DETERMINATION AND ANALYSIS OF SOMATIC CHROMOSOME NUMBERS IN SWEETPOTATO CULTIVARS, RELATED *Ipomoea* SPECIES, AND INTERSPECIFIC HYBRIDS

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ABSTRACT

The somatic chromosome numbers (2n) in seven sweetpotato cultivars, four diploid (2x) *Ipomoea* species, tetraploid (4x) and hexaploid (6x)*I. trifida* strains, and twenty selected hybrids between sweetpotato and 6x*I. trifida* were determined using a Feulgen-acetocarmine squash technique designed for*Ipomoea* chromosomes. The data revealed that euploid counts of 2n=30, 60 and 90 were the modes for the 2x, 4x, and 6x *Ipomoea*, respectively. These counts coexisted with aneuploid cells having either less (hypoploid) or more (hyperploid) chromosomes than the euploid or modal counts. The hypoploid cells were majority among the aneuploid variants. The percentage frequency ratio of euploid to aneuploid cells were 60%:40% among diploids, 45%:55% among tetraploids, and 30%:70% and 34%:66% among the 6x *I.trifida* and sweetpotatoes, respectively. The wide hybrids exhibited extreme aneuploidy with 16%:84% euploid to aneuploid cell ratio. Two hybrids did not show cells with 2n=90. In general, the hybrids resembled the sweetpotato parents in having chromosome numbers closer to 6x or 90 whereas the 6x*I. trifida* and the 4x strains exhibited somatic counts encompassing the 2x, 4x and 6x counts. The results suggest that the prevailing cytogenetic system among the*Ipomoea* is that of somatic euploidy-polyploidy combined with aneuploidy. Further, the amount of aneuploid cells appeared higher with taxa of higher ploidy and highest among the hybrids. The findings are discussed in relation to sweetpotato breeding, germplasm conservation and evolution of new phenotypes through vegetative propagation.

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KEY WORDS: Aneuploidy. Cytogenetics. Euploidy. Evolution. *Ipomoea*. Somatic cells. Sweetpotato breeding. Wide hybrids. 2n.

INTRODUCTION

Ever since a majority of the species within the genus *Ipomoea* were found to have chromosome numbers in multiples of 15 (King and Bamford, 1937), the hypothesis that the basic chromosome number in this genus is

15 has been supported by various workers. The chromosome numbers 2n=30, 2n=60 and 2n=90 were assigned to different species within the genus (Nishiyama and Teramura, 1962; Jones, 1968, 1980; Krishnan, *et al.*, 1969; Magoon, *et al.*, 1970; Nishiyama, 1971; Nishiyama, *et al.*, 1975; Yen, 1976; Shiotani and Kawase, 1987; Orjeda, *et al.*, 1990) and other multiples of 15 were assigned to polyploid hybrids within the genus (Austin, 1977; Bai, 1984; Shiotani and Kawase, 1987). In these reports, 2n=90 was assigned to sweetpotato and to a wild Mexican form of sweetpotato identified as *I. trifida* (H.B.K.) G. Don. (Acc. K123, Nishiyama and Teramura, 1962) which was also considered as an extreme segregate of sweetpotato (Jones, 1967). In this study, the 6x descendants of Acc. K123 and Dr. A. Jones' Acc. 7949-3, identified as *I. sp.*, are named as *I. trifida* (Table 1). In addition to the above mentioned euploid *Ipomoea* forms, aneuploid sweetpotato cultivars and aneuploid variants of 4x hybrids between sweetpotato and 2x *I. trifida* (H.B.K.) Don. have been reported (Oracion, *et al.*, 1990). The term euploid refers to cells, tissues and individuals that have either the basic chromosome number (x) of a genus or complete multiples thereof, *i.e.*, 2x, 3x, 4x, 5x, 6x, *etc.*, whereas aneuploids have incomplete multiples of the x-number (Schulz-Schaeffer, 1980). Aneuploids therefore represent a loss or addition of members of the basic chromosome set of the genus resulting in hypoploid or hyperploid chromosome numbers, respectively. Further, some Philippine sweetpotato cultivars were observed to have variable somatic chromosome numbers but with 2n=90 as the count in highest frequency (Oracion and Saladaga, 1988). The latter observations included a few *Ipomoea* species from ViSCA, Baybay, Leyte, Philippines and wild forms identified as 2x, 4x and 6x *I. trifida* introduced from Japan. These *Ipomoea* were also found to have various somatic chromosome numbers.

