The Ipomoea trifida Complex Closely Related to Sweet Potato

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SUMMARY

The concept of the "Ipomoea trifida complex" is proposed after field, herbarium and experimental studies on Ipomoea species belonging to the section Batatas. All wild plants that can be crossed with cultivated sweet potato belong to this complex.

Morphological and cytological observations were carried out using newly introduced Ipomoea species from tropical America in 1979 and 1980. Diploids, tetraploids and hexaploids were recognized by studying the somatic chromosome numbers. It was impossible to detect accurately the ploidy level only on the basis of the morphological characteristics.

Most diploid plants of the complex bear no tuberous roots but some accessions produced somewhat thickened roots. This thickness of roots strongly suggests that diploid forms have the potential to produce tuberous roots.

In 1955, Nishiyama collected in Fortin, Mexico a wild hexaploid (6x, 2n=90) that could be crossed with sweet potato. This observation contributed to the initiation and promotion of sweet potato breeding in Japan using wild species. Thus, two varieties, including the wild germplasm, were developed along with several promising strains which are now being tested for adaptability to various areas. Phylogenetic studies of sweet potato have also been progressing using wild related species. With the progress of breeding experiments using wild species and phylogenetic research, some problems were likely to arise and interfere with international exchange of research information, such as the taxonomic confusion and discrepancy in identification of the wild species relating to sweet potato.

Although researchers in this field are combining increasingly aware of the problem, a satisfactory solution has not yet been found. The purpose of this paper is to offer precisely some solutions to this problem, chiefly on the basis of experimental results obtained in Japan and observations made in tropical America.

Taxonomic situation of the wild relatives of sweet potato

Discrepancies in species names have been associated with the studies on wild plants resembling morphologically sweet potato. Difficulty in species identification of plants closely related to sweet potato can be ascribed to the existence of an inadequate taxonomic system and subjective interpretation of taxonomic

data by each researcher. In general, the following three factors have contributed to these discrepancies: (1) the species are not well defined morphologically, (2) morphological characteristics which were used to distinguish one species from another by taxonomists show continuous variations, and (3) some species can be easily crossed with others, producing intermediate types between them.

Many taxonomists, as reviewed recently by Austin (1978), have attempted to establish a taxonomic system of Ipomoea species from each viewpoint. Reports from Van Ooststroom (1953), Verdcourt (1963) and Austin (1978) appear to be most useful since these authors investigated the interrelationship and geographical distribution of wild relatives closely related to sweet potato. Van Ooststroom recognized the existence of an interrelationship among I. triloba, I. trifida, I. tiliacea, I. gracilis, and I. batatas species, and he included these five species in the section Batatas. Austin adopted the concept of Ipomoea batatas complex at the section level of taxonomy, and included 11 species and 3 natural hybrids into this complex.

Austin studied the taxonomic literature, the geographical distribution and herbarium specimens extensively, and attempted to analyse the interrelationships among species belonging to the complex. However, he did not interpret correctly the experimental results which had been obtained for the past twenty years presumably due to the taxonomic confusion of Ipomoea species closely related to sweet potato. Nishiyama (1961) designated the wild plant, K123, as I. trifida (H.B.K.) G. Don, and he claimed that this hexaploid species might possibly be the ancestor of sweet potato. The fact that this wild plant had the same number of chromosomes as sweet potato was both and advantage and a shortcoming. The advantage was that K123 could be used readily for varietal improvement of sweet potato. Many researchers focussed their attention on the utilization of wild plants, and several wild Ipomoea species could be introduced thereafter. On the other hand, the incomplete identification of this wild plant made the taxonomic confusion even more conspicuous, and the experimental results thereafter were not highly evaluated by some researchers. In any case, the greatest achievement of Nishiyama was to have initiated research work in this field and promoted breeding studies for the utilization of wild plants as the gene source in Japan.

Nishiyama's report stating that the progenitor of sweet potato had been identified gained the attention of researchers worldwide. Jones (1967) pointed out that Nishiyama's identification was incomplete morphologically and cytologically. Jones believed that K123 was not a separate species but a weedy feral derivative of cultivated Ipomoea batatas, i.e. sweet potato. Jones' assumption has been accepted by many researchers for a long time. If the wild plant first collected had been a diploid plant instead of a hexaploid, the situation would have been different and a great deal of confusion thereafter could have been avoided. The diploid species was collected in Acapulco, Mexico in 1960 by Tamari and Kobayashi. This Ipomoea species was identified as I. leucantha Jacq. by Teramura who was a co-worker of Nishiyama (Teramura et al., 1967). The misconception that K123 could be identified as I. trifida (H.B.K.) G. Don and inaccurate definition of the species by taxonomists certainly contributed to perpetuate the confusion. The plant identified as I. leucantha resembled I. trichocarpa described by Martin and Jones (1972) except for the following two characters: (1) the absence of a pigmented substance at the bottom of the flower tube, making a white asterisk pattern as shown in Figure 1, and (2) the existence of self-incompatibility and several incompatibility groups among plants. At present, it is believed that this diploid species was not I. leucantha but a typical I. trifida.

