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THEORETICAL AND APPLIED GENETICS

Genetic Analysis of Incompatibility in the Diploid *Ipomoea* Species Closely Related to the Sweet Potato

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Summary. In order to identify the genotypic constitutions of incompatibility in the diploid species, *Ipomoea leucantha* Jacq. (K221), which is most closely related to the sweet potato, the progenies derived from the reciprocal crosses, backcrosses and testcrosses were analysed. All the plants examined were self-incompatible, and pollen germination was inhibited on the stigma after incompatible pollinations. No reciprocal differences were found in the incompatibility reactions. In the progenies three incompatibility groups were observed which showed the rather simple segregation ratios. The homozygous plants for incompatibility alleles were obtained in the progenies. The experimental results demonstrated a sporophytic type of incompatibility controlled by a single locus with multiple S-alleles exhibiting a dominance relationship in both the pollen and the stigma. The plants obtained in the progenies had the following genotypes: S_1S_2, S_1S_3, S_2S_2, S_2S_3 and S_3S_3.

Key words: *Ipomoea* – Sporophytic incompatibility – Genetic analysis – *S*-alleles – Sweet potato

Introduction

Since Terao (1934) first pointed out the presence of three intra-incompatible, intercompatible groups in cultivated varieties of the sweet potato, *Ipomoea batatas* (L.) Lam., a large number of varieties and seedlings have been classified into several incompatibility groups by many workers (Togari and Kawahara 1942; Shigemura 1943; Van Schreven 1953; Shinjo and Omura 1962; Fujise 1964; Hernandez and Miller 1964; Wang 1964; Martin and Cabanillas 1968). The genetic analysis of incompatibility in the sweet potato has not yielded consistent results among investigators. Fujise (1964) postulated that the genetical system of incompatibility was sporophytically controlled at three loci, each with two alleles exhibiting dominance and epistasis. Martin (1965, 1968) explained Fujise's experimental results in a simpler way, in which two loci with multiple alleles were assumed. He also interpreted the results of Van Schreven (1953) as a sporophytic control of the incompatibility at two loci or at one locus with multiple alleles. These inconsistent explanations of the incompatibility in the sweet potato can principally be explained by the nature of the hexaploidy, which complicates a genetical analysis and also results in more or less sterility of gametes. Furthermore, the mode of interactions of incompatibility genes in a polyploid state has not been clarified as yet in the genus *Ipomoea*.

A few self-incompatible diploid species have been reported in the section *Batatas* of the genus *Ipomoea*, and it has been suggested that the sweet potato could have developed from one of them (Nishiyama 1961; Jones and Deonier 1965; Wedderburn 1967; Martin 1970; Martin and Jones 1972). Martin (1968) gave the interpretation that the incompatibility system in the diploid species, *I. setifera* Poir., is a sporophytic type at one locus with multiple alleles. However, the *I. setifera* is not taxonomically classified as a species in the section *Batatas*, but in the section *Pharbitis* (Jones 1968; Austin 1975). Nishiyama et al. (1975) and Teramura (1979) suggested that three species in the section *Batatas*, viz., *I. leucantha* Jacq. (2×), *I. littoralis* Blume (4×) and *I. trifida* (H.B.K.) Don. (6×), were probable progenitors of the sweet potato, and that these wild species and the sweet potato were grouped in a series of autoploidy with the B genome of *I. leucantha*. The diploid species, *I. leucantha* (Accession number K221) was collected in Acapulco, Mexico and in 1961 was introduced into the Kyushu Agricultural Experiment Station (KAES), Japan for utilization of wild relatives in sweet potato breeding. Thereafter, this species was recognized to be self-incompatible and occasionally was hybridized

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with varieties of the sweet potato (Miyazaki and Kobayashi 1976). In addition, three different incompatibility groups (designated L_A, L_B and L_C) were also found in the species and one of them (L_C) was common to the incompatibility group (C) of the sweet potato (Miyazaki and Sakamoto 1974).

As the first step for elucidating the genetical and physiological mechanisms of incompatibility in the sweet potato, it is important to analyse the genetical system of incompatibility in the diploid species closely related to the sweet potato. The present study was carried out to identify the genotypic constitutions of the diploid species, *I. leucantha* (K221) on the incompatibility and to obtain plants with various genotypes on this character.

