The sweet potato *Ipomoa batatas* (L.) Lam.) is an asexually propagated vegetable that is grown mainly in tropical and subtropical regions. Its exact center of origin is not known but is probably just south of the Isthmus of Panama. In the temperate United States it provides variety to the diet. In Japan it is used as a source of industrial starch and in the tropics it is an important staple of subsistence farmers. The vines, as well as the roots, may be eaten or fed to animals (Yen, 1974, 1976).

**I. PARENTAL MATERIAL**

The sweet potato is a member of the *Convulvulaceae* and the only known natural hexaploid morning glory (*6n = 90*) (Jones, 1965). Most other species of the genus are diploids (*2n = 30*), although there are some wild tetraploids (*4n = 60*) (Jones, 1968; Martin et al., 1974; Martin and Jones, 1973). A 90-chromosome wild plant collected in Mexico and reported as *I. trifida* (H.B.K.) G. Don has received considerable attention. The author and others do not accept that classification as correct but believe it to be *I. batatas* (Jones, 1967; Martin et al., 1974). The most recent taxonomic report on *Ipomoa* was prepared by Austin (1978).

To cross other species with the sweet potato, it is necessary to develop bridging types to overcome the ploidy differences (Austin, 1977). Japanese workers have succeeded in synthesizing 90 chromosome plants from diploid and tetraploid sweet potato relatives (Nishiyama et al., 1975; Kobayashi and Miyazaki, 1976). These results show that hybridization with other species of the genus is possible. Unfortunately, because of taxonomic difficulties, considerable uncertainties still exist relative to the exact species involved (Martin and Jones, 1973; Martin et al., 1974).
Because the sweet potato is the only natural hexaploid species presently known in the genus, hybridization is largely restricted to crosses within the species. Variability within the species is extensive and we have only begun to utilize what is available. Every trait I have studied from wide genetic backgrounds have varied over an extensive range. I firmly believe that with proper screening procedures one can find desirable plant types for almost any need within the species. Each seedling plant is heterozygous and genetically different from any other. Each cultivar represents vegetative multiplication by roots or stems from one seedling. Inheritance patterns are better described in quantitative genetic terms rather than in qualitative terms because of the continuous range of plant types that occur in any lot of seedlings (Jones, 1966; Yen, 1974).

The quantitative mode of inheritance influences breeding strategies (Jones et al., 1976). Although the following discussion will deal in some detail with techniques of crossing two selected parental plants, the best breeding strategy for some objectives may be to use open-pollination or polycross breeding methods.

The exchange of breeding materials is rather informal. There is no one main center for maintenance of genetic collections. I maintain a considerable collection of named cultivars, breeding lines from discontinued programs, plant introductions, and true seed from various open pollinated populations. Most sweet potato breeders maintain similar collections and exchange material freely within the constraints of quarantine regulations and national policies.

II. PLANT CULTURE

A. Field

There are genetic differences in flowering incidence, as well as strong environmental influences (Yen, 1974; Martin and Jones, 1971; Jones, 1965). The seasonal flowering response of cultivars observed in temperate climates may be lost in a tropical climate (Warmke and Cruzado, 1949). More recent work shows that sweet potatoes actually vary widely in photo-period responses. Some flower in the spring, others in the fall, some in the spring and fall, some in the summer, and others flower all season (Jones, 1966; Martin and Jones, 1971). The lack of flowering of U.S. cultivars and breeding lines may be due to chance associations in the original plants used and a history of forcing normally non-flowering plants into flower, thus perpetuating the non-flowering trait in subsequent generations. In population studies where selection for good flowering has been very effective, no adverse associations of good flowering with agronomic characters have been found (Jones and Dukes, 1976; Jones et al., 1976; Martin et al., 1974). It may be best to use sparse flowering plants only as a last resort or to make a special cross. Excessive dependence on plants forced into flower can only enforce the sparse flowering problem.

