THE STERILITY-INCOMPATIBILITY COMPLEX OF THE SWEET POTATO

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Sex has been well- established as the almost universal method of reproduction among animals and plants. The sexual process has many advantages to the species, chief of which is that it results in a constant reassortment of the genetic material, thus giving rise to new combinations which may have superior value. But the sexual process is complicated and demands a high order of control of physiological processes, and exact timing of events. The genetic information must be systematically halved, and the two halves from different parents intimately re-united. The newly formed individual must then be nurtured to a state of independence from either parent. Because the process is complex, it may be disrupted in numerous ways. Capricious external forces, inner physiological disturbances, or inadequate information from the genes themselves may interrupt any of the long series of steps in the normal reproductive process, reducing the potential number of progeny. We call this result sterility, but sterility is but an end product. In animals and plants, the study of sterility producing systems may not only be fascinating, but has numerous practical ramifications in everyday life.

It is interesting and noteworthy that plants in contrast to animals, usually have the two sexes in one individual, very often within a single flower. Thus, mating of identical male and female may occur, which restricts exchange of the genetic material, and leads successively to a more homogenous and uniform progeny. In such cases the advantage of sex may be lost. It is not surprising, therefore, that various physiological processes have developed in flowering plants to impede the process of self-fertilization or increase the likelihood of crossing. Some of these mechanisms are self-evident. For example, bright-coloured, odorous flowers attract insects which inadvertently carry pollen and affect fertilization. In some cases, parts of one sex mature before the corresponding parts of the other, thus leaving an interval when crossing can occur but not selfing. A series of related processes in which self-fertilization or seed production is impeded by internal physiological systems are grouped under the name self-incompatibility.

It is important to distinguish here between self-incompatibility and sterility. In the case of self-incompatibility, all sexual processes are normal. Viable gametes are produced. But gametes from the same or genetically distinct plants, may function perfectly. Thus, the plant is not sterile *per se,* except in matings to itself Therefore, self-incompatibility has sometimes been called self-sterility. The distinction between sterility and incompatibility is of particular importance when one begins to study poor fruit or seed set in specific plants. Fortunately for the geneticist, these processes usually occur separately, and thus can be studied independently.

But when sterility and incompatibility occur in the same species, separating and understanding the various systems may indeed be a puzzle. Now so far I have talked as if sterility were the exact opposite of fertility, and self-incompatibility the exact opposite of self-compatibility. Thus, I might have given the impression that these two kinds of behaviour are each expressed in only two ways. But in reality, all sorts of intermediate behaviours occur, which we might call partial sterility or partial self-incompatibility. I have the good fortune of presenting to you today some data and some opinions concerning a plant that demonstrates very well the complexities of both kinds of behaviour, the sweet potato.

The sweet potato ranks third in importance among vegetables in the United States. It is now widely distributed through both temperate and tropical areas. Although discovered by the first Europeans in the Caribbean, some studies suggest that the sweet potato was well distributed by man throughout the Pacific, at a still earlier date. Because the sweet potato is fleshy and herbaceous, its remains have not been well preserved among archaeological relics. Storability of the tubers and the ease of propagation from the stems have contributed to the sweet potato's popularity before and now.

What kind of a plant is the sweet potato? When the geneticist asks this question he is really asking, "What kind of a breeding system does it have, in contrast to other plants ?" The sweet potato is a hexaploid with 90 chromosomes. In contrast, all but a few species of *Ipomoea* have 30 chromosomes. The chromosomal behavior of the sweet potato is normal, but some secondary pairing during meiosis suggests that similarity exists between the different pairs of chromosomes. It is probable that the sweet potato is the result of hybridization of two *Ipomoea* species followed by chromosomal doubling.

The flower of the sweet potato is pinkish and attractive. It readily draws insects, especially honey bees. But propagation by cutting is the usual practice. There is some suggestion that even the more primitive sweet potato varieties are highly selected. Progeny of superior varieties include large numbers of off-types, including those with only small storage roots, and twining, climbing habit. Very little of the genetics of the species is known.

