Potato

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The potato of commerce in the United States, Europe, and other temperate and subtropical climates is *Solanum tuberosum*, subspecies *tuberosum*. This crop is often referred to as the Irish potato or white potato to differentiate it from the sweet potato. Both names are misleading in that the origin of potato is not Irish and they have colors other than white. Native cultivars of the same subspecies grow in Chile. The subspecies *andigena* is widely cultivated at high elevations from Argentina to Mexico with a center of concentration in Peru, Bolivia, and Ecuador. Some believe that North temperate clones were derived from subspecies *andigena* through selection for adaptation, but others believe that Chilean tuberosum was the source (Grun et al., 1977).

I. PARENTAL MATERIAL

*Solanum* contains about 2,000 species, of which about 150 are tuber-bearing. These occur in five cytological groups, with somatic chromosome numbers of 24, 36, 48, 60, and 72.

About 70% of all potato species are diploid (Hawkes, 1958). Most of these are self-incompatible and are able to produce seeds only when they are pollinated with pollen containing a different S allele. Diploid species which are self-compatible are *S. morelliforme*, *S. polyadenium*, and *S. verrucosum*. A prominent cultivated diploid is *S. phureja*, which is grown in mountain valleys throughout South America. It is distinguished by an absence of tuber dormancy, which permits immediate replanting in areas where continuous cropping is possible. This species has been used extensively as a pollinator to produce haploids of *S. tuberosum* cultivars, as a bridg-
ing parent between other diploid species and *S. tuberosum*, and as a base for genetic studies (Peloquin et al., 1966). Other cultivated diploids are *S. stenotomum*, which is cultivated in regions similar to where *S. phureja* is grown; *S. ajanhiure*, a hardy species grown in the highlands of Bolivia where its tubers are used for production of tunta, a freeze-dried produce; and *S. goniocalyx*, which is grown in the lower valleys in Peru.

Tetraploid, tuber-bearing *Solanums* may be self-fertile. Cipar et al. (1964) showed that haploids (diploids) of the tetraploids contain the same self-incompatibility system as the diploid species. The system conforms with the *Nicotiana* scheme of oppositional S alleles. Presumably the tetraploids are self-compatible when the pollen possesses two S alleles which induce mutual weakening. Even though the majority of diploid species are self-incompatible, variation exists within species. One cause for this variation may be the spontaneous production of unreduced gametes in plants which are heterozygous for S alleles. The other is the occurrence of an S-bearing translocation (Olsder and Hermsen, 1976), which would have the same mutual weakening effect as long as the translocation carried a different S allele.

Crosses between tetraploids and diploids rarely produce triploid offspring because of a “triploid block” arising from an imbalance of endosperm factors in the nucleus (den Nijs and Peloquin, 1977b). A few triploid clones are cultivated, but these are sterile and are preserved by asexual propagation. The non-bitter triploid cultivars are often classified as *Solanum × Chaucha*. The hybrids *Solanum × Jupeyczukii* are assumed to be hybrids between the frost-resistant, tetraploid species, *S. acaule*, and cultivated diploids. Christiansen (1977) has identified more than 120 different clones and described the impact of these “bitter potatoes” upon the economy and nutrition of people living in the Altiplano region of Peru and Bolivia.

Tetraploids form about 15% of the tuber-bearing species. Clones of *S. tuberosum* subspecies *andigena* will cross readily with clones of subspecies *tuberosum*, but generally produce late maturing hybrids unless the *andigena* parent has been selected for earliness. Clones of this subspecies are valuable sources for many desirable characters.

The predominant form of chromosome pairing in tetraploids is as bivalents. Swaminathan and Howard (1954) reported an average quadrivalent and trivalent frequency of two to three per nucleus. Tetraploids may be hybridized with diploids directly or by first doubling the chromosome number of the diploid with colchicine. Tetraploid offspring are produced in crosses between diploids and tetraploids as a consequence of the unreduced gametes produced in small frequency by most diploids and in high frequency by a few. Hanneman and Peloquin (1968) obtained 91.9% tetraploid progeny in crosses between tetraploid × diploid parents and 94.8% in the reciprocal crosses. The diploid pollen appears to have a competitive advantage over the haploid pollen, and when crossed to a tetraploid species, the triploid block permits only the tetraploid ovules to develop.