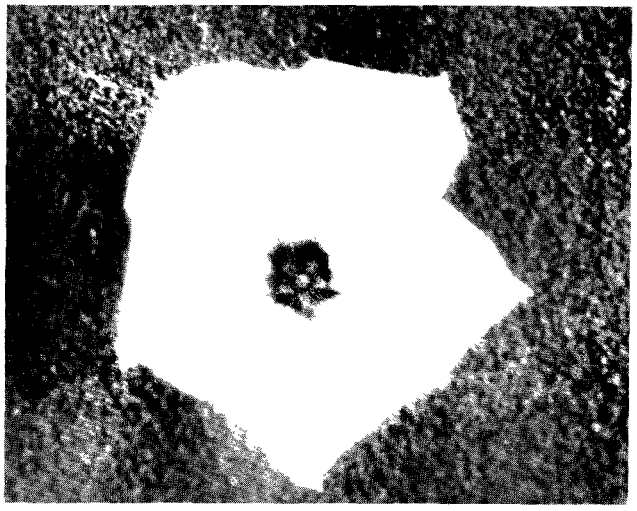

Figure 1. Asterisk pattern at the bottom of the flower tube.

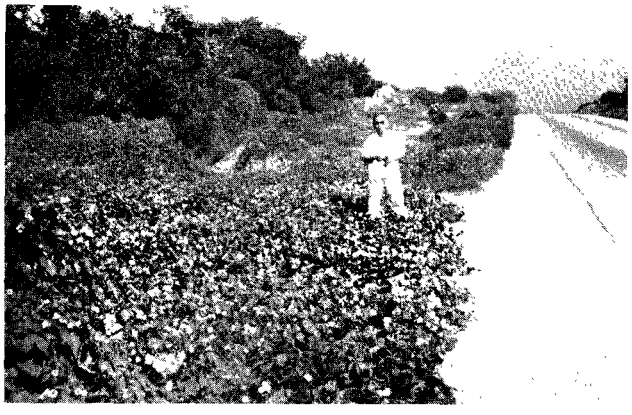

Figure 2. Diploid I. trifida specimens growing near Santa Marta, Colombia.

Triploid Ipomoea seeds were also collected in the same are in Acapulco where the diploid species had been collected. All eight seeds from a single plant were found to be triploid, having a somatic chromosomal number of 45. It was interesting to note that triploid plants could occur naturally, and further, that hybridization among triploids produced several hexaploids. Natural triploid seeds were also collected by Shiotani in Mexico in 1974 (Shiotani and Kawase, 1980).

Since the original triploids and hexaploids derived from the triploids resembled morphologically K123 which had been designated as I. trifida, these triploid plants were called tentatively triploid I. trifida. Collection of natural triploid plants suggested: (1) diploid and tetraploid species must be growing near the area where the triploid seeds were collected, and (2) natural hexaploids must occur naturally and K123 was thus presumed to have originated from such hexaploid plants.

A tetraploid plant was collected in Veracruz, Mexico by Muramatsu in 1962. The leaves of this plant were rather small and appeared thickened. Since the morphological characters seemed to differ considerably from those of I. trifida

