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## The Evolution, Maintenance, and Loss of Self-Incompatibility Systems

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Self-incompatibility, the inability of a fertile hermaphrodite plant to produce viable seeds upon self-pollination, is the principal and most effective mechanism preventing self-fertilization in flowering plants. While its manifestations are diverse, in all cases, the major effect is to promote outcrossing between genetically different individuals of the same species. Discrimination between self and nonself is not usually the result of incompatibility between the gametes themselves, or between gametophytes. Instead the siphonogamous habit (with pollen tubes) of angiosperms enables direct interaction between the male gametophyte and the female-acting sporophyte, the parent of the female gametophyte.<sup>57</sup> Systems of self-incompatibility are widely distributed among flowering plant taxa and are reported from at least 19 orders and 71 families.<sup>6,22</sup> These include both dicotyledons and monocotyledons, plants from all geographical regions, and virtually all life forms.

Recently, several new hypotheses have been proposed to explain the selective forces involved in the evolution and maintenance of plant breeding systems.<sup>33,128</sup> Sexual selection, the optimal allocation of resources to maternal and paternal function, and strategies for coping with environmental uncertainty have all been invoked to explain the evolution of different reproductive modes. Self-incompatibility systems have remained relatively immune from these considerations. The traditional view of inbreeding avoidance as an explanation for the evolution of self-incompatibility has been largely unchallenged, since the evidence in support of the role of self-incompatibility systems as outbreeding devices is strong. This is not to imply that no difficulties exist in explaining the functional significance of different systems of incompatibility and their evolutionary relationships with one another. As the floral biology of a broader range of plant species has been investigated, it has become apparent that some revision of our concepts of self-incompatibility may be in order, since several types of self-incompatibility that have been recently discovered do not readily fit into existing classifications.

In this chapter, I review current research on the evolution and genetics of self-incompatibility. The discussion is organized into three main topics: (1) evolutionary relationships among incompatibility systems, (2) maintenance of self-incompatibility in natural populations, and (3) genetic modifications and evolutionary loss of self-incompatibility systems. Since the literature on self-incompatibility is vast, I have

made no attempt to be comprehensive and in many cases have cited only recent references on a particular topic. Initially, a brief review of the major classes of self-incompatibility and their general properties is given. For more detailed treatments of self-incompatibility, the reader is referred to general reviews of the topic.<sup>2,47,71,85</sup>

## TYPES OF INCOMPATIBILITY

Self-incompatibility systems can be divided into two distinct groups: gametophytic self-incompatibility, in which the incompatibility phenotype of the pollen is determined by its own haploid genotype, and sporophytic self-incompatibility, in which the incompatibility phenotype is governed by the genotype of the pollen-producing parent. The difference may arise from the time of *S* gene action, which in sporophytic systems appears to be premeiotic (or at the latest meiotic) before individualization in the tetrads, but in gametophytic systems occurs after the first metaphase of meiosis in pollen mother cells.<sup>85</sup>

Whereas all mating types in gametophytic self-incompatibility systems are morphologically similar (homomorphic), sporophytic self-incompatibility can be further subdivided into homomorphic and heteromorphic systems on the basis of whether or not the mating types are morphologically alike. Two classes of heteromorphic incompatibility are known (distyly and tristily), depending on whether there are two or three mating groups. The mating groups usually differ in style length, anther height, pollen size, pollen production, and incompatibility behavior. The reader is referred to general reviews of heteromorphic self-incompatibility systems.<sup>51,114</sup>

Within the major types of self-incompatibility there occurs a variety of systems that differ from one another largely in their genetic basis (Table 5.1). Typically, in homomorphic systems a single locus (*S*) with multiple alleles controls incompatibility, although in recent years systems involving two to four loci and multiple alleles have been demonstrated,<sup>78</sup> and several cases of the polygenic control of self-incompatibility have been claimed.<sup>38,113</sup> In heteromorphic systems, distyly is controlled by a single locus with two alleles and tristily by two loci each with two alleles and epistasis operating between the loci.<sup>51</sup>

Despite the variation in patterns of inheritance within gametophytic and sporophytic systems, each possesses distinctive cytological and physiological characteristics. For example, with few exceptions, in gametophytic systems pollen is binucleate and pollen tubes are inhibited in the style, whereas in sporophytic systems pollen is trinucleate and the rejection response is on the stigmatic surface. These differences may arise because of the contrast in the timing of *S* gene action. Although these differences break down in heteromorphic systems, where pollen can be bi- or trinucleate and inhibition stigmatic or stylar, the relationship between pollen cytology and site of inhibition within individual heterostylous species appears to be maintained.<sup>92</sup>

As research on self-incompatibility continues several "anomalous" systems have been identified, forcing us to reconsider and perhaps revise our views on the classification and overall properties of the different types of self-incompatibility. While it seems unlikely that the general dichotomy between sporophytic and gametophytic systems will be affected by recent discoveries, we may need to alter our thinking about the evolutionary origins and relationships among the major classes of self-incompatibility. Three examples of pollen-pistil interactions that are not readily interpretable

Table 5.1. Systems of Self-Incompatibility in Flowering Plants<sup>a</sup>

Major Types	Genes	Alleles	Allelic interaction	Stage of inhibition	Effect of polyploidy	Selected families
<b>HOMOMORPHIC</b>						
1 Gametophytic	1	Many	Codominant	Style	Breakdown	30 Rosaceae, Leguminosae, Solanaceae
2 Gametophytic	2	Many	Codominant	Style	None	1 Gramineae
3 Gametophytic	4	Many	Codominant	Style	None	2 Ranunculaceae, Chenopodiaceae
4 Sporophytic	1	Many	Dominant	Pollen germination	None	20 Cruciferae, Compositae, Rubiaceae
5 Sporophytic	3-4	Many	Dominant codominant	Pollen germination and stigma penetration	None	1 Cruciferae ( <i>Eruca sativa</i> )
6 Sporophytic/gametophytic <sup>b</sup>	1	Many	—	Ovary	—	1 Sterculiaceae ( <i>Theobroma cacao</i> ) (perhaps many)
7 Polygenic <sup>b</sup>	many	?	—	Ovary	—	1 Boraginaceae ( <i>Borago officinalis</i> )
<b>HETEROMORPHIC</b>						
8 Distyly	1	2	Dominant	Pollen germination, stigma penetration, and style	None	23 Primulaceae, Linaceae, Turneraceae
9 Tristyly	2	2	Dominant	Style and ovary	None	3 Lythraceae, Oxalidaceae, Pontederiaceae
10 Distyly "anomalous" <sup>b</sup>	1	2 floral many SI	Dominant	Ovary	None	2 Boraginaceae ( <i>Anchusa</i> ) Amaryllidaceae ( <i>Narcissus</i> )
11 Enantiostry <sup>b</sup>	1?	2?	—	—	—	2 Haemodoraceae ( <i>Wachendorfia</i> ) ? Tecophilaeaceae ( <i>Cyanella</i> )

<sup>a</sup>Modified from Lewis.<sup>71</sup>

<sup>b</sup>These reports of self-incompatibility are not well understood and require further study (see text for references).

within the traditional classification schemes will serve to illustrate this point. In each case workers examining these phenomena have suggested that self-incompatibility mechanisms are involved, but a critical appraisal of the nature of these systems is required.

### *Late-Acting Self-Incompatibility*

Early studies of pollen tube growth in self-incompatible species suggested that inhibition of self-pollen tubes in the ovary occurred only rarely in flowering plants. Ovarian inhibition of self-pollinations, either pre- or postzygotically, was generally considered an aberrant or maladaptive condition since, in some cases (e.g., *Theobroma cacao*<sup>24</sup>), ovules were apparently irreversibly sterilized by selfs. Numerous reports of ovarian inhibition have appeared in the literature recently, suggesting that late-acting incompatibility systems are more widespread than had been previously thought. Seavey and Bawa<sup>103</sup> have reviewed the subject and discuss the nature, occurrence, and functional significance of various ovarian phenomena. They distinguish three types of response: (1) ovarian inhibition of self-pollen tubes before ovules are reached, (2) prefertilization inhibition in the ovules, and (3) postzygotic rejection. Most workers have not considered postzygotic effects as involving a true self-incompatibility system, the former being usually reserved for prezygotic interactions between the pollen and pistil. The postzygotic rejection of selfs is often excluded from definitions of self-incompatibility owing to the difficulty of distinguishing such an effect from inbreeding influences. Embryo abortion due to the action of recessive lethals uncovered by selfing may be similar in appearance to a true self-rejection reaction. Seavey and Bawa<sup>103</sup> discuss these difficulties and outline how the effects of inbreeding may be distinguished from late-acting self-incompatibility.

Models of genetic load do not anticipate levels of deleterious recessives sufficient to obtain zero or low levels of seed set upon selfing (although see Sorensen<sup>108</sup>). In addition, it seems unlikely that the expression of inbreeding depression upon selfing would be concentrated in only the early embryonic phase of the life history. Thus measures of seed set upon selfing and the subsequent evaluation of growth of selfed progeny might be useful in distinguishing between inbreeding depression and a true self-rejection response, since inbreeding effects would be manifest at a variety of different developmental stages. In contrast, a late-acting self-incompatibility system would be expected to operate at a specific developmental period of embryo growth. Thus, detailed studies of embryo development might distinguish such effects.

If the genetic basis of late-acting self-incompatibility is similar to gametophytic and sporophytic systems in the possession of mating types, then these should be detectable as cross-incompatible matings. Such mating groups would not be anticipated from inbreeding unless consanguineous matings were involved. The distinction here may be particularly difficult if late-acting self-incompatibility phenomena are polygenically based, since the expectations for both involve quantitative variation as opposed to clear segregation of seed set values.

### *Cryptic Self-Incompatibility*

The distinction between self-incompatibility phenomena and inbreeding effects is also relevant to plant species exhibiting cryptic self-incompatibility systems. In families

with both homomorphic and heteromorphic incompatibility, pollen tube growth is often significantly faster in cross-pollen compared to self-pollen (prepotency) in self-compatible relatives. This effect was studied by Darwin<sup>41</sup> and has been termed cryptic self-incompatibility by Bateman.<sup>16</sup> It may be more widespread in angiosperms than previously thought, since the usual method of testing for self-incompatibility will not reveal its presence. Where this type of behavior occurs, differential fertilization of selfs and crosses can reflect the presence of weak self-incompatibility or it may be a reflection of inbreeding effects. In the latter case it is not always clear whether pre- or post-zygotic influences are at work, unless direct observations of differential pollen tube growth are made.

Using controlled pollen mixtures and the style length locus as a genetic marker in self-compatible, distylous *Amsinckia grandiflora*, Weller and Ornduff<sup>24</sup> showed that self and intramorph pollen were at a competitive disadvantage to intermorph pollen. Hence the cryptic self-incompatibility system found in this species resembles a weaker version of that occurring in related distylous species of the family, which show inhibition of cross-pollen among individuals of the same floral morph. The existence of cryptic self-incompatibility in *Amsinckia* has been questioned by Carey and Ganders (unpublished data cited in Ganders<sup>51</sup>) who failed to find differences in pollen tube growth in *Amsinckia grandiflora* or in any other distylous species in the genus. This has led to the suggestion that selective abortion of embryos may occur in *Amsinckia*.<sup>26,27</sup> However, Weller (unpublished data) has recently repeated the pollen tube experiments on *Amsinckia grandiflora* with results similar to his earlier findings and hence there seems little doubt that the species exhibits a true cryptic dimorphic-incompatibility system.

