G.J. Jellis & D.E. Richardson (eds.), The Production of New Potato Varieties: Technological Advances. Cambridge University Press, pp. 248-261.

BREEDING STRATEGIES FOR TRUE POTATO SEED

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INTRODUCTION

The utilization of true potato seed (TPS) for potato production has developed rapidly in many parts of the world since 1978, when TPS was adopted as a principal research programme at the International Potato Center (CIP) in Peru. By 1984, the range of TPS activities had become extensive (International Potato Center 1984). In 34 countries, research on TPS was being conducted at the experiment station level, while 10 countries were involved in on-farm research. TPS was being used at that time by farmers in Sri Lanka, the People's Republic of China, Rwanda, Samoa and in the Philippines.

Much of the early work on TPS agronomy was carried out using open pollinated seed collected from cultivars which produced large quantities of true seed. One of the problems with this true seed was the heterogeneity of some of the progenies, because of the high heterozygosity of the mother plants, which could not be compared with clones in terms of uniformity. Initially it was felt that complete uniformity might not be necessary for potatoes from TPS. Researchers at CIP had been encouraged in this belief by the fact that they had observed farmers in Costa Rica (Central America) mixing white-skinned and red-skinned varieties at harvest. It was thought that this might also be typical of the situation in other countries. Subsequent studies have indicated however that uniformity is important, not only with regard to phenotype in the field, but also with regard to maturity, pest and disease resistance and cooking quality. Uniformity must be given due consideration in any breeding programme if potatoes from TPS are to achieve their potential in many countries.

This review of breeding for TPS covers some of the genetical studies which have formed the basis of breeding research, the breeding schemes which are currently having most impact, namely the use of hybrid progenies from 4*x* x 2*x* crosses and open pollinated progenies, as well as longer term research on inbreeding and apomixis. Aspects of seed production are discussed in relation to breeding priorities as well as some points concerning the types of potatoes to be raised from true seed.

THE NATURE OF GENETIC VARIABILITY FOR TPS TRAITS

When research commenced in the late 1970s, little was known about the genetic basis and inheritance of traits such as berry number, per cent seed germination and transplant survival, which were considered to be important for potatoes grown from true seed. Furthermore characters such as seedling vigour and uniformity had never been previously considered in the context of a field crop of potatoes, as all breeding efforts prior to this time had concentrated on the production of clonally propagated varieties. The determination of the heritabilities of these traits in different progenies has provided a basis for much of the breeding research.

The estimation of genetical parameters for TPS traits has been undertaken in CIP and at Cornell University in the United States. The results have differed depending upon the nature of the genotypes used in each experiment. For example, Mendoza (1980) and Thompson et al. (1983), using a North Carolina Design I (Comstock & Robinson 1952) to analyse a Neotuberosum population, found no additive genetic variance for yield *per se*, although estimates for additive variance for the components of yield, such as tuber number and tuber size, were high. The high negative correlation between these characters indicated that selection for an increase in one should decrease the other. Tuber size was positively correlated with days to maturity, size uniformity and eye depth, whereas tuber number was negatively correlated with these characters. Tuber size gave a higher estimate of narrow sense heritability (h^2) than tuber number, but a lower estimate of the additive genetic by environment interaction variance. Hence response to selection for tuber size should be more rapid than for tuber number. Heritability estimates for seedling vigour and uniformity in the nursery and seedling vigour at 60 days were high enough to indicate that these characters could be improved by selection. Transplant survival, on the other hand, gave a low estimate of heritability. Nonadditive variance was the most important component in the control of uniformity of colour.

In terms of seed production, the positive genetic correlations between number of berries and transplant survival, tuber size, uniformity of tuber size, and depth of eyes in this material are advantageous because selection for improvement in these characters should result in increased seed production. The relatively high estimates of heritabilities and low estimates of genotype by environment interactions for tuber size and other tuber yield and quality related traits indicate that individual plant selection should be considered instead of family selection. Thompson *et al.* (1983) also suggested that the significant estimate of nonadditive variance for yield favours F_1 hybrids as the optimum type of progeny for TPS production.