Because of the variability in sweet potato, it is difficult to specify optimum environmental conditions that will hold for all plants. In Argentina, Folquer (1974) obtained best seed yields during a period of minimum daily
temperatures from 12.8 to 18.6 C, maximum daily temperatures of 23 to 34 C, relative humidity from 62 to 75%, and a photoperiod of about 14.5 hours. The high seed set during this period was related to good flowering and may not represent ideal conditions for seed set. In the United States, a number of studies on improved flowering have indicated optimum photoperiods to be about 12 hours (Edmond and Ammerman, 1971). Personal observations would indicate that seed do not set well in very low humidities, even when flowering is abundant. Therefore, environmental factors do affect seed set in ways other than flowering rate, but few controlled studies have been conducted (Montelaro and Miller, 1951). Personal observations indicate that sweet potatoes set more seed when under environmental stress. Seed set is reduced when vine growth is rapid and vigorous. Low nitrogen fertility and low soil moisture probably improve set.

It is known that insects and diseases can reduce seed set and that chemical treatments can alleviate the problem (Yen, 1974; Jones and Jackson, 1968; Jones, 1964; Jones et al., 1977). I have seen corn earworm (Heliotis zea (Boddie)) and fall armyworm (Spodoptera frugiperda (Smith)) infestations so severe that virtually every flower contained at least one worm. When using chemical sprays, one should treat in the evenings when bee activity is less to avoid killing insect pollinators. Contact sprays or baits should be favored over sprays with residual activity for the same reason.

B. Growth Chamber and Greenhouse

Many sweet potatoes rarely flower under normal temperate conditions and special efforts are necessary if they are to be used for breeding (Miller, 1937; Edmond and Martin, 1946). Some respond to short day lengths and can be crossed in the greenhouse during winter months. Edmond and Ammerman (1971) and Wang (1975) have reviewed ways to induce flowering. Various physiological shocks, including grafting, girdling and chemical treatment, seem to encourage flowering. The primary stem can be cut about half way through in a slanting direction and prevented from healing back by inserting a wooden wedge or a piece of cardboard. Terminal portions of stems with 6 to 8 nodes can be grafted to other species which flower freely.

Greenhouse crossing is generally done during the winter months when days of about 12 hours are favorable and temperatures are not excessively high. Montelaro and Miller (1951) found about 24 C to be optimum. Edmond and Martin (1946) considered 16 to 17 C night temperatures and 24 to 30 C day temperatures to be optimum. Some breeders use ground beds while others use benches, a choice which is probably more a factor of availability than of plant growth. Plants are generally tied on stakes, canes, wires, or strings. Care must be taken not to over fertilize so as to not produce excessive vine growth. Transplanting vine cuttings from flowering plants may promote more flowering in the greenhouse. Sometimes restricting root growth by planting in a pot or by restricting nitrogen fertilization will improve flowering. In general, a large plant is not necessary for good seed set and rapid vine growth is not desirable.
III. FLORAL CHARACTERISTICS

Flowers of sweet potatoes are similar to those of other morning glories with cultivar differences occurring in size, shape, and color (Fig. 1). They occur in axillary inflorescences of 1 to 22 buds which open singularly or in groups of two or more (Jones, 1966). The corolla is funnel shaped, generally with white limbs and lavender to light purple throats. The depth of the tube varies from 28 to 63 mm and the width of the limb from 26 to 56 mm. Color varies from pure white through degrees of lavender of various patterns to complete lavender (Yen, 1974; Jones, 1966). Each of the five fused petals has a stamen attached at the base with anthers that are usually white, but may be light to dark lavender. Filaments vary in length from 5 to 21 mm among cultivars and within the flower of one plant filaments may vary in length and placement in relation to the stigma, such that any number of anthers may be below, equal to, or above the stigma. The stigma is bilobed and generally white, but sometimes light or dark lavender. Styles may be from 8 to 29 mm long. The pistil has two ovaries, each containing two ovules. Sepals are leaf-like and persistent and may be glabrous or pubescent. Conspicuous yellow glands that contain nectar which attracts insects are at the base of the corolla (Martin and Jones, 1973). Mature capsules may be glabrous or pubescent and contain one to four seeds.

