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TRUE POTATO SEED

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I. Introduction

There are many examples of cultivated plants, that were first grown as heterogenous, seed propagated populations, but plant breeding led to the production of uniform, high yielding, vegetatively propagated clones to be used as cultivars. Going the opposite way, from vegetative propagation to the use of botanical seed, can draw on few earlier examples except among ornamentals.

Potato tubers as planting material are expensive. They may propagate diseases if seed tuber certification programmes are not enforced. Production and testing of clean seed is expensive. Potato tubers are heavy and bulky and perishable.

The constraint formed by the high cost or unavailability of high quality seed became particularly evident in the efforts of the International Potato Center (CIP) to improve production and expand potato cultivation to new areas in the developing world. Seed tubers are usually imported at high prices, they may arrive at the wrong time for planting and have the wrong physiological age. They are difficult to store and to transport.

Two solutions were possible: Find ways to make high quality seed tubers available at a more reasonable price, or circumvent the difficulties of disease propagation, perishability, heaviness and bulk, by dismissing potato tubers as planting material. Botanical seed does not transmit most of the viruses, it is very lightweight and easy to transport.

Both ways are used in order to promote potato production in developing countries. In vitro propagation and/or rapid multiplication of pathogen tested selected cultivars, in combination with selection of the best season and locality for field production of seed tubers in national programmes, is improving the availability of seed tubers in many developing countries. Botanical seed is already an alternative for some areas. Some competition is apparent. The final outcome has yet to be seen.

II. History

The story of true potato seed is one where the beginning looses itself in the distant past and the future is not yet known.

We believe that the first cultivation of potatoes could have resulted from the collection of tubers, some of which produced plants, which gave botanical seeds, which accidentally produced plants, some of which gave better tubers and so on. We know that potatoes in the Andes are still produced from botanical seed at intervals (Malagamba & Monares, 1987; Salaman, 1949).

We know that attempts to use botanical seed for potato propagation were made soon after the introduction of potatoes to Swedish agriculture. In a letter to the Academy of Science in Sweden (Wimmermark, 1751) a description is given of how in 1748 Mathias Kylander, Linköping, collected botanical seed, which was sown in the spring of 1749 and transplanted to the field. He harvested potatoes the size of a nut, which he saved and planted again in the field the following spring. In the autumn he harvested potato tubers which were higher yielding and of different shape and with a thicker peel than those in the rest of the field. He intended to repeat the harvest of botanical seeds from these plants to see if in this way he could make the plants increasingly tolerant to cold.

This short paper by a clergyman/farmer in 1751 gives in a nutshell many of the advantages and disadvantages of true potato seed - the improved yield the second year, but also the longer time needed for development from true seed. He used methods recommended now - transplanting seedlings in order to harvest tubers, which because of their small size were most suitable for use as seed tubers. The crop produced was different from the original plants, and variable, which gave him the idea that further generations could give even better material. Breeding had started. But a continued use of botanical seed for propagation did not take place. May we conclude that if it had proved to be a usable method, TPS cultivation would have continued, and we would now have improved cultivars for TPS propagation?

Records can be found of similar occurrences in other countries during the 19th century, e.g. when botanical seed was imported to Europe after the blight epidemic in 1845 (Haan, 1953). Experiments were made in India in the 1940s (Upadhya, 1979).

The first attempts at producing potato cultivars for botanical seed propagation during modern times were probably made in the USSR. Publications started to appear in the 1950s, and recent surveys indicate that breeding is carried out at several institutes (Trinkler et al., 1984; Budin, 1985). At least three TPS-cultivars have been released, intended for production of seedling tubers.

In the People's Republic of China research on true potato seed started 1959 (Li & Shen, 1979; Song, 1984; Song et al., 1987; Wang, 1985). The work was initiated in Inner Mongolia by Dr. Chang Hung Quin, and led to the decision to begin a large-scale TPS production programme in 1972.

The reason for this decision was two problems in Chinese potato production; high virus incidence and lack of late blight resistant varieties. Two high yielding cultivars, expected to have satisfactory resistance to late blight, had been identified in 1968. These produced berries after open pollination, and their progenies had sufficient uniformity and attractive tuber characteristics. This material has been used in Inner Mongolia and in the Southwest mountainous region in China for the production of seedling tubers in nursery seedbeds or after direct sowing or transplanting to the field in different regions, depending on the length of the growing period. Further multiplication may take place up to five or six times, depending on the danger of virus spread in the area.

Work on TPS started in New Zealand in 1976. Experiments indicated that potato seedlings could be raised directly in the field (Bedi, 1978) and that favourable yields could be

harvested from direct-sown or transplanted seedlings, but with higher yields from the latter (Bedi & Smale, 1978). Experiments were reported on in comparison with vegetative seed of an established cultivar, as well as management practices for various phases of TPS work (Bedi et al., 1979), and optimism was expressed of the possibility of producing commercially acceptable TPS cultivars. An open pollinated line, Waitangy, was distributed by a local seed firm for the amateur home grower (Anon., 1981).

A commercial project was started in the United States in 1976 (Leue, 1984), by a company which had already developed cultivars propagated via botanical seed from normally vegetatively propagated ornamentals and strawberries.

Potatoes from true seed were expected to be attractive for home gardens, and the initial concept was of potatoes as a new vegetable in the bedding plant market. A potato from true seed was not expected to be suitable for large scale production, although later the potential for international use in tropical and subtropical countries came into focus.

Considerable effort went into all the steps of developing the product, from production and handling of the botanical seed, to the development of detailed cultural recommendations for bedding plant growers for production of seedlings and for home growers for transplanting and culture of the seedlings.

The variety Explorer was introduced in 1981, and agressively marketed in many parts of the world.

By this time a world wide interest in TPS had been aroused through the work of CIP. CIP brought out the considerable advantages of botanical potato seed for developing countries, created the expression TPS, and the slogan »A handful of seed replaces two tons of tubers«. Work started in 1977, and since then has grown fast. The first planning conference on TPS was held in 1979 in Manila, the Philippines. Experiments were started in many countries, developed and developing, around the world. A working group within EAPR was formed in 1984. For this presentation it was initially my intention to try to map the countries, which have experimented on TPS. I had to give this up except for developing countries, where data have been provided by CIP for countries with which they collaborate. The majority of such experiments have not, at least not yet, been reported on in scientific journals. My impression is that nearly all countries that do any potato research at all, have also had at least exploratory experiments with TPS.

III. Present status of adoption of TPS technology

The rather massive experimentation and evaluation of TPS technology that has taken place during the last decade, has led to a start in adopting the technology in some developing countries, but so far not in developed countries.

III. 1. Survey of research and adoption in developing countries.

A survey of the status of TPS work in countries of the developing world which collaborate with CIP was made in 1983 and again in 1986 (Table 1). The questionnaire involved a total of 68 countries. Research on TPS was listed as in progress in 36 countries in 1983, and in 38 in 1986. In 1983 TPS was grown in farmers' fields in 3 countries, in 1986 this figure had increased to 8. The majority of those were in South Asia and the Far East.

For the countries in the table both total acreage and acreage under potatoes and TPS vary to an extreme degree. Many of the countries are very small. The People's Republic of China is counted as only one country, although it has many provinces, which might be more comparable units. The amount of TPS shipped form Inner Mongolia to the Southwest Mountainous region in China was given as 1000 kg as early as 1978. In 1979 15.000

Table 1. Number of developing countries in different regions, where research on TPS is carried out, or TPS is grown in farmers' fields, compared with the number of countries with research on or application of vegetative propagation based *in vitro*.
(Data from CIP surveys 1983 and 1986)

Region (number of countries)	*TPS research*		*TPS farmer*		*Tuber seed based in vitro*	
	83	*86*	*83*	*86*	*83*	*86*
Andean Latin America (5)	3	2		2	2	5
Non-andean Latin America (5)		4			3	4
Central America (6)	5	1			3	2
Eastern Africa (16)	10	9			2	5
Near and Middle East (7)	4	5		1	2	1
North and West Africa (7)	2	5				2
South Asia (6)	4	5	1	1	3	4
Far East (15)	6	6	1	3	2	7
The People's Republic of China (1)	1	1	1	1	1	1
Total countries (68)	36	38	3	8	18	31

ha of TPS was grown in the Sichuan province. A total of 20.000 ha was reached in China, but production has later stagnated. There appears to be two main reasons for this; the material used originally carried the potato spindle tuber viroid, which was not known at the time, and material which produced sufficiently uniform progenies has not yet been available to replace it (Wang, 1985; Shen, personal communication).

