

INTRA AND INTERSPECIFIC CROSSES IN THE GENUS *MANIHOT*

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As long as selection in cassava is limited to the testing of cultivars, seed production is not a factor of importance. It becomes, however, very important when in the case of breeding purposes, large populations of seedlings are necessary either from free-pollinated plants or from artificially cross-pollinated plants. In the latter case, especially, it is desirable that from hand operated pollinations are obtained as much fruits and from each fruit as much seeds as possible.

Koch (1934) in his thesis does not pay much attention to this problem and gives only a few figures. He mentions that in 1933 from 22,000 cross pollinations a total of 1500 fruits were obtained signifying a success of 7%. On the behaviour of the various cultivars used as parent clones nothing is mentioned. More data are given by him on the crosses between *Manihot utilisima* and *M. glaziovii*, but here the number of pollinations is so small that expression in percentages may lead to erroneous conclusions. The same objections must be made in relation to figures given by Nichols (1947). He notes that from his crosses between different cultivars, the percentages of success fluctuate between 0 and 56, with averages of 13.6 and 14.6 which have relation to respectively 27 and 32 crosses in the F_1 and F_2 generations. Nothing is said, however, about the behaviour of the different parent clones. He concludes that a low percentage of success is a striking feature within the species. In those cases where he got no success at all he assumes that incompatibility may exist.

In his interspecific crosses he generally finds low success and sometimes no success at all. With species hybrids he is sometimes faced with selfsterility. Back crossing with cassava-parent generally gave much better results.

MATERIAL AND METHODS

In the description of his crossing technique Nichols (1947) mentions that both male and female flowers are enclosed in muslin bags before and after pollination. Koch (1934) however, reports that pollination is effectuated by capping the female flower with a male one. The latter one drops after one or two days when the female flower is no more receptive. Enclosing in muslin bags after pollination is thus superfluous.

Under the conditions of the tropical lowland climate in Java, several cultivars did not flower at all or only very late. Flowers borne at tall plants necessitate working on ladders which leads to a decrease in number of flowers being pollinated per day. Koch (1934) found that by planting his cultivars at an altitude of at least 3000 feet above sea level, nearly all cultivars produced flowers at an earlier age and at such a height that pollination could be effected much more easily. In this way two native assistants could perform 2500 pollinations in two days.

RESULTS

For the sake of clearness, our results are classified in three groups viz.:

- a. Crosses within the species *Manihot utilissima*
- b. Crosses between *M. utilissima* and *M. glaziovii*
- c. Crosses between *M. utilissima* and *H. saxicola*.

a. The results of different crosses within *M. utilissima* over four years with percentages of success, number of seeds harvested and number of seeds per fruit are given in Table I. Crosses with less than 200 pollinations are excluded from this compilation.

Table I. Results of pollinations between various cultivars of *Manihot utilissima*.

Year	number of pollinations	number of fruits	% success	number of seeds harvested	mean number of seeds per fruit
1937	2344	156	15	—	—
1939	17689	1706	10	3588	2.1
1940	19565	2823	14.4	3672	1.3
1941	13969	2495	17.8	4307	1.7

The compiled results in Table I give no idea on the differences in success with respect to the different combinations of parents, and the mean number of seeds per fruit. These, however, were fairly large. In Table II the extreme values are given for the different years.

Table II. Extreme values of percentages of success in different years.

year	% success		mean number of seeds per fruit	
	highest	lowest	highest	lowest
1937	17.—	3.—	—	—
1939	20.—	0.3	2.6	1.1
1940	25.9	1.—	1.9	0.4
1941	37.—	1.—	2.6	0.6

From the detailed results per crossing which cannot be given here on account of space, it was clear, however, that crosses with a higher success than 10% were only to be found if one or both parents belonged to a group of four cultivars i.e. F.357, Boger, S(as) P(edro) P(reto) and Mangi. The first two are hybrids selected at Buitenzorg, whereas S. P. P. and Mangi are imports from Brazil. Most of the crosses were made reciprocally with, on the average, the same degree of success. With the cultivar Mangi, however, most flowers dropped during flowering, which becomes obvious in the crosses where Mangi was used as the female parent. In 1939 the cross S.P.P. x Mangi gave 18% success, the reciprocal cross however only 3%. This phenomenon also occurred in reciprocal crosses when using a hybrid E 17 which had Mangi for one of the parents. Very bad results were obtained with cultivar Singapore which was used as female parent in 1940 and 1941. In combination with six different male partners the success did

not exceed 1% with five of them, with F 357, the success was 22.5%, with only 0.4 seed per fruit.

b. Crosses between *M. utilis* and *M. glaziovii*. Under this heading come also crosses between F_1 hybrids and backcrosses of F_1 hybrids with the cassava parent.

Table III. Results of reciprocal crosses between *M. utilis* and *M. glaziovii*.

Cross	number of pollinations	number of fruits	% success	number of seeds harvested
M. util. x M.glaz	730	42	6.—	50
M. glaz. x M.util.	453	8	2.—	—

Of the cassava parent used crosses involving F 357 cultivar always gave good results. From Table III it is clear that only some success could be obtained when the cassava was used as the female parent.

