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SELF- AND CROSS-FERTILIZATION IN PLANTS. I. FUNCTIONAL DIMENSIONS

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Many functional—ecological, morphological, and physiological—factors affect the occurrence of self-fertilization. Six modes of self-pollination are distinguished. These differ in whether they utilize specialized flowers, whether they involve the transfer of pollen within or between flowers, whether they are autonomous or mediated by vectors, and their timing relative to opportunities for outcrossing. The various modes of selfing are subject to different structural constraints. Prepotency, the preferential success of cross-pollen in achieving fertilizations when it competes with self-pollen, influences the frequency of self-fertilization in some species. The amount of self-fertilization may depend on environmental conditions and the vector species visiting each flower and may vary among the flowers of one plant. To gain information on the prevalence of autonomous self-pollination, 66 species for which the degrees of self-compatibility and autofertility (seed set in isolation) have been published were surveyed. Partially self-incompatible species (in which the seed set is lower after self-pollination than after separate outcrosses) have on average lower autofertility than self-compatible species (in which self- and cross-pollinations succeed equally well), but some partially self-incompatible species have considerable autofertility and some self-compatible species have none. A number of features of floral morphology and phenology are associated with high Autofertility Indices.

Introduction

The comparison of self- and cross-fertilization is the central topic of floral biology. Following the discovery by Knight (1799) and Darwin (1868, 1876) that cross-fertilization is advantageous because it produces superior progeny, there was a period of intense activity in pollination biology in the later decades of the nineteenth century. Flower structures that encourage cross-fertilization and reduce self-fertilization were studied widely. After considerable debate during this period, it was also acknowledged that some plants are adapted to regular self-fertilization and have floral syndromes that contrast strongly with those associated with outcrossing (see Darwin [1876] and Henslow [1879] for divergent viewpoints and Müller's [1883] brilliant resolution of the issue).

Floral biology became popular again in the second half of the twentieth century. In this period, genetic studies have dominated comparisons of self- and cross-fertilization. The genetic studies have provided much-needed empirical information on several aspects of self- and cross-fertilization, including frequencies of self-fertilization (Barrett and Eckert 1990), the expression and causes of inbreeding depression (Charlesworth and Charlesworth 1987; Barrett and Charlesworth 1991), and the genetic structures of outcrossing and selfing populations (Brown 1990; Hamrick and Godt 1990; Ritland 1990). The theoretical effects of the mating system on the genetic structures of regularly selfing and outcrossing populations have also been analyzed widely (Brown 1990; Ritland 1990).

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The functional approach to the study of self- and cross-fertilization contrasts with the genetic one in emphasizing the operation of pollination mechanisms and aspects of the natural history of flowers. Functional studies of mating systems examine ecological, morphological, and physiological perspectives. They have continued from the last century to the present day with little change and currently constitute a useful but rather static aspect of mating systems. In recent years, many topics of floral ecology have been rejuvenated by innovative studies of reproductive strategies for deploying adaptive mechanisms, but the new paradigm has had hardly any impact on the traditional topic of cross- versus self-fertilization.

We believe that functional aspects of self-fertilization have been underemphasized and offer unrealized opportunities to increase our knowledge of the evolution and selection of mating systems. A number of major functional factors, including prepotency, pollen discounting, the effects of selfing on the outcrossed seed production, and reproductive assurance, remain entirely or almost entirely unstudied (Lloyd 1992; Schoen and Lloyd 1992). Moreover, self-pollination is not a single unvarying process that occurs in the same manner in all species that practice any selfing (Lloyd 1979). On the contrary, self-pollination occurs in several fundamentally different ways, which we describe as the “modes” of self-pollination. There have been few attempts to determine their relative frequencies experimentally. In addition, a number of operational factors can cause the amount of self-fertilization to vary within a population, including environmental conditions and different pollinator species; these too have rarely been examined.

In this and the following articles we examine these major functional dimensions of self- and cross-fertilization and attempt to integrate them with genetic approaches to the subject. This article introduces functional aspects of self- and cross-fertilization by describing the various modes by which selfing occurs and the ecological, morphological, and physiological factors that influence their frequencies. It also reviews published work on spontaneous self-pollination to examine functional factors that contribute to variation in the frequency of self-fertilization. The two following articles present a phenotypic model of the selection of self-fertilization (Lloyd 1992) and describe and illustrate experimental procedures for estimating the selective forces and partitioning the full complement of self-fertilization into its component modes (Schoen and Lloyd 1992).