Although no conclusions about acreages can be drawn from the table, it demonstrates that interest in TPS research is increasing in developing countries. This can be corroborated by success stories from individual countries. Promising results with high yields are especially apparent in e.g. the Philippines and Bangladesh. It should be specially pointed out that what TPS is intended to compete with at present in the developing countries is available seed tubers, not the best possible future seed tuber quality. Even in such comparisons, however, experimental results are often in favour of TPS.

III. 2. TPS adoption in developed countries

According to Bedi (personal communication) the Waitangy open pollinated line released in New Zealand for amateur home growers met with mixed success. The interest was great because the seed was cheap. Some growers, who used transplanting and followed growing instructions, produced good crops, but many failed. Later attempts were made to have commercial nursery men germinate the seed, and sell transplanted seedlings in pots. Problems arose when seedlings were ready for sale; if not sold immediately they became root-bound, and began to tuberize in the pots. This adversely influenced their subsequent performance. Attempts to have efficient farmers produce tubers after transplanting were successful as far as yield and appearance were concerned. Tuber yield was lower than from tuber seed, but the small tubers were very uniform, and were sold washed in supermarkets. Consumer response on the quality of the tubers was mixed. Because of the expensive packaging, transport and distribution, the cost was relatively high. A better line, also from open pollination, since the use of hybrid seed is regarded as out of question because of expensive labour, is now being tested. Among its traits are mentioned higher yield and wider adaptability than Waitangy, and it is being tested e.g. in France and Korea.

The Explorer variety from USA, which was marketed in many countries, met with mixed success (Leue, 1984) for similar reasons. Seedlings were weak and delicate, and even well grown plants needed more sales promotion than other bedding plants. Johnston et

al. (1984) in a Canadian advisory leaflet analysed the reasons for the failure that many growers had experienced; the variety was too late, about 180 days were needed to produce a crop; the material was not adapted to Canadian conditions; genetic variability in plant size, maturity and tuber traits was too large. Advice was given to use the material in a two year cycle instead, starting the seed indoors and then transplanting to flats outdoors for harvest of seedling tubers the first year, which could be planted the next year, and used for food or even for selection of new varieties.

According to Leue (1984) TPS breeding for the U. S. home garden market was not regarded as justified by the sales, although trials had shown that considerable improvement over Explorer were possible. A further reason for this was the extreme variability from season to season in yield of botanical seed. Breeding and seed production continues, however, in warmer countries.

III. 3. Ways of utilization of TPS

The experiences that seedlings are difficult to use for direct ware production agree with the statements in publications from the People's Republic of China (Song, 1984), Taiwan (Tsao & Chang, 1982) and USSR (Trinkler et al., 1984), that production of seedling tubers for use as tuber seed, and not ware production, can be recommended.

CIPs results also indicate that seedling tuber production will have the major importance at least within the near future. In some areas, where climatic conditions are adverse for tuber production and storage, and a tradition exists for growing vegetable crops, transplanting of seedlings may be made for direct ware production.

Most striking is the variety of ways in which utilization of TPS is adapted to local conditions (Monares et al., 1983; Ninez, 1985; Haugerud & Nyirazikwiye, 1986; Wiersema & Booth, 1987). The development is a very interesting one, and which way or ways of utilization will have the greatest future impact is difficult to tell.

III. 4. Advantages and disadvantages of TPS

A more detailed list of advantages and disadvantages of TPS can be made now, based on experimental results, than the reasons listed in the introduction, that led to the attempts to introduce the TPS technology.

What were seen as the most important advantages - low cost planting material, reduced pathogen transmission, inexpensive and non-bulky storage and transport, longer term storage - remain as high in importance, but with modifications. Since the experience is that production of seedling tubers rather than direct ware production is expected to become more widely adopted, the time a seedling is exposed is prolonged, which necessitates breeding for virus resistance as well as for TPS production. Production of the botanical seed meets with difficulties in warm tropical areas with a short photoperiod.

The importance of the expected disadvantages, among which the lack of uniformity and the longer growing period needed, resulting in an expected low yield, were seen as the foremost, has proved to be exaggerated.

The yield levels, even when open pollinated progenies have been used, have been very good especially when compared with available local seed tubers in developing countries. The variability in plant and tuber characteristics, maturity, dormancy etc. has generally not been seen as a major problem in developing countries.

Improved genetical material is asked for, understandably, since in progenies used for experimentation major improvements to traits of importance for TPS production have

not been possible in the 10 years since the start. These traits include seedling vigour and increased tuber size in transplanted seedlings.

Compared to tubers, and also compared to most agricultural crops grown from botanical seed, potato seedlings are delicate and difficult to handle. Damping off and insect attacks have made pesticide application an expensive necessity. In areas where a tradition exists in growing small seeded horticultural crops the raising of the potato seedlings has not caused difficulties, however.

Obviously, only in certain areas are favourable weather conditions present in two seasons to make it possible to produce seedling tubers of an ideal physiological age at the optimal planting time.

Conclusions made at CIP about the general agro-economic conditions most favourable for adoption of TPS technology (Malagamba, 1984, 1987) were that mesothermal tropical zones, where seed tubers are costly and their quality rapidly deteriorates due to high temperature and the incidence of tuber-transmitted diseases, appear as those with the highest potential for adopting TPS.

IV. Production of botanical seed and seed quality

In order for TPS to become an alternative for potato production, it must be possible to produce sufficient amounts of botanical seed of an acceptable quality and a satisfactory genetic background at a cheaper price than that of tuber seed. This seed must give the potential to produce a crop of tubers with an acceptable yield, uniformity and culinary quality under the ecological conditions in question.

The economy of production of botanical seed is influenced by the flowering and seed setting capacity of the parental material, of the inputs of material and labour necessary, the cost of which is country specific. The quality of the seed produced also influences its commercial value, as does the genetic characteristics and uniformity of the crop that can be produced from the seed. Let us, however, postpone the discussion of future demands on combination of traits in TPS cultivars and uniformity until later, and first discuss mainly tetraploid progenies produced after crossing or open pollination, i.e. the type of material, which has been used in the exploratory work on TPS production, and also has been found satisfactory for ware production in many developing countries.

IV. 1. Flowering and berry production

For planting one hectare of transplanted seedling crop, about 100 g of botanical seed are needed.

It is well known to all potato workers that many cultivars never flower in the field, even under long day conditions, which are the most conducive of flowering. In earlier breeding conscious or unconscious selection has taken place for reduced berry production. It is not needed, it may divert assimilates from tuber production, seeds spilled in the field may cause problems in later crops. Breeders have worked out management methods and treatments to improve flowering and berry setting sufficiently for most genotypes to be used in breeding programmes. In those a few thousand seeds are sufficient, and considerable effort may be justified in order to produce a good progeny.

The situation is different when cheap production of kilograms of high quality seed is needed. Production of large amounts of botanical seed may be difficult, especially in low latitude warm climates. This has been pointed out in several publications from CIP and other programmes (Accatino & Malagamba, 1982; Kim et al., 1983; Tsao, 1981; Upadhya et al., 1984). The well known influence of photoperiod/temperature was demonstrated in

Table 2. Influence of environment on production of botanical seed. Malagamba, 1986.

Location	*Latitude*	*Flowers per plant*	*Botanical seed g/m*
Osorno, Chile	40.40°S	69.5	7.7
Lima, Peru	12.05°S	1.6	0.8
San Ramon, Peru	11.08°S	0.2	negligible

an experiment in Peru (Table 2). Tsao & Chang (1982) found that only 47 out of 900 tested accessions set fruit under a 12 h photoperiod. They also found that flowering could be induced in almost all of these if daylength was extended artificially. Breeders know, however, that many of the desirable progenitors refuse to produce sufficient seed quantities even under continuous light. This is true particularly of early maturing clones. However, genetic variability in flowering and seed setting traits is considerable, and selection has been found to give rapid improvement. Especially clones selected as parents under high temperature conditions, may also produce berries under high temperature/short day conditions (Malagamba, 1987).

Availability of sufficient amounts of high quality pollen is necessary, and storability and storage conditions for good pollen quality have been investigated. Environmental conditions influence both flowering and gamete fertility. Many pesticides have a negative effect on gamete fertility (Pallais et al., 1984), and application should be avoided.

IV. 2. Seed quality

A number of seed quality characters may be listed (Upadhya, 1983, 1986; Pallais, 1987), which influence germination rate and early growth of seedlings. They may be influenced both by the genetic constitution of the maternal plant and of the pollen, and by environment and agronomic practices. Soil nutrition, light conditions and temperature during fruit and seed development, fruit maturation period, seed extraction methods, seed moisture content at harvest, and storage conditions and duration, also influence the quality and performance of the seed (Sadik, 1983; Pallais, 1987).

Botanical potato seed is usually dormant for at least six months after harvest (Simmonds, 1963). On the other hand it retains germinability for very long periods, at least up to 25 years. Pallais et al. (1984) reported that fermentation in connection with seed extraction gave faster and more uniform germination.