In order to overcome disease susceptibilities, considerable work has been expended to breed and improve the sweet potato, and such efforts continue. The usual method has been to cross-pollinate varieties having characteristics desired in a single variety, and to select among the progeny for the desired type. New varieties are released after much elimination during years of testing. Thus, each variety represents something carefully screened and chosen as the almost ultimate expression of the desired characteristics. Two problems have impeded breeding efforts. One of these is the reluctance of varieties to flower under temperate zone conditions. This problem can be avoided to some extent by various flower-inducing procedures. The second problem has been the occurrence of relatively low levels of seed set after both self- and cross-pollination. And, of course, that problem is the one we are concerned with today.

Let us take a look at some fertility measurements of the sweet potato. Ultimately, fertility must be considered the ability to produce offspring, seed. If we take a large number of sweet potato crosses made under ideal conditions, and classify the crosses by number of seed per pollination, we obtain a hyperbolic distribution (Table I). From the table it is evident that the vast majority of the crosses set few seeds. It is also evident that very few crosses set even 50 per cent of the available ovules. If we examine another measure of fertility, fruit per pollination, we see a similar curve. Now what do these two curves mean ? What do they tell us about the breeding system of the plant? They say that the normal situation is reduced seed set, or partial sterility. Why not incompatibility? A brief discussion will show why this curve is produced primarily by sterility systems and only secondarily by incompatibility.

Table 1. Distribution of fruit and seed set in crosses of the sweet potato

Percentage Class	Number of examples 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

In the simplest possible case of self incompatibility when only two self-incompatible, inter-compatible types exist, half of the crosses would be fertile and half would be incompatible (Table 2). By adding another plant the number becomes 2/3 fertile and 1/3 incompatible. Similarly, each newly added incompatibility type increases the percentage of fertile and decreases the percentage of incompatible matings.

Table 2.—Percentage of compatible matings as compared to number of compatibility groups.

Incompatibility Number of groups	*Kind of Number of matings**	*Incompatibility Number of matings*	*Fertile Percentage matings*
2	4	2	50
3	9	3	67
5	25	5	80
10	931	10	99

* Including self-pollinations.

Note: These figures are based on the assumption that the groups are represented by equal numbers in the population.

In the case of systems in which fertile crosses are very highly fertile, and incompatible crosses are very incompatible, fertility would follow bimodal distributions. In perfect systems the two modes would be represented by straight lines. In actual practice, genes of minor effect usually widen out the curves without destroying the bimodality. But the fertility curves of the sweet potato are not bimodal. Instead, they suggest that the plant is partially sterile, and that self-incompatibility plays a minor role in the fruit setting picture. Nevertheless, there are reasons to believe that self-incompatibility is also important.

Up to the present time, investigators have tried to explain the poor fruit and seed set of sweet potato on the basis of self-incompatibility. The technique for studying incompatibility is simplicity itself. One takes a number of plants, 20 will do for a start, and crosses them in all combinations. On the basis of fruit and seed set, the crosses are divided into 2 kinds, fertile and incompatible. One then compares the plants to each other and decides which plants act alike. He tries to divide the plants into groups that are incompatible in crosses within the groups but fertile in crosses between groups. This is an old and fruitful technique, usually successful, and our present understanding of self-incompatibility has rested on the fact that one can usually judge between fertile and incompatibility classes, and that one can classify plants with similar behaviour. But this is only the first step. To understand the genetic control of incompatibility one must make crosses among selected cross-fertile individuals, test the compatibilities of parents and offspring, make further back-crosses and second generation crosses, and finally draw up an explanatory model of gene number and gene action. To understand the physiological control one must study pollen behaviour in fertile and incompatible matings, during the process of germination, tube growth, fertilization, and sometimes also the processes of ovule and embryo development. In the sweet potato, not all these steps have been systematically followed.

Now, when one has a fertility distribution such as one sees in sweet potato, how can one classify plants into groups ? In reality all the crosses are sterile or partially sterile. I believe the answer is that sweet potato data have been squeezed and juggled to fit preconceived models of the incompatibility system, and discrepancies have been overlooked or discounted. But it is worth our time, I believe, to see how others have dealt with these problems.

