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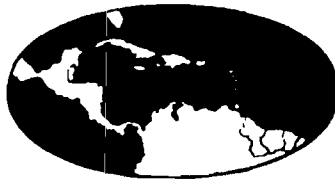
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## MECHANISMS RESTRICTING SEED SET IN THE SWEET POTATO

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### INTRODUCTION

Improvement through breeding of the sweet potato is hampered by poor seed production following open or controlled self- or cross-pollination. Part of the poor fertility is due to self-incompatibility (7), but sterility has also been ascribed to chromosomal mechanisms (8) and to "unbalanced gametes" (1). Fungal disease of the pollen itself may also lead to sterility (4). In the case of strong incompatibilities, failure of pollen germination appears to be the principal incompatibility mechanism (9). But the presence of partial or intermediate incompatibilities, and the fact that full seed set in the sweet potato is rare suggest that other mechanisms are operating also. These mechanisms have been suggested to be parent-controlled differences in capacity for growth on the part of pollen tubes, and of growth stimulation by the stigma (9). Our observations that an abundance of pollen can germinate on the stigma, even in poorly-fertile crosses led us to investigate post-pollination barriers to seed production, the results of which are reported herein.

### MATERIALS AND METHODS

The sweet potato varieties used were a series of 19 seedlings selected from breeding plots of their abundant flowering. A large number of controlled crosses were made among the seedlings by Dr. Alfred Jones, Tifton, Georgia. We continued crossing these seedlings, but harvested stigmas and/or styles 5 hours after pollination for observations of pollen germination and tube growth, using a fluorescent technique (5). Germination counts were based on 5 pollinated stigmas and styles per combination. Clones were classified into incompatibility groups on the basis of their crossing relationships. Crosses illustrating the various types of behavior were selected for detailed analysis.

The course of anthesis, stigma receptivity, and abscission was observed in emasculated flowers without pollination, or with compatible

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or incompatible pollinations were made with a flat-bladed needle washed in alcohol and dried after each combination. The efficiency of this technique was determined by pollen counts of stigmas crushed in acetocarmine a few hours after pollination. We studied the rate of germination and growth of pollen by harvesting pistils at varying times after pollination, and observing length of pollen tubes. After determining the time necessary for pollen tubes to traverse the style, certain crossing relationships including cases of unilateral and weak incompatibility were studied in detail.

## RESULTS

### Crossing relationships

Among 142 crosses based on 5 pollinations or more, 39 were completely incompatible. Percentage of flowers setting fruit in the remainder varied from less than one to 94. The distribution of crossing results are given in Table 1 for both capsule and seed set data. The curves of the two fertility estimates are similar in shape. High fertility in capsule or seed setting rarely occurred, and most crosses could be characterized as only partially compatible. These distributions are similar to those obtained by other authors (3).

Percentage Class	Number of plants per class	
	Fruit Set	Seed Set
0.0	38	39
0.1 - 6.0	20	47
6.1 -12.0	19	18
12.1 -18.0	13	17
18.1 -24.0	6	7
24.1 -30.0	7	7
30.1 -36.0	5	3
36.1 -42.0	6	2
42.1 -48.0	5	1
48.1 -54.0	5	0
54.1 -60.0	5	0
60.1 -66.0	5	0
66.1 -72.0	1	0
72.1 +	7	0

The 19 clones fell into at least 4 groups with respect to crossability (Table 1). Varieties of group I, II, and III were intra-incompatible, whereas varieties of groups IV were intrafertile. The crossing relationships among the groups can be summarized as follows (arrows point from male to female).

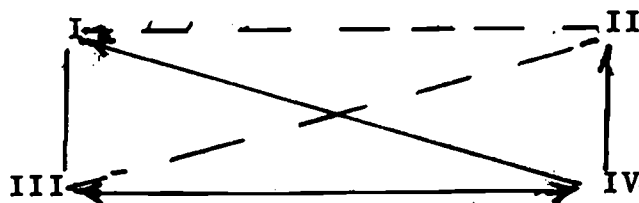


TABLE 3

Relation of number of pollen tubes to time after pollination and to portion of pistil in some fairly fertile crosses