Pollen fertility of interspecific hybrids frequently is dependent on the species used as female. Lamm (1953) reported ssp. *tuberosum* cytoplasm to be sensitive to *S. acaule* nuclear factors. Dionne (1961) reported male sterility in crosses between *S. demissum* and diploid species when *S. demissum* was used as a female. Grun et al. (1977) studied various manifestations of
male sterility in *tuberosum* and its possible ancestors. They described eight cytoplasmic factors for male sterility which differentiated spp. *tuberosum* from ssp. *andigena*, *S. vernei*, and *S. stenotonum-S. phureja*. The ssp. *tuberosum* clones considered were from the northern hemisphere and from coastal Chile. In general, clones of ssp. *tuberosum* from both sets behaved the same. Sources were bilaterally fertile in crosses to each other, whereas ssp. *tuberosum × ssp. andigena* hybrids usually will display male sterility, although the reciprocals do not.

*Solanum × curtilibium* is a pentaploid, presumably a cross between *S. × juzepczukii* and subsp. *andigena*. *Solanum × curtilibium* and *S. × juzepczukii*, constitute the “bitter potatoes” grown on the Altiplano of the Andes.

Hexaploid species constitute about 8% of the tuber bearing *Solanum* species. These are generally self-fertile. They can be crossed directly to tetraploid cultivars with a small percentage of success or they may be crossed to a diploid to produce a tetraploid hybrid, which is then crossed to a tetraploid cultivar. The hexaploid species most widely used by potato breeders has been *S. demissum* which grows at high elevations in Mexico. This species served as the source of the major *R* genes for late blight resistance.

Major collections of tuber bearing Solanums are maintained at the International Potato Center in Peru, the IR-1 project at Sturgeon Bay, Wis., the Commonwealth Potato Collection at Pentlandfield, Scotland, the German-Dutch Potato Collection at Braunschweig, West Germany, the Central Colombian Collection at Bogota, Colombia, and the Potato Collection at Balcarce, Argentina. The International Potato Center has the best collection of cultivated species, particularly *andigena*, *phureja*, and the “bitter potatoes”. The IR-1 collection is an excellent source of the wild species, as well as many accessions of the cultivated species. Because of quarantine restrictions on importation of tubers into the United States, the IR-1 project is an invaluable source of germplasm for interested users in the United States. Quarantine restrictions do not apply to the importation of true seeds, if material is desired from the other collections.

II. PLANT CULTURE

A. Field

Clones of temperate zone *tuberosum* will generally bloom 60 days after planting in the field. Pollination of the flowers on the plant in the field is generally unsuccessful for producing seeds. Many breeding programs overcome this difficulty by using the technique of cut stems described by McLean and Stevenson (1952) and developed further by Peloquin and Hougas (1959). This method involves cutting a stem that contains a large inflorescence with several unopened buds. The stem is cut 20 to 30 cm long with at least one fully expanded leaf. The cut stem is immediately placed in tap water and carried to an air-conditioned greenhouse or growth chamber. Any opened flowers are removed.
Where nurseries are grown as a source of cut stems for pollination, the plants should be at a spacing that will facilitate identification and access. Rows approximately 2 m apart and plants 1 m apart in the rows will accomplish this. The planting stock should be virus-free and the nursery managed to avoid infection by contact or aphids. If possible, the nursery should be planted where irrigation can be applied during the time of flower development, if rainfall is insufficient. The nursery should be a short distance from the place where the cut stems are maintained.

B. Growth Chamber and Greenhouse

When using cut stems, the greenhouse or growth chamber should have at least 16 hours of sunlight or 20 klux of artificial light. It is important that the temperature be maintained at about 19 °C with a high relative humidity during the period of pollination. Usually an inflorescence will produce flowers for 5 to 10 days. After fertilization has been achieved, the stems can be placed in a warmer greenhouse if space is limiting. The most critical aspect of this technique is to keep the cut stems from rotting. This can be done if the water in the containers is replaced with fresh water two or three times a week during the first 2 weeks. Few stems will rot if 5 to 10 ppm of streptomycin sulfate are added to the water, and the water is changed once a week while at the 19 °C temperature. If rot does begin, the stem can be saved by trimming it back. Stems treated in this fashion can develop mature fruits that can be harvested in about 6 weeks. Some breeders use milk bottles to hold individual stems. Another technique, more amenable to changing the water, is to use plastic paint pails with chicken wire over the top to support four stems.

