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GENETIC AND PHYSIOLOGICAL BASIS FOR BREEDING AND IMPROVING THE SWEET POTATO

Bases Physiologiques et Génétiques de Sélection et d'Amélioration de la Patate

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SUMMARY

Sweet potato is a trailing vine ot the tropics and of temperate summers that produces an edible storage root. In this review the physiological and genetic basis for improving the sweet potato are discussed. The sweet potato is daylength sensitive, and flowers chiefly during short days. The species is self incompatible, and in addition partially sterile. It is a hexaploid probably of origin from two or more species. Pedigree methods of plant breeding have been useful but are labor intensive. Mass selection is described as the technique of choice. It consists of selecting 20 or more individuals with the best expressions of the characteristic desired, stimulating them to flower in a polycross block and crossing by honeybees. Seeds produced are germinated for the next round of selection, and the process is repeated. This results in rapid accumulation of major dominant genes, and slower accumulation of others.

RESUME

La Patate est une liane rampante des tropiques et des saisons estivales tempérées qui produit un tubercule comestible. Dans cet article de synthèse les bases génétiques et physiologiques de l'amélioration de la Patate sont discutées. La Patate est sensible à la durée du jour et fleurit surtout en jour court. L'espèce est autoincompatible et de plus partiellement stérile. C'est un hexaploide probablement issue de deux espèces au moins. Les méthodes de sélection pédigrées ont été utiles mais sont fastidieuses. La sélection massale est présentée comme la méthode par excellence. Elle consiste à sélectionner 20 individus ou davantage possédant la meilleure expression de la caractéristique désirée, à stimuler leur floraison en polycross avec pollinisation par des abeilles. Les graines obtenues sont mises en germination pour le cycle de sélection suivant, et le processus se répète. Il s'en suit une

accumulation des gênes majeurs dominants et l'accumulation plus lente des autres.

INTRODUCTION

The sweet potato is 6th or 7th in food production among all food of the world (FAO, 1980). However, about 2/3 of the world production is utilized in one country, China (Villareal, 1982). Sweet potato is a staple food only in Papua New Guinea where daily consumption of several kilograms is not unusual (Garrett, 1974), and in a few isolated areas of the tropics. Although the sweet potato is well distributed throughout the tropics and warmer parts of the temperate zone. However it is seldom a daily food and is often replaced at the table with other foods when family income rises.

Reluctance to eating of sweet potato may be due to several factors (Tsou and Villareal, 1982), not only interest in a variet diet, but also disdain, the attitude that sweet potato is a poor man's food (this reflects the fact that sweet potato is easy to produce). Sweetness itself may be a deterent. A sweet dish is hardly likely to become a staple one. Sweet potatoes often have distinct flavors that do not appeal to everyone. Finally, sweet potatoes produce gas (flatulence) in some persons, and this may be painful as well as socially distressing.

Developement of better sweet potatoes is important to the improvement of their image and utilization. The taste and preference for currently existing varieties varies tremendously (Lin, et al., 1983). There appears to be a growing interest in non-sweet or low-sweet sweet potatoes, types that now can be considered only in the experimental stage (Villareal, 1982). Futhermore, there is considerable promise in sweet potato as an industrial substrate, especially for alcohol production.

Improvement of the sweet potato requires an understanding of what the sweet potato is and what it can be. There is both a physiological and a genetic basis for this understanding.

PHYSIOLOGY OF THE SWEET POTATO

The sweet potato, *Ipomoea batatas* (L.) Lam., is a trailing vine of the morning glory family (Convolvulaceae) characterized by its succulent, edible tuberous storage roots. Sweet potatoes are propagated principally from cuttings obtained from sprouted roots of from established vines. Plants are seldom more than 0.5 meters in height but if given space may cover several square meters with dense foliage. The cropping season is short, 3 to 6 months.

Sweet potato is tropical in origin and needs a hot climate for adequate growth. However, because of its short growth period, it is often grown during summers in the temperate zone. Cool weather, including cool nights, significantly retard growth and storage root production. Adaptation of the sweet potato to the temperate zone requires heated storage of roots during the winter, followed by resprouting of the roots, often with the stimulation of applied heat, to obtain planting material. In the tropics sweet potatoes are almost always propagated from cuttings of the vines. Where weather is warm enough, the sweet potato can be grown at any time of the year.

Growth of the sweet potato is closely related to the availability of sufficient water. Water and adequate aeration are particularly important during the establishment of the cutting. The tuberized roots form from specialized roots arising from the cutting. If moisture is critical during the first few weeks of growth, these roots become lignified, and will not enlarge (HAHN, 1975). However, once the root system is well developed, sweet potatoes can tolerate drought well, and are often considered to be drought resistant.