Sweet potato flowers open soon after daybreak and generally are fading by noon depending on environmental conditions. On cloudy days, flowers may remain open longer than on hot, sunny days. Each flower opens for only a short time, then withers, and the corolla drops off. Charles et al. (1974) found that within 3 hours of opening the anthers showed signs

Fig. 1—Views of an intact sweet potato flower from above (A) and the side (B). Parts of the flower (C) with calyx and corolla removed on one side, and (D) with calyx and corolla completely removed.
of withering, and that by evening the styles began to shrivel. Not much is known about sweet potato pollen longevity and viability because no one has successfully germinated it in culture. Studies with fresh pollen indicate 80 to 85% viability (Togari and Kawahara, 1942; Jones, 1965; Jones, 1966). Even though some pollen grains germinate within minutes after pollination, germination may continue for 3 or 4 hours (Martin and Cabanillas, 1966). Pollen tubes may be detected in the ovary 4 hours after pollination and by 8 hours pollen tube growth is essentially complete.

IV. ARTIFICIAL HYBRIDIZATION AND SELF-POLLINATION

A. Equipment

Equipment needed for controlled hybridization is a pair of tweezers, small marking tags (about 1.3 to 1.9 cm), paper clips, and some means of protecting the emasculated flowers, such as soda straws or small glassine bags (Wang and Burnham, 1968).

B. Preparation of the Female

Buds that will open the next day are easily recognized because they are much larger than other buds (Fig. 3). Emasculation can be done after about 1400 hours by slitting the corolla into two parts from the sepals through the tip with tweezers or some other sharp instrument, and pulling each half of the corolla down and out with the forefinger and thumb (Edmond and Ammerman, 1971; Edmond and Martin, 1946). The attached stamens will be removed with the corolla and the pistil will be exposed (Fig. 2B). The pistil can be protected with a glassine bag or a short piece of soda straw pinched over at one end to prevent insect entry (Fig. 2C). The soda straw or bag also serves to identify emasculated buds.

C. Pollination

During the same time of day that emasculations are made, buds to be used in self-pollinations and as pollen sources are prevented from opening the next morning by placing a paper clip or piece of soda straw over their tips (Fig. 3D and E). The clips or straws can be knocked off easily by wind movement, people, or even bumblebees, so the breeder should prepare more than one expects to use. The next morning, pollinations can be made as soon as anthers begin dehiscing, about 0500 to 1000 hours (Edmond and Ammerman, 1971; Hernandez et al., 1967). The anthers are removed from the protected flowers with tweezers and the pollen applied to stigmas of desired female parents. The same flowers used as male parents may be selfed by removing the corolla and protecting the corolla against outcrossing. If the stigmas and anthers are the same height, self-pollination may be accomplished by shaking the corolla and leaving the straw or paper clip in place. The straw or bag is replaced over the pistil after pollination, and a tag attached giving the male parent’s designation and any other information de-
Fig. 2—Emasculation and self-pollination of a sweet potato flower: (A) flower at the stage for emasculation; (B) emasculated flower; (C) emasculated flower with soda straw protecting the stigma; (D) and (E) closing pollinator flowers with a soda straw or paper clip.

Fig. 3—View of the seed capsule from the side (A). The seeds (B) are usually dark brown to black, sometimes speckled or tan.
sired. Tags of different colors may be used to designate different parental lines or types of crosses. After 2 days, the protective covering should be removed. Crossed buds should be observed closely to prevent younger buds from growing through the string of the tag, which could result in misidentification of the cross.

