



INNOVATIVE METHODS for PROPAGATING POTATOES

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INTERNATIONAL POTATO CENTER (CIP)

P.O. Box 5969 Lima - Peru. Cables: CIPAPA - Lima
Telex: 25672 PE. Telephones: 366920 - 354354

Inbreeding and True Potato Seed Production

M.T. Jackson, L. Taylor and A.J. Thomson

Introduction

The successful introduction of TPS technology in developing countries, particularly where the potato is not a traditional crop, demands a reappraisal of conventional potato breeding strategies, not only in terms of breeding procedures, but also of the end-product developed through breeding, in order to exploit fully the potential of the potato as a sexually propagated crop. As a contribution to TPS research, a joint project between the University of Birmingham and the Plant Breeding Institute, in collaboration with the International Potato Center, and funded by the U.K. Overseas Development Administration has been developed to evaluate the potential of inbreeding for the production of TPS. Inbreeding as a strategy has received relatively little attention from potato breeders. In this paper we shall put forward some ideas in support of using an inbreeding strategy for producing true seed potatoes.

The Uniformity of Potatoes from TPS

Uniformity is the norm when potatoes are grown from tubers. In contrast seedling generations exhibit considerable heterogeneity because of the great heterozygosity which is 'locked-up' in the potato as a result of vegetative reproduction. Several approaches to breeding the genetic uniformity necessary for TPS have been evaluated in recent years. These approaches have included the selection of tetraploid parental materials (Mendoza, 1979; Peloquin, 1979; Kidane-Mariam et al., 1984), the use of dihaploids and diploids which produced diplandroids and diplogynoids (Mendiburu & Peloquin, 1971, 1977; Mok & Peloquin, 1975; Peloquin, 1979) and their use in $4x-2x$ crosses. These methods are compromises between maximizing heterozygosity, maintaining the necessary level of gametic uniformity, and relative ease of seed production. Inbreeding, which achieves the highest level of gametic uniformity, 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. The choice between these approaches is dependent on whether heterosis must be equated with heterozygosity.

Inbreeding Depression vs Heterosis

In proposing an inbreeding strategy we agree with Jinks & Lawrence (1983) in questioning the widespread belief that the best phenotypes, particularly for yield, are produced by heterozygotes rather than 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, some of which will become homozygous for these deleterious recessives. Concerning the genetical basis of inbreeding depression, Jinks & Lawrence (1983) have indicated that it is due to the fact that the characters of interest are determined by genes with non-additive effects, of which those whose effects are deleterious are but a subset of such genes. These genes will segregate upon inbreeding.

Heterosis is the converse of inbreeding depression. Heterosis has been utilized as a productive breeding strategy in a variety of crop species, but its genetic base is still the subject of some debate. The two main genetic models of heterosis are the overdominance model (Hull, 1945), 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). However, 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. Although they do not dispute that overdominance may occur, they argue that there are few substantiated cases of major genes showing overdominance.

The quantitative model developed by Jinks, Pooni and co-workers at Birmingham (Jinks, 1981, 1983) argues that heterosis results from the dispersal of dominance and non-allelic interactions by linkage and linkage disequilibrium, and that, if these genetic parameters are estimated for a given cross using the triple test cross mating design, then the frequency of important transgressive segregants in inbred lines derived from the F_2 by single seed descent can be predicted.

What are the Effects of Inbreeding in Potatoes?

