

MUTATIONS AND CROP IMPROVEMENT.

III. IPOMOEA BATATAS (L.) POIR.

(CONVOLVULACEAE)

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I. INTRODUCTION

1. General references

WAITE, 1907 (mode and area of cultivation); GROTH, 1911 (ditto); BAILEY, 1922 (ditto); THOMPSON and BEATTIE, 1922 (classification of American varieties); ARTSCHWAGER, 1924 (anatomy of the root); WESTER, 1924 (Philippine cultivation); THOMPSON, 1929 and 1949 (cultivation and production); ISBELL, 1931 (regeneration of leaf cuttings); ELMER, 1950 (varieties in Kansas); SAUER, 1950 (South-American cultivation); COOLEY, 1951 (origin and primitive storage); YEN, 1963 (New Zealand and Maori cultivation).

2. Origin and cytogenetical constitution

Ipomoea batatas (sweet potato, "kumara") probably originated in tropical America (NISHIYAMA, 1961). It is said to have been in cultivation for 5000 years (ABRAHAM, 1957). Already before Columbus it was cultivated over large areas of the new as well as the old world (MANSFELD, 1959). In 1519 according to REINHARDT (1911, p. 361), it became known in Europe. It is now widely cultivated in southern USA, tropical America, Africa, India, Indonesia, China, Japan, Malaysia, New Zealand and ranks among the foremost crops in these areas.

The sweet potato is a hexaploid species with $2n=90$ chromosomes. The basic chromosome number of *Ipomoea*, section *Batatas*, is 15. Diploid, tetraploid and hexaploid species have been recorded ($2n=30, 60$ and 90). See articles by KANO (1929); WALCOTT (1937); KING and BAMFORD (1937); WATANABE (1939, 1940); TING and KEHR (1953); TING

et al. (1957); SHARMA and DATTA (1958); NISHIYAMA *et al.* (1961 a); NISHIYAMA and TERAMURA (1962). Meiosis of *Ipomoea batatas* is mostly regular, with 45 bivalents at the first meiotic metaphase, although some cases of lagging univalents and other disturbances have also been noted. So-called secondary association of bivalents was reported by TING *et al.* (1957), possibly suggesting a general affinity of corresponding chromosome pairs. Multivalent formation seems to be rare.

SHARMA and DATTA (*l.c.*) conclude that *I. batatas* has four long chromosomes with satellites (A-type), two medium-sized chromosomes with satellites (I-type), ten medium-sized chromosomes without satellites (4 of J-type, 6 of K-type), and 74 short chromosomes (44 of L-type and 30 of M-type). The karyotype should thus have the following constitution: 4 A, 2 I, 4 J, 6 K, 44 L and 30 M.

These facts indicate that *Ipomoea batatas* is of allopolyploid origin, arisen by crossings of some diploid and tetraploid species with subsequent doubling of the hybrid chromosome number ($2n=30 \times 2n=60 \rightarrow 2n=45 \rightarrow 2n=90$). However, *Ipomoea batatas* seems to be closely related to the wild American species *Ipomoea trifida* which is also hexaploid (NISHIYAMA *et al.*, 1961 a and b). This species does not usually form edible tubers, although roots may become thickened. It could possibly be considered an ancestor of the cultivated sweet potato on the basis of morphological, cytological and genetical evidence (NISHIYAMA, 1961; NISHIYAMA and TERAMURA, 1962). The two species form fertile F_1 hybrids without meiotic disturbances. Species like *Ipomoea triloba* ($2n=30$), *tiliacea* ($2n=60$), *gracilis* ($2n=60$) might be involved in the allopolyploidization of *Ipomoea batatas* (or its possible predecessor *I. trifida*). In 1908 HOUSE postulated that *Ipomoea batatas* was derived from the tropical American species *Ipomoea tiliacea* (see also COOLEY, 1951). A change of this species into *Ipomoea batatas* by means of simple domestication is impossible owing to differences in chromosome number. As shown by TING *et al.* (1957, p. 201) *Ipomoea tiliacea* is a tetraploid species.

Autopolyploid *Ipomoea batatas* ($2n=180?$) was produced by colchicine treatment and analysed for morphological characters and root yield by PI and WANG (1961). It was in fact definitely inferior in productivity to the parent type.