In another set of experiments using a North Carolina Design II (Comstock & Robinson 1952) with a CIP breeding population comprising *Solanum tuberosum* ssp. *tuberosum* and ssp. *andigena*, *tuberosum* x *andigena* hybrids, as well as *tuberosum* x *phureja* hybrids. Thompson & Mendoza (1984) determined the genetic parameters for 11 traits. Narrow sense heritability estimates were above 0.52 for berry number, tuber number, tuber size, yield, tuber smoothness and uniformity of tuber colour. No additive genetic variance was found for uniformity of tuber size. Significant estimates of non-additive variance were also obtained for berry number, yield, tuber smoothness, uniformity of tuber colour and uniformity of tuber size. What is interesting about these results is the high estimate of h^2 for yield, in contrast to the estimates determined for the Neotuberosum material in earlier experiments (Thompson *et al.* 1983). With respect to berry number, tuber number and tuber size, there was coincidence in heritability estimates between the different experiments. The high genetic correlations between yield-related traits form the basis for the adoption of a selection index method of improvement. Based on the material studied and the use of a selection index, they suggested that improvement in yield, tuber smoothness, and uniformity of colour and shape should be rapid at the locations used in their study.

Mendoza (1985) has described the performance of different types of progeny developed from the material used by Thompson & Mendoza (1984). The parental clones used in the N.C. Design II were selfed and bulk pollinated; open pollinated seed was also collected. Multilines were created by mixing equal numbers of seeds of four of the crosses in each set. With respect to per cent germination, transplant survival, number of plants harvested and yields, the hybrid progenies were better than the selfed or open pollinated progenies, which were considered to be partially inbred. With regard to tuber weight, there were no differences amongst the different progenies. Furthermore, the selfed and open pollinated progenies were equal to or better than the hybrids in tuber uniformity and depth of eyes. There were no significant differences in tuber weight, but the hybrid progenies yielded more because of the greater number of tubers per plant.

BREEDING FOR POTATOES FROM TRUE POTATO SEED

The production of acceptable TPS progenies is a compromise between the ease of their production, either as open pollinated progenies or as hybrids, and the cost of their production. Several breeding strategies have been outlined to achieve uniformity in TPS progenies. They include (i) the use of open pollinated seed from selected tetraploid clones; (ii) 4*x* x 2*x* hybridization with unreduced gametes from First Division Restitution (FDR) in the diploids; (iii) inbreeding; and (iv) exploitation of various aspects of apomixis in potatoes.

Hybrids vs. open pollinated TPS

The most detailed information from breeding studies for TPS to date have come from Peloquin and his associates in Wisconsin. Two of the breeding schemes outlined by Peloquin (1983) are based on unilateral and bilateral sexual polyploidization, which have been shown to be efficient methods of exploiting diploid species for widening the genetic base of tetraploid varieties, but which have also been applied successfully for producing superior TPS progenies. Peloquin (1983) has demonstrated that the genetic diversity for both valuable qualitative and quantitative traits and the allelic variation necessary for maximum heterozygosity, can be transferred almost intact to such progenies. Unreduced gametes produced by FDR do transmit a considerable proportion (80%) of the heterozygosity and epistasis of the parents to the offspring. The superiority of the hybrid progenies is interpreted however in terms of heterozygote advantage. Most comparisons have been made between 4*x* x 2*x* hybrid and open pollinated progenies. In almost all cases, hybrid progenies have outyielded cultivars and open pollinated TPS from tetraploid clones (see chapters by Hermundstad & Peloquin and others, this volume). Macaso-Khwaja & Peloquin (1983) stated that the low yields of 4*x* open pollinated progenies were probably an effect of inbreeding depression. The increase in homozygosity and decrease in intra and interallelic interactions, due to the reduction in number of alleles per locus as a result of selfing, were the basis of low yields. In fact, Hermsen (1983) has discounted the use of homozygous lines in breeding true seed potatoes, suggesting that they cannot have the vigour of hybrids which is commonly attributed to the high frequency of tetra-allelic loci and favourable epistatic effects.