The hybrids grown from seeds harvested were given H numbers. When intercrossed, these H-hybrids generally gave very unsatisfactory results. Out of 10 combinations totalling 1003 pollinations only 16 seeds were obtained, ten from which were the result of one single combination. Backcrossing of the species hybrids with the cassava parent (F 357) gave much better results.

The results of these backcrosses are compiled in Table IV.

Table IV. Results of backcrosses of F_1 species hybrids with the cassava parent.

year	cross	number of pollinations	number of fruit	% success	number of seeds harvested	mean number of seeds per fruit
1940	F 357 x H 5/9	1115	335	30	449	1.3
	H 5/9 x F 357	1056	87	8	—	—
	F 357 x H 5/2	1105	7	1.1	—	—
	H 3/2 x F 357	1341	182	18	407	2.2
1941	F 357 x H 5/9	1280	49	3.7	59	1.2
	H 5/9 x F 357	620	142	11.—	242	1.7
	H 5/8 x F 357	197	—	—	—	—
	H 5/3 x F 357	89	—	—	—	—
	S.P.P. x H 5/9	1100	162	14.—	375	2.3
	Singapore x H 5/9	600	2	—	5	2.5

From the data in Table IV it is clear that a reasonable amount of success can only be expected when cassava is used as the female parent. The majority of the species hybrids produced very few flowers and only two of the nine hybrids available could be used with some success. Cultivar Singapore again proved to be a bad parent.

Plants grown from the seeds of these backcrosses were a very variable lot from which ultimately only four remained as promising. From these four, 17 proved to be the best one. Combinations of the F_2 hybrids yielded much better

results than those of the F_1 hybrids. Whereas in the case of the F_1 hybrids 1003 pollinations produced 16 seeds, four combinations of the F_2 hybrids succeeded in 113 fruits with 155 seeds out of 2398 pollinations.

Backcrossing of these F_2 hybrids with a cassava parent also gave generally much better results than those of the F_1 hybrids. The results of a number of backcrosses are compiled in Table V.

Table V. Results of backcrosses of F_2 species hybrids with different cassava parents.

cross	number of pollinations	number of fruits	% of success	number of seeds harvested	mean number of seeds per fruit
17 x F 357	940	46	5.—	27	0.6
F 357 x 17	1740	180	10.5	225	1.2
17 x 269	150	34	22.5	16	0.5
269 x 17	1120	16	1.4	3	0.2
S.P.P. x 17	1160	257	22.—	562	2.2
Singapore x 17	1200	10	1.—	9	0.9
17 x Bogor	500	51	2.5	7	0.5

From these results it is clear again that the best success may be expected when cassava is used as the female parent. In contrast to the crosses with F_1 hybrids, no combination appeared to be an entire failure.

c. Crosses between *M. utilissima* and *M. saxicola*. Under this heading are backcrosses with the F_1 hybrids and crosses of *M. saxicola* with an F_2 hybrid (17) of a *glaziovii* — cassava cross. A description of *M. saxicola* has been given by Bolhuis (1953). Seeds were obtained from Surinam yielding a number of very uniform plants which at Buitenzorg flowered profusely. Crossing was affected with the cassava cultivar Basiorao, a Brazilian import, which flowered simultaneously. The results of these crosses are shown in Table VI.

Table VI. Results of crosses between *M. utilissima* and *M. saxicola*.

cross	number of pollinations	number of fruits	% of success	number of seeds	number of seeds per fruit
M. sax. x Bas.	335	125	36.7	76	0.6
Bas. x M. sax.	96	47	49.—	80	1.7

Particularly striking is the high percentage of success which is far in excess of the percentages found in crosses within the species *M. utilissima*. It makes it even questionable as to whether *M. saxicola* is sufficiently different from *M. utilissima* to consider it as a separate species, since both crosses have such a high percentage of success. There is, however, a considerable difference

in the number of seeds per fruit. The hybrids resulting from these crosses were backcrossed with cultivar F 357 as cassava parent. The results are being compiled in Table VII.

Table VII. Results of backcrosses of sax. — util. hybrids with a cassava parent.

cross	cross	number of pollinations	number of fruits	% of success	number of seeds	number of seeds per
(M. sax. x Bas)	x F357	2990	1466	49	1070	0.7
(Bas x M. sax.)	x F357	2440	275	11.3	251	0.9

In these backcrosses it matters whether *M. sax.* or the cultivar *Basiorao* is used as the female parent in the first cross. The yield in seeds per fruit is however low in both combinations.

Save for these crosses *M. saxicola* was also crossed reciprocally with 17. The results are shown in Table VIII.

Table VIII. Results of reciprocal crosses between *M. saxicola* and an F_2 hybrid of *M. util.* and *M. glaziovii*.

cross	number of pollinations	number of fruits	% of success	number of seeds	number of seeds per fruit
17 x M. sax	633	4	6.5	10	0.25
M. sax. x 17	527	55	10.4	16	0.3

It appears that the making of a triple species hybrid is quite feasible. The data of the reciprocal crosses do not differ very much and the very low number of seeds per fruit in both combinations is remarkable.

