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Origin of Complementary Incompatibility Systems in Flowering Plants

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Summary. The complementary incompatibility system, characterized by co-operative control of a single S specificity by alleles of two or more distinct S genes, has raised interesting questions regarding the origin and evolutionary significance of this system. What were the factors which led to the appearance of the complementary system of self-incompatibility. Is complementary incompatibility a primary or secondary development?

Lundqvist and Østerbye have suggested that the fundamental characteristic of this system - lack of dominance and competitive interactions between alleles of the same and different series - developed once, early in the evolution of angiosperms, at a stage when self-incompatibility was controlled polygenically. In one line of development, where two or more such incompatibility genes were strengthened by specific modifiers at the expense of the rest, co-operation among loci was favoured to promote increased interplant compatibility in the population. In this evolutionary line, allelic or intergenic interactions were excluded. In the other line of development, where only one incompatibility locus was strengthened, there was no need for such selection and alleles of this locus retained the property of allelic interaction in the pollen.

In this article an alternative hypothesis has been proposed for the origin of complementary incompatibility. It is suggested that this type of incompatibility system, conforming with generally held views on the evolution of self-incompatibility systems, developed secondarily, and polyphyletically, after the breakdown of the original one-locus, multiallelic, gametophytic system. In the re-revolution of self-incompatibility through introgression with a related self-incompatible taxon, the essential action of the presumed physiologically integrated self-compatible complex led to the exclusion of allelic or intergenic interaction as a prerequisite for evolution of complementary control. According to this hypothesis, breakdown of the original self-incompatibility and re-evolution of self-incompatibility, in the manner suggested above, could have occurred many times in the evolution of angiosperms and such systems might therefore be expected to occur scattered among different phylogenetic lines.

Introduction

Breeding systems in flowering plants show phylogenetic relationships which can be traced from the most primitive to the most advanced angiosperms. Self-incompatibility occurs widely and is believed to have evolved very early, indeed at the very beginning, in the evolution of angiosperms (Whitehouse 1960: Pandey 1960a, 1969a; Crowe 1964; Heslop-Harrison 1967).

Among self-incompatible plants the one-locus (S), multiallelic, gametophytic system of self-incompatibility is considered to be the most primitive, and it occurs widely among homomorphic plants. There are, however, a number of species where self-incompatibility is controlled by two loci. There is considerable evidence to suggest that the two-locus systems are secondary derivatives of the one-locus system (Lewis 1966; Lewis and Crowe 1958; Whitehouse 1960; Pandey 1956a, 1957a, 1960a, b, 1962a; Lundqvist 1954, 1956; Darlington 1963; Crowe 1964). The second locus may arise through either euploidy or aneuploidy, or through a structural change in the chromosome which does not involve variations in the original chromosome number. It may also occur through hybridization. Evidence suggesting incorporation of one or more S-gene duplications in the genome early in the history of the various phylogenetic branches of angiosperms, has been discussed elsewhere (Pandey 1969b).

In plants which have a newly acquired duplicate S locus three types of relationship between S alleles are possible in the pollen: (a) Competitive interaction between the two genes so that neither is able to express fully, leading to breakdown of self-incompatibility; (b) Dominance (or epistasis) of one gene over the other so that, in effect, only one gene is expressed (in autopolyploids the second S locus will usually be an identical duplicate of the first, but in alloploids the two genes may or may not be directly homologous; however, for simplicity, the term "dominance" will be used to cover both situations in this article); and (c) Independent action so that the cell has the combined properties of both genes (Lewis 1947, 1954).

Capacity for allelic interactions (dominance and competition) or independent action in pollen, although modifiable by genetic background, are inherent properties of genes and specific to allelic pairs.

In a gametophytically self-incompatible species duplication of the S locus would often lead to breakdown of self-incompatibility, owing to competitive interaction in the pollen (competition for substrates - Lewis 1947; or for ribosomes - Heslop-Harrison 1967; Mackenzie et al. 1967). However, if outbreeding continued to be advantageous self-incompatibility would be favoured and restored in various ways. Four such mechanisms have been identified so far: -

(i) Mutation and/or loss of function at one locus

In *Trifolium repens*, T. *medium* (Pandey 1956b, 1957a, 1969b) and in a number of *Solanum* species (Nath 1953; Pandey 1957b, 1960b) the second locus is believed to have mutated and lost its function in the breeding system, so that self-incompatibility, for all practical purposes, has returned to the original one-locus system.