A different phenomenon appears to operate in self-compatible tristylous *Eichhornia paniculata* where inbreeding effects seem to be more important in regulating the parentage of offspring. Using pollen mixtures and an isozyme marker locus (GOT-3) Glover and Barrett<sup>52</sup> observed an approximately twofold advantage to cross-pollen over self-pollen. The treatments involved both intramorph and intermorph cross-pollen. In both, a similar advantage to cross-pollen was observed, a result not expected if a weak trimorphic incompatibility system was functioning. An additional treatment also compared the competitive ability of both legitimate (between anthers and stigmas of equivalent level) and illegitimate (between anthers and stigmas at different levels) cross-pollen. The two classes of pollen were equally competitive, again an outcome not expected in a conventional trimorphic incompatibility system.

While in this study it seems unlikely that cryptic trimorphic incompatibility is responsible for the observed advantage to cross-pollen, it is by no means clear at what stage the advantage to the cross treatment is manifest. While prepotency of cross-pollen may occur, it is possible that there is some selective elimination of selfed zygotes through embryo abortion. Here, as in putative cases of late-acting self-incompatibility, detailed dissection of the complete reproductive cycle from pollination to seed set is required to distinguish between the possibility of incompatibility phenomena and inbreeding effects. In the former case, we are dealing with a mechanism operated by the maternal parent and controlled by its genotype and that of the pollen donor. In contrast, inbreeding depression is a process acting in the progeny zygote determined by its own genotype. While it is conceptually straightforward to distinguish between these factors, in practice it may not always be clear which of these processes is responsible for the reduced seed set after selfing compared with outcrossing.

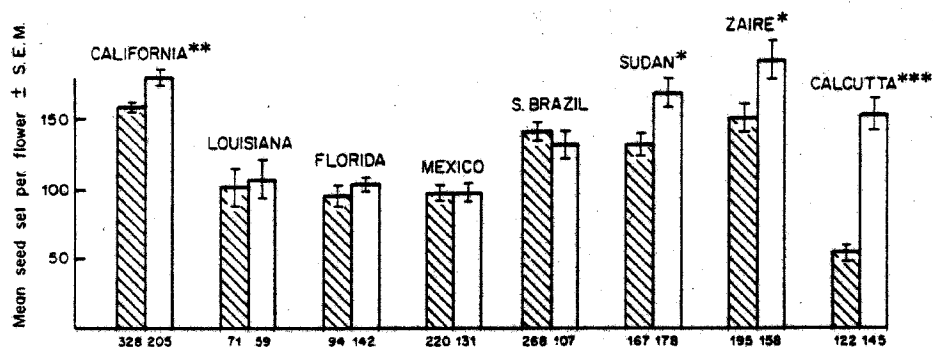


Fig. 5.1. Seed production following controlled self- and cross-pollinations of *Eichhornia crassipes* clones. All cross-pollinations involved a single clone from Costa Rica. Sample sizes are the number of flowers pollinated. ▨ = self-pollinations, □ = cross-pollinations, \* $p < .025$ , \*\* $p < .01$ , \*\*\* $p < .001$ . Significant differences in seed set between self- and cross-pollination may result from weak self-incompatibility and/or inbreeding depression. (After Barrett.)

This problem is often encountered in interpreting results of controlled pollination studies. Figure 5.1 illustrates such a difficulty from the results of controlled self- and legitimate cross-pollinations of tristylous *Eichhornia crassipes*.<sup>24</sup>

#### Anomalous Heteromorphic Incompatibility Systems

A final example in which the incompatibility phenomena described do not readily fit into conventional schemes involves two distinctive types of floral heteromorphism. In both cases, controlled pollinations indicate reduced seed set on selfing, but it is by no means clear what mechanism is operating, whether or not inbreeding depression is involved, and how the systems are related to typical heteromorphic incompatibility.

In the Boraginaceae both self-incompatible and self-compatible distylous taxa are known.<sup>26</sup> Experimental studies on *Anchusa officinalis*<sup>93,101,102</sup> and *Anchusa hybrida*<sup>44</sup> have revealed a distinct and unusual form of floral heteromorphism, which may also occur in *Narcissus*.<sup>43</sup> In both *Anchusa* species there is considerable variation in style length in natural populations, although the ratio of style length to anther height shows a clear bimodal distribution. In *Anchusa officinalis*, surveys of morph ratio indicate that in all populations the long-styled morph is far in excess of the short-styled morph.<sup>93</sup> Yet curiously, genetic studies of inheritance of style length are suggestive of the common pattern for distylous plants with a single diallelic locus governing style length variation.<sup>102</sup> High frequencies of the long-styled morph might occur if this morph experienced a high degree of self-fertilization, but controlled self-pollinations of both morphs yield little to no seed.<sup>93</sup> Of particular interest is the observation that both intramorph and intermorph pollinations are compatible (Table 5.2). Because of this finding, workers studying these species have concluded that *Anchusa* possesses a multiallelic incompatibility system unlinked to the locus governing floral dimorphism. Observations of pollen tube growth in selfs indicate that pollen tubes reach the ovary and enter the micropyle, suggesting that the recognition reaction resides in the ovules.<sup>101</sup> Detailed studies of the genetic basis of the incompatibility system of *Anchusa* are hindered by the generally low female fertility of crosses. Despite this, it would seem worthwhile to investigate further the cause of self rejection in the species,

Table 5.2. Seed Set of Intrafamilial Pollinations in *Anchusa officinalis*.<sup>a,b</sup>

Plant number	Plant number									
	S 1	S 2	S 3	L 4	L 5	S 6	S 7	L 8	S 9	S 10
S 1	0	6	<b>38</b>	<b>0</b>	5	31	6	19	<b>25</b>	0
S 2	10	0	<b>10</b>	13	<b>0</b>	25	13	<b>50</b>	0	19
S 3	5	0	0	<b>38</b>	20	<b>44</b>	<b>19</b>	50	25	<b>25</b>
L 4	<b>38</b>	<b>44</b>	<b>63</b>	0	31	<b>38</b>	31	6	31	<b>50</b>
L 5	31	<b>13</b>	19	31	0	13	56	50	50	19
S 6	45	6	6	25	25	0	19	75	31	25
S 7	35	25	0	<b>38</b>	25	25	0	19	63	25
L 8	20	0	25	10	56	50	63	0	44	44
S 9	0	0	6	19	15	6	25	38	0	13
S 10	0	25	25	0	15	25	13	6	63	0

<sup>a</sup>After Schou and Philipp.<sup>102</sup><sup>b</sup>The numbers are the percentage of maximum seed set, boldface numbers indicate the seven cases in which a difference in compatibility is manifested in a complete absence of seeds in one cross. All plants are from a single family.

particularly since the apparent absence of clear-cut mating groups and the fact that ovarian phenomena are involved suggest that inbreeding depression may also be a factor.

The data for *Anchusa* resemble those obtained by Crowe<sup>38</sup> for the related nonheterostylous *Borago officinalis*. She argued that in this species self-incompatibility is polygenically controlled and is expressed postzygotically. Evidence to support this claim was obtained from pollen chase experiments (prior application of self-pollen before cross-pollen) in which a sterilization effect was observed from self-pollinations. However, prezygotic rejection mechanisms operating in the nucellus or micropyle may also block subsequent compatible pollen tubes and thus it may be premature to conclude that postzygotic mechanisms are at work in this species.

One mechanism by which incompatibility could operate postzygotically involves the postponement of the rejection response relative to recognition. This would require labeling of the developing zygote by a product synthesized during the recognition period. No such chemical has yet been demonstrated in species in which postzygotic incompatibility has been claimed and, therefore, it may be more satisfactory to reserve the term incompatibility for prezygotic interactions.

A second distinctive form of heteromorphic incompatibility involves differences among mating types in style orientation and has been observed in two monocotyledonous families (Haemodoraceae, Tecophilaeaceae).<sup>46,89,90</sup> In the genera *Wachendorfia* and *Cyanella*, some plants have styles that are sharply deflected to the right, while in others the style bends to the left. This condition is referred to as enantiostyly and is interpreted as an outbreeding mechanism promoting pollination between floral morphs in a manner similar to heterostyly.

In *Wachendorfia paniculata*, controlled self- and cross-pollinations within and between plants with right- and left-bending styles suggest that intermorph crosses produce more seeds than self- or intramorph pollinations. On the basis of these results, Ornduff and Dulberger<sup>90</sup> concluded that a weakly developed self- and intramorph

incompatibility system is present in the species. The occurrence of 1 : 1 ratios of the two morphs in four *Wachendorfia* populations<sup>38</sup> suggests that intermorph matings may predominate under field conditions and that the mechanism of inheritance of floral enantiostyly may be similar to that found in heterostylous plants. Since no relatives of enantiostylous plants are heterostylous, it seems unlikely that the polymorphisms are related in any way, except in as much as they may represent distinctive and independent responses to selection favoring outcrossing. More detailed genetic and ecological studies of these curious polymorphisms are required before any firm conclusions on their adaptive significance can be reached. In addition, controlled selfs and crosses among the morphs combined with observations of pollen tube growth are required to firmly establish the presence of a self-incompatibility system in the species.

### ***Heterosis Model of Self-Incompatibility***

The examples reviewed above indicate some of the difficulties in distinguishing the various forms of self-incompatibility from the influences of inbreeding depression. Recently, Mulcahy and Mulcahy<sup>43</sup> have attempted to extend the significance of inbreeding effects to encompass typical style-mediated gametophytic self-incompatibility systems. They have questioned the conventional genetic model of gametophytic self-incompatibility by one or a few multiallelic loci with oppositional effects and have instead argued that many loci, which are spread throughout the genome with complementary effects, govern the incompatibility response. According to this view, gametophytic self-incompatibility is simply an expression of genetic load mediated via extensive pollen style interactions. This model, called the "heterosis model" of gametophytic self-incompatibility, is based on the assumption that if the pollen and style carry dissimilar allelic combinations, there will be heterotic interactions between them, resulting in increased pollen tube growth rates. In contrast, if both the pollen and style share the same deleterious recessive alleles, pollen tube growth will be reduced accordingly. The actual growth rate of the pollen tube will be the sum of all pollen–style interactions, and incompatible pollinations are due not to specific inhibitory molecules (oppositional model) but rather to the growth of pollen tubes being too slow to allow fertilization.

The heterosis model and evidence used to support it have been strongly criticized by Lawrence *et al.*,<sup>66</sup> who argue that much of the evidence used by the Mulcahys against the oppositional hypothesis is either not relevant or not inconsistent with it. They point out difficulties concerned with the genetic and biochemical basis of the model, the most serious of which is that it is not capable of providing an explanation for the compatibility relationships observed in either single locus or multilocus systems, unless in the latter case it is assumed that the constituent loci of the proposed supergenes which govern self-incompatibility are very tightly or completely linked.

