seedlings and the second clonal year (Table 3.21b), although the general trends were the same. If

Table 3.20a Observed (Obs.) and expected (Exp.) number of clones which would have been selected (+) and rejected (-) in the glasshouse (GH), first (FCY), second (SCY) and third (TCY) clonal years according to overall breeders' preference scores on 200 clones.

GH	FCY	SCY	TCY	Obs.	Exp.
+	+	+	+	15	1.53
+	+	+	-	1	2.56
+	+	-	+	8	4.73
+	-	+	+	6	4.25
-	+	+	+	8	3.34
+	+	-	-	9	7.88
+	-	+	-	3	7.09
+	-	-	+	4	13.11
-	+	+	-	3	5.56
-	+	-	+	2	10.28
-	-	+	+	10	9.25
+	-	-	-	17	21.85
-	+	-	-	7	17.13
-	-	+	-	3	15.42
-	-	-	+	22	28.51
-	-	-	-	82	47.52

χ^2_8, by pooling rows 1-4; 5-6; 7-8; 9-10 and 11-12 = 41.49 ($p<0.001$)

Table 3.20b Observed number of clones which were selected (+) and rejected (-) in the glasshouse (GH) first (FCY) and second (SCY) clonal year from amongst only those clones that were selected in the second clonal year according to overall breeders' preference.

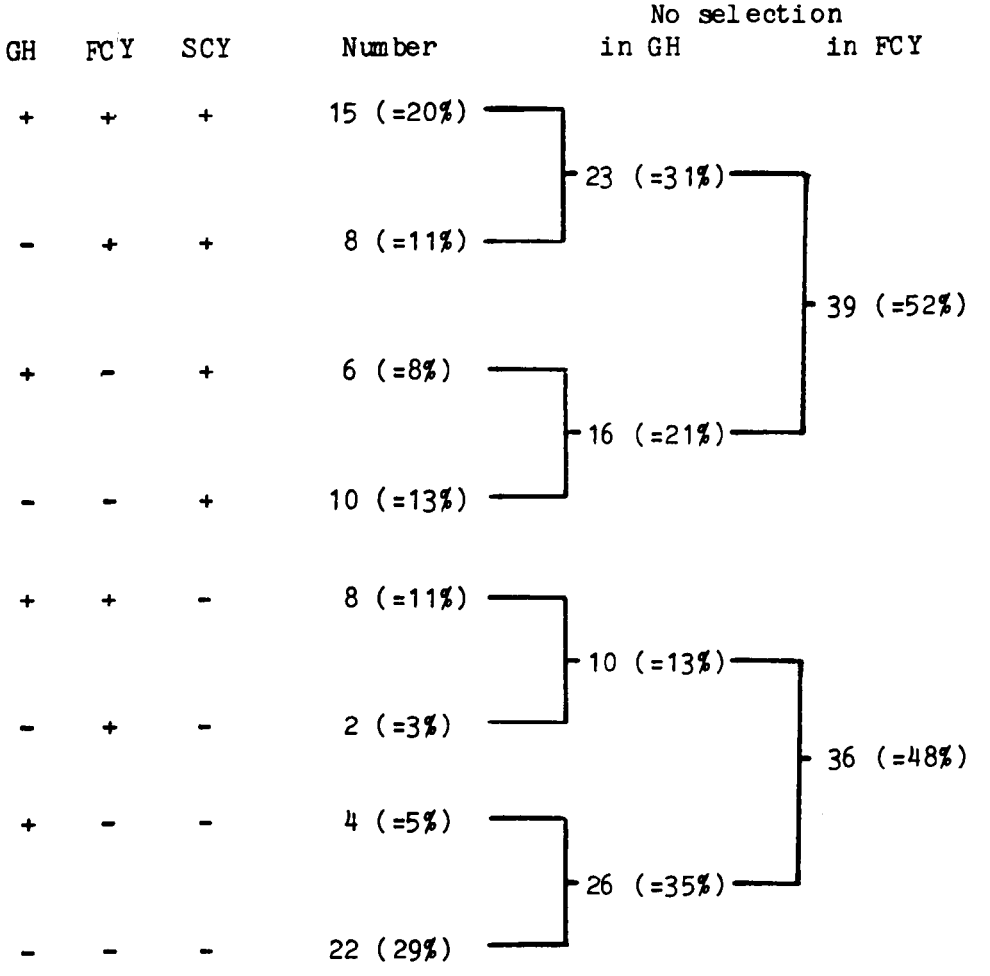


Table 3.21 Selection ratios for overall breeders' preference with varying selection intensities between a) the glasshouse (GH) and the second clonal year (SCY), based on 560 clones and b) between the glasshouse (GH) and the third clonal year (TCY), based on 200 clones.

a) GH v SCY

1%	-	-	-	-	-	-	9.4	5.1	9.0
4%	-	4.5	1.6	2.2	2.8	4.5	3.9	3.4	2.3
10%	5.8	3.2	1.8	2.0	2.1	2.2	2.1	2.1	1.9
25%	14.1	4.6	2.6	2.3	2.1	2.3	2.1	2.3	2.4
42%	4.0	2.3	2.0	2.0	1.7	1.7	1.6	1.7	1.7
64%	2.0	1.5	1.4	1.4	1.4	1.4	1.3	1.4	1.5
83%	1.4	1.3	1.3	1.2	1.2	1.2	1.2	1.2	1.2
93%	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1
	91%	81%	71%	58%	46%	34%	24%	16%	10%

Glasshouse

b) GH v TCY

4%	-	1.4	2.4	3.8	6.0	2.2	2.2	3.4	0.8
7%	-	2.8	2.2	3.5	3.4	1.5	1.1	1.3	0.4
16%	3.3	3.1	1.9	2.4	3.2	2.0	1.8	1.7	1.4
28%	5.8	2.6	1.8	2.2	2.3	2.1	1.8	1.8	1.9
40%	4.1	2.1	1.8	1.7	1.9	1.7	1.6	1.5	1.4
53%	1.9	1.5	1.6	1.5	1.5	1.5	1.5	1.5	1.7
66%	1.6	1.4	1.4	1.3	1.4	1.4	1.4	1.4	1.5
77%	2.5	1.4	1.3	1.1	1.2	1.2	1.2	1.2	1.2
89%	1.4	1.3	1.2	1.1	1.1	1.1	1.1	1.1	1.1
	91%	84%	74%	65%	54%	43%	31%	22%	14%

Glasshouse

approximatly 25% of clones are selected in the third clonal year (underlined in Table 3.21), the reduction in efficiency with increasing intensity of selection can be seen (i.e. largest selection ratios being obtained when a high proportion of glasshouse seedlings are retained).

Selection ratios between the first and second clonal years were on average twice as large as those between seedlings and first clonal generations (Table 3.22a). A clone selected in the first clonal year was over 4 times more likely to be selected in the second clonal year than one discarded in the first clonal year. The selection ratios between the first and third clonal years were, however, on average only 2.40 (Table 3.22b). If selection was carried out at approximately the 25% level there was (as in Table 3.21) again a reduction in selection efficiency associated with increased selection intensities at the first clonal year stage. However, selection in the first clonal year did appear to be marginally more effective than selection at the seedling stage.

The highest selection ratios were found between the second and third clonal years (Table 3.23). On average a selection ratio of 6.26 was obtained between the second and third clonal years. As with previous selection ratios increased intensity in the second clonal year resulted in reduced ratios while increased intensity in the third generation increased the ratios. If 28% of the third clonal year plots were selected, selection ratios of 19.3, 13.1, 5.1 and 3.7 were obtained when 74%, 50%, 31% and 15% respectively were selected in the second generation.

3.3.2 Yield and yield components.

Mean squares from the analyses of variance of total tuber weight, mean tuber weight and number of tubers per plant on 200 genotypes

Table 3.22 Selection ratios for overall breeders' preference with varying selection intensities between a) the first clonal year (FCY) and the second clonal year (SCY), based on 560 clones and b) between the first clonal year (FCY) and the third clonal year (TCY), based on 200 clones.

a) FCY v SCY

1%	-	-	-	-	8.4	-	6.6	-	-
4%	-	3.4	9.0	6.9	6.5	2.1	10.6	6.9	14.7
10%	-	5.0	13.2	7.6	6.8	4.1	5.2	4.6	5.0
25%	-	8.3	8.0	5.3	4.0	3.1	3.1	3.0	2.0
42%	-	5.2	4.0	3.0	2.6	2.5	2.4	2.3	2.4
64%	16.7	3.9	2.3	2.0	1.8	1.7	1.6	1.6	1.6
83%	5.6	2.5	1.6	1.4	1.3	1.3	1.2	1.2	1.2
94%	2.2	1.5	1.2	1.1	1.1	1.1	1.1	1.1	1.1
	95%	85%	68%	45%	26%	14%	5%	3%	1%

First clonal year

b) FCY v TCY

4%	-	-	2.7	2.4	2.3	1.5	5.7	4.6	-
7%	-	-	5.3	5.3	3.4	2.2	2.7	2.3	-
17%	-	-	5.9	5.9	3.1	2.2	3.1	3.2	-
28%	-	6.8	4.9	4.3	2.5	2.3	2.9	2.5	1.8
40%	2.4	3.5	3.1	3.1	1.9	1.9	2.5	2.2	2.6
54%	2.7	2.5	2.0	1.8	1.7	1.7	1.8	1.6	1.9
66%	1.6	2.2	2.0	1.6	1.4	1.4	1.4	1.3	1.6
77%	1.9	1.5	1.5	1.3	1.2	1.3	1.2	1.1	1.3
89%	1.5	1.4	1.3	1.2	1.2	1.2	1.1	1.1	1.1
	98%	89%	72%	55%	31%	19%	6%	3%	1%

First clonal year

Table 3.23 Selection ratios for overall breeders' preference with varying selection intensities between the second clonal year (SCY) and the third clonal year (TCY), based on 200 clones.

4%	-	-	-	-	15.6	9.4	24.0	33.0	28.4
8%	-	-	-	-	14.5	15.6	8.8	15.3	14.3
16%	-	-	11.2	15.5	8.3	5.3	6.4	6.4	6.2
28%	-	-	19.3	13.1	5.1	3.7	3.5	3.7	3.7
40%	-	-	13.7	8.0	3.4	2.6	2.8	2.6	2.6
53%	-	-	6.0	3.9	2.2	2.0	2.0	1.9	1.9
66%	-	8.8	2.7	2.4	1.7	1.6	1.6	1.5	1.5
77%	-	4.1	2.0	1.6	1.4	1.2	1.2	1.3	1.3
89%	2.9	2.4	1.5	1.3	1.2	1.1	1.1	1.1	1.1
	97%	88%	74%	50%	31%	15%	4%	1%	0.5%

Second clonal year

grown in four consecutive years are shown in Table 3.24. The error term is the pooled sites x clones within progenies terms from the individual analyses of each clonal generation (Table 3.8). There were significant differences between years and progenies for total tuber weight and yield components. Clones within progenies were significant for total tuber weight and mean tuber weight but not for number of tubers. The years x progeny interaction was significant for all variates while the interaction years x clones within progenies was non-significant.

The efficiency of selection for yield and yield components was examined by correlation of data recorded in different seasons (Table 3.25). In general, the largest correlation coefficients were obtained for total tuber weight and the lowest for number of tubers. The highest correlations were always between the second and third clonal years. Correlation coefficients between seedling total tuber weight and total weight in the three clonal generations showed a similar pattern to that found for breeders' preference, with a reduction in coefficient with increased years from true botanical seed. Similar results were also found for mean tuber weight although this trend was not observed for tuber number.

From correlation analyses between years, it appears that selection for total tuber weight would be more effective than selection for either of the yield components. Therefore, the efficiency of selection for total tuber weight will be further examined. The 560 clones grown in the glasshouse, first and second clonal years were divided into eight categories according to whether each clone was selected (top 20%) or rejected (bottom 80%) in each season (Table 3.26a). Also shown are the expected number of clones, based on 20% selected in each year and complete independence between seasons. The number of clones selected in all years (19) and rejected

Table 3.24 Mean squares from the analyses of variance of total tuber weight (TTW), mean tuber weight (MTW) and number of tubers per plant (TNU) recorded on 200 clones (from eight progenies) in four consecutive years.

Source	df	TTW	MTW	TNU
Years (Y)	3	1018.3 '''	6.05 '''	1558.9 '''
Progenies (P)	7	94.1 '''	1.77 '''	117.9 '''
Clones w. Prog (C)	192	13.5 ''	0.26 ''	16.1 ns
Y x P	21	26.3 ''	0.46 '''	29.5 ''
Y x C w. P	576	5.3 ns	0.09 ns	6.2 ns
Error	1296	10.1	0.19	13.1

The error term is the pooled sites x clones within progenies terms from the analysis of individual years (Table 3.8).

ns = not significant; ' = 0.05>p>0.01; '' = 0.01>p>0.001; ''' = p<0.001.

Table 3.25 Coefficients obtained by correlating total tuber weight (TTW), mean tuber weight (MTW) and number of tubers per plant (TNU) recorded in four years, the glasshouse (GH), first (FCY), second (SCY) and third (TCY) clonal years. a) correlations based on 560 clones, b) correlations based on 200 clones.

a) 560 clones

	GHvFCY	GHvSCY	GHvTCY	FCYvSCY	FCYvTCY	SCYvTCY
TWT	0.51'''	0.26'''	-	0.54'''	-	-
MTW	0.28'''	0.24'''	-	0.46'''	-	-
TNU	0.20'''	0.13'	-	0.10'	-	-

b) 200 clones

	GHvFCY	GHvSCY	GHvTCY	FCYvSCY	FCYvTCY	SCYvTCY
TWT	0.48'''	0.24''	0.20''	0.24''	0.49'''	0.52'''
MTW	0.38'''	0.21''	0.19''	0.48'''	0.40'''	0.60'''
TNU	0.25'''	0.17'	0.31'''	-0.04ns	0.33'''	0.32'''

ns = not significantly; ' = 0.05>p>0.001; '' 0.01>p>0.001; ''' = p<0.001.

Table 3.26a Observed (Obs.) and expected (Exp.) number of clones which were selected (+) and rejected (-) according to total tuber weights recorded in the glasshouse (GH), first clonal year (FCY) and second clonal year (SCY). The selected clones were those in the top 20% ranking in each year.

GH	FCY	SCY	Obs.	Exp.
+	+	+	19	4.4
+	+	-	28	17.9
+	-	+	16	17.9
-	+	+	25	17.9
+	-	-	49	71.6
-	+	-	39	71.6
-	-	+	52	71.6
-	-	-	332	287.4

χ^2_6 (pool first two rows) = 39.5 ($p<0.001$)

Table 3.26b Observed number of clones which were selected (+) and rejected (-) according to total tuber weight in the glasshouse (GH) and first clonal year (FCY) given that all clones (112 genotypes) were selected (top 20%) in the second clonal year.

GH	FCY	
+	+	19 (=17%)
+	-	16 (=14%)
-	+	25 (=22%)
-	-	52 (=46%)

41 (=37%)

93 (83%)

in all years (332) were greater than expected if there had been no association between years. There was, however, a large number of clones which would have been selected in one year and discarded in one, or both, of the others. If the second clonal year assessment is taken to be the most accurate then 112 clones would be considered to have relatively high tuber yields. From amongst these 112 clones (Table 3.26b), only 17% would have been selected as producing high yield in the glasshouse and first clonal year. A further 37% would have been discarded in one of the previous generations while almost half (46%) would have been in the lower yielding 80% in both previous years.

When total tuber weight in the third generation is included a similar result is obtained (Table 3.27a). Under normal selection practice only two clones would have survived selection in all four years, although this is a considerably higher number (0.02) than would have been expected if selection was on a random basis. If it is now assumed that the third clonal year provides the best estimate of yielding ability, then 20 clones should have potential for high yield (in relation to the others). From these, 18 clones (90%) would have been discarded as producing a low yield in at least one of the previous years (Table 3.27b) and 35% would never have been selected in any of the previous seasons. Selection in the early generations for yielding ability will therefore result in the loss of potentially high yielding clones.

The efficiency of selection for yielding ability was also examined by studying selection ratios. Selection ratios from seedlings (Table 3.28a and 3.28b), first clonal year (Table 3.29a and 3.29b) and second clonal year (Table 3.30) all showed similar results to that found when breeders' preference was examined. In all cases, increased selection intensity was associated with a reduction in

Table 3.27a Observed (Obs.) and expected (Exp.) number of clones (based on 200 clones) which were selected (+) and rejected (-) according to total tuber weight, recorded in the glasshouse (GH) and the first (FCY), second (SCY) and third (TCY) clonal years. Selected clones were those ranking in the top 20% in each year.

GH	FCY	SCY	TCY	Obs	Exp.
+	+	+	+	2	0.02
+	+	+	-	1	0.16
+	+	-	+	0	0.15
+	-	+	+	0	0.16
-	+	+	+	4	0.16
+	+	-	-	4	1.47
+	-	+	-	1	1.56
+	-	-	+	1	1.47
-	+	+	-	1	1.56
-	+	-	+	1	1.47
-	-	+	+	5	1.56
+	-	-	-	10	14.01
-	+	-	-	6	14.01
-	-	+	-	6	14.82
-	-	-	+	6	14.01
-	-	-	-	152	133.42

χ^2_5 (pooling first 11 rows) = 58.5 ($p<0.001$)

Table 3.27b Observed number of clones which were selected (+) and rejected (-) according to total tuber weight recorded in the glasshouse (GH), the first (FCY) and second (SCY) clonal years. Only the highest yielding clones (top 10% = 20 clones) from the third clonal year are included.

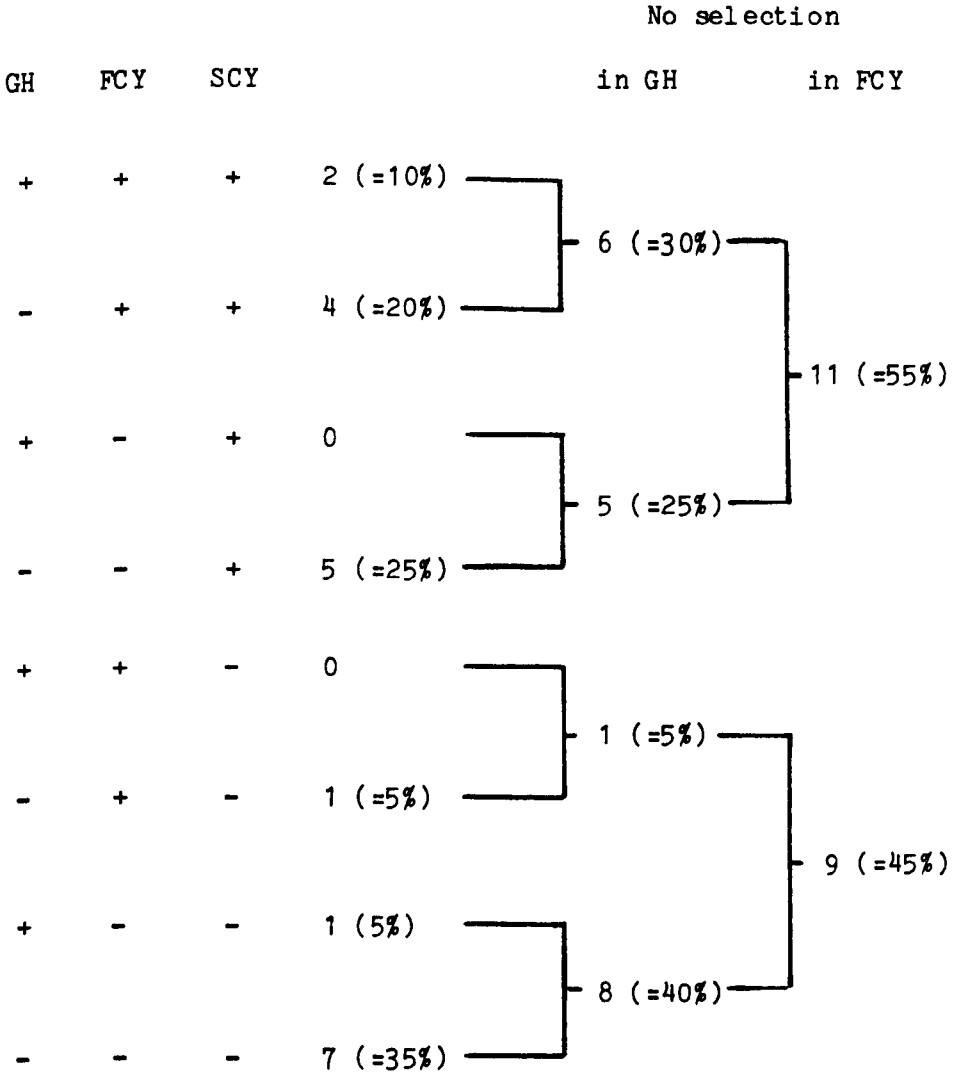


Table 3.28 Selection ratios for different selection intensities of total tuber weights recorded between a) the glasshouse (GH) and the second clonal year (SCY), based on 560 clones and b) the glasshouse and the third clonal year (TCY), based on 200 clones.

a) GH v SCY (560 clones).

10%	6.0	2.5	2.2	1.8	1.5	1.7	1.5	1.6	1.3
20%	3.0	3.2	2.4	1.8	1.6	1.8	1.8	1.9	1.3
30%	2.9	2.7	2.0	1.6	1.5	1.5	1.5	1.7	1.5
40%	2.6	2.2	1.7	1.4	1.5	1.5	1.5	1.6	1.4
50%	2.1	1.9	1.7	1.5	1.6	1.6	1.5	1.5	1.4
60%	1.6	1.5	1.4	1.3	1.3	1.4	1.3	1.3	1.3
70%	1.5	1.4	1.3	1.2	1.2	1.3	1.2	1.2	1.2
80%	1.5	1.3	1.2	1.1	1.2	1.2	1.2	1.2	1.2
90%	1.2	1.2	1.1	1.1	1.1	1.1	1.1	1.1	1.1
	90%	80%	70%	60%	50%	40%	30%	20%	10%

Glasshouse seedlings

b) GH v TCY (200 clones).

10%	2.1	2.3	1.9	1.6	1.6	1.6	1.7	1.2	2.0
20%	4.2	2.2	1.8	2.0	2.0	2.1	1.8	1.8	2.1
30%	2.0	1.6	1.5	1.6	1.5	1.6	1.6	1.6	1.9
40%	1.6	1.3	1.3	1.3	1.3	1.5	1.5	1.4	1.6
50%	1.4	1.4	1.3	1.2	1.2	1.3	1.2	1.1	1.4
60%	1.2	1.3	1.3	1.2	1.1	1.1	1.2	1.1	1.3
70%	1.4	1.4	1.3	1.3	1.2	1.2	1.3	1.2	1.2
80%	1.2	1.2	1.2	1.1	1.1	1.1	1.1	1.0	1.1
90%	1.1	1.1	1.1	1.1	1.1	1.1	1.0	1.0	1.0
	90%	80%	70%	60%	50%	40%	30%	20%	10%

Glasshouse seedlings

Table 3.29 Selection ratios for different selection intensities of total tuber weights recorded between a) the first clonal year (FCY) and the second clonal year (SCY), based on 560 clones and b) the first clonal year (FCY) and the third clonal year (TCY), based on 200 clones.

a) FCY v SCY (560 clones)

10%	-	6.7	7.5	5.5	3.0	2.9	3.1	4.0	4.2
20%	-	4.4	4.9	4.3	3.3	2.7	2.6	2.6	2.8
30%	18.0	4.9	3.5	3.6	2.9	2.4	2.4	2.6	2.6
40%	12.1	4.4	3.4	3.1	2.5	2.1	2.0	2.1	2.1
50%	15.1	4.3	3.2	2.8	2.3	1.9	1.9	2.0	2.0
60%	9.1	3.2	2.6	2.2	1.9	1.6	1.6	1.7	1.7
70%	7.0	2.5	2.2	1.8	1.6	1.5	1.4	1.4	1.4
80%	3.9	2.2	1.7	1.5	1.4	1.3	1.2	1.3	1.3
90%	2.4	1.6	1.3	1.2	1.2	1.2	1.1	1.1	1.0
	90%	80%	70%	60%	50%	40%	30%	20%	10%

First clonal year

b) FCY v TCY (200 clones).