(ii) Incomplete loss of function at one locus but elimination of competition between alleles of the two loci

In *Solanum pinnatisectum* and S. *ehrenbergii* (Pandey 1960b, 1962), the second locus has mutated, but retains two or a small number of mutant alleles with abnormal properties which still affect the breeding system. The two loci show dominance but competitive interaction has been eliminated.

(iii) Two fully functional multiallelic S loci without competition

In *Physalis ixocarpa* (Pandey 1957a), the second locus remains normal and multiallelic, but alleles of both loci showing competitive interaction have been eliminated. Self-incompatibility is therefore controlled by two multiallelic loci, which as in (2) show dominance but no competitive interaction.

(iv) Two fully functional multiallelic S loci without competition or dominance but with co-operation between loci

In the Gramineae different alleles of the two multiallelic loci, S and Z, are not only devoid of both competition and dominance interactions, but are complementary (Lundqvist 1956, 1964). Any two alleles, one of each locus, are able to cooperate to produce a unique specificity. Recently Lundqvist et al. (1973) found a similar system in two unrelated plants, *Ranunculus acris* (Ranunculaceae) and *Beta vulgaris* (Chenopodiaceae).

What is the origin of co-operation between loci?

Hypothesis

It is proposed that complementary incompatibility, like many other genetic systems of self-incompatibility in angiosperms, developed secondarily and polyphyletically. The following steps are believed to be involved in this evolution:

(1) Breakdown of the original self-incompatibility, and integration of the S_C gene complex in the normal physiology of reproduction.

(2) Introgression with related self-incompatible form or species giving an S_IS_C hybrid.

(3) Selection for outcrossing, while both the S_I and S_C loci remain essential for reproduction.

(4) Selection against dominance, epistasis, or any other form of interaction.

(5) Acquisition of another, independently acting, S_I locus, e.g. through chromosomal rearrangement or ploidy.

(6) Restriction of metabolites in the pollen leading to co-operation between S loci.

Thus, historically, the complementary system would be a product of self-compatibility, hybridization and re-evolution of self-incompatibility, and could have arisen independently in unrelated flora.

Arguments Leading to the Hypothesis

In the following discussion, this proposed series of events leading to the rise of the complementary system of incompatibility is elucidated.

1. Introgression and Selection

Numerous cases have been reported in the genera *Solanum*, *Oenothera*, *Nicotiana* and *Lycopersicon*, in which the action of particular units, or a major part of the S complex, occurred precociously, leading to varying degrees of sporophytic determination (Nath 1953; McGuire and Rick 1954; Crowe 1955; Pandey

1957b, 1962, 1968, 1973a). This change in the time of *S* gene action occurred in intra- or inter-specific hybrids derived from a normal self-incompatible pollen parent and a female parent carrying a mutant self-compatibility allele. In interspecific hybrids of *Oenothera* (Crowe 1955; Pandey 1960a) the evidence suggested that the *S* elements controlling production of the presumed specific pollen growth substance acted precociously (sporophytically), but the elements controlling the presumed specific incompatibility precursors acted gametophytically as usual. Recent discovery of the two forms of *S* gene (S_I and S_C) within the polymorphic species *Nicotiana glauca* has led to a better understanding of this behaviour. In $S_I S_C$ hybrids between self-incompatible (S_I) and self-compatible (S_C) strains, there is obligate independent action of *S* alleles, S_C acting sporophytically, presumably in the floral primordia, and S_I acting gametophytically in the microspores (Pandey 1973a, 1974).

Occurrence of a long-established self-compatibility allele together with a self-incompatibility allele in the same plant gives rise to an anomalous situation with regard to incompatibility expression. In the pollen the two types of gene show obligate independence at the "primary gene action phase" since they act at different developmental stages and in different cells. However, they may show dominance or competition as a result of product interaction at the "incompatibility reaction phase" when pollen and stigma are brought together (Pandey 1973a). Depending on the alleles involved, competitive interaction or dominance of S_C (or S_f) over S_I could lead to breakdown of incompatibility. In a phylogenetic line derived from such a hybridisation, restoration of self-incompatibility could therefore occur by selection of S_I alleles which showed no competitive interaction with self-compatibility alleles, and which were also dominant over them.