IV. 2. 1. Freedom from diseases and pests

In this respect true seed has substantial advantages over seed tubers, since most virus diseases and nematodes are not carried by botanical seed (Jones, 1982). The potato spindle tuber viroid and the few virus types that can be transmitted can be avoided by the use of carefully tested parents. A number of fungi have been found on the seed surface, but surface sterilization is possible.

IV. 2. 2. Seed weight and seed size

Seed size influences emergence and seedling weight and a positive correlation has been found between 100 - seed weight and tuber yield (Dayal et al., 1984). Seed sizes vary normally between about 1.8 (large) and 1.3 (small) mm. Seed size and seed weight are in-

fluenced by parent genotype/environment interaction as well as maturity at harvest. Large variations in 100-seed weight have been found, and heritability was high in the material investigated (Upadhya, 1986).

IV. 2. 3. Management to improve production and quality of botanical seed

Dosages of nitrogen and phosphorous applied to the mother plant have a considerable influence on flowering and berry set, and for optimal production and quality of botanical seed almost twice the nitrogen level from that considered optimal for tuber production seems to be needed (Pallais et al., 1984; Upadhya, 1986).

Training of vines may facilitate field operations. This also improves berry setting and seed quality (Pallais et al., 1984). Upadhya (1986) found it possible, under Indian conditions, to reduce costs through the use of single eye seed pieces instead of whole tubers for maternal parents. This not only reduced the cost of planting material, but gave single stemmed, sturdy plants, which did not require staking. Pruning of plants and decreasing the number of flowers gave increases in berry size and 100-seed weight (Aimekinders & Wiersema, 1985).

A balance has to be found between management practices that influence the total number of botanical seeds produced per hectare and the quality of that seed, since influence of berry size, which in turn is influenced by berry number per plant, influences 100-seed weight, which in turn is expected to influence rate and uniformity of germination and early growth (Upadhya et al., 1984; Pallais et al., 1986).

IV. 2. 4. Production costs for botanical seed

The yield and uniformity of open pollinated vs hybrid seed, and their possible future role, will be discussed later.

Open pollinated seed of some genotypes may be produced in large amounts under field conditions without any special measures taken. Malagamba (1983 a) estimated seed yields at Huancayo, Peru (high altitude, cool conditions) to be about 28 kg, or 36,000,000 seeds, per hectare, enough for the seeding of 360 hectares. Open pollinated seed is expected to result from self-pollination to varying degrees, from nearly 100% in genotypes where the style is shorter than the anther cone to 50-60% in some genotypes when bumble-bees are present.

Hand pollination is needed in order to produce hybrid seed of most of the parental material available at present.

With hand pollination a production of 150 kg/hectare of hybrid seed was calculated to be possible in India (table 3, Upadhya, 1986). In Chile 200 kg/hectare have been produced (Malagamba, personal communication).

Costs vary very much between countries, and the comparison of hours of labour and relative cost of the different operations are more appropriate than the actual cost. Emasculation has been found to be a very expensive part of seed production (table 4).

Table 3. Amount of hybrid seed that can be produced on one hectar. Upadhya, 1986.

Assumed production per berry	200 seeds
Assumed 100 seed weight	100 mg
Seed production per berry	200 mg/berry
Single bunch stem produces 5 berries	1 g/stem
Stem density 15 m = 150,000 stems ha	150 kg/ha

Table 4. Production cost of 1 kg of hybrid botanical seed at INIA, Osorne, Chile, 1986. Source of data CIP Progress report 1986, Monares et al.

	Range (4 crosses)
Total cost (in US $)	128-188
Per cent of cost for different operations	
Growth and management of parental clones	8-20
Flower and pollen collection	8-9
Emasculation	29-36
Pollination	17-22
Berry harvest	3-5
Seed extraction and processing	15-22

Many ways have been discussed to reduce the cost of producing hybrid seed or genetically equivalent heterozygous seed through elimination or reduction of the cost of emasculation and/or pollination.

The most sophisticated and elegant, but time consuming, way is the creation of potato cultivars with autonomous apomixis (Hermsen, 1980; Liorek, 1984).

Male sterility, preferably of a type where the flowers were still attractive for bumblebees (Peloquin, 1983; Brown, 1984) is another alternative. Also with the necessity of hand pollination, male sterility would be favourable, since emasculation cost is so large. Cybrids have already been produced, with the nucleus of a desirable maternal parent in the cytoplasm with the male sterility inducing mitochondria of a clone with cytoplasmic male sterility. Gametocides have also been discussed (Pallais et al., 1984).

It may be, however, that emasculation can be omitted for hybrid production in most of the parental material already in use and under testing, if hand pollination is retained. Upadhya et al., (1984) found no adverse effects of non-emasculation on seeds/berry and TPS quality under Indian conditions. Similar experiences have been reported from Chile (Anon., 1986). Emasculation, even when made by an experienced person, damages the gynoecium to some extent and styles may be broken. Seed production may benefit from the omission of emasculation. A small amount of selfing would have little effect on the yielding capacity of the progeny. The prerequisite is, however, that attention should be paid to the morphology of the flower. The stigma must protrude and be longer than the anther cone. The protruding stigma is quite common in existing material. The stigma of the female parent should also be receptive well before anther dehiscence. This is also quite common. The breeding effort in order to facilitate pollination of non-emasculated flowers would thus be minimal compared to the introduction of male sterility or apomixis.

The reason for continued major efforts to introduce apomixis or male sterility would then be demand for uniformity and indispensibility of heterozygosity to attain sufficient yielding ability. I will return to these questions later.

V. Agronomy of TPS production

Two main systems can be distinguished for the utilization of TPS:

A) Ware potatoes may be produced directly from botanical seed
   or
B) Tubers (seedling tubers) may be produced for use as seed for a second crop, or even repeated generations.

For both purposes two different methods may be used

a) direct field sowing of the botanical seed
b) transplanting seedlings from an nursery to seed beds or to the field.

Most of the method development has been made using hand labour or very simple machinery, since the experimentation is intended mainly for developing countries. Ghate et al. (1986) discuss possible methods for mechanization.

V. 1. *Direct field sowing*

Experiments with direct sowing has given variable results. Emergence is often slow (Bedi & Smale, 1978; Martin, 1983) and establishment has often been poor. Few experiments have led to yields that could be reported. Optimal conditions of soil structure, temperature and absence of weeds are required. Although e.g. Sadik (1983) postulated that direct sowing of potato seed would be unlikely to be more difficult than for other small-seeded crops, which can be handled by vegetable growers, and e.g. seed pelleting and fluid drilling to facilitate the handling have been discussed, direct sowing is not recommended at present.

V. 2. *Seedling management for transplanting or production of seedling tubers*

Seedlings can be successfully grown in small areas that can be managed intensively. In seed beds it is possible to overcome the problems with low early vigour and lack of uniformity in emergence.

Detailed investigations have been made on the management of seedlings (Malagamba, 1983 a and b; Martin, 1983; Engels et al. 1984; Wiersema, 1984 a; 1986 b), in order to make recommenations on choice of seed bed substrate, sowing methods, spacing and spatial arrangement of seedlings, fertilization requirements, temperature requirements for seed germination and establishment, shading, factors which induce tuberization (tuberization already in the seed bed has a negative influence on the continued development of transplanted seedlings), herbicide treatment, use of fungicides and insecticides, etc.

Damping off caused by *Rhizoctonia* and other pathogens is often encountered (Elango, 1983, 1986), and the delicate plants are attractive to insects, e.g. *Diabrotica*, in warm climates. The costs of pesticide applications in this phase are considerable.

V. 3. *Transplanting and seedling establishment*

For ware production seedlings should be transplanted to the field approximately 35 days after sowing.

Transplanted seedlings are to be preferred in warm tropical areas because of the difficulty of storage of tubers and the rapid spread of diseases under those conditions.

Good progenies may yield quite well when grown as transplanted seedlings. Examples may be found of bulking rates as high as those in crops grown from tuber seed of established cultivars (table 5).

Table 5. Bulking studies, Bangladesh. Yield of tubers (t/ha) at consecutive harvests. Source of data CIP Progress report 1986, Sikka.

Days after transplant	*TPS Hybrid CIP 1*	*TPS Hybrid CIP 2*	*TPS Hybrid CIP 3*	*TPS Local OP*	*Patrones tuber*	*Local cv tuber*
45	1.92	1.98	1.73	0.09	1.26	0.43
60	5.43	3.72	3.87	0.47	3.53	0.26
75	11.44	11.48	7.51	2.92	11.36	2.19
90	18.00	15.18	11.88	6.36	14.84	4.57
105	24.95	16.37	15.38	11.63	19.77	4.96

Transplanting experiments have shown that seedlings need considerable time to recover their original growth rate after transplanting (Malagamba, 1984). Management practices, e.g. the use of rooting blocks made of compost, may reduce transplanting shock. Differences between progenies were pronounced, and in general hybrids recovered faster than open pollinated progenies.