3. Mode of propagation, flowering and seed setting

In cultivation *Ipomoea batatas* is generally reproduced vegetatively by means of roots or cuttings. The cuttings can, according to SOLPICO

(1937), be classified as vine or stem cuttings, terminal shoot cuttings, leaf cuttings or root cuttings. Although the species throughout its area of cultivation is almost exclusively propagated by vegetative means, preferably by vine cuttings, clones and varieties can under certain conditions be forced to flower. Some bloom spontaneously. Field collections made in Peru, Bolivia, Ecuador, Colombia as well as in the Pacific Islands (YEN, 1961 a), indicated that in no case was purposeful propagation by seed done either in practice or by local tradition. In USA, Puerto Rico, India, Japan, New Zealand etc. numerous varieties fail to flower (ROSA, 1926; MILLER, 1935, 1937; EDMOND and MARTIN, 1946; WARMKE and CRUZADO, 1949; ZOBEL and HANNA, 1953; TING and KEHR, 1953; KEHR *et al.*, 1954; VAN SCHREVEN, 1954; FUJISE *et al.*, 1955; POOLE, 1955; LAM and CORDNER, 1955; ABRAHAM, 1957; LAM *et al.*, 1959; NISHIYAMA and TERAMURA, 1962; YEN, 1963; FUJISE, 1964). Evidently there is considerable genetic variability in the physiological control of flowering (TIOUTINE, 1935). Recently procedures have been worked out (*v.* the authors mentioned) to induce flowering and increase seed setting by the help of grafting on alien root stock, for instance on *Ipomoea Bona-nox*, greenhouse cultivation and special climatic control (variation in temperature, day length, humidity), training the vines on bamboo trellise, use of hormones etc. In this way artificial hybridization has also become possible. However, pronounced seed sterility is often noticed in crosses, often depending on incompatibilities but also on climatic conditions. "Out of 6000 crosses made in 1950 hundred and thirtyfive seeds were obtained and 92 of these germinated" (ABRAHAM, *l.c.*). Similar results of sterility were reported by WARMKE and CRUZADO (*l.c.*) and FUJISE *et al.* (*l.c.*). In POOLE's experimentation (1955, pp. 18—19) 800 seeds gave rise to 452 seedlings obtained after self-pollination, 334 of which flowered; only 19 suggested any degree of self-fertility in any flowering season, and only one produced spontaneously self-pollinated seed.

Diploid species of *Ipomoea* are generally self-compatible (NISHIYAMA and TERAMURA, *l.c.*). Hexaploid *Ipomoea batatas* and *trifida* are, however, largely self-incompatible (*cf.* also TIOUTINE, 1935; and HERNANDEZ and MILLER, 1962). In the latter species 17 out of 20 clones examined were completely self-incompatible, two were partially self-compatible and one was self-compatible. These 20 clones could be divided into seven compatibility groups (NISHIYAMA, 1961). This author also found that *Ipomoea trifida* and *batatas* have a genetic system in common for incompatibility. According to him four incompatibility groups

have so far been certified in Japanese varieties of *Ipomoea batatas*. In 1954 SCHREVEN described six such groups in *Ipomoea batatas*. According to FUJISE (1964) the incompatibility is ascribed to three gene loci, T, S, Z, with T and S epistatic to Z, the pollen reaction being sporophytic. POOLE (1955, p. 6) found a prolific self-fertile plant (HES 107-C), which gave the opportunity of determining the segregation ratios of heterozygous genes (3:1, 9:7, 13:3).

II. SPONTANEOUS MUTATIONS

It is an old experience that sports (vegetative mutations) are fairly common in sweet potato cultivation. MILLER (1935) refers to studies by himself as well as by other authors, for instance HARTER (1926) and ROSA (1926). See also WHITE (1933), as well as ELMER (1950) who described a series of mutants released as new cultivars. MILLER (*l.c.*) reports that in the commercial sweet potato district of Louisiana, the variations occur so frequently that the "laborers who are engaged in harvesting and packing have learnt to recognize and to discard these off-type potatoes" (p. 460). He made collections of distinct mutations of the Porto Rico sweet potato, classifying them into five groups mostly distinguished with regard to skin colour: Porto Blanco, Porto Rubio, Porto Morado (this sport type has been distributed under various names), Porto Orado, Porto Matoso. As a special precaution in MILLER's study, no mutant was selected unless it was found attached to a plant identified as being a Porto Rico plant.

The mutations were tested for yield and chemical properties (primarily starch and sucrose content). Two mutants (Porto Blanco and Porto Rubio) outyielded the Porto Rico parent when the plantings were made early. They behaved as long-season varieties. Moreover they were higher in starch content than the Porto Rico, but at the same time decidedly lower in sugar. Possibly they would imply improvements in starch manufacturing. ELMER (1950) stated that the varieties Orange Little Stem, Rolo and Orlins arose as mutants from Little Stem Jersey, and Nancy Gold and Red Nancy, in turn, as mutants from Nancy Hall. He maintained that the mutant cultivars were the results of a series of mutations. "In no case was the final intensity of skin color or the final carotene content of the roots obtained as a single mutation" (*l.c.* p. 8). Some mutants showed A- and C-vitamin contents appreciably above those of the parent strains.

