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INCOMPATIBILITY STUDIES IN OENOTHERA*

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The complex-heterozygotes of the subgenus *Euoenothera* which occur throughout North America can be classified into five phylogenetic groups on the basis of their cytogenetical and morphological characteristics. In one of these, the *biennis* group 1, a gametophytic incompatibility system has been demonstrated (STEINER 1956, 1957). It is of interest to know whether such an incompatibility mechanism is also present in the other phylogenetic groups. Because these differ in certain details from the *biennis* group 1, the method used to demonstrate incompatibility alleles in the *biennis* 1 forms is not practical for the other groups. During the course of an earlier study dealing with this problem (STEINER 1961) an improved method for the detection of incompatibility alleles in complex-heterozygotes was devised. This method, which also gives information regarding the identity of the alleles in different races, was tested using relatively few races. The present paper reports the results of an analysis which has been extended to a number of additional strains of complex-heterozygotes.

The term "complex-heterozygote" describes the specialized cytogenetic mechanism exemplified by many *oenotheras*. A complex-heterozygote possesses two genomes or "complexes", each composed of seven chromosomes. The two sets of chromosomes differ completely in the arrangement of their end segments. As a result, at meiosis a circle of fourteen chromosomes is formed and because the adjacent chromosomes in the circle regularly go to opposite poles, each complex remains intact in the meiotic products. Thus only two kinds of gametes occur. Because these plants are naturally self-pollinated, one would expect to find among the offspring homozygotes of each complex as well as heterozygotes like the parent. A balanced lethal system, however, prevents the occurrence of the homozygous combinations.

The two complexes which make up such a structural heterozygote differ in (1) the segmental arrangement of their chromosomes, (2) the phenotype which each produces, and (3) the frequency with which each is transmitted through the egg or through the pollen. The complex which in a series of outcrosses is more often transmitted through the egg than through the pollen is called the alpha complex. The complex which is predominantly transmitted through the pollen is known as the beta.

If it is present in a race, the incompatibility allele (S_I) is found in the alpha complex. At the homologous locus of the beta complex a self-compatibility

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allele (S_C) occurs. In self-pollinations the pollen carrying the alpha complex does not grow because the same incompatibility allele is present in the stigmatic and stylar tissue. Pollen carrying the beta complex, on the other hand, develops normally. The incompatibility allele is, in a restricted sense, a type of pollen lethal, and prevents the occurrence of alpha·alpha homozygotes among the offspring from self-pollination of a complex-heterozygote.

Materials and Methods

The races used in this investigation are listed in Table 1 according to the phylogenetic group to which they belong. For particulars concerning most of these forms, see CLELAND (1958). The characteristics of the races, *Ashland D*, *eriensis*, *Whartoniae* and *York Springs* have not as yet been fully analyzed.

Each race was crossed as the female parent to a synthetic *biennis* group I hybrid, alpha *Hot Springs*·beta *Camp Peary L*. The latter is a complex-heterozygote which almost without

Table 1. *Races used in the current study*

<i>Biennis 1</i>	<i>Strigosa</i>
Mifflintown	Forsberg
Whartoniae	Granger
York Springs	Heber
<i>Biennis 2</i>	Minturn
Ashland D	Monett
Buck Creek	North Colorado
Elma V	Springs
Routhierville	Iowa II
Shulliana	<i>Parviflora</i>
Tonawanda I	angustissima
Tonawanda II	Iron Mountain
<i>Unclassified</i>	Manistique
Camas	muricata
eriensis	Nobska

exception transmits the alpha *Hot Springs* complex through the pollen rather than the beta *Camp Peary L* which is normally a pollen complex. A series of hybrids was produced in which each hybrid carried the alpha complex of a different race in combination with alpha *Hot Springs*. Alpha *Hot Springs* is known to possess an incompatibility allele. If the alpha complex with which alpha *Hot Springs* is combined also carries an incompatibility allele, the hybrid should be self-incompatible.

Hybrids which proved to be self-compatible were interpreted as carrying a self-compatible allele in the alpha complex derived from the race parent and were not tested further.