Materials and methods

The materials used in the present study were three plants, K221-A, K221-B and K221-C, each of which was chosen, respectively, from different incompatibility groups, L_A, L_B and L_C of *Ipomoea leucantha* Jacq. (K221) (Miyazaki and Sakamoto 1974). These plants were received in July 1976 from KAES. Reciprocal crosses (F_1) between K221-A and K221-B, and backcrosses (BCF_1) and testcrosses (TCF_1) of the F_1 hybrids were made in 1976, 1977 and 1979, respectively, after emasculation to avoid casual selfing. In order to stimulate the formation of flower buds, all the plants were grown in pots and received short day treatment (10 hours light period) for about two weeks after four weeks from planting. The three plants mentioned above were also used for the classification of progeny plants into the different incompatibility groups.

Determination of the incompatibility groups of the progeny was made in the following manner: Prior to anthesis, mature buds were removed from plants each afternoon. Those to be used as female were emasculated and placed in petri dishes with water-agar medium at 23°C from the evening to the next morning. Buds to be used as pollen sources were put in small vials with water. Pollination was made in the morning between 8 and 10 a.m. by transferring pollen grains to the stigma. The pollinated flowers were left in the petri dishes at 28°C for 5 to 6 hours after pollination to stimulate pollen germination, and then the stigmas were excised and stained on slide glass with a drop of lactolphenol cotton blue. For each pollen-stigma combination, 5 to 6 stigmas were prepared as replicates. After one or more days, success or failure of pollen germination on the stigma was observed under a microscope. Failure of pollen germination on the stigma may have occurred not only from incompatible pollination, but also from pollen sterility. To distinguish them, pollen fertilities of all the plants used in pollinations were estimated from the stainability of pollen with lactolphenol cotton blue.

Table 1. Incompatibility relationships among the three plants used in the study

♀ \ ♂	K221-A	K221-B	K221-C
K221-A	–	+	+
K221-B	+	–	+
K221-C	+	+	–

+ = compatible; – = incompatible

Results

Reciprocal Crosses and Segregation of the Incompatibility Groups in the F_1 Progeny

The three plants, K221-A, K221-B and K221-C were confirmed to be self-incompatible and reciprocally cross-compatible with each other, as shown in Table 1. Pollen fertilities of the three plants, K221-A, K221-B and K221-C were 89.1 ± 6.5%, 92.6 ± 8.3% and 80.2 ± 11.5%, respectively. Seed set percentages amounted to 70-80% in the reciprocal crosses between K221-A and K221-B. F_1 progenies derived from the crosses K221-A × K221-B and K221-B × K221-A were raised in 1977 and designated strain number L10 and L11, respectively. Eighty plants of L10 and 93 plants of L11 were all self-incompatible and had fairly high pollen fertilities, i.e. 76.9 ± 16.0% on the average. Table 2 shows the incompatibility reactions of

Table 2. Incompatibility reactions of some F_1 plants to the three plants, K221-A, -B and -C

Strain -plant no.	Cross combination	Selfing	Crossing with the three plants						Incompatibility group determined
			as male			as female			
			K221-A	K221-B	K221-C	K221-A	K221-B	K221-C	
L10-74	K221-A × K221-B	–	–	+	+	–	+	+	L_A
L10-78	"	–	+	–	+	+	–	+	L_B
L10-13	"	–	+	+	–	+	+	–	L_C
L11-68	K221-B × K221-A	–	–	+	+	–	+	+	L_A
L11-54	"	–	+	–	+	+	–	+	L_B
L11-86	"	–	+	+	–	+	+	–	L_C

+ = compatible; – = incompatible

Table 3. Segregation of the F_1 hybrids between K221-A and -B into three incompatibility groups

Strain no.	Cross combination	Number of plants observed	Segregants of each incompatibility group			P value in X^2-test[a]
			L_A	L_B	L_C	
L10	K221-A × K221-B	80	35	24	21	0.3 – 0.5
L11	K221-B × K221-A	93	38	22	33	0.05 – 0.1
Total		173	73	46	64	0.05 – 0.1

[a] X^2-test for expected ratio of 2:1:1, based on the assumption described in 'Discussion'

some F_1 plants to the three plants representing the three incompatibility groups. This result indicates that reciprocal pollinations with the three plants whether as male or female gave the same results. From these compatibility relationships, it was determined that the plants, for example, L10-74, L10-78 and L10-13 belonged to L_A, L_B and L_C groups of incompatibility, respectively. In this manner, all the F_1 plants of strains L10 and L11 were divided into the three incompatibility groups as shown in Table 3. Observed segregation ratios of the plants belonging to the three incompatibility groups (L_A: L_B: L_C) were 35:24:21 in strain L10, and 38:22:33 in strain L11. These segregation ratios showed no significant differences from the expected ratio of 2:1:1 in X^2-test, which based on the assumption described in the following discussion. The reciprocal crosses between two parents gave the similar segregation ratios.