10%	-	-	8.4	1.3	1.3	1.3	2.1	2.9	4.2
20%	-	4.7	5.3	1.8	1.9	1.7	2.4	3.0	2.7
30%	-	2.7	3.8	2.2	2.3	2.1	2.7	2.9	2.6
40%	8.4	3.0	3.3	2.5	2.3	2.3	2.6	2.7	2.3
50%	5.2	3.3	2.8	2.2	2.2	2.1	2.3	2.3	2.1
60%	2.6	2.8	2.8	2.4	2.0	1.8	2.0	2.0	1.8
70%	2.0	1.9	1.9	1.9	1.7	1.6	1.6	1.6	1.5
80%	2.0	1.9	1.6	1.5	1.4	1.4	1.4	1.3	1.2
90%	1.5	1.4	1.2	1.2	1.1	1.2	1.1	1.0	1.0
	90%	80%	70%	60%	50%	40%	30%	20%	10%

First clonal year

Table 3.30 Selection ratios for different selection intensities of total tuber weights recorded between the second clonal year (SCY) and the third clonal year (TCY), based on 200 clones.

10%	-	-	8.6	13.1	19.6	4.7	3.7	2.4	2.7
20%	-	-	17.1	26.1	19.3	5.2	4.0	3.7	3.5
30%	-	15.0	8.4	9.4	7.6	4.5	3.8	3.3	3.1
40%	-	4.9	5.4	4.2	3.7	3.3	2.6	2.3	2.1
50%	-	4.0	3.6	2.7	2.3	2.3	2.1	1.9	1.8
60%	13.3	2.5	2.7	2.3	1.9	1.9	1.8	1.7	1.7
70%	3.8	2.1	2.1	1.9	1.7	1.6	1.5	1.5	1.4
80%	2.8	1.6	1.7	1.7	1.5	1.4	1.3	1.3	1.3
90%	2.1	1.4	1.4	1.3	1.2	1.2	1.2	1.1	1.1
	90%	80%	70%	60%	50%	40%	30%	20%	10%

Second clonal year

selection ratio. Selection ratios from seedlings and the first clonal year were so low in magnitude to question the resource that selection would involve. Selection at moderate intensity would, however, be possible in the second clonal year. The highest ratio was obtained by selecting at the 60% level in the second clonal year and selecting the top 20% in the third year.

3.3.3 Other tuber characters.

Mean squares from the analyses of variance of progenies and clones over four years showed significant differences between the eight crosses for uniformity of tuber shape, distribution of tuber size, absence from growth cracks and tuber dormancy (Table 3.31). The error term used for the interactions was the pooled sites x clones within progenies terms from the analysis of individual clonal years (Table 3.11). Main effects were tested against the appropriate interaction term. There were significant differences between years for shape, distribution and dormancy. Clones within progenies were significantly different for shape, growth cracks and dormancy but not for distribution of size. The interaction of tuber shape between years and progenies was significant although all other interactions were non-significant.

Efficiency of selection for tuber characters was examined by correlating the assessments between different years (Table 3.32). Coefficients based on 560 observations (Table 3.32a) were significantly greater than zero between seedling and first clonal year assessments for shape, stolon persistence and eye depth. The correlations for all variates were significant between the seedlings and second clonal year. Over all the tuber characters, larger coefficients were obtained by correlation between the first and second clonal years. When the 200 clones which were also grown in the third

Table 3.31 Mean squares from the analysis of variance of uniformity of tuber shape (Shape), distribution of tuber size (Dist), absence from growth cracks (Grow) and tuber dormancy (Dorm) assessed on 200 clones grown in three consecutive years.

Source	df	Shape	Dist	Grow	Dorm
Years (Y)	3	31.14'''	47.72'''	0.640	19.96'''
Progenies (P)	7	29.46'''	14.41'''	14.886'''	52.30'''
Clones W Prog (C)	192	3.75''	2.57ns	2.080''	8.17'''
Y x P	21	4.69'''	2.51ns	0.368ns	0.75ns
Y x C W P	576	1.19ns	1.50ns	0.398ns	0.14ns
Error	1296	1.26	2.40	1.060	2.84

Error term is the pooled sites x clones within progenies terms from the analysis of variance of each individual season (see Table 3.11).

ns = not significant; ' = $0.05>p>0.01$; '' = $0.01>p>0.001$; ''' = $p<0.001$.

Table 3.32 Coefficients obtained by correlating uniformity of tuber shape (Shape), stolon persistence (Stolon), absence from growth cracks (Grow), tuber dormancy (Dorm), distribution of tuber size (Dist) and depth of eyes (Eyes) assessments in different seasons (the glasshouse (GH), the first (FCY), second (SCY) and third (TCY) clonal year).

a) 560 clones.

Variate	GHvFCY	GHvSCY	GHvTCY	FCYvSCY	FCYvTCY	SCYvTCY
Shape	0.27'''	0.30'''	-	0.59'''	-	-
Stolon	0.15''	0.27'''	-	0.59'''	-	-
Grow	0.09ns	0.32'''	-	0.68'''	-	-
Dorm	0.06ns	0.25'''	-	0.41'''	-	-
Dist	0.04ns	0.15''	-	0.31'''	-	-
Eyes	0.41'''	0.46'''	-	0.69'''	-	-

b) 200 clones.

Variate	GHvFCY	GHvSCY	GHvTCY	FCYvSCY	FCYvTCY	SCYvTCY
Shape	0.31'''	0.22''	0.28'''	0.59'''	0.44'''	0.65'''
Stolon	0.12'	0.18'	-	0.24''	-	-
Grow	0.04ns	0.09ns	0.11'	0.13'	0.26'''	0.41'''
Dorm	0.23''	0.20''	0.19'	0.23''	0.36'''	0.83'''
Dist	0.11'	0.16'	0.05ns	0.36'''	0.20''	0.34'''
Eyes	0.39'''	0.19''	-	0.49'''	-	-

ns = not significant; ' = $0.05>p>0.01$; '' = $0.01>p>0.001$; ''' = $p<0.001$.

clonal year were considered (Table 3.32b), large coefficients were obtained for tuber shape, and relatively large coefficients obtained for tuber dormancy. Correlation between seedlings and the three clonal years were low for distribution of size and absence from growth cracks. Overall there was a trend of increasing coefficient with increasing years. For example correlations between seedlings and first clonal year tended to be smaller than between seedlings and second clonal year which in turn were smaller than between seedlings and third clonal year. Correlation coefficients between the glasshouse and field years, although often statistically significant, were mostly too low to merit selection at the seedling stage. The correlation for tuber shape between the first and second clonal years was larger than for the other characters and may merit selection for regularity of shape at this stage. There did, however, appear to be a good relationship between the second and third clonal years for regularity of tuber shape and tuber dormancy.

3.4 Conclusions.

In each of the environments examined, the four breeders selected (preference score equal to or greater than 5) different proportions of clones. Despite this variation, the breeders were in good agreement about which clones were most desirable in each trial. The agreement, as measured by correlation coefficients between pairs of breeders, increased with increasing clonal generations from true potato seed. This is most likely to be the result of greater plot sizes used in the later generations. This result was in agreement with Brown (1985) where four breeders were in better agreement in the first clonal year than when scoring seedlings. Greater discrepancies between breeders in the glasshouse and earliest clonal generations must therefore add to the inefficiency of selection.

When assessing breeders' preference, the four breeders were all greatly influenced by the total tuber weight of each plot and also by uniformity of tuber shape. The variates mean tuber weight and number of tubers influenced scores, but to a lesser extent. In the second and third clonal year, where plots rather than single plants were assessed, the breeders scores were related also to the frequency of growth cracking.

The correlations between BB and MURR were significant for each breeder in each year. The correlation between BB and MURR for overall preference (the average preference score from the four breeders) gave higher coefficients than for any of the individual breeders. This would suggest that greater accuracy of assessment would be achieved by having breeding material scored by more than one breeder.

The correlations between BB and MURR were significantly greater than zero for total tuber weight and the two yield components as well as for uniformity of tuber shape, tuber dormancy and depth of eyes. Distribution of tuber size was found to be the least repeatable character between the two sites while stolon persistence was only found to be correlated in the second and third years.

Despite the formal levels of significance obtained for yield, preference and the tuber characters, there was always a large proportion of the total sum of squares that would not have been accounted for by regression of one site's assessments on to the other. Also, a high proportion of clones that would have been selected with high total tuber weights or preference scores at one of the two sites would have been discarded for the same character at the other. From this study it is not possible to determine whether the assessments carried out at BB are more meaningful in commercial terms than those from MURR (or vice versa), however it does show that a great deal of genotype x site interactions exist.

From the analysis of variance over years, the interactions of clones within progenies x years were significant for most of the variates examined. The correlation coefficients between the seedling and clonal generations were significantly greater than zero for overall preference, total tuber weight and mean tuber weight. The correlations between years for tuber number were lower, although these were also generally significant. In addition, with only a few exceptions, there appeared to be a reasonbable agreement between the assessment of tubers characters in different clonal years. The correlation coefficients for overall preference, total tuber weight and mean tuber weight between different years all showed a trend of having the largest coefficient with the next succeeding generation and a reduction in coefficients with increasing generations. For example the correlation between seedlings and the first clonal year was greater than between seedlings and the second clonal year which in turn was greater than between seedlings and the third clonal year. This is perhaps a reversal of what would have been expected as increasing generations had larger plot sizes. This result does, however, suggest a "carry over" effect between years as a result of planting seed tubers which had themselves been assessed the previous year. It is also interesting that the tuber number and the other tuber characters did not follow the pattern of decreased coefficients with increasing years. These variates did in fact show the expected relationship. Brown (1985) found that breeders' preference, total tuber weight and mean tuber weight recorded in the first clonal year were all highly correlated with the weight of seed tuber planted. It is also interesting to note that he found the relationship between seed tuber weight and the other tuber characters to be much lower. A more detailed examination of the effect of seed tuber weight is presented in section 4.2.

Although the correlations between different generations were significant, a more detailed examination of overall preference and total tuber weight showed that a high proportion of potentially desirable clones would be discarded if selection was carried out at either the seedling or first clonal year generations. If selection, by breeders' preference, had been carried out in the glasshouse and the first clonal year then from the 115 clones considered worthy of selection in the second clonal year, only 27% would have been retained to that stage. Had selection been carried out only in the first clonal year then still only 56% would have been retained. A similar result was obtained when selection for total tuber weight was examined. Thus selection in the first two years would seem to carry a high cost in terms of losing clones which have, in fact, commercial potential.

Examination of selection ratios between different year's assessments of breeders' preference and total tuber weight showed an increase in selection ratio with increasing proportions of clones being retained from the seedling and first clonal years. In order to obtain a worthwhile selection ratio between the seedling year or the first clonal year with either the second or third clonal years, the proportion of clones which need to be retained in the first two years is so high as to question the resources that such selection would require. The ratios between the second and third clonal years, however, suggested that a reasonable level of selection could be performed at this stage in a breeding scheme.

The effects of selection can be compared directly in the fourth clonal year. Eighteen clones from the A1 cross that had been selected for three years in the normal breeding scheme at SCRI were grown alongside 18 random clones from the same cross. Mean squares from the analysis of breeders' preference, total yield, uniformity of shape,

growth cracks, tuber dormancy and foliage maturity are shown in Table 3.33. In the analyses the effects ascribed to clones were partitioned, using orthogonal contrasts, into the difference between the selected and random clones, the difference within random clones and the difference within selected clones. The selected clones had on average higher preference scores ($p<0.001$), higher yield ($p<0.001$), better shapes ($p<0.001$) with larger tubers ($p<0.05$). The two groups were not different for absence from growth cracks, tuber dormancy or foliage maturity. It would therefore appear that selection in the first three years was having the desired effect but where this effect could be traced is uncertain and it should also be remembered that the "selected" clones originated from an original population of 1000 seedlings.

Although the selected clones were on average superior to the random sample, there was greater variation within the randoms than was found within the selected group for all characters recorded, with the exception of tuber size. Breeders are in general not interested in increasing the average values of a group of genotypes but are rather searching for the one, or perhaps two, genotypes which are superior. The highest 6 ranks and lowest 6 ranks from amongst the 36 clones in this trial are shown in Table 3.34. Each variate and rank position is assigned as either R, a random clone, S, a selected clone or R/S, a random and selected clone tying. From this it can be seen that only a third of the top six clones were from the random group and only one from the top six from the random group for overall preference and uniformity of shape respectively. However, for total yield, tuber size, absence from growth cracks and foliage maturity, it was equally likely that a random clone or selected clone would be in the top six positions. Also, there was a suggestion that selection had been counter productive for tuber dormancy, where the top six were predominantly randoms. A different result was found when the bottom

Table 3.33 Mean squares from the analysis of variance of 18 random selections alongside 18 selected clones from the potato breeding scheme at SCRI from the cross Pentland Crown x Desiree (A1). In the analysis the effect of clones is partitioned into the difference between random and selected clones, variation within the random group and variation within the selected group.

Source	df	Pref	Shape	Size	Grow	Sprout	Matu	Yield
Blocks	1	1.51	0.80	5.51	7.20	1.51	0.11	26.22'''
Clones								
Random v Select	1	39.20'''	22.05'''	7.81''	6.05	0.11	2.11	34.12'''
within Random	17	4.27'''	3.37'	4.31'''	7.10'''	12.38'''	4.71'''	9.22'''
within Select	17	2.64'	3.29'	5.11'''	2.35	5.01'	2.22''	2.99
Replicate Error	35	1.14	1.64	0.98	2.02	1.96	0.75	1.59
Mean of randoms		4.09	4.02	6.01	8.05	7.20	4.52	10.10
Mean of selects		5.49	5.07	6.64	8.60	7.27	4.85	11.41

' = 0.05>p>0.01; '' = 0.01>p>0.001; ''' = p<0.001.

Table 3.34 Top and bottom six rankings of total yield, breeders' preference uniformity of tuber shape, tuber size, dormancy, absence from growth cracks, and foliage maturity of 18 selected clones (S) and 18 random clones (R).

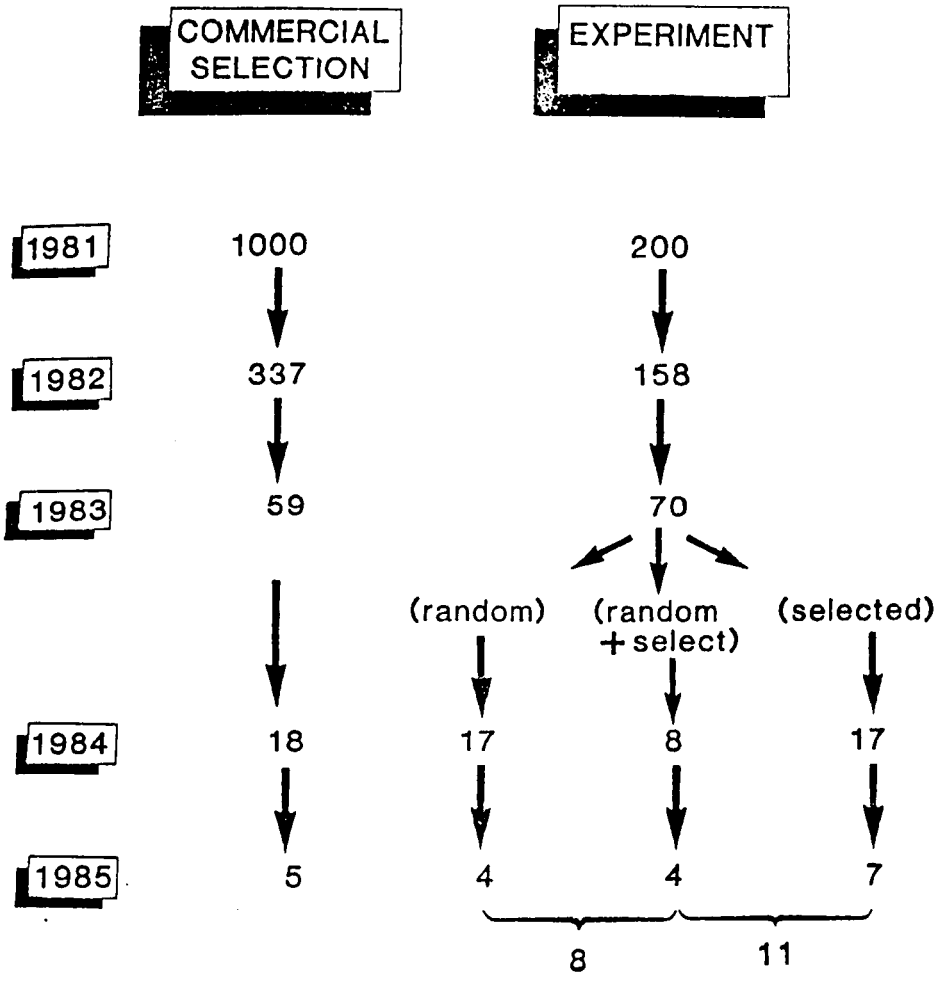
Rank	TWT	Pref	Shape	Size	Dorm	Grow	Matu
1	R	S	S	R	R/S	R/S	R
2	S	S	S	R	-	-	S
3	S	S	R	S	R/S	R/S	R/S
4	R	R	S	S	-	-	-
5	R	S	S	R	R/S	R/S	R/S
6	S	R	S	S	-	-	-
31	R	R	R	R	R	R	S/R
32	R	S	R	R	S	R	-
33	R	R	R	R	S	R/S	R/S
34	R	R	R	R	R	-	-
35	R	R	R	R	R	S	R/S
36	R	R	R	S	R	S	-

six ranks were examined. For total yield, preference, shape and size the poorest clones were always from the random group. However, there was little difference between the groups for the remaining variates.

Overall therefore, it would appear that selection in the first three years of a potato breeding programme is producing a result in the required direction. There was not, however, a great difference between the random and selected group, especially when it is considered that this selected group should be around the best 2% of the initial clones from this cross. Also, it was possible to identify a fairly large proportion of clones with high expression of each variate within the random group. It should also be borne in mind that if the random group is a representative sample, it should by definition contain clones which equal the best in the selected group, thus the observed differences may merely be one of frequency. If a breeder did not select in these generations he would certainly begin with a greater sample than 18 clones, which, under the circumstances, he could afford to do.

The potential loss of material due to selection carried out at the seedling and early clonal generations can also be examined directly. At the same time as this experiment was set up, seeds from each of the eight crosses were sown in the SCRI 'Commercial Potato Breeding Programme'. The number of clones from one of these crosses (A1, the cross also examined above) as it passes through clonal generations is shown in Figure 3.1 for the commercial scheme and also the experiment. In the normal breeding scheme, where selection was carried out annually, 18 clones survived (these are the same 18 clones examined above) to the third clonal year and this reduced to five based on selection in that third clonal year. The experiment started with 200 seedlings but these were reduced at random to 70 by the second clonal year. On the basis of the second clonal year results,

Figure 3.1 Comparison of clones from the cross Pentland Crown x Desiree (A1) passing through the commercial potato breeding programme at SCRI and in the experiment where they were reduced in number at random.



25 clones were selected at random and 25 were selected as having commercial merit, of which eight were common to the two groups. These were grown in the third clonal year, alongside those from the breeding scheme. Of the 25 selected clones 11 were again re-selected while from out of the 'random group' eight were selected. Therefore, if the breeding scheme had started with 70 clones, which were all retained with no selection until the second clonal year, 11 would have survived the next two rounds of selection, ie. 1 in 6.4. However, in the commercial scheme starting with 1000 seedlings and carrying out annual selection, only five clones have survived, ie. 1 in 200. If it is assumed that the reduction from 1000 to 59 in the second clonal year is merely reducing the numbers at random (ie. equivalent to the experiment where they were deliberately reduced at random) then from these 59 clones, five were selected, ie. 1 in 11.8, a ratio which is somewhat worse than from the experiment. With such small numbers it is unwise to place too large an emphasis upon the apparent decrease but clearly there is no evidence of any positive effect due to selection in these two early generations when compared in a practical breeding scheme. Within the experiment, however, there was a suggestion that selection in the second clonal year, if clones are grown at two locations and replicated at both, would produce a better than random effect.

The seven other progenies from the 'A' material were also sown and assessed in the commercial scheme in parallel to those used in the experiment. However, no clones survived commercial selection to be examined in the fourth clonal year. From this experiment on the other hand, 45 clones were considered good enough to be trialled at this stage. These 45 clones, along with the 19 selected from cross A1 (64 clones in total) were grown in the fourth and fifth clonal year trials of the commercial breeding programme in the same trials as survivors from the commercial scheme. In the sixth clonal year trial of the

commercial scheme in 1987, the stage where clones are trialled at a number of locations throughout the UK and the Mediterranean, nine of these 64 clones had survived. From the many thousands (approximately 100,000 seedlings) that were grown and screened in the commercial scheme only 30 showed a similar degree of desirability. These nine clones from the experiment are shown in Table 3.35, along with whether each was selected (+) or rejected (-) as seedlings and at BB and MURR in the first, second and third clonal years. It can be seen that none of these clones would have been selected on normal breeding criteria in all environments. Five of them would have been discarded as seedlings, five would have been discarded at BB and three at MURR in the first clonal year. In the second clonal year, only one was discarded at BB, but four discarded at MURR, while in the third clonal year three would have been discarded at BB and one discarded at MURR.

These results demonstrate very clearly that, at best, selection on seedlings and in the first clonal year is random, but there is perhaps an indication of a negative effect. Some of the factors which could be responsible for the inefficiency of selection in the early generations are examined in the following chapter.

Table 3.35 Clones from the 'A' experiment which have survived three rounds of selection in the normal breeding programme of the potato breeding programme at SCRI along with their performance (either +, overall preference greater than, or equal to, 5, or -, overall preference less than 5) at the seedling stage (GH) and in the first (FCY), second (SCY) and third (TCY) clonal year trials at BB and MURR.