The most important factor responsible for recovery from transplanting shock was found to be the capacity of the seedlings to regenerate adventitious roots quickly. Selection methods based on this have been worked out. In order to identify progenies with fast recovery after transplanting, seedlings are exposed to an induced shock by immersion of the roots in a PEG solution. The plants are inserted in a sponge support, and the root system is mist irrigated. A recovery index based on quantity of roots regenerated, and on wilting, is worked out (Malagamba, personal communication).

V. 4. *Seed tubers derived from TPS*

The production and utilization of seed tubers derived from true potato seed (Wiersema, 1984 a; 1986 a) is seen as a potential combination of the rapid plant development from seed tubers with the high health standards and low cost of TPS. Seedling tubers are produced in densely planted beds, where suitable conditions can be created for direct sowing or seedling transplanting, and where weeds and diseases can be controlled.

Yields and proportions of marketable tubers are considerably higher when the same progenies are grown from seedling tubers, than when transplanted seedlings are used (table 6). The use of seedling tubers has proved to be the most reliable method for TPS utilization according to almost all results of experimentation so far (e.g. Malagamba, 1984, 1987; Wiersema, 1984 a; Tsao, 1983; Rowell et al., 1986 c).

Table 6. Range of yield of 15 progenies at Huancayo, Peru, when grown as transplanted seedlings and as seedling tubers (tuber weight 5-10 g).
Source of data CIP Progress Report 1986, Malagamba et al.

	Total yield t/ha	*% marketable (>3.5 cm)*
Transplanted seedlings	14.6-45.8	58-81
Seedling tubers	30.3-68.6	71-93

For the production of seedling tubers, direct sowing in seed beds, followed by thinning and hilling by the addition of at least 2-3 cm of substrate to increase number of stolons and tubers, was regarded as the most labour saving method (Wiersema, 1984 b). In comparison with transplanting this also reduced the total growing period from sowing to maturity by about 15 days, the time taken for the seedlings to recover from transplanting shock. The length of the growing period under conditions in Lima varied from 110 to 150 days depending on TPS line and season.

For seed bed production Wiersema (1986 b) found the optimum density to be about 100 seedlings/m^2 in a square pattern. Total tuber number and tuber weight increased with increasing density due to faster canopy cover and increased selection pressure, weak plants being eliminated. Densities higher than 100 seedlings were found impractical for management of the beds.

With good management very high yields of seedling tubers can be achieved in small areas. Wiersema (1984 a) reported yields up to 12 kg/m^2 bed. Many small tubers are produced by the seedlings. Maximum numbers larger than 1 g - the size found usable for multiplica-

Table 7. Evaluation of 18 TPS progenies directly sown in nusery beds at Lima. Source of data CIP Progress report 1986. Wiersema et al.

	No tubers · kg m⁻²	*Total yield kg m⁻²*	*Mean tuber weight (g)*
Range	224-812	2.55-8.97	6.7-20.3

tion - harvested by Wiersema were 1200 tubers/m² bed. Table 7 gives results from another experiment, which also indicates the genetic variation that exists.

Storability of small tubers is an important issue. Only few reports have been published up to now, but results by Wiersema & Cabello (1987) indicate that although weight loss during storage was higher in small tubers, yields were not adversely affected. The reaction to temperature during storage of small tubers appears to differ from that of large ones. Practical experience (e.g. Vu et al., 1987) has not indicated small tuber size to be a problem.

VI. Uniformity and yield

The traits needed for TPS production are in many respects different from those which have been important for production of vegetatively propagated cultivars.

A key question affecting both decisions on breeding objectives and TPS-breeding methodology, is what level of uniformity is necessary. It has been argued that at least for developing countries uniformity is of little importance, and an acceptable level is easily achieved in existing material.

Kidane-Mariam et al. (1985 b) state »(tuber) uniformity may not be as critical a factor as once believed«, and also cite a number of other studies in support of the statement, e.g. Accatino & Malagamba, (1982); Macaso-Khwaja & Peloquin (1983); Rowell & Ewing (1984). The statement is based on ratings of tuber uniformity as a score which combines visual impression of skin colour, tuber shape and tuber size. In many cases this score compares very well with the uniformity score for cultivars. Similar high levels of uniformity have been noted in progenies of different origins; 4x x 4x crosses within Tuberosum, and between Tuberosum and Neo-Tuberosum, as well as 4x x 2x crosses.

Table 8. Specific gravity and mean scores for quality characters after steam cooking. TPS transplant trial at Lincoln, New Zealand. Bedi et al., 1979.

TPS line	*Specific gravity*	*Palatability*	*s.d.*
S V93	1.099	21.03	2.12
S 440022	1.086	18.47	2.42
S 52404	1.086	18.30	2.25
S 6100103	1.087	20.00	2.42
S 917013	1.092	18.33	2.21
S 1015015	1.083	17.45	2.56
C 1055	1.076	18.45	2.52
C 1405	1.085	19.00	2.42
C 1329	1.080	18.35	2.46
C 1458	1.084	18.20	3.41
C 1245	1.087	18.85	2.80
C 1482	1.076	16.51	2.77
cf Rua. control	1.091	23.17	1.85

S = seed from self-pollinated berries.
C = seed from cross-pollinated berries.
Maximum attainable score for palatability = 30.

Table 9. Specific gravity and mean scores for quality characters after steam cooking. TPS trial et Riwaka. New Zealand. Bedi et al., 1979.

TPS line	*No. of plants tested*	*Specific gravity*	*s.d.*	*Palatability*	*s.d.*
SV170013	10	1.076	8.94	18.8	1.20
S595027	8	1.053	7.68	16.2	2.84
S52404	23	1.059	9.63	17.9	1.32
SV17004	9	1.073	9.32	19.7	1.29
S726014	10	1.062	12.83	17.0	1.17
S440022	10	1.063	7.54	18.6	1.33
S595013	9	1.062	16.2	15.4	1.58
SV94	9	1.065	9.83	18.5	1.58
SV93	9	1.093	14.62	18.9	1.71
C1055	9	1.058	7.0	20.3	2.07
C1329	9	1.068	9.9	18.4	1.95
C564	9	1.062	8.96	20.2	1.95
C1245	7	1.080	17.79	18.0	0.77
C1458	10	1.067	18.14	18.7	1.68
C1408	10	1.067	10.2	19.4	1.84
C1405	11	1.072	17.65	19.8	1.43
C1467	10	1.073	22.75	17.6	1.03

Range in standard diviation

	Specific gravity	*Palatability*
S-progenies	7.54-16.2	1.17-1.86
C-progenies	7.0 -22.75	1.03-2.07

S = seed from self-pollinated berries.
C = seed from cross-pollinated berries.
Maximum attainable score for palatability = 30.

For characters which influence cooking quality, very few results have been published from analyses of progenies tested for use as TPS. Bedi et al. (1979) give data on specific gravity and palatability tests of a number of TPS lines grown in New Zealand. Table 8 is an example of such results, where a number of TPS lines were compared with a tuber seed propagated control.

As expected, variability in palatability was larger in the TPS progenies than in the cultivar. Standard deviations for specific gravity were not given for this experiment. However, in another experiment (table 9), where no comparison with tuber propagation was included, within-line variation in specific gravity was very high. Dry matter content was generally low. This was ascribed to immaturity at harvest. Note also that ranges in specific gravity and palatability were not as wide in selfed progenies as in crosses.

Published investigations where quality data on individual clones are given, which demonstrate the variation in unselected progenies used in the breeding of vegetatively propagated cultivars are also rather scarce. Such data often stay in the breeder's files, and I will use some data from the Svalöf breeding work.