Backcrosses of the F_1 Hybrids and Segregation of the Incompatibility Groups in the BCF_1 Progeny

The plants with high pollen fertility, i.e., L10-74, L10-78 and L10-13, were selected as the representatives from each of three different incompatibility groups, L_A, L_B and L_C, respectively, and backcrossed with their parental plants. The progenies from the backcrosses, L10-74 × K221-B, L10-78 × K221-A, L10-13 × K221-A and L10-13 × K221-B were raised in 1978 and designated strain number L12, L13, L14 and L15, respectively (Table 4). All these BCF_1 plants were pollen fertile (the average fertility amounting to 80-90%), and were self-incompatible. The segregation of incompatibility groups was observed separately in each BCF_1 progeny as shown in Table 4. Even though two BCF_1 strains L12 and L13, were produced from the phenotypically same parental cross-combinations, i.e. between L_A and L_B groups, strain L12 produced L_A and L_B type plants with a segregation ratio of 44:48 (nearly 1:1), while strain L13 segregated L_A, L_B and L_C type plants with a ratio, 31:12:10 (P-value in the X^2-test for a ratio of 2:1:1 was 0.3-0.5, based on the assumption described in 'Discussion'). The progenies of strain L14 and L15 were divided into the same incompatibility groups as the parents in the backcrosses; that is, strain L14 from the cross, L_C × L_A produced L_A and L_C type plants, and strain L15 from L_C × L_B gave L_B and L_C type plants, with a segregation ratio of 1:1 in both strains.

Testcrosses of the BCF_1 Hybrids and Segregation of the TCF_1 Progeny into Three Incompatibility Groups

Out of 92 plants of strain L12 belonging to either the L_A or L_B group, 10 representative plants in each group were chosen and crossed with a plant, L14-37, of L_C group in strain L14. The progenies obtained from the crosses of L14-37 with L_A and L_B type plants of strain L12 were designated L16 to L25, and L26 to L35, respectively

Table 4. Segregation of the backcrossed progenies into three incompatibility groups

Strain no.	Cross combination	Number of plants observed	Segregants of each incompatibility group			P value in X^2-test[b]
			L_A	L_B	L_C	
L12	L10-74(L_A) × K221-B(L_B)[a]	92	44	48	0	0.5 – 0,7[c]
L13	L10-78(L_B) × K221-A(L_A)	53	31	12	10	0.3 – 0.5[d]
L14	L10-13(L_C) × K221-A(L_A)	60	30	0	30	1.0[c]
L15	L10-13(L_C) × K221-B(L_B)	60	0	29	31	0.99 – 1.0[c]

[a] Incompatibility group of the parental plants is shown in parentheses

[b] c and d represent P-values tested against 1:1 and 2:1:1 ratio, respectively, based on the assumptions described in 'Discussion'

Table 5. Segregation of the testcrossed progenies into three incompatibility groups

Strain no.	Cross combination	Number of plants observed	Segregants of each incompatibility group		
			L_A	L_B	L_C
L16	L14-37(L_C) × L12-64(L_A)[a]	7	3	4	0
L21	" × L12-74(L_A)	7	3	4	0
L23	" × L12-79(L_A)	7	3	4	0
L24	" × L12-82(L_A)	7	1	6	0
L25	" × L12-85(L_A)	7	4	3	0
L17	" × L12-65(L_A)	7	5	0	2
L18	" × L12-66(L_A)	7	3	0	4
L19	" × L12-70(L_A)	7	4	0	3
L20	" × L12-71(L_A)	7	4	0	3
L22	" × L12-76(L_A)	7	4	0	3
L27	" × L12-61(L_B)	7	0	4	3
L29	" × L12-63(L_B)	7	0	3	4
L30	" × L12-67(L_B)	7	0	2	5
L31	" × L12-69(L_B)	7	0	4	3
L32	" × L12-72(L_B)	7	0	3	4
L33	" × L12-73(L_B)	7	0	6	1
L26	" × L12-60(L_B)	7	0	7	0
L28	" × L12-62(L_B)	7	0	7	0
L34	" × L12-75(L_B)	7	0	7	0
L35	" × L12-77(L_B)	7	0	7	0

[a] Incompatibility group of the parental plants is shown in parentheses

(Table 5). The segregations of three incompatibility groups in these strains were investigated with 7 plants for each strain. The results obtained are shown in Table 5. Among the strains derived from the test-crosses between a L_C plant (L14-37) and L_A plants of L12, 5 strains (L16, L21, L23, L24 and L25) segregated L_A and L_B type offspring, and other 5 strains (L17, L18, L19, L20 and L22) gave L_A and L_C type plants. Consequently, the ratio of the strains segregating L_A and L_B to those segregating L_A and L_C, was 5:5. Among the strains derived from the testcrosses of a L_C plant (L14-37) with L_B plants of L12, 6 strains (L27, L29, L30, L31, L32 and L33) segregated L_B and L_C type offspring, and 4 strains (L26, L28, L34 and L35) gave only L_B type plants, suggesting that the parental plants of these four strains are homozygous at the incompatibility locus. Then the ratio of strains segregating L_B and L_C to those producing L_B was 6:4.