		FCY		SCY		TCY	
Clone code	GH	BB	MURR	BB	MURR	BB	MURR
A1/12	+	-	+	+	-	+	+
A1/113	-	+	+	+	+	+	+
A2/37	-	+	+	+	-	+	-
A2/66	+	-	-	+	+	+	+
A5/45	-	-	-	+	-	-	+
A6/188	-	+	+	+	+	-	+
A7/32	+	-	-	+	+	+	+
A7/153	+	+	+	-	-	+	+
A7/171	-	-	+	+	+	-	+

CHAPTER 4

FACTORS AFFECTING THE EFFICIENCY OF SELECTING INDIVIDUAL GENOTYPES IN THE EARLY GENERATIONS OF A POTATO BREEDING PROGRAMME

4.1 Introduction

In the previous chapter, the efficiency of selecting individual genotypes in the early generations of a potato breeding programme was examined. The findings indicated that selection at the seedling and also the first clonal year stage of a potato breeding scheme resulted in, at best, a random reduction in genotype numbers. Selection was therefore deemed to be ineffective in these early generations.

The first two generations of a breeding scheme have characteristics which may cause this inefficiency of selection. At the seedling stage the phenotypic expression of genotypes may be adversely influenced by the following effects:

(1) genotypes are grown from true botanical seed, whereas in later generations they are propagated clonally from planted tubers;

(2) The seedlings are grown in small pots rather than in ridged drills;

(3) Seedlings are raised in an aphid proof glasshouse rather than under field conditions.

In addition, at the first clonal year stage, phenotypic expression may be further affected by the fact that:

(1) Evaluation of genotypes is carried out on the produce of a a single plant plot;

(2) First clonal year plants are raised by planting seed tubers which have been produced by seedlings;

(3) Clones are assessed, in the case of the BB site, under conditions suited to high grade seed production (for

necessarily be the most favourable environment to assess genotypes which will perform well under ware conditions.

In traditional potato breeding schemes, where genetic variation is produced by sexual hybridisation, it is impossible to avoid growing the first generation from true botanical seeds. Similarly, because of the heterozygous nature of cultivated tetraploid cultivars, each seedling is genetically unique and hence the largest possible plot size at this stage (ignoring micro-propagation or stem cuttings) is a single plant.

In designing a breeding strategy breeders can manipulate, to a certain extent, the growing conditions of seedling and first clonal year plants. Optimum conditions for growing seedlings under glass requires manipulation of temperature, day length and water supply and variation in these factors can result in large differences in tuber yields (Krug, Wreidt & Weber, 1974a and 1974b). It has also been suggested that many of the problems associated with glasshouse grown seedlings can be avoided if they are grown in large pots or under field conditions (Zadina, 1971; Swiezynski, 1978).

A "carryover" effect from the seedling stage is the size of seed tuber used to plant the first clonal year. The size of seed tuber planted in the first clonal generation can influence the number of clones that are visually selected by breeders (Mullin, Blomquist & Lauer, 1961; Blomquist & Lauer, 1962; Louwes & Neele, 1978), larger seed tubers resulting in a higher frequency of selected clones. Moreover, Brown et al. (1984) have noted that there can be a significant correlation between breeders' preference, a visual appraisal of commercial worth, and the weight of tuber planted in the first clonal stage.

The effect of seed tuber size on potato yields has been well documented (see Allen 1978). In the majority of these past studies, seed tubers had previously been field grown, and they were generally larger than those which are produced by seedlings grown in small pots. Correlation coefficients between seed tuber weight and resulting yield in the first clonal generation have been shown to range between 0.15 to 0.49 (Brown & Caligari, 1986) and between 0.41 to 0.62 (Mullin, Blomquist & Lauer, 1966). In the latter study a 1/4 inch (0.64 cm) increase in seed tuber size was associated with an increase in tuber yield between 0.26 to 0.39 lb (0.12 kg to 0.18 kg) per plant.

Maris (1986) also found that differences in seed tuber weight had a large effect on many agronomic characters in the first clonal year. He also examined the effect of seed tuber weight used to plant first clonal year plants on performance of second clonal generation plants. He found correlations between seed tuber weight used in the first clonal year and second clonal year performance of 0.26 for plant height and foliage maturity; 0.29 for breeders' preference; 0.33 for mean tuber weight and 0.40 for total tuber weight.

The plot size used in the early generations of a potato breeding programme tends to be small because of the limited number of tubers available for planting. If evaluation is carried out on the phenotypic performance of a single, unreplicated, plant plot, micro-environmental variation may hamper effective selection (Davies & Johnston 1965, 1968 and 1974). If, however, the inefficiency of selection at the first clonal year stage is due primarily to some other factor (for example the effects of planting tubers which have been produced from seedlings) the efficiency might be improved by delaying selection until field grown seed tubers are available. This has to be balanced against the fact that if selection is carried out on a single plant basis then many more genotypes can be evaluated than

with larger plots and greater replication.

Finally, Simmonds (1969) has noted that selection under seed production conditions will result in a higher proportion of early maturing clones than would perhaps be desired.

In this chapter some of these factors which may be affecting phenotypic performance, and hence the efficiency of selection, in the early breeding stages are examined. In order to examine the seedling stage, seedlings were grown in different sized pots (the 'B' material) and also grown under field conditions (the 'C' material) to investigate whether altering the growing conditions would increases selection efficiency. The effect of seed tuber weight used to plant the first clonal year trials was examined in two experiments. In the first, the effect of seed tuber weight used to plant the first clonal generation was examined in relation to performance of genotypes grown in the field for three consecutive years (using clones from the 'A' material). In the second, tuber size of seedlings was artificially controlled by growing seedlings in different pot sizes (the 'B' material). Genotypes were then also evaluated in the field for three consecutive clonal generations.

Most previous work on the efficiency of single plant selection in potato breeding has been carried out by comparing selection of single plants at the first clonal year stage with selection on larger plots in a later year. This chapter compares the efficiency of single plant selection when small and larger plots were grown in the same field and year, and where both plots sizes use common origin, field grown, seed tubers. This comparison was made posible by growing a single plant plot, at MJRR, of all 'A' material clones which were evaluated at the third clonal year stage in two replicates of five plant plots at that site. Finally, the effect of selecting clones under seed growing conditions, rather than ware conditions, can be simulated by

examination of data collected on the 'A' material over three years under seed conditions (BB) as well as under ware condition (MURR).

4.2 The effect of growing environment on seedlings

To examine the efficiency of selection when seedlings were grown in the field, rather than in small pots in a glasshouse, seeds from four potato crosses were sown into peat blocks and after 10 weeks of growth these seedlings were transplanted into ridged drills in the field. Full details of the material and methods of this experiment (the 'C' material) are given in section 2.4.

The average total tuber weight, mean tuber weight and number of tubers per plant produced by seedling transplants is shown in Table 4.1. On average, seedlings grown in the field produced just over 0.5kg per plant which was lower than the average of the same clones grown in the first clonal year. Similarly, the seedling transplants produced smaller tubers (0.04kg) than in the first clonal year although the transplants did produce more numerous tubers. The yield of tubers produced by seedling transplants were however greatly in excess of those reported by Howard (1963) or Brown (1985) growing seedlings in small pots under glass. The yield of seedlings grown in the field was also greatly increased over those grown in small, medium or large pots under glass (see section 4.3).

Correlation coefficients between seedling transplants and first clonal year plots for total tuber weight, mean tuber weight and number of tubers per plant were all positive although not large (Table 4.2). Simple linear regression of yield characters recorded on transplants and those on first clonal year plants accounted for only 7.5%, 4.7% and less than 1% of the total variation in the first clonal year for total tuber weight, mean tuber weight and number of tubers respectively. Similar coefficients, obtained by correlating yield

Table 4.1 Average total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT) per plant of seedlings transplanted into the field (Seedlings) and also the same clones grown fron seed tubers in the first clonal year (FCY).

	Seedlings	FCY
TTW (kg)	0.598	0.774
MTW (kg)	0.040	0.067
NT	14.67	11.56

Table 4.2 Correlation coefficients between seedling transplants and first clonal year plot (Seed v FCY) for total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT) per plant. Also similar coefficients obtained by correlation between the two replicates grown in the first clonal year (Rep 1 v Rep 2).

	Seed v FCY	Rep 1 v Rep 2
TTW	0.272 '''	0.687 '''
MTW.	0.218 '''	0.559 '''
NT	0.068	0.753 '''

''' = $p<0.001$

characters recorded on each of the two replicates grown in the first clonal year were significantly larger, accounting for 47.1%, 31.2% and 56.7% of the total variation in total tuber weight, mean tuber weight and number of tubers between replicates. Therefore, the efficiency of selection at the seedling stage will not be increased by simply growing the seedlings under field conditions.

The effect of growing seedlings in small pots, under glass, was examined using the 'B' material (for details see section 2.3). Seedlings from this material were grown in three differnt pot sizes and hence can be used to determine whether the use of larger pots would give more efficient results than smaller ones. Coefficients obtained by correlating variates recorded in the first and second clonal year, where seedlings were raised in different pot sizes, are shown in Table 4.3. Seedlings grown in very small pots gave rise to coefficients which were consistently lower than seedlings which were grown in either medium or large pots for breeders' preference, and all yield characters. For all variates examined, there was a general trend of greater association between first and second clonal years with increasing pot size used to grow seedlings. However, even where the largest pots were used, linear regression between the first and second clonal years only accounted for 4.7%, 4.4%, 3.0% and 1.1% of the total variation in second clonal year assessments of breeders' preference, total tuber weight, mean tuber weight and number of tubers respectively. Therefore, unless the efficiency of selection in later generations is greatly improved by increasing the seedling pot size, such practice could not be justified.

4.3 The effect of seed tuber size used in the first clonal year

The effect of seed tuber size planted in the first clonal year, on subsequent performance of clones in the first, second and third

Table 4.3 Coefficients obtained by correlation of breeders' preference (Pref), total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT) between the first and second clonal years. Clones were grouped according to whether they were grown in small, medium or large pots at the seedling stage.

	Small	Medium	Large
Pref	0.017	0.204'	0.218'
TTW	0.033	0.147	0.211'
MTW	0.044	0.089	0.174
TN	0.076	0.068	0.106

' = $0.05>p>0.01$

clonal generations was examined in two experiments. In the first experiment (Experiment 1), the effect of seed tuber weight used to plant the first clonal generation was examined in relation to performance of genotypes grown in the field for three consecutive years. The weight of each seedling-produced tuber planted in the first replicate of the 'A' material was recorded. Using this data, it was possible to examine the performance of these clones in the first, and following two years, in relation to the weight of tuber planted in the first clonal year. Details of materials and methods for this experiment are given in section 2.2; however, only data from BB are included in the present analysis, as BB provided the seed tubers for each subsequent trial. In the second experiment (Experiment 2), tuber size was artificially controlled by growing seedlings in different pot sizes (see the 'B' material; section 2.3 in Material and Methods). These genotypes were also evaluated in the field for three consecutive years.

Experiment 1

Coefficients, obtained by correlation of seed tuber weight in the first clonal year with breeders' preference, total tuber weight, mean tuber weight and number of tubers/plant recorded in the first, second and third clonal generations are shown in Table 4.4. Correlations from the first clonal generation were significantly greater than zero for all variates examined. The highest correlation from the first clonal year was for total tuber weight; this accounted for 26% of the total variation. The lowest correlation in this year was for number of tubers/plant, which accounted for only 4% of the total variation. Correlation coefficients between the weight of seed tuber planted in the first clonal year and performance in the second clonal generation were greatly reduced in magnitude, for all characters, compared to those from the first clonal year. However, correlations obtained in

Table 4.4 Correlation coefficients between the weight of seed tuber planted in the first clonal year against breeders' preference, total tuber weight, mean tuber weight and number of tubers/plant recorded in the first clonal year (FCY), second clonal year (SCY) and third clonal year (TCY) from Experiment 1. Correlations based on 200 observations.

	FCY	SCY	TCY
Breeders' preference	0.37 '''	0.21 '	0.12 ns
Total tuber weight	0.51 '''	0.14 '	0.01 ns
Mean tuber weight	0.28 ''	0.23 '	-0.00 ns
Number of tubers/plant	0.22 '	-0.06 ns	0.12 ns

ns=not significant; '=0.05>p>0.01; ''=0.01>p>0.001; '''=p<0.001.

the second clonal generation were still significantly greater ($p<0.05$) than zero for breeders' preference, total tuber weight and mean tuber weight. The correlations between weight of seed tuber used in the first clonal year with variates recorded from the third clonal generation did not differ significantly from zero. Overall, therefore, the size of tuber planted in the first clonal year greatly influences performance of clones at this stage, with bigger seed tubers resulting in more desirable produce. In the third clonal year, however, the performance of clones was not related to their ability to produce large tubers when grown as seedlings.

Before assessing each generation, the breeders had agreed that a preference score of 5, or more, would indicate that the particular plot would, under normal selection practise, have been selected for re-evaluation. On this basis, clones were grouped according to those which would have been selected and discarded in each year, and the mean seed tuber weight planted in the first clonal year was calculated for each group (Table 4.5). In the first clonal year trial, selected clones had on average been grown from seed tubers weighing 18.35g, while the average weight of seed tubers in the discarded clones was lighter by 3.99g. Similarly, clones which were selected in the second clonal year generation had, on average, seed weights derived from seedlings that were 2.77g heavier than the group of clones that were discarded in that year. In the third clonal year trial the two groups of selected and discarded clones were not significantly different with respect to the weight of seed tuber used in the first clonal generation.

The effect of seed tuber weight used at the first clonal year stage can be seen for breeders' preference (Figure 4.1) and total tuber weight (Figure 4.2) recorded in the first, second and third clonal years. In the figures, the total number of clones were divided

Table 4.5 Mean weight of tuber planted in the first clonal year of clones that were selected (breeders' preference $\geq$ 5), or rejected (breeders' preference < 5) in the first clonal year, second clonal year and third clonal year.

	Selected	Discarded	Difference (selected-discarded)
First clonal year	18.35	14.36	3.97 '''
Second clonal year	17.04	14.27	2.77 ''
Third clonal year	15.68	14.80	0.88 ns

ns=not significant; ''=0.01>p>0.001; '''=p<0.001

Figure 4.1 Relationship in Experiment 1 between weight of seed tuber produced by seedlings (g) and overall breeders' preference in the first (FCY), second (SCY) and third (TCY) clonal years.

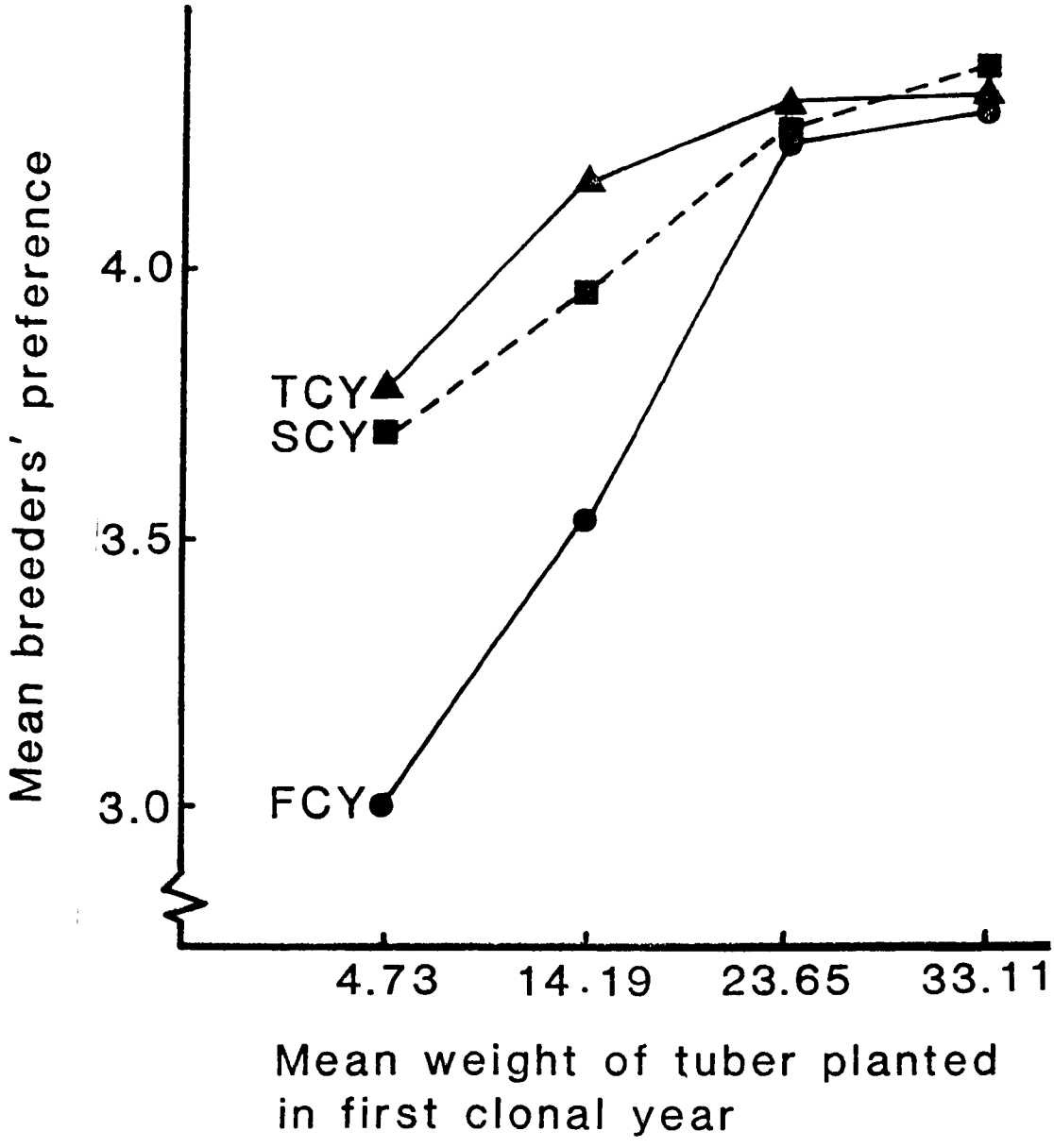
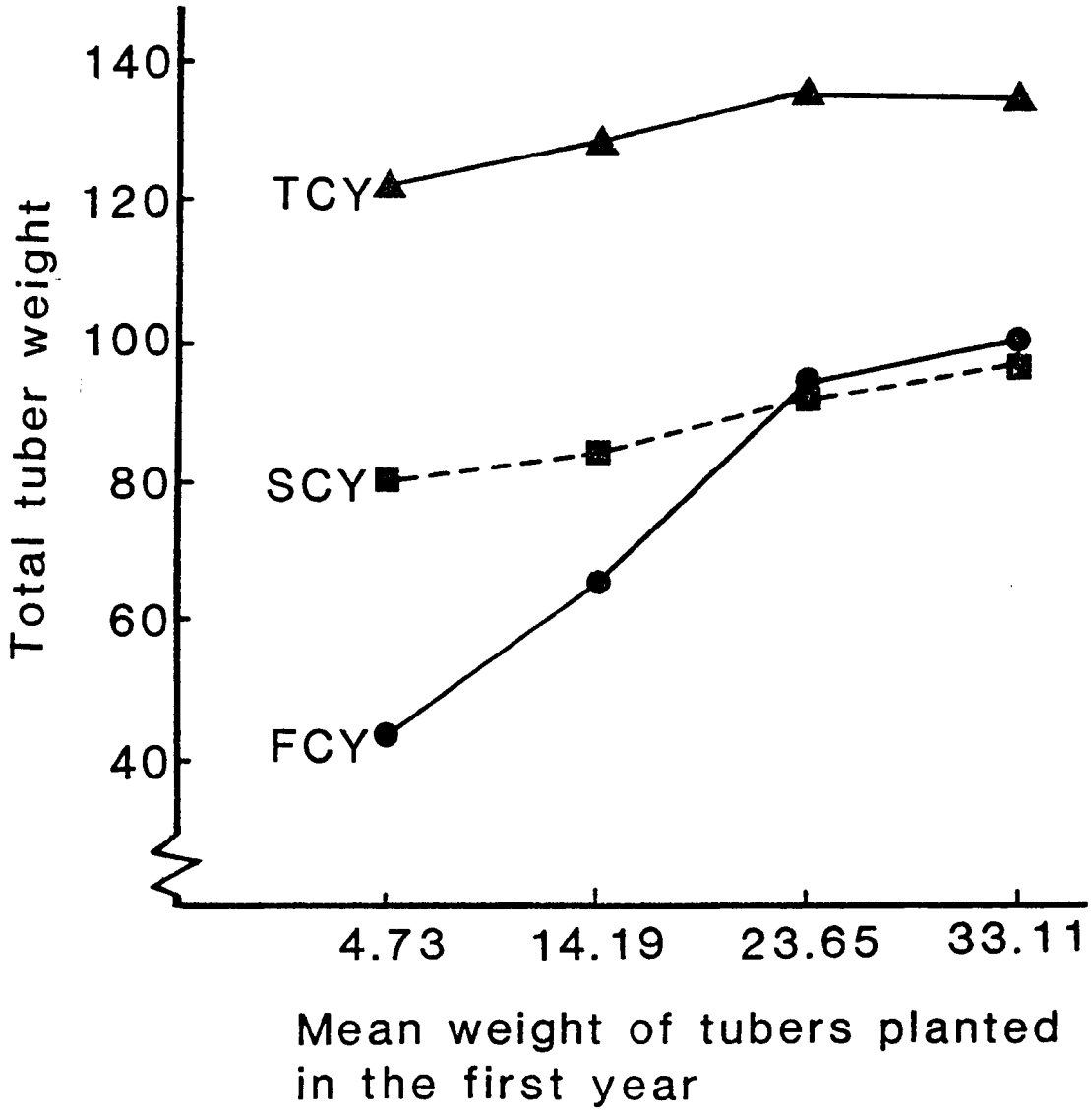


Figure 4.2 Relationship in the Experiment 1, between weight of seed tuber produced by seedlings (g) and total tuber weight (kg x 10^{-2}) in the first (FCY), second (SCY) and third (TCY) clonal years.



into four groups with mean seed tuber weights derived from seedlings of 4.73g, 14.19g, 22.65g and 33.11g. As the weight of seed tuber increases there was a rapid increase in total tuber weight and breeders' preference in the first clonal generation. The average total tuber weight produced from first clonal year plants was 0.44kg when seed weights averaged 4.7g but this increased to 1.02kg/plant when the largest seed tubers were grown. Similarly in the first clonal year, breeders' preference was 3.05 in the group with the lightest seed tubers and 4.27 for the heaviest. In the second clonal year the difference between the four groups was not as large as in the first clonal generation for total tuber weight and breeders' preference, although there was obviously still a relationship whereby total tuber weight and breeders' preference increased with increasing seed tuber weight. In the third clonal generation the total tuber weights of the four groups were relatively constant although clones with the heaviest seed tubers at the first clonal year stage obtained a higher breeders' preference (4.31) than did the group with the lighest seed tubers (3.74).

Experiment 2

Mean squares from the analyses of variance of five crosses, grown in the glasshouse with three pot sizes and two sowings, for total tuber weight, mean tuber weight and number of tubers are shown in Table 4.6. The first sowing produced significantly higher total tuber weights ($p<0.001$) and mean tuber weights ($p<0.001$) although there was no significant difference between the number of tubers per seedling. There were also significant differences ($p<0.001$) for all yield characters between the three pot sizes. The largest pots produced highest total tuber weights, mean tuber weights and more tubers while the small pots were lowest for all characters. Despite the formal significance of the sowing x pot-size interactions for total tuber

Table 4.6 Mean squares from the analysis of variance of total tuber weight (TTW), mean tuber weight (MTW) and number of tubers/plant (NT) on five crosses grown in small, medium and large pots in two glasshouse sowings.