Most sweet potato cultivars are daylength sensitive. Short days promote flowering and storage root growth (PORTER, 1979). The effect of daylength vary among varieties; and it is seldom possible in a given case to distinguish between the effects of daylength and of other cultural and environmental factors except in careful experiments.

Sweet potatoes are often produced without added fertilizer. They need nitrogen, however, for initial growth of foliage. An excess of nitrogen can lead to overdevelopment of foliage, and thus shading of the lower leaves. This, then, results in underdevelopment of roots. Potassium is of great importance, particularly during the period of storage root growth (Tsuno and Fujise, 1965). Sweet potatoes are efficient in use of phosphorous, and this nutrient seldom limits production.

The production cycle of the sweet potato must be considered seriously modified from a true annual cycle, whether in the temperate zone or the tropics. The storage root can be regarded as a mechanism for survival of the plant during adverse times, especially during the annual dry season. Nevertheless, the root has no clearly established resting period, and will readily resprout after the foliage is removed or after harvest. The growth of sweet potatoes under natural conditions has not been described.

The cycle of the cultivated sweet potato is well known. The cutting passes through a critical period of adjustment when roots that will become tuberized are initiated, and when the plant adjusts to its new environment (WILSON and LOWE, 1973). The foliage develops rapidly following a typical sigmoid curve. As the foliage reaches its peak and begins to decline, the rate of tuberization increases.

Finally, a state is reached in which the foliage has been debilitated, and the storage root grows little if at all. Although theoretically the sweet potato root can continue to enlarge indefinitely, in actual practice it reaches a maximum size. This maximum size occurs after an optimum size when shape and quality are at their best. If sweet potatoes are left longer in the field, growth defects such as cracking increase.

Sweet potatoes often, or perhaps under field conditions, are always infected by viruses which can limit foliar and root growth under certain conditions. Some varieties are much more tolerant to viruses than are others. The evidence suggests that during vigorous growth of the sweet potato the plant grows more rapidly than the virus multiplies, so that the virus charge or titer decreases, and there may be no symptoms. However, under any conditions that slow down the growth of the plant, the virus titer may increase and the virus itself may then limit further growth. A given clone may become so charged with virus that practical production is no longer possible. By furnishing excellent growing conditions it appears possible to reclaim a diseased variety. Meristem tip culture can also be used for this purpose.

One frequently reads, especially in the older literature, about the running out or the running down of varieties. There is no evidence at the present time that this is anything more than a poor physiological state of the plant and/or a heavy virus infection. Spontaneous mutations do occur, however, but the evidence is not clear whether they contribute to varietal degeneration. Thus, it is possible to improve the sweet potato from a purely physiological standpoint.

The techniques for such physiological improvement include maintaining beds of sweet potatoes as sources of cutting, fertilizing, watering, and controlling pests in such beds, taking cuttings when the plants are growing vigorously, about 2-3 months of age, using only the 30-50 cm of the tip of the vine as cuttings. These tasks should normally be in the hands of the farmer himself, and they are task that must be done on a continuous basis.

Yields depend on many other factors, of course, but these will not be discussed here.

REPRODUCTIVE BIOLOGY OF THE SWEET POTATO

The sweet potato, *Ipomoea batatas* belongs to a genus characterized by chromosome numbers built on multiples of 30 (2X=30). Within the section Batatas normal chromosome numbers are 30 (diploid), 60 (tetraploid) and 90 (hexaploid). Twelve species (see table 1) have been studied extensively in an attempt to unravel their relationships, especially with respect to the origin of the sweet potato, a hexaploid. While not all experts have reached the same conclusions,

Table 1. The species and hybrids of section Batatas, genus *Ipomoea* (adapted from Austin, 1983).

Species	Chromosome number	Geographical range
I. trichocarpa Elliott	30	North and South America
I. lacunosa Linn.	30	Eastern USA
I. x *leucantha* Jacquin	30	Widespread in the tropics and the temperate zone
I. triloba Linn.	30	Widespread, from Caribbean and Central America
I. tenuissima Choisy	30 (?)	Caribbean Islands
I. ramosissima (Poir) Choisy	30 (?)	Central and South America
I. trifida (H.B. & K.) G. Don	30, 60, 90	Central America, Mexico
I. tiliaceae	60	Circum-Caribbean
I. cyanchifolia Meisner	30 (?)	Brazil
I. x *grandiflora* (Dammer) O'Donnell	30 (?)	Southeast South America
I. peruviana O'Donnell	Unknown	Peru
I. gracilis R. Brown	60	Australia
I. littoralis Blume	60	Pacific Islands, Mexico
I. batatas (L.) Lam.	90	American tropics, now widespread

the work of NISHIYAMA et al. (1975) represents a prominent pole of opinion. NISHIYAMA believes that a prototype of what he calls the *I. trifida* complex such as *I. leucantha* crossed with a tetraploid derived from the same source, such as *I. littoralis*, and that following non-reduction of gametes a hexaploid *I. trifida* was produced. He believes the sweet potato was selected from this hexaploid. Crossing of *I. leucantha* and *I. littoralis* to form new hexaploids has been accomplished. Thus, the origin would be autopolyploidy.