The Japanese geneticist Terao (1934) was the first to attempt to classify sweet potatoes into incompatibility groups. His classification was simple and straightforward, 51 varieties classified into 3 intra-incompatible, and inter-compatible groups. This system was expanded to include a 4th group by Nishiyama (1961) and later by Shinjo (1962). Finally, Fujise (1964) broadened the number of varieties classified and ended up with 8 groups. Hernandez and Miller (1964), and Wang (1964) followed the system in classifying American varieties into 6 groups. Van Schreven, on the other hand, classified her varieties into 6 groups but the groups had some very different crossing relationships. Some of her crosses did not fall into strictly intra-incompatible and inter-compatible classes. Without exception, the published results of these investigators show internal discrepancies, such as fertility where incompatibility was expected, and incompatibility where fertility was expected. It must also be realized that judgment of fertility versus incompatibility was always made on a subjective basis. It could only be done in that fashion, for in all studies fruit and seed were distributed similarly.

I think the best evidence for the existence of a system of self-incompatibility in sweet potato is that similarities among varieties do exist, and these do make classification possible. But the incompatibility relationships are masked by a more powerful and generally-occurring sterility system.

Before leaving the subject of incompatibility classification, I would like to discuss the only attempts to my knowledge to study incompatibility in the sweet potato in the progeny of controlled crosses. As I have pointed out, without such crosses it is impossible to test models of genetic control of the behaviour. Van Schreven (1953) crossed two varieties of sweet potato, and compared the offspring to the parents (Table 3). She found 4 incompatibility groups among the offspring, two of which were like the parents and 2 of which were entirely different. It is interesting to note that the pattern of crosses found by Van Schreven almost duplicates the pattern of classification found in her varieties. Evidently, Van Schreven did not notice these resemblances, for she did not mention them, nor did she test the progeny against non-parental varieties.

Table 3.—Crossabilities of sweet potato varieties, and a family of seedlings (Van Schreven, 1953)

Varieties as females	Varieties as males				
	I and II	III	IV	V	VI
I and II	Some Fertile	Yes	Yes	Yes	Yes
III	Yes	No	No	No	Yes
IV	Yes	No	No	Yes	Yes
V	Yes	No	Yes	No	Yes
VI	Yes	Yes	Yes	Yes	No

Seedlings as females	Seedlings as males			
	A	B	C	D
A	No	No	No	Yes
B	No	No	Yes	Yes
C	No	Yes	No	Yes
D	Yes	Yes	Yes	No

I have constructed a simple genetic model to explain these results. The model depends on principals of gene action known to occur in other incompatibility systems. It suggests that incompatibility is controlled by two pairs of genes, of the so-called *Primula* type. Each dominant gene is epistatic to the recessive allele of the other. Or to express the system more clearly, each type of plant is incompatible with plants of the same genotype. In addition, the cross-compatibility or incompatibility between plants is determined by the dominant genes present. All crosses are fertile except those that have even one dominant gene in common.

Unfortunately, this model cannot be tested, for Van Schreven did not carry the studies through another generation.

A second attempt to classify the incompatibilities of progeny from controlled crosses was made by Fujise (1964). Working with the groups first delimited in Japan, he classified for incompatibility the progeny from crosses among the A, B and C types (Table 4). This table indicates the 3 kinds of crosses and the kinds of progeny actually obtained from each cross. You will immediately note that some crosses are within incompatibility groups where successful crossing would not be expected. But as I explained, in sweet potato the incompatibilities are seldom absolute, so that by making lots of pollinations eventually some seeds can be obtained in most crosses. Fujise's model to explain these results is extremely complicated and will not be fully explained here. The model assumed 3 loci, each with 2 or 3 alleles. The epistatic relations vary among the alleles, and some alleles only reduce or weaken the incompatibility. I am certain that this hypothesis will not hold up, especially as a more conservative hypothesis can be developed.

Table 4.—Progeny of crosses among A, B, and C varieties, according to Fujise

Parents	Type of Cross	Possible Progeny
A x A	Pseudo compatible	A, B, C
B x B	”	B, C
C x C	”	C
A x B	Compatible	A, B, C
A x C	”	A, B, C
B x A	”	A, B, C
B x C	”	B, C
C x A	”	A, B, C
C x B	”	B, C

My model to explain Fujise's data is presented in the next table (5). This model has the advantage that it is based on only 2 genes of 2 alleles each. Weakened self-incompatibility is assumed to be due to other independent genes not a part of the specificity control system. The model depends upon a single epistatic action of one dominant gene *T*, over the other, *S*. Only when *T* is represented by its recessive allele does the *S* gene function. The model agrees with what we know about incompatibility in other plants. It is conservative and explanatory. Unfortunately, as in the case of the model designed to explain Van Schreven's data, no second generation or backcross data are available and thus the model cannot be tested. Finally, I would like to say that no model proposed can be easily extended to include other incompatibility groups. But I am not presently worried about such conflicts. I think we have not yet classified incompatibilities accurately enough to be sure of relationships. When we can be sure of relationships, we can construct models to explain the data, and then we can test them.