(6x) or I. leucantha (2x), the tetraploid plant was considered to be a different species, and was identified as I. littoralis Blume presumably due to its adaptability to the environment of coastal areas (Teramura, 1979). Based on the crossing experiments and cytological observations made be several workers in Japan, Nishiyama (1971) described the genetic origin of sweet potato. A tetraploid species originating from a collection made in Mexico by G. Chapman was supplied to our laboratory by A. Jones. This tetraploid species had been designated as I. gracilis R. Br. (Jones, 1970). This plant belonged definitely to the same species as the tetraploid called I. littoralis in Japan. Austin (1977) believed that this tetraploid plant was neither I. littoralis nor I. gracilis, but resulted from the hybridization of I. batatas and a diploid species, probably I. trifida (H.B.K.) G. Don. The assumption made by Austin seems to be plausible both morphologically or genetically. However, we have some reservations and we would like to suggest that this tetraploid may be an ecotype of I. trifida derived from an autotetraploid originating from the diploid I. trifida as described later in more detail. Tetraploid Ipomoeas closely resembling sweet potato were also collected in Colombia and Ecuador in the 1970s (Martin et al., 1974; Kobayashi, 1978). Furthermore, specimens resembling these tetraploids were collected in Mexico and Guatemala (Muramatsu and Shiotani, 1974). Those tetraploid plants were considered to be closely related to sweet potato, but could not be given any species name due to the taxonomic confusion prevailing at that time. Austin (1977) also postulated that these tetraploid plants had the same origin as I. littoralis or I. gracilis mentioned above. We considered that those tetraploids observed from the Andes to Mexico were derived from the autopolyploid of diploid I. trifida. With the promotion of Ipomoea collections, ecological and genetic information on these plants has accumulated. A plant group which shows the ability of being crossed with sweet potatoes should have a common genome though the ploidy level may be different. Since this group was recognized to be a Mendelian population, Nishiyama (1971) proposed the name of Ipomoea batatas to this plant group including diploids, tetraploids and hexaploids. On the other hand, Austin described 14 kinds of plants belonging to the Ipomoea batatas complex. Species characterization or definition by austin was much more accurate than those of the previous taxonomists. It is, however, still impossible to identify all our collections according to his descriptions. The main reason for this difficulty lies in the continuous variations including sepal characters which Austin considered as being an important taxonomical key to identification.

Ipomoea trifida (H.B.K.) G. Don is the species in which we have been very much interested because it was thought that the complexity of the situation might be alleviated by observing "true" or "standard" I. trifida specimens. As well known, the taxonomic origin of this species dates back to the plants collected on the banks on the Orinoco River by Humboldt and Bonpland at the time of their expedition to tropical America during 1799 to 1804. The plant identified as I. trifida (H.B.K.) G. Don by Van Ooststroom is preserved at the Rijks Herbarium, Leiden. This specimen was collected in Santa Marta, Colombia according to Muramatsu who once compared this herbarium specimen with Nishiyama's K123 wild plant. On the basis of this information, we visited Venezuela and Colombia in 1979, and other regions of Central America and the northern part of South America including seven countries in 1980, with a view to gaining more information and collecting typical I. trifida.

Distribution of plants which can be crossed with sweet potato

It is comparatively easy to determine if a plant can be crossed with sweet potato by simply observing the floral characteristics as reported earlier (Kobayashi and Miyazaki, 1976). Several communities of I. trifida were observed

along the coast of Santa Marta, Colombia. This specimen was considered to be the same plant as that identified by Van Ooststroom as I. trifida (H.B.K.) G. Don. The plants occurred profusely in places at elevations of 5 to 20 m. above sea level (Figure 2). We could observe this plant even in areas at elevations of about 1,000 m above sea level.

Seed setting was not high compared to flowering number, pointing to allogamous characteristics. Plants occurring at higher elevations can produce tuberous roots (Figure 3). This species is propagated vegetatively naturally as well as by seeds. Similar plants occurring in the vicinity of Santa Marta were observed widely in Maracay, Venezuela, and we reconfirmed its identification by comparing it with I. trifida preserved at the Venezuela National Herbarium in Caracas. Austin also considered that this specimen was a typical I. trifida (H.B.K.) G. Don (Austin, personal communication).

Observations were made after growing specimens of I. trifida collected in Santa Marta and Maracay the following year from seeds under the same environmental conditions. Wide genetic variations including flowering time were recognized. All plants were diploid (2n=30), and allogamous with at least six incompatible groups. Mexican diploid species were also considered to be I. trifida though these species had long been identified as I. leucantha Jacq. in Japan. Figure 4 indicates the itinerary of the trip we made in 1980 and the areas where I. trifida specimens were observed. Specimens collected in Santa Marta and Maracay were all diploid, but tetraploid and hexaploid individuals were also included in the plants identified as I. trifida on the basis of their morphological characteristics and distribution. It can be said in general that larger leaves, thicker vines and fewer flowers were produced as the ploidy level became higher. However, the