Evidence has been given earlier to show that maintenance of self-incompatibility by selection against competitive alleles has occurred repeatedly in nature (Pandey 1957a, 1960b, 1962).

As outlined in the Introduction, it is apparent that many plants with duplicate functional *S* loci had their self-incompatibility restored through selection against competition only, all reconstituted self-incompatibility systems still possessing dominance interaction. It is likely that the preservation of dominance had an intrinsic advantage. If plants lacked the metabolic capacity to produce two independent specificities in the microspore, selection of alleles capable of dominance interaction would allow one specificity to be functionally expressed, making restoration of self-incompatibility possible.

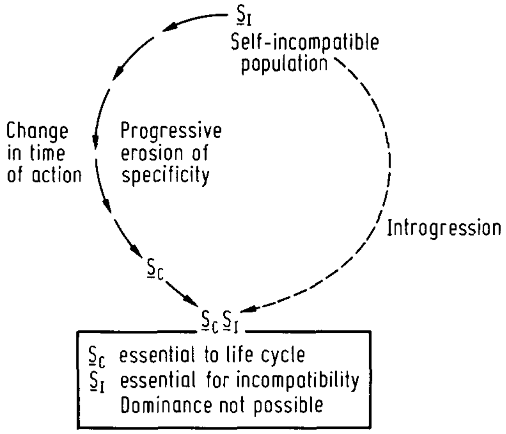

Fig. 1. Proposed evolutionary events in the exclusion of dominance (epistasis) interaction between *S* genes

Dominance interaction therefore provides insurance against metabolic deficiency in the microspore.

However, under special conditions, selection for dominance of self-incompatibility genes over self-compatibility genes may not be possible.

2. Integration of the *S* Complex and Selection Against *S* Interaction

In a taxon which has been well established as a self-compatible form or species - but in which the *S* allele, although it has lost its self-incompatibility, is only partly eroded (Pandey 1969a, 1973a) - the breeding system is adjusted to the efficient functioning of the various components of the *S* complex. The *S*-elements controlling the production of growth substances and enzymes involved in the normal complementary pollen-style physiology will still be functional even if those controlling the incompatibility specificities are lost or mutated. During evolution following change to self-compatibility, including subsequent *S* erosion and concomitant genetic adjustments, the complex may be physiologically integrated to the extent that it cannot be entirely replaced by a new *S* gene of a different genetic architecture, functioning at a different stage in development, without loss of viability (Fig. 1).

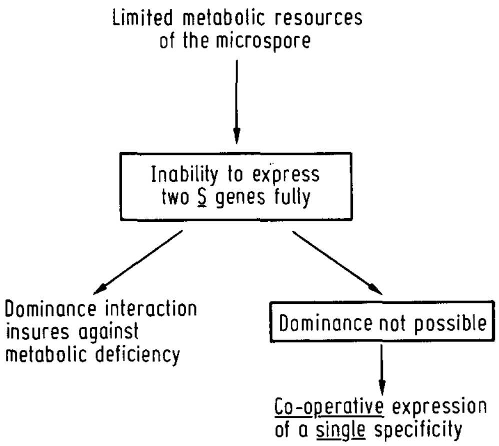

Fig.2. Limited metabolic resources of the microspore as an initiating factor in the origin of co-operative expression of specificity

The existence of such integrated self-compatibility genes can be visualised by considering the two-locus system of self-incompatibility in *Solanum ehrenbergii* and *S. pinnatisectum* (Pandey 1960b, 1962). Here the second $\underline{S}$ locus is occupied by only two eroded forms with sporophytic action, while the main multiallelic $\underline{S}_I$ gene acts gametophytically. Since this two-locus system apparently represents a reduction in the efficiency of sexual reproduction, maintenance of the second locus with its two partly deleterious alleles implies an intrinsic advantage associated with its activity. A small further loss of residual specificity affecting intraspecific incompatibility would revert the species to a one-locus incompatibility system even though expression of the eroded $\underline{S}$ complex might still be maintained. The existence of such a system is suggested by observations of Nath (1953) and Pandey (1957b) on *Solanum aracc-papa (S. sparsipilum)*. Intraspecific crosses revealed only a normal one-locus gametophytic incompatibility system. Crosses with *S. subtilius (S. chacoense)*, however, indicated the presence of a duplicate self-compatibility gene ($\underline{R}$) acting sporophytically in the pollen.