Source	df	TTW	MTW	NT
Sowings (S)	1	628.10'''	27.663'''	10.40ns
Pot size (P)	2	96.87'''	9.820'''	263.00'''
Crosses (C)	4	6.99'''	0.243ns	42.01'''
S x P	2	134.34'''	3.045'''	4.97ns
S x C	4	4.35'''	0.321ns	11.99ns
P x C	8	0.46ns	0.159ns	10.37ns
S x P x C	8	0.99ns	0.205ns	1.83ns
Residual	570	1.60	0.107	5.25

ns = not significant; ''' = $p<0.001$

Residuals are all terms including clones within blocks and blocks within sowings.

weight and mean tuber weight, inspection of the relative magnitudes (Table 4.7) showed that the trend towards reduced yield in small pots was consistent. It is also obvious from Table 4.7 that growing seedlings in different pot sizes had indeed produced populations which have different sizes of largest tuber. It is these largest tubers that were used to plant the first clonal year trial.

Mean squares from the analyses of variance of breeders' preference, total tuber weight, mean tuber weight and number of tubers recorded from the first clonal year trial are shown in Table 4.8. There were significant differences ($p<0.001$) between sowings for all characters. Genotypes from the first sowing (the one which produced the largest seed sizes) were higher yielding and were assessed as being of superior preference to those from the second sowing. There were also significant differences between pot sizes for breeders' preference ($p<0.01$), total tuber weight and number of tubers per plant ($p<0.001$). There were significant differences between crosses for breeders' preference but not for the yield characters. The interaction sowings x crosses was significant at the 5% level whereas all other two-way interactions were not significant. A similar analysis of variance was carried out on the second clonal year trial but there were no significant differences between sowings or pot sizes and all interaction terms were non-significant.

The relationship between total tuber weight derived from small, medium and large pots at the seedling stage can be seen in Figure 4.3a. In the first clonal year genotypes derived from small pots only produced 0.74kg per plant while those from large pots gave 1.04kg per plant. In the second and third clonal year all three pot groups produced similar yields. Examination of the total tuber weight from genotypes derived from the two sowings (Figure 4.3b) shows that genotypes from the first sowing (those which had the heaviest seed

Table 4.7 Mean total tuber weight (TTW), mean tuber weight (MTW), number of tubers (NT) and weight of the largest tuber (WLT) obtained from growing seedlings in small, medium and large pots in two glasshouse sowings.

TWT

	Small	Medium	Large	Mean
Sowing 1	1.10	2.92	5.85	3.29
Sowing 2	0.60	1.06	2.08	1.25
Mean	0.85	1.99	3.97	

MTW

	Small	Medium	Large	Mean
Sowing 1	0.34	0.71	1.03	0.70
Sowing 2	0.17	0.25	0.37	0.27
Mean	0.26	0.48	0.70	

TN

	Small	Medium	Large	Mean
Sowing 1	3.34	4.47	5.93	4.58
Sowing 2	3.42	4.14	5.34	4.43
Mean	3.38	4.30	5.66	

WLT

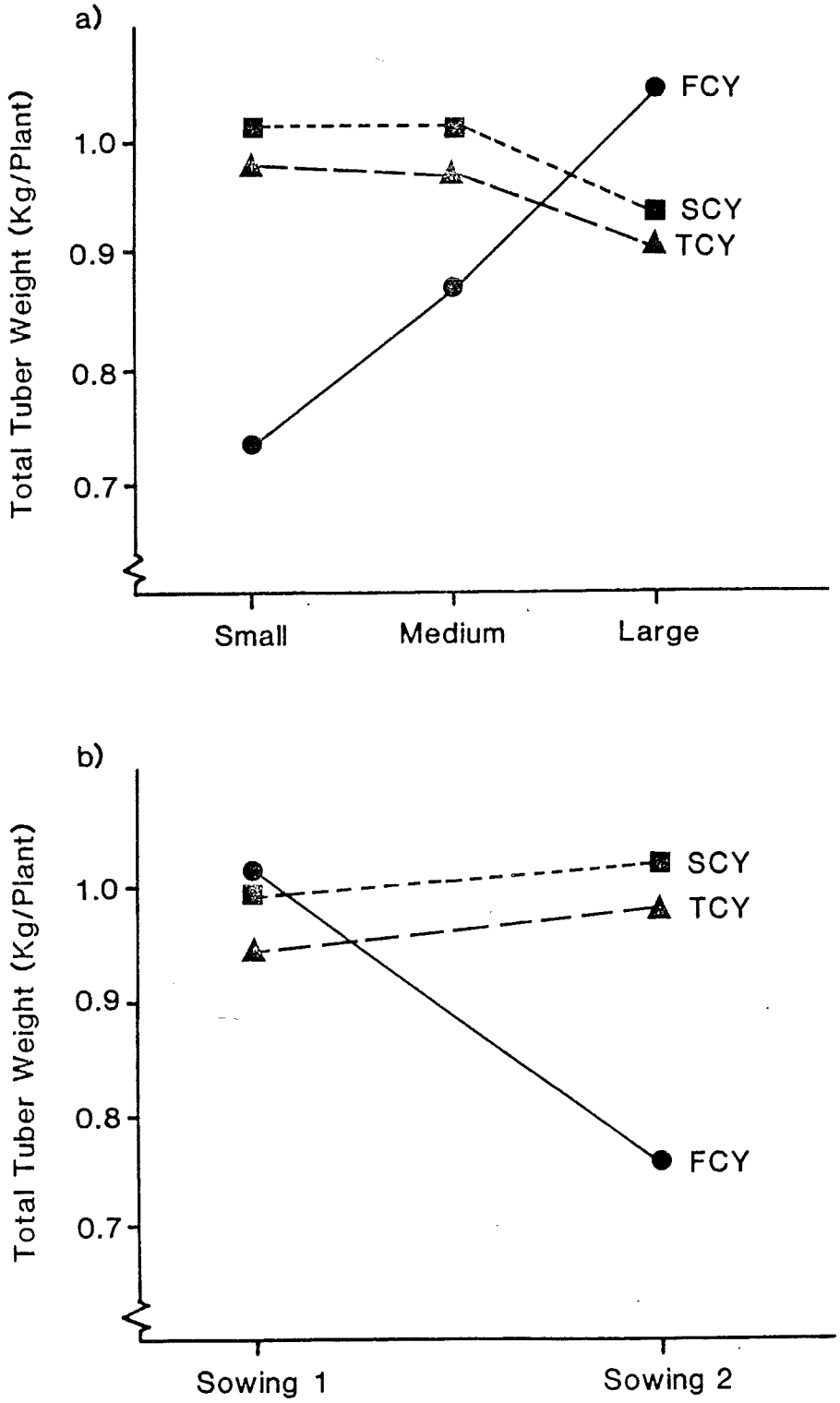
	Small	Medium	Large	Mean
Sowing 1	0.62	1.23	1.47	1.11
Sowing 2	0.29	0.51	0.76	0.52
Mean	0.46	0.87	1.12	

Table 4.8 Mean squares from the analysis of overall breeders' preference (Pref), total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT) from 5 crosses grown in the first clonal year. Seed tubers were from seedlings grown in small, medium and large pots in two glasshouse sowings the previous year.

Source	df	Pref	TTW	MTW	NT
Sowings (S)	1	26.108'''	4.640'''	4.946'''	1302.1'''
Pot size (P)	2	7.420''	2.427'''	0.245ns	285.3'''
Crosses (C)	4	14.800'''	0.721ns	0.672ns	97.1ns
S x P	2	1.133ns	0.400ns	0.190ns	73.3ns
S x C	4	0.981ns	0.372ns	0.799'	65.8ns
P x C	8	0.782ns	0.162ns	0.218ns	13.9ns
S x P x C	8	2.416ns	0.591''	0.193ns	75.0''
Residual	270	1.530	0.2198	0.315	25.8

ns = not significant; '' = 0.01>p>0.001; ''' = p<0.001

Figure 4.3 Relationship in Experiment 2 between (a) pot size used to raise seedlings and total tuber weight in the first (FCY), second (SCY) and third (TCY) clonal years and (b) early and late sowings at the seedling stage with total tuber weight in the first (FCY), second (SCY) and third (TCY) clonal years.



tuber weights) gave higher yields than those from the second in the first clonal year. However, in the second and third clonal years the total tuber weights were relatively constant.

The trend found with total tuber weight was also observed for breeders' preference, number of tubers and mean tuber weight (Figure 4.4a and Figure 4.4b). In the first clonal year increased pot size at the seedling stage was associated with greater preference, with more and heavier tubers, while in the second clonal year the groups were relatively constant. Similarly, the heavier seed tubers from the first sowing gave more tubers, higher preference scores and smaller tubers than those from the second sowing. In the second clonal year the genotypes from the two sowings were constant for these characters.

4.4 The effect of increasing plot size

The efficiency of single plant selection compared to selection based on two replicate five plant plots was examined by analysis of the third clonal year trial of the 'A' material grown at MJRR. Details of the trial are given in section 2.1.5.

The between sample error variances from the analysis of variance of the data recorded on the six control cultivars, grown in single plant plots and in five plant plots are shown in Table 4.9. The error variances from the two plot sizes were compared using Bartlett's test (Bartlett, 1937). There was no significant difference between the error variance from single plant plots and that from the five plant plots for breeders' preference. However, the error variance from the single plant plots was significantly larger than in the five plant plots for total tuber weight , mean tuber weight and number of tubers/plant. Therefore greater accuracy was acheived by evaluation in five plant plots over single plant measurements.

Figure 4.4 Relationship in Experiment 2 between (a) pot size used to raise seedlings and (i) overall breeders' preference; (ii) number of tubers; (iii) mean tuber weight in the first (FCY), second (SCY) and third (TCY) clonal years and (b) early and late sowings at the seedling stage with (i) overall breeders' preference; (ii) number of tubers; (iii) mean tuber weight in the first (FCY), second (SCY) and third (TCY) clonal years.

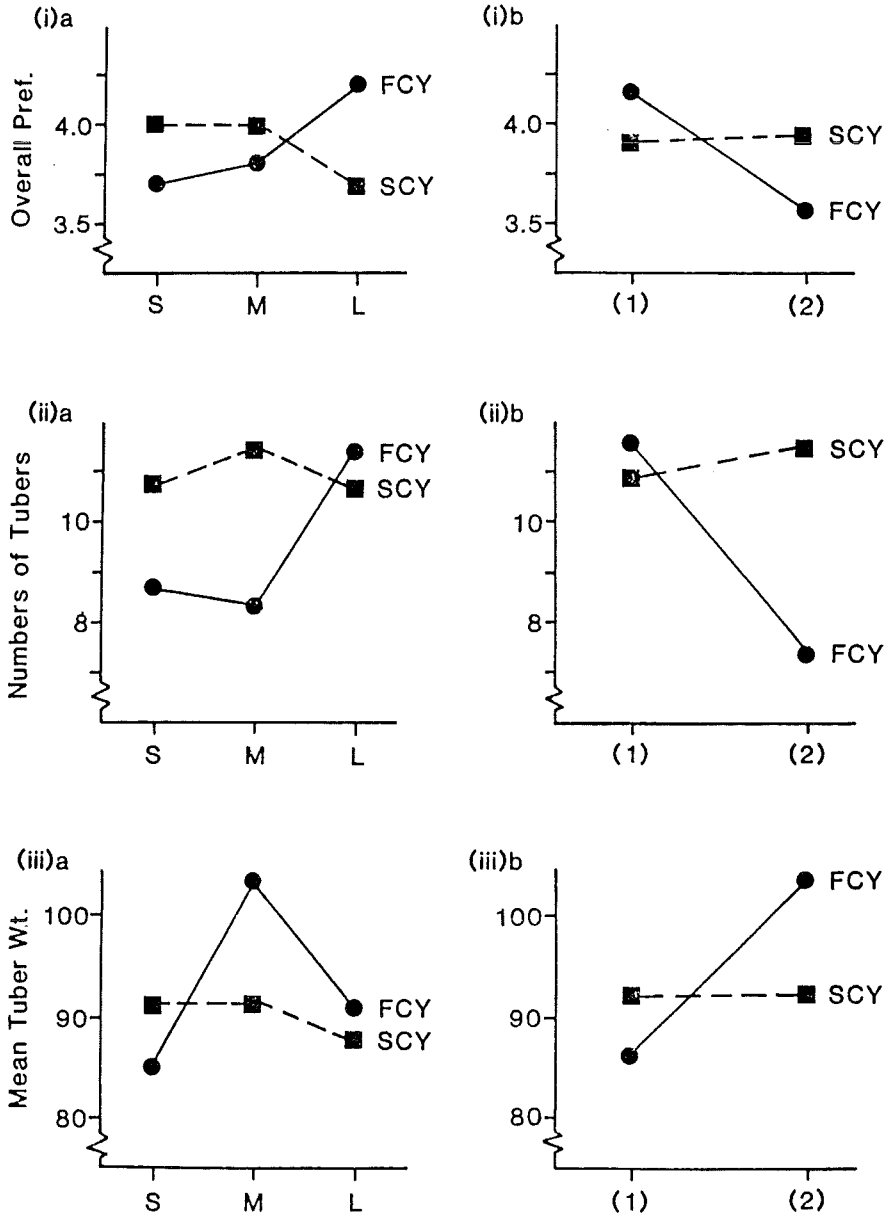


Table 4.9 Error variances of breeders' preference (Pref), total tuber weight in kgs per plant (TTW), mean tuber weight in grams per plant (MTW) and number of tubers per plant (TN) from the analysis of variance of six control cultivars grown in a single replicate of one plant plots and two replicates of five plant plots.

	df	Pref	TTW	MTW	TN
2 x five plant plots	36	0.7309	0.0361	479	4.04
Single plant plot	18	0.6013	0.2019	7764	14.88
χ^2 (Bartletts test)	1	0.18 ns	15.56 '''	38.34 '''	8.96 ''

ns=not significant; ''=0.01>p>0.001; '''=p<0.001

Correlations for breeders' preference, total tuber weight, mean tuber weight and number of tubers per plant between the single plant plots and the five plant plots were all found to be significantly greater ($P<0.001$) than zero (Table 4.10). The largest correlation coefficient ($r=0.64$) was for total tuber weight while the lowest correlation coefficient ($r=0.54$) was found for mean tuber weight. The correlation coefficients for the four variates examined were consistently larger between the two replicates of the five plant plots than between the single and the mean of two five plant plots.

It would appear from the correlation coefficients between the single and five plant plots, that it should be possible to select on a single plant basis. However, the simultaneous distribution of breeders' preference scores on the single plant plots and the mean score of two five plant plots (Table 4.11) shows that many clones given high scores in the five plant plots were assessed as having a poor preference in the single plant plots, and vice versa. As noted, a score of more than 5 indicates that a particular plot is considered to have "commercial" worth, and hence, under a normal breeding scheme, would have been selected for re-trial. From this information 202 clones (67%) would have been discarded in both the single and five plant plots, while 26 clones (9%) would have been selected in both plot sizes. However, 27 clones (9%) would have been selected when grown in a single plant plot but discarded when grown in a five plant plot, and 45 clones (15%) would have been selected in the five plant plots but discarded as a single plant plot. It should be noted that a higher proportion of clones was selected from the five plant plots (24%) than was selected in the single plant plots (18%). Despite this, it is obvious that a high proportion of clones that would have been selected (breeders' preference ≥ 5) in either plot size (26, selected in both plot sizes + 27, selected only in the single plant plots + 45, selected only in the five plant plots = 98 clones) would

Table 4.10 Coefficients of correlation between breeders' preference, total tuber weight, mean tuber weight and number of tubers per plant recorded on a single plant basis (Single) and the mean, averaged over two replicates, of five plant plots (2x5t). The correlation between the two replicates of the five plant plots (Rep 1 and Rep 2) is also shown. All coefficients are significantly greater ($p<0.01$) than zero.

	Single v 2x5t	Rep 1 v Rep 2
Breeders' preference	0.57	0.76
Total tuber weight	0.64	0.84
Mean tuber weight	0.54	0.74
Number of tubers per plant	0.61	0.69

All correlation coefficients are significantly greater ($p<0.001$) than zero.

Table 4.11 Simultaneous distribution of breeders' preference scores recorded on single plant plots and two five plant plots.

Single plant plots	Mean of two five plant plots							
	1.0	1.1-2.0	2.1-3.0	3.1-4.0	4.1-5.0	5.1-6.0	6.1-7.0	7.1-8.0	8.1-9.0
8.1-9.0	.	.	.	.	.	.	.	.	.
7.1-8.0	.	.	.	.	1	.	1	.	.
6.1-7.0	.	.	.	3	6	4	2	.	.
5.1-6.0	.	.	3	8	6	13	4	2	.
4.1-5.0	.	.	8	13	28	21	10	.	.
3.1-4.0	.	6	25	29	21	12	1	.	.
2.1-3.0	1	10	18	10	8	.	.	.	.
1.1-2.0	1	4	9	2	2	.	1	.	.
1.0	3	4	.	.	.	.	.	.	.

have been discarded on the basis of the score from either the single or five plant plots. From these 98 clones, 73% would have been discarded in one of the two plot sizes.

The similarity of total tuber weight recorded on a single plant and a five plant plot can be compared in a similar way (Table 4.12). If the top 20% of clones were retained, according to total tuber weight, then 218 clones (73%) would have been discarded on both the single and five plant plots, while 38 clones (13%) would have been selected in both plot sizes. Also 22 clones (7%) would have been selected for total tuber weight on the basis of the mean of two five tuber plots but discarded on the basis of a single plant. Similarly 22 clones would have been selected as a single plant but discarded on the basis of the mean total tuber weight of two five plant plots. In summary, from the 60 clones which would have been selected on the basis of the mean total tuber weight from two five plant plots, only 63% of these would have been selected on their performance as a single plant plot.

Although the clones used in this study were a random sample, in that no deliberate selection pressure had been exerted on them, each clone had been assessed for breeders' preference the year prior to this experiment (1983). If the clones are grouped into four classes based on scores in 1983 (at most 3; greater than 3 but at most 4; greater than 4 but at most 5; and greater than 5) the similarity within each group between performance as a single plant, and the mean of two five plant plots can be examined. The correlation coefficients for breeders' preference (Table 4.13) are found to decrease in magnitude as the preference scores of the group in the previous year increased. For example, the correlation coefficient for breeders' preference scores on the group which were assessed to be at most 3 in 1983 was 0.70, while the corresponding correlation coefficient of the

Table 4.12 Simultaneous distribution of total tuber weight recorded on a single plant plot and five plant plots. The data are expressed as the percentage selected in each plot size. For example, if the 300 clones were ranked (1=highest) according to total tuber weight, then 1-10% would be clones ranked 271st to 300th, 10-20% would be clones ranked 241st to 270th and so on. The category 90-100% is of course the highest yielding clones, ranked 1st to 30th.

91-100%	1	.	.	.	.	.	2	1	9	17
81-90%	.	.	2	3	1	4	2	6	4	8
71-80%	1	1	.	.	3	4	2	8	10	1
61-70%	.	2	3	2	3	10	4	2	3	1
51-60%	.	2	4	5	3	3	5	6	1	1
41-50%	3	4	5	3	6	2	2	2	2	1
31-40%	6	4	2	4	3	3	4	4	.	.
21-30%	2	4	6	7	4	.	6	.	1	.
11-20%	6	7	3	3	6	2	2	1	.	.
1-10%	11	6	5	3	1	2	1	.	.	1
	1-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100

(%)

Mean of two five plant plots

Table 4.13 Correlation coefficients between single plant plots and the mean of two five plant plots for breeders' preference, total tuber weight, mean tuber weight and number of tubers per plant. Clones are grouped according to breeders' preference scores in the previous year.

	<3 (n=75)	≥3<4 (n=106)	≥4<5 (n=64)	≥5 (n=31)	Control (n=24)
Breeders' preference	0.70'''	0.50'''	0.43'''	0.33	0.46'
Total tuber weight	0.74'''	0.57'''	0.50'''	0.65'''	0.13
Mean tuber weight	0.49'''	0.52'''	0.48'''	0.56'''	0.45'
Number of tubers per plant	0.65'''	0.59'''	0.60'''	0.66'''	0.39'

' = $0.05>p>0.01$; ''' = $p<0.001$.

group which were assessed as greater than 5 in 1983 was only 0.33. There was an implication of a similar relationship, although not so strong, for total tuber weight. Similarly, the correlations for the control cultivars in the experiment were generally small in comparison to the random sample of clones. There was, however, no evidence that the correlations differed in the different groups for mean tuber weight or number of tubers per plant.

4.5 The effect of selection under seed growing conditions

Since growing conditions for seed production at BB differ from those where potatoes are grown for ware (ie. at MURR) it is questionable whether selection under BB conditions would produce genotypes which will perform to a high standard at a ware site. It has already been shown in section 3.2 that the relationship and repeatability of selection between BB and MURR in any one year is not high. This relationship in now further studied by correlating the results from the third clonal year (using the 'A' material) with those from the previous two years for the two sites taken separately (Table 4.14). For all three yield characters, the correlations were generally larger within sites as opposed to between sites, although usually not greatly so. In fact, of the 12 sets, 10 showed this relationship while the the remaining two, both involving tuber number, showed a slightly reversed trend.

Although the differences are not large there are effects due to the site of selection or assessment. These may be due to the shorter growing season at BB and be a reflection of foliage maturity. Again using the 'A' material, maturity (measured on a 1-9 scale of increasing lateness) was correlated with total tuber weight and also the two yield components (Table 4.15). Correlation of maturity on to total tuber weight and also on to mean tuber weight resulted in

Table 4.14 Correlations for total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT) between BB and MURR in the third clonal year (TCY) compared with the first (FCY) and second (SCY) clonal years.

		FCY		SCY	
		BB	MURR	BB	MURR
BB - TCY	TWT	0.39'''	0.22''	0.65'''	0.38'''
	MWT	0.31'''	0.21''	0.54'''	0.37'''
	TN	0.34'''	0.21''	0.39'''	0.11ns
MURR - TCY	TWT	0.37'''	0.45'''	0.28'''	0.36'''
	MWT	0.31'''	0.40'''	0.45'''	0.46'''
	TN	0.31'''	0.21''	0.34'''	0.21''

ns = not significant; '' = $0.01>p>0.001$; ''' = $p<0.001$.

Table 4.15 Correlations between foliage maturity (averaged over three years) and total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT) recorded at BB and MURR in the first (FCY), second (SCY) and third (TCY) clonal years.

		TTW	MTW	NT
BB	- FCY	-0.08ns	-0.20''	0.19'
	SCY	-0.23''	0.06ns	-0.10ns
	TCY	-0.05ns	-0.18'	0.21''
MURR	- FCY	0.21''	0.03ns	0.21''
	SCY	0.04ns	0.03ns	0.08ns
	TCY	0.38'''	0.10ns	0.21''

ns = not significant; ' = $0.05>p>0.01$; '' = $0.01>p>0.001$; ''' = $p<0.001$.

negative coefficients (ie. early maturity was associated with higher yield and greater tuber weights). At MURR, on the other hand, the reverse was true and higher total tuber weights tended to be associated with later maturity. The number of tubers per plant showed a positive relationship at both sites, with higher numbers being produced by later maturing clones.