D. Factors Affecting Efficiency

Field nurseries are used during the frost free months by southeastern U.S. breeders to make controlled crosses. If prolific early flowering types are selected as parents, field nurseries probably can be used anywhere sweet potato breeding is conducted. Procedures similar to those established by Miller (1937) generally are followed. This involves spacing plants about 3 m apart and training them up hog-wire trellises in a fan shape. If open-pollinated seed as well as those from controlled crosses are desired, the nursery should be nearly square rather than a few long rows to better insure random crossing. Nutrition must be carefully controlled to prevent excessive vine growth. Good air movement probably contributes to disease control and higher seed set. Therefore, weed control is important and one may consider using herbicides or mulches of black plastic or pine straw.

Sterilities, incompatibilities and environmental conditions all affect capsule set percentages (Folquer, 1974; Fujise et al., 1955; Martin and Cabanillas, 1966; Martin and Jones, 1971; Jones et al., 1977; Montelaro and Miller, 1951; Edmond and Martin, 1946; Wang and Burnham, 1968). The success rate in the same crossing block normally varies from 1 to 47% for different female parents and an average success of 35% should be considered good. Success from selfing seldom exceeds 3% capsule set (Yunoue and Hirosaki, 1975; Edem, 1975). The average number of seed per capsule seldom exceeds 1.7.

Complex compatibility and sterility systems complicate crossing of sweet potatoes. The literature has been reviewed by Martin (1965) and Williams and Cope (1967). Different theories have been developed to explain the systems and to put certain plants into compatibility groups, but none has held up when applied to plants from different origins. Jones (1965) studied the cytology and fertility of sweet potato and concluded that although chromosome behavior in some plants is cytologically abnormal, pairing generally is highly regular. Burnham (1967) and Wang and Burnham (1968) found that some plants with female sterility have ovaries with less than the normal four ovules. The hexaploid nature of the species also obviously could contribute to the general low fertility observed. Apparently a heavy load of deleterious genetic factors can be tolerated by this vegetatively propagated crop. These factors are expressed at various stages in the sexual process as low seed germination, low seedling vigor, abnormal plant types, reduced flowering, ovule abortion, ineffective pollen tube growth or embryo abortion, and poor seed set.

Several techniques have been developed to observe pollen tube growth in vivo which are useful for determining whether a particular cross is likely to be successful and which direction of a cross is more likely to be obtained. Buds that are to open the next day can be collected and held in vials of water in the laboratory (Fig. 2A). Reciprocal pollinations can be made as they
open the next morning and the relative rates of pollen tube growth measured with the use of various stains and rapid squash techniques. With each procedure of staining used, the stigmas and styles of about five flowers are excised 4 to 5 hours after pollination. One staining procedure is to place the stigmas and styles on a glass slide, stain with 0.5% cotton blue in lactophenol, place a cover glass over the stained organs, and press with the finger. The prepared slides are kept at room temperature for microscopic observations the next day (Togari and Kawahara, 1942). Another procedure is to fix the material in formalin-alcohol-acetic acid, stain with aniline blue, and examine the material under UV light of 365 mu wavelength (Martin, 1959). The pollen tubes fluoresce a dark yellow while the stigma and stylar tissue fluoresce a light yellow (Charles et al., 1974; Martin and Ortiz, 1966). With compatible crosses, pollen grains will adhere to the stigma and pollen tubes can be seen penetrating the stylar tissue.

Genetic markers are not used in sweet potato breeding as a rule, however, parental characteristics often can be recognized in progeny.

V. NATURAL HYBRIDIZATION

Much of the intensive labor required by controlled crossing procedures can be avoided through the use of open-pollination by naturally occurring insects. Less elaborate trellises than used in controlled crossing can be constructed by use of metal reinforcing rods, stakes, or bamboo canes placed by each plant. These are tied together by a single cord near the top of the supports and anchored at the ends of the rows. These trellises are more easily constructed and more easily removed at the end of the season than hog-wire trellises commonly used for controlled crossing. Each plant is secured to its support with a string tied at the base, twined around the plant and support, and again tied higher near the top of the support. Each plant should be identified with a wooden pot label rather than a tag because the latter usually does not last for the whole season.