Hour after pollination	Portion of pistil	Number of pollen tubes							
		Crossing combination and group							
1		193 x 94 I x II	94 x 100 IV x III	85 x 93 III x II	99 x 101 III x I	89 x 94 III x IV	101 x 85 I x III		
	Stigma	4	1.5	10	5	25+	16		
	Style	0	0	0	0	0	0		
	Ovary	0	0	0	0	0	0		
2		17	5	16	15	25+	25+		
	Stigma	2	0.7	0	2	2	3		
	Style	0	0	0	0	0	0		
	Ovary								
4		25+	22	13	17	25+	25+		
	Stigma	4	2.5	0	2.5	2	8		
	Style	1.5	0	0	1	1	3		
	Ovary								
8		25+	14	17	13	25+	25+		
	Stigma	5	4	2	4	4	8		
	Style	4	4	2	1.5	2	4		
	Ovary								

As indicated in Table 1, there were a number of exceptions to this classification. Nevertheless, we were not able to classify these clones by any more satisfactory scheme. The continuous distribution of partial fertilities makes a more exact classification difficult. The existence of similarities in crossing behavior between certain parents is striking, and suggests the operation of a relatively few genes affecting the major incompatibility relationships.

A basic question concerns whether or not parents act similarly in reciprocal combinations. Comparison of 60 reciprocal crosses by correlation showed that both capsule set and seed set were correlated ( $r$  for capsule set = 0.01;  $r$  for seed set = 0.52,  $p$  0.01) in reciprocal crosses. Nevertheless, clear-cut reciprocal differences occurred between Groups I and IV, and in other isolated instances.

The use of two methods of measuring fertility in Table 2 might be questioned. In crossing combinations from which both types of data were obtained, there is a strong indication that both methods give similar results (Table 2). Inspections of stigmas may be accomplished rapidly, the same day as pollinations, if desired, and promises to be a useful technique in the rapid assessment of incompatibilities.

#### Duration of stigma and style

Numerous authors (2) have previously demonstrated that the sweet potato flower opens during early morning hours, and is highly receptive to pollination for several hours thereafter. Our concern was whether the stigma and style remained in reasonable condition long enough to permit pollen tubes to fully penetrate them. Therefore, times of color change (browning of stigma; yellowing of style) and of abscission were noted. Whether pollinated or not stigmas remained fresh-looking for 8 to 12 hours. If exposed to rain or intense sunlight, stigmas turned brown no sooner than 6 hours after anthesis. Stigmas were abscised from 16 to 24 hours after anthesis. On the other hand, styles remained fresh in appearance up to 72 hours after anthesis. If pollinated in a compatible fashion they began to wither at that time, but if not, they were abscised with the flower by 96 hours after anthesis.

#### Efficiency of pollination

The average number of pollen grains placed on a stigma by the usual technique was 36.0 ( $s = 16.3$   $\bar{C}$  ; range = 12-71).

#### Pollen germination and pollen-tube growth

Pollen germination begins within a few minutes after compatible pollination, and by one hour a small percentage of grains are firmly attached to the stigma by pollen tubes (Table 3). But grains continue to germinate up to 3 or 4 hours after pollination. The stigmatic

TABLE 2

Relation between pollen germination on the stigma and capsule and seed setting in controlled crosses

Type of behavior	Stigma observed		Combinations observed	
	Number		Number	
No germination	37		19	
Weak germination	41		16	
Good germination	20		5	

Capsule and seed set					
Pollinations		Capsule set		Seed Set	
Number	Number	Percent	Number	Percent	
470	38	8.1	49	2.6	
416	61	14.6	90	5.4	
116	37	31.8	53	11.8	

TABLE 1

A division of 19 clones of sweet potatoes into 4 compatibility groups, and their crossing relationships 1/

	Group I				Group II				Group III				Group IV						
	87	91	105	101	86	93	97	110	96	98	92	95	89	100	85	88	99	90	94
Group I	87	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	91	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	105	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	101	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	86	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	93	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Group II	97	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	110	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	96	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	98	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Group III	92	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	95	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	89	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	100	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	85	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	88	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	99	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Group IV	90	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	94	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

1 = incompatible (capsule set 10 percent or less; 0-1 tubes per stigma)  
W = weak fertility (capsule set 10-20 percent; 2-4 tubes per stigma)  
F = fertile (capsule set 30 percent; 5 or more tubes per stigma)



tissue is transversed in about an hour, so that by 2 hours after pollination some pollen tubes may be seen in the style. Four hours after pollination pollen tubes may be detected entering the ovary, and by 8 hours after pollination pollen tube growth is essentially complete. Further increases were not detected after 16 and 24 hours. Characteristically, large number of pollen grains germinate on the stigma. We have seen as many as 50 tubes in stigmatic tissue. Yet only a fraction of these tubes penetrate the style. Once having penetrated the style, the tubes appear to grow into the ovary without further interruption. Pollen tube growth is slower in some combinations (for example, 95 x 93) than in others, but in all fertile crosses so tested, pollen tubes grew the length of the style within 8 hours. The differences between number of pollen tubes in stigma and in style were significant for all combinations, and at all but the earliest hours. These results suggest that neither abortion of stigma nor style could reduce fertility, but that pollen tube growth between stigma and style is restricted.