Traditionally potato crosses have been made in the greenhouse during the winter when the temperature can be maintained at 19 °C. The day length must be extended to 16 hours from the time of emergence to pollination. Lights with a high light level such as metal halide lamps, result in the best growth. Flowering will be benefitted if the fertility is somewhat restricted and tuberization is reduced. Dutch breeders have developed a system of placing the potato seed piece on a brick and covering it with sand (Thijn, 1954). As soon as the roots have penetrated the soil, the sand is washed away and tubers removed as they are formed. Another technique is to plant the tubers in 20 cm clay pots and set them on the greenhouse bench or ground bed. This constricts the root growth and promotes flowering. The plants need to be pruned to one or two main stems and tied to 2 m stakes.

III. FLORAL CHARACTERISTICS

It is difficult to classify the cultivated tetraploid potato as to extent of natural cross-pollination. It displays the inbreeding depression characteristic of cross-pollinated species, yet most of the seeds obtained from open-pollinated fruits are the result of self-fertilization. This is discussed in greater detail in section V.
The inflorescences are borne terminally on the stems and the number of flowers ranges from 1 to 30, with 7 to 15 being the most usual (Fig. 1A). The number of inflorescences per plant and the number of flowers per inflorescence are greatly influenced by the cultivar. About the time the first flowers are fully expanded, a new shoot develops at the proximal leaf axis and ultimately grows beyond the first flower cluster to produce a second inflorescence.

The flower is 3 to 4 cm in diam with five petals which give the flower the shape of a star (Fig. 1B). The size of the flowers and their distribution in the inflorescence make them easy to locate and to manipulate. The five anthers are 5 to 7 cm long, and openly displayed in a column surrounding the pistil (Fig. 1C). The stigma generally protrudes beyond the ring of anthers (Fig. 1D). The corolla may be white or a complex range of blue, red, and purple depending on the anthocyanins present. The anthers are a bright yellow, except for male-sterile clones in which they may be light yellow or

Fig. 1—Emausculion and anthesis of potato. (A) The four buds of the inflorescence marked by arrows are at proper stage for emasculation; (B) emasculated flower at the stage for pollination; (C) complete single flower prior to anthesis; (D) anthers ready to shed pollen.
yellow green. The stigmas are usually green, though some clones may have pigmented stigmas. The extrusion of the stigma beyond the anthers can range from essentially none to the style being half again as long as the anthers. The petals generally will conceal the anthers in the mature bud, though in some clones the petals of the bud will not be expanded fully enough to conceal the anthers. The stigma generally will not be extruded through the tip of the anther cone in the mature buds until a day before the flower opens.

The flowers on the branch closest to the base are the first to open with two or three opening each day. Flowers will remain open 2 to 4 days resulting in inflorescences with 5 to 10 flowers open at the time during the height of bloom. The receptivity of the stigma and duration of pollen production is about 2 days (Janssen and Hermson, 1976). Clarke (1940) found that fertilization can occur as early as 36 hours after pollination. Hoopes (1977) found that pollen tubes of _tuberosum × andigena_ hybrids grew the length of the styles within 20 hours. Viable embryos can be excised 14 days after pollination (Haynes, 1954). Six weeks after pollination is the minimum time for full development of viable seed (Simmonds, 1963b).

**IV. ARTIFICIAL HYBRIDIZATION AND SELF-POLLINATION**

**A. Equipment**

If many flowers are to be pollinated with one pollen source or a bulk collection of pollen is required, a mechanical vibrator will facilitate pollen collection. These vibrators may be constructed using a flashlight case with a modified door bell unit fastened to it (Fig. 1D) (Sanford and Hanneman, 1977). In operation, the looped wire fastened to the vibrating arm of the buzzer is placed against the base of the flower and the anthers vibrated to release the pollen (Fig. 1C). The pollen can be collected in small test tubes filled with paraffin to within 1 cm of the top, in gelatin capsules, or in modified plastic syringes where the plunger can regulate the depth of the pollen.

**B. Preparation of the Female**

Cut stems are best made in the field in the early morning. The opened flowers should be removed at that time and mature unopened buds can be emasculated. The buds at this stage are plump, the petals appear ready to separate, and display their final color (Fig. 1A).

When potatoes are grown in winter in closed greenhouses, and not subjected to vigorous shaking by ventilation air currents, opened flowers generally fail to set fruit unless they are hand pollinated. Consequently, emasculation is not essential in the greenhouse if the consequences of a chance selfing are not very serious. Where complete control is required, the emasculation can be accomplished easily as a consequence of the simple flower structure and large anthers. Either forceps or a scalpel reduced to about half its normal blade width can be used to remove the five anthers. Since pollina-
tions are made in the morning after the petals have reopened, the emasculation of buds can be done in the afternoons. The petals can be forcibly opened to reveal the anthers (Fig. 1). Usually the anthers can be removed in groups of two or three without breaking the style. The emasculated flowers do not require protection under the conditions of crossing described, and generally are obvious enough not to require special identification at this stage (Fig. 1B).