Kidane-Mariam et al. (1985a) compared 30 TPS families from 4x x 2x crosses and open pollination, for tuber yield and plant uniformity. The hybrid families were from crosses between 4x clones and 2x Phureja-haploid Tuberosum hybrids producing pollen by FDR. The open pollinated (OP) families were from three categories of 4x parents: (a) DTs - 4x derived from 4x x 2x crosses; (b) advanced clones which were highly male fertile; and (c) advanced clones known to possess variable male fertility in which pollen stainability ranged from <3% to 10-30% during the flowering period.

The average tuber yield of the hybrids was 28% higher than that of the highest yielding OP group and about 48% higher than the combined mean yield of the three groups of OP families. The heterotic response of the hybrid 4x x 2x progenies was interpreted on the basis of the mode of 2n pollen formation (FDR), and the level of heterozygosity transmitted to the progeny. On the basis of these results, Kidane-Mariam et al. (1985a) state that the 4x x 2x approach is the best breeding scheme for the development of TPS progenies. Nevertheless the yield and other characteristics of some of the OP families was sufficiently high to warrant further study, and because of the substantially lower cost of seed production (about 10-20% of the cost of hybrid seed) their use for potato production would be economically advantageous in many situations, even though yields are lower on average than those of hybrids.

While acknowledging the breeding value of the 4x x 2x progenies, Hermsen (1983) has expressed some concern about the narrow genetic base of the diploids used by Peloquin and others, because these clones trace back to a few ssp. tuberosum dihaploids and a few clones from S. phureja. He advised that these points should be borne in mind when considering parental materials because these should be complementary for horticultural traits and resistances to pests and diseases, as well as abiotic stress conditions. A further point which should also be considered is the glycoalkaloid content of some of the hybrid progenies from 4x x 2x crosses, since some wild species are included in these breeding schemes.

The use of locally-adapted tetraploid cultivars for the generation of TPS progenies has been examined by Kidane-Mariam et al. (1985b). The performances of 262 single and bulk cross hybrids and four families from open pollination were evaluated at three locations in Peru. Significant differences were observed among families in tuber yield, uniformity and transplant survival in the field. Hybrid TPS families gave higher yields and more uniform tubers than families from open pollination. This difference was attributed to inbreeding depression due to selfing in the open pollinated materials.

Hybrid TPS progenies from intermating selected tetraploid stocks can produce good yields and have satisfactory uniformity. However, the significant family-environment interaction for tuber yield in this study indicated that if TPS families are generated from 4x x 4x crosses, then it is important to determine whether the parental stocks have a good level of adaptation to the specific locality where the TPS materials are to be grown.

Open pollinated seed and inbreeding

Farmers could produce TPS themselves by collecting seed resulting from natural pollinations in their own fields, and in fact some may have no reasonable alternative but to save open pollinated seed. However, the reluctance of some potato breeders to accept open pollinated progenies probably rests on the assumption that such materials will become substantially inbred through selfing, and that this should be avoided at all costs.

The quantity and quality of seed from open pollination is related to parental genotype, but also to pollinator activity. Atlin (1985) has discussed the effects of collecting open pollinated seed over several generations and argued that it would lead to inbreeding. There is some evidence to suggest however, that potato populations may in general be more outbred than expected from some pollination studies, where high selfing rates were observed (Glendinning 1976; White 1983). Kidane-Mariam et al. (1985 a) compared first, second and third generation open pollinated progenies from several potato clones, and found no significant difference for yield. The explanation they gave for this was that the individual plants serving as seed parents for the next generation were either the most heterozygous of the selfed progeny or were the product of outcrossing. The indications from this study and one carried out in San Ramon, Peru (Atlin 1985) were that inbred individuals were much less viable and fertile than individuals resulting from cross pollination. It also appeared that inbreeding depression was more severe under conditions of stress, causing even low levels of inbreeding to result in large yield declines. Furthermore, S_1 and S_2 progenies produced less pollen per flower and pollen of a poorer quality than did parental hybrids, suggesting that inbred parents contribute little to the pool of male gametes in a mixed population, and that the level of selfing was very much lower than the average estimate of 80% obtained by the use of genetic markers.