While the Mulcahys' model may be inconsistent with available information for gametophytic systems of self-incompatibility, it may help explain other facets of pollen–pistil interactions such as those involved with pollen prepotency, optimal outcrossing, and extraneous pollen advantage in interpopulation crosses.<sup>69,115</sup> Observations of pollen germination, pollen tube growth, and the fertility of crosses within and between subpopulations at different spatial scales would be useful in assessing whether or not the genetic relatedness of sexual partners can influence pollen–pistil interactions in ways that mimic incompatibility phenomena.



## EVOLUTION OF SELF-INCOMPATIBILITY SYSTEMS

Two contrasting views on the evolutionary origins of self-incompatibility systems are evident in the literature. The first, originally proposed by Whitehouse,<sup>125</sup> suggests that self-incompatibility arose once in association with the origin of flowering plants. Following this interpretation, the present range of self-recognition systems is fundamentally similar because of the presence of an ancient, but strictly conserved, *S* locus in all families. Variation among systems arises from superimpositions on the basic mechanism underlying self-rejection. An alternative view follows Bateman,<sup>15</sup> who argued against the monophyletic origin of self-incompatibility systems and suggested that it was more probable that weak polygenic incompatibility had arisen *de novo* several times and that progressive genetic modifications had taken place to give the range of systems observed today. Modifications involved either selection of nonspecific modifiers influencing all loci or specific modifiers increasing the effectiveness of one or two loci at the expense of the rest.

Each view on the evolutionary origin(s) of self-incompatibility has its supporters, but until more information on the taxonomic distribution, genetic basis, and physiological properties of incompatibility systems is available, the question is likely to remain unresolved. The problem may eventually be solved by molecular characterization of the *S* gene from species with different systems of incompatibility.

### *Primitive Systems of Incompatibility*

While controversy exists over the phylogenetic relationships between the different types of sporophytic self-incompatibility (see below), there is general consensus that the primitive system of self-incompatibility in flowering plants is gametophytic. In addition to the single locus form of control, more complex systems with three, four, and perhaps even more loci are known.<sup>78,91</sup> Since these occur in species from relatively unspecialized families (Ranunculaceae, Chenopodiaceae), it is possible that they may be similar to the original forms of self-incompatibility with the common one-gene system derived by progressive homozygosis or deactivation (silencing) of all but one of the genes. The observation of ovarian self-incompatibility in the primitive *Pseudowintera colorata* (Winteraceae) by Godley and Smith<sup>34</sup> is also of interest, and raises the possibility that unspecialized forms of polygenic self-incompatibility, with rejection mechanisms residing in the ovary, may have evolved first in the angiosperms, and that, later in evolution, progression to stylar and finally stigmatic inhibition with monogenic control occurred.

Detailed genetic data from species with late-acting (ovarian) self-incompatibility systems are badly needed to enable an assessment of their relationships to sporophytic and gametophytic systems. Unfortunately, since many of the plants in which these systems have been observed are tropical woody species, this may be some time in coming. The only data available for a species with this type of self-incompatibility system (*Theobroma cacao*) are difficult to interpret and suggest that genetic control is gametophytic for the pollen and sporophytic for the ovules.<sup>34</sup> A similar system may also operate in the related *Sterculia chicha*,<sup>111</sup> where ovarian inhibition has been observed.

The view that gametophytic self-incompatibility is phylogenetically primitive whereas sporophytic self-incompatibility is derived has recently been challenged by Zavada<sup>134</sup> and Zavada and Taylor<sup>135</sup> on the basis of fossil evidence. Studies of early Cretaceous angiosperm pollen indicate that many taxa possess reticulate exine sculpturing, a feature of extant plants with sporophytic self-incompatibility. In addition, current fossil evidence indicates that the style did not evolve until the Lower Cretaceous or lower Upper Cretaceous, thus postdating the occurrence of pollen types indicative of sporophytic systems. Since gametophytic self-incompatibility depends primarily on interactions between the pollen tube and style, this observation is difficult to reconcile with the view that gametophytic self-incompatibility is ancestral, unless the early plants with this system possessed stigmatic recognition mechanisms such as those that occur in *Papaver*. Zavada and Taylor<sup>135</sup> suggest that early angiosperm self-incompatibility may have involved a system similar to that found in *Theobroma cacao*, with stigmatic recognition but with the rejection response resulting in abortion of the carpel. According to this view, the subsequent development of pollen tube inhibition, without the accompanying abortion of reproductive structures as a result of incompatible pollinations, provided energetic advantages as well as opportunities for prezygotic mate assessment.<sup>128</sup>

#### ***Relationships Between Homomorphic and Heteromorphic Self-Incompatibility***

Current information on the distribution of homomorphic self-incompatibility systems is fragmentary but suggests that not only are sporophytic and gametophytic systems found in different families but heteromorphic incompatibility occurs in yet another group of families distinct from these.<sup>30,31</sup> Despite contrary views,<sup>131</sup> there are no convincing genetic data indicating that homomorphic and heteromorphic systems of sporophytic incompatibility co-occur in the same family, with the exception of the large family Rubiaceae. This point is of relevance to ideas on the evolution of dimorphic incompatibility.<sup>80</sup> Following the view of a unitary, strictly conserved *S*-locus in flowering plants, Muenchow<sup>81</sup> has developed a theoretical model for the evolution of distyly by loss of alleles from an existing multiallelic sporophytic system. Rather than invoking genetic drift,<sup>131</sup> Muenchow's model suggests that selection for maximal cross-incompatibility can, under rather restricted conditions, remove incompatibility alleles in such a way that remaining alleles display the pattern of dominance and recessiveness found in distylous groups. Until closely related taxa with both homomorphic and heteromorphic systems of sporophytic incompatibility are discovered, however, the model may have no more than theoretical value.

The physiological and biochemical properties of incompatibility systems are still relatively poorly understood, but available data hardly support the view of a unitary *S* gene for sporophytic systems. It is possible that the recognition factors normally associated with the tapetum in homomorphic systems have no role to play in the incompatibility systems of heterostylous plants and that physiological differences between pollen tubes and the pistil mediate incompatibility.<sup>110</sup> In this connection, it is worth noting that inhibition sites in heterostylous species can involve the stigma, style, or ovary.<sup>1,17,96,104</sup> Charlesworth<sup>30</sup> has suggested that if the general properties of heteromorphic incompatibility turn out to be fundamentally different from homo-

morphic systems, the conventional use of the term *S* gene should probably not be applied to the incompatibility locus in heterostylous plants.

### *Selective Forces*

Few workers have considered the selective forces that have given rise to two distinctly different types of incompatibility in flowering plants, namely the gametophytic and sporophytic systems. Beach and Kress<sup>19</sup> suggest that the answer may stem from the conflict created by the contrasting reproductive behaviors of the sporophytic and gametophytic generations. In order for the male gametophyte to be evolutionarily successful, it must fertilize an egg, or none of the gametophyte's genes will be transmitted to the next generation. The quality of the resultant zygote is not open to choice since the male gametophyte is already "committed." In contrast the female sporophyte does not benefit by indiscriminate male gametophyte success but rather by inhibiting self-pollen and promoting cross-pollen. Beach and Kress<sup>19</sup> propose that the development of sporophytic incompatibility from gametophytic incompatibility may represent an evolutionary response by sporophytes that is due to opportunities available to "committed" gametophytes for circumventing the inhibition mechanisms of gametophytic systems. Sporophytic systems can be viewed as more effective in discriminating against committed male gametophytes since they operate before the haploid genome is expressed, as a result of the biochemical labeling of pollen with sporophytically derived products in the exine.<sup>63</sup> Willson<sup>127</sup> considers other aspects of conflict between male and female function in self-incompatible plants. While these ideas are both novel and plausible, they provide little opportunity for experimental analysis and as a result the hypotheses are unfortunately largely untestable.

## MAINTENANCE OF SELF-INCOMPATIBILITY SYSTEMS

Our understanding of the evolutionary development of incompatibility systems is largely speculative and based on an imperfect knowledge of their distribution and general characteristics. A rich literature has, however, developed on their maintenance and function in contemporary plant populations. Much of this work is theoretical and there is considerable scope for experimental field studies on the ecology and population genetics of self-incompatible species to assess the validity and predictions of the theoretical models.

The major selective force proposed to explain the maintenance of incompatibility systems is substantial inbreeding depression in the fitness of selfed progeny due to the expression of largely recessive deleterious mutations in homozygotes. Virtually every natural outbreeding plant and animal population that has been examined displays the complementary effects of inbreeding depression and heterosis.<sup>130</sup> The total inbreeding depression, in normally outcrossing species, that results from selfing is frequently greater than 50%, and the average individual is typically heterozygous for one or more recessive lethal factors.<sup>39,64</sup>

Unfortunately, the magnitude and quantitative patterns of inbreeding depression have not been examined in natural populations of many self-incompatible species, although numerous reports of the deleterious effects of inbreeding in cultivated self-incompatible species are available in the agricultural and horticultural literature. A

paucity of data for natural populations of self-incompatible species may in part be a consequence of the difficulties in obtaining selfed seed. Bud pollinations and other techniques can be employed to circumvent this problem, but these approaches are frequently time-consuming and technically difficult.<sup>65</sup> For example, by using bud pollinations in self-incompatible *Turnera ulmifolia*, substantial inbreeding depression has been demonstrated for vegetative and reproductive traits in several diploid populations (J. S. Shore and S. C. H. Barrett, unpublished data). However, the yield from bud selfs differs between the style morphs and the amount of seed obtained is generally low. An alternative approach for examining inbreeding depression in self-incompatible plants involves the use of sib-matings. This could be of particular interest in species with contrasting incompatibility systems since the control of sib-mating differs markedly between them.<sup>71</sup> Unfortunately, since different systems of incompatibility rarely, if ever, occur within related taxonomic groups, it seems likely that other factors (e.g., life history, dispersal mechanism, population size) would overwhelm effects on inbreeding that could be ascribed to the system of mating alone.

Olmstead<sup>66</sup> has recently considered the relationship between the breeding system of self-incompatible species and the level of inbreeding in populations. He proposes that the evolution and maintenance of self-incompatibility may have been largely independent of the level of inbreeding in the population as a whole. This is because the avoidance of selfing, the primary outcome of all self-incompatibility systems, has a negligible influence on the level of inbreeding in comparison with population size effects. Since many flowering plants are characterized by small effective population sizes and considerable genetic substructure, they are likely to experience considerable inbreeding. Olmstead argues that inbreeding has beneficial effects (reduced cost of meiosis, maintenance of coadapted gene complexes), and an optimal level exists in plant populations. Following this view, the maintenance of self-incompatibility primarily results from differences in the relative fitness of selfed and outcrossed progeny, not from any positive influence brought about by increased outbreeding.