4.6 Discussion

4.6.1 Growing seedlings in the field.

The results obtained after growing seedlings in field conditions did not indicate that selection would be any more effective than if seedlings were grown in pots under glass. In fact there was greater association, for all variates recorded, between glasshouse grown seedlings and the first clonal year than between seedling transplants and the first clonal year. In the year following that reported for the transplants, a similar experiment was organised. In this year, potato seeds were sown directly in the field and from this experiment all, but a few, plants failed to grow. The main reasons for this are not known, although drought appeared to be a large factor, as did competition from weeds. Despite the difficulties that occur when seedlings are grown in the field, the seedling transplants did produce vast numbers of daughter tubers. This may allow for greater multiplication of breeding stocks which would subsequently enable more precise replicated trials with larger plots in earlier clonal generations. Other than greater multiplication properties, however, there was no advantage to growing seedlings in field conditions as found in Scotland and it is, therefore advised, for ease of management, to grow seedlings in pots. In countries with a different climate further investigations are required.

4.6.2 Growing seedlings in larger pots.

Examination of correlation coefficients for variates recorded in the first and second clonal year where seedlings had been grown in different pot sizes indicated that greater efficiency of selection would be achieved if seedlings were grown in larger pots. However, the increase in coefficients between, for example, medium and large pots was not sufficiently large enough to justify the extra glasshouse space that the larger pots would occupy. Along with greater glasshouse area, the larger pots also required a greater volume of compost which would increase costs. As was the case with growing seedlings in the field, however, growth of seedlings in larger pots resulted in larger yields and also a greater number of tubers per seedling. This, in turn, might accelerate clonal multiplication.

4.6.3 Seed tuber weight used in first clonal year.

When clones from Experiment 2 were grown in the first clonal year, seedlings from the largest pots produced on average, higher yields and yield components and were assessed as having higher preference. The clones from the small pots were lowest yielding and assessed as lowest preference. Similarly, clones from the first sowing appeared to be commercially more attractive than those from the second sowing. It should be noted that seed tubers derived from the first sowing, as well as being larger seed, were also physiologically older than those from the second sowing. Physiological age of potato seed can influence yield (O'Brein, Allen, Bean, Griffith, Jones & Jones, 1983) and may, therefore, have been a factor in the increased desirability and yield of the first sowing group. In the second clonal year the effects of pot size and different sowings were almost completely eliminated from the performance of clones.

In Experiment 1 there was a strong relationship observed between

weight of seed tuber and tuber characters recorded in the first clonal year. There was also a similar, although reduced, relationship between seed tuber weight planted in the first clonal year and performance in the second clonal year. In the third clonal year the relationship was non-significant. If seedlings are selected on their ability to produce large tubers, then selected clones will appear more desirable in the first clonal year, slightly more desirable in the second year and not significantly better in the third clonal year, when compared with clones rejected on this criterion.

Maris (1986) found a similar relationship, with decreasing association between seedling seed-tuber weight and increasing generations from true seed. He examined only the first two clonal generations and, as found in this study, recorded a significant correlation between seedling seed tuber weight and performance in the second clonal year. He concluded that seedlings which produce large tubers will have a "genetic advantage". The results from this study agree in part with Maris's conclusions. However, when seed tuber weight is artifically manipulated (Experiment 2) then the weight of seed tuber, produced by seedings, will only influence clonal performance in the first generation. In Experiment 1, where seed weight effects are confounded with genetic effects it would appear that the largest proportion can be attributed to non-genetic effects in that the relationship between seedling seed tuber weight and clonal performance decreases rapidly with increased generations from true seed. The non-genetic effects almost certainly will contribute to the inefficiency of selection at this stage in a potato breeding programme. It seems advisable, therefore, that no selection is carried out until field-grown tubers are available for planting.

4.6.4 Increased plot size.

The error variances for yield characters of the control

cultivars, were significantly larger when estimated from single plant plot than from the five plant plots. The error variances of the controls, however, were not significantly different for breeders' preference. Also, for all characters examined, there was greater agreement between the two replicates of the five plant plots compared to that between the single plant plots and the mean of two five plant plots. Therefore, greater accuracy was achieved by assessing two five plant plots rather than single plant plots.

Coefficients obtained by correlating data recorded on a single plant plot with mean data recorded from two five plant plots were of greater magnitude than those reported for breeders' preference, and yield characters (see Chapter 3, Table 3.18 and 3.25, respectively). The analyses reported in Chapter 3 involved comparing single plant observations from first clonal year plots with the mean of two five plant plots grown in the third clonal year. In the experiment reported here, the coefficients were expected to be larger because the single and five plant plots were both grown in the same field and in the same year. However, the greater correlations may also be due to both plot sizes being grown from common origin, field grown, seed tubers whereas the correlations reported in Chapter 3 involved single plant plots where seed tubers were produced from seedlings grown in pots.

Despite the relatively high correlation coefficients obtained between single and five plant plots, examination of the distribution of scores from both plot sizes showed that many clones would have been discarded on the basis of a single plant observation, but selected on the data recorded on two five plant plots. Examination of the selection ratio (as defined in section 2.1) showed that a genotype that was selected on a single plant basis, was 2.69 times more likely to be selected if grown in two five plant plots, than a clone that was

discarded on the basis of a single plant plot.

The size of plot needed to differentiate "good" clones from "poor" ones is likely to be associated with the heritability of a character within the population that is being selected. In this experiment the population had not been selected, and the correlations between single and five plant plots for breeders' preference and total tuber weight were positive and quite high. However, when the total number of clones examined was partitioned according to breeders' preference scores from the previous year, the correlation for breeders' preference between single plant plots and the mean of two five plant plots was found to decrease as the previous years' assessment increased. Also it is interesting that the control cultivars showed lower correlations between plot sizes, and it is reasonable to assume that these cultivars had previously been selected, not only for breeders' preference, but also for yield characters.

Replication effectively raises the broad sense heritability (Falconer, 1964). However increase in replication, or plot size, would result in either greater areas of land being needed to assess a set number of genotypes, or alternatively, a reduction in the total number of genotypes screened per fixed area of land. Obviously more genotypes can be evaluated in the same area of land if the plot size is kept to a minimum, without replication. Aikman & Langton (1983) were of the opinion that the most effective method, in the initial stages of selection, is to assess the maximum number of genotypes in single plant plots. Bos (1982) agreed that non-replicated trials are optimal if the broad sense heritability is greater than, or equal to, 0.5. In the experiment reported here, approximately 3,000 genotypes could have been grown in the same land area that was used to grow 300 clones in five plant plots, with two replicates. Also, if only 60

clones are to be retained for re-trial, then the "best" 20% of the 300 clones would be selected but only the "best" 2% of the 3,000 would be kept. If the top 10% of clones were selected on the basis of total tuber weight of a single plant, then all but one of these clones will be found within the top 60% of the two five plant plots (Table 4.12). It should, however, be noted that land availability may not be the limiting resource. Single plant plots are invariably harvested by hand digging while plots can be mechanically harvested. Also, if each individual plot requires weighing, the resources to handle 3,000 weighings may not be available. It will take little or no more effort or time to weigh the produce from a five plant plot than it would to weigh the produce from a single plant.

In conclusion, single plant selection in potato breeding will result in the loss of many potentially valuable clones. Also, clonal selection on single plant plots will be most effective when the population has not been selected. However, once selection pressure has been applied, or should the initial population be less diverse than the one examined here, then more than a single plant (ie. greater replication or larger plots) will need to be be grown to select superior genotypes with any degree of certainty.

4.6.5 Selection under seed conditions.

The results made clear that selection under seed growing conditions (ie. at BB) produced clones which were more likely to perform well under BB conditions than under MJRR conditions. Although the difference in magnitude of correlation coefficients between: (i) common sites and (ii) different sites, was not large it was relatively consistent and may need to be taken into account. Also it was found that selection under such seed conditions will tend to produce early maturing cultivars. If these are the clonal types required it would then be desirable to select under seed conditions. It should also be

remembered that the reverse situation was also observed (ie. the selections at MJRR were later maturing and more adapted to MJRR conditions than BB). Because potatoes are invariably grown for profit as both seed and ware crops, the only feasible solution would be to evaluate breeding material under both conditions and to retain only those genotypes which perform adequately in both environments. In the earliest selection stages of a potato breeding scheme this would, however, be costly both in land and labour.

Cross referencing assessment information on a large number of clones grown at more than a single location is of course possible and indeed can be relatively simple using computer technology to collect and sort information, plus database packages such as CHIP (Brown, 1983) or AGRITRIAL (Hampson 1986) to analyse and interpret such results quickly.

4.7 Conclusions

None of the factors examined, which may have been responsible for the inefficiency of selection in the early generations of a potato breeding programme, indicated that selection of individual clones could be made markedly more effective. Delaying selection of individual, superior clones until at least the second clonal year would appear to be the most feasible option to avoid the loss of a high proportion of potentially valuable clones. If field grown seed tubers are used for planting then low levels of selection, to eliminate the very worst clones may be possible but this will still carry the risk of discarding desirable clones. The effect of seedling-produced tubers on the performance of clones in the first and also the second clonal generations was evident, and will adversely affect selection at these stages.

The overall conclusions from this chapter are rather negative in

that no single factor investigated was found to be responsible for poor efficiency of selection during the early generations of a potato breeding programme. The results indicate, however, that phenotypic expression of seedlings is as much a reflection of being grown from true seed as it is a consequence of the environmental conditions under which seedlings are cultivated. Seedling-produced seed tubers, single plant pots and locational effects all contribute to the inefficiency of selection in the first and, to a lesser degree, the second clonal generations. Therefore, based on the current findings, no selection of individual clones should be carried out until at least the second clonal year, and in that year, selection should only be imposed at a relatively low intensity.

CHAPTER 5

CROSS PREDICTION METHODS

5.1 Introduction

Univariate cross prediction has been applied to a number of inbreeding species based on the work of Jinks & Pooni (1976) with Nicotiana rustica. Predictions of the proportion of recombinant inbred lines that will transgress either, or both, parents (T) are based on the evaluation of the integral:

$$\int_{T}^{\infty} f(x_i)\, dx$$

where the variate of interest is normally distributed, and the function $f(x_i)$ is based on $\underline{m}$, the mean of all possible inbreds for the character and $\underline{D}$, the additive genetic variance for the character. These parameters can be estimated by using various appropriate experimental methods.

These methods have also been applied to a variety of inbreeding species, particularly wheat (Snape, 1982, Snape & Parker, 1986) and barley (Thomas & Tapsell, 1983; Tapsell & Thomas, 1983). The use of such methods has been proposed in inbreeding species to allow for selection of progenies with the highest probability of producing desirable recombinant lines in plant breeding. Thus avoiding the problems associated with early generation selection in such species. These problems fall into two main categories (i) the difficulty of selecting highly heterozygous material, where dominance effects can be large, for genotypes that will produce superior homozygous lines, and (ii) the inaccuracy of selection on small plots (initially individual plants) because the basic error and sampling variation, and also because the surrounding plots are of different genotypes and hence open to the possibility of competition interactions (Powell, Carigari, Goudappel & Thomas, 1985; Caligari & Powell, 1986). The cross prediction methods have been further extended to cover second cycle hybrids (Pooni & Jinks, 1985; Pooni, Jinks & Yohannes, 1985). Other

workers have shown that small numbers of doubled haploid lines, particularly in barley, produced from different crosses may be used in prediction (Reinbergs, Park & Song, 1976; Simpson & Snape, 1979; Caligari, Powell & Jinks, 1985; Powell, Caligari, McNicol & Jinks, 1985). The use of doubled haploids produces a sample of inbred lines which are used to provide an estimate of the population mean and additive genetic variance and hence the distribution of inbred lines that would be expected from a particular cross.

Until now, such cross prediction methods have not been considered in relation to breeding programmes of clonally reproduced crops such as potatoes, (Solanum tuberosum). This may partly be due to the fact that heterozygosity is not a problem, in other words, although the initial material (ie. true seeds) are all genetically unique and highly heterozygous, they are subsequently multiplied clonally and so are fixed in the sense that they are the actual genotypes which may be commercially exploited. However, all the other problems of selection efficiency are still pertinent and have been discussed in Chapter 3 and Chapter 4. It was shown that such conventional phenotypic selection in these early generations was ineffective. It would therefore seem appropriate to investigate the possibility for cross prediction methods in potatoes, particularly as Brown (1985) reported that progeny means appear to be repeatable over the early generations, even though these environments are as diverse as seedlings grown in small pots in a glasshouse to material grown in the field from tubers.

A new cultivar will usually not be successful simply because of high expression in a single character, but rather it needs to have an overall improvement in a number of morphological, pathological and quality characters. This problem can partially be overcome by considering a variate such as breeders' preference, which is based on a visual assessment of characters by the breeder and has been likened

to a multivariate character (Frey, 1962). This will however have some limitations since other characters, such as disease resistance or cooking quality cannot readily be incorporated into this one variate. Thus more than one variate needs to be considered. Evaluation of crosses in a breeding programme has been shown to be effective in Nicotiana rustica (Pooni & Jinks, 1978) and also in Hordeum vulgare (Powell, Caligari, McNicol & Jinks, 1985). Such predictions are based on the multivariate distribution:

$$\int_{T_1}^{\infty}\int_{T_2}^{\infty}\cdots\int_{T_i}^{\infty} f(x_1),f(x_2),\ldots,f(x_i)\, dx_1, dx_2, \ldots, dx_i$$

where the function $f(x_1, x_2, \ldots, x_i)$ is a multi-normal distribution with parameters $\underline{m}$, the mean of all possible inbred lines for each character, $\underline{D}$, the additive genetic variance of each character and $\underline{r_D}$, the additive genetic correlation between the characters of interest.

Cross prediction, as described above, involves hybridisation of chosen parents and evaluation of a subset of the progeny from each cross to estimate the parameters which form the basis of the prediction. It would therefore be desirable if superior hybrid combinations could be identified without actually making the crosses. Parental choice would be more effective if breeders had some knowledge of quantitative inheritance of the major economic characters (Killick, 1976).

However, almost all biometrical theory has been developed on the basis of disomic inheritance and that parents are either in panmictic equilibrium, or are inbred lines. These genetic study techniques are therefore not applicable to cultivated potatoes which have tetrasomic inheritance and where parental lines are highly heterozygous and usually with unknown genetic structure.

Combining ability analysis (Griffin, 1956) produces statistical, rather than genetic, parameters which are independent of the genetic status of the crop and hence offer an alternative approach to potato breeders. The terms general combining ability and specific combining ability were originally defined in the analysis of full diallel crosses by Sprague & Tatum (1942). They defined general combining ability to "designate the average performance of a line in a hybrid combination" while specific combining ability "is used to designate those cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved". The performance of progeny from any cross combination is defined as:

$$y_{ij} = u + g_i + g_j + s_{ij}$$

where y_{ij} is the expression of the progeny derived from the cross between the ith and jth parents; u is the overall mean of all crosses; g_i is the general combining ability of the ith parent; g_j is the general combining ability of the jth parent and s_{ij} is the specific combining ability of the cross between the ith and jth parents. Where general combining ability effects are predominant over specific combining ability effects it will be possible to predict properties of hybrid crosses according to the combining abilities of the parents concerned. If however most variation is accounted for by specific combining ability, no predictions can be made without evaluation of individual cross combinations.

Most combining ability studies on potatoes have been carried out using a number of test crosses. Half diallel designs were used by Killick (1976), while North Carolina II designs were employed by Plaisted, Sanford, Federer, Kehr & Peterson (1962) and Killick & Malcolmson (1973). All possible cross combinations were not completed

by any of these authors due to problems of fertility and missing cells had to be estimated. To avoid fertility problems, Tai (1976) suggested the use of partial diallels (Kempthorn & Curnow, 1961) as the best approach because, apart from their statistical advantages, they avoid sterility problems and the need to complete every possible cross combination.

The majority of combining ability studies in potatoes have concerned yielding ability where specific combining ability has been found to be large in relation to general combining ability (Plaisted et al., 1962; Killick, 1976; Tai, 1976). High specific combining ability for yield was found to be the result of high specific combining ability for number of tubers rather than mean tuber weight, which showed high general combining ability (Tai, 1976). From other characters examined, foliage maturity has shown good general combining ability (Johansen, Miller, Vewson & Fonerot, 1967 and Killick, 1976) as did resistance to the white potato cyst-nematode (Phillips & Dale, 1982), starch content (Pika & Tarasenko, 1985), Streptomyses scabies (Pfeffer & Effmert, 1985) and crisp fry colour (Chitsay, 1984). Characters which have shown a predominance of specific combining ability include P. infestans (Killick & Malcolmson, 1973), specific gravity of tubers (Plaisted & Patterson, 1963) and tuber blackening after cooking (Dalianis, Plaisted & Paterson, 1966 and Pika, Tarasenko & Mitsko, 1984).

In this chapter the feasability of using univariate and multivariate cross prediction methods by examination of a sub-sample of clones from each cross are examined. To determine the merits of univariate cross prediction, the character breeders' preference is considered and to examine multivariate predictions total tuber weight, mean tuber weight, number of tubers and uniformity of tuber shape are considered simultaneously. Examination of progeny performance in

relation to performance of parental lines was also carried out to determine whether any estimates of hybrid performance can be obtained based on parental performance.

5.2 Cross prediction based on progeny evaluation.

Crosses from the 'A' material are used to examine univariate and multivariate cross prediction by evaluation of a sub-sample of progeny from each cross. Details regarding parents and growing conditions of the progenies are given in Section 2.2.

5.2.1 Univariate Cross Prediction.

In the second clonal year the number of clones per progeny had been reduced to 70 and therefore these clones were used to form the basis of the prediction. The means and square roots of the variances (σ^2) of these 70 clones are given in Table 5.1 for the first three years. In the glasshouse no replication was possible, since each true-seed is unique, and hence only the total between clone variation was available, ie. the phenotypic variance, the square root of which is given (σ_p). In the first clonal year the replicates were confounded with the mother tuber size and hence again no true replicate variance is available to correct the phenotypic variance for environmental effects. In the second clonal year, however, true replication was possible and so the square root of the genotypic variance (σ_g) is given along with that from the phenotypic variance (σ_p).

The means and σ^2's given in Table 5.1 were used following the methods of Jinks and Pooni (1976) to calculate the proportion of lines expected to transgress a particular target value. The probabilities were estimated as the sum of the normal probability integrals corresponding to the value:

Table 5.1. Means ($\bar{x}$) and standard deviation (ie. σ - the square root of the between clone variance) estimated from 70 clones for each of the eight progenies, as seedlings in GH as well as at BB and MURR in the first clonal year (FCY) and second clonal year (SCY) in. In the SCY true replication was present, thus it was possible to estimate σ_g, the between clone variance having removed the environmental component ie. the genetic component.

	FCY						SCY					
	GH		BB		MURR		BB			MURR		
	$\bar{x}$	σ_p	$\bar{x}$	σ_p	$\bar{x}$	σ_p	$\bar{x}$	σ_g	σ_p	$\bar{x}$	σ_g	σ_p
C1	4.36	1.52	3.43	0.86	3.75	0.85	4.07	0.79	1.11	3.61	0.58	0.91
C2	4.01	1.65	3.34	1.25	3.50	1.22	3.41	0.40	0.87	3.02	0.79	1.05
C3	3.61	1.50	2.87	0.87	3.64	0.98	3.13	0.00	0.77	3.20	0.46	0.84
C4	4.17	1.23	3.31	1.05	3.72	0.90	3.29	0.70	1.05	3.07	0.65	0.95
C5	3.04	0.91	2.90	0.80	3.33	0.77	3.40	0.58	0.97	2.92	0.59	0.91
C6	3.68	1.52	3.55	0.99	3.71	1.06	3.90	0.61	0.99	3.53	0.76	1.03
C7	4.21	1.36	3.95	1.27	4.22	1.09	4.10	0.61	0.99	3.53	0.62	0.94
C8	3.29	1.44	2.72	1.12	2.43	0.81	2.67	0.51	1.06	2.37	0.53	0.88

$$\frac{T-\bar{X}}{\sigma} \quad \text{or} \quad \frac{\bar{X}-T}{\sigma}$$

depending on whether the predictions are for values greater than (or equal to) or less than (or equal to) the target, where T stands for the target value and $\bar{X}$ is the cross mean.

Initially, a breeders' preference score of 5.0 was chosen as the target value. This value was chosen since, on the original 1-9 scale of assessment, it had been decided that 5 represented the value above which a clone would have been retained in the normal selection process within the breeding programme. In other words a score of less than 5 would have the clone as discarded while 5 or greater would mean that it was commercially acceptable and therefore have been retained for testing in the next clonal generation. In fact a range of commercially grown cultivars were included in the randomisation of the experiment and their means are given in Table 5.2. As can be seen in most of these cases these control cultivars would not have been selected (ie preference score of greater than 5).

The predicted proportion of clones falling into the category of greater than (or equal to) an average score of 5.0 are given in Table 5.3 for each of the three years and the two sites in the first and second clonal years. The predictions for the second clonal year are shown based on the genotypic as well as on the phenotypic variance. The observed proportions, given in the lower part of the table, are based on all the clones raised on each occasion ie. 200 clones in the seedling and first clonal year, 70 clones in the second clonal year and 25 clones in the third clonal year. It should be noted that the clones used for prediction are not independent of those providing the overall results which can lead to spuriously high correspondence between observed and predicted from the same environment. The

Table 5.2. Mean visual appraisal scores for the commercial cultivars grown with the experiment in the first (FCY), second (SCY) and third (TCY) clonal years.

	FCY		SCY		TCY	
	BB	MJRR	BB	MJRR	BB	MJRR
P. Crown	3.58	3.93	3.62	3.87	5.37	5.64
P. Dell	3.96	4.06	4.64	4.40	6.13	6.34
P. Squire	3.79	3.10	3.90	4.04	4.62	5.36
M. Piper	4.75	5.28	5.71	4.96	4.75	4.74
Desiree	3.67	3.25	3.87	3.63	4.87	4.94

Table 5.3 Predicted (a) and observed (b) proportions of clones falling into the category of mean score greater that 5.0 (predictions made using the $\bar{x}$ and σ).

a. Predicted using $\bar{x}$ and σ .