Table 5. A model that can explain Fujise's results

Parental combinations and possible genotypes	Genotypes and Classifications of possible progeny
A (Tt --) and A (Tt --)	A (Tt –), B (tt S-), C(tt ss)
B (tt S -) and B (tt S -)	B (tt S-), C (tt ss)
C (tt ss) and C (tt ss)	C (tt ss)
A (Tt --) and B (tt S-)	A (Tt –), B (tt S-), C(tt ss)
A (Tt --) and C (tt ss)	A (Tt –), B (tt S-), C(tt ss)
B (tt S -) and C (tt ss)	B (tt S-), C (tt ss)

Now I must confess that so far I have not told you much about my own work. I have proceeded on the assumption that the poor seed-setting behaviour of sweet potato is due to both sterility and incompatibility, and that one system cannot be worked out without also considering the other. So I have taken a completely different approach. Although we are crossing sweet potatoes, and trying to classify varieties, our principal objective has been to see what happens after pollination occurs. Thus, we have used various fixing and staining techniques in order to allow us to trace the pathway of the pollen through the female tissue.

These studies have revealed a great deal to us. Before I tell you what we found I need to tell you something about the structure of the pistil. The female organ is so normal or typical in structure that it could actually serve as a model for flowering plants in general. The floral parts are the stigma, the style and the ovary.

The stigma consists of two adjacent spherical bodies, each about 1 mm. in diameter, mounted on a slender tapering style, 0.4 — 1.2 mm. in diameter and 10 to 25 millimeters long. Each spherical lobe actually consists of 50 to 75 radiating branches from a central core. The branches are covered with papilionaceous cells, and the cells exude a sticky substance. In our trials, pollen grains adhered to the surface of the stigma by mechanical entrapment among the branches of the stigma, and by surface tension of the viscous exudate.

The main body of the stigma is composed of large, spherical or ovoid cells arranged in columns radiating from the stigma-style juncture to the branches. Branches completely cover the tissue core. Each consists of 25-75 files of parenchymatous cells which appear to be continuous with the files in the body of the stigma, and these in turn are continuous with the files of cells in the central core of the style.

In favourable transverse sections files of cells may be traced from stigma branches, through the stigma body, to the central core of the style. However, the cells of the style core are much smaller in diameter than the cells of the stigma. Thus, the stigma-style junction is characterized by a series of intergrading cell sizes where the files of cells from the branches pass to the style. Rough counts of cell numbers in stigma versus style suggest that in addition to increased cell size, more files of cells occur in the stigma than in the style.

The boundary between the parenchymatous cells of the stigma, and the papillae of the epidermis is strongly defined by heavier cell walls.

The epidermis of the stigma is composed entirely of dumbell-shaped papilionaceous cells. These cells are large (60-110 microns in length), and typically consist of a definite base, a constricted region, a broadened region, and a narrow nipple. The nucleus is usually in the broadened portion of the papilla. A distinctive feature of these cells is the presence of numerous spherical particles. Larger particles (4-6 microns in diameter) are often grouped around the nucleus whereas smaller particles are dispersed through the cytoplasm. Haematoxylin staining suggests that larger particles are plastids, whereas the smaller particles may be mitochondria. In contrast, the parenchymatous cells are not so rich in particles.

The central part of the style consists of a pollen tube conducting tissue of long, narrow cells. This column of cells is of uniform size throughout the length of the style. The surface of the style is covered with a uniform epidermis. Between the epidermis and the conducting tissue is a layer of collenchyma which tapers in thickness from the style-ovary junction to the junction of stigma and style. Two bundles of xylem and phloem are imbedded in the collenchyma.