In the light of the reported numerical chromosomal variants among members of the genus *Ipomoea*, as well as intraclonal variation in somatic chromosome numbers, the present study was conducted to determine the somatic chromosome number in selected sweetpotato cultivars, *Ipomoea* relatives, and hybrids between sweetpotatoes and their closely related 6x *I. trifida* to ascertain the prevailing cytogenetic system of the somatic cells within clones of these vegetatively propagated *Ipomoea*. The study is part of a cytogenetic investigation involving sweetpotato and *Ipomoea* relatives which were entered in a wide crossing scheme under tropical conditions at ViSCA. This paper presents a basic discussion of the results in the context of sweetpotato breeding, germplasm conservation, and possible mode of evolution of new phenotypes through vegetative propagation.

Table 1. Source and description of *Ipomoea* species or strains.

Ipomoea	Source	Description
I. batatas		
VSP-1, VSP-2, VSP-7	ViSCA, Leyte, Philippines	New sweetpotato variety released by the Philippine Seed Board; produced from intervarietal crosses
VSP-8		[Also named Philippine Seed Board Sweetpotato 14 (PSBSP 14)]
Ciete Flores		Native cultivar; original source not known
Miracle		Native cultivar collected from Dulag, Leyte, Philippines
Naveto		Native cultivar introduced from Papua, New Guinea
I. trifida 6x strains	Mie University, Japan (Dr. I. Shiotani)	Open-pollinated seeds from F1 progeny from clonal stocks collected from Fortin, Veracruz, Mexico (Acc. K123, identified as *I. trifida*) and the plant from the seeds labelled as 79,12 by Dr. A. Jones (Acc. 7949-3, identified as *I. sp.*)
4x strains		Open-pollinated seeds from F1 progeny of clonal stocks collected from Boca del Rio, Veracruz, Mexico (Acc. ECAL 2326 (1)-1) and from Veracruz, Mexico (Acc. 8053), both stocks identified as 4x *I. trifida*
I. aquatica (cultivated)	ViSCA, Leyte, Philippines	Cultivated in wet areas for shoots as vegetable and animal feed; locally called "tangkong"
I. aquatica (wild)		Wild, weedy strain used as a substitute for the cultivated type
I. triloba		Weed; locally called "mote-mote"
I. cairica		Weed but sometimes cultivated for ornamental purposes
I. pes-caprae		Shoreline weed locally named "lambayong"

Table 2. Identity or source of twenty sweetpotato x 6x*I. trifida* F1 hybrids used in the study.

Accession Number	Cross Combination	Total Number of Selected Hybrids
B12	TIS-2544 x 6x *I. trifida*	4
B13	V7-21 x 6x *I. trifida*	1
B14	V29-1180 x 6x *I. trifida*	2
B15	Naveto x 6x *I. trifida*	1
B16	Wanmun Small x 6x *I. trifida*	1
B17	V29-5 x 6x *I. trifida*	1
B22	V30-688 x 6x *I. trifida*	1
B23	V30-731 x 6x *I. trifida*	2
B24	VSP-7 x 6x *I. trifida*	3
B25	V30-866 x 6x *I. trifida*	4
Total		20

MATERIALS AND METHODS

The *Ipomoea* plants used were obtained as shoot cuttings from clones of seven sweetpotato cultivars, namely: VSP-1, VSP-2, VSP-7, VSP-8, Ciete Flores, Miracle and Naveto; two strains of*I. aquatica* (cultivated and wild); three other *Ipomoea* species identified as *I. triloba, I. cairica* and *I. pes-caprae*; wild *Ipomoea* strains, identified as 4x and 6x*I. trifida*; and twenty hybrids selected for good storage root-forming ability out of progenies from crosses between sweetpotato and 6x *I. trifida*. All plant materials and their sources aré shown in Tables 1 and 2. The method used in preparing mitotic chromosomes is that described by Oracion (1993) for*Ipomoea* species and hybrids. Fifteen to 70 mitotic metaphase-arrested cells with intact cell walls were analyzed for each sweetpotato cultivar, species, or wild strain; eight to 56 cells were analyzed for the hybrid genotypes. From the chromosome counts made for each species or strain, the following statistics were determined: range, mode, means and percentage frequency distribution of somatic counts (2n) according to classes. The 2n classes assigned were: 2n counts equal to the euploid number, *i.e.*, 2n=30, 2n=60 or 2n=90; 2n counts below the euploid number, *i.e.*, 2n<30, 2n<60 or 2n<90; and 2n counts above the euploid number, *i.e.*, 2n>30, 2n>60 or 2n>90.