Discussion

The lengths of the stamens and of the style are frequently different among the plants used in the present study. It is also true in sweet potato varieties (Van Schreven 1953). However, the incompatibility reaction could not be associated with their lengths (Van Schreven 1953; Fujise 1964). These facts suggest that *Ipomoea* species show homomorphic incompatibility, as pointed out by Martin (1965). The characteristics of the incompatibility system found in the present study are as follows: 1) All the plants tested were self-incompatible; 2) Pollen germination was inhibited on the stigma after incompatible pollinations; 3) Pollinations in reciprocal directions gave rise to no difference in the incompatibility reactions; 4) Plants incompatible with one of the parents and those belonging to different incompatibility groups were segregated in the F_1 and BCF_1 generations; and 5) The progenies in F_1, BCF_1 and TCF_1 showed simple segregation ratios of different incompatibility groups, and the occurrence of homozygous plants for incompatibility alleles (S-alleles)

Table 6. Incompatibility relationships among the five genotypes identified in the present investigation

♀ \ ♂		S_1S_2 (L_A)	S_1S_3 (L_A)	S_2S_2 (L_B)	S_2S_3 (L_B)	S_3S_3 (L_C)
S_1S_2	(L_A)	–	–	+	+	+
S_1S_3	(L_A)	–	–	+	+	+
S_2S_2	(L_B)	+	+	–	–	+
S_2S_3	(L_B)	+	+	–	–	+
S_3S_3	(L_C)	+	+	+	+	–

+ = compatible; – = incompatible; ( ) = Phenotype of the incompatibility

was suggested. All these features can not be explained by a gametophytic system of the incompatibility, but can lead to the interpretation that the genetical system of the incompatibility in the present materials is sporophytically controlled at one locus with multiple alleles. The second characteristic of the system mentioned above coincides with the general rule that the stigmatic surface is the site of incompatibility reactions in plants with sporophytic control of incompatibility, with a few exceptions (Brewbaker 1957). The third characteristic suggests that S-alleles hold the same interallelic relationship in the pollen as in the stigma, because reciprocal differences of incompatibility reactions might be resulted if the action of S-alleles in the pollen is different from that in the stigma and if the alleles express interallelic relationships of independence, interaction or mutual weakening in either the pollen or the stigma.

Considering the results mentioned above, the following assumptions can be made to identify the genotypic constitutions on the incompatibility of the progenies from the various crosses:

1. The incompatibility is under control of the multiple alleles belonging to a single locus.
2. Phenotype of the pollen is sporophytically determined.
3. The *S*-alleles, which are designated by S_1, S_2, S_3 and S_4, are in a regular, sequential dominance order of $S_1 > S_2 > S_3 > S_4$ in both the pollen and the stigma. These alleles determine in their homozygosity incompatibility groups, L_A, L_B, L_C and L_D, respectively, in both the pollen and the stigma.

Under these assumptions, the genotype of each parental plant is considered to be one of the followings; S_1S_1, S_1S_2, S_1S_3 or S_1S_4 for K221-A, and S_2S_2, S_2S_3 or S_2S_4 for K221-B. Of all the possible cross-combinations among these genotypes, only three cross-combinations, i.e., $S_1S_3 \times S_2S_3$, $S_1S_3 \times S_2S_4$ and $S_1S_4 \times S_2S_3$, agree with the results obtained in the F_1 generation (i.e., with the strains L10 and L11), in which the three incompatibility groups (L_A, L_B and L_C) were observed. If the parental cross-combination, K221-A × K221-B, were $S_1S_3 \times S_2S_4$ or $S_1S_4 \times S_2S_3$, then L_D group (S_4S_4) could be observed in the BCF_1 progeny (either strain L14 or L15). From the results presented in Table 4, the possibility of the two parental cross-combinations, $S_1S_3 \times S_2S_4$ and $S_1S_4 \times S_2S_3$ could be rejected. Therefore, the S_4 allele was not present in the parental plants and thus the parental genotypes are determined to be S_1S_3 for K221-A, and S_2S_3 for K221-B. From these genotypes, the F_1 progenies of the reciprocal crosses between them are expected to segregate L_A, L_B and L_C type plants into a ratio of 2:1:1; the results of the strains L10 and L11 confirmed it (Table 3). Consequently, the genotype of L10-78 (L_B group) and that of L10-13 (L_C group) should be S_2S_3 and S_3S_3, respectively. The L_A group in the F_1 progeny includes two genotypes, S_1S_2 and S_1S_3. The former genotype is represented by a plant L10-74 as strain L12, obtained from the backcross, L10-74 × K221-B (S_2S_3), segregated L_A and L_B type plants into a 1:1 ratio. The segregation ratios obtained in the four BCF_1 progenies (strains L12 to L15) agreed precisely with those expected from the genotypes deduced above (Table 4).