#### *Number and Frequency of S Alleles*

The number and frequency of *S* alleles that can be maintained in finite populations of self-incompatible plants with multiallelic systems has been the subject of extensive theoretical treatment<sup>133</sup> but little empirical work. Until the recent studies by Lawrence and co-workers on the field poppy, *Papaver rhoeas*,<sup>65</sup> the sum total of our knowledge was based on Emerson's pioneering work on *Oenothera organensis*<sup>48,49</sup> and the less detailed studies of *Trifolium repens*<sup>3</sup> and *Trifolium pratense*.<sup>129</sup>

Work on *Papaver rhoeas*<sup>24,25,65</sup> is sufficiently detailed so that the data can be compared validly with those of Emerson. The first point is that in both studies similar numbers of *S* alleles were found within populations of the two species. However, while in *Oenothera organensis* the frequency of *S* alleles was not significantly different, in *Papaver rhoeas* large differences in frequency were evident in each of three populations examined (Fig. 5.2). Two hypotheses could account for the unequal frequencies of *S* alleles in *Papaver rhoeas* populations. The first proposes that the alleles are subject to selection unrelated to that associated with the incompatibility system, either directly or via close linkage with other genes. The alternative hypothesis invokes random genetic drift, associated with repeated colonizing episodes, and assumes that populations were not at equilibrium when sampled. While the first hypothesis predicts

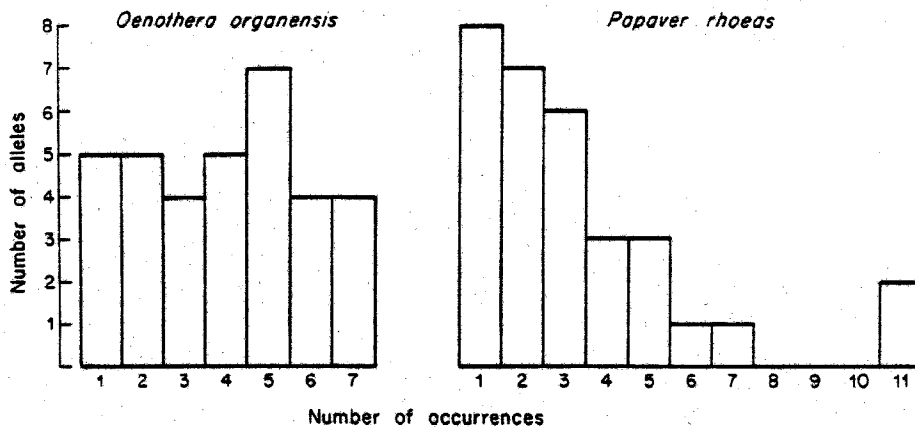


Fig. 5.2. Distribution of *S*-alleles in populations of *Oenothera organensis* and *Papaver rhoeas*. (After Emerson<sup>49</sup> and Campbell and Lawrence.<sup>25</sup>)

that the same alleles will occur at high frequency in different populations, the second does not. The fact that *Papaver rhoeas* is a weed of arable land and disturbed sites certainly appears to favor the nonequilibrium hypothesis since weed species are usually subject to repeated colonizing episodes. However, the number of *S* alleles found in each of the three populations is large,<sup>26,30,31</sup> suggesting that genetic bottlenecks may be of less importance than might be indicated from a consideration of the population ecology of the species.

Lawrence and O'Donnell<sup>65</sup> believe that, despite its weedy tendencies, *Papaver rhoeas* is a permanent and stable member of arable weed communities and that the large dormant seed bank found in the species may buffer populations against the chance effects associated with restrictions of population size. The cause(s) of the differences in *S* allele frequencies within populations, therefore, still remains unresolved. Cross-classification of *S* alleles among populations is necessary to determine if the same alleles predominate in different populations. If this turns out to be the case, differential selection among heterozygotes may be involved.

### *Mating Groups in Heterostylous Species*

Identification of mating types in species with homomorphic incompatibility can be ascertained only by extensive pollination programs, and this probably accounts for the paucity of data from natural populations. In contrast the frequencies of mating types in species with heteromorphic incompatibility can be readily obtained by visual inspection of plants within populations. In addition, equilibrium genotype frequencies at the heterostyly loci can also be determined, although in tristylous species this involves progeny testing and complex mathematical analysis.<sup>61</sup>

There is considerable information on the population structure of both distylous and tristylous species. Survey data from distylous populations typically indicate that the long- and short-styled morphs are equally frequent (isoplethy), although in some species unequal morph frequencies (anisoplethy) are a feature of populations.<sup>68,89</sup> Owing to the rarity of floral trimorphism, there are fewer observations of tristylous

species, and both isoplethic and anisoplethic population structures are reported.<sup>14</sup> Studies of style morph frequency in heterostylous plants are of special interest because they can provide information on the dynamics of selection at the loci controlling mating system.<sup>8,28</sup>

Heuch<sup>58,59</sup> has shown theoretically that, provided no fitness differences among the style morphs occur, an isoplethic equilibrium is the only possible condition in large populations with disassortative mating. This outcome follows from the genetic systems that govern heterostyly. Where unequal morph frequencies prevail, several possible factors may be involved. These can include founder effects and clonal propagation,<sup>11</sup> mating asymmetries among the style morphs,<sup>8,94</sup> differential selfing owing to relaxation of self-incompatibility,<sup>29</sup> or modification and breakdown of heterostyly.<sup>8,28,117</sup>

Of interest to problems concerned with the maintenance of heteromorphic incompatibility is a consideration of the minimum population size required for the polymorphisms to remain stable. This issue is relevant mainly to tristylous species because of their complex systems of inheritance. In a study of 16 populations of tristylous *Lythrum salicaria* on Finnish islands, Halkka and Halkka<sup>56</sup> found that the three style morphs were present in all populations, despite their small size. They concluded that gene flow between the islands must be frequent in order for populations to remain tristylous. However, as Heuch<sup>60</sup> has shown theoretically, the genetic system governing tristily in *Lythrum salicaria* can remain stable in isolated populations consisting of as few as 20 plants. Loss of style morphs occurs with regularity in populations below this size, and when this happens the short-styled morph is lost more frequently, since the dominant *S* allele governing this phenotype is only carried by short-styled plants. Fluctuations in population size, associated with colonizing episodes and drought, are postulated as the major factor leading to deficiency and loss of this morph from populations of tristylous *Eichhornia* species.<sup>8,11</sup>

### ***Function of Floral Polymorphisms in Heterostylous Species***

Although mating types in self-incompatible species are maintained in populations by frequency-dependent selection, it is by no means clear what selective forces are responsible for the evolution and maintenance of the complementary set of floral polymorphisms that is associated with the incompatibility groups in heterostylous species.<sup>51,132</sup> The most widely accepted explanation of the functional significance of floral heteromorphism was originally formulated by Darwin,<sup>42</sup> who hypothesized that the reciprocal placement of stamens and styles in the floral morphs is a mechanical device to promote insect-mediated cross-pollination among morphs with anthers and stigmas at equivalent levels (legitimate pollination). Although statistically significant levels of legitimate pollination have been demonstrated in both distylous<sup>50</sup> and tristylous<sup>12</sup> species, in many studies heterostyly appears to have little effect on pollination patterns. With random pollination, however, sufficient numbers of compatible pollen grains are usually deposited on naturally pollinated stigmas of heterostylous plants to ensure maximum seed set.<sup>72</sup>

Observations of random pollination in heterostylous species have led to the development of several alternative hypotheses to explain the maintenance of heterostyly. These hypotheses view heterostyly as a floral mechanism that (1) reduces self-pollination,<sup>82</sup> (2) is maintained by sexual selection and the optimal allocation of sexual

resources,<sup>77,112,126</sup> (3) avoids mutual pollen-stigma interference and stigmatic clogging,<sup>77,116</sup> and (4) enhances pollen carryover.<sup>115</sup> A major challenge will be to devise experimental tests to distinguish among these hypotheses. It is possible that in some heterostylous species the floral polymorphisms are selectively neutral under contemporary conditions and are maintained because of a close developmental association with the incompatibility system. More information on the developmental genetics of heterostyly is required to assess this possibility. Dulberger<sup>45</sup> and Richards and Barrett<sup>97</sup> discuss the developmental relationships between the floral polymorphisms and incompatibility in heterostylous species.

## MODIFICATION AND LOSS OF INCOMPATIBILITY

Comparative studies of closely related taxa with contrasting breeding systems provide strong evidence for the repeated loss of self-incompatibility in flowering plants.<sup>109</sup> The tendency of incompatibility loci to mutate toward increased self-compatibility has been demonstrated in both homomorphic and heteromorphic systems.<sup>70,85,107</sup> Various types of genetic modification leading to self-compatibility occur. These include (1) mutation of the incompatibility gene(s), (2) alteration of the genetic background in which *S* alleles function, (3) occurrence of polyploidy in gametophytic systems (excluding *Ranunculus*, *Beta*, and monocotyledons), and (4) homostyle formation in distylous species as a result of crossing-over in the supergene controlling the heterostylous syndrome. Whether or not self-compatible variants establish and spread is dependent on their ability to compete with their outbreeding progenitors or establish in novel environments.<sup>62,76</sup> Inbreeding depression is likely to be the major factor restricting spread, particularly if population sizes are large in the outcrossing progenitor, resulting in high genetic loads. Sporadic pollinator failure in zoophilous species and population bottlenecks on a time scale of less than 100 generations can, however, promote selection for a highly self-fertilizing mode of reproduction since these processes reduce genetic load and hence the magnitude of inbreeding depression.<sup>64</sup> Of course, mutations at incompatibility loci do not necessarily mean that self-compatible individuals are self-fertilizing. The degree of selfing will depend on a range of factors of which floral morphology and the abundance of pollen vectors are usually the most important.<sup>100</sup>

### *Homomorphic Incompatibility*

Among homomorphic systems, loss of self-incompatibility has been particularly well documented in *Leavenworthia*, in which several species (e.g., *Leavenworthia crassa* and *Leavenworthia alabamica*) exhibit both self-incompatible and self-compatible populations.<sup>99</sup> Self-compatible populations have developed adaptations (e.g., introrse anthers, small flower size) that increase the efficiency of self-pollination. These have been documented in detail by Lloyd.<sup>74</sup> In some cases, loss of self-incompatibility may be associated with speciation, as has been proposed for *Stephanomeria malheurensis*<sup>55</sup> and *Lasthenia maritima*.<sup>35</sup> In both cases, it appears that genetic modifications at loci governing sporophytic incompatibility have initiated the events leading to reproductive isolation. In neither case is the genetic basis of the change in incompatibility behavior known. The genetic basis of self-compatibility in *Stephanomeria* has recently been investigated (see Brauner and Gottlieb<sup>28a</sup>).

Most of the detailed information on genetic modifications at incompatibility loci in homomorphic systems is based on studies of agricultural and horticultural plants.<sup>85</sup> Plant breeders have endeavored to select for self-compatibility to facilitate production of homozygous lines. Unfortunately, there is relatively little information on the variation in expression of self-incompatibility in populations of most wild species. Occasional self-compatible individuals in normally self-incompatible species (pseudocompatibility) have been studied in detail by Ascher.<sup>73,98</sup> The extent of this variation in natural populations, how it is maintained, and its influence on the mating system of populations are largely unknown.

### *Breakdown of Dimorphic Incompatibility*

While the evolution of heteromorphic incompatibility systems presents a complex problem that is still poorly understood,<sup>29,32</sup> breakdown of these genetic polymorphisms has been documented in many heterostylous families.<sup>28,31</sup> Modifications include replacement of one type of outcrossing mechanism by another, such as the evolution of distyly from tristily (see below) and the origin of dioecism from distyly.<sup>18,75</sup> More frequently, heterostylous systems break down in the direction of increased self-fertilization by the formation of homostylous population systems. Two recent studies of this shift in breeding system illustrate how similar genetic pathways can result in different outcomes with regard to the mating system.