In those hybrids which were self-incompatible, the self-incompatibility could result not only from the presence of an incompatibility

allele in the complex under study, but also from the occurrence of a pollen lethal. "Pollen lethal" is here taken in the broad sense to describe a genetic factor which prevents the germination or development of the pollen which carries it, regardless of the genetic constitution of the stigma upon which it is placed.

In order to distinguish between these alternative explanations, the cross-compatibility relationships between all self-incompatible hybrids were determined. If the pollen of a particular hybrid failed to develop when placed upon the stigma of all the remaining hybrids, the presence of a pollen lethal is suggested. On the other hand, if the pollen proved to be compatible with at least one of the other hybrids, the self-incompatibility of the pollen parent must result from the action of an incompatibility allele.

The crosses between the various hybrids having alpha *Hot Springs* in common should also reveal, in those cases where incompatibility alleles are present in the complexes associated with alpha *Hot Springs*, which of these carry identical alleles. If, however, a complex bears a pollen lethal, there is no way of determining from such crosses whether an incompatibility allele is also present but its effect masked by the lethal.

Both self- and cross-compatibility were tested by determining pollen tube growth. Flowers were emasculated and the styles allowed to mature on the plant. When the stigmas were receptive, the emasculated flowers were removed and placed in vials of water. The stigmas were pollinated and the flowers incubated at 28°C for six to ten hours. The styles were then fixed and processed as previously described (STEINER 1956). With this technique the pollen tubes are readily recognized by the deeply stained, spindle-shaped starch grains which they contain.

Because the self-incompatibility of these hybrids could be explained in some cases by the action of pollen lethals, it seemed desirable to determine the percentages of normal-appearing pollen grains produced by each hybrid. Pollen grains were mounted in IKI-lactic acid. The appearance of pollen from a structural homozygote (*hookeri* race) was used as the criterion for normal. No attempts were made to correlate the appearance of the various types of pollen grains with their ability to germinate and grow.

Results

Only two of the hybrid combinations, alpha *Minturn*·alpha *Hot Springs* and alpha *Heber*·alpha *Hot Springs*, proved to be self-compatible. All other combinations were self-incompatible; these are listed in Table 2. This table also shows

Table 2. Cross-compatibility between alpha-alphas having alpha *Hot Springs* in common

alpha <i>Hot Springs</i> with alpha of:	chrsmc config.	Whartoniae	York Springs	Iowa II	Angustissima	Mifflintown	Shulliana	Ashland D	Monett	Manistique	Muricata	Iron Mountain	Eriensis	Buck Creek	Routherville	North Col. Springs	Granger	Nobska	Camas	Forsberg	Elma V	Tonawanda I	Tonawanda II	
Whartoniae	7prs.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
York Springs	04,04,3prs.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Iowa II	08,04,1pr.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Angustissima	010,2prs.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Mifflintown	7prs.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Shulliana	08,3prs.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Ashland D	08,04,1pr.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Monett	010,2prs.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Manistique	014.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Muricata	010,2prs.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Iron Mountain	06,04,04.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Eriensis	014.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Buck Creek	010,2prs.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Routherville	012,1pr.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
North Col. Springs	08,04,1pr.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Granger	012,1pr.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Nobska	undeter.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Camas	08,04,1pr.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Forsberg	08,04,1pr.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Elma V	010,2prs.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Tonawanda I	010,2prs.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗
Tonawanda II	010,2prs.	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗

the compatibility relationships between the alpha complexes of the various races. The hybrids are grouped into three classes:

1. Hybrids whose pollen develops in the styles of all others tested. (Those carrying the alpha complexes of *Whartoniae*, *York Springs*, and *Iowa II*.)

2. Hybrids whose pollen develops in the styles of certain of the hybrids and not in those of others (Those bearing the alpha complexes of *angustissima*, *Mifflintown*, *Shulliana*, *Ashland D*, *Monett*, *Manistique*, *muricata*, *Iron Mountain*, *eriensis*, *Buck Creek*.)