In these experiments using open pollinated seed, the mixtures of clones have been considered more or less as synthetic varieties composed of a number of parents, because of the observed absence of a decline in yield between first and second generations of natural pollination (Atlin 1985). Some inbreeding is still to be expected in such populations, but could be reduced by using methods of male sterility to develop synthetic varieties with low selfing rates. Cytoplasmic sterility as proposed by Brown (1984) or that recently identified in the progeny of Atzimba x IVP-35, in which abundant stainable pollen is produced but which does not function in fertilization would be one way of achieving this.

Another option which has received little attention is to develop clones which are tolerant of inbreeding and from which open pollinated seed could be collected for the production of homozygous, uniform potatoes, without any decline in yield over generations. In a recent paper, Jackson et al. (1985) have proposed an inbreeding strategy for the production of TPS, through single seed descent in diploid potatoes. Inbreeding may be exploited either through the production of F_1 hybrids between inbred lines (Yashina & Pershutina 1971), a strategy in which heterozygosity is favoured at the expense of ease of seed production, or by the use of autogamous inbred lines in which gametic uniformity is due to homozygosity. These methods are compromises between maximizing heterozygosity, maintaining the necessary level of gametic uniformity and the relative ease of seed production. The choice between these approaches is dependent on whether heterosis is related to heterozygosity.

Jinks & Lawrence (1983) have questioned the widespread belief that the best phenotypes, particularly for yield, are produced by heterozygotes rather than by homozygotes. In outbreeding crops, breeders attempt to avoid inbreeding depression, which is expressed as a reduction in vigour, fertility and yield. The usual explanation of inbreeding depression is that it is due to the fixation of unfavourable or deleterious recessives. Inbreeding increases the frequency of loci which are homozygous and some will become homozygous for these deleterious recessives. Jinks & Lawrence (1983) have indicated that inbreeding depression is due to the presence of genes in the base population that display dominance, or dominance and epistatic effects, and that control characters of primary interest to the breeder such as yield.

Heterosis is the converse of inbreeding depression. Its genetical base is still the subject of some debate. The two main genetic models of heterosis are the overdominance model (Hull 1945), favoured by Mendoza & Haynes (1974) to explain the genetic control of yield in autotetraploid potatoes, and the dominance model (Williams 1959; Sinha & Khanna 1975). The overdominance model, which proposes that heterozygosity is intrinsically advantageous, has been expanded to a multilocus model by Li (1967), and to include multiallelic effects by Mendoza & Haynes (1974). Equally, in support of the dominance model, it has been shown that heterosis may result from additive x additive and additive x dominance effects at a few loci (Seyffert & Forkman 1976), or from linkage and linkage disequilibrium (Sved 1972; Arunchalam 1977). In recent theoretical work on the genetical basis of heterosis, Jinks (1981; 1983) has argued that heterosis is not dependent on heterozygosity per se, but on the genic content of the individual, and therefore that heterosis may be 'fixed' in homozygous recombinants produced through inbreeding. It is suggested that heterosis results from linkage disequilibrium of genes with dominance and epistatic effects. Although Jinks & Lawrence (1983) do not dispute that overdominance may occur, they argue that there are few substantiated cases of major genes showing overdominance.

They further point out that the effect of selection in cultivated species will be to raise the frequency of genes for favourable expression of the selected character(s), that is, those genes which display dominance in the desired direction, and therefore, when such material is inbred, the resultant inbreeding depression is proportional to the response that has previously been obtained by selection. Jinks & Lawrence (1983) further argue that although in such populations heterozygotes, on average, may be superior in fitness terms to homozygotes because of dominance, the objective of plant breeding is to identify individuals whose performance is well above average, and that these individuals, in the absence of overdominance, are as likely to be homozygotes as heterozygotes. That is, the apparent correlation between yield and heterozygosity is spurious.