The cytological evidence does not clearly support this hypothesis. The finding by TING and KEHR (1953) of secondary associations at meiosis can be interpreted as close relationships among the 6 sets of chromosomes that presumably are homologous. However, cultivars differ in the presence or absence of meiotic abnormalities. JONES (1965) found meiotic activity to be highly regular in 40 clones observed.

Multivalents were relatively low in number. Thus, it would appear that the ancestral parents in the origin of the sweet potato were not closely related, and sweet potato may therefore be an allopolyploid. However, if this is so, the ancestral species have not yet been identified. Furthermore, the variation within the sweet potatoes is so extensive that most investigators would favor interpretation of the sweet potato as an alloploid of still unrecognized species. AUSTIN (1983) interprets the hexaploid collections of *I. trifida* as feral sweet potatoes, and the wild tetraploids as the results of crosses among diploid and the hexaploid sweet potato.

The present evidence on the origin of the sweet potato fails to account for the presence of tuberous roots, non-climbing vines, red root periderm color, and orange (high carotene) roots, characteristics not found in primitive species. Thus, the question of the origin of the sweet potato is still far from resolved.

Since most sweet potatoes are daylength sensitive, as days shorten there is a tendency for growth to shift from production of foliage to increased tuberization and to flowering. Cultivars differ in this respect. Some flower readily at any season. Others flowers only when days are short. Still others do not flower under any normal conditions. Sweet potato that do not flower readily can often be stimulated to flower by grafting on other Ipomoea species (STINO, et al., 1969). A simpler technique is to train the vines to trellises during the season of short days. Lack of flowering may be a severe impediment to use of a particular sweet potato as a parent in controlled crosses.

The flower of the sweet potato is conspicuous. The corolla is entire, usually lavender-colored, and attractive to insects. The long style bears an almost globular, lobed stigma. Five stamens arranged around the anther are of varying height, yet it is not correct to call the flower distylous nor to interpret its structure as heteromorphic.

On the contrary, the flower is well adapted to self or cross pollination by bees, and in some cultivars self pollination is frequent even when bees are not present. The flower opens in the morning and closes in the afternoon. It is easy to emasculate and to cross pollinate by hand. A short piece of soda straw is often used to protect the emasculated flower before and after pollination.

The sweet potato is almost always self-incompatible. This and other seed-limiting processes that can be classed as sterility have severely restricted the understanding of the breeding system of the sweet potato. However, a clear interpretation has been achieved. The system of self incompatibility in *Ipomoea* is of the sporophytic multiple allelic type. A series of alleles at one locus controls the genotype of the parent. The incompatibility reaction of each plant is determined by the interaction of the two alleles and all pollen grains exhibit the same incompatibility phenotype (MARTIN, 1968). Some of the features of this incompatibility in a diploid species include more than two incompatibility groups, unilateral incompatibility between some groups, incompatibility between some parents and their progeny, two or four incompatibility groups in a family, the occurence of parental groups in some families, and the physiological control of incompatiblity on the basis of inhibition of pollen germination.

On the basis of knowledge of the incompatibility system in a diploid it is possible to interpret the incompatibility of the sweet potato on the assumption that the incompatibility locus has been duplicated or triplicated (MARTIN, 1968). All data collected are compatible with this assumption.

Data on crossing relationships of sweet potato as developed by VAN SCHREVEN (1953) are presented in table 2, together with an interpretation based on the sporophytic, multi-allelic system of self-incompatibility. It is not necessary to specify a duplication of the incompatibility locus to explain the results. On the other hand, data by FUJISE (1964) can only be explained when two incompatibility loci, R and S, are specified (table 2).

Serious physiological problems often impede seed production even when a cross is compatible. Occurring principally as post-pollen germination barriers to fertility, MARTIN and CABANILLAS (1966) have shown how pollen tube growth and embryo development fail at varied times after pollination. Thirteen detectable failures in sweet potato reproductive process were outlined by MARTIN (1982).

Finally, insect and disease problems affect seed production. Since the effects are often subtle, they may be confused with those of incompatibility and sterility. Pod and seed production in sweet potato can be dramatically increased by treatment of flowering, open pollinated plants with suitable fungicides and insecticides (JONES, et al.,

Table 2. Incompatibility groups in *Ipomoea setifera* and sweet potato according to the sporophytic multiple allele system 1/.