Strain L12, which segregated phenotypically into L_A and L_B type plants, is expected to consist of four kinds of genotypes; S_1S_2 and S_1S_3 for L_A group, and S_2S_2 and S_2S_3 for L_B group. On the other hand, the plant L14-37 (L_C), used as the female in testcrosses, has the genotype S_3S_3 since strain L14, derived from the backcross L10-13 (S_3S_3) × K221-A (S_1S_3), segregated L_A (S_1S_3) and L_C (S_3S_3) type plants into a 1:1 ratio. Segregation data presented in Table 5 on the incompatibility groups of 20 strains, L16 to L35, derived from the testcrosses of L12 progeny with L14-37 (S_3S_3), confirmed the followings: Five parental plants, L12-64, -74, -79, -82 and -85 all had the genotype S_1S_2 since they segregated L_A and L_B type plants into a 1:1 ratio in the testcross; five plants, L12-65, -66, -70, -71 and -76, which segregated L_A and L_C type plants into a 1:1 ratio in the testcross, had the genotype S_1S_3; six plants, L12-61, -63, -67, -69, -72 and -73, which segregated L_B and L_C type plants into a 1:1 ratio in the testcross, had S_2S_3; and the remaining four plants, L12-60, -62, -75 and -77 were homozygous for S_2-allele. The observed ratio, 5:5:4:6 for four genotypes, S_1S_2, S_1S_3, S_2S_2 and S_2S_3 in strain L12, coincides with the expected ratio, 1:1:1:1. Accordingly, five different incompatibility genotypes, S_1S_2, S_1S_3, S_2S_2, S_2S_3 and S_3S_3, were identified, in which two were homozygous for *S*-alleles. Incompatibility reactions among these genotypes are summarized in Table 6.

The segregation data obtained in all the progenies of the F_1, BCF_1 and TCF_1 generations, supported the assumption that the incompatibility in *I. leucantha* (K221) is sporophytically determined by multiple alleles in a single locus. This type of incompatibility has been reported in Compositae (Gerstel 1950; Hughes and Babcock 1950; Crowe 1954), Cruciferae (Bateman 1954, 1955; Sampson 1957, 1964; Odland 1962) and other families (Knight and Rogers 1955; Thompson 1979). The present results support the suggestion made by Martin (1968) that the incompatibility of Convolvulaceae is of the same type as mentioned above.

Relationships of dominance, independence or competition between S-alleles in pollen and/or style have been reported in the species of the above-mentioned families. Three S-alleles identified in the present materials exhibited a simple dominance relationship in both the pollen and stigma. However, four other incompatibility groups (L_D to L_G) besides the three studied here have been found in *I. leucantha* strains collected at other locations in Mexico (Ko-

wyama, unpublished data), and this species widely distributes throughout tropical America and the Pacific islands (Austin 1978). Therefore, it is expected that additional *S*-alleles and, accordingly, other types of the interallelic relationships would be found in the future.

Ipomoea species in the section *Batatas* have received considerable attentions in the phylogenetical study with a special reference to the origin of the sweet potato. The interspecific relationships between the sweet potato and the wild relatives have been discussed from morphological, cytogenetical and taxonomical points of view (Ting et al. 1957; Sharma and Datta 1958; Jones and Deonier 1965; Magoon et al. 1970; Martin et al. 1974; Nishiyama et al. 1975; Austin 1977; Teramura 1979). A comparative investigation on the distribution of *S*-alleles in both wild *Ipomoea* species and the sweet potato will shed a new light on the origin of the latter. The plants of whose genotypes were identified in the present investigation, will be useful for such a study and for physiological studies on the incompatibility in the genus *Ipomoea*.

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