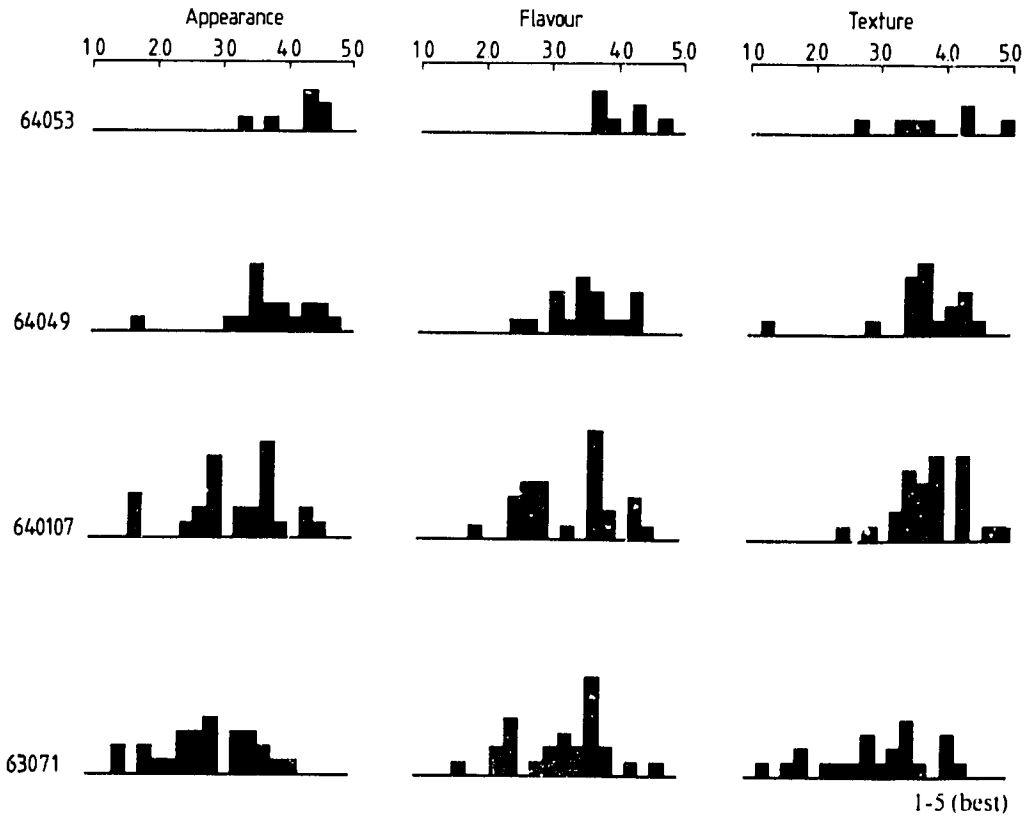

Fig. 1. Distribution of cooking quality in unselected hybrid populations. Analyses of individual clones grown in the field in South Sweden, sensory evaluation by a test panel of 5 persons.

VI. 1. Sensory evaluation

Sensory evaluation of a number of unselected hybrid progenies was made in material grown in South Sweden. Fig. 1 demonstrates both the variability within progenies and the appreciable difference that may be found between different progenies. A point to note is that an extremely low frequency of the clones in the progenies are comparable to the standard, in this case cv Bintje, which also was one of the parents in one of the crosses.

Discoloration after cooking, one of the factors influencing rating for appearance, was also quite variable (fig. 2)

For colour rating of chips (crisps) (fig. 3) similar great variation exists, which under Swedish conditions can be ascribed also to the genetic differences in earliness.

VI. 2. Starch

Percentage of starch is very important for culinary quality and processing, and uniformity particularly important for processing. Fig. 4 gives the distribution in three populations produced in controlled crosses between parent clones medium to high (16-21%) in starch (Umaerus, 1969). One hundred clones per progeny were field grown in South Sweden from 20-30 mm seed tubers, and 45-55 mm tubers were analysed after harvest approximately 3 months after planting. The range is about 10 per cent units between the highest and the lowest clone.

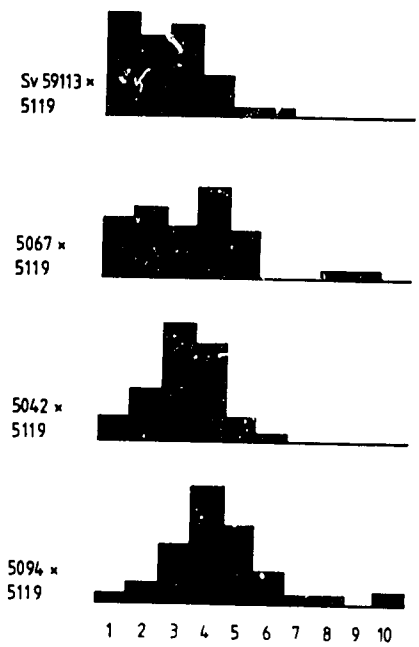

Fig. 2. Distribution of discoloration after cooking in unselected hybrid populations. Analyses of individual clones grown in the field in South Sweden. Discoloration estimated in the scale 1-10 (darkest) one hour after boiling of peeled tubers.

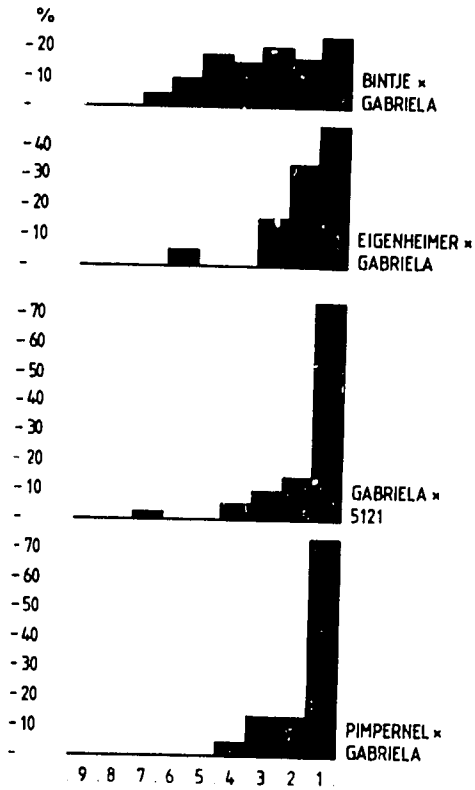

Fig. 3. Distribution of colour of crisps (chips) in unselected hybrid populations. Analyses of individual clones grown in the field in South Sweden. tubers stored for three months at +4 C. Scale 9-1 (darkest).

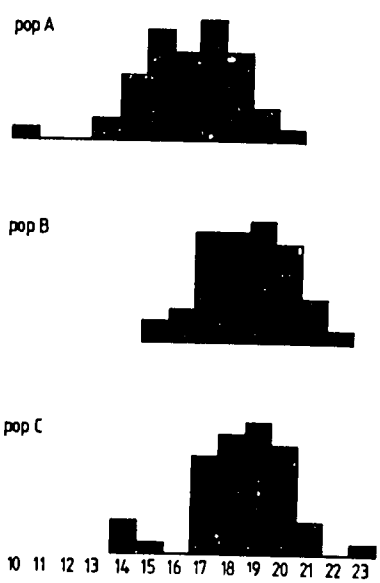

Fig. 4. Distribution of percentage of starch in unselected hybrid populations. Analyses of tuber harvests from individual plants grown in the field in South Sweden.

VI. 3. *Chlorogenic acid*

In this experiment 20 clones per progeny of a number of crosses were grown together with their parents from 20-30 mm tubers at several locations in Sweden, harvested after 90 (North Sweden) to 120 days (South Sweden), and stored until January. Two populations will be used as examples (fig. 5). The variation is large, larger in some progenies than in others, and larger in North Sweden than in South.

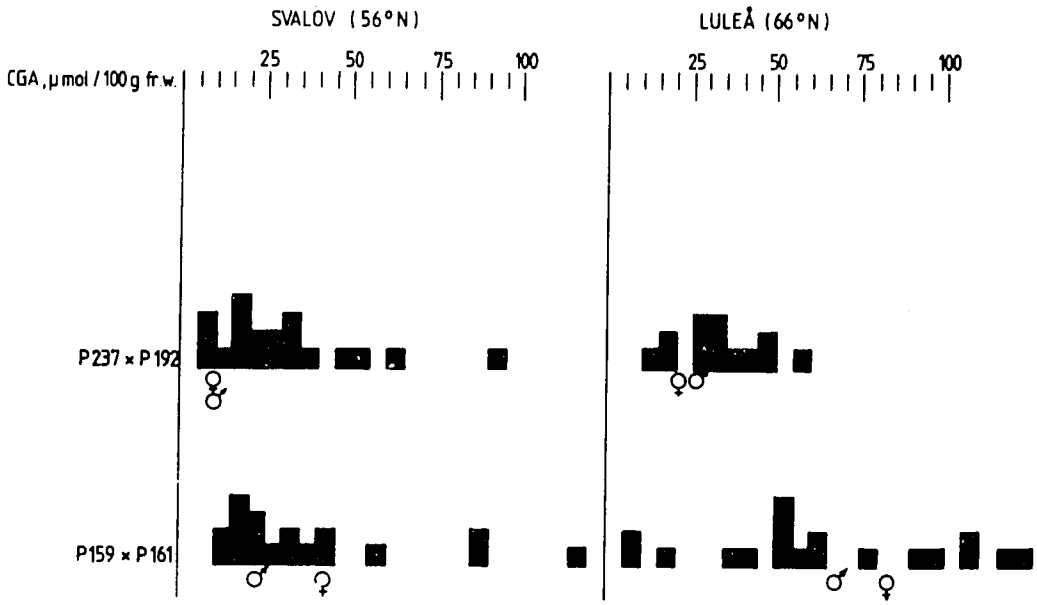

Fig. 5. Distribution of chlorogenic acid in unselected populations (20 plants per population) and parental clones grown in South and North Sweden. Samples of cortex from the crown end of the tuber, peel removed.