RESULTS AND DISCUSSION

Following the theory of x=15 as the basic chromosome set in the genus *Ipomoea* and using the modal count as basis for ploidy, all the studied sweetpotato cultivars from ViSCA, Philippines were hexaploids, and the other *Ipomoea* species from ViSCA were diploids; the wild strains introduced from Japan were either tetraploids or hexaploids (Table 3). On the other hand, ten of the twenty hybrids had modes of 2n=90, which would qualify as hexaploids, but four of these hybrids exhibited one or two other modes aside from 2n=90 (Table 4). Thus, B12-2 had another mode of 2n=88 while B15-1 and B24-3 had 2n=92 as the second mode; B12-3 showed two other modes of 2n=87 and 2n=89 in addition to 2n=90. The rest of the hybrids showed aneuploid modal counts that were either lower or higher than 90.

The means among the different species and sweetpotato cultivars were generally lower than their respective modes (Table 3). Notably, the 6x*I. trifida* had lower means than the*I. batatas* cultivars, a characteristic which indicated a major difference between the two taxa. On the other hand, means among their F1 hybrids varied (Table 4). Those having modes of 2n=90 or higher had means lower than their modes, whereas the remaining three hybrids with modes of 2n=80, 81, or 82 had means higher than their modes but below 90. In general, means among the hybrids were higher than those of the 6x *I. trifida* and closer to sweetpotato, which suggested a closer resemblance to sweetpotato than the wild parents. This is an expected consequence since the hybrids were selected for good storage root forming ability, a character present only in the sweetpotato parents but non-existent among the wild parents.

The ranges in chromosome counts suggested that a relatively high number of chromosome losses were tolerated by the different taxa but not chromosome additions. Only the 4x *I. trifida* strain 4x-2 appeared to have tolerance to a high number of chromosome additions as well as tolerance to chromosome losses as shown by its somatic counts ranging from 25 to 90 (Table 3). This indicated that the 4x strain could tolerate both the 2x and 6x chromosome numbers. The 6x *I. trifida* strains also contained 2x, 4x and 6x cells, whereas six of the seven sweetpotato cultivars showed a narrow range of counts from 69 to 92 (Table 3), thereby differing largely from the wild 6x. This indicated that the cultivated 6x*I. batatas* had mostly cells with chromosome numbers approximating hexaploidy. On the other hand, the interspecific hybrids also showed a narrow range from 70 to 96, which indicated a similarity to the sweetpotato parents rather than to the*I. trifida* parents. Again, this may be correlated with good storage root forming ability, a trait found only in the sweetpotato parents and not in the*I. trifida* parents.

The percentage frequency distribution by 2n classes among sweetpotato cultivars (Table 3) revealed that only 21.05% (VSP-7) to 53.85% (VSP-2) of the cells analyzed had 2n=90 and were interpreted as euploids with a mean of 33.75% across cultivars. A bigger percentage of the cells observed belonged to the hypoploid class 2n<90 ranging from 42.31% (VSP-2) to 76.47% (Ciete Flores) with a mean of 62.31% across cultivars. Only 3.91% of the cells across cultivars were hyperploids with 2n>90. A similar pattern

Table 3. Range, mean, mode, number of cells analyzed and percentage frequency distribution by classes of somatic chromosome numbers (2n) in *Ipomoea* species, strains or cultivars.