C. Pollination

Pollination is most successful in the morning soon after the flowers are fully open. On dark days in the winter, it may be necessary to wait for about an hour after artificial lights are turned on. A pollination schedule of 3 days per week will generally catch most available flowers and reduce the extent of double pollination of individual flowers.

Flowers with plump, bright yellow anthers with a brownish tip are most apt to be good sources of pollen (Fig. 1D). Pollen is generally most abundant in the morning. Most flowers can be used as a pollen source for 2 days after the corolla first opens (Janssen and Hermson, 1976). If flowers from the field are used as a source of pollen, stems of the male plants may be cut the day before pollination and held in water. If pollen is collected directly in the field, an early morning collection is most apt to be successful.

Potato pollen is robust, if it is kept cool and dry. It can be stored for a month at 2.5 °C or a year at −24 °C (Blomquist and Lauer, 1962). Longevity is improved if the storage is dry, such as a dessicator with silica gel (Howard 1958). Pollen stored at room temperature and humidity loses its viability after 1 day.

When only a few pollinations are to be made with a single pollen source, the pollen can be removed from mature anthers by inserting a blunted, narrowed scalpel at the base of the suture in the anther lobe and scraping it the length of the anther (Fig. 2A). If the clone is a good pollen source, this will produce sufficient pollen to pollinate three or four stigmas.

Mature, unopened buds and flowers which are newly opened are receptive to pollination. The pollen can be applied in many ways, including touching the stigma with the tip of the pollen-bearing scalpel (Fig. 2B) or inserting the stigma into the vial of collected pollen. A coating of germinating pollen is an effective barrier against further pollination.

When selfing is desired, the unemasculated flowers are allowed to open and the pollen is removed from an anther and applied to the stigmas of the opened flowers on that plant. Dipping the scalpel in alcohol will prevent contamination between pollinations. If volumes of selfed seed are needed, the vibrator can be used, inserting the stigma in the pollen as it is being collected among plants within that clone.

Generally all the flowers of a single inflorescence are assigned to the same pollen source. When the pollination is made, a string tag, which identifies the male or both the female and the male, can be looped about the stem. A color code for the tags can be used to simplify the search of flowers for pollination on subsequent days.
The success in cross-pollination is dependent upon the two parents. If parents of unknown value are used, success greater than 50% is good. If the female is known to produce good mature flowers and the male to produce good pollen, the percentage success is higher, but is not guaranteed. Pollination with bulk pollen from several clones can produce 90% success.

D. Factors Affecting Efficiency

In some breeding programs, potatoes are grafted onto tomato roots to promote flowering of difficult clones. The amount of flowering and duration of flowering will be improved and the abscission of newly pollinated flowers will be reduced. This technique is particularly useful for those clones which tend to abort their flowers prior to pollination.

Fig. 2—Pollination and seed. (A) Collecting pollen from a single anther using a blunt scalpel; (B) applying pollen to a stigma with the scalpel; (C) collecting bulk pollen using a vibrator; (D) battery operated vibrator; (E) mature fruits ready for seed extraction.
The most efficient marker for identifying hybrid seed is an embryo spot described by Dodds and Long (1956) and used by Peloquin and Hougas (1959). This marker was found in the diploid species S. phureja. The dominant genes $B^c$ and $B^d$ in the presence of $P$ or $R$ condition a blue or red spot at the cotyledonary node of the embryo. The most efficient mature plant markers are also anthocyanin pigments, which are inherited as dominant genes. Simply inherited disease resistance alleles like the $H_i$ gene for Race A golden nematode resistance also can be used.

V. NATURAL HYBRIDIZATION

Many cultivars of potatoes, particularly those of recent vintage, will bear fruits in the field if the weather during blooming is cool and humid. The primary insect visiting the flowers is the bumblebee. Unopened flowers on fertile plants do not set fruits if they are protected by screened cages. Glendinning (1976) described bumblebee behavior: "...bee alights on the anther-cone and its weight causes the flower to hang down. It then vibrates the anthers, and pollen falls onto its abdomen and also onto the stigma. If it obtains much pollen it hangs from the flower while collecting it to its pollen baskets; occasionally, when pollen is abundant, it may renew its grip on the anther and repeat the process. Visits to less productive flowers are briefer and do not involve collection of pollen to the pollen baskets". Estimates of cross-pollination in the field range from zero to about 20% (Glendinning, 1976; Cunningham, 1977).