In a taxon which had acquired a new, multiallelic, normal, $\underline{S}_I$ locus whilst still retaining its essential integrated $\underline{S}_C$ complex in the background, dominance (epistasis) of $\underline{S}_I$ would lead to suppression of the integrated self-compatibility gene complex and would therefore not be possible. Self-incompatibility might be restored, however, by selection against dominance as well as competitive interactions between the two loci.

Selection for complete independence of various $\underline{S}_I$ and $\underline{S}_C$ forms (Pandey 1973a) could presumably be achieved only by complete loss of the property of allelic interaction. Selected $\underline{S}_I$ alleles would not only be incapable of interacting with the integrated $\underline{S}_C$ locus against which they had been selected, but would also show no interaction among themselves, a relationship not subjected to direct selection. This view is supported by observations in *Physalis ixocarpa*, which has a two-locus incompatibility system (Pandey 1957a). In this species, selection against interaction between alleles of the two normal, multiallelic, $\underline{S}_I$ loci has eliminated the property of allelic interaction completely, for induced autopolyploidy fails to produce competitive interaction between alleles of the same locus, and autopolyploids remain self-incompatible.

3. Metabolic Limitation in the Young Microspore and Selection for $\underline{S}$ Co-operation

In the absence of $\underline{S}$ interaction, self-incompatibility could only be restored (1) if the pollen possessed the metabolic resources for independent action of two genes; or, if that was not possible (2) a mechanism was adopted which allowed cooperation between the two genes very early in their activity, perhaps at the transcription phase (Pandey 1976), so that both genes could be expressed with the maximum metabolic economy of the cell (Fig.2).

Physical isolation of the haploid microspore from the maternal sporophyte and the probale wholesale replacement of the cell's metabolic machinery at the diploid-haploid phase change undoubtedly creates a heavy demand on the limited resources of the microspore (Heslop-Harrison 1967; Mackenzie, Heslop-Harrison and Dickinson 1967; Pandey 1973b). Hence, with continued selection for self-incompatibility, a situation likely to produce co-operation between two incompatibility loci would include: -

(i) lack of dominance interaction so that one $\underline{S}$ gene could not be expressed alone;

(ii) lack of sufficient $\underline{S}$-specific metabolites in the microspore, so that full independent expression of both genes would not be possible; and/or

(iii) an increased selective premium on the evolution of complementary interaction between $\underline{S}$ genes to lower

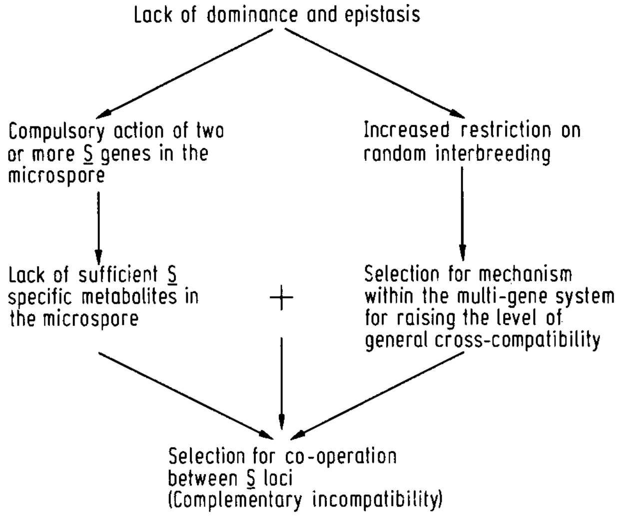

Fig. 3. Suggested selective factors involved in the origin of complementary incompatibility

the level of cross-incompatibility (Lundqvist 1975). An increase in the number of cross-compatible genotypes would be particularly favoured in a restricted population with few alleles at each locus.