VI. 4. *Tyrosine*

The same experiment with 20 clones per progeny was used for analysis of tyrosine levels. The variation was appreciable, and of different magnitude in different progenies, but with an opposite trend to chlorogenic acid between the two localities.

VI. 5. *Total glycoalkaloids*

Data from Sanford & Sinden (1972) illustrate the variation in content of total glycoalkaloids found within a number of progenies grown in Maine (fig. 6). Clones within a progeny often exceed the higher of the parents.

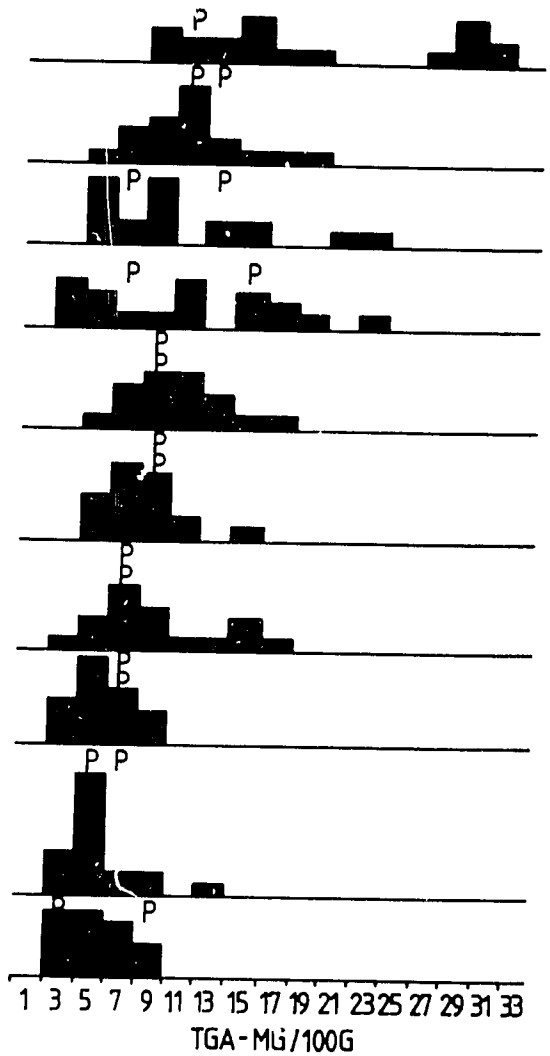

Fig. 6. Distribution of total glycoalkaloids in unselected populations and parental clones. After Sanford & Sinden, 1972.

VI. 6. *Need of uniformity*

The examples given above indicate that appreciable variability in quality traits must be expected.

Earliness variation and variations in dormant period will also exist in the progenies and influence quality factors as well as being important themselves.

There seems to be little doubt that some improvement is needed in comparison with the majority of progenies that can be produced through crossing or selfing of existing cultivars and progenitors. Uniformity may become more important for developing countries in the future, if more abundant food becomes available. In western countries the quality concept includes uniformity, and the processing industry demands uniformity. The established cultivar concept also strongly emphasizes uniformity.

VI. 7. *Uniformity vs yield*

Several breeding approaches, leading to different levels of uniformity, have been proposed (Hermsen, 1977, 1983; Plaisted, 1977; Peloquin, 1979; Peloquin et al., 1984). Since

yield is another key question, the choice between different possible approaches depends on whether heterozygosity is a prerequisite of sufficient yielding ability.

The most elegant, but also probably the most time consuming way, which can utilize all positive gene interactions in a heterozygous, genetically uniform material would be the production of potatoes with autonomous apomixis (Hermsen, 1980).

Inbreeding, and if heterozygosity is necessary hybrids between inbreds, are other approaches for high levels of uniformity (Hermsen, 1977; Yashina & Pershutina, 1971).

For the long term solution of how breeding should be performed, the TPS advance has thus promoted the desirability of understanding the causes for inbreeding depression and its converse; heterosis. Heterosis breeding has led to very spectacular results in breeding of allogamous crops, although the theoretical background is still debated, and has been seen at times as a somewhat academic question.

There are numerous investigations which have shown that inbreeding depression is often pronounced in potatoes with regard to vigour, yield and fertility. Heterosis has been demonstrated in species crosses, the advantages of heterozygosity have been demonstrated many times, and the advantage of multiallelism demonstrated in potatoes by Mendoza & Haynes (1974) supported the theory of overdominance as a cause of heterosis.

Jackson et al. (1984) and Jackson (1987) on the basis of theoretical work by Jinks (1981, 1983) arguing that the genic content of the individual rather than heterozygosity per se is the background of heterosis, and heterosis thus could be fixed in a homozygous condition, proposed inbreeding for the production of TPS lines. Results from USSR (Trinkler et al., 1980, 1984; Budin & Soboleva, 1978) as well as recent experiences at CIP indicate that inbreeding depression is not always present.

VII. Implications for future utilization of TPS

We have seen that at present the emerging most widespread utilization of TPS appears to be in developing countries as seedling tubers or in some areas as transplanted seedlings.

Climatic conditions, food habits, labour costs in different areas, as well as the suitability of available genetic material, will influence the extent and localization of future utilization.

I will try to survey the different options for TPS use, and also the advantages and constraints for the different ways. I will do it in the approximate order of present adoption. The patterns which are now emerging may not be lasting, however, depending on the rate of adoption of competing technologies.

VII. 1. Botanical seed used for production of tubers for further multiplication.

Higher and more reliable yields of tubers can be produced from seedling tubers than from transplanted seedlings, as examplified in table 6. The largest acreages in the world from true seed have been grown in this way in the People's Republic of China.

VII. 1. 1. Repeated tuber production from open pollinated seed.

Open pollinated botanical seed is collected from selected parents. After production of a first generation of seedling tubers in greenhouses, beds or the field, repeated generations of tubers may be produced for use as seed tubers, and in part for consumption.

Advantages

Flexibility. Production of the botanical seed can take place centrally or be made by the farmer, depending on parent genotype and suitability of environment. Seedling tuber production may be centralised or be made by the farmer. Easily adaptable to different areas. The same seed source may be used for different areas, and propagated for different numbers of generations depending on e.g. virus spread in different areas or different seasons.

Low cost of both breeding in the initial phases, production of botanical seed, and distribution of initial planting material.

No change of production technology in ware production needed compared to vegetatively grown conventional cultivars.

Disadvantages

Lack of uniformity.
Yield depression because of inbreeding.
As discussed earlier these constraints may not be at all as serious as anticipated in the initial phases of TPS experimentation.

In present material, selection takes place in the seedling generation through competition between seedlings (table 10, Wiersema, 1986 b). The weakest seedlings resulting from inbreeding in open pollinated progenies are automatically selected out. This might allow open pollination to be used even if inbreeding reduces yield. Further selection may be applied for yield and/or uniformity (Rowell et al., 1986 b). Also, the economic returns rather than yield per se should be considered - even a somewhat reduced yield compared to hybrid seed might be preferred because of the low cost of planting material.

Potential areas of adoption

a) Countries where food habits with regard to potato quality are not fixed.
b) Production for uses of potatoes where uniformity demands are limited to few traits, e.g. starch production. It might be possible to select parental material which produces progenies with an acceptably high average starch percentage in the tubers in combination with acceptable tuber yields. The economic returns would depend on the cost of production of seedling tubers compared to the cost of presently used systems, i.e. in most cases a seed production and certification system based on meristem derived tuber seed. In both cases the health standard of the seed used for ware production depends on the number of generations, the rate of flush out through the system. Calculations would have to be made for individual countries.

Implications for breeding

The first objective is the identification of progenitors which flower and produce reasonable amounts of good quality botanical seed, and produce progeny with an average maturity suitable under the growing conditions in the area for which it is intended. This has already been achieved for some areas.

Short term introduction does not have to rely on a long period of breeding, since most traits are similar to vegetatively propagated cultivars. Breeding for changes in seedling traits may not have to be made, or be limited to some improvement of e.g. germinability and early seedling vigour. The seedlings can be given intensive care for the first tuber production, since only small acreages are needed.