		FCY		SCY		SCY	
Progeny	GH	BB	MURR	BB	MURR	BB	MURR
C1	33.7	3.4	7.1	11.9	8.9	20.0	6.4
C2	27.4	9.3	10.9	0.0	0.6	3.4	3.1
C3	17.6	0.7	8.2	0.0	0.0	0.8	1.6
C4	25.1	5.4	7.8	0.7	0.1	5.2	2.2
C5	1.5	0.4	15.4	0.3	0.0	5.0	1.2
C6	19.2	7.2	11.3	3.5	2.7	13.3	7.8
C7	28.1	20.3	28.9	7.1	8.9	18.1	5.8
C8	11.7	2.1	0.1	0.0	0.0	1.4	0.1

b. Observed

		FCY'		SCY''		TCY'''	
Progeny	GH	BB	MURR	BB	MURR	BB	MURR
C1	21.7	4.6	6.1	15.7	5.7	32.0	24.0
C2	17.0	8.6	6.1	2.9	1.4	16.0	8.0
C3	12.7	2.0	5.4	0.0	1.4	4.0	0.0
C4	13.7	3.7	5.2	5.7	4.3	12.0	4.0
C5	3.8	1.2	1.2	4.3	1.4	12.0	20.0
C6	13.1	5.3	9.1	5.7	8.6	24.0	20.0
C7	21.4	14.6	22.2	17.1	5.7	20.0	28.0
C8	8.0	2.8	0.0	2.9	1.4	4.0	0.0

' = based on 200 clones; '' = based on 70 clones; ''' = based on 25 clones.

predicted and observed results were correlated and the estimated coefficients are given in Table 5.4. As can be seen all the correlations are positive and are generally quite high. It should be noted however that some of the correlations, although close to significance, were not formally so at the 5% level. This was mainly due to the correlations being based on only eight crosses but the consistency and magnitude of their average values shows that they are meaningful. Clearly any of the environments, even the most atypical of normal agricultural growing conditions, ie. seedlings grown in small pots in the glasshouse, gives reasonable cross prediction. This stands somewhat in contrast to findings with barley (Caligari et.al. 1985; Powell, Caligari, Phillips and Jinks, 1986). where significant genotype by environment interactions were found to affect predictions. The use of the phenotypic variance compared with the genotypic variance is also of some interest. Although the genotypic variance should, on theoretical grounds, give more accurate predictions, the phenotypic variance give a similar set of predictions. This raises the question of how much of a contribution the variance makes to prediction at the target level set here. The relative contribution of mean and σ to the prediction was investigated by regression of the predicted value onto (a) means alone and (b) the multiple regression onto the mean and σ. From these two regressions the coefficient of determination (R^2) was calculated as the percentage of the regression item to the total sum of squares in the regression analysis. The differences between the two R^2's are given in Table 5.5, not only for a target value of 5, but also for targets of 3, 4 and 6. As might be expected the differences increase in general as the target value rose. A target value of 3 showed differences in R^2 ranging from only 0.1 to 0.9 while with a target value of 6 the difference ranged from 6.9 to 17.4. Thus it would seem, not surprisingly, that the variance becomes more important as the target value rises. Higher target values have

Table 5.4 Correlation coefficients between predicted and observed proportions of clones having an average score greater than 5.0. Predictions were based on the mean and σ' of the 70 clone samples.

Predicted from			FCY		SCY		TCY		
		GH	BB	MURR	BB	MURR	BB	MURR	Mean
	GH '	**0.96**	0.59	0.53	0.59	0.46	0.61	0.24	0.57
FCY	BB '	0.65	**0.98**	0.93	0.62	0.44	0.36	0.51	0.64
FCY	MURR '	0.30	0.69	**0.79**	0.50	0.39	0.32	0.71	0.51
SCY	BB ''	0.73	0.40	0.49	**0.91**	0.63	0.85	0.74	0.68
SCY	MURR ''	0.79	0.64	0.71	0.96	**0.61**	0.78	0.79	0.75
SCY	BB '	0.70	0.55	0.66	**0.93**	0.80	0.90	0.88	0.77
SCY	MURR '	0.68	0.52	0.63	0.66	**0.91**	0.89	0.74	0.72

' = prediction based on σ'_p ; '' = prediction based on σ_g

The figures in bold type are those where observed and predicted are not independent as at least some of the data are in common. The figures in italies are correlations where the prediction were made in a later generation than the observed and so in practical breeding terms are not useful but are included for completeness.

Table 5.5 The average difference between the coefficient of determinations (R^2) obtained by the linear regression of the prediction, based only on the progeny means, and and the observed and the prediction, based on the mean plus σ and the observed for target values of 3, 4, 5 and 6.

Environment		⩾3	⩾4	⩾5	⩾6
	GH	0.8	1.2	4.2	6.9
FCY	BB	0.6	0.1	2.8	9.2
FCY	MURR	1.9	5.8	0.4	12.4
SCY	BB	1.3	3.8	9.4	12.1
SCY	MURR	0.1	1.0	7.3	17.4

not been considered here since only an extremely small proportion of clones were observed in practise, sampling effects became large and the commercial cultivars grown suggested that such values were inappropriate.

The means of the 70 clones alone were therefore taken as the prediction of a cross's worth and correlated with the observed numbers greater than (or equal to) 5 (as was done for the mean plus σ), the coefficients of which are presented in Table 5.6(i). As might be expected from the above, the agreement between the predicted and observed was not materially different when only the mean was used compared with when the mean and σ was used. A further method of prediction is available. As was suggested by Powell, Caligari, McNicol and Jinks (1985) the actual number of lines falling into the required phenotypic category (in this case a score of greater than or equal to 5) can be used as a predictor. The correlation coefficients for predictions based on sample numbers with these observed are given in Table 5.6(ii). No values are given for predicted and observed at the same site in the second clonal year, since these data are by definition identical. Using this method it can be seen that again there is reasonably good agreement between predicted and observed numbers even over sites and years. The overall mean correlation for all these three prediction methods are 0.668, 0.688 and 0.628 for using the mean plus σ, using only the mean alone and using the number observed in a sample respectively. These three are obviously very similar in magnitude to each other.

Although the correlation between the predicted and observed numbers as discussed above, is of interest to plant breeders, in most circumstances breeders are more concerned with ranking the crosses in terms of their ability to provide clones that are above the set target value. In other words it is of considerable interest to compare the

Table 5.6 Correlation coefficients for the relationship between predicted and observed numbers of lines scoring greater than 5.0.

(i) Predictions based only on the mean of the 70 clones.

			FCY		SCY		TCY		
		GH	BB	MURR	BB	MURR	BB	MURR	Mean
	GH	0.94	0.59	0.57	0.65	0.49	0.61	0.29	0.59
FCY	BB	0.78	0.86	0.89	0.77	0.75	0.72	0.70	0.78
FCY	MURR	0.67	0.57	0.77	0.57	0.56	0.56	0.59	0.61
SCY	BB	0.69	0.58	0.71	0.80	0.76	0.90	0.90	0.76
SCY	MURR	0.75	0.47	0.69	0.70	0.81	0.81	0.70	0.70

(ii) Predictions based on the actual number of lines observed in a sample.

			FCY		SCY		TCY		
		GH	BB	MURR	BB	MURR	BB	MURR	Mean
	GH	0.93	0.53	0.51	0.56	0.55	0.61	0.20	0.56
FCY	BB	0.64	0.99	0.92	0.63	0.39	0.36	0.54	0.64
FCY	MURR	0.74	0.96	0.98	0.64	0.48	0.42	0.54	0.68
SCY	BB	0.72	0.63	0.69	-	0.60	0.75	0.81	0.70
SCY	MURR	0.49	0.37	0.55	0.60	-	0.76	0.62	0.56

The figures in bold type are those where observed and predicted are not independent as at least some of the data are in common. The figures in italics are correlations where the predictions were made in a later generation than the observed and so in practical breeding terms are not useful but are included for completeness.

predicted and observed rankings. The rank correlations were estimated for the three different prediction systems for the target value of 5 are presented in Table 5.7. As can be seen the picture is very similar to that for the numbers although the correlations are on average marginally higher. The predictions were also made for the target values of 3,4 and 6 and means averaged over years and sites as shown in Table 5.8 along with those from the target value of 5. The correlations are all reasonably high with the highest target value (ie ≥ 6) giving the lowest values but even here they are still high enough to be useful, bearing in mind the problems of sampling variation when only a few clones are involved.

It was noted in Section 2.1 that the two sites were subject to somewhat different agronomic conditions mainly in terms of BB having a shorter growing season. The question arises as to whether cross prediction carried out from the results of one site is, on average, a better prediction for that site as opposed to the other one. In Table 5.9 the rank correlation coefficients are given having been averaged over years for BB and MURR. The correlation coefficients are not very different but of the 24 cases given, 18 have a higher correlation with the same site. Of the remaining 6 cases, one shows the correlation to be equal while five are the opposite way round. This perhaps suggests a tendency for the prediction to favour the site at which they are made but not to a great extent. A further point of note is that of the 5 cases with a lower correlation, 4 are associated with the highest target values. Although the significance of this is difficult to assess they should be viewed alongside the findings in Section 4.5 where individual clones were selected at BB and MURR.

So far in this section only one variate (overall breeders' preference) has been considered. Such univariate predictions could, however, have been carried out with any other characters recorded. To

Table 5.7 Rank correlation coefficients between the predicted and observed proportions of lines scoring greater than 5.

(i) Predictions based on mean plus σ of the 70 clones per cross.

			FCY		SCY		TCY		
		GH	BB	MURR	BB	MURR	BB	MURR	Mean
	GH	**1.00**	0.79	0.72	0.64	0.57	0.73	0.58	0.72
FCY	BB	0.71	**0.98**	0.78	0.52	0.55	0.57	0.46	0.65
FCY	MURR	0.50	0.76	**0.90**	0.34	0.52	0.46	0.42	0.56
SCY	BB	0.69	0.55	0.61	**0.96**	0.86	0.89	0.88	0.78
SCY	MURR	0.67	0.79	0.90	0.75	**0.87**	0.92	0.79	0.81

(ii) Predictions based on only the mean of the 70 clones per cross.

			FCY		SCY		TCY		
		GH	BB	MURR	BB	MURR	BB	MURR	Mean
	GH	**0.98**	0.71	0.66	0.71	0.64	0.70	0.55	0.71
FCY	BB	0.74	**0.83**	0.92	0.81	0.83	0.89	0.85	0.84
FCY	MURR	0.81	0.59	**0.74**	0.81	0.78	0.66	0.65	0.72
SCY	BB	0.74	0.74	0.86	**0.81**	0.73	0.92	0.95	0.82
SCY	MURR	0.73	0.50	0.79	0.65	**0.82**	0.76	0.62	0.70

(iii) Predictions based on the actual number of lines observed in a sample.

			FCY		SCY		TCY		
		GH	BB	MURR	BB	MURR	BB	MURR	Mean
	GH	**0.96**	0.67	0.60	0.68	0.62	0.67	0.50	0.67
FCY	BB	0.73	**0.99**	0.79	0.58	0.57	0.65	0.56	0.70
FCY	MURR	0.77	0.95	**0.90**	0.52	0.57	0.65	0.56	0.70
SCY	BB	0.64	0.55	0.58	-	0.83	0.77	0.85	0.70
SCY	MURR	0.57	0.59	0.72	0.83	-	0.81	0.67	0.70

The figures in bold type are those where observed and predicted are not independent as at least some of the data are in common. The figures in italics are correlations where the predictions were made in a later generation than the observed and so in practical breeding terms are not useful but are included for completeness.

Table 5.8 Rank correlation coefficients averaged over all years and sites for the target values 3, 4, 5 and 6.

(i) Prediction based on mean and σ of a 70 clone sample.

		⩾3	⩾4	⩾5	⩾6
	GH	0.59	0.69	0.72	0.46
FCY	BB	0.82	0.65	0.65	0.37
FCY	MURR	0.80	0.68	0.56	0.43
SCY	BB ''	0.74	0.71	0.78	0.53
SCY	MURR ''	0.82	0.76	0.81	0.54
SCY	BB	0.79	0.69	0.78	0.53
SCY	MURR	0.86	0.74	0.78	0.61

'' = prediction based on σ_g , all other predictions based on σ_p .

(ii) Prediction based on only the mean of a 70 clone sample.

		⩾3	⩾4	⩾5	⩾6
	GH	0.75	0.69	0.71	0.47
FCY	BB	0.82	0.79	0.84	0.63
FCY	MURR	0.82	0.65	0.72	0.50
SCY	BB	0.83	0.78	0.82	0.63
SCY	MURR	0.80	0.66	0.70	0.55

(iii) Prediction based on observed number in a sample.

		⩾3	⩾4	⩾5	⩾6
	GH	0.59	0.57	0.67	0.48
FCY	BB	0.83	0.73	0.70	0.21
FCY	MURR	0.81	0.61	0.70	0.56
SCY	BB	0.78	0.73	0.70	0.50
SCY	MURR	0.79	0.70	0.70	*

* No coefficient is given here as no clones were observed with a score of 6 or more.

Table 5.9 Rank correlation coefficients averaged over all years and sites for the four target values (3, 4, 5 and 6) for the three prediction methods.

(i) Prediction using the mean and σ of a 70 clone sample.

	⩾3		⩾4		⩾5		⩾6	
	BB	MJRR	BB	MJRR	BB	MJRR	BB	MJRR
BB	0.89	0.73	0.72	0.66	0.76	0.72	0.40	0.55
MJRR	0.79	0.87	0.72	0.73	0.70	0.76	0.38	0.66

(ii) Prediction using only the mean of a 70 clone sample.

	⩾3		⩾4		⩾5		⩾6	
	BB	MJRR	BB	MJRR	BB	MJRR	BB	MJRR
BB	0.90	0.79	0.81	0.77	0.83	0.86	0.57	0.78
MJRR	0.76	0.86	0.61	0.66	0.66	0.73	0.38	0.65

(iii) Prediction using sample numbers.

	⩾3		⩾4		⩾5		⩾6	
	BB	MJRR	BB	MJRR	BB	MJRR	BB	MJRR
BB	0.84	0.82	0.79	0.65	0.71	0.69	0.19	0.40
MJRR	0.75	0.86	0.65	0.65	0.72	0.68	0.37	0.73

avoid repetition the results from the predictions using these other characters are not included in detail. The correlations between progeny means recorded as seedlings and first clonal year plants and those recorded in the second and third clonal years for total tuber weight, mean tuber weight and number of tubers are given in Table 5.10. Similar coefficients for uniformity of tuber shape, distribution of tuber size and absence from growth cracks are also given in Table 5.11. All coefficients between the early generations and later generations were positive although only some were formally significant. The range in values for these coefficients did however suggest that some degree of prediction would be possible for any of these other characters.

5.2.2 Multivariate cross prediction.

To consider the merits of multivariate cross prediction three methods of cross prediction were examined:

(1) the multivariate probability;

(2) the sum of ranks;

(3) the frequency in a sub-sample.

Multivariate probabilities were calculated using a computer program developed at SCRI (Powell et al., 1985) which was based on an algorithm by Schervish (1984). The parameters used in the probability estimates for each cross were the mean and phenotypic variance for each of the characters (total tuber weight, mean tuber weight, number of tubers and uniformity of tuber shape) together with the phenotypic correlation between them. The sum of ranks (for a detailed description see Kendel, 1962) was obtained by ranking the eight crosses for each of the four individual variates then summing them to give a total for each. The observed frequencies in the sub-samples as well as over all clones were obtained by simply counting the number of

Table 5.10 Coefficients obtained by correlation of total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT) produced by eight crosses grown as seedlings (Seed) and in the first clonal year (FCY) with those from the second (SCY) and third (TCY) clonal years. FCY, SCY and TCY data were recorded at BB and MURR.

TWT	BB-SCY	MURR-SCY	BB-TCY	MURR-TCY
Seed	0.11	0.34	0.22	0.17
BB-FCY	0.86''	0.77'	0.84''	0.51
MURR-FCY	0.39	0.79''	0.42	0.82''
MTW				
Seed	0.75'	0.84''	0.66'	0.64'
BB - FCY	0.72'	0.56	0.73'	0.51
MURR-FCY	0.46	0.72'	0.24	0.68'
TN				
Seed	0.14	0.40	0.46	0.38
BB - FCY	0.21	0.45	0.71'	0.50
MURR-FCY	0.26	0.78'	0.92'''	0.71'

' = $0.05>p>0.01$; '' = $0.01>p>0.001$; ''' = $p<0.001$; all other coefficients are not significant.

Table 5.11 Coefficients obtained by correlation of uniformity of tuber shape (Shape), distribution of tuber size (Dist) and absence from growth cracks (Grow) produced by eight crosses grown as seedlings (Seed) and in the first clonal year (FCY) with those from the second (SCY) and third (TCY) clonal years. FCY, SCY and TCY assessments were obtained from BB and MURR.

Shape	BB-SCY	MURR-SCY	BB-TCY	MURR-TCY
Seed	0.61	0.27	0.36	0.65'
BB-FCY	0.83''	0.65'	0.51	0.69'
MURR-FCY	0.83''	0.41	0.17	0.41
Dist				
Seed	0.06	0.55	0.13	0.34
BB - FCY	0.85''	0.29	0.41	0.89''
MURR-FCY	0.73'	0.62	0.44	0.62
Growth				
Seed	0.94'''	0.83''	0.99'''	0.69'
BB - FCY	0.92'''	0.76'	0.86''	0.43
MURR-FCY	0.63	0.42	0.79'	0.74'

' = $0.05>p>0.001$; '' = $0.01>p>0.001$; ''' = $p<0.001$; all other coefficients are not significant.

clones that were observed to be greater than the target values set for each of the four variates simultaneously. The target values used for each year and site were the overall means of each variate, averaged over all eight crosses.

The effectivness of estimation within a single environment will be considerend first. Two sample sizes 70 clones per cross and 25 clones per cross were examined. The predictions based on both sub-sample sizes were correlated with the frequency of clones that were observed when all clones were examined (Table 5.12). It should be noted that the correlation coefficient with the sum of ranks will tend to be negative because the lower the sum of ranks the greater is the probability of the cross producing desirable clones. As expected the predictions using a sub-sample of 70 clones per cross gave higher correlation coefficients with the observed frequencies when all clones were included than did the 25 clone samples. The multivariate probability predictions, in general, resulted in higher correlation coefficients than either sum of ranks or observed sub-sample frequencies based on 70 clones per cross. The sum of ranks produced higher correlation coefficients than the sub-sample frequency with the 25 clone sub-samples. However the reverse was found when a larger sub-sample (70 clone per cross) was examined. There was a loss of accuracy in estimating the multivariate probabilities or sum of ranks when the sample examined was reduced from 70 to 25 clones per cross but it was not large. The observed frequency showed much lower correlations when the sample was reduced. Overall, however, it was found that a 25 clone sub-sample per cross produced a reasonable estimate of the observed frequency of clones in a larger sample within the same environment.

The target values used to define the lower bounds of total tuber weight, mean tuber weight, number of tubers and regularity of tuber

Table 5.12. Correlation coefficients obtained by correlating the observed frequency of clones (based on all clones examined) with the predicted frequency greater than the mean value of total tuber weight, mean tuber weight, number of tubers per plant and uniformity of tuber shape within each of five different environments. The predicted frequencies are based on (1) multivariate probabilities; (2) sum of rankings and (3) the observed frequency in a sub-sample of the progeny.

Environment	Prediction based on 70 clones			Prediction based on 25 clones		
	(1)	(2)	(3)	(1)	(2)	(3)
GH	0.92	-0.80	0.92	0.76	-0.63	0.68
BB-FCY	0.91	-0.94	0.89	0.81	-0.74	0.54
MURR-FCY	0.89	-0.82	0.98	0.71	-0.62	0.82
BB-SCY'	0.92	-0.69	-	0.61	-0.84	0.57
MURR-SCY'	0.80	-0.66	-	0.42	-0.72	0.69

' Observed percentages based on 70 clones per cross, all other obeseved percentages based on 200 clones per cross.

shape in the predictions were the mean value of each character, averaged over all crosses, in each environment. The frequency of clones which were observed to be greater than the target value of the four variates simultaneously in a sample of 200 clones per cross and from a 25 clone per cross sample were estimated (Table 5.13). The predicted frequency, based on multivariate probabilities, with the same target values used above, and the sum of rankings both based on the same four variates are also shown in Table 5.13.

Cross prediction in most practical plant breeding situations will involve the estimation of the worth of a progeny in one environment, by evaluation of a sub-sample of genotypes from each cross under investigation. The prediction aims to estimate the performance of genotypes from the crosses in the later stages of a selection scheme where larger numbers of clones are grown from each cross. This was simulated by correlating predicted frequencies (based on evaluation of 25 clones per cross) with the observed frequencies, based on a larger sample of genotypes, and in the different site and years. The correlation coefficients obtained from multivariate probabilities (Table 5.14), sum of rankings (Table 5.15) and observed frequencies, on a 25 clone sample (Table 5.16) were generally significantly different from zero despite a relatively small sample size (ie only eight crosses). As with the comparison between predicted and observed frequencies in a single environment (Table 5.12), the multivariate probability predictions provided the best estimate of what was observed in a larger sample of genotypes in a different environment. Averaged over all possible combinations of environments, linear regression of predicted frequency (based on multivariate probabilities) on to observed frequency in a different environment, with a greater sample of genotypes, accounted for over 30% of the total variation in the latter. Similar regressions were carried out for the sum of ranking and observation frequencies, based on a 25

Table 5.13. Observed frequency of clones (200 and 70 clones per sample), expected frequency based on multivariate probability (based on 25 clones per sample, MVP), observed frequency of clones (based on 25 clones per sample) that were greater than the overall mean of all crosses in the glasshouse (GH) and at Blythbank (BB) and Murrays (MURR) in FCY and SCY. Also the sum of rankings of each cross in these environments, rank sums are the sum of the rankings of variates above.

	Progeny	GH	BB FCY	MURR FCY	BB SCY	MURR SCY
Obs.(all clones)						
	1	6.06	12.50	12.21	28.58	11.42
	2	12.42	3.17	7.63	7.25	10.00
	3	15.03	2.78	6.80	2.86	8.57
	4	8.57	9.77	10.46	15.94	5.71
	5	0.54	4.71	8.38	14.29	4.28
	6	4.35	5.55	7.63	14.29	12.58
	7	15.51	16.57	30.91	10.00	7.41
	8	3.00	0.71	2.20	5.15	0.00
MVP.(based on 25)						
	1	8.32	10.32	18.28	15.17	12.98
	2	13.00	6.97	9.65	8.41	11.78
	3	5.56	0.55	5.37	4.30	3.41
	4	8.19	5.54	15.39	11.06	1.99
	5	0.08	4.81	9.10	15.79	15.08
	6	7.49	9.01	13.23	22.71	6.89
	7	15.71	11.64	20.94	13.98	7.62
	8	2.29	1.21	0.00	5.89	0.04
Obs.(based on 25)						
	1	8.00	8.00	23.64	16.00	11.11
	2	16.67	4.17	0.00	8.33	5.88
	3	4.17	0.00	0.00	4.17	5.00
	4	4.17	0.00	4.17	8.33	0.00
	5	0.00	0.00	4.17	12.50	5.26
	6	4.17	4.17	0.00	20.83	5.00
	7	12.50	4.17	26.09	18.33	6.76
	8	0.00	0.00	0.00	4.17	0.00
Sum of ranks						
	1	12	15	18	7	16
	2	13	21	23	21	22
	3	20	24	19	29	14
	4	13	16	11	20	22
	5	27	22	20	17	18
	6	22	13	14	10	12
	7	13	13	12	15	14
	8	24	20	27	25	26

Table 5.14. Correlation coefficients obtained by correlating observed frequency of clones (based on all clones per cross) against predicted frequency (based on 25 clones per cross) estimated by the multivariate probability integral, that are greater than the mean value for total tuber weight, mean tuber weight, number of tubers per plant and regularity of tuber shape.