Modes of self-pollination

CLEISTOGAMY

In morphological terms, the most distinct mode of selfing is cleistogamy (Kuhn 1867; Lord 1981), which occurs in closed flowers that are structurally specialized for self-fertilization and do not outcross. Cleistogamy differs from all other modes of selfing in several respects. It is the only mode that occurs in morphologically distinct flowers. Hence, it can be recognized immediately and its frequency can be measured simply by counting the numbers of cleistogamously and chasmogamously produced seeds. Moreover, cleistogamy is unique among modes of selfing (Schoen and Lloyd 1984; Lively and Lloyd 1990) in possessing an advantage over outcrossing (the "cost of outcrossing") that is derived from a cost of producing males, as modeled by Maynard Smith (1971), rather than a cost of meiosis, as described by Williams (1971). Cleistogamous flowers cost less to produce because the cost of pollen and attractants is very low. Cleistogamy is also distinct in that in many species the cleistogamously and chasmogamously derived seeds differ in their size, dispersal, germination, and survival characteristics (Campbell et al. 1983; Schmitt and Gamble 1990). Altogether, the operation and selection of cleistogamy differ widely from those of other modes of selfing (Schoen and Lloyd 1984). In this series of articles we confine our attention to the chasmogamous modes of selfing that occur in flowers that can also engage in self-pollination.

GEITONOGAMY

Geitonogamy is the most distinct of the chasmogamous modes of selfing because it involves transfer of pollen between flowers and requires the same pollination mechanism as cross-pollination. Consequently, it has the ecological prop-

erties of cross-fertilization and the genetic properties of self-fertilization. The distinctive nature of geitonogamy has led to its being the only mode of chasmogamous selfing that was distinguished traditionally (Kerner 1895). A certain amount of geitonogamy is virtually inevitable in self-compatible plants that produce a number of flowers at anthesis at the same time. Geitonogamy is probably the most widespread mode of self-pollination, but it may never achieve the predominance that the autonomous modes acquire in habitually selfing species. It would be even more important but for the fortunate and still largely unexplained habit shared by virtually all flower visitors of visiting only a fraction of the available flowers on a plant before moving to the next plant (Frankie et al. 1976; Kadmon and Shmida 1992; Robertson 1992).

Charles Darwin (1859, 1876) recognized the importance of geitonogamy when he argued that trees are likely to be self-pollinated more frequently than other plants because they display more flowers at one time. Darwin postulated that this could explain the higher frequency of species with separate sexes among the trees of the United Kingdom, New Zealand, and the United States (but not Australia) than among other plants of the same regions. A century later, Arroyo (1976) proposed that the occurrence of geitonogamy may be an important factor in the selection of self-incompatibility as well as separate sexes.

A few recent studies have examined the relationship between the frequency of geitonogamy and flower number that Darwin implied (Crawford 1984; Geber 1985; Handel 1985; Hensing 1988; Robertson 1992). The amount of geitonogamy is influenced not only by the flower display but also by factors that affect the extent of pollen carryover (Robertson 1992). Other aspects of geitonogamy, such as its distribution among the flowers on a plant, variation with pollinator abundance and type, changes throughout a flowering season, and the relative degree to which it displaces cross-fertilization and the autogamous modes of selfing, remain unexplored. All these factors influence the measurement or selection of geitonogamy.

FACILITATED SELF-POLLINATION

In the course of foraging for rewards, flower visitors may cause some autogamy as well as geitonogamy (Knuth 1906–1909; Estes and Brown 1973; Hinton 1976; Schneider and Buchanan 1980; Pazy 1984). Like geitonogamy and competing selfing (see below), such facilitated selfing (so named by Schneider and Buchanan 1980) occurs at the same time as outcrossing. Facilitated selfing is primarily a by-product of adaptations for outcrossing, again resembling geitonogamy (Lloyd 1992). In flowers that present pollen and

stigmas during the same visits, facilitated selfing is almost impossible to eliminate completely unless there is a mechanism that ensures that stigma contacts in a flower strictly precede pollen contacts, as in *Cypripedium* species (van der Pijl and Dodson 1966) or species with sensitive stigmas (Newcombe 1922).

The amounts of facilitated selfing that animal visitors cause in the course of their foraging activities are likely to vary enormously, depending on the way visitors move, the time they spend on each flower, and the positions of the anthers and stigmas. There are no data available, but, following Heine (1937), we expect that less specialized visitors that forage on promiscuously pollinated flowers are likely to cause more facilitated selfing than specialized visitors with more precise movements.

THE THREE MODES OF AUTONOMOUS SELF-POLLINATION

Prior, competing, and delayed self-pollination are similar in being autonomous modes of selfing that occur without the participation of an external agent. The three modes differ in their timing (Lloyd 1979). They occur before, during, and after opportunities for outcrossing in a flower, respectively. As a result of their different timing, they also differ in the degree to which they displace cross-fertilization (Ockendon and Currah 1978) and in the conditions required for their selection (Lloyd 1979, 1992).

Numerous but brief anecdotal accounts concerning when and how autonomous selfing occurs in various species are scattered through the literature. Earlier observations were collected by the German encyclopedists (Müller 1883; Kerner 1895; Knuth 1906–1909). A notable modern example is the work on the self-pollination of orchids by Catling (1990), who made careful observations of floral behavior that showed exactly when and how, though not precisely how much, autonomous self-pollination occurs in various species. We know of no experimental attempts to determine the relative importance of the three modes of autonomous selfing in any species.