The relationships among the above factors are illustrated in Fig. 3.

4. Origin of the "Complementary Incompatibility System"

The system in Gramineae

Once hybridisation and selection had produced a one-locus gametophytic incompatibility system lacking the capacity for allelic interaction, duplication of the $\underline{S}_I$ locus would not break down incompatibility by competitive interaction. However, since full or partial duplication of such a genome carrying a background self-compatibility locus would necessitate expression of, not two, but three or four, $\underline{S}$ loci in the pollen, incompatibility might sill break down in plants with insufficient $\underline{S}$-specific metabolites in the microspore for full expression of multiple $\underline{S}$ genes. In such cases, possibly the only means of restoring self-incompatibility would be for two or more independently functional $\underline{S}_I$ genes to co-operate in the expression of incompatibility within the metabolic limits of the microspore. In addition, the actual events of hybridization and genomic restructuring, including polyploidy, would be likely to generate small, genetically isolated populations carrying few alleles at each $\underline{S}$ locus. Selection for a higher degree of cross-compatibility within such a population would also favour complementary expression of $\underline{S}$ genes. The complementary self-incompatibility system of the Gramineae may have arisen in this way.

Implications of the Hypothesis

1. Lack of Allelic Interaction in *Tradescantia paludosa*

In a phylogenetic line where incompatibility was restored by selection against interaction, selection against the background self-compatibility locus would maintain independently acting $\underline{S}_I$ alleles in a diploid species with a functionally normal one-locus incompatibility system. Owing to the absence of potentially interacting alleles, there would be no breakdown of self-incompatibility following autopolyploidy. *Tradescantia paludosa* may be such a species. It has a normal one-locus, multiallelic, gametophytic system, but investigations of numerous autopolyploids have revealed a total absence of allelic interaction (Annerstedt and Lundqvist 1967).

T. paludosa belongs to the family Commelinaceae, which is related to the Gramineae but is more primitive. There is also evidence suggesting a lack of allelic interaction in the family Bromeliaceae (Kerns and Collins 1947), a sister family of the Commelinaceae in the order Commelinales. Based on these relationships, Annerstedt and Lundqvist (1967) have suggested that lack of allelic interaction in the Gramineae may have had an earlier origin in the evolutionary line common to all these taxa.

2. Mono- or Polyphyletic Origin

A recent study has suggested that the incompatibility systems in two diploid dicot species, *Ranunculus acris* (Ranunculaceae) and *Beta vulgaris* (Chenopodiaceae), are similar to that found in the Gramineae (Lundqvist et al. 1973). Both have more than one incompatibility locus - *R. acris*, a minimum of three; *B. vulgaris*, a minimum of four - alleles of which co-operate to produce one unique specificity. Lundqvist et al. (1973) have suggested that the complementary system of incompatibility evolved monophyletically "from a common ancestral gametophytic S-locus lacking allelic interaction." The dicot families Chenopodiaceae and Ranunculaceae are considered to be derived from a common evolutionary branch (Takhtajian 1969) which is also believed to be ancestral to the monocotyledons (von Wettstein 1935).

According to the present hypothesis, a monophyletic origin for the complementary system implies breakdown of ancestral self-incompatibility, followed by integration of a self-compatibility locus, in the common progenitors of a large body of lowering plants, including the monocot group as a whole. Temporary loss of self-incompatibility may in itself have been a significant factor in the explosive evolution of this line of descent, permitting rapid fixation of successful characteristics followed by a return to outbreeding in response to crucial evolutionary pressures. A possible example of the stabilization of primitive characteristics caused by an early breakdown in incompatibility may be found in the Magnoliales, supposedly the most primitive living angiosperms. The only recorded occurrence of self-incompatibility in this order is in the Anonaceae (Brewbaker 1957).

However, while complementary incompatibility in the monocots and certain related dicots may have a monophyletic basis, the alternative possibility that this system may have been derived polyphyletically in response to common causal conditions must not be ignored. Indeed, two major factors in the present hypothesis, hybridisation and the restoration of self-incompatibility after temporary self-compatibility, must be regarded as recurrent responses to changing evolutionary conditions throughout the flowering plants (Darwin 1859; Darlington 1940, 1963; Stebbins 1959; Pandey 1968, 1969a; Grant 1971).