Demands on virus resistance do not have to be very high, since a stock of seed to replace diseased material can be kept available. For diseases not disseminated through the

tuber, resistance of similar levels as in vegetatatively propagated material would be needed, with different emphasis in different areas. The heterogeneity of seedlings in disease resistance, especially of the race specific type, might be an advantage, similar to a multiline effect.

The crucial question for how much breeding effort will have to be put in, is what level of uniformity is needed. Plaisted (1977) advocated population breeding, the conventional approach in low-cost breeding of allogamous crops, and listed as one of the objectives of this approach selection for uniformity in market attributes. Thompson & Mendoza (1984) determined genetic parameters for a number of TPS traits including uniformity of tuber colour and shape, and concluded that selection could lead to rapid improvement.

Uniformity in currently available populations is regarded as acceptable in some areas already, but not everywhere and not for all purposes. Rapid improvement has been achieved through very simple breeding techniques - the identification of parental material which produces more uniform progenies - for the traits where uniformity has been looked for: tuber uniformity in colour, shape, eye depth and size. It is not possible to predict at present if similar rapid progress is possible for the many traits necessary for cooking and processing quality, although available data indicate that variation is available. It is also not possible to predict what levels of uniformity are indispensible. The closer to the marginal areas for potato production we go, the larger becomes the environmentally induced variation, and thus it will be more difficult to accept an increase in genetic variability.

In a longer term uniformity would be expected to become more important . Genetic uniformity, guaranteeing the least possible phenotypic heterogeneity, could be achieved in two ways: through inbreeding, which is used in breeding programmes in the USSR and the People's Republic of China, or through the creation of potato cultivars with autonomous apomixis (Hermsen, 1980). Both ways would make it possible to use only one clone for production of botanical seed, and the production of botanical seed would thus be cheap compared to hybrid seed production, provided clones with acceptable berry production can be produced. Both are long term breeding approaches for complete or high level uniformity to be achieved.

There appears to be considerable hope that tetraploid progenies with no or minor effects of inbreeding on yield can be identified (Trinkler et al., 1984, Mendoza, personal communication). Faster progress is possible (Jackson et al., 1984) by using anther culture or single seed descent on the diploid level;

VII. 1. 2. Hybrid seed for repeated tuber production.

Hybrid populations after controlled crosses on the tetraploid level may be used for seed tuber production a number of generations in the same way as described for open pollinated seed.

Advantages

The same as for open pollinated seed as concerns low cost of breeding and distribution of initial planting material, and similarity in production technology in ware production compared to vegetatively grown cultivars.

Most of the flexibility seen as an advantage under VII. 1.1. is retained, plus possibly a higher potential yield. Mendoza (1984) reports on a comparison where a large number of single crosses as well as bulk crosses and multilines where compared with selfed and open pollinated material. Significant differences were found in favour of hybrid material in

germination, transplant survival and tuber yield. Because of the higher potential yield Kidane - Mariam et al. (1984) stated that the use of OP seeds for commercial production should be viewed as a stop-gap until a method is developed to produce inexpensive hybrid seed. It is, however, doubtful if these advantages are important when seedling tubers are used (table 10).

Table 10. Mean yield of tubers (t/ha >28 mm) from 5 hybrid and 6 open pollinated progenies. Source of data CIP Progress Report 1986, Wiersema et al.

	Transplanted seedlings	*Seedling tubers*
F₁ progenies	29.7	51.4
OP progenies	24.3	51.4
F-test	**	NS
** P< 0.01		

Disadvantages

The considerably greater difficulty and higher cost of production of botanical seed, compared to open pollination.

A slight disadvantage in uniformity in present material: According to Mendoza (1984) tetraploid hybrids were equal or inferior to open pollinated progenies in uniformity and eye depth. Variability in cooking quality appeared to be larger in hybrids than in open pollinated progenies in one of the few reports on cooking quality of TPS (Bedi, 1979).

Potential areas of adoption

The same as for VII. 1. 1. Both hybrid and open pollinated botanical seed would be expected to be cheaper alternatives than conventional tuber seed. Incentive for adoption will depend on availability of hybrid seed, which is more difficult to produce for the farmer himself, and the relation between cost of hybrid seed vs open pollinated.

Implications for breeding

While combinations of desirable traits in the progenies are similar to those mentioned for open pollination, more emphasis would have to be put on flower characteristics, to facilitate insect pollination or make hand pollination cheaper by avoiding emasculation.

Different types of hybrid families have been suggested; crosses within group Tuberosum; crosses with Neo-Tuberosum; use of dihaploids and diploids in 4x x 2x crosses (Hermsen, 1977; Plaisted, 1977; Peloquin, 1979; Peloquin et al. 1984.) These types of progenies have been evaluated in later investigations, in most cases as transplanted seedlings and not grown from seedling tubers, however. They have all been found to give acceptable yields and uniformity.

Kidane-Mariam et al. (1985 b) evaluated 262 hybrid progenies after conventional intermating of tetraploid parental lines. Several families gave yields similar to standard cultivars, estimated to be equivalent to 34 - 36 tonnes per hectare. It was concluded that the use of crosses at the tetraploid level allows for more flexibility than other approaches, e.g. in using locally adapted cultivars in crossing programmes.

Neo-Tuberosum crosses (Rowell et al., 1986 a) also yielded similar to standard cultivars, 30 - 34 tonnes per hectare, and uniformity in tuber appearance was comparable to

standard cultivars in several progenies. The authors stated that the high yields are consistent with the well documented heterosis exhibited by hybrids of Neo-Tuberosum and Tuberosum, and that in addition to the yield advantages resistances to many important potato diseases are found within the Neo-Tuberosum populations.

The 4x x 2x breeding scheme intended to maximize heterozygosity and give better than average uniformity has been shown in many investigations by Peloquin & co-workers to generate high-yielding progeny with good uniformity (Macaso-Khwaja & Peloquin, 1983; Kidane-Miriam et al., 1985 a; Concilio & Peloquin, 1987), and has been extended theoretically with a number of schemes to allow e.g production of hybrid seed without hand pollination (Peloquin, 1983).

Selection for general combining ability for tuber uniformity appears to have given good results both within Tuberosum and utilizing combinations with Neo-Tuberosum (Thompson & Mendoza, 1984; Rowell et al., 1986 b).

If, in the long run, heterozygosity is found to be a prerequisite for high yield, and apomixis has not been achieved, hybrid progenies could be produced through crosses between inbred lines. Since the tetraploid level, with possibilities of multiallelism, would then be expected to be superior (Mendoza & Haynes, 1974), double crosses would be expected to be superior to single crosses with respect to yield.

VII. 1. 3. »Farmers' varieties«.

As an extension of the system described under VII. 1. 1. and VII. 1. 2., a production of »farmer's varieties« may take place. A continued selection over a number of years in farmers' fields of the clones or groups of clones with attributes seen as desirable under the local conditions is not only possible, but probable. This appears to be taking place in e.g. Rwanda in TPS material distributed by CIP, and has happened in India.

Advantages

This would be a parallell to what took place when potatoes were introduced in northern Europe, and lead to a situation with a multitude of local cultivars. Seed certification specialists have fought battles against the remains of these up to this century in many countries. In retrospect it was an efficient way of adapting the potato to long day. It may be a much more efficient way of adapting the potato to warm climates, since the variability of the material that can be made available for selection to work on is much wider.

Disadvantages

Identical to the use of seed tubers.

Potential areas of adoption

Countries where seed tubers of established cultivars are not easily available, and seed certification is not enforced. Areas with moderate spread of viruses and climatic conditions which allow storage of tubers.

VII. 1. 4. Ware production from seedling tubers.

Seedling tubers of open pollinated or hybrid progenies may be used for ware production without further multiplication.

Advantages

In addition to most of those mentioned under VII. 1. 1. and VII. 1. 2. less danger of virus infection because of rapid replacement of seed.

Disadvantages

Compared to VII. 1. 1. and VII. 1. 2. more labour intensive because of the need for continuous production of seedling tubers in larger quantitites, and a continuous supply of botanical seed.

Potential areas of adoption

The areas for adoption would be those where the danger of disease spread is too large to allow further tuber multiplication.

Implications for breeding

Flowering and seed production traits that influence the cost of production of botanical seed need more emphasis, since larger quantities are needed.

Since larger areas of seedlings would be needed for the production of seedling tubers, than with repeated tuber multiplication, and consequently cost would be more influenced by labour and chemical input in this phase, more emphasis would be needed to improve seedling traits; uniformity of germination, early seedling vigour, seedling resistance to damping off.

The considerations regarding open pollination or hybrid seed are the same as above.

VII. 2. Ware production from botanical seed.

The expected advantages of TPS - cheap, lightweight, disease free, non- perishable planting material - are more fully realised when botanical seed is used for direct ware production.