Ipomoea	Number of Cells Analyzed	Statistics			Frequency Distribution (%)		
		Range	Mean	Mode	2n=Mode	2n<Mode	2n>Mode
I. aquatica[1]	26	27-34	29.84	30	53.84	26.92	19.23
I. aquatica[2]	15	28-34	30.06	30	46.66	26.66	26.66
I. triloba	17	28-30	29.17	30	52.94	47.05	0
I. cairica	16	28-30	29.62	30	75.00	25.00	0
I. pes-caprae	47	20-31	29.38	30	65.95	31.91	2.12
I. trifida							
4x-1	72	33-63	57.67	60	47.22	45.83	6.94
4x-2	79	25-90	59.24	60	41.77	39.24	18.99
4x-3	72	30-74	56.99	60	47.22	45.83	6.94
I. trifida							
6x-1	70	40-91	78.64	90	27.14	68.57	4.29
6x-2	79	30-91	80.80	90	36.71	59.49	3.80
6x-3	70	26-95	75.01	90	25.71	67.14	7.14
I. batatas							
VSP-1	16	80-92	86.38	90	31.25	56.25	12.50
VSP-2	26	72-90	86.84	90	53.85	42.31	3.85
VSP-7	19	69-92	83.26	90	21.05	73.68	5.26
VSP-8	19	76-91	85.57	90	31.57	63.15	5.26
Ciete Flores	17	77-90	84.94	90	23.52	76.47	0
Naveto	15	76-90	85.40	90	33.33	66.66	0
Miracle	80	41-95	85.40	90	46.25	50.00	3.75

[1]Cultivated
[2]Wild

Table 4. Range, mean, mode, number of cells analyzed and percentage frequency distribution by classes of somatic chromosome numbers (2n) in 20 sweetpotato x 6x *I. trifida* F1 hybrids.

Hybrid	Number of Cells Analyzed	Statistics			Frequency Distribution (%)		
		Range	Mean	Mode	2n=90	2n<90	2n>90
B12-1	35	78-94	86.14	90	22.86	68.57	8.57
B12-2	18	75-91	87.00	88;90	22.22	72.22	5.56
B12-3	56	82-92	87.78	87;89;90	17.86	75.00	7.14
B12-4	17	85-91	88.53	91	11.76	64.71	23.53
B13-1	45	72-92	82.49	80	4.44	93.33	2.22
B14-1	32	70-94	85.19	82	9.38	75.00	15.62
B14-2	19	80-96	83.05	90	26.32	68.42	5.26
B15-1	10	76-94	88.80	90;92	20.00	30.00	50.00
B16-1	15	84-95	90.27	94	13.33	40.00	46.67
B17-1	22	80-90	85.36	81	9.09	90.91	0
B22-1	21	74-93	86.90	91	9.52	57.14	33.33
B23-1	8	82-91	87.00	91	0	75.00	25.00
B23-2	19	75-91	86.74	90	31.58	57.89	10.53
B24-2	18	81-93	87.33	90	22.22	66.67	11.11
B24-3	21	81-93	84.38	90;92	23.81	33.33	42.86
B24-4	23	72-92	87.78	90	34.78	52.17	13.04
B25-1	21	77-93	84.86	93	0	76.19	23.81
B25-2	18	77-93	87.50	90	22.22	55.56	22.22
B25-3	12	82-92	88.25	92	16.67	50.00	33.33
B25-4	26	78-95	87.69	91	11.54	53.85	34.62

was observed among the 6x *I. trifida* strains. The hybrids, however, varied in their percentage frequency distributions of somatic counts (Table 4). Out of the 20 hybrids, nine followed the trend exhibited by the parents; seven exhibited the class of 2n>90 as second in rank to the 2n<90 class; one showed equal percentage means between the 2n=90 class and the 2n>90 class; and three showed the 2n>90 class as the highest in frequency. Two hybrids, B23-1 and B25-1, did not exhibit any cell with 2n=90. However, majority of the aneuploid cells were of the hypoploid types, which suggested that chromosome losses in the *Ipomoea* genomes were tolerated and prevailed more than chromosome additions to the euploid complements.