Since potatoes have such a high percentage of self-pollination in the field, crossing blocks are rarely used in most potato breeding. They are used however, when population development, involving a large number of clones, is the objective. This system is particularly appropriate for diploid species which are generally self-incompatible, so that all the seed that is produced is from cross-pollination. When field nurseries are used in these programs, they should be planted at latitudes or altitudes where prolonged high temperature and low humidity can be avoided. The field should not be subject to volunteer plants from previous crops and should be isolated from other plantings. The plants should be spaced approximately 1 m apart in and between rows to facilitate the harvest and identification of the fruits. Insect control should be done with systemic insecticides or with target specific chemicals during the period of bloom to avoid killing the bumblebees.

VI. SEED DEVELOPMENT, HARVEST, AND STORAGE

Enlargement of the ovary can be observed within a week after pollination and usually is a sign of a successful cross; however, parthenocarpic development can occur and be misleading. The fruits which develop are shaped like tomatoes about 2.5 cm in diam (Fig. 2E). As they reach maturity, they become soft and change from a dark green color to a grey-green. To avoid the loss of seed, about 4 weeks after pollination, each
cluster of fruits should be inserted in a paper bag, and the bag stapled around the stem. When the fruits begin to soften, they should be removed from the plant or stem cutting and held in storage until the seed can be extracted. This will be 1.5 to 2 months after pollination (Simmonds, 1963b; Lam and Grenade, 1976).

The safest technique for threshing fruits is to half fill a liter beaker with tap water and squeeze the ripe fruits in the water. The seeds will sink and the pulp can be decanted off. The decanting is repeated once or twice until the beaker contains only seed and clear water. The water and seeds are poured onto a cheesecloth stretched over a pail and held by a rubber band. The seeds can be scooped from the cheesecloth onto a paper towel with a spoon. The tag from the bag holding the fruits is attached to the towel. The towels are laid upon a counter top for 2 or 3 days to dry. When the seeds are dry, the towels can be folded in half and the halves rubbed together to loosen the seeds. The seeds are stored in suitable envelopes.

An alternate technique which can be used more efficiently with large lots of seeds is to put the fruits with a small volume of water into a food blender. It is important that the blades be blunted and that the time of exposure to the blade action be only momentary or seed damage will occur. The contents of the blender can be poured through a small sieve to remove most of the pulp. The rest of the procedure can be the same as for the hand extraction. Some workers digest the pulp by adding 1% volume of HCl and soaking the seeds for 1 hour (Sloombicki, 1961).

Seeds that have been dried and stored in coin envelopes at room temperature in a cabinet containing a room dehumidifier have maintained germinability more than 10 years. Storage life can be extended to 20 years by drying the seeds over silica gel and storing them in sealed glass vials or sealed envelopes of metalized polyester film with low water vapor permeability at 5°C (Ross, 1969; Howard, 1975).

Seeds of tetraploid potatoes will be dormant about 6 months, with some maintaining this dormancy as long as 2 years (Lam and Erickson, 1966; Simmonds, 1963a; Ross, 1969). Some breeding programs hold seeds for 1 year to overcome this dormancy. When it is necessary to overcome the dormancy, the seeds can be soaked for 24 hours with 2,000 ppm of gibberellic acid (Spicer and Dionne, 1961; Lam and Erickson, 1966).

**VII. TECHNIQUES FOR SPECIAL SITUATIONS**

Embryo culture has not been used extensively in potato breeding, probably because the frequency of unreduced gametes in diploids is sufficient to permit diploid × tetraploid crosses.

The special technique of using selected clones of _S. phureja_ to derive haploids of tetraploid clones has created many opportunities in potato breeding. The haploids present a convenient means for producing hybrids with diploid species. They are also a means of conducting genetic analyses at the diploid level. The hybrids between haploids and _S. phureja_ clones which produce a high percentage of 2n gametes by first division restitution may offer an opportunity for greater heterosis in tetraploid breeding programs (den Nijs and Peloquin, 1977a; Mendiburu and Peloquin, 1977; and
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Mok and Peloquin, 1975). The basis of this concept is that much of the heterozygosity of the diploid hybrid will be transferred intact to the tetraploid. The selection of elite S. phureja × haploid hybrids could produce progenies with more predictable performance and uniformity.

REFERENCES


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