3. Hybrids whose pollen fails to grow in the styles of all others tested (Those carrying the alpha complexes of *Routhierville*, *North Colorado Springs*, *Granger*, *Nobska*, *Camas*, *Forsberg*, *Elma V*, *Tonawanda I*, and *Tonawanda II*.)

Table 3. Percentages of normal pollen produced by alpha·alpha hybrids

alpha <i>Hot Springs</i> with alpha	% of normal pollen	total no. of grains counted
<i>angustissima</i>	22.8	2714
<i>Ashland D</i>	27.1	3913
<i>Buck Creek</i>	40.1	2401
<i>Cama</i>	27.0	2441
<i>Elma V</i>	24.3	2104
<i>eriensis</i>	23.2	2257
<i>Forsberg</i>	13.0	2206
<i>Granger</i>	27.9	2385
<i>Heber</i>	13.9	2677
<i>Iowa II</i>	14.4	2999
<i>Iron Mountain</i>	13.3	3206
<i>Manistique</i>	0.7	2177
<i>Mifflintown</i>	8.0	2131
<i>Minturn</i>	27.9	2150
<i>Monett</i>	42.3	1979
<i>muricata</i>	0.6	2172
<i>Nobska</i>	32.3	2846
<i>North Colorado Springs</i>	3.4	2100
<i>Routhierville</i>	21.3	2633
<i>Shulliana</i> (jugens)	30.9	2367
<i>Tonawanda I</i>	25.0	2004
<i>Tonawanda II</i>	18.6	2423
<i>Whartona</i>	31.4	2055
<i>York Springs</i>	17.0	1985

Hot Springs), in other cases (e.g. alpha *Ashland D*·alpha *Hot Springs*) the same pollen parent may show a limited number of tubes in some crosses and a normal number in others. A limited number of pollen tubes might be expected when a hybrid produces very little normal pollen; this seems to be the case in alpha *Iron Mountain*·alpha *Hot Springs* and alpha *Manistique*·alpha *Hot Springs*, which produce only 13% and 0.7% respectively, normal-appearing pollen grains (Table 3). On the other hand, alpha *Monett*·alpha *Hot Springs* and alpha *Ashland D*·alpha *Hot Springs* produce as much normal-appearing pollen as those hybrids which show a normal number of pollen tubes in compatible pollinations.

Table 2 also shows a number of instances in which pollen tubes developed only in the stigma. These must be considered incompatible, although the incompatibility reaction is somewhat delayed. Whether such a delayed reaction occurs depends upon the particular hybrid used as the female parent.

The experiments reported here were performed in Köln, Germany and utilized certain of the strains employed in the earlier study done in Ann Arbor, Michigan.

In the second category are included cases in which cross-compatibility is rare (e.g. alpha *Buck Creek*·alpha *Hot Springs* used as pollen parent), instances in which cross-incompatibility is exceptional (e.g. alpha *angustissima*·alpha *Hot Springs*), and finally, cases in which cross-compatibility and cross-incompatibility approach equal frequency.

Among the crosses of the first and second classes taken together, there are thirty-five which show in their reciprocals the opposite compatibility reaction.

Attention must be called to a considerable number of crosses, which although compatible, show only a limited number of pollen tubes in spite of abundant pollination. In such cases the number of pollen tubes may be on the order of three to fifteen or twenty. In a normal compatible pollination a hundred or more pollen tubes can be observed. Although a limited number of tubes may be characteristic when certain hybrids are used as pollen parents (e.g. alpha *Monett*·alpha

The summer was unusually cool and wet. It is interesting to note that although the compatibility tests were carried out under conditions identical with those used in the previous experiments, the four hours which had earlier been sufficient for the growth of pollen tubes to the base of the style in control pollinations proved to be too short a time in the present tests. The growth period was thus increased to at least six hours in order to be certain that the pollen tubes had sufficient time to develop. Thus environmental conditions under which plants are growing prior to pollination as well as conditions immediately after pollination appear to influence pollen tube development.