The breakdown of distyly to homostyly in *Primula* is one of the classic examples of the evolution of self-fertilization in flowering plants. Homostyles are interpreted as products of crossing-over within the supergene that controls heterostyly. The product is an allelic combination and phenotype, which combines the style length and compatibility group of one morph with the stamen length and compatibility of the alternate morph. Homostyles are thus self-pollinating, due to the close proximity of sexual organs, and self-compatible.

Whether or not homostylous variants will spread following their origin depends on several factors, including the mating system of morphs, the relative fitness of their progeny, and the availability of pollinating agents.<sup>28</sup> A controversy exists concerning the presence of locally high frequencies of homostylous variants in populations of *Primula vulgaris* in two regions of England (Somerset and the Chilterns). Crosby's early studies<sup>36,37</sup> predicted that homostylous variants would increase in frequency and eventually replace the distylous morphs as a result of their high selfing rates. This view was disputed by Bodmer,<sup>20,21</sup> who suggested, based on garden studies, that homostyles were up to 80% outcrossed as a result of marked protogyny. Two recent studies have clarified some of these issues. Using isozyme loci as genetic markers, Piper *et al.*<sup>34,35</sup> have shown in several populations that the homostylous morph is highly self-fertilizing ( $s = 0.92$ ) while, as expected, the long- and short-styled morphs are highly outcrossed (and see Cahalan and Gliddon<sup>29</sup>). Comparison of several components of fitness in natural populations (e.g., flower production, seeds per capsule, total seed production) demonstrated that homostyles were significantly more fertile than the other morphs. However, this difference varied in both time and space, owing to fluctuations in pollinator service due to differences in rainfall. Although surveys of *Primula* populations in Somerset have been conducted over a 25- to 40-year period,<sup>40</sup> they indicate only small changes in morph frequency, preventing any firm conclusion about whether a stable equilibrium has been reached, or whether homostyles are slowly replacing the



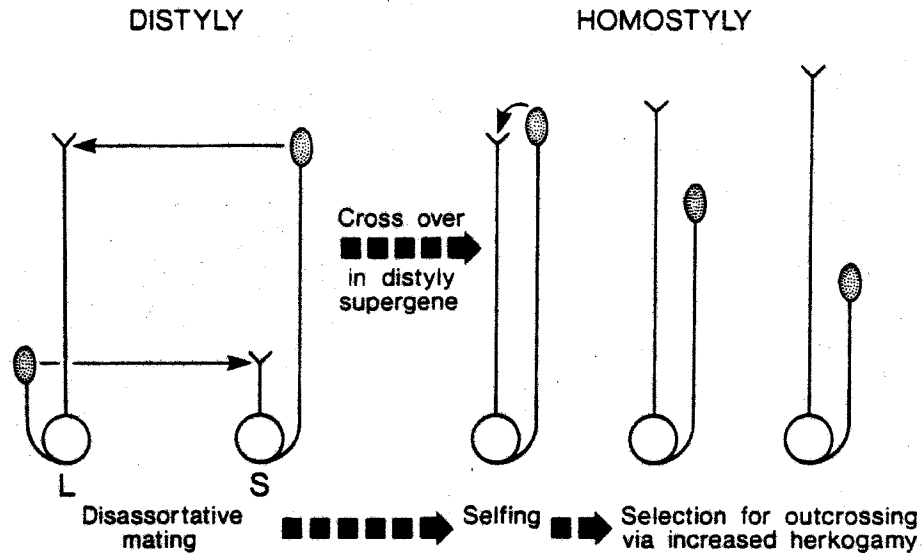


Fig. 5.3. Breeding system evolution in the *Turnera ulmifolia* complex. (For details see Barrett and Shore.<sup>13</sup>)

distylous morphs. Clearly, without long-term demographic work, it is extremely difficult to provide conclusive evidence about the net direction of selection on the mating system, particularly in long-lived perennial plants.

There are many cases in which the close relatives of heterostylous taxa are homostylous. This suggests that the shift in breeding system from outcrossing to selfing may be frequently associated with speciation events. Homostylous taxa are often found at the geographical margins of the progenitor's range, raising the possibility that reduced pollinator service may have favored their establishment and spread. This geographical pattern is evident in *Turnera ulmifolia*, a Neotropical polyploid complex of perennial weeds. Our studies of this group<sup>4,13,105-107</sup> have revealed the striking lability of breeding systems and cast doubt on the frequently held view that the evolution of selfing involves a unidirectional change (Fig. 5.3).

The *Turnera ulmifolia* complex is composed of diploid, tetraploid, and hexaploid varieties. Diploids and tetraploids exhibit typical dimorphic incompatibility, whereas hexaploids are self-compatible and homostylous.<sup>13,105</sup> The three homostylous varieties of *Turnera ulmifolia* that we have studied experimentally are differentiated for morphological traits and isozyme patterns as well as being intersterile. They occur at different margins of the range of the species complex, indicating that dimorphic incompatibility has broken down to homostyly on at least three separate occasions in the complex, always in association with the hexaploid condition. The reason for the association between homostyly and hexaploidy is unclear. Hexaploids synthesized using colchicine remain distylous, indicating that at its inception hexaploidy per se does not cause homostyle formation.<sup>107</sup>

Cytological studies indicate that while tetraploid varieties in the complex form quadrivalents and appear to be autopolyploids, hexaploids form bivalents and are therefore likely to be allopolyploids. Evidence to support this comes from isozyme studies,

which indicate that tetraploids exhibit tetrasomic inheritance for enzyme loci, whereas hexaploids display considerable fixed heterozygosity (J. S. Shore and S. C. H. Barrett, unpublished data). This raises the possibility that, following their origin, homostyles might spread more easily in hexaploid populations as a result of a reduction in the magnitude of inbreeding depression associated with allopolyploidy. Lande and Schemske<sup>64</sup> consider the influence of polyploidy on inbreeding depression.

The patterns of floral variation in *Turnera ulmifolia* are particularly complex in the Caribbean region. On large islands (e.g., Greater Antilles) populations are either tetraploid and distylous or hexaploid and homostylous. However, on smaller islands (e.g., Bahamas) only homostyles occur. Presumably, repeated colonizing episodes and the facility for establishment after long-distance dispersal favor homostyles over the self-incompatible distylous morphs in island colonization. On Jamaica, populations are uniformly hexaploid and self-compatible but display a range of floral phenotypes from long homostyle (long stamens and long styles) to plants with flowers resembling those of the typical long-styled morph from distylous populations. Barrett and Shore<sup>13</sup> interpret these latter phenotypes as resulting from selection for outcrossing in homostylous colonists (Fig. 5.4). This may be more readily achieved by the development of herkogamy (spatial separation of stigmas and anthers) in homostylous stocks, through selection on polygenic variation, than by the de novo development of alternative outbreeding mechanisms.

To test the hypothesis that the range of homostylous floral variants on Jamaica is secondarily derived from distylous ancestors, crosses between homostylous and distylous forms were conducted.<sup>13</sup> The predicted crossing relationships from the cross-over model for the origin of homostyly were revealed in all floral phenotypes (see Table 4 in Ref. 51). Hence, despite possessing "short-level" anthers, the herkogamous populations exhibit the residual incompatibility reaction of long-level anthers of the short-styled morph. It is remarkable that, despite the absence of distylous populations on Jamaica, both the pistils and pollen of homostylous forms retain their ancestral incompatibility behavior. Unlike unilateral interspecific incompatibility,<sup>45</sup> the incompatibility behavior expressed in crosses between heterostylous and homostylous forms is usually reciprocal in nature.

Although there is no evidence of changes in floral traits owing to selection for outcrossing in homostylous variants of *Primula vulgaris*, this may have occurred in other taxa in the genus. Many monomorphic relatives of heterostylous *Primula* species are known that possess large flowers and outcrossing adaptations. Similar patterns are also evident in *Linum*.<sup>79</sup> Whether homostyles maintain selfing or redevelop outcrossing adaptations may depend in part on the capacity of other components of the genetic system to influence recombination, as well as local selection pressures favoring outcrossing.

In both of the above examples, the breakdown of dimorphic incompatibility arises as a result of recombination in the supergene that controls distyly. This may not be the only genetic pathway by which incompatibility can be modified, as a number of distylous taxa are known in which the style morphs are highly self-compatible.<sup>51</sup> Since it seems unlikely that floral dimorphism can evolve in the absence of incompatibility,<sup>32</sup> these taxa have most likely secondarily lost their incompatibility systems. The genetic basis of self-compatibility in these taxa has not been studied in detail. Shore and Barrett<sup>107</sup> have examined the inheritance of a range of self-compatible variants in

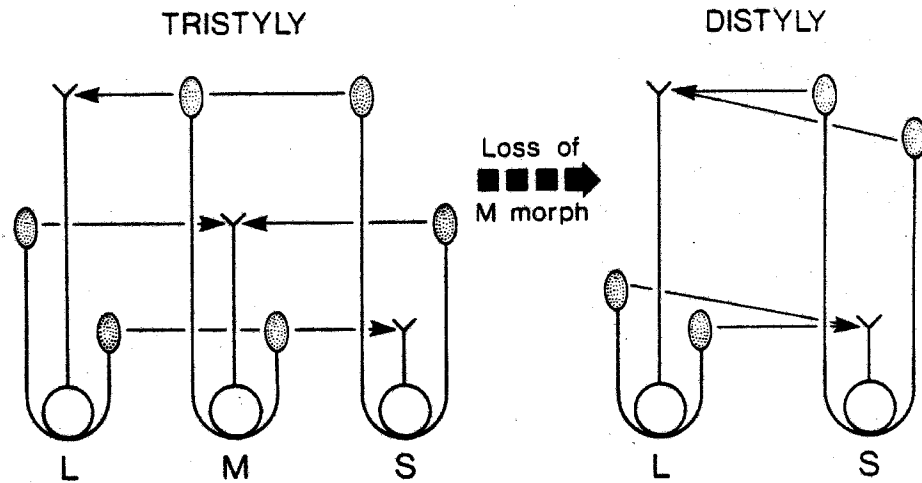


Fig. 5.4. Evolution of distyly from tristyly in *Oxalis alpina*. (For details see Weller.<sup>117</sup>)

distylous *Turnera ulmifolia* populations. The variants display varying degrees of self-compatibility as a result of either aberrant style or pollen behavior and the genetic control of compatibility behavior is polygenic in nature.

#### **Modification and Loss of Trimorphic Incompatibility**

Modification and loss of trimorphic incompatibility have been reported from each of the three tristylous families.<sup>29</sup> Current work on two cases illustrates the complexity of these systems; the first involves the multiple origins of distyly from tristyly in *Oxalis* and the second the evolution of selfing in *Eichhornia*.