Results on somatic mutations were also discussed by MATUNAGA (1934, cited from KAGAWA, 1939), KAGAWA (1939), PAIS DE CAMARGO

(1952) and KUWATA (1952). In PAIS DE CAMARGO's studies two mutants were tested for yield: a 98-Castelo mutant with cream-coloured periderm and an 18-Dahomey mutant with purple-reddish periderm and cream-coloured cortex. The mutants ranked among the best varieties available for cultivation. HERNANDEZ *et al.* (1956) state that in 1952 the latest sweet potato improvement in Louisiana resulted from the selection of a dark copper skin mutation in "Goldrush". Except for the difference in skin colour the two varieties were identical in all characteristics studied and the new variety was released with the idea of replacing the original Goldrush. The authors also reported the frequency of sectorial chimeras. In the variety Unit I Porto Rico 6 per cent of the offspring had white sectorials, 0.1 per cent deep orange sectorials. In Goldrush 0.3 per cent and in Earlyport 9 per cent had white sectorials. Skin mutations arose to 3 per cent in Unit I Porto Rico, and to 0.7 per cent in Goldrush.

In 1964 HERNANDEZ *et al.* published another analysis of spontaneous mutation in four varieties of sweet potato: Unit I Porto Rico, Goldrush, Copperskin Goldrush and Heartogold. The skin mutability rates compared as percentage of roots with one or more mutations were respectively: 2.9 %, 0.7 %, 0.7 %, 0 % (no skin mutations were found in Heartogold). Most of the skin mutations consisted of white and purple streaks. The authors also studied flesh mutability in Unit I Porto Rico, Earlyport and Goldrush. Mutation rates were 6.2 %, 0.3 % and 9.3 % respectively. Only in Unit I Porto Rico were a few orange sectorial mutations discovered, otherwise they were of the white sectorial type. Three purple skin mutations of Unit I Porto Rico yielded as well or slightly better than the parent clone. Copperskin Goldrush roots were found to mutate back to the original Goldrush skin colour. A vegetative mutant of Earlysweet, developed in Georgia and named Red Earlysweet, is said to have all the desirable characters of the parent variety together with an attractive red skin (Plant Breed. Abstr. 1962, Vol. 32: p. 792, No. 4409).

An interesting case of a sweet potato chimaera was reported by KUWATA (1952). In the variety Gokoku a chlorophyll deficient mutant was found. This mutant had four nodes; the shoot from the lowest node had normal leaves and stems, while the shoots from the other three nodes showed chimerical leaves and stems in white and green, or in red and green. By studying this plant and its offspring, the sectorial, periclinal and mericlinal states of chimerical constitution were analysed. Finally in 1963, in his paper on New Zealand varieties, YEN (1963) recorded a

series of mutants in leaf shape and tuber colour. Most deviations involving the flesh colour of the root represent increases in carotene content. This leads to an improvement in nutritional value and to a more attractive product. Mutations in the reverse direction do occur and some selection of high-colour roots is desirable to retain a high level of carotene in commercial sweet potato stocks (H. B. CORDNER, 1964, in litt.).

III. RADIATION GENETICS AND INDUCED MUTATION

MILLER (1935) was the first to report X-ray induced mutations in *Ipomoea batatas*. "The five X-rayed potatoes were planted for vine production immediately after radiation together with a corresponding set of untreated potatoes which had been produced from the same root unit. As soon as vines developed from these potatoes, two plantings were made of 20 hills each. At harvest time when comparative studies were made, it was found that vines grown from potatoes which had been given the above treatment produced potatoes having a creamy white flesh color while the parent Porto Rico had an orange-yellow to salmon-colored flesh. This induced mutation resembles one of the natural mutations, Porto Rubio, which has been described. The chief difference between the two is that the induced mutation has a sweeter taste than the natural mutation" (p. 463).

CHENG (1958) reported treatments of tubers of the early variety P-30 using X-irradiation with 1250 and 5000 r. Half of the tubers gave "sport mutations with variegated leaves". Cuttings of these sports gave rise to "many vegetative variations". One plant was found to mature earlier and to yield "significantly better" than the original P-30 variety. Another plant had a light-red skin different from the original white. Most plants of the sport mutations were abnormal, however.