The effects of inbreeding in cultivated tetraploid potatoes have been examined by a number of authors (Krantz, 1924, 1946; Krantz & Hutchins, 1929; Guern, 1940; Neciporcuk, 1949; Hagberg & Tedin, 1951; Feistritzer, 1952; Gowen, 1956; Engel, 1957; Rudorf, 1958; Deshmukh & Verma, 1960; Pushkarnath, 1960; Mullin & Lauer, 1966; Zadina, 1973). In general, severe reductions in vigour, yield and fertility with successive generations of inbreeding were observed. However, several researchers including Krantz & Hutchins (1929), Krantz (1946), and Pushkarnath (1960), have noted differences between the responses of different lines to inbreeding. More recently, Trinkler et al. (1976) have stated that they were able to select inbred lines which showed little or no inbreeding depression. Trinkler et al. (1980) compared the performance of secondary inbred lines ($I_1 - I_4$) derived from crosses of inbred lines ($I_1 \times I_1$, $I_2 \times I_2$, and $I_3 \times I_3$), and found no inbreeding depression. The secondary inbred lines had yields of up to 50% greater than the initial F_1 . Budin & Soboleva (1978) obtained I_1 to I_3 lines from spontaneously-doubled F_2 hybrids of dihaploid S. tuberosum ssp. andigena with S. phureja, S. stenotomum, and S. pampasense which showed no significant inbreeding depression.

Similarly, at the diploid level, inbreeding depression has been observed. De Jong & Rowe (1971) found that I_2 inbred lines derived from dihaploid Group Tuberosum x Group Phureja and Group Stenotomum hybrids had an average yield in the I_2 of only 36% of the I_0 , but that the four families did respond differently to inbreeding. Abdalla (1970) found that the responses of different lines of self-compatible S. verrucosum to selfing varied considerably.

The Effects of Inbreeding in Other Outbreeding Crops

Considerable variation in response to inbreeding has been observed in a number of other predominantly outcrossing species. Ockendon & Currah (1982) found that seven of 11 inbred lines of runner bean (Phaseolus coccineus L.) showed no significant inbreeding depression. Inbred clones of Trifolium pratense L. have been produced which equalled or excelled the parental clones in all characters examined (Taylor et al., 1970). Schuster & Michael (1976) produced I_7 and I_8 generation lines of Brassica napus oleifera with higher yields than the parental material. In alfalfa (Medicago sativa L.) Hill (1975, 1976) found clones which showed little or no inbreeding depression, Melton et al. (1969) and Melton (1970) observed a wide range of responses to selfing, and Panella & Lorenzetti (1966) observed that the I_3 generation was more vigorous than the I_2 .

The Attainment of Homozygosity

There are several ways in which homozygosity can be achieved, amongst which anther culture and single seed descent are two important strategies, and which will be used in this project. Anther culture techniques to produce dihaploids from tetraploids, or even monohaploids as proposed by Wenzel et al. (1979) can be used to produce homozygous lines. It is apparent, however, that no general anther culture protocols are available, and that different potato genotypes differ in their 'tissue culture ability'. Single seed descent is a breeding strategy in which selection is deferred until a suitable level of homozygosity is achieved.

We propose to attempt to inbreed diploid potatoes. The reasons for this are primarily logistical. Achieving the desired degree of homozygosity at the diploid level will require far fewer generations of single seed descent, and much less material than would be required at the tetraploid level. Nevertheless inbreeding at the diploid level does present other problems. The tuber-bearing *Solanums* have a gametophytic system of incompatibility, but polyploids are self-fertile probably due to competitive interaction or mutual weakening of S-alleles (Dodds & Paxman, 1961). As a general rule, most diploid species are self-incompatible, but there are notable exceptions among the wild species, including *S. verrucosum*, *S. etuberosum*, *S. brevidens*, *S. morelliforme* and *S. polyadenium* (Hawkes, 1958, 1963). While some species are strictly self-incompatible, self-compatible genotypes are found within others such as *S. phureja* (Dodds, 1956; Cipar, 1964; Hermsen & Sawicka, 1979). Olsder & Hermsen (1976) have also found self-compatible dihaploids derived from *S. tuberosum*. Self-compatible genotypes have been identified in diploid populations developed at the Scottish Crops Research Institute-Pentlandsfield (C.P. Carroll, personal communication). In several crops, such as brassicas (Taylor, 1982), sweet potato (Sood et al., 1982) and rosaceous tree fruits (Visser, 1981; Visser & Verhaegh, 1980; Visser & Oost, 1982), successful methods at breaking self-incompatibility barriers have been developed. These include pollen irradiation, 'pioneer' and 'mentor' pollen, heat treatments and enhanced CO₂ atmospheres. Several of these approaches will be used in an attempt² to break self-incompatibility, although the identification of self-compatible genotypes at an early stage would be advantageous. A study of incompatibility in diploid potatoes is the subject of a separate research project at Birmingham.