With regard to potatoes, different lines seem to behave differently to inbreeding (Krantz & Hutchins 1929; Krantz 1946; Pushkarnath 1960). Trinkler et al. (1976) have stated that they were able to select inbred lines which showed little or no inbreeding depression, and Trinkler et al. (1980) found no inbreeding depression when comparing the performance of secondary inbred lines. As Atlin (1985) has stated, most inbreeding studies have not continued past the S_1 generation, so full evaluations of its application to potatoes have not been made. The research project of Jackson et al. (1985) should contribute valuable data in this respect.

Exploiting apomixis in potatoes

Hermsen (1983) put forward the idea that autonomous apomixis could be introduced into potatoes, as another way of producing genetically uniform potatoes from true seed. Gametophytic apomixis is characterized by apospory and diplospory. The existence of these mechanisms in potatoes, and their choice for breeding true seed potatoes, has been the subject of some controversy.

Peloquin (1983) has considered the use of apospory in two breeding schemes. In one of these, crosses are made between diploid hybrids. In one 2*x* hybrid, there must be a high frequency of 2*n* eggs which are highly heterozygous. Such gametes can be formed either through apospory, or meiotically with no crossing-over followed by FDR. In the other, highly heterozygous male gametes must be formed at meiosis in which there is no crossing-over followed by FDR. Consequently all the male and female gametes would have the same gentoypes as their respective sporophytes. Meiotic mutants for 2*n* pollen which fulfil these criteria have already been identified. The sy_3 mutant (which produces only univalents at the first division of meiosis) and *ps* (parallel spindles) at the second division have been combined, and consequently 100% of the parental genotype is transmitted to the male gametes. The production of 2*n* eggs through apospory or FDR with no crossing-over, and their identification, are the principal constraints to the development of this breeding scheme.

In the other scheme, the formation of seeds asexually is envisaged on desirable 4*x* hybrid clones. In order to achieve this, 4*x* seed may be formed either by apospory or by no crossing-over followed by FDR; fertilization can be circumvented by parthenogenesis or pseudogamy. Irikura (in Peloquin 1983) reported that apomictic seeds were induced in diploid and tetraploid potato cultivars with 2,4-D sprays on emasculated flowers. The chemical induction of aposporous apomictic seed, i.e. clonal true seed, has also been discussed by Iwanaga (1983).

Jongedijk (this volume) has discussed the experimental induction of diplosporic apomixis, through desynapsis and FDR 2*n* egg formation. He states that the induction of diplosporic apomixis in potato appears to offer the best prospects because the genetically controlled elements of the system are already available. These include strongly reduced crossing-over in megasporogenesis, the formation of unreduced megaspores and embryo sacs, and the parthenogenetic development of the unreduced egg cell.

Production of true seed

True seed production on a commercial scale is dependent upon the flowering characteristics of the parental material, the quality of TPS produced and the economics of TPS production (Upadhya et al. 1985). Genetical studies have shown a correlation between berry number and the components of yield (Thompson & Mendoza 1984), and Dayal et al. (1984) have shown that there is a positive and significant correlation between 1000-seed weight, tuber yield per plant and tuber number per plant.

Almekinders & Wiersema (1985) have shown that the position of the inflorescence on potato plants is related to seed weight. More stems per plant had a favourable effect on TPS production through reduced flowering period, fewer axillary branches and a larger proportion of berries originating from first and second position inflorescences. By decreasing the number of flowers per inflorescence, berry size and 100-seed weight could be increased. It is also clear from the work of Pallais et al. (1985) that potatoes grown for the production of true seed have specific needs, such as nutritional requirements, that differ from those grown for commercial production.