3. Complementary Incompatibility - Primitive or Derived?

Evidence that complementary incompatibility may have evolved early in the ancestral line common to monocots and a related evolutionary branch of dicots led Lundqvist (1975) to speculate that the complementary multilocus system might be the primitive form of incompatibility from which the more common single locus system was secondarily derived. Elaborating on this theme, and on earlier suggestions of Bateman (1952) and Pandey (1959), Østerbye (1975) proposed that the most primitive type of incompatibility was a gametophytic, polygenically controlled system which developed once, early in the phylogenetic history of the angiosperms. Subsequently, specific modfiers increased the effectiveness of either a single S locus or a few loci at the expense of the rest. Thus, early in evolution there emerged two distinct lines of development. In one, where more than one S locus was strengthened by modifiers, in order to preserve self-incompatibility and at the same time facilitate the widest possible cross-compatibility, alleles of the different loci were "enforced to evolve properties counteracting allelic competition" (and dominance). In the other line, where only one S locus was strengthened by modifiers, there was "no need, nor any opportunity, of evolving the ability of counteracting this competition" (and dominance). Østerbye pointed out, as also suggested by Hayman (1956), "that the ability to function under coexistence may be a rather fundamental quality, developed at the same time, or in connection with, an increasing effectiveness of the S loci in question".

The elegant Lundqvist-Østerbye hypothesis differs from the older and widely accepted view that the common one-locus, gametophytic, multiallelic system of incompatibility is the primitive one, and that all other systems arose either directly from it, or were secondary developments after the breakdown of this system.

Both the Lundqvist-Østerbye hypothesis and the hypothesis outlined in this paper recognise the lack of allelic interaction as a fundamental property in the generation of complementary incompatibility. However, in the Lundqvist-Østerbye hypothesis the loss of allelic interaction is an indirect result of the action of "modifiers" on multiple S loci during a unique period of development which occured only once during the evolution of the angiosperms. In the current hypothesis, on the other hand, loss of allelic interaction is the result of the presence in the genome of a concealed S_C locus (essentially also a "modifier"). The breakdown of incompatibility to generate such S_C alleles has apparently occurred independently at many times in the evolution of the angiosperms. The bringing together of S loci, resulting firstly in modification of the property of allelic interaction and secondly in development of the multiallelic systems, depends on the process of hybridization and polyploidy which are also recurrent themes throughout angiosperm evolution.

The two hypotheses lead to quite different theoretical evolutionary patterns of incompatibility and should be readily distinguishable with further research into the genetic structure of incompatibility systems throughout the angiosperms:

(1) The distribution of complementary multilocus systems is monophyletic in the Lundqvist-Østerbye hypothesis. Therefore such systems would not be expected to occur in families unrelated to the monocot-Ranunculaceae-Chenopodiaceae line of descent. Systems without allelic interaction (including complementary systems) would not be expected to occur in lines which also showed allelic interaction. More specificially, complementary incompatibility could not arise from ancestral lines possessing one- or two-locus interacting systems. Furthermore, although the possibility has been considered by Østerbye (1975, Fig. 17), it seems unlikely that a one-locus non-interacting system could arise from an ancestral line with a one- or two-locus interacting system.

In the present hypothesis, however, systems without allelic interaction, including complementary systems, are quite likely to have arisen more than once during evolution and to occur in a scattered fashion among the angiosperms. Interacting and non-interacting single- or multiple-locus systems might very well occur in the same line of descent. (This is not to deny a possible direct relationship among the complementary systems of the monocots, Ranunculaceae and Chenopodiaceae as discussed in the preceding section.)

(2) Numbers of S loci in non-interacting multiple systems would be expected to be higher among the more primitive taxa according to the Lundqvist-Østerby hypothesis in which the primitive system was polygenic.

In the current hypothesis, however, in which the single locus, gametophytic, system is considered primitive, multiple non-interacting systems would be expected to be found predominantly amongst the more derived taxa.