A TPS Ideotype

What sort of a plant do we expect to produce by inbreeding at the diploid level? Yield comparisons between diploid and tetraploid potatoes are usually made under a conventional production system. Undoubtedly tetraploid potatoes do exhibit a yield advantage over diploids (Mendoza & Haynes, 1976; Mendiburu & Peloquin, 1977), but this advantage does not appear to be due to polyploidy per se (Rowe, 1967; De, Maine, 1984). While Mendoza (1979)) has argued that the yield advantage of tetraploids is due to multiallelic interactions and heterozygosity, based on the overdominance model of heterosis (Mendoza & Haynes, 1974, 1976), Sanford & Hanneman (1982) have suggested that there is a possible heterotic threshold of yield in potatoes.

Jinks & Lawrence (1983) have pointed 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 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 specious.

Despite the potentially greater yield in tetraploid cultivars, elite diploid lines have been identified. Carroll & De, Maine (1981) found that four out of ten diploid hybrids obtained by crossing Tuberosum dihaploids were not significantly different in yield from the top yielding control cultivar cv. Desiree. Swiezinski (1984) has produced several diploid families in Poland which have yields greater than the average for tetraploid families, even though the mean of the diploids was lower.

One can question the validity of comparisons of yields obtained from plants grown from TPS and those grown from tubers. A TPS seedling is a one-stemmed plant. Perhaps the ideotype we should aim to select is one which produces only one (or just a few) tubers of marketable yield per plant. Such an ideotype would channel all its productivity into this small number of tubers, rather than into many, of which only a proportion would be of marketable yield. Under such circumstances the apparent yield disadvantages of diploid potatoes would become less important as long as each plant yielded in this manner. We envisage that TPS will be used directly for the production of a ware crop rather

than for a seed tuber crop. Consequently marketable yield per unit area is of greater importance than total yield per plant. The sizes of tubers acceptable as marketable yield varies from country to country. Variation in tuber size in potatoes 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 TPS is utilized directly, especially 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 different genotypes in producing a range of tuber sizes, and could be reduced in importance by the choice of suitable parental material.

In many developing countries the potato is utilized as a vegetable and not as a staple food. Consequently it is unrealistic to imagine the potato replacing important staple crops in the near future. The inclusion of the potato into new cropping systems, or its introduction into new environments, might be achieved more readily if we no longer continue to think of it being grown in the traditional way as from tubers on ridges, but look for new ways in which it may be cultivated. One can visualize that the potato may be adopted as a vegetable crop, with seedlings transplanted to the field in raised beds, as is typical with vegetable production in many countries. The manipulation of planting densities would then allow the achievement of acceptable yields. Such a system would be suited to the needs of small farmers in developing countries of the tropics. The successful adoption of TPS technology in many parts of the developing world will ensure that the potato becomes a valuable dietary supplement.

Conclusions

We have outlined some arguments in favour of an inbreeding strategy for TPS production, even though we recognize that important practical constraints will be faced. Once a sufficient level of homozygosity has been achieved, it can be exploited in the interim through the production of F_1 hybrids, although the production of inbred lines is the ultimate aim of the research project.

Inbreeding in potatoes presents a considerable challenge, but one for which the potential rewards are great. This is an area of TPS research which has received no emphasis until now. It is our hope that this project will make a contribution to the utilization of TPS in developing countries.

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