The juncture of the style and ovary can only be traced satisfactorily through serial sections. As the style enters the ovary, it becomes continuous with the septum dividing the two locules of the capsule. The central core of conducting tissue begins to spread laterally at the base of the septum, and is widest at the point of juncture with the ovules. Each ovule is attached to the placenta by a short funicular strip, which also delimits the micropyle. Part of the tissue of the funicular strip appears similar to and is continuous with the pollen tube conductive tissue, of the style. This cell type can be traced from the style to funiculus, to base of the ovule, through the integument of the ovule, upwards and over the upper part of the ovary, and down again to the region of the egg.

Upon germination, the tubes pass through the cuticle, between cells of the epidermis, through the region of thickened cell walls, and between the cells of the parenchyma, crushing cells to the side as they pass through. Old pollen tubes in the stigma are completely filled with callose. As the tubes pass into the style, they are confined to the central core of conducting tissue. The passage of 5 to 10 tubes through this tissue results in an obliteration of cell outlines, possibly through enzymatic breakdown of cell walls, and also by lateral pressure from the tube itself. The amount of callose within the tube varies from little or none, to irregular masses or complete plugs. Pollen tubes are not necessarily circular in cross section. Evidently the first tubes to pass through the style are crushed or distorted by the passage of later tubes.

Within the ovary, the tubes follow the circuitous path of the conducting tissue.

We are now in a position to talk about what happens after pollination. Togari (1942) observed some years ago that pollen fails to germinate on the stigma of the sweet potato after self-pollination. It has been assumed since then that the physiological basis for self-and cross-incompatibilty in the sweet potato is pollen germination failure. Togari used these observations in a re-classification of the Japanese self-incompatibility groups and came up with essentially the same results as Terao, namely that Japanese varieties could be divided into 3 intra-incompatible, inter-compatible groups. His final analysis showed almost complete pollen germination failure after self-or after within-group cross-pollinations. But problems were encountered in the crosses between groups. To use his words, "Even in the compatible crosses there exist remarkable variations in regard to the percentage of pollen germination as well as the growing velocity of pollen tube." To explain this behaviour, Togari postulated other properties directly related to the incompatibility group. These assumptions are that the germinability and growing rate of the pollen tubes were controlled by the same genotype as that which gave group specificity, and that the three groups differed with respect to the strength of these processes. He also postulated that the groups differed in the strength of the stimulus to germination provided by the style. I think all investigators would agree that the physiological system of incompatibility depends on pollen germination failure. Likewise, it is certain that pollen germination is restricted even in fertile matings. But Togari's conclusions with respect to group differences have not proved accurate and in later studies have been discounted. I think the problem here is that pollen germination failure is due in some cases to sterility rather than incompatibility. I shall come back to this point when I try to draw up a new theory for the poor fruit set of the sweet potato.

We have looked at thousands of sweet potato styles and have counted the number of pollen grains on the stigma, the number of tubes in the stigma, and the number of tubes in the style. These counts serve as fertility indices, and we can graph their distribution in the same manner that we graphed the distribution of fruit and seed setting data (Table 6). It is very interesting to see that the curves representing distribution of tubes per stigma and tubes per style not only have the same shape, but their shape is exactly the same as those of fruit and seed set distribution. Just as we concluded that lack of bimodality of fruit and seed setting distribution curves represented sterility instead of incompatibility, we must now admit that these two new indices are also indices of sterility. What I am saying is that failure of pollen to germinate is one of the characteristics of sterility in the sweet potato. This does not contradict the hypothesis that the mechanism of self-incompatibility is also pollen tube failure. But any particular example of pollen germination failure cannot arbitrarily be considered as due to incompatibility, for sterility of varying degrees will always be present.

Table 6. Distribution in numbers of pollen tubes in stigma and in style after crossing

Pollen tubes in stigma Tubes per stigma	Number of crosses	*Pollen tubes in style* Tubes per style	Number of crosses
0.0	72	0.0	111
0.01 — 3.0	100	0.01 — 0.40	70
3.1 — 6.0	54	0.41 — 0.80	45
6.1 — 9.0	44	0.81 — 1.20	39
9.1 — 12.0	27	1.21 — 1.60	44
12.1 — 15.0	12	1.61 — 2.00	16
15.1 — 18.0	11	2.01 — 2.40	4
18.1 — 21.0	7	2.41 — 2.80	3
21.1 — 24.0	2	2.81 — 3.20	0
24.1 +	3	3.21 +	2