In contrast to the fairly fertile crosses above, weakly compatible crosses were characterized by either reduced pollen germination or reduced penetration of tubes into the style and ovary (Table 4). In the case of incompatible crosses, germination was reduced to zero or nearly so. All comparisons were made 8 hours after pollination.

TABLE 4

Germination of pollen and growth of pollen tubes  
in weakly compatible and incompatible crosses

Combination	Groups	Compatibility	Number of tubes in		
			Stigma	Style	Ovary
85 x 101	III x I	Weak	6.25	1.50	1.25
85 x 98	III x II	Weak	3.25	.75	.50
101 x 100	I x III	Weak	25	7.50	1.00
100 x 93	II <sub>1</sub> x I	Weak	25	3.00	0.
94 x 101	III x I	Incompatible	1.50	1.00	.25
85 x 98	III x II	Incompatible	0	0	0
93 x 101	I x I	Incompatible	0	0	0
100 x 98	III x II	Incompatible	0	0	0

Thus in both fertile and partially fertile crosses there is a suggestion that not all pollen tubes in the style enter the ovary, but tubes were frequently obscured or difficult to trace in ovarian tissue. Tubes in the ovary were often mishapen or of corkscrew

appearance. We did not observe the tubes entering the micropile, and our technique appears to be inadequate for that purpose.

Restriction of pollen-tube penetrance in the ovary was also suggested in the case of 3 unilaterally incompatible crossing combinations (Table 5). In each, the reciprocal cross showed fairly normal behavior.

TABLE 5

Differences in pollen tube penetrance between reciprocal crosses of three different combinations

Combination:	Group	:Stigmas : Numbers of tubes in			:Compatibility :(fruit set)
		:observed:	Stigma	Style Ovary	
94 x 87	IV x I	14	8	5 0	I
87 x 94	I x IV	14	56	27 24	F
99 x 93	III x I	6	31	15 0	I
93 x 99	I x III	6	34	16 12	F
85 x 87	III x I	6	27	3 0	I
87 x 85	I x III	6	90	25 10	F

#### Embryo abortion

A further possible post pollination barrier to seed production in sweet potato may be abortion of the young embryo. However, we have not completed a study of this alternative. At this particular point, it appears that such abortion does not take place.

#### Morphology of the stigma and style

One approach that we have used in attempts to determine the nature of post pollination barriers has been to study the morphology of stigma and style. The stigma has a roughly spherical form, but below the dissecting microscope one can see that the spherical body is actually composed of numerous cylindrical branches. These branches in turn are covered by dumbbell-shaped papillae of single cells. Below this specialized epidermis is a barrier, perhaps only thickened cell walls. The papillae contrast with the internal, parenchymatous cells of the stigma branch in being richly supplied with particles.

At the time of pollination, the individual grains of pollen come in intimate contact with the papillae of the stigma. At that point, the incompatibility reaction must take place as an interaction of substances diffusing from pollen or stigma, or both, for pollen germination fails entirely. This inhibitory process may be either strong,

resulting in complete failure of germination, or weak, resulting in germination of some few pollen grains. As only one stigma, presumably with only one strength of reaction, participates in any single pollination, germination of some pollen grains and failure of others on the same stigma must be associated with differences in the pollen grains themselves. Thus the stigmatic surface may be conceived of as the site of the primary incompatibility reaction, and constitutes a region where certain pollen grains are accepted, and may develop tubes into the stigma while certain others are rejected.

Within the stigma, the parenchyma is quite uniform except for the occurrence of xylem and phloem. Pollen tubes pass freely through this tissue. My observations have been that tubes pass between rather than within cells.

The style is a long cylinder tapering from ovary to stigma, composed of several distinct tissue layers. These include a cutinized epidermis, and a cortex of parenchymas and collenchyma. Two vascular bundles run through this tissue. Finally, in the center of the style is a column of long, very narrow cells through which the pollen grains must travel during their trip to the ovary. The junction between the small-diameter cells of the style and the larger cells of the stigma is quite abrupt, suggesting to me that the failure of pollen tubes to pass from stigma to style is in part a mechanical problem. However, the possibility of a second physiological reaction inhibiting pollen tube growth must not be ruled out. Once in the style, however, pollen tubes evidently have a uniform road to the ovary.