When the hyperploid and hypoploid cells were put together in a 2n class then compared to the euploid counts as the other class, the resulting pattern in euploid to aneuploid cell ratio among the *Ipomoea* showed increase in number of aneuploid cells with increase in ploidy. This was demonstrated

by the grand mean ratio of 59%:41% euploid to aneuploid cells among the diploids; 45%:55% euploid to aneuploid cells among the tetraploids; and 30%:70% and 34%:66% euploid to aneuploid cell ratio among the 6x *I. trifida* and sweetpotatoes, respectively. Euploidy is often necessary for survival among sexually-reproducing organisms wherein every chromosome is necessary for genome balance, which in turn is necessary to produce fertile gametes and physiologically balanced seeds. In the genus *Ipomoea*, however, asexual propagation or reproduction appears to be the rule, therefore the need to maintain pure euploid clones could be bypassed and the aneuploid cell lines, when present, could be perpetuated through asexual propagation. Among the *Ipomoea* forms studied, the diploids showed 46% to 75% euploid cell content whereas the tetraploids and hexaploids showed less than 50% or much lower amount of euploid cells. This indicates that the diploids still need to maintain a higher number of the expected physiologically balanced euploid cells having complete chromosome sets in order to survive. The polyploids, however, are able to tolerate higher amounts of aneuploid cells as the extra genomes, *i.e.*, two more in the tetraploids and four more in the hexaploids, function as genetic buffers in such polyploid systems. It is therefore logical to expect that with more extra genomes present or a high ploidy level, a high number of aneuploid cells may be tolerated along with the high buffering capacity of the extra genomes. This may explain why with high ploidy level, a high aneuploid cell content was observed among the *Ipomoea* forms studied. The hybrids showed a 16%:84% euploid to aneuploid ratio, indicating extreme aneuploidy. Two hybrids, B23-1 and B25-1, did not show any cell with 2n=90. This suggests that interspecific hybridization caused an increase in aneuploidy among somatic cells of the hybrids. Specific gene combinations or interactions are probably responsible for the increase. The exact mechanism causing aneuploidy is not known.

The clones were therefore composed of cytogenetically heterogeneous cells or tissues that lie side by side within the organism, leading to the formation of "chromosomal mosaics" or "chromosomal chimeras." According to Schulz-Schaeffer (1980), these terms refer to organisms that are not genetically uniform throughout and have cells differing in chromosome structure or number. Among the *Ipomoea* forms studied here, only differences in somatic chromosome numbers were analyzed. This cytogenetic system of somatic euploidy-polyploidy combined with aneuploidy leading to chromosome mosaicism in *Ipomoea* species has high chances of being perpetuated because of the inherent capacity of most *Ipomoea* to be propagated by vegetative means.

It has been reported that somatic mutations in sweetpotato occur in a remarkably high frequency with some cultivars having a higher tendency to mutate than others (Hernandez, *et al.*, 1964; Kukimura, 1986). Because of this tendency to mutate, hill individual plant selection has been deemed necessary to preserve cultivars and is an integral part of plant certification programs (Edmond and Ammerman, 1971). This tendency of sweetpotato to undergo genetic changes within a clone is probably related to its having a cytogenetically heterogeneous population of cells to a certain degree within a clone. Such inconstancy in the chromosome complements of vegetatively propagated plants is common, examples of which are found in the Aroid family (Sharma and Das, 1954; Mookerjea, 1955; Sharma and Bhattacharya, 1966), some *Musa* species and hybrids (Imperial, 1967; Oracion, 1985; Castañares, 1986) and other monocotyledons (Sharma and Bhattacharya, 1966). These findings led Sharma and co-workers to formulate a theory of speciation in vegetatively propagated or reproducing plant species. The theory states that cells or cell initials with chromosome composition or numbers deviating from those of the parent plant, may participate in the formation of shoots that give rise to new kinds or phenotypes.

The improvement of sweetpotato before the techniques of flower induction were perfected has been largely by clonal selection of desirable somatic mutations (Ting and Kehr, 1953; Hall *et al.*, 1992). Although this method of sweetpotato improvement is still being practiced through discoveries of desirable natural mutants (Annual Report of Sweet Potato Breeding, 1993) or through mutation breeding (Oracion and Saladaga, 1988; Kukimura, 1986), intervarietal hybridization followed by selection of desirable recombinants is being practiced more in planned breeding programs (Annual Report of Sweet Potato Breeding, 1989, 1991, 1992, 1993; Kukimura *et al.*, 1988; A program for varietal improvement of Sweet Potato in the Philippines Progress Reports for 1986, 1989). Wide hybridization is also being explored to further enrich the sweetpotato germplasm (Kukimura *et al.*, 1988; Oracion and Shiotani, 1992; Orjeda *et al., 1992).* In addition, the new era of genetic engineering or biotechnology is now in process (Hall *et al.*, 1992; Collins, 1992). The results of the present study may suggest that *in vitro* culture of a highly heterogeneous group of cells of a clone or hybrid would offer wide possibilities in producing new genotypes from the individual cells of such a clone for breeding purposes. However, *in vitro* culture of such cells or tissues should pass through appropriate screening procedure(s) if the main purpose is to conserve the genetic purity of clones. Results of this study suggest, too, that a means of favoring the growth and development of cells whose chromosome number approaches 90 should be considered in the somatic cell culture of sweetpotato.