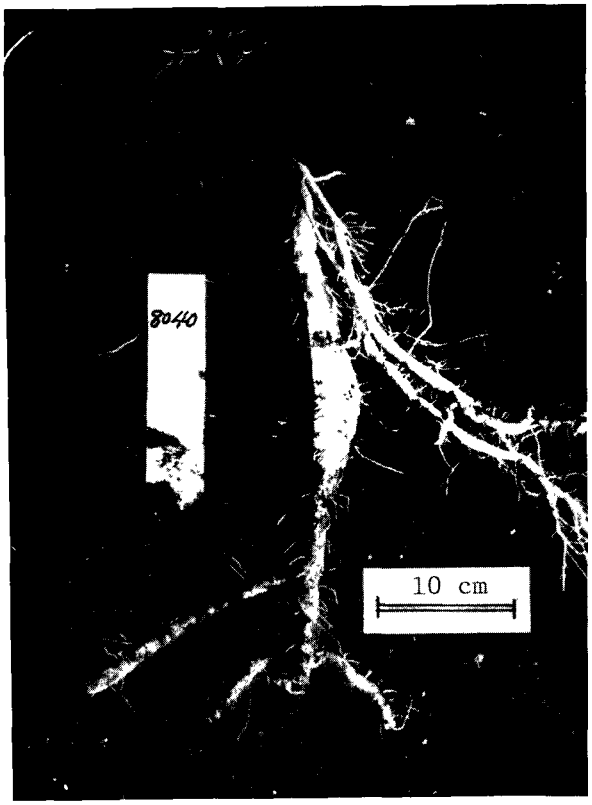

Figure 3. Tuberous root produced by diploid I. trifida.

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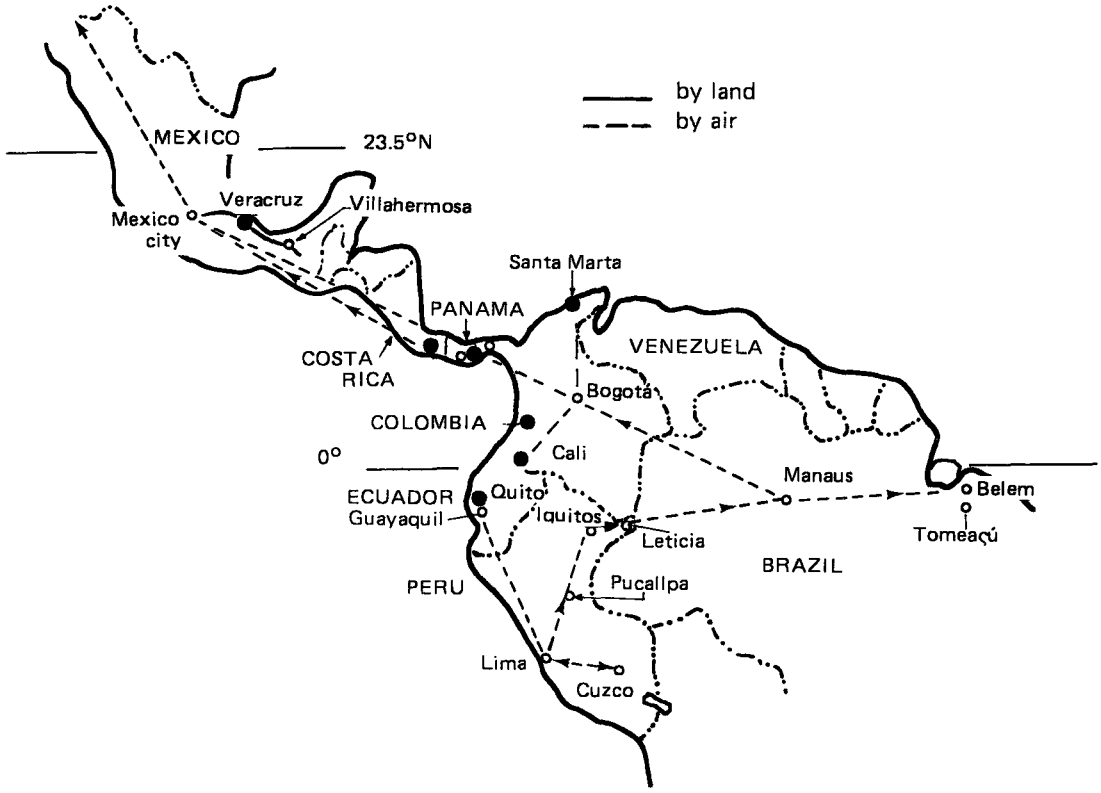

Figure 4. Route map and locations (solid dots) of I. trifida specimens collected in 1980.