Finally, we have not yet succeeded in tracing the exact path of pollen tubes from the style to the ovule, but we believe that the principal barriers to pollen tube growth do not occur at that point.

#### DISCUSSION AND CONCLUSION

In conclusion, the sweet potato presents a complex picture of sterilities and incompatibilities. The wide range of fertility values encountered in typical crosses decreases the ease of analysis of the system of incompatibility, and increases the quantity of data needed and the opportunities for misclassification. The incompatibility classification scheme presented herein must therefore be thought of as tentative. Nevertheless, in its essential features it resembles crossing relationships previously found (6). In contrast to fruit-set data, observations of stigma and style may resolve incompatibilities into their component parts, inhibition of pollen germination, and inhibition of pollen tube growth between stigma and style. The fact that the two types of inhibition did not always occur together suggests that they are controlled by separate systems. Inhibition of germination, the principal incompatibility mechanism, must be controlled by a powerful physiological system working at the level of pollen and stigma surface. It should be possible to resolve the nature of this control by histochemical, enzymatic, and immunochemical studies.

On other hand, the more widespread inhibition of pollen tubes between stigma and style could be due to a variety of mechanisms such as: mechanical barriers to pollen tube penetration; weak chemotropic guidance of tubes; or failure of tube growth of weak or unbalanced gametes. The possible existence of other mechanisms operating in the ovary itself must not be overlooked, but embryo abortion does not appear to be one of such mechanisms. Among the problems that remain, two would seem to be nearer resolution. Analysis of the incompatibility system might be possible if decisions are based on pollen germinability alone. Such observations would have to be followed by controlled crosses and analysis of progeny. The second problem, prediction of crossabilities between selected varieties, has now been simplified. Observations of pollen germination on the stigma and the growth in the style should permit ready identification of strong and intermediate incompatibilities. But very weak compatibilities can only be measured with actual fruit-setting trials.

The presence of barriers to seed set other than self-incompatibility is not too surprising. The existence of partial homologies between chromosomes of the separate genomes constituting the sweet potato genome and the inevitable duplication of genic functions must inevitably lead to inharmonious combinations in some gametes. Nevertheless, the stigma and style constitute a strong screening mechanism whereby the stronger gametophytes can and do compete successfully with those of lesser strength. The fact that full seed set is so rare in sweet potato suggests to us that the concept of unbalanced gametes is not a complete explanation of the post-germination barriers to seed set. The significance of the stigma-style barrier, and its relation to the self-incompatibility system must still be worked out, and to do so we are using self-incompatible diploid relatives of the sweet potato.

#### SUMMARY

Sweet potato crosses are characterized by a variable level of sterility, whereas full fertility is rare. Sterility has been ascribed to self-incompatibility, chromosomal aberrations, and inviable gametes. We are studying barriers to seed set among 19 seedlings selected for abundant flowering. Fruit and seed set among these seedlings are distributed in a curve resembling the right-hand half of a normal curve with mode at zero. The 19 seedlings can be divided into 4 incompatibility groups, but numerous exceptions occur to any grouping. Even in fertile crosses between groups, seed-setting is restricted to about 50 percent of full potential. Examinations of stigmas and styles after pollination reveal that inhibition of pollen germination is the physiological mechanism of incompatibility. Most of the exceptions to the classification scheme were due to pseudocompatibility (weak self- and cross-incompatibility). However, among fertile crosses other barriers were found. The chief of these is failure of pollen tubes to pass from stigma to style. Once in the style, tube growth is not inhibited. A second inhibition may occur when the tubes pass from style to ovary or ovule. Finally, embryo abortion is suspected to reduce seed-set in some cases. The interplay

of these barriers, and of self- and cross-incompatibility is sufficient to explain the variable seed-set observed. Incompatibilities and sterilities reduce the efficiency of plant breeding efforts. They can be partially avoided by open pollination among lines selected for desirable characteristics. The potentialities of various breeding and improvement systems were discussed.

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#### CONTROL OF PAPAYA BUNCHY TOP VIRUS DISEASE IN JAMAICA

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The first official record of a virus disease affecting papaya, Carica papayae was informed by F. E. V. Smith in Jamaica in 1928. (4). He reported that a large number of plants around Kingston were affected and from then until the present, virus diseases have been the predominant limiting factor to the successful growing of papaya in Jamaica and some of the other Caribbean islands.