Rows can be spaced sufficiently far apart to allow tractor cultivation between them and plants can be spaced about 1.5 m in the row. No special field layout is necessary, except to avoid long narrow nurseries where cross pollinations would not likely be random. This kind of nursery has worked well for mass selection (Jones et al., 1976). Isolation requirements have not been determined specifically, but one probably should avoid other flowering sweet potatoes by a few hundred meters.

Natural pollination is accomplished during the early morning hours, chiefly by Hymenoptera. Very little information has been published on this subject, but many insects have been observed working the flowers and undoubtedly affect some pollination. There are hive differences in honey bee preference for sweet potato flowers. In some locations, large numbers of honey bees work these flowers while in other locations very few can be found working them even though hives are close by. Large numbers of bumble bees can be found working sweet potato flowers.

Bee hives may be placed near the end of the trellis if natural populations of insect pollinators are low. Two self-incompatible but cross-compatible parents can be planted in isolation from other flowering sweet potatoes and crossed by naturally occurring insects or honey bees.
VI. SEED DEVELOPMENT, HARVEST, AND STORAGE

Seed mature in about 1 month, a little sooner under hot, summer temperatures and later in cool, fall temperatures. When the capsules are completely dry and brown, the seeds are mature (Fig. 3). Each capsule contains a maximum of four seeds, but the average is much less, about 1.1 to 1.7 (Wang and Burnham, 1968; Fujise et al., 1955; Jones, 1965; Jones, 1966). Mature seed are about half their maximum green size. They have diameters of 3 to 5 mm and are flat on two sides and round on the other (Martin and Cabanillas, 1966). The usual color is dark brown or black, but some are tan and others speckled. The seed weigh about 2 g per 100 seeds, but this may vary with parental types from about 1.3 to 3.0 g (Fujise et al., 1955; Martin and Cabanillas, 1966; Jones and Dukes, 1976).

Since flowering is over an extended time, seed harvest also is extended. Some plants hold mature seed well and do not need frequent harvesting while others, if not harvested promptly, drop the capsules to the ground where they rot and allow the seed to sprout. In some plants, the capsules open soon after drying and the seed shatter. Seed are usually threshed by hand and stored in envelopes properly identified with their origin.

The seed are hard and retain viability for long periods. Under favorable conditions of 50% relative humidity and 18 C, they may maintain viability for 20 years or more. Because of the hard seed coat, germination is very irregular unless some means of seed scarification is used (Miller, 1937; Montelaro and Miller, 1951). The method of Steinbauer (1937) or some modification of it is still most commonly used (Martin, 1946). Seed are soaked in concentrated sulfuric acid for 20 to 60 min, immediately washed in water or neutralized with a solution containing baking soda, and rinsed in clear water. Seed also may be scarified by mechanical means, such as rubbing with emery paper or pricking each seed with a sharp instrument (Martin, 1946). Percent germination can be increased by putting seed in water and discarding those that float. A high proportion of those that sink are viable.

A seed weevil, Megacerus impiger Horn., can infest seed under field conditions and reinfest other seed during storage (Jones and Cuthbert, 1971). Satisfactory control has been obtained by enclosing a small segment of a household pest strip (20%, 2,2-Dichloroxynil dimethyl phosphate) in a plastic bag with the seed for about 1 week.

VII. TECHNIQUES FOR SPECIAL SITUATIONS

The frequency of somatic mutations in sweet potato is quite high and some cultivars tend to have higher mutation rates than others (Hernandez et al., 1964). Many of the 'Jersey' types are mutations from older cultivars. Orange flesh types may mutate to lighter color and vine lengths and coloration may change. Some mutations may improve market value, such as occurred with 'Goldmar', a mutation of 'Redmar' (Anon., 1972). Because of this tendency to mutate, hill selection is necessary to preserve cultivars and is an integral part of certification programs (Edmond and Ammerman, 1971).
REFERENCES


SWEET POTATO