But what about after pollen germination? What happens next? I have already described the pollen tube pathway through the stigma, style and ovary. Because we had reason to believe that some seedless crosses were nevertheless characterized by excellent pollen germination, we made a study in which the pollen tubes in the stigma, and in upper, mid, and lower style were counted and compared to the number of seed actually set in the fruit. This study was very rewarding (Table 7). It can be seen from the table that in both a fairly fertile cross, A, and a fairly infertile cross, B, that there is a drastic reduction of numbers in pollen tubes between stigma and style. Within the style there is no statistical difference in number of tubes in the various regions. But in both crosses many more pollen tubes are found in the style than seeds are produced in the ovary. We have seldom seen pollen tubes in the ovary, but I believe some pollen tube elimination does take place between style and ovule. Thus, from these data and many, many other observations of hundreds of crosses I am forced to conclude that the reproductive potentiality of sweet potato is limited by reduction in number of pollen tubes between stigma and style, and between style and ovule.

Table 7. Pollen tube growth and fruit set in two sweet potato crosses

Cross	Pollinations	*Pollen Tubes* Stigma	Upper style	Mid style	Lower style	% capsule Set	Seeds per pollination
A	42	19.6	6.1	5.7	5.0	42.8	0.86
B	94	16.1	0.92	0.74	0.61	6.4	0.10

Yet some tubes do find their way to ovules and some seeds are set, but fertilization does not finish the story. Sweet potato fruits seldom contain more than one seed, but if one determines from a series of pollinations and subsequent fruit set data the probability that a single ovule is set, one can then determine the expected frequency of occurrence of fruits of 2, 3 or 4 seeds. This we have done, and we find that seed set is at random, with a low probability at best that any particular ovule grows to be a seed. What happens to the rest of the ovules? To determine this we have observed the development of ovules in the ovary and found two distinct developmental rates. Some ovules enlarge only a small amount, while others grow rapidly. These differences result in the production of two kinds of products at maturity, which I believe, came from unfertilized ovules, and seeds. The distribution of weights of ovule products from a good number of fruits from which all 4 products were obtained is given in the next table (8). You can clearly see that two kinds of products are produced, with absolutely no overlap. When one tries to germinate the seed, one finds that smaller seed do not germinate well, and in fact, there is a rather strong line of demarcation between the 50 per cent of the seeds that germinate and the 50 per cent that do not. I interpret these data to mean that most ovules are not fertilized, and of those that are, only about half produce embryos sufficiently viable to germinate. Herein one sees two more signs of sterility.

Table 8.—Distribution of sizes of mature seed and aborted ovules of sweet potato, with respect to germination

Weight of seed or ovule (mg.)			Number of examples	Percentage germinated
0.0	—	0.5	329*	0.0
1.1		1.5	15	0.0
1.6		3.0	17	0.0
3.1		7.0	12	0.0
7.1		11.0	17	11.7
11.1		15.0	34	29.6
15.1		19.0	35	68.6
19.1		23.0	40	97.5
23.1		27.0	16	100.0
27.1		31.0	5	100.0

* The average weight of these scales was about 0.02 mg.

But sterility does not stop at that point. We have grown sweet potato populations and find that as many as 10 per cent of the plants are small, weak, spindly, and ready to die. These we do not plant in the field. In field plantings, we find that perhaps another 10 per cent of the plants are weak, unproductive, easily killed or crowded out.

I think now I can synthesize the sterility story for you (Table 9).

Table 9. Characteristics of sterility in sweet potato.

1. Some pollen germination failure.
2. Disorientation and failure of some pollen tubes to pass from stigma to style.

3. Disorientation and failure of some pollen tubes to pass from style to ovule.
4. Production of some poor seed.
5. Production of some poor plants.

The cause of the sterility problem lies in the nature of the sweet potato itself. It is a hexaploid with 90 chromosomes. Although chromosomes pair normally, considerable secondary association occurs, indicating that partial homology exists among the genomes constituting the sweet potato. Thus gametes may not always carry a well balanced set of chromosomal material. Poor germination of seeds and weakness of seedlings are probably due to such imbalances. Although much more difficult to document, it is highly probable that a large portion of gametes produced by any sweet potato variety are weak or imbalanced. Such weakness could be expressed during critical growth phases of the pollen tube.