Discussion

The results of the current experiments are in general the same as those obtained in the previous study. Evidence from the compatibility tests supports the conclusion that the alpha *biennis* 1 complexes, *Mifflintown*, *Whartoniae*, and *York Springs*, each possesses an incompatibility allele. *Angustissima*, a *parviflora* race with a *biennis* type alpha complex, likewise carries an incompatibility factor. It seems safe to venture the prediction that most alpha complexes of the *biennis* type, regardless of whether they occur in races belonging to the *biennis* 1, *biennis* 3, or the *parviflora* phylogenetic groups, carry incompatibility alleles.

Among the alpha *biennis* 2 complexes, alpha *Ashland D*, alpha *Buck Creek*, and *jugens* (*Shulliana*) show evidence of incompatibility factors. When the *angustissima*, *Mifflintown*, and *jugens* hybrids serve as pollen parents, there is in each instance one cross-incompatible combination. These can most readily be explained by the assumption that they represent cases of identity of S_I alleles.

The complexes, alpha *Iowa II* and alpha *Monett*, may be added to those of the *strigosa* group for which there is evidence of incompatibility alleles. The *parviflora* races, *Iron Mountain*, *Manistique*, and *muricata* all possess alpha complexes of the *strigosa* type; these are incompatible in most crosses, but each series has certain combinations in which a limited number of pollen tubes develop. Such cross-compatibility when coupled with self-incompatibility indicates the presence of incompatibility alleles.

A number of alpha complexes belonging to the *strigosa* and *biennis* 2 groups show no cross-compatible combinations. These are the alpha complexes of *Elma V*, *Forsberg*, *Granger*, *North Colorado Springs*, *Routhierville*, *Tonawanda I*, and *Tonawanda II*. Although admittedly it is impossible to be certain that with additional tests such complexes may not prove to be cross-compatible in at least one instance, the conclusion that these complexes carry true pollen lethals appears on the basis of the present data to be justified. It is not possible, however, to establish whether incompatibility alleles are present in addition to the pollen lethals, since in the current experiments the latter prevent the detection of the former.

Even though pollen lethals prevent the detection of incompatibility alleles in many races, such alleles have been demonstrated in enough other races to amply confirm the earlier conclusion that they occur in all phylogenetic groups of complex-heterozygotes. It is highly unlikely that the incompatibility system evolved after the complex-heterozygotes had already originated. Therefore, if incompatibility alleles occur in some races, one would expect to find them in

most others unless there have been frequent mutations to the S_C allele. If this were the case, however, it would be difficult to understand why such mutations have not occurred to any extent in the *biennis* group 1.

The crosses in which alpha *Buck Creek*·alpha *Hot Springs* and alpha *eriensis*·alpha *Hot Springs* served as pollen parents show in each series only one compatible pollination. This argues for the absence of a pollen lethal and suggests the presence of an incompatibility allele. The large number of incompatible crosses would then have to be explained by assuming that in each case the alpha complex coming from the female parent carries an S_I allele identical with that of alpha *Buck Creek* or of alpha *eriensis*. Such extensive identity of S_I alleles seems improbable. In the first place, this does not appear to be the case in the *biennis* group 1, in which almost every race has a distinctive incompatibility allele. Secondly, a gametophytic incompatibility system by definition must possess a large number of different alleles; widespread identity of alleles would make it ineffective. It is true that the function of these alleles in the complex-heterozygotes is different from that in a structural homozygote, but, as pointed out before, the system must have evolved before the origin of the complex-heterozygotes; if incompatibility alleles are present at all, their diversity should still persist unless a particular phylogenetic group could be traced back to a single or relatively few ancestral forms.

Finally, strong evidence against the identity of alleles as an explanation for much of the cross-incompatibility can be found in certain crosses of Table 2 which show reciprocal differences. For example, in the series in which alpha *Ashland D*·alpha *Hot Springs* is used as the pollen parent, the cross with alpha *Whartoniae*·alpha *Hot Springs* is incompatible. The reciprocal cross, alpha *Ashland D*·alpha *Hot Springs* X alpha *Whartoniae*·alpha *Hot Springs*, is compatible. Numerous other crosses in the series are compatible so that a pollen lethal as the cause of incompatibility is excluded. If the two complexes, alpha *Ashland D* and alpha *Whartoniae* carried identical incompatibility alleles, the cross should be incompatible in both directions. As previously pointed out, in classes I and II there are thirty-five such cases of reciprocal differences (Table 2). Class III can here be disregarded, since a reciprocal difference is normally expected if a complex without a pollen lethal is crossed with one which carries such a factor.