Should further research reveal scattered occurrence of non-interacting systems throughout the angiosperms, and a prevalence of higher multiple systems amongst comparatively evolved taxa, this would seem to render the Lundqvist-Østerbye hypothesis untenable, and would favour the alternative hypothesis presented here. That is, lack of allelic interaction leading to complementary incompatibility systems evolved secondarily and polyphyletically through hybridization and selection, from plants which originally had the one-locus, interacting, multiallelic, gametophytic system.

Further, in discussing the probable absence of sporophytic incompatibility among the monocots and certain related dicot lines which show multilocus complementary incompatibility, Østerbye suggested that in the course of evolution of these systems the S genes may have achieved "a specialization which makes them unfit for the development of a sporophytic system". In fact, since sporophytic incompatibility is characterised by dominance interaction between pairs of alleles in diploid tissue, the loss of allelic interaction alone is a sufficient "specialization" to preclude sporophytic incompatibility in lines with non-interacting S genes.

Finally, the apparently anomalous relationships between the incompatibility system and pollen cytology among the monocots and related dicots with complementary incompatibility may, in fact, be logical on the basis that sporophytic incompatibility is precluded in these lines. During evolution there has been a tendency for the sporophyte to support or actually take over the physiological functions of the increasingly reduced male gametophyte. In lines where S genes retained the property of allelic interaction, not only was it possible for the second pollen mitosis to occur early in contact with the sporophyte, but earlier S gene action in diploid tissue could give rise to a functional sporophytic incompatibility. This would lead to the observed correlation between sporophytic incompatibility and trinucleate pollen. However, in lines without allelic interaction, although an early second pollen mitosis might still be possible, earlier S gene action would seriously impair the efficiency of incompatibility owing to increased cross-incompatibility. Thus, selection may have maintained gametophytic incompatibility in non-interacting lines, in spite of a

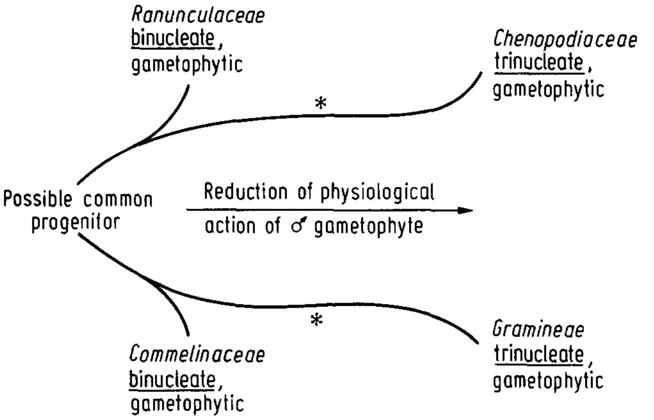

Fig. 4. Possible phylogenetic correlation between incompatibility systems and pollen cytology in lines with non-interacting S genes. * A change to sporophytic incompatibility could have occurred at these points in evolution if the incompatibility systems had been capable of allelic interaction (see text)

general tendency for earlier completion of gametophytic physiology (Fig. 4).

4. Multiplicity of the S Loci

In the one-locus, gametophytic incompatibility system maximum cross-compatibility is achieved through creation of a large number of alleles, each having a unique specificity. With two complementary loci, where any two alleles of different loci combine to produce a unique specificity, a large number of composite specificities are possible even with a small number of alleles at each locus. Thus the complementary system is furnished with an evolutionary alternative for multiplying specificities: an increase in the number of loci, each with a relatively small number of alleles, as opposed to an increase in the number of alleles at few individual loci.

As discussed earlier, in a taxon the number of S loci may increase only within the strict metabolic limitations of the microspore. The structure of the S complex, and its associated genetic environment, may be such that only a relatively limited number of alleles capable of complementary action is possible at a particular locus. Hence, under continuing restriction of inbreeding, limited multiplication of S loci, each presumably with a relatively small, but possibly varying, number of alleles, may be the most suitable method for increasing specificities in the complementary system. *Ranunculus acris* (3 loci) and *Beta vulgaris* (4 loci) may represent products of such a process.

In conclusion, the present hypothesis is consistent with the large body of observations recorded so far in the flowering plants. The evolutionary implications of this hypothesis differ significantly from those of the Lundqvist-Østerbye hypothesis. Further research should be illuminating.

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