In both the Lythraceae and Oxalidaceae, distyly is derived from tristyly by loss of one of the style morphs. The most detailed investigations of this change in breeding system are those of Weller<sup>117-123</sup> on *Oxalis alpina* (Fig. 5.4). In populations of this species from southeast Arizona, the mid-styled morph ranges in frequency from 0–46%. Where populations exhibit high frequencies of this morph, the floral architecture and incompatibility relationships of the morphs are typical of most taxa with trimorphic incompatibility. However, in populations in which the mid-styled morph is rare or absent the reproductive morphology and incompatibility behavior of the long- and short-styled morphs are typical of distylous species.<sup>117</sup> Crossing studies<sup>120</sup> among populations with the two breeding systems indicate that distylous populations have diverged more substantially from one another than have tristylous populations. This pattern is consistent with the view that contrasting selection pressures in populations have resulted in the evolution of distyly in some and the retention of tristyly in others.

The difficulty arises in trying to determine the selective forces responsible for loss of the mid-styled morph from populations. Weller has examined a number of hypotheses, and several have been clearly falsified. These include preferential foraging by pollinators on the style morphs<sup>121</sup> and differences in clonal propagation and ovule and seed fertility of the morphs.<sup>127</sup> The most likely hypothesis concerns the loss of incompatibility differentiation in mid-level stamens of the long- and short-styled morphs.<sup>117</sup> This could favor these forms as male parents, since pollen capable of fer-

tilizing their ovules would be more likely derived from these morphs than from the mid-styled morph. However, detailed progeny tests conducted over a 3-year period that had been designed specifically to evaluate this hypothesis gave unexpected results.<sup>123</sup> The mid-styled morph was disproportionately represented in families derived from this morph, and there was no clear evidence of its reduced male fertility as anticipated. The progeny test results also indicated large deficiencies of the short-styled morph in mid-styled families and suggested that anomalous transmission of alleles at the *S* and *M* loci may occur. To detect the differential transmission of alleles by gametophytic selection during megasporogenesis or through embryo abortion, controlled crosses among known genotypes and progeny analysis will be required. At this time it is too early to evaluate whether or not these phenomena are involved in the origin of distyly, but it is difficult to believe that the loss of incompatibility differentiation in tristylous populations has no role to play. Several other cases of genetic modification of trimorphic incompatibility in the genus *Oxalis* are equally difficult to interpret.<sup>67,67</sup>

Breakdown of trimorphic incompatibility in the Pontederiaceae involves the repeated shift to semihomostyly and selfing,<sup>8</sup> rather than the evolution of distyly or other outcrossing systems. These changes may or may not be associated with speciation events. In species in which incompatibility is maintained, as in the genus *Pontederia*, it is variable in expression, with the mid-styled morph displaying a high level of self-compatibility in comparison with the long- and short-styled morphs.<sup>10</sup> Barrett and Anderson<sup>10</sup> have proposed a developmental model to explain the weak expression of self-incompatibility in the mid-styled morph and discuss its implications for the breakdown of tristily.

In *Eichhornia*, floral trimorphism is associated with high levels of self-compatibility and the occurrence of autogamous semihomostylous variants in each of the tristylous species.<sup>5,6,9</sup> The breakdown process has been studied in detail in *Eichhornia paniculata*, in which populations exhibit modifications ranging from complete tristily in northeast Brazil to semihomostyly on the island of Jamaica. Proposed stages in the breakdown process are illustrated in Fig. 5.5. Critical events involve loss of the *S* allele (and hence the short-styled morph) through stochastic influences on population size

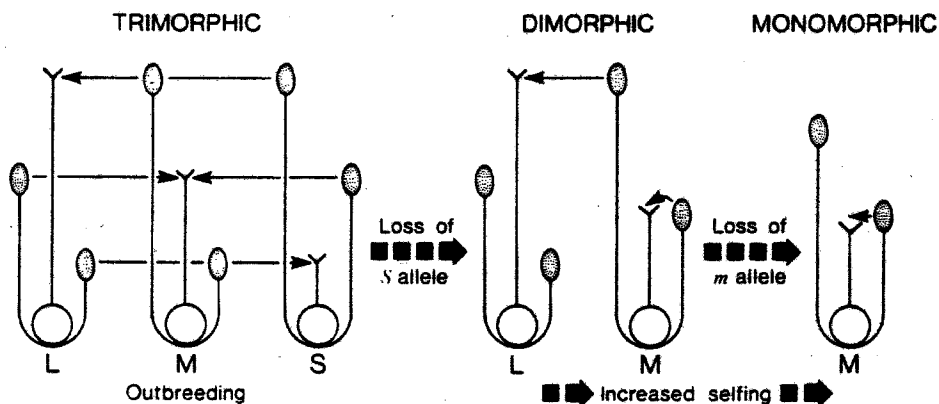


Fig. 5.5. Evolutionary breakdown of tristily to semihomostyly in *Eichhornia paniculata*. (For details see Barrett<sup>8</sup> and Glover and Barrett.<sup>52</sup>)

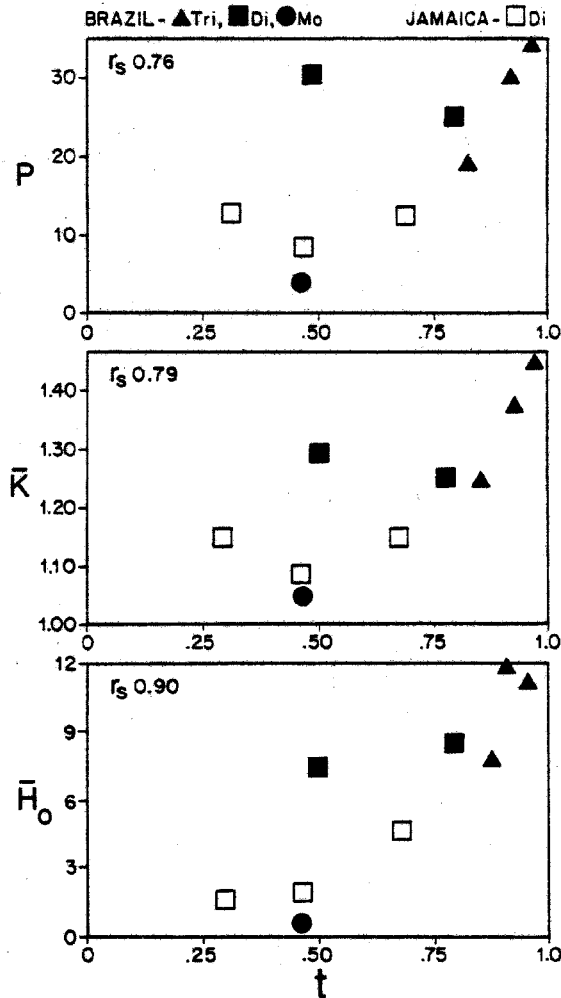


Fig. 5.6. The relationship between outcrossing rate ( $t$ ) and several population genetic parameters ( $P$  = proportion of loci polymorphic,  $\bar{K}$  = mean number of alleles per locus,  $\bar{H}_0$  = mean observed heterozygosity) in populations of *Eichhornia paniculata*. (After Glover and Barrett.<sup>53</sup>)

and loss of the  $m$  allele (and hence the long-styled morph) in association with the automatic selection of genes modifying the position of short-level stamens in the mid-styled morph.<sup>8</sup> All monomorphic populations so far examined are composed exclusively of semihomostylous mid-styled individuals. These populations are frequently small, suggesting that the facility for self-pollination is advantageous at low density.

The breakdown of tristylty in *Eichhornia paniculata* involves a shift in mating system from predominant outcrossing to high levels of selfing. This has been verified by multilocus estimates of outcrossing rate, using isozyme loci as genetic markers.<sup>52</sup> Lack of electrophoretically detectable isozyme variation in semihomostylous populations from Jamaica precluded quantitative estimates of their mating systems. However, the

lack of variation and the highly autogamous behavior suggest that they are predominantly selfing. Associated with the evolutionary change in mating system of *Eichhornia paniculata* is a reduction in levels of genetic variation and heterozygosity (Fig. 5.6). Tristyloous populations are significantly more variable than dimorphic or monomorphic populations.<sup>53</sup> The breakdown of tristily in *Eichhornia* species depends in large part on the initial relaxation of self-incompatibility. Self-compatible populations are likely to be more sensitive to demographic and ecological factors (e.g., plant density, pollinator levels) that influence mating patterns. While it is evident that populations of species with trimorphic incompatibility contain considerable genetic variation for self-compatibility,<sup>10</sup> it is not obvious how this variation is maintained and what selective factors lead to its eventual loss independently of changes in floral form.

## CONCLUSIONS

Self-incompatibility systems in flowering plants can be classified according to different criteria including the time of gene action, the inhibition site of self-pollen tubes, the association with floral polymorphism, and the number of loci and alleles governing the incompatibility reaction. Future research on this diversity is likely to benefit considerably from recent advances in molecular biology. Molecular characterization of incompatibility systems through the use of recombinant DNA technologies<sup>54</sup> and comparison of gene homologies in contrasting systems (sporophytic versus gametophytic and homomorphic versus heteromorphic) by hybridization techniques should enable a more rigorous assessment of phylogenetic relationships. Other topics that are likely to provide promising avenues for research include (1) clarification of the general properties (genetics, inhibition mechanisms) of "late-acting" and "cryptic" self-incompatibility systems, (2) evaluation of the role of inbreeding depression in the maintenance of self-incompatibility, (3) estimation of mating system parameters (e.g., levels of inbreeding through sib-mating) in populations of self-incompatible species, and (4) ecological, demographic, and life history correlates of different self-incompatibility systems. It will be of particular interest to see whether the classical view of self-incompatibility as an outbreeding mechanism survives the challenge of alternative hypotheses that will undoubtedly be formulated in the coming years.

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## REFERENCES

1. Anderson, J. M., and Barrett, S. C. H., Pollen tube growth in tristylous *Pontederia cordata* L. (Pontederiaceae), *Can. J. Bot.* **64**, 2602-2607 (1986).
2. Arasu, N. N., Self-incompatibility in angiosperms: A review, *Genetica* **39**, 1-24 (1968).
3. Atwood, S. S., Oppositional alleles in natural populations of *Trifolium repens*, *Genetics* **29**, 428-435 (1944).