Reciprocal differences suggest the possibility of a cytoplasmic effect. The crosses shown in Table 2 do not, however, reveal any pattern of cytoplasmic inheritance which would not require further assumptions for which no evidence is currently available.

The cross-compatibility behavior of the alpha·alpha hybrids of classes I and II might be explained through the assumption that in addition to the presence of an incompatibility allele certain complexes carry a type of pollen lethal which may not have a lethal effect on the stigma and style of some genetic combinations. This lethal action would depend not upon the presence of a specific incompatibility factor, but rather upon the total genetic constitution of the female parent. Such a factor would be intermediate between a true pollen lethal as defined earlier, and an incompatibility allele which is only a lethal when the stigmatic and stylar tissue carries the identical allele.

The latter explanation has merit in that it does not demand the assumption of a modified gametophytic incompatibility system in order to explain the reciprocal differences in compatibility behavior; such an altered incompatibility mechanism would be difficult to reconcile with the results obtained with the *biennis* 1 races as well as with some of the races belonging to the other groups. Further, it is well-known that the complex-heterozygote allows the accumulation in its complexes of lethal as well as detrimental mutations, some of which very possibly may produce effects such as assumed above. Whether the failure of pollen tube development which results from the presence of this type of lethal should be classified as an incompatibility reaction is questionable. Although such a reaction falls within the definition of heterogenic incompatibility as proposed by ESSER (1959), the fact that it depends upon a more or less chance combination of entire genomes suggests that it resembles more closely a sterility reaction such as found commonly in interspecific crosses.

Unfortunately, the current data provide no better test for the latter hypothesis than for that suggesting a cytoplasmic effect. In either case extensive additional work will be necessary before other than a working hypothesis can be proposed.

Zusammenfassung

Es wird weiteres Material vorgelegt, um die allgemeine Aussage zu stützen, daß Inkompatibilitätsallele in allen phylogenetischen Gruppen der komplex-heterozygoten Arten der nordamerikanischen *Euoenothern* zu finden sind. Eine Anzahl von Rassen der *strigosa*-*biennis* 2-, und *parviflora*-Gruppen scheinen Pollenletalfaktoren zu enthalten, welche die Entwicklung des Pollens verhindern, unabhängig von der Konstitution des Griffels, auf dem er sich befindet. Solche Letalfaktoren haben in den vorliegenden Versuchen die Entdeckung der Inkompatibilitätsallele verhindert, falls die letzteren in diesen Rassen vorhanden sein sollten.

In der vorgelegten Untersuchung werden die Inkompatibilitätsbeziehungen zwischen 22 verschiedenen selbstinkompatiblen $\alpha \cdot \alpha$ -Bastarden bestimmt. In einer Gruppe dieser Bastarde zeigte jedes Glied, so bald es als Pollenelter benutzt wurde, Anzeichen sowohl für Kreuzungskompatibilität als auch für Kreuzungsinkompatibilität. Die Kreuzungsinkompatibilität kann in vielen Fällen nicht erklärt werden durch die Annahme einer Identität der S_I -Allele, weil die reziproken Kreuzungen häufig kompatibel waren. Als Arbeitshypothese wird vorgeschlagen, daß diese Fälle von Kreuzungsinkompatibilität entstehen durch einen Typ von Letalfaktoren, welche im Gegensatz zu den oben erwähnten nicht unabänderlich den Pollen ausschalten, in dem sie enthalten sind, sondern deren Wirkung sich erst entfaltet in Wechselwirkung mit der gesamten genetischen Konstitution des Griffels, auf dem sich der Pollen befindet.

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