In the path of the pollen tube are three critical areas. The first is the surface of the stigma, and many pollen grains fail to pass this obstacle even in fertile matings. The second obstacle is the stigma-style juncture where the pollen tube pathway is suddenly and drastically restricted. A change in pollen-tube physiology probably occurs at this point. The third obstacle is the style-ovary juncture where the pollen tube pathway becomes irregular and less well-defined. We venture the hypothesis that the sterility barriers of the sweet potato are no more than the sites or processes where weak or inadequate gametes are eliminated. Elimination may occur for mechanical or physiological reasons either before or after pollination or fertilization. We also hypothesize that these weaknesses are general in occurrence, multigenic in control, and can only be corrected by a long period of mass selection for fertility.

I think now that we understand a little better the sterility, that we shall soon be able to put together a unified theory of the incompatibility. Some of the facts and suppositions are summarized in Table 10. We are interested in and working with both the genetic and physiological aspects of this problem. From the genetic point of view we have three programmes in progress. The first programme is a study of self-incompatibility in a diploid species of *Ipomoea*. This species was selected from 11 self-incompatible species found in a survey of the family Convolvulaceae. Because of its diploid status and high fertility, we expect to find a simple system of incompatibility not masked by sterility. We have completed 3 generations, and expect to finish the job with confirming generations in 1967-68. We have already made some interesting progress, and can predict that the analysis of this system will help us understand and interpret the system in the sweet potato.

Table 10.—Some characteristics of the self-incompatibility of the sweet potato

Characteristic	*In sweet potato*
Floral morphology	—Homomorphous
Site of inhibition	—Stigma
Nuclei of pollen	—Two or three ?
Pollen cytokinesis	—Simultaneous
Loci involved	—Two or three ?
Alleles per locus	—Two or more ?
Site of control	—Sporophyte
Number of groups	—Low (4-8)
Gene action, pollen	—Dominance & epistasis ?
Gene action, stigma	—Dominance & epistasis ?

A second study is of the incompatibility groups in 28 varieties we have collected. We have crossed these in as many combinations as possible, and have developed statistical indices of the degrees of resemblance among them. With these data we expect to eliminate a good part of the human errors of judgment. The analysis should be finished this spring or summer. We have progressed far enough to recognize another of the basic reasons for poor fruit set in North America. It is simply that most varieties belong to the same incompatibility group.

The third genetic study concerns the control of self-incompatibility in the sweet potato itself. For the study we have selected as parents some clones with rather strong self-incompatibility, but better than average cross-fertility. The back-cross generations are now in the field waiting for our tests, and we will try to complete the analysis in 1967-68. With the completion of these 3 programmes, I think we shall have the essential facts concerning genetics of the phenomenon.

But questions regarding the physiological control remain. The specialized structure of the papillae of the stigma is suggestive of the role these cells must play in the incompatibility reaction. Exudate on the stigma comes from the papillae, and this could be rich in enzvmes or inhibitors. We do not yet know whether sweet potato pollen has the ability to grow on stigmas in general, is actively inhibited from growing on some, or whether the pollen lacks the ability to grow on its own stigmas unless it is stimulated. I believe we can get useful information on this subject by a series of experimental pollinations including such treatments as double pollinations, transfers of pollen from one stigma to another, mutilation of the stigma, collection of stigmatic exudates on agar, etc. We would also like to examine the enzymes of the stigma histochemically, if possible. Especially, we would like to know if the stigma has a cutin and the pollen a cutinase system. These are characteristic of all other incompatibility systems in which pollen fails to penetrate the stigma. Preliminary tests suggest that the incompatibility of sweet potato does not depend on a cutin-cutinase system, and thus may be unique.

A final task that we would like to be able to do is to use serological techniques to actually discriminate between different incompatibility substances. With such techniques we could identify incompatibility groups without the necessity of cross pollinations. A visionary task, perhaps, but something that has recently been done successfully at Cornell with the family Cruciferae.

To conclude, I would like to say that untangling the relationships of incompatibility and sterility in sweet potato has been a fascinating pastime. The sweet potato has proved to be an excellent example of an imperfect species, a species in which evolution has not yet straightened out the reproductive processes and in which sex is thus only a second-best method of reproduction.

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