ploidy level could not be accurately deduced by only observing morphological characters in the field. Species regarded as hexaploid I. trifida could not actually be distinguished from some plants that were probably derived from cultivated sweet potatoes. Intermediate plants between I. trifida (H.B.K.) G. Don and I. batatas (L.) Lam. were observed profusely in Cali - Buenaventura (1,500 - 2,000 m.a.s.l.), Colombia, San Jose - Turrialba (600 - 1,800), Costa Rica, and around Veracruz (5 - 10), Mexico. Many tetraploid plants identified as I. trifida were observed in the vicinity of Cali, Colombia and along the coast of the Caribbean Sea near Veracruz, Mexico. Many intermediate types between the typical I. trifida and plants called I. littoralis or I. gracilis were observed along with plants of the so-called I. littoralis type that were adapted well to the coastal environment as reported previously by other researchers. Since we observed several intermediate types and no sexual isolation system was recognized, it was eventually concluded that these tetraploid plants represent one of the ecotypes of tetraploid I. trifida and it is believed that these tetraploid plants are neither a separate species nor natural hybrids.

Concept of the Ipomoea trifida complex

It was considered that the various specimens collected could be distinguished by giving a name to each species based on the discontinuity of morphogenetical variations that had occurred at an earlier time. However, it was recognized after field observation and comparison of the materials grown under the same environmental conditions that the name given to a species did not necessarily correspond to the plant group that could be crossed with sweet potatoes.

By now, many intermediate types between known plants which have different species names and some variant forms of I. trifida (Table 1) have been recognized. It is comparatively easy to connect the links of the chain of the respective germplasms within the group in spite of differences in ploidy level. In nature also, exchange of germplasm is presumed to occur due to the existence of incompatibility that is common to this group. The assumption made by Jones concerning the Mexican hexaploid, and Austin's interpretation on the tetraploid plants as being hybrids cannot be refuted theoretically or experimentally. However, such interpretations could be modified on the basis of the following aspects: natural occurrence of triploid plants is not rare; hexaploid plants can be produced easily from triploid plants; various types of diploid and tetraploid plants occur in tropical America; plant density of this ecological group is far higher than that of sweet potato.

Table 1. Variant forms belonging to I. trifida complex.

Acc. No.	2n	Origin	Specific characteristics
7915	30	Colombia	Blooms freely without seasonal influence
8040	30	Colombia	Tuberization of roots
8043			
8051	30	Panama	Miniature plant type with normal flowers
7948	60	Colombia	Intermediate plant type between typical I. trifida and I. littoralis type

After observing the species occurring in tropical America environment and considering the evolutionary trend of polyploidy based on the experimental results, it was eventually concluded that both the hexaploid and tetraploid plants could have been derived from diploid I. trifida originally.

To gain a proper insight into the ecological genetics of the wild plants closely related to sweet potato, the concept of the "Ipomoea trifida complex" was proposed, as shown in Figure 5. This complex refers to an ecological group including plants with different ploidy levels ranging from diploids to hexaploids and different ecotypes presumably adapted to the special environments.

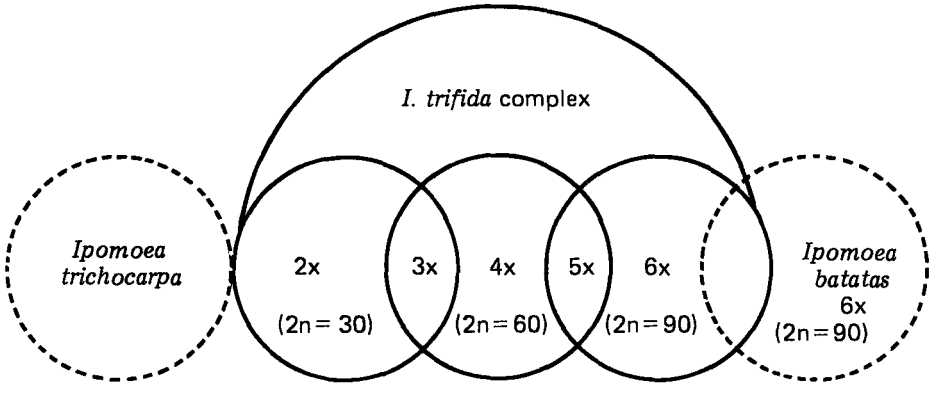

Figure 5. Concept of the Ipomea trifida complex.

The main problems relating to the taxonomy of the wild relatives of sweet potato could be solved through this concept, in particular the phylogenetic relationships of sweet potato. To corroborate the validity of the concept of I. trifida complex, the following aspects can be considered: (1) plants belonging to the I. trifida complex and sweet potato have a common genome (Shiotani and Kawase, 1980); (2) the sphere of adaptability widens as the ploidy level becomes higher; (3) such important characteristics for sweet potato evolution as the presence of tuberous roots and root pigmentation can be observed even in diploid I. trifida (Shiotani, unpublished).

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