The production of hybrid seed is a feature of TPS research which needs particularly careful consideration. Upadhya et al. (1985) and Pallais et al. (1985) have given figures for the hand emasculation and hand pollination of potato flowers in the field. In India, for example, it has been calculated that the cost of production of 100 g of hybrid true seed (sufficient to plant 1 ha) would be about US$6.00, if emasculation was carried out, but less than US$2.00 if flowers are pollinated without emasculation. The quality of seed produced is also dependent upon the pollen load. Pollination of the stigma three times within the receptivity period of 18-36 hours produced the largest number and size of berries, as well as the highest quantity and quality of true seed (Upadhya et al. 1985).

Although the use of hand labour for pollination appears feasible in certain situations, it is clearly not in others. What alternatives are there? Under field conditions, potatoes are pollinated by bees. Since potatoes do not produce nectar or other food 'rewards', they depend mainly on their pollen content to attract pollinators. White (1983) has reported that bee pollination is important for the production of open pollinated seed. In a series of field experiments at Huancayo (3200 m) in central Peru, bees were observed to forage within single clones for short periods, but also to switch occasionally to different clones. Consequently much of the seed from open pollinated clones resulted primarily from self or intraclonal pollinations. For the production of hybrid seed or synthetic varieties using natural pollination, White (1983) suggested that studies should be undertaken to determine the effects of border rows and planting patterns on rates of cross pollination.

Given that a considerable amount of self pollination occurs naturally in the field, the use of bees to produce hybrid seeds will only be effective if one of the parents is male sterile. Bees rarely visit sterile flowers because of the lack of pollen. Consequently incorporation through breeding of the tetrad sterility identified by Brown (1984) offers promise in this respect. Bees visit flowers of the tetrad sterile clone and can pollinate these flowers with fertile pollen from an adjacent male fertile clone. The flowers of the tetrad sterile clone look normal and shed copious amounts of tetrad pollen when vibrated. The production of hybrid seed, or even the efficient production of open pollinated seed is also dependent upon a greater understanding of the ecology of the pollinators, Bombus spp., and why they sometimes fail to pollinate.

A TPS ideotype

Agronomic comparisons between potatoes grown from TPS and from seed tubers have little justification. While the use of seedling tubers, as indicated by Wiersema (1983; 1985) gives farmers many of the advantages of TPS while still handling seed tubers, the use of TPS for direct production of a ware crop presents several problems. A TPS seedling is a one-stemmed plant and does not have the food reserves in tubers upon which rapid early growth of clonally propagated potatoes is based. TPS progenies often take longer to reach maturity. Although total yields from some of the 4*x* x 2*x* hybrid progenies reported by Macaso-Khwaja & Peloquin (1983) are high, the important feature to consider is marketable yield per unit area.

Satisfactory yields could also be obtained from TPS seedlings which produce only a small number of tubers per plant, but all of which fall within the marketable size. Such a plant would channel all its productivity into this small number of tubers, rather than into many of which only a small proportion would be of marketable size. Variation in tuber size affects both total and marketable yield, and is due to several factors including (i) space per plant; (ii) stems per plant; (iii) size of stems; (iv) date of emergence; and (v) tuber sizes on one stem. When seedlings are transplanted, the first four of these factors would be reduced or eliminated. The only factor of significance would be due to differences between genotypes in producing a range of tuber sizes, and this could be improved by choice of suitable parental material. Total yield would then be manipulated through planting density. What is clear is that the use of TPS presents potato researchers with a unique opportunity to develop new ways of growing the potato; that is, it would be a mistake to think solely in terms of how the crop is currently raised from seed tubers.

CONCLUSIONS

Considering that virtually nothing was known about growing potatoes from TPS before the late 1970s, the fact that true seed progenies are not only now being evaluated under experimental conditions but also being utilized by farmers is an indication of the rapid development of this technology. The close association of breeders, geneticists, agronomists and physiologists in breeding TPS progenies has been the basis of the rapid progress which has been made in such a short period of time.

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