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LITERATURE CITED

Annual Report of Sweet Potato Breeding. 1989. Sweet Potato Breeding Laboratory, Kyushu National Agricultural Experiment Station, MAFF, Japan. 22 pp.

Annual Report of Sweet Potato Breeding. 1991. Sweet Potato Breeding Laboratory, Kyushu National Agricultural Experiment Station, MAAF, Japan. 27 pp.

Annual Report of Sweet Potato Breeding. 1992. Sweet Potato Breeding Laboratory, Kyushu National Agricultural Experiment Station, MAAF, Japan. 27 pp.

Annual Report of Sweet Potato Breeding. 1993. Sweet Potato Breeding Laboratory, Kyushu National Agricultural Experiment Station, MAAF, Japan. 29 pp.

AUSTIN, D.F. 1977. Hybrid polyploids in *Ipomoea* section *batatas*. J. Heredity. 68:259-300.

BAI, K.V. 1984. Pentaploids in sweet potato and their prospective role in sweet potato improvement. Proc. Sixth Symp. of Inter. Soc. for Trop. Root Crops, CIP, Lima, Peru, Feb. 21-26, 1983.

CASTAÑARES, A.G. 1986. Somatic chromosome number and mitotic behavior in abaca (*Musa textilis* Nee), "agotay" (*Musa* sp.) and their F1 hybrid. Unpublished BS Thesis, Visayas State College of Agriculture, Baybay, Leyte, Philippines. 40 pp.

COLLINS, W.W. 1992. Practical applications of biotechnology for sweetpotato improvement. *In* W.A. Hill, C.K. Bonsi and P.A. Loretan (eds.). Sweetpotato Technology for the 21st century. Tuskegee University, Alabama, USA. 607 pp.

EDMOND, J.B. and AMMERMAN, G.R. 1971. Sweet potatoes: Production, Processing, Marketing. AVI Pub. Co., Westport, Conn. Cited by Jones, A. (1980). *In* W.R. Fehr and H.H. Hadley (eds.). Hybridization of Crop Plants. Am. Soc. of Agron- Crop Sci. Soc. Am., Madison, Wisconsin, USA. p. 653.

HALL, M.R., LABONTE, D.R. and BONSI, C.K. 1992. New techniques and conventional breeding of sweetpotato. *In* W.A. Hill, C.K. Bonsi and P.A. Loretan (eds.). Sweetpotato Technology for the 21st century. Tuskegee University, Alabama, USA. 607 pp.

HERNANDEZ, T.P., HERNANDEZ, T. and MILLER, J.C. 1964. Frequency of somatic mutations in sweet potato varieties. Proc. Am. Soc. Hort. Sci. 85:430-433.

IMPERIAL, C.B. 1967. Chromosome number of BC1 and BC2 Pacol x Abaca. Unpublished BS Thesis, University of the Philippines at Los Baños, College, Laguna. 14 pp.

JONES, A. 1967. Should Nishiyama's K123 (*Ipomoea trifida*) be designated *I. batatas*? Econ. Bot. 21(2):163-166.

JONES, A. 1968. Chromosome numbers in *Ipomoea* and related genera. J. Heredity 2:274-279.

JONES, A. 1980. Sweet Potato. *In* W. R. Fehr and H. H. Hadley (eds.) Hybridization of Crop Plants. Am. Soc. of Agron-Crop Sci. Soc. Am., Madison, Wisconsin, USA. p. 42-45.

KING, J.R. and BAMFORD, R. 1937. The chromosome number in *Ipomoea* and related genera. J. Heredity 28:279-282.

KRISHNAN, R. MAGOON, M.L. and VIJAYA BAI, K. 1969. The pachytene chromosome of *Ipomoea crassicaulis*. Theor. Appl. Genet. 39:274-279.