GH	*0.7506*				
BB-FCY	0.6206	*0.8047*			
MURR-FCY	0.7055	0.7081	*0.7866*		
BB-SCY'	0.0343	0.6131	0.6439	*0.6085*	
MURR-SCY'	0.5128	0.5925	0.5564	0.4895	*0.4190*
	GH	BB-FCY	MURR-FCY	BB-SCY	MURR-SCY

Expected based on multivariate probibility

' = Observed frequencies based on 70 clones per cross, all other observed frequencies are based on 200 clones per cross. Correlations in italics are observed and predicted in the same environment.

Table 5.15. Correlation coefficients obtained by correlating observed frequency of clones (based on all clones per cross) against observed frequency (based on 25 clones per cross), that are greater than the mean value for total tuber weight, mean tuber weight, number of tubers per plant and regularity of tuber shape.

GH	*0.6859*				
BB-FCY	0.3967	*0.5424*			
MURR-FCY	0.5054	0.3795	*0.8207*		
BB-SCY'	0.0050	0.6333	0.5582	*0.5683*	
MURR-SCY'	0.5336	0.7223	0.2192	0.5801	*0.6892*
	GH	BB-FCY	MURR-FCY	BB-SCY	MURR-SCY

Observed percentage based on 25 clones/cross

' = Observed frequencies based on 70 clones per cross, all other observed frequencies are based on 200 clones per cross. Correlations in italics show observed frequencies from the same environment.

Table 5.16. Correlation coefficients obtained by correlating observed frequency of clones (based on all clones per cross) against sum of the rankings of each of the variates total tuber weight, mean tuber weight, number of tubers per plant and regularity of tuber shape.

GH	-0.6314				
BB-FCY	-0.6509	-0.7411			
MURR-FCY	-0.5154	-0.5748	-0.6241		
BB-SCY'	-0.3416	-0.5486	-0.3685	-0.8464	
MURR-SCY'	-0.4564	-0.3825	-0.4268	-0.5534	-0.7408
	GH	BB-FCY	MURR-FCY	BB-SCY	MURR-SCY

Sum of ranking of individual variates

' = Observed percentages based on 70 clones per cross, all other observed frequencies are based on 200 clones per cross. Correlations in italics show that the observed frequencies and sum of rankings are from the same environment.

clone sample. It was found from these regression analysis that, on average, regression of rank sums on to observed frequencies accounted for 23% of the total variation in the observed frequencies while regression of the observed frequencies (25 clones) on to the observed frequencies only accounted for 10% of the total variation in the large sample frequencies.

Both the multivariate probability and observed frequency based on 25 clone sub-samples estimated on seedlings performance in the glasshouse, resulted in an extremely low correlation coefficient when correlated with the observed frequency from BB in the second clonal year. This result was mainly due to the performance of one cross. This cross had the fewest number of tubers per seedling in the glasshouse and a very high number of tubers per plant at BB in the second clonal year. The reason for this is not apparent.

5.3 Cross prediction using parental values.

A half-diallel design (described in Section 2.5) was used to determine the possibility of predicting superior crosses by evaluation of parents. The parents used in the half-diallel were included in the randomisation of the second clonal year trial of the 'D' material. Each parent was grown at both BB and MURR and was replicated four times at each location. From the analyses of variance (Table 5.17) breeders' preference scores were significantly greater ($P<0.001$) at MURR than at BB. Similarly, total tuber weight and mean tuber weights were significantly greater ($P<0.001$) at the MURR site. The effect of parents was only significant for breeders' preference while this effect was non-significant for total tuber yield and the yield components as tested against the interaction of sites by parents. There were, however, highly significant interactions between sites by parents for yield and the yield components. It should be noted that

Table 5.17 Mean squares from the analyses of variance of breeders' preference (Pref), total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT) per plant recorded at BB and MURR for five parent clones used in the half-diallel cross.

Source	df	Pref	TTW	MWT	NT
Sites	1	6.40'''	2.380'''	3019'''	3.80ns
Parents	4	9.49'''	0.076ns	63ns	10.21ns
Sites x Parents	4	1.84 ns	0.417'''	69'''	24.90'''
Error	31	1.192	0.0404	10.8	0.758

ns = not significant; ' = 0.05>p>0.001; '' = 0.01>p>0.001; ''' = p<0.001.

parents and sites were treated as random effects in the analyses of variance (Table 5.17) and hence tested against the site x parents interaction. With respect to breeders' preference this model may be correct in that the parents can be considered as a random sample of cultivars grown in the UK. For the other characters considered however, these parents were deliberately chosen to represent a range of early and late maturing cultivars which also produced a range of tuber numbers and sizes. Hence the random model used may be inappropriate and a fixed model should be employed. When the fixed effect model is applied there were indeed significant differences between parents for both yield components. The choice of site can also be considered to be fixed or random. BB and MURR can be considered as a random seed production site and random ware site but the effect of sites in the analysis must be considered as fixed and hence tested against the error term, although this would not alter the results.

Inspection of the parent means at both sites (Table 5.18) and also their ranking within each site showed that the interactions were more than mere scalar effects. At BB, Wilja was the highest yielding parent (total tuber weight) and Cara was the lowest yielding. When grown at MURR, however, Cara was in fact highest yielding whereas Wilja only ranked fourth. Inspection of rankings within sites for mean tuber weights would suggest that Wilja was largely responsible for the interaction, along with Desiree. Wilja having second heaviest mean tuber weights at BB and ranking last at MURR, while Desiree ranked as having lowest mean tuber weights at BB and produced the heaviest mean tuber weights at MURR. It should be noted that Wilja is a cultivar which is early bulking and Cara matures later than the other parents. The interactions for yield and yield components would therefore be accounted for, at least in part, by the wide range in maturity and bulking rates of the parents coupled to the contrasting

Table 5.18 Average value (plus ranks, in parenthesis) of five parent clones used in a half-diallel cross for total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT) when grown at two locations (BB and MURR).

BB	Pref	TWT	MWT	TN
Pentland Ivory	4.25(3)	1.22(4)	119(2)	10.3(4)
Baillie	4.50(2)	1.61(2)	104(3)	15.4(1)
Wilja	6.00(1)	1.67(1)	128(1)	13.0(2)
Cara	3.75(4)	0.90(5)	106(4)	8.5(5)
Desiree	2.75(5)	1.29(3)	105(5)	12.3(3)

MURR	Pref	TWT	MWT	TN
Pentland Ivory	5.75(2)	1.73(2)	176(1)	9.8(5)
Baillie	4.25(4)	1.73(2)	162(3)	10.7(4)
Wilja	6.75(1)	1.69(4)	152(5)	11.1(3)
Cara	3.75(5)	2.07(1)	153(4)	13.5(1)
Desiree	4.75(3)	1.09(5)	168(2)	11.3(2)

long and short growing season of MURR and BB respectively.

Mean squares from the analyses of variance of 10 progenies (from a 5x5 half-diallel without selfs) grown at BB and MURR are shown in Table 5.19. The effect of progenies was partitioned, according to the method of Griffin (1956), into general combining ability (GCA) and specific combining ability (SCA). In the analyses, the interaction of sites by SCA was consistently smaller than the error (the within progeny variation) and hence this latter term was used to test the other interaction and also the main effect SCA. GCA effects were highly significant ($P<0.001$) for all characters. SCA was significant ($P<0.001$) for mean tuber weight and just significant at the 5% level for breeders' preference. The interaction, sites x GCA, was significant for total tuber weight ($P<0.05$) and highly significant for mean tuber weight ($P<0.001$).

Significant GCA effects from the analysis should indicate a possibility of predicting the performance of crosses according to the phenotype of the parents. Three methods of estimating progeny performance will be considered: (a) Univariate prediction based on performance of seedlings (as detailed in Section 5.2); (b) prediction based on the simplest genetic model, that of mid-parent values and (c) prediction based on mid-self values. The ranking of 10 crosses according to performance averaged between BB and MURR in the second clonal year is given along with the ranking according to univariate prediction on seedlings, mid-parent values and mid-self values (Table 5.20). Visual inspection of the three prediction methods against the observed performance indicates that all prediction methods do in fact provide some indication as to the superior crosses. The accuracy of prediction can be investigated further by correlation of the three prediction methods onto observed progeny performance in the second clonal year (Table 5.21). All correlation coefficients were positive

Table 5.19 Mean squares from the analysis of variance for total tuber weight TTW, mean tuber weight, MTW, number of tubers, NT and breeders' preference, Pref. recorded on a 5x5 half diallel without selfs. (G. C. A. = general combining ability; S. C. A. = specific combining ability)

Source	d. f.	TTW	MWT	NT	Pref
G. C. A.	4	32.97'	9.86ns	4581'''	11.53'''
S. C. A.	5	3.41ns	8.24'''	444ns	4.92ns
Sites x G. C. A	4	4.70'	15.78'''	318ns	2.15ns
Sites x S. C. A	5	0.12ns	1.18ns	174ns	1.37ns
Error	480	1.93	1.73	227	1.92

ns = not significant; ' = $0.05>p>0.01$; ''' = $p<0.001$

Error terms are clones within progenies plus clones within progenies x sites.

Table 5.20 Progeny rankings based on (a) prediction made on seedlings (based on progeny mean and phenotypic variance); (b) mid-parent values; (c) mid-self values; (d) and observed performance of progenies in the second clonal year for breeders' preference (Pref.), total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT).

	Pref.				TTW				MWT				NT			
Cross	(a)	(b)	(c)	(d)	(a)	(b)	(c)	(d)	(a)	(b)	(c)	(d)	(a)	(b)	(c)	(d)
B12	7	5	4	9	10	6	8	10	8	3	3	2	10	7	8	9
B13	8	1	7	1	8	6	8	7	3	2	4	8	6	8	10	7
B14	10	6	10	10	9	10	10	8	1	5	2	1	2	10	9	10
B15	9	6	9	7	7	9	7	9	6	1	1	3	9	9	7	8
B23	5	2	1	2	3	1	3	3	4	6	10	5	1	1	5	4
B24	4	8	3	8	4	4	6	5	2	10	8	9	5	3	4	1
B25	6	8	2	6	6	3	1	6	7	7	7	7	3	2	1	6
B34	3	3	6	4	5	4	5	4	5	7	9	10	4	5	6	5
B35	1	3	4	4	1	2	1	1	10	4	6	4	7	4	3	3
B45	2	10	8	2	2	8	4	1	9	9	5	5	7	6	2	2

Table 5.21 Phenotypic and rank correlation coefficients obtained by correlation of predicted (based on mean and variance of seedlings (Seed), mid-parental values (mid-parent) and mid-self values (mid-self)) onto observed values (mean of progeny at BB and MURR) for breeders' preference (Pref.), total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT).

Phenotypic correlation

	Pref.	TTW	MTW	TN
Seed	0.48	0.90''	0.46	0.11
Mid-parent	0.41	0.55	0.40	0.71'
Mid-self	0.26	0.76'	0.68'	0.79'

Rank correlations

	Pref.	TTW	MTW	TN
Seed	0.48	0.95'''	0.19	0.11
Mid-parent	0.39	0.51	0.48	0.71
Mid-self	0.16	0.72	0.68	0.80

' = $0.05>p>0.01$; '' = $0.01>p>0.001$; ''' = $p<0.001$; all other coefficients are not significant.

although more than half of them were formally short of significance. Univariate prediction based on the mean and variance of crosses as seedlings provided the best indication of breeders' preference while the mid-self value was least accurate for this character. Total tuber weight was also most accurately estimated by seedling evaluation. Linear regression of predicted from seedlings onto performance in the second clonal year accounted for 81% of the variation in the later generation. For total tuber weight, mid-self value provided a better estimation of progeny worth than the mid-parent value. The most accurate estimation for both yield components was found from the mid-self values, accounting for 50% and 62% of the total variation in the second clonal year for mean tuber weight and number of tubers respectively.

Until now, predictions have been based on the average performance of parents, self and also progenies between BB and MURR. From above, it has been shown that the five parental clones were of contrasting types and resulted in large genotype by environment interactions when grown at BB and MURR. Correlation between predicted (based on mid-self and mid-parent) at each individual site showed a consistent tendency for higher correlation between predicted and observed in a common location rather than predicted in one environment and observed in the other (Table 5.22). Some of these relationships were large. For example, consider the mid-parent predictions first. When the predictions were made from parental data collected at BB, correlation between predicted and observed were higher at BB than MURR for breeders' preference, total tuber weight and mean tuber weight and equal for number of tubers. When predictions were based on parental performance at MURR, however, correlation coefficients between predicted and observed were always of higher magnitude, in a number of cases significantly so, at MURR rather than at BB. An almost identical result was found when the mid-self predictions were

Table 5.22 Phenotypic correlations between predicted (based on mid-parent and mid-self) and observed values of 10 crosses for breeders' preference (Pref.), total tuber weight (TTW), mean tuber weight (MWT) and number of tubers (NT).

	Pref.		TTW		MTW		TN	
	BB	MJRR	BB	MJRR	BB	MJRR	BB	MJRR
BB -Mid-parent	0.31	0.25	0.27	0.01	0.47	-0.17	0.31	0.31
MJRR -Mid-parent	0.35	0.40	0.02	0.35	-0.12	0.57	0.50	0.53
BB -Mid-self	0.37	-0.21	0.63	0.78	0.26	-0.54	0.48	0.54
MJRR -Mid-self	0.04	0.59	0.82	0.84	-0.11	0.82	0.67	0.74

' = 0.05>p>0.01; '' = 0.01>p>0.001.

Coefficients in italics are predicted and observed in a common environment.

examined. Overall therefore, prediction by mid-parent or mid-self is affected by the environment in which either the parents or selfs are evaluated or in which its progenies are grown.

When the GCA effect is large in relation to SCA effects it is not only posible to identify the superior crosses but also the better parents. Inspection of the third clonal year performance of progeny in which each parent featured (i.e. each parents general combining ability), its parental performance, the performance of selfs and also the average performance of glasshouse grown seedlings in which the parent featured (Table 5.23) showed that again some degree of prediction was possible. Wilja was assessed as the better parent at the seedling stage, the better parent on parental evaluation and also the parent which showed highest mean progeny performance in the second clonal year. Pentland Ivory was the lowest yielding parent, was the parent with the lowest yielding self, produced seedlings with lowest yield and also gave the lowest GCA. Wilja was found to be highest yielding and was ranked second, first, and second when seedlings, parents and selfs, respectively were examined. The yield components were also dominated by the parent Pentland Ivory which consistently produced large tubers (heaviest total tuber weight) and also fewer tubers than the other parents.

The accuracy of parent assessment was also considered by correlation of predicted by seedling evaluation, by parent evaluation and by self evaluation onto GCA (Table 5.24). All correlations were positive but, with one exception, were not significantly greater than zero. It should however be noted that these coefficients were based on only 4df. Over the three prediction methods, evaluation of seedlings in the glasshouse provided the best estimate of breeders' preference, mid-parent predictions provided the best estimate of total tuber weight while mid-self values gave the highest correlations for

Table 5.23 Parental worth determined by average ofspring grown as seedlings (Seed), parental expression (Parent) and average expression of selfs along with progeny performance in the second clonal year (SCY) of the five parental lines Pentland Ivory (PI), Baillie (Ba), Wilja (Wi), Cara (Ca) and Desiree (De) for breeders' preference (Pref), total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT).

Pref.	Seed	Parent	Self	SCY
PI	0.079 (5)	5.00 (3)	2.55 (5)	3.91 (5)
Ba	0.181 (4)	4.37 (4)	3.48 (1)	4.06 (3)
Wi	0.245 (1)	6.37 (1)	3.22 (3)	4.46 (1)
Ca	0.198 (3)	3.75 (5)	2.68 (4)	4.05 (4)
De	0.240 (2)	4.50 (3)	2.84 (3)	4.19 (2)

TTW	Seed	Parent	Self	SCY
PI	0.029 (5)	1.47 (5)	0.67 (5)	1.24 (5)
Ba	0.168 (4)	1.67 (2)	0.96 (3)	1.38 (4)
Wi	0.226 (2)	1.68 (1)	0.98 (2)	1.55 (1)
Ca	0.213 (3)	1.49 (4)	0.88 (4)	1.43 (3)
De	0.262 (1)	1.59 (3)	1.06 (1)	1.45 (2)

MWT	Seed	Parent	Self	SCY
PI	0.216 (2)	150 (1)	49 (5)	123 (1)
Ba	0.161 (4)	133 (4)	101 (3)	110 (4)
Wi	0.169 (3)	142 (2)	97 (4)	107 (5)
Ca	0.237 (1)	129 (5)	112 (2)	115 (2)
De	0.068 (5)	139 (3)	129 (1)	112 (3)

TN	Seed	Parent	Self	SCY
PI	0.082 (5)	10.1 (5)	6.2 (5)	11.2 (5)
Ba	0.208 (1)	13.1 (1)	11.2 (2)	13.8 (4)
Wi	0.175 (2)	12.0 (2)	10.4 (4)	14.9 (1)
Ca	0.140 (3)	11.0 (4)	10.8 (3)	14.0 (3)
De	0.078 (5)	11.8 (3)	11.9 (1)	14.2 (2)

Table 5.24 Correlation coefficients between predicted parental performance, based on seedlings progeny trial (Seed), mid-parent (Mid-Par) and mid-self (Mid-Self) values and observed preformance for breeders' preference (Pref), total tuber weight (TTW), mean tuber weight (MTW) and number of tubers (NT).

	Seed	Mid-Par	Mid-Self
Pref.	0.73	0.77	0.48
TTW	0.95'	0.52	0.84
MWT	0.48	0.43	0.89
TN	0.49	0.67	0.90

' = 0.05>p<0.01; all other coefficients are not significant.

mean tuber weight and number of tubers.

5.4 Discussion and Conlusions.

For the character overall breeders' preference, the mean and σ provide a good prediction of the number of clones that will exceed (or equal) a given target value. These predictions hold good over a number of years at two contrasting locations. Further, it was clear that σ added increasingly to the accuracy as the target value increased but was not a major component in the prediction. It was therefore not surprising that using the mean alone gave acceptable predictions. Another method of prediction which utilised the observed number of clones in a sample to predict the number that would be obtained in larger samples and in different environments was also satisfactory.

Plant breeders are generally more concerned with the ranking of crosses, in terms of their ability to produce commercial cultivars, than the predicted numbers per se. When predictions were carried out on this basis rank correlations showed good agreement between observed and expected. There appeared to be a slight tendancy for the predictions to agree more closely with observations at the same site than at the other site, when averaged over years. This tendency was not great but might need to be taken into account in a plant breeding programme where large numbers of progenies are being handled and hence even small differences could produce effects of practical significance.

Although univariate cross prediction was only considered for one of the variates, breeders' preference, the correlation between progeny means recorded in the early generation with those in the later generations indicated that such prediction methods would have been applicable for any of the characters measured.

When multivariate predictions were considered, all three methods used to predict which crosses would produce the highest frequency of clones in the later generations, having expression greater than the targets for four variates simultaneously, proved to be successful. However, cross prediction based on the evaluation of the multi-normal distribution was best. It was found that even when the cross means, within progeny variances and correlation between variates were estimated in the most atypical potato growing environment, that of seedlings grown in a glasshouse, a good indication of the frequency of clones that would transgress the target values was obtained. Predicting the frequency of clones that would transgress the target values was poorest when they were estimated from the observed frequencies on a sample of 25 clones. This prediction only accounted for 10% of the variation in the observed frequency of a larger sample in a later generation. The weakness of these latter estimations is almost certainly due to the effects that sampling variation can play when so few clones are involved. Inspection of Table 5.12, where a 70 clone sample was used showed that correlations between such predicted frequencies and those observed were considerably larger. This supports the contention of the overriding effects of sampling variation when using the observed frequency in a sub-sample as a prediction system unless the number of clones is reasonably large, at least larger than 25.

It was interesting that the relative magnitude of the sum of ranking gave a good estimate of the observed frequency that exceeded the target values. This is perhaps not surprising as the target values set were in fact the mean value of each variate, averaged over all clones and crosses. From Section 5.2 it was found, in univariate prediction, that the genotypic, or phenotypic, variance of each cross added little to the univariate prediction. It was, however, observed

that the within progeny variance became of greater importance when the target value was increased. Perhaps the same would be true here. With the target value set as the mean of each variate, then the cross means (directly related to the ranking) are of greatest importance. If, however, the target values are increased, the variance of each variate and also the covariance between variates are likely to be increasingly important in the predictions. In these cases the sum of rankings would not provide such a good prediction since they are only based on the mean value of each variate for each cross. With the use of electronic computers it is now relatively easily to calculate areas under a multi-normal distribution (Caligari et al., 1985). The method of cross evaluation for more than a single character using the sum of ranks could however be useful in cases where computers are not available, or where many crosses are to be examined.

The clones examined in this study were entered into the normal selection scheme of the potato breeding department at SCRI. Athough the clones were a random sample, in that no selection had been carried out before they were included into the breeding scheme, they were entered to the third clonal year stage of the breeding scheme in 1984. Since that time they have been subject to the same selection criteria as the clones that were already in the system. The number of clones from each cross that were considered suitable for re-trial in the fourth, fifth and sixth clonal year (1985 to 1987 inclusively) are shown in Table 5.25. Alongside these data are the cross rankings, according to the univariate predictions on breeders' preference (Table 5.25a) and also the multivariate probability predictions (Table 5.25b) estimated from seedlings and also from BB and MURR in the first clonal year. The first point to note is that there were only 39 selections which merited re-trial in the sixth clonal year from all the seedlings that were grown in 1981. Clones which derived from this experiment accounted for just under one quarter of these. Insofar as these

Table 5.25a. Cross rankings according to univariate probability predictions based on overall breeders' preference ($\bar{x}$ plus σ) estimated on seedings in the glasshouse (GH) and at BB and MURR in the first clonal year. Also the number of clones from each cross which were selected for re-trial in the fourth, fifth and sixth clonal year stage of the commercial breeding scheme at SCRI.

Cross	GH	BB FCY	MURR FCY	Number of clones that survived to year Four	Five	Six
C1	1	5	7	15	3	2
C2	3	2	4	9	3	2
C3	6	7	5	1	0	0
C4	4	4	6	2	0	0
C5	8	8	2	10	3	1
C6	5	3	3	11	6	1
C7	2	1	1	12	7	3
C8	7	6	8	0	0	0

Table 5.25b. Cross rankings according to multivariate probability predictions estimated on seedings in the glasshouse (GH) and at BB and MURR in the first clonal year. Also the number of clones from each cross which were selected for re-trial in the fourth, fifth and sixth clonal year stage of the commercial breeding scheme at SCRI.

Cross	GH	BB FCY	MURR SCY	Number of clones that survived to year Four	Five	Six
C1	3	2	2	15	3	2
C2	2	4	5	9	3	2
C3	6	8	7	1	0	0
C4	4	5	3	2	0	0
C5	8	6	6	10	3	1
C6	5	3	4	11	6	1
C7	1	1	1	12	7	3
C8	7	7	8	0	0	0

clones were derived from a random sample of only 200 clones (25 from each of eight crosses) at the third clonal year stage, selection carried out in the normal breeding scheme appears not to have been very effective before the third clonal year stage.