DISCUSSION.

When breeding cassava by means of cross pollination the plant breeder generally wants as large a number of plants as possible to be able to select extremes. Being a vegetatively propagated crop plant, the cassava is very heterozygous and heterogenous. In this respect, it is important to know whether a reasonable amount of seeds can be expected from controlled crosses. From the data given in Table II and from experiences with several cultivars, it is clear that in Java this amount of success can only be expected when a relatively small number of cultivars is used as parent clones. Other cultivars generally yielded very poor or no results at all. With the right combinations of parents, a percentage of success can be expected of at least 25%. From Table II it can be seen that in the consecutive years the percentage of success can be increased by the right choice of parents. Large differences are to be expected in the number of seeds per fruit, which, however, may be influenced in a large measure by the weather in the ripening period. Of all the combinations of cultivars, only two had no success at all. Nichols (1947), however, found many sterile combinations. He attributes this to incompatibility, but according to our data, this has still to be proved. In one year, the combination Singapore x Bogor gave no success at all, in another year, this combination yielded very poor results. Nichols conclusions are obviously based on a too low number of pollinations.

Large differences occur also in the number of seeds per fruit. This may

be caused by unfavourable weather conditions as was the case in 1940 (see Table I) when a lot of seed failed to develop in the fruits. At harvest, only sound normally developed seeds were counted. With certain crosses, the average number of seeds per fruit, however, is so low that other causes may be taken into consideration. Both Koch (1934) and Nichols (1947) assume that this may be caused partly by parthenocarpy; cytological and morphological research may lead to a better insight in this matter.

In the Ivory Coast, Meige (1954) found in the cultivar collection of the ORSTOM, different types of sterility; male sterility, female sterility and total sterility. His cytological research was, however, restricted to only one example of male sterility wherein he found that meiosis was normal, and that the pollen grains degenerated before maturing. In the case of total sterility he mentions that parthenocarpy may be present or not. Crosses of partly sterile cultivars with fertile ones, however, were not attempted.

Abraham (1957) made a large number of cassava crosses but he does not mention any percentages of success or number of seeds per fruit. Cours and Fritz (1960) mention that there is no pollen formation at all in certain of their cassava hybrids; the male flowers being sterile. This fact is, however, neither mentioned by any other author nor borne out by the results of the crosses at Buitenzorg where also cassava hybrids were used as the male parent.

The results of crosses with *M. glaziovii* (Ceara rubber) are in accordance with the data given by both Koch (1934) and Nichols (1947). Koch (1934) mentions a fair amount of fruit-setting in free pollinated F_1 hybrids, but after some weeks most of the developed fruits dropped off. Doughty *et al.* (1955) report very low seed set with glaz. — cassava hybrids when selfed and also when backcrossed with the cassava parents. Much better seed production, however, was noted when they were intercrossed. These data are not in accordance with the findings at Buitenzorg.

From our experiences at Buitenzorg it can be concluded that the first backcross hybrids can be useful for practical growing.

Abraham (1957) made thousands of pollinations with Ceara rubber as female parent without any success. With cassava as the female parent, however, he got 1% success. This is entirely in accordance with our findings.

Comparison of the results of crosses with *M. saxicola* at Buitenzorg with those of Nichols (1947) in Tanzania is not possible due to the great sensitivity of this species to cassava mosaic. He made only a few crosses and left his F_1 hybrids to pollinate freely among themselves.

Jennings (1959) crossed cassava with *Manihot melanobasis* and found the hybrid to be very fertile but the mean number of seeds recovered per fruit was rather low. Crosses of his F_1 hybrids with *M. glaziovii* gave better results. According to Koch (1934) crosses of cassava with *M. dichotoma* were entirely unsuccessful. Nichols (1947), however, records success in both ways, but his F_1 hybrids proved to be entirely sterile.

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CONCLUSIONS.

1. Crosses of cassava cultivars show largely different results. At Buitenzorg

only a few cultivars proved to give fairly good results when used as parents in hybridisation work. When based on the right cultivars a percentage of success of at least 20% may be expected.

2. Some cultivars proved to be very bad parents, in crosses hardly any or no seeds were harvested. In how far this is due to incompatibility has yet to be proved.
3. Cassava can be crossed with several other species of *Manihot*. The percentage of successful pollinations, however, is generally very low. Moderate good success of these interspecific hybridisations is only to be expected if cassava is used as the female parent.
4. F₁ hybrids between cassava and *M. glaziovii* show a high rate of sterility when intercrossed. Backcrossing of the hybrids with the cassava parent gave fairly good results provided a good cassava cultivar is used which gave also success in cassava crosses.
5. Crosses of cassava with *M. saxicola* gave a high percentage of successful pollinations which makes it doubtful whether *M. saxicola* should be considered as a separate species. Backcrossing of the hybrids with a cassava parent gave exceptionally good results when in the original interspecific cross *M. saxicola* is used as the female parent.
6. It is proved by two authors that hybrids containing the "blood" of three species can be obtained.
7. In the majority of crosses the mean number of seeds per fruit was rather small. Further investigation as to the nature of this phenomenon are worthy of recommendation.

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