MASIMA and SATO (1959) made irradiation experiments using young shoots. After X-ray treatment the shoots were cut into pieces having one leaf each. Dosage varied from 5000 to 20,000 r. Lethality became pronounced above 10,000 r. At a dose of 20,000 r, survival was between 30 and 40 per cent (Fig. 1). Variations in leaves, stems and tubers were recognized in the X_1 generation. In the next generation (X_2)—one X_1 tube gave rise to an X_2 row—a number of variants appeared in the treated materials, having yellow white or purple red tubers instead of the parental brown red colour (Fig. 2). Twelve selected mutant lines showed some altered characteristics in stem and tuber colour. The most conspicuous changes consisted of long or short, thick or slender stems and yellow white or purple red tubers.

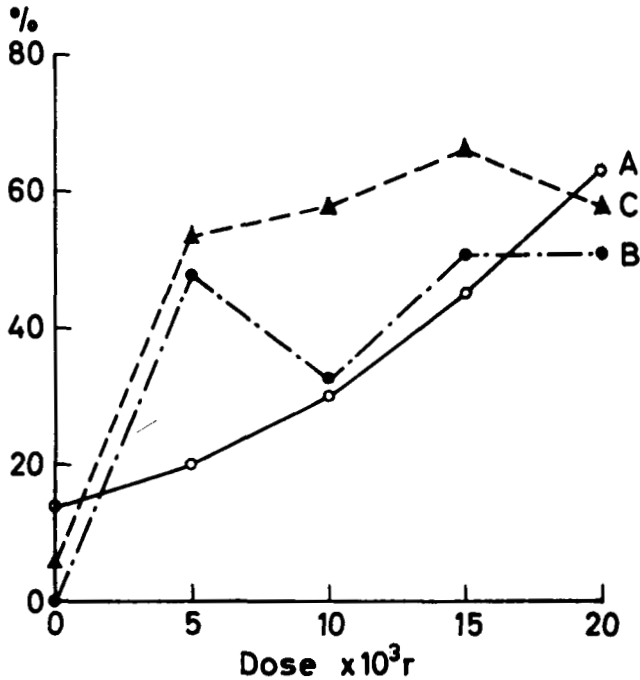


Fig. 1. Relations between X-ray dosage and rate of lethality (A), rate of X_1 chimeras (tuber colour) (B), and rate of X_2 mutations (C). (Redrawn after MASIMA and SATO, 1959).

NISHIYAMA *et al.* (1959) irradiated various parts of vine cuttings: (1) the ends of leaf stalks, (2) whole leaves except the leaf-stalk ends, (3) the middle parts of the leaf stalks. Doses ranged from 1245 to 7470 r-units of X-rays. In experiments 2 and 3 no lethality was found, either with regard to the number of leaves developing or the number of roots per leaf; with regard to experiment 1, on the other hand, there was a pronounced irradiation damage as to leaf number developing above 4000 r, and at an even lower dose with regard to total root length per leaf. A slight stimulation effect was noticed at the lowest dose applied (Table 1).

In their paper of 1964, cited above in connection with spontaneous mutations, HERNANDEZ *et al.* also reported results of γ -irradiation (10,000—50,000 r) of roots of three varieties (Unit I Porto Rico, Goldrush and Heartogold). Goldrush was most sensitive to irradiation (no survival above 20,000 r), Unit I Porto Rico was medium sensitive, and Heartogold was least sensitive with very little reduction in plant number and vigour at 40,000 r, although there was a significant reduction at