The cross which was ranked highest according to the multivariate probability prediction based on four variates and also ranked second or highest in the univariate prediction (C7) provided 12 clones for re-trial in the fourth year, 7 in the fifth year and 3 in the sixth year trials. Over all crosses, there is good agreement between the rank at the seedling or first clonal year stage and the number of clones that survived selection. Correlation between the rank of crosses at the seedling and first clonal year stage and the number of clones that survived commercial selection are shown in Table 5.26a and 5.26b. Inspection of the multivariate predictions showed that five correlation coefficient, from the possible six, between predicted ranking from the first clonal year and clones that survived to later stages in a breeding scheme, were significant. The other coefficient being was just short of significance at the 5% level. Correlations between univariate prediction ranks and the number of surviving clones were of a similar magnitude to the multivariate ones. Overall however, the multivariate predictions proved a better indication of progeny worth than the univariate of breeders' preference. The correlation between multivariate predicted ranking estimated from seedlings were in general lower than those from the first clonal year trial. They were, however, sufficiently large in magnitude to suggest that even these predictions would have merit in a potato breeding scheme. There was no increase in accuracy between the seedling and first clonal stage when univariate predictions were considered.

Analyses of a half-diallel resulted in a predominance of GCA effects for breeders' preference, total tuber weight and number of

Table 5.26a Correlation coefficients obtained by correlating the cross ranks of the univariate probability predictions of overall breeders' preference in the glasshouse (GH) and at BB and MURR in the first clonal year with the number of clones that were selected for re-trial in the fourth, fifth and sixth clonal year stage of the commercial breeding scheme at SCRI.

	Rank of crosses based on univariate probabilities		
	GH	BB-FCY	MURR-FCY
Survived to fourth year	-0.56	-0.38	-0.36
Survived to fifth year	-0.41	-0.62	-0.69
Survived to sixth year	-0.70	-0.65	-0.54

Table 5.26b Correlation coefficients obtained by correlating the cross ranks of the multivariate probability predictions in the glasshouse (GH) and at BB and MURR in the first clonal year with the number of clones that were selected for re-trial in the fourth, fifth and sixth clonal year stage of the commercial breeding scheme at SCRI.

	Rank of crosses based on multivariate probabilities		
	GH	BB-FCY	MURR-FCY
Survived to fourth year	-0.47	-0.79	-0.68
Survived to fifth year	-0.81	-0.85	-0.70
Survived to sixth year	-0.50	-0.86	-0.62

tubers while SCA effects were large for mean tuber weight. This was in contrast to results found by other workers. Rowell, Ewing & Plaisted (1986) also found significant GCA for yield and tuber characters when hybrids between Neotuberosum and S. tuberosum were examined as did Masson (1985) who examined 4x hybrids by first division restitution crosses between 4x and 2x material. In both these studies the parental material was genetically diverse and in cases where a broad genetic base exists between parents the SCA effects are expected to be reduced (Phillips & Dale, 1982). Although all parents used in this study were S. tuberosum ssp. tuberosum they were from different origins. The clones Pentland Ivory and Baillie were from the SCRI breeding programme, Desiree and Wilja were from Dutch breeding programmes and Cara was bred at the Oak Park Research Institute, Eire. They are therefore perhaps representative of a wide genetic base and this may have increased GCA over SCA effects.

It was possible to obtain an indication of progeny worth by evaluation of parental clones and using the simplest genetic model of mid-parent values. The predictions were, however, greatly influenced by prediction x environment interactions. Predictions when parents were grown at MJRR were only useful in predicting performance of progeny at that site and visa versa at BB. If parental predictions are to be useful in a potato breeding programme then it is essential that the parents are evaluated under the environmental conditions that the eventual cultivars will be grown. It may in fact be necessary to evaluate parents at many locations, and perhaps also over a number of years, before accurate estimates can be made. Results did however show that parental predictions would be useful if only to eliminate the worst parents. Clones from the half-diallel study were, like the 'A' material, entered and evaluated alongside clones from the normal breeding material from the SCRI potato breeding programme. To date these clones have been evaluated in the system for three years and

clones have only continued in the scheme if they satisfy the standard selection criteria. From amongst the five clones examined Pentland Ivory was shown to be the worst parent for all characters except mean tuber weight. After three rounds of selection only three clones have survived in which Pentaland Ivory featured as a parent. Predictions based on seedling performance and also mid-parent performance ranked the cultivar Baillie fourth and this parent contributed only four clones to the standard SCRI fifth clonal year trials. The other three parents were shown to have greater merit, according to the predictions, and this was again reflected in that Wilja contributed eight clones, Desiree contributed nine clones and Cara contributed ten clones to the later stage in the breeding scheme. The ranking of parental worth according to either seedling performance, mid-parent or mid-self performance did not give an exact relationship to the number for survivors at the later stages in a breeding scheme. It is interesting to note however that cross prediction of seedlings can provided a good prediction of the better parents as well as identifing the superior cross combinations. Also, mid-parent or mid-self values allowed at least the worst parents to be identified.

Mid-self values provided a good prediction of progeny worth, in most cases a more accurate estimation than the mid-parent. Estimating parental worth using a single test cross was found to correlate highly with the estimation where four test crosses were used (Rowell et al., 1986). It is possible therfore that selfing has much the same effect as a single test cross system. Although mid-self values provided better predictions than mid-parent, it should be remembered that evaluation of selfs will be more time and labour intensive than simply evaluating parents. Neither mid-parent or mid-self predictions were as good in predicting either total tuber weight or breeders' preference than evaluating seedlings in the glasshouse.

Overall therefore it is suggested that parental assessment should be employed in order that only the most undesirable parents are not used in crosses hence saving time and resources. Both univariate and multivariate cross prediction is possible in the early generations of a potato breeding programme and either can be used to identify superior cross combinations of superior parents. Greater accuracy of estimating the superior crosses, as measured against the proportion of advanced clones with each progeny, was by multivariate, over univariate, prediction. It should however be added that breeders' preference scores can be assessed relatively quickly, and hence offer the prospect of assessing many more crosses than would perhaps be possible if each indivudual seedling or first clonal year plant requires to be weighed and tubers counted. It is therefore the simplest assessment which will probably be most useful when applied on a large scale.

CHAPTER 6

FINAL DISCUSSION AND CONCLUSIONS

Potatoes are still one of the world's major food crops. In terms of total world output they are only surpassed by wheat, corn and rice. The importance of the crop is, therefore, obvious and the potential contribution made by potato breeders to the world food supply is great. Despite the lengthy process of breeding a potato variety, a newly introduced cultivar will only remain on the Official List of cultivars for an average of 7.5 years (Hoppner, 1978), with only one variety in ten remaining on the list for more than 20 years (Hunnius, 1975). If breeding objectives are to be efficient, breeders must attempt to predict the likely market needs of the future crop some 10 to 20 years hence. Moreover, they must aim to ensure that a proper breeding and selection strategy is adopted such that the probability of success is maximised.

In recent years, there has been a tremendous research effort in the development of genetic engineering and novel *in vitro* techniques, some of which will have uses in plant breeding. In fact, the regeneration properties of potatoes make this crop ideal for the utilisation of such techniques. Although a lengthy discussion of these techniques is outwith the scope of this study, it would be wrong not to consider the possible implications of these new technologies to future potato variety production. Most of the new techniques are concerned with the control and induction of genetic variability, and are, therefore, likely to affect the organisation of and strategies used in a breeding programme.

Potatoes can be infected by *Agrobacterium tumefaciens*, an organism that is used as a vector to transfer new genes into chromosomes of many dicotyledonous species (Flavell, 1987). A major difficulty associated with this form of gene transfer arises in the identification of a gene, or genes, of interest; the extraction and

cloning of these genes; insertion of them into a suitable genotype; ensurance that the genes are functional only in specific desired areas of the plant; and finally, absence of deleterious non-allelic interactions with the host genotype. Despite these difficulties, the potential to plant breeding of the transfer and function of specific gene insertions could be immense. Gene insertion techniques are however, a long way removed from becoming routine procedures. It may therefore, be many years before such techniques realise their full potential. There is also difficulty in handling characters controlled by polygenic systems.

Plants which are regenerated from callus tissue (somaclones) may exhibit differences from the original genotype (Shepard, 1982). It has, therefore, been suggested that somaclonal variation can be used to remove defects from present cultivars. Variation in plantlets regenerated from callus tissue has been observed for a range of characters, albeit limited in number (i.e. resistance to Streptomyces scabies Gunn, 1982). However, in many respects somaclones are identical to the parent cultivar from which they were derived (Secor & Shepard, 1981). The occurrence of somaclonal variation may, therefore, hinder other techniques which involve in vitro culture (where variation is not desirable) rather than provide useful variation for future plant improvement.

Protoplast fusion (somatic hybridisation) offers more prospect to potato breeders. However, regeneration of plants from isolated wall-less cells (protoplast) does however show a marked genotype response (Jones, 1987). The aim of somatic fusion is to hybridise selected dihaploid protoplasts or to hybridise dihaploid clones with diploid wild species. The use of somatic fusion will, therefore, offer breeders a greater range of possible hybrid combinations than might be available with traditional sexual hybridisation. The most

difficult aspect of this technology, however, concerns the selection of fused heterokaryons from unfused or self-fused parental protoplasts.

Most of the novel techniques currently being investigated require in vitro propagation at some stage. This provides opportunities for some degree of selection at the in vitro stage. Indeed it is possible to extract exotoxins from abiotic cultures of P. infestans and use these to identify blight resistant plantlets in vitro (Behnke, 1979). It is also possible to select for herbicide resistance/tolerance in vitro (W. de Greef, Plant Genetics Systems Ltd., 1988, personnal communication).

In addition to genetic engineering and in vitro work other avenues are being explored. Although most potato breeding in the Northern hemisphere is conducted at the tetraploid level, in recent years there has been increased interest in breeding at the diploid level. It is now a relatively standard procedure to produce dihaploid plants (2x=2n=24) from tetraploid clones through parthenogenisis following hybridisation between S. tuberosum and selected clones of S. phureja (Hougas & Peloquin, 1957). Pollination of S. tuberosum with S. phureja produces a mixture of tetraploid, triploid and dihaploid offspring. After discovering plants of S. phureja that act as good male parents, and which are homozygous for a seed marker (Hermsen & Verdenius, 1973), female parthenogenesis has become a routine method for producing many thousands of diploids in a single season (Van Breukelen, Ramanna & Hermsen, 1977). Such dihaploids can of course form part of the genetic base in a diploid breeding scheme, and in general, diploid breeding offers several advantages over tetraploid breeding. Diploids are more readily crossed with wild species, which are predominantly diploid. Moreover, in theory, it takes fewer rounds of recurrent backcrossing to eliminate any undesirable wild species

genes. Finally, by using diploids it should be possible to obtain a better understanding of the inheritance of quantitative characters; also parental clones which are multiplex for important qualitative characteristics are more easily obtained. Set against these advantages, it is unlikely that commercial cultivars will be developed at the diploid level as they lack vigor. Therefore, it will be necessary to return to the tetraploid level as a final stage in variety production (Hermsen, 1977). This would be accomplished by mitotic doubling or through protoplast fusion.

One possible development which would have a great impact on potato breeding strategy would be the combination of monohaploid breeding and protoplast fusion (Hermson, 1977). Monohaploids can be produced from tetraploids by anther culture, parthenogenesis (see above) or a combination of both techniques. Colchicine-doubled monohaploids are completely homozygous diploid potatoes. Hence monohaploids and doubled monohaploids offer the prospect of producing hybrid varieties as in F_1 and double cross hybrids in maize. The majority of doubled-monohaploids already produced are pollen sterile (Van Breukelen et al., 1977) and hence conventional sexual hybridisation between them is not possible. This problem can, however, be overcome by somatic hybridisation techniques.

Another development which has yet to be achieved on a routine basis in potatoes involves reproduction via apomixis (Hermsen, 1980), i.e. asexual production of true botanical seed. If apomixis became available and easily applicable to potatoes, it might lead to a major change in the way that the crop is grown and bred. All seeds produced by apomixis would be genetically identical, although each seed may be highly heterozygous in itself. The advent of apomixis would surely result in a far higher proportion of the potato crop, especially in warmer regions, being grown from true potato seeds (TPS). The primary

disadvantage of TPS production at present is the lack of uniformity in the crop. In regions not suited for TPS production, first clonal year seed tubers would be grown. Using true potato seedlings many of the diseases which are transmitted by seed tubers would be reduced and hence would not need to be considered in the breeding objectives. If apomixis is to be used in potato production it must be relatively easy to develop. The best method would perhaps be by chemical induction. Very little has been published on chemical apomixis, although some success has been reported by Iwanaga (1983). Chemically induced apomixis would, of course, be patented and hence offer the prospect for large financial gains to the developing company and this may in part have limited the amount of published works in this area.

Combining monohaploid and doubled-monohaploids with advances in protoplast fusion and the development of apomixis in potatoes would therefore offer potato breeders the possibility of a different approach. Hybrid varieties could be developed where the breeders have far greater control of the genetic constitution. Once produced, these cultivars would be multiplied by apomictic techniques hence avoiding many of the inherent difficulties of seed tuber health.

Despite all the progress achieved in the development of "novel techniques" and gene transfer systems in recent years and the potential that such techniques offer plant breeders, it is likely that traditional potato breeding methods will predominate for a great many years to come. It should also be noted that the products of a non-conventional breeding system will still need to be subjected to the rigorous selection procedures that are imposed in a traditional breeding programme. The new methods are, therefore, just as likely to fail through ineffective selection procedures methods, as are the more traditional schemes studied in this thesis. The results found in this thesis will, therefore, also have relevance if, or when, these

non-conventional techniques are routinely used. In any case, such techniques are unlikely to be of use in handling a range of qualitative characters all at one time.

In simple terms, desirable traits are either qualitatively or quantitatively inherited. Qualitatively inherited characters are little affected by environment and hence do not pose great problems of selection to breeders. Indeed, a number of important major gene characters can be effectively selected in the early generations of a potato breeding scheme. This is true especially for the single gene (H_1) which confers resistance to potato cyst nematode (G. rostochiensis), and the genes Rx and Ry which offer resistance to virus X and Virus Y, respectively. It should, however, be ensured that selection for major gene characters does not adversely affect the population for other important traits.

Major gene characters can also be handled by multiplex breeding (Toxopeu, 1953). The aim of multiplex breeding is to produce parents which are either triplex (AAAa) or quadriplex (AAAA) for one, or more, important dominant major genes. When used as one of the parents in a tetraploid cross, there will be no need to test for the presence of the gene amongst the progeny, as (in the absence of double reduction) each clone will contain the gene, at least at the simplex (Aaaa) level. It was believed at first that the production of multiplex parents would be a long and laborious task. If, however, suitable progeny screens are available, the procedure can be relatively simple, enabling rapid success (Mackay, 1987). The production of multiplex parents can be further accelerated by the production of dihaploids.

In general, it is the quantitatively inherited characters which pose the greatest difficulties to breeders, as well as to novel technologists and microbiologists. Arguably, these characters are also those of greatest value in a breeding programme (ie. yield,

quality or horizontal disease resistance).

In potatoes, high heterozygosity is believed necessary for high vigour and yield (Simmonds, 1969). It has been argued on theoretical grounds, that heterosis is not dependent on overdominance *per se*, but is rather a consequence of the dispersion of dominant alleles (Jinks, 1983). Therefore, it should be possible to obtain homozygous segregants of high fitness through inbreeding. This theory has been substantiated in *Nicotians rustica* (Jinks, 1981) and *Hordeum vulgare* (Caligari, Powell & Jinks, 1987) where inbred lines have been found which surpass the performance of both parents and also the "heterotic" F_1. In potatoes, Trinkler, Kalachev & Matenkoya (1976) were able to select clones from selfed crosses that showed little or no inbreeding depression. Moreover, it has also been reported (Trinkler, Denisova & Mikhalev, 1980) that no inbreeding depression in true potato seed performance occurs in secondary inbred lines. However, most inbreeding studies on potato have not continued past the first round of selfing (Atlin, 1985) so the full immplications of inbreeding depression have still to be evaluated. In any event, it is unlikely that homozygous potatoes will be produced by selfing, because of the resulting pollen sterility problems.

The high heterozygosity in potato parental lines leads to the segregation of many important characters following crossing, and because of the vast array of recombinant genotypes produced, there is a very low probability of detecting superior genotypes. It follows that to breed an improved variety, an enormous number of seedlings must be raised each year.

Despite these difficulties, it was established from the work conducted for this thesis that out of a random sample of 200 clones of the 'A' material (derived from eight different crosses) nine clones had sufficient merit to be trialled at the stage of the sixth clonal

year. From all of the breeding material generated at SCRI in the year that the 'A' material was produced, only another 28 clones, from many thousands of seedlings raised, were carried forward to the same stage of selection. Hence, based on these findings, it appears that the frequency of potentially desirable clones is much higher among segregants of a cross than previously believed. One might conclude, therefore, that in future it may not be necessary to begin a potato breeding programme with the large number of seedlings that are conventionally grown, especially if, as shown here, selection in the first two years brings about, at best, only a random reduction in the number of clones.

Maris (1964a) and Tai & Young (1984) obtained similar results to those found in this study when they examined early generation selection efficiency. Their correlation studies between successive assessment years gave coefficients of a similar magnitude to those obtained here. The conclusion of these authors was that only negative selection should be carried out at the seedling and first clonal year stage. By this they indicated that only the very worst genotypes should be discarded. The efficiency of selection, in this, and almost all previous instances, was examined in randomised, and occasionally replicated, experiments. The accuracy of estimation from these studies are, therefore, likely to overestimate the actual efficiency which will exist when selection is carried out in practice where many more genotypes are evaluated and in most cases without either randomisation or replication. Taking this into account it must be seriously questioned as to the profit in carrying out relatively accurate assessment trials with the prospect of only rejecting a small proportion of material, especially as there has been a suggestion in this study, and also that of Anderson & Howard (1981) that selection was in fact having a negative effect. It would surely be more beneficial simply to multiply seed tubers from clones until the

necessary quantities were available to allow assessment trials which would give a truer indication of genotypic worth.

Results from this thesis showed the cause of ineffective selection in the early generations to be complex. The efficiency of selection could have been slightly improved by delaying single plant selection until field grown tubers were available for planting, evaluation of clones at more than a single site and by increasing pot size used at the seedling stage and also plot size in field assessment trials.

Seed tuber size planted in the first clonal year had a large effect on yield, mean tuber weight and the likelihood of selection. To avoid the effects of seedling-produced seed tuber size variation, it has been suggested that seed tubers should be size graded before planting so that comparisons can be made between clones with a more uniform seed tuber size (Lowes & Neele, 1987a). It has also been suggested in first clonal year yield studies that the weight of seed tubers should be subtracted from the first clonal year yield in order that any potential bias is removed (Lundu, 1960). If the size of seed tuber planted at the first clonal year was the only factor affecting the inefficiency of selection then any, or both, of these suggestions might have merit. However, this effect, although major, was only one of the measurable, contributing factors observed in the present studies and hence would not justify the extra time or resource that their employment would necessitate. The overriding conclusion, therefore, did not change, that selection for quantitativley inherited tuber characteristics on individual clones should not be practiced in the first two growing years of a potato breeding programme.

Experiments conducted in the present study were only concerned with the efficiency of selection for yield and other tuber characters, as these are the ones on which the majority of early generation

selections are based. It is, however, feasible that clone numbers could be reduced by early generation selection for other traits (Lacey, Jellis, Carrel & Starling, 1987). Indeed there is evidence that polygenic resistance to Phytophthora infestans can be identified at the seedling stage (Caligari, Stewart & Waistie, 1983; Caligari, Mackay, Stewart & Waistie, 1985). It has also been suggested that mild selection for fry colour on seedling tubers is possible (Louwes & Neele, 1987b). A degree of caution should, however, be attached to the work on fry colour as these conclusions were based on growing cultivars in pots under glass rather than by evaluation of true seedlings. It should also be noted that selection for any trait, as well as needing some degree of efficiency, must be shown not to adversely effect other more important characters. Selection for resistance to several diseaseswas found to cause undesirable shifts in the population for other traits (Plaisted et al., 1984). For example, there is a tendancy for clones resistant to foliage blight (Phytophthora infestans) also to be late maturing. Therefore, if early maturity is desired, selection for blight resistance should be attempted with caution.

Breeders have, for manyyears, suspected that selection for most characters, in the early generation was not effective. However, there seemed to be no alternative available to those who believed that large numbers were needed to achieve success. The results from this thesis are that cross prediction would be a powerful tool in identifying superior cross combinations and also in identifying desirable parents in the early generations of a breeding programme. It, therefore, offers an alternative to the ineffective selection of individual genotypes at these stages.

In this study, cross prediction was only investigated with relatively few crosses compared to the numbers which are likely to be

evaluated in a practical breeding programme. Brown, Caligari, Dale, Swan & Mackay (1988) however have completed a subsequent study (as a result of findings presented in this thesis) and examined the progeny from 191 crosses. Their findings were in agreement with the results found here. The system that is now used in the early generations of the Potato Breeding Department at SCRI is to evaluate 200-300 crosses each year at the seedling stage. The evaluation is based on breeders' preference of 2, or more, breeders independently. The superior 10%-20% of crosses are identified and larger quantities of seed from these crosses are sown, and grown as seedlings and first clonal year single plants without selection. It is only after this that any selection of individual clones is carried out. This system has been in operation now for four years and the first batch of resown material has reached the stage of yield trials. Far fewer individual seedlings have been raised although the indications are that the general standard of clones is superior for yield and most other tuber characters than those previously observed.

Cross prediction has several advantages over the more traditional methods of potato breeding. First, it allows effective selection to be carried out amongst glasshouse grown seedlings. This study has shown that even with glasshouse grown seedlings, the most atypical environment, progeny assessment, as opposed to individual clone selection, can be effective. This is the stage where most clones can be easily grown. Thus selection pressure can be increased by screening large numbers of crosses at this stage. Secondly, if the progeny sample assessed is representative of the whole progeny then, effectively, the breeder is assessing the whole potential of the cross i.e. as though he had grown a progeny of infinite size from the cross. Thirdly, the technique can provide the basis for rapidly assessing the success of parental genotypes in producing desirable progenies without delaying these decisions until long term selection

data are available (as suggested by Tai, Jui, & Young, 1986). It therefore allows selection to be practiced among the multitude of parental genotypes that are available and increases the power of selection that the breeder can apply. Fourthly, because of the simplicity of the trials that are needed (Brown et al., 1988) and the fact that only a sample of clones is required, the material can be tested in many different environments. Finally, it is easy to extend this approach to encompass more than one variable. Indeed at SCRI cross prediction has not only been successfully carried out over the last three years for mean preference but also crosses have been assessed for resistance to tuber blight and foliage blight (Caligari et al. 1983; Caligari et al. 1985), as well as potato cyst nematodes (G. pallida) Pa2/Pa3 (Phillips, 1981) and potato leafroll virus (Solomon, Brown & Mackay, 1987). Investigations are presently underway to extend the use of such cross prediction techniques to cover resistance to common scab, gangrene, tobacco rattle virus and to assess cooking quality characters such as after cooking blackening and fry colour.

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