Data interpreted	Incompatibility group (phenotype)	Proposed genotype
Martin (*I. setifera*)	1 (R_1)	R_1R_3
	2 (R_1R_2)	R_1R_2
	3 (R_2)	R_2R_3
	4 (R_3)	R_3R_3
Van Schreven (*I. batatas*)	1 (R_1)	R_1R_2
	2 (R_1R_3)	R_1R_3
	3 (R_2)	R_2R_3
	4 (R_3)	R_3R_3
Fujise (*I. batatas*)	A (R_1)	$R_1R_2S_1S_2$
	B (S_1)	$R_2R_2S_1S_2$
	C (S_2)	$R_2R_2S_2S_2$

1/ Adapted from Martin (1968), Van Schreven (1953), and Fujise (1964).

1976).

Problems of incompatibility and sterility impede controlled pollination in sweet potato. Some crosses are not now possible, and practically all crosses produce much less than the potential 4 seeds per pod.

The practical consequences of self-incompatibility and sterility must be recognized. It is almost impossible to produce seed by self-pollination except in a few self-fertile cultivars. Because of the high sterility, vigor is rapidly lost using any kind of inbreeding. Hand crossing cannot result in more than 4 seeds per cross, and usually the result is fewer. Therefore, breeding techniques should not rely on hand pollination. When two varieties are cross compatible, seed can be produced in quantity if they are stimulated to flower side by side, in an isolated area.

Because of its polyploid status, the sweet potato is not a suitable species for studies of traditional or Mendelian genetics. Each gene may be represented by 6 alleles. The segregation ratios in particular crosses are usually complex, but may be simple and Mendelian when only a single dominant allele is present. Thus, it is not surprising that simple genetic ratios have been reported in the literature (POOLE, 1955). However, since the simple ratios are artifacts due to homozygosity for some genes, inheritance studies often have found discrepancies, not so frequently with respect to dominance relationships, but frequently with respect to segregation patterns. Hexaploid segregation patterns are varied and complicated (JONES, 1967). If dosage effects occur, something that can often be expected, segregation will be continuous and discrete ratios will not be seen, even when a single locus is responsible for a character.

Because of these considerations the majority of the characteristics of importance in the sweet potato are inherited quantitatively or appear to be so inherited. The questions that are of importance are those of quantitative genetics.

The theoretical basis for quantitative genetics in the sweet potato has been developed by JONES et al., (1976) and he and others have measured the genetic components of variance, and have estimated the heritability of many economic traits (Table 3), using several different methods. The formal heredity estimates suggest that progress is possible in the selection for any trait that can be recognized and defined. Estimates are usually intermediate in size, further suggesting that progress in selection will be slow. This is not surprising when the high number of chromosomes of the sweet potato is considered.

Table 3. Narrow sense heritability estimates in the sweet potato 1/.

Character	Heritability estimates
Root weight	25, 41, 44
Growth cracking	37, 51
Flesh color	53, 66
Flesh oxidation	64
dry matter	65
Protein content	
Fiber	47
Skin color	81
Sprouting	37, 39
Vine length	60
Leaf type	59
Flowers/inflorescence	50
Fusarium wilt resistance	50, 86, 89
Nematode egg mass index	57, 69, 75
Insect complex resistance	45
flea beetle resistance	40
Weevil resistance	84

1/ Adapted from JONES, 1980.

RECOMMENDED BREEDING TECHNIQUE

Some type of recurrent selection appears to be desirable in sweet potato breeding. The selection procedure should permit minor and recessive genes to be expressed and to be selected, with a progressive increase in a population of favorable genes.

Mass selection has been developed as the technique of choice. First proposed in 1965 (JONES), the technique uses the principales of genetics, especially of quantitative genetics as appropriate guidelines. In its simplest form mass selection consists of the selection of a number of sweet potato clones for one or more desirable characteristics, the stimulation of the selections to flower, and their hybridization in a polycross block by natural pollinators (chiefly honeybees). Seedlings of the cross are screened for the same characteristics and the best are utilized, with or without the best of parents, , in the production of a new polycross.

This technique should result in a rapid accumulation of major genes, eventually breaking of linkages of unfavorable genes in repulsion, and a slower accumulation of favorable minor genes. The theoretical basis, methodology, and practical applications were studied for two decades and have established mass selection as a useful technique, especially for charactistics weakly expressed and controlled by many genes.

Mass selection must be complemented with a screening technique, and in the case of some characteristics, the identification and measurement of the character is the weakest link. During screening, selections can be made not only for the strongest expression of the characteristic but also for other desirable characteristics. Furthermore, plants from seeds are potential varieties, and may be used as such without further modification.

Any breeding program depends on techniques. The techniques that have been found useful in a practical breeding program, including details of handling seeds and plants, have been described by JONES (1980), and complement the information given here.

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