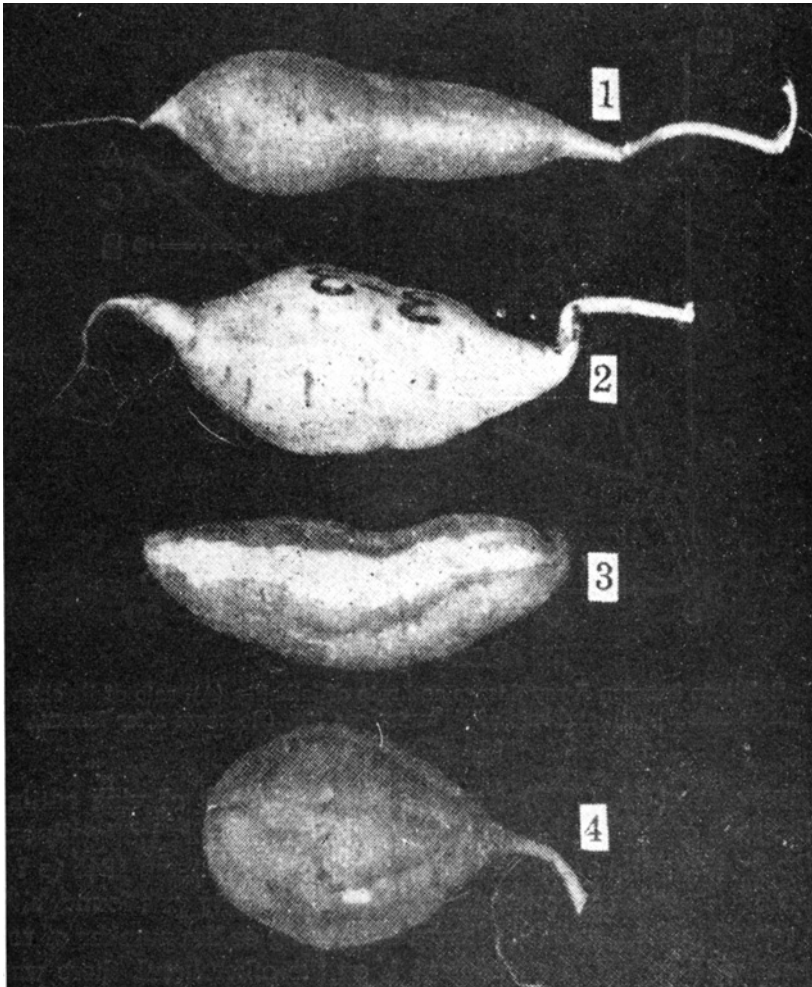


Fig. 2. Mutations of sweet potato induced by X-irradiation. (1) Control, Norin No. 1. Tuber brown-red. (2) Mutant X-3. Tuber yellow-white. (3) Chimerical tuber of brown-red and yellow-white. (4) Mutant X-28, Tuber purple-red. (After MASIMA and SATO, 1959).

50,000 r. In the next generation white sectorial mutations were discovered, the lowest rate being found in Goldrush (*cf.* also the paper by HERNANDEZ *et al.*, 1959).

OSBORNE and LUNDEN (1961) reported experiments involving irradiation of roots of sweet potato. They found that 20,000 r of ^{60}Co - γ -rays decreased survival by circa 50 per cent. The neutron dose resulting in a

TABLE 1. *X-ray irradiation and lethality of leaf cuttings in Ipomoea batatas (from NISHIYAMA 1959, experiment 1).*

Dose	Percentage of leaves developing (25 leaves in each treatment)	Root length per leaf, cm
Control	76	20.3
1245 r-units	96	20.9
2490 "	76	12.5
3735 "	72	7.8
4980 "	16	0.4
6225 "	16	0.4
7470 "	16	0.6

similar degree of survival seemed to lie around "150 neutron reps" (*l.c.*: Tables I and III).

POOLE (1959) and POOLE and TANAKA (1963) found yield differences between sister subclones of irradiated and control materials. Two clonal irradiation groups yielded higher and one group yielded lower than the check group. The studies indicated that clones with no other distinguishing characteristics than yield differences may be identified by careful statistical analysis. It is not clear from the report to what extent the yield differences are really hereditary and due to induced mutation.

Some data on γ -irradiation are also found in a brief abstract by MATSUMURA and FUJII (1958).

CONCLUSIONS

Production capacity and quality are the chief objectives in breeding programs of sweet potato. Starch manufacturers would prefer varieties high in starch and low in sugar. Table quality, on the other hand, as stressed by MILLER (1935), would require a high sucrose content. Carotene content is of great importance (CORDNER *et al.*, 1959). Further improvement of sweet potato varieties will benefit from the control of flowering ability and the subsequent possibility of hybridization (F_1 heterosis and gene recombination) and selection work of suitable parent strains and hybrid segregates. Wild hexaploid *Ipomoea trifida* possesses genes for resistance to nematodes and black rot (NISHIYAMA *et al.*, 1961 b) which if necessary may be transferred to sweet potato. Vegetative mutations in high-productive varieties having good quality could no doubt be induced advantageously or be selected for in natural materials. X, γ or neutron irradiation of cuttings and roots could easily be

carried out on a large scale; in the case of sparsely ionizing radiations by using doses around 4000 r for leaf stalks treated according to method (1) in the report of NISHIYAMA *et al.* (1959), or 20,000—40,000 r if roots are irradiated as outlined by HERNANDEZ *et al.* (1964). In fact, vegetative mutants (sports), high in yield, are commonly distributed in practice and their number may certainly increase through utilization of irradiation methods or, possibly, of chemical mutagens.

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