4. Barrett, S. C. H., Heterostyly in a tropical weed: The reproductive biology of the *Turnera ulmifolia* complex (Turneraceae), *Can. J. Bot.* **56**, 1713–1725 (1978).
5. Barrett, S. C. H., The floral biology of *Eichhornia azurea* (Swartz) Kunth (Pontederiaceae), *Aquat. Bot.* **5**, 217–228 (1978).
6. Barrett, S. C. H., The evolutionary breakdown of tristily in *Eichhornia crassipes* (Mart.) Solms. (water hyacinth), *Evolution* **33**, 499–510 (1979).
7. Barrett, S. C. H., Sexual reproduction in *Eichhornia crassipes* (Water Hyacinth) I. Fertility of clones from diverse regions, *J. Appl. Ecol.* **17**, 101–112 (1980).
8. Barrett, S. C. H., Ecological genetics of breakdown in tristily, in *Structure and Functioning of Plant Populations. 2. Phenotypic and Genotypic Variation in Plant Populations* (I. Haeck and J. W. Woldendorp, eds.), pp. 267–275. North-Holland Publ. Co., Amsterdam, 1985.
9. Barrett, S. C. H., Floral trimorphism and monomorphism in continental and island populations of *Eichhornia paniculata* (Spreng.) Solms. (Pontederiaceae), *Biol. J. Linn. Soc.* **25**, 41–60 (1985).
10. Barrett, S. C. H., and Anderson, J. M., Variation in expression of trimorphic incompatibility in *Pontederia cordata* L. (Pontederiaceae), *Theor. Appl. Genet.* **70**, 355–362 (1985).
11. Barrett, S. C. H., and Forno, I. W., Style morph distribution in New World populations of *Eichhornia crassipes* (Mart.) Solms-Laubach (Water Hyacinth), *Aquat. Bot.* **13**, 299–306 (1982).
12. Barrett, S. C. H., and Glover, D. E., On the Darwinian hypothesis of the adaptive significance of tristily, *Evolution* **39**, 766–774 (1985).
13. Barrett, S. C. H., and Shore, J. S., Variation and evolution of breeding systems in the *Turnera ulmifolia* complex (Turneraceae), *Evolution* **41**, 340–354 (1987).
14. Barrett, S. C. H., Price, S. D., and Shore, J. S., Male fertility and anisoplethic population structure in tristylous *Pontederia cordata* (Pontederiaceae), *Evolution* **37**, 745–759 (1983).
15. Bateman, A. J., Self-incompatibility systems in angiosperms, I: Theory, *Heredity* **6**, 285–310 (1952).
16. Bateman, A. J., Cryptic self-incompatibility in the wallflower: *Cheiranthus cheiri* L., *Heredity* **10**, 257–261 (1956).
17. Bawa, K. S., and Beach, J. H., Self-incompatibility systems in the *Rubiaceae* of a tropical lowland forest, *Am. J. Bot.* **70**, 1281–1288 (1983).
18. Beach, J. H., Pollinator foraging and the evolution of dioecy, *Am. Nat.* **118**, 572–577 (1981).
19. Beach, J. H., and Kress, W. J., Sporophyte versus gametophyte: A note on the origin of self-incompatibility in flowering plants, *Syst. Bot.* **5**, 1–5 (1980).
20. Bodmer, W. F., Natural crossing between homostyle plants of *Primula vulgaris*, *Heredity* **12**, 363–370 (1958).
21. Bodmer, W. F., Genetics of homostyly in populations of *Primula vulgaris*, *Phil. Trans. R. Soc. London, B* **242**, 517–549 (1960).
- 21a. Brauner, S., and Gottlieb, L. D., A self-incompatible plant of *Stephanomeria exigua* sub sp. *coronaria* (Asteraceae) and its relevance to the origin of its self-pollinating derivative *F. malheurensis*, *Systematic Botany* **12**, 299–304 (1987).
22. Brewbaker, J. L., Pollen cytology and incompatibility systems in plants, *J. Hered.* **48**, 217–277 (1957).
23. Cahalan, C. M., and Gliddon, C., Genetic neighbourhood sizes in *Primula vulgaris*, *Heredity* **54**, 65–70 (1985).
24. Campbell, J. M., and Lawrence, M. J., The population genetics of the self-incompatibility polymorphism in *Papaver rhoeas*. I. The number and distribution of S-alleles in families from three localities, *Heredity* **46**, 69–79 (1981).
25. Campbell, J. M., and Lawrence, M. J., The population genetics of the self-incompatibility polymorphism in *Papaver rhoeas*. II. The number and frequency of S-alleles in a natural population (R106), *Heredity* **46**, 81–90 (1981).
26. Casper, B. B., Self-compatibility in distylous *Cryptantha flava* (Boraginaceae), *New Phytol.* **99**, 149–154 (1985).
27. Casper, B. B., and Charnov, E. L., Sex allocation in heterostylous plants, *J. Theor. Biol.* **96**, 143–149 (1982).
28. Charlesworth, B., and Charlesworth, D., The maintenance and breakdown of heterostyly, *Am. Nat.* **114**, 499–513 (1979).
29. Charlesworth, D., The evolution and breakdown of tristily, *Evolution* **33**, 486–498 (1979).
30. Charlesworth, D., On the nature of the self-incompatibility locus in homomorphic and heteromorphic systems, *Am. Nat.* **119**, 732–735 (1982).
31. Charlesworth, D., Distribution of dioecy and self-incompatibility in angiosperms, in *Evolution—Essays*

- in Honour of John Maynard Smith (J. J. Greenwood and M. Slatkin, eds.), p. 237. Cambridge Univ. Press, Cambridge, 1985.
32. Charlesworth, D., and Charlesworth, B., A model for the evolution of heterostyly, *Am. Nat.* **114**, 467-498 (1979).
  33. Charnov, E. L., *The Theory of Sex Allocation, Monographs in Population Biology* No. 18. Princeton Univ. Press, Princeton, 1982.
  34. Cope, F. W., The mechanisms of pollen incompatibility in *Theobroma cacao* L., *Heredity* **17**, 157-182 (1962).
  35. Crawford, D. J., Ornduff, R., and Vasey, M. C., Allozyme variation within and between *Lasthenia minor* and its derivative species, *L. maritima* (Asteraceae), *Am. J. Bot.* **72**, 1177-1184 (1985).
  36. Crosby, J. L., Selection of an unfavourable gene-complex, *Evolution* **3**, 212-230 (1949).
  37. Crosby, J. L., Outcrossing on homostyle primroses, *Heredity* **13**, 127 (1959).
  38. Crowe, L. K., The polygenic control of outbreeding in *Borago officinalis*, *Heredity* **27**, 111-118 (1971).
  39. Crumpacker, D. W., Genetic loads in maize (*Zea mays* L.) and other cross-fertilized plants and animals, *Evol. Biol.* **1**, 1-131 (1967).
  40. Curtis, J., and Curtis, C. F., Homostyle primrose re-visited. I. Variation in time and space, *Heredity* **54**, 227-234 (1985).
  41. Darwin, C., *The Effects of Cross and Self Fertilization in the Vegetable Kingdom*. Appleton, New York, 1876.
  42. Darwin, C., *The Different Forms of Flowers on Plants on the Same Species*. Murray, London, 1877.
  43. Dulberger, R., Flower dimorphism and self-incompatibility in *Narcissus tazetta* L., *Evolution* **18**, 361-363 (1964).
  44. Dulberger, R., Floral dimorphism in *Anchusa hybrida* Ten., *Isr. J. Bot.* **19**, 37-41 (1970).
  45. Dulberger, R., S-gene action and the significance of characters in the heterostylous syndrome, *Heredity* **35**, 407-415 (1975).
  46. Dulberger, R., and Ornduff, R., Floral morphology and reproductive biology of four species of *Cyanella* (Tecophilaeaceae), *New Phytol.* **86**, 45-56 (1980).
  47. East, E. M., The distribution of self-sterility in flowering plants, *Proc. Am. Philos. Soc.* **82**, 449-518 (1940).
  48. Emerson, S., The genetics of self-incompatibility in *Oenothera organensis*, *Genetics* **23**, 190-202 (1938).
  49. Emerson, S., A preliminary survey of the *Oenothera organensis* population, *Genetics* **24**, 524-537 (1939).
  50. Ganders, F. R., Disassortative pollination in the distylous plant *Jepsonia heterandra*, *Can. J. Bot.* **52**, 2401-2406 (1974).
  51. Ganders, F. R., The biology of heterostyly, *N.Z. J. Bot.* **17**, 607-635 (1979).
  52. Glover, D. E., and Barrett, S. C. H., Variation in the mating system of *Eichhornia paniculata* (Spreng.) Solms. (Pontederiaceae), *Evolution* **40**, 1122-1131 (1986).
  53. Glover, D. E., and Barrett, S. C. H., Genetic variation in continental and island populations of *Eichhornia paniculata* (Pontederiaceae), *Heredity* **59**, 7-17 (1987).
  54. Godley, E. J., and Smith, D. H., Breeding systems in New Zealand plants *S. Pseudowintera colorata* (Winteraceae), *N.Z. J. Bot.* **19**, 151-156 (1981).
  55. Gottlieb, L. D., Genetic differentiation, sympatric speciation, and the origin of a diploid species of *Stephanomeria*, *Am. J. Bot.* **60**, 545-553 (1973).
  56. Halkka, O., and Halkka, L., Polymorphic balance in small island populations of *Lythrum salicaria*, *Ann. Bot. Fenn.* **11**, 267-270 (1974).
  57. Heslop-Harrison, J., Self-incompatibility: Phenomenology and physiology, *Proc. R. Soc. London*, **B 218**, 371-395 (1983).
  58. Heuch, I., Equilibrium populations of heterostylous plants, *Theor. Popul. Biol.* **15**, 43-57 (1979a).
  59. Heuch, I., The effect of partial self-fertilization on type frequencies in heterostylous plants, *Ann. Bot. (London)* **44**, 611-616 (1979b).
  60. Heuch, I., Loss of incompatibility types in finite populations of the heterostylous plant, *Lythrum salicaria*, *Hereditas* **92**, 53-57 (1980).
  61. Heuch, I., and Lie, R. T., Genotype frequencies associated with incompatibility systems in tristylous plants, *Theor. Popul. Biol.* **27**, 318-336 (1985).
  62. Jain, S. K., The evolution of inbreeding in plants, *Annu. Rev. Ecol. Syst.* **7**, 469-495 (1976).
  63. Knox, R. B., Heslop-Harrison, J., and Heslop-Harrison, Y., Pollen-wall proteins: Localization and characterization of gametophytic and sporophytic fractions, in *The Biology of the Male Gamete* (J. G. Duckett and P. A. Racey, eds.), p. 177. *Biol. J. Linn. Soc.* (1975).