Open pollinated or hybrid botanical seed may be used. The same considerations apply as under VII. 1., but inferiority of open pollinated populations has been more clearly documented when used for ware production than when seedling tubers are produced (table 10).

VII. 2. 1. Transplanted seedlings.

Advantages

In comparison with production from seedling tubers: Storage of tubers will not be necessary. Apparent uniformity of tubers better than when ware is produced from tubers.

In comparison with direct sowing: Better survival and establishment of the stand. Some selection can be made at the time of transplanting, to improve progenies.

Disadvantages

Longer growing period because of delay in plant growth caused by transplanting shock.

Labour intensive. Seedlings delicate and difficult to produce and handle. Damping off

Table 11. Yield of tubers >28 mm from 11 TPS progenies.
Source of data CIP Progress report 1986, Wiersema et al.

	Transplanted seedlings	*Seedling tubers*
Mean yield, t/ha	26.7	51.3
Range, t/ha	15.0-44.6	40.6-64.2
Ranking of progenies	1	3-4
	2	8
	3	1
	4	7
	5	6
	6	3-4
	7	11
	8	2
	9	5
	10	9
	11	10

caused by *Rhizoctonia* is often a problem, as well as weeds. Considerable cost for pesticides and herbicides.

The tubers produced are small compared to those produced from tuber seed.

Possible areas of adoption

Warm tropical areas, where tuber storage and transport of tubers are difficult.

Implications for breeding

Several improvements in seedling traits would be needed, some of which have been shown to be feasible; genetic variation exists. Survival after transplanting and reaction to transplanting shock varies between progenies, and improved recovery is already selected for. Seedling vigour, which is related to quality of the botanical seed, can be improved.

Hybrid seed has shown more superiority over open pollinated seed when TPS is used for transplanting than when seedling tubers are utilized (Atlin & Wiersema, 1988), which is ascribed to the selection taking place in a dense stand. It seems then to be desirable that weak seedlings are automatically eliminated, and it is somewhat doubtful if major changes in seedling structure and sturdiness should be the objective.

Evaluation of progenies has to take place both as transplanted seedlings and seedling tubers, since ranking of progenies has been formed to be different (table 11).

VII. 2. 2. Direct sowing for ware production

Advantages

The same as for transplanted seedlings plus the possibility of reduced labour.

Disadvantages

Difficult to establish a good stand of plants, delicate seedlings, damping off, weeds, insects, low utilization of light in early phases of development, poor yield, small tubers.

Areas of adoption

Field cultivation is not regarded to be feasible with present material. Production in beds may give high production per unit area, and home garden production under climatic conditions where repeated sowing is possible has been estimated to be able to satisfy a family's need the year round.

If major improvements through breeding can be made, and mechanization developed, a potential might exist in all parts of the world which do not have too short growing period.

Implications for breeding

In order to make this ultimate goal of TPS utilization possible a major reconstruction of the potato seedling is probably necessary. Analogies may be seen with other cultivated plants, which have been very drastically changed through breeding. Many of those changes occurred very long ago - the development of the corn plant with large seeds unable to be distributed except with the aid of man, or the loss of the brittle rachis in the cereals. Other changes, which have taken place during recent times, include the creation of cereal cultivars with short, stiff straw, and minimum development of tillers in order to produce a uniform stand of large spikes of the same age, leafless peas, topless broad beans and so on.

The potato seedling is still a wild plant in its characteristics. Its strategy is to produce many small seeds, most of which do not survive in nature.

Seeing the availability of genetic variability in all traits where it has been looked for, it seems worthwile to make an effort to try to define the combination of traits that would make it possible to grow potatoes with direct sowing of true seed. Very drastic changes would be needed in my opinion, but I do not expect it to be impossible to create them. Attempts to define the ideal plant type for TPS production have been made earlier, e.g. by Jackson et al. (1984).

I will list some of the traits I believe are desirable;

A large botanical seed - variation exists, but genotypes which produce sufficient size may not yet have been identified.

A larger seed is easier to handle, and produces a more vigorous seedling, but probably this is not enough. A much sturdier and thicker, but not very tall, stem would be desirable. Care must be taken not to make the plant too short in stature, however, at least for areas wher there is a danger of lack of water, because this might give a correlated response in root development.

Seedlings are single stemmed, but produce a number of above ground branches. It would be desirable to identify genotypes which produce a single, unbranched stem. This would allow fairly dense stands, in order to produce an early canopy large enough for satisfactory utilization of the light.

The plant should produce few tubers. This would make it possible to produce large enough tubers also in a dense stand.

The plant should flower and produce sufficient, but not overmuch, seed to be self reproducing. Independence of daylength would be desirable, but different genotypes for different areas may be possible, and are of course desirable from other aspects.

Self fertility and no negative response to inbreeding are desirable for low cost production of botanical seed. This eliminates the need of hand pollination or pollinating insects.

Is the production of such cultivars possible?

I think so, but with considerable breeding efforts.

Will the production of such cultivars be worth the effort, time and money?

This is more difficult to answer.

If the use of TPS is seen as a temporary solution in order to supply seed for remote areas while a tuber seed programme is being built up, and if in this case the creation of such a tuber seed programme is seen as a realistic possibility for all the areas of the world, where it would be an advantage for human nutrition or economy to produce potatoes, then it is doubtful.

If on the other hand it seems realistic to breed not only for plant type, but also for the many quality traits that I believe would be needed for TPS to compete where high culinary quality clonal varieties are available, the answer may be yes. However, the breeding inputs for creating material which combines quality traits, resistance traits, and uniformity with a restructuring of the plants need to be very large, and would be acceptable from an economic point of view only if the material produced could be expected to be utilized over very large acreages.

For the adoption of TPS in temperate developed countries with a short growing season, I doubt if even such a drastic change would be enough. The reserve of the tuber which allows the quick start in spring becomes more important for yield and maturity the shorter the available growing season is.

VIII. Conclusions

The work on TPS is quickly making a number of the established truths of potato production obsolete. Many of the unsurmountable difficulties that were envisaged when the use of botanical seed was first discussed, can be overcome or circumvented in more or less ingenious ways. However, other difficulties remain, and some of the advantages have not been realised, at least not yet.

It was believed that open pollination was almost equivalent to selfing. There is considerable variation, and the realised level of inbreeding may be only 40-60% (Atlin, 1984).

It was believed that inbreeding depression was invariably too serious in potatoes to allow selfing. This is undoubtedly so in many genotypes, but selfing or open pollination without detrimental effects on yield has been found much more frequently than expected.

It was believed that open pollination repeated generation after generation would lead to contiuned yield decrease. This has not been found to be so.

It was believed that emasculation, which is labour intensive and therefore expensive, or male sterility, would be necessary in order to produce hybrid botanical seed using hand pollination. Experiences at CIP indicate that for practical purposes effects of a small frequency of inbred plants on yield of the progeny is probably negligible, and emasculation can be omitted.

It was seen as one of the most important possible advantages of using botanical seed instead of tuber seed, that viruses could be excluded from the list of harmful parasites. Expensive tuber seed production, virus testing and seed certification would be less necessary. Breeding for virus resistance would not have to be considered for material for TPS production. The agronomic difficulties with direct sowing or transplanting for ware production from TPS have made this advantage difficult to realise immediately. In the breeding program for TPS at CIP it is now seen as important to include resistance to the most important viruses

For the same reason it will take time before the slogan »A handful of seed replaces two tons of tubers« becomes more than in part reality. The use of TPS is taking a number of different routes. It is difficult to predict at present if this conglomerate of ways to utilise TPS will remain - perhaps TPS will turn out to be just a repetition, applied in the developing world, of the introduction of the potato to North Europe, i.e. a farmer's breeding

of new cultivars, a multitude of genotypes to be tried out, of which a few will remain as vegetatively propagated a hundred years from now?

This adaptation breeding on a gigantic scale would be an important enough result. The introduction of cell- and tissue culture in seed programmes in developing countries is advancing very fast. With this method as a basis for a national supply of healthy seed, tuber propagation may be preferred.

On the other hand potatoes may be transformed to an autogamous crop. If inbreeding continues to show promise, and high yielding cultivars can be produced, which also set sufficient seed after open pollination, it might be possible to replace meristem based seed programmes with a cheaper system for production of healthy seed all over the world. In a long time perspective breeding might even lead to direct ware production from botanical seed for countries with favourable climates.

TPS has quickened the pace in potato research, widened our knowledge and imagination. Whether the work will lead to a large scale worldwide use of TPS is still uncertain, and will depend on available funding and economic considerations. Even if TPS turns out to be only a passing phase for the promotion of potato cultivation in developing countries - and I believe it will be more than that - TPS will have served a good purpose.

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