KUKIMURA, H. 1986. Mutation breeding in root and tuber crops: A review. Gamma Field Sympo. No. 25, Inst. of Radia Breed, NIARMAFP, Japan. p. 109-127.

KUKIMURA, H., KOMAKI, K. and YOSHINAGA, M. 1988. Current progress of sweetpotato breeding in Japan. Paper presented at the 8th Symposium of the International Society for Tropical Root Crops (ISTRC) in Bangkok, Thailand. 14 pp.

MAGOON, M.L., KRISHNAN, R. and BAI, V.K. 1970. Cytological evidence on the origin of sweet potato. Theor. Appl. Genet. 40:360-366.

MOOKERJEA, A. 1955. Cytology of different species of Aroids with a view to trace the basis of their evolution. Caryologia 7:221-291.

NISHIYAMA, I. 1971. Evolution and domestication of sweet potato. Bot. Mag. Tokyo 84:377-387.

NISHIYAMA, I., MIYAZAKI, T. and SAKAMOTO, S. 1975. Evolutionary autoploidy in the sweet potato (*Ipomoea batatas* (L.) Lam.) and its progenitors. Euphy. 24:197-208.

NISHIYAMA, I. and TERAMURA, T. 1962. Mexican wild forms of sweet potato. Econ. Bot. 16(4):305-318.

ORACION, M.Z. 1985. Cytogenetics of *Musa textilis* Nee X *Musa balbisiana* Colla hybrids in the Philippines. Unpublished MS Thesis, University of the Philippines at Los Baños, College, Laguna. 161 pp.

ORACION, M. Z. 1993. A technique for making preparations of mitotic and meiotic chromosomes from *Ipomoea* species and hybrids. Ann. Trop. Res. 15:31-36.

ORACION, M.Z., NIWA, K. and SHIOTANI, I. 1990. Cytological analysis of tetraploid hybrids between sweet potato and diploid*Ipomoea trifida* (H.B.K.) Don. Theor. Appl. Genet. 80:617-624.

ORACION, M.Z. and SALADAGA, F.A. 1988. A preliminary study on inducing mutation in sweet potato using EMS combined with adventitious bud technique. Philipp. J. Crop Sci. 10:S11.

ORACION, M.Z. and SALADAGA, F.A. 1988. Somatic chromosome number in *Ipomoea* species from the Philippines and Japan. Philipp. J. Crop Sci. 10:S11.

ORACION, M.Z. and SHIOTANI, I. 1992. Cytology and fertility of sweetpotato x diploid *Ipomoea trifida* F_1 hybrids and their potential in analytic breeding of sweetpotato. *In* W.A. Hill, C.K. Bonsi and P.A. Loretan (eds.) Sweetpotato Technology for the 21st century. Tuskegee University, Alabama, USA. 607 pp.

ORJEDA, G., FREYRE, R. and IWANAGA, M. 1990. Production of 2n pollen in diploid *Ipomoea trifida*, a putative wild ancestor of sweet potato. J. Heredity. 81:462-667.

ORJEDA, G., IWANAGA, M., and FREYRE, R. 1992. Use of *Ipomoea trifida* germplasm for sweetpotato improvement. *In* W.A. Hill, C.K. Bonsi and P.A. Loretan (eds.). Sweetpotato Technology for the 21st century. Tuskegee University, Alabama, USA. 607 pp.

SCHULZ-SCHAEFFER, S. 1980. Cytogenetics. Springer-Verlag New York, Inc., USA. 446 pp.

SHARMA, A.K. and BHATTACHARYA, G.N. 1966. A cytotaxonomic study on some taxa of Araceae. Genet. Iberica 18:237-263.

SHARMA, A.K. and DAS, N.K. 1954. A study of karyotypes and their alteration in Aroids. Agron. Lusit. 16:23-48.

SHIOTANI, I. and KAWASE, T. 1987. Synthetic hexaploids derived from wild species related to sweet potato. Japan J. Breed. 37:367-376.

TING, Y.C. and KEHR, A.E. 1953. Meiotic studies in the sweet potato (*Ipomoea batatas* Lam.). J. Heredity 44(5):207-211.

YEN, D.E. 1976. Sweet potato. *In* N. W. Simmonds (ed.). Evolution of Crop Plants. Longman, London. p. 42-45.