64. Lande, R., and Schemske, D. W., The evolution of self-fertilization and inbreeding depression in plants. I. Genetic models. *Evolution* 39, 24-40 (1985).
65. Lawrence, M. J., and O'Donnell, S., The population genetics of the self-incompatibility polymorphism in *Papaver rhoeas*. III. The number and frequency of S-alleles in two further natural populations (R102 and R104). *Heredity* 47, 53-61 (1981).
66. Lawrence, M. J., Marshall, D. F., Curtis, V. E., and Fearon, C. H., Gametophytic self-incompatibility re-examined: A reply. *Heredity* 54, 131-138 (1985).
67. Leach, C. R., Fluctuations in heteromorphic self-incompatibility systems. *Theor. Appl. Genet.* 66, 307-312 (1983).
68. Levin, D. A., Plant density, cleistogamy and self-fertilization in natural populations of *Lithospermum caroliniense*. *Am. J. Bot.* 59, 71-77 (1972).
69. Levin, D. A., and Clay, K., Extraneous pollen advantage in *Phlox cuspidata*. *Heredity* 54, 145-148 (1985).
70. Lewis, D., Structure of the incompatibility gene. III. Types of spontaneous and induced mutation. *Heredity* 5, 399-414 (1951).
71. Lewis, D., *Sexual Incompatibility in Plants*. Edward Arnold, London, 1979.
72. Lewis, D., Incompatibility, stamen movement and pollen economy in a heterostyled tropical forest tree, *Craetoxylum formosum* (Guttiferae). *Proc. R. Soc. London, B* 214, 273-283 (1982).
73. Litzow, M. E., and Ascher, P. D., The inheritance of pseudo-self compatibility (PSC) in *Raphanus sativus* L., *Euphytica* 32, 9-15 (1983).
74. Lloyd, D. G., Evolution of self-compatibility and racial differentiation in *Leavenworthia* (Cruciferae). *Contrib. Gray. Herb.* 195, 3-134 (1965).
75. Lloyd, D. G., Evolution towards dioecy in heterostylous populations. *Plant Syst. Evol.* 131, 71-80 (1979).
76. Lloyd, D. G., Demographic factors and mating patterns in Angiosperms, in *Demography and Evolution of Plant Populations* (O. T. Solbrig, ed.), p. 67. Blackwell, Oxford, 1980.
77. Lloyd, D. G., and Yates, J. M. A., Intrasexual selection and the segregation of pollen and stigmas in hermaphrodite plants, exemplified by *Wahlenbergia albomarginata* (Campanulaceae). *Evolution* 36, 903-913 (1982).
78. Lundquist, A., Complex self-incompatibility systems in angiosperms. *Proc. R. Soc. London, B* 188, 235-245 (1975).
79. Mosquin, T., Biosystematic studies in the North American species of *Linum*, section *Adenolinum* (Linaceae). *Can. J. Bot.* 49, 1379-1388 (1971).
80. Muenchow, G., An S-locus model for the distyly supergene. *Am. Nat.* 118, 756-760 (1981).
81. Muenchow, G., A loss-of-alleles model for the evolution of distyly. *Heredity* 49, 81-93 (1982).
82. Mulcahy, D. L., and Caporello, D., Pollen flow within a tristylous species: *Lythrum salicaria*. *Am. J. Bot.* 57, 1027-1030 (1970).
83. Mulcahy, D. L., and Mulcahy, G. B., Gametophytic self-incompatibility reexamined. *Science* 220, 1247-1251 (1983).
84. Nasrallah, J. B., Kao, T. H., Goldberg, M. L., and Nasrallah, M. E., A cDNA clone encoding an S-locus-specific glycoprotein from *Brassica oleracea*. *Nature (London)* 318, 263-267 (1985).
85. Nettancourt, D. de, *Incompatibility in Angiosperms*. Springer-Verlag, Berlin, 1977.
86. Olmstead, R. G., Self-incompatibility in light of population structure and inbreeding, in *Biotechnology and Ecology of Pollen* (D. L. Mulcahy et al., eds.), p. 239. Springer-Verlag, New York, 1986.
87. Ornduff, R., The breeding system of *Oxalis suksdorfii*. *Am. J. Bot.* 51, 307-314 (1964).
88. Ornduff, R., Heterostyly in South African flowering plants: A conspectus. *J. South Afr. Bot.* 40, 169-187 (1974).
89. Ornduff, R., Heterostyly, population composition and pollen flow in *Hedyotis caerulea*. *Am. J. Bot.* 67, 95-103 (1980).
90. Ornduff, R., and Dulberger, R., Floral enantiomorphy and the reproductive system of *Wachendorfia paniculata* (Haemodoraceae). *New Phytol.* 80, 427-434 (1978).
91. Osterbye, U., Self-incompatibility in *Ranunculus acris* L. I. Genetic interpretation and evolutionary aspects. *Hereditas* 80, 91-112 (1975).
92. Pandey, K. K., Overcoming incompatibility and promoting genetic recombination in flowering plants. *N.Z. J. Bot.* 17, 645-663 (1979).
93. Philipp, M., and Schou, O., An unusual heteromorphic incompatibility system: Distyly, self-incompatibility, pollen load and fecundity in *Anchusa officinalis* (Boraginaceae). *New Phytol.* 89, 693-703 (1981).

94. Piper, J. G., Charlesworth, B., and Charlesworth, D., Breeding system evolution in *Primula vulgaris* and the role of reproductive assurance, *Heredity* 56, 207-217 (1986).
95. Piper, J. G., Charlesworth, B., and Charlesworth, D., A high rate of self-fertilization and increased seed fertility of homostyle primroses, *Nature (London)* 310, 50-51 (1984).
96. Richards, A. J., and Ibrahim, H. B. T., The breeding system in *Primula veris* L. II. Pollen tube growth and seed set, *New Phytol.* 90, 305-314 (1982).
97. Richards, J. H., and Barrett, S. C. H., The developmental basis of tristylly in *Eichhornia paniculata* (Pontederiaceae), *Am. J. Bot.* 71, 1347-1363 (1984).
98. Robacker, C. D., and Ascher, P. D., Effect of selection for pseudo-self-compatibility in advanced inbred generations of *Nemesia strumosa* Benth, *Euphytica* 31, 591-610 (1982).
99. Rollins, R. C., The evolution and systematics of *Leavenworthia* (Cruciferae), *Contrib. Gray. Herb.* 192, 3-98 (1963).
100. Schemske, D. W., and Lande, R., The evolution of self-fertilization and inbreeding depression in plants. II. Empirical observations, *Evolution* 39, 41-52 (1985).
101. Schou, O., and Philipp, M., An unusual heteromorphic incompatibility system. 2. Pollen tube growth and seed sets following compatible and incompatible crossings within *Anchusa officinalis* L. (Boraginaceae), in *Pollen: Biology and Implications for Plant Breeding* (D. L. Mulcahy, ed.), pp. 219-227. Elsevier, New York, 1983.
102. Schou, O., and Philipp, M., An unusual heteromorphic incompatibility system. 3. On the genetic control of distyly and self-incompatibility in *Anchusa officinalis* L. (Boraginaceae), *Theor. Appl. Genet.* 68, 139-144 (1984).
103. Seavey, S. R., and Bawa, K. S., Late-acting self-incompatibility in angiosperms, *Bot. Rev.* 52, 195-219 (1986).
104. Shivanna, K. R., Heslop-Harrison, J., and Heslop-Harrison, Y., Heterostyly in *Primula* 2. Sites of pollen inhibition, and effects of pistil constituents on compatible and incompatible pollen tube growth, *Protoplasma* 107, 319-337 (1981).
105. Shore, J. S., and Barrett, S. C. H., Morphological differentiation and crossability among populations of the *Turnera ulmifolia* L. complex (Turneraceae), *Syst. Bot.* 10, 308-321 (1985).
106. Shore, J. S., and Barrett, S. C. H., The genetics of distyly and homostyly in *Turnera ulmifolia* L. (Turneraceae), *Heredity* 55, 167-174 (1985).
107. Shore, J. S., and Barrett, S. C. H., Genetic modifications of dimorphic incompatibility in the *Turnera ulmifolia* L. complex (Turneraceae), *Can. J. Genet. Cytol.* 28, 796-807 (1986).
108. Sorensen, F., Embryonic genetic load in coastal Douglas-fir, *Pseudotsuga menziesii* var. *menziesii*, *Am. Nat.* 103, 389-398 (1969).
109. Stebbins, G. L., *Flowering Plant Evolution above the Species Level*. Belknap Press of Harvard University Press, Cambridge, 1974.
110. Stevens, V. A. M., and Murray, B. G., Studies on heteromorphic self-incompatibility systems: Physiological aspects of the incompatibility system of *Primula obconica*, *Theor. Appl. Genet.* 61, 245-256 (1982).
111. Taroda, T., and Gibbs, P. E., Floral biology and breeding system of *Sterculia chicha* St. Hil., *New Phytol.* 90, 735-743 (1982).
112. Taylor, P. D., Evolutionarily stable reproductive allocations in heterostylous plants, *Evolution* 38, 408-416 (1984).
113. Varopoulos, A., Breeding systems in *Myosotis scorpioides* (Boraginaceae) I self-incompatibility, *Heredity* 42, 149-157 (1979).
114. Vuilleumier, B. S., The origin and evolutionary development of heterostyly in the angiosperms, *Evolution* 21, 210-226 (1967).
115. Waser, N. M., and Price, M. V., Optimal and actual outcrossing in plants, and the nature of plant-pollinator interaction, in *Handbook of Experimental Pollination Biology* (C. E. Jones and R. J. Little, eds.), Chapter 17. Van Nostrand Reinhold Company Inc., New York, 1983.
116. Webb, C. J., and Lloyd, D. G., Selection to avoid interference between the presentation of pollen and stigmas in angiosperms. II Herkogamy, *N.Z. J. Bot.* 24, 163-178 (1986).
117. Weller, S. G., Breeding system polymorphism in a heterostylous species, *Evolution* 30, 442-454 (1976).
118. Weller, S. G., The genetic control of tristylly in *Oxalis* section *Ionoxalis*, *Heredity* 37, 387-393 (1976).
119. Weller, S. G., Dispersal patterns and the evolution of distyly in *Oxalis alpina*, *Syst. Bot.* 3, 115-126 (1978).

120. Weller, S. G., Variation in heterostylous reproductive systems among populations of *Oxalis alpina* in southeastern Arizona, *Syst. Bot.* 4, 57-71 (1979).
121. Weller, S. G., Pollination biology of heteromorphic populations of *Oxalis alpina* (Rose) Knuth (Oxalidaceae) in southeastern Arizona, *Bot. J. Linn. Soc.* 83, 189-198 (1981).
122. Weller, S. G., Fecundity in populations of *Oxalis alpina* in southeastern Arizona, *Evolution* 35, 197-200 (1981b).
123. Weller, S. G., Factors influencing frequency of the mid-styled morph in tristylous populations of *Oxalis alpina*, *Evolution* 40, 279-289 (1986).
124. Weller, S. G., and Ornduff, R., Cryptic self-incompatibility in *Amsinckia grandiflora*, *Evolution* 31, 47-51 (1977).
125. Whitehouse, H. L. K., Multiple-allelomorph incompatibility of pollen and style in the evolution of the angiosperms, *Ann. Bot. (London)* 14, 198-216 (1950).
126. Willson, M. F., Sexual selection in plants, *Am. Nat.* 113, 777-790 (1979).
127. Willson, M. F., *Plant Reproductive Ecology*. John Wiley and Sons, New York, 1983.
128. Willson, M. F., and Burley, N., *Mate Choice in Plants: Tactics, Mechanisms, and Consequences, Monographs in Population Biology No. 19*. Princeton Univ. Press, Princeton, 1983.
129. Williams, R. D., and Williams, W., Genetics of red clover (*Trifolium pratense* L.) compatibility, *J. Genet.* 48, 67-79 (1947).
130. Wright, S., *Evolution and the Genetics of Populations. Vol. 3 Experimental Results and Evolutionary Deductions*. Univ. of Chicago Press, Chicago, 1977.
131. Wyatt, R., Pollinator-plant interactions and the evolution of breeding systems, in *Pollination Biology* (L. Real, ed.), Chapter 4. Academic Press, Orlando, Florida, 1983.
132. Yeo, P. F., Some aspects of heterostyly, *New Phytol.* 75, 147-153 (1975).
133. Yokoyama, S., and Hetherington, L. E., The expected number of self-incompatibility alleles in finite plant populations, *Heredity* 48, 299-303 (1982).
134. Zavada, M. S., The relation between pollen exine sculpturing and self-incompatibility mechanisms. *Plant Syst. Evol.* 147, 63-78 (1984).
135. Zavada, M. S., and Taylor, T. N., The role of self-incompatibility and sexual selection in the gymnosperm-angiosperm transition: A hypothesis. *Am. Nat.* 128, 538-550 (1986).