Prior selfing occurs when anthers dehisce and stigmas are receptive before anthesis and the two pollinating surfaces are positioned and oriented so there is contact between them in unopened buds. Some self-fertilizing species regularly engage in bud pollinations (Hagerup 1952). Many species may undergo an increase in prior selfing when flower opening is postponed in poor weather and herkogamy is less fully developed (again there are no firm data).

Competing selfing resembles facilitated selfing in that it occurs during the same interval as cross-pollination, but it differs in being achieved autonomously and, hence, it is more easily selected

(Lloyd 1992). The original definition of competing selfing (Lloyd 1979) did not distinguish it from facilitated selfing and was therefore broader than the present definition. The two modes can be separated experimentally in animal-pollinated species (Schoen and Lloyd 1992). Competing selfing is probably relatively unimportant in abiotically pollinated plants, which are often unisexual or completely dichogamous.

Competing selfing occurs by a variety of mechanisms. In some species, such as many self-compatible Brassicaceae in which the paired anthers surround the stigma, competing selfing results simply from the close proximity of pollen and stigmas during anthesis. In other species, the exact temporal relationships between selfing and crossing events, and thus the degree to which competing selfing preempts outcrossing, are more complex. They depend in part on the pattern of dichogamy. In incompletely protogynous species, the stigmas have an opportunity to receive outcrossing pollen first. In incompletely protandrous species, competing selfing that occurs when stigmas become receptive takes place during the same interval as outcrossing and is therefore likely to have a greater effect on the amount of cross-fertilization. An intermediate situation occurs in flowers that open and close daily for several days if they undergo competing selfing only when the petals are moving or when they are closed (Meehan 1876).

Delayed selfing occurs when the movements of flower parts at the end of anthesis lead to pollen-stigma contacts and the fertilization of ovules that have not been previously cross-fertilized. In species that are herkogamous during the period when cross-pollination occurs, flower movements during senescence may cause self-pollination. In certain Campanulaceae and Asteraceae, e.g., the style arms curl around and touch the style where pollen has been presented secondarily (Faegri and van der Pijl 1979). In some species with epipetalous stamens, the fall of senescent corollas may cause a portion of any remaining pollen to be brushed against the stigmas (Hagerup 1957; Dole 1990, but compare Dudash and Ritland 1991).

Factors that influence the frequency of self-pollination

The amount of self-fertilization in a plant is affected by a number of factors that provide further functional dimensions of self- vs. cross-fertilization.

CONSTRAINTS ON THE MODES OF SELF-POLLINATION

The morphological and phenological features of flowers impose distinct constraints on each mode of self-pollination. Species that have any degree of dichogamy, either protandry or protog-

yny, cannot engage in prior selfing. Conversely, delayed selfing cannot take place in species in which the pollen is no longer viable, or stigmas are no longer receptive, when the opportunities for cross-pollination in a flower are over. If the structure of flowers allows pollen to be picked up during a pollinator visit only after the stigmas have been contacted, facilitated selfing cannot occur. In many herkogamous species, the pollen and stigmas are too distantly separated during anthesis for competing selfing to be possible. The degree of anther-stigma separation affects the frequency of self-pollination in some species (Rick and Dempsey 1969; Schoen 1982; Barrett and Shore 1987; Holtsford and Ellstrand 1992). Moreover, the amount of selfing may depend on whether the stigmas or anthers are higher (approach or reverse herkogamy) (Sobrevila and Arroyo 1982; Kohn and Barrett 1992).

Geitonogamy is the most constrained mode of chasmogamous self-pollination. A considerable amount of geitonogamy is often unavoidable as a consequence of the movement of pollinators between flowers of the same plant. The amount of geitonogamy may be varied by altering the number or disposition of flowers or their individual attractiveness, which alters the number of successive visits that a pollinator makes to the flowers of a plant, or by changing floral structure so that the amount of pollen carryover is altered (Robertson 1992). All these changes, however, alter not only the amount of geitonogamy but also that of cross-pollination.

The operation of these structural and behavioral constraints means that a particular species of plants may be able to employ, or prevent, only a limited fraction of the modes of self-pollination.

THE RELATIVE COMPETITIVE ABILITIES OF SELF- AND CROSS-POLLEN

The competitive abilities of self- and cross-pollen influence the amount of self-fertilization, particularly when selfing occurs over the same period as crossing (the geitonogamous, competing, and facilitated modes). Darwin (1876) demonstrated that a number of species are highly self-fertile when isolated and yet produce predominantly outcrossed progeny when they are surrounded by different varieties of the same species or different individuals of the same variety. The observations were made by growing plants in close proximity and identifying outcrossed plants by their characters (when from different varieties) or vigor (when from individuals of the same variety). Darwin postulated that the "prepotency" of outcrossing pollen was the most important factor in limiting the natural frequency of self-fertilization.

In modern times there have been a number of

observations of the prepotency of cross-pollen in competition experiments with nominally self-compatible species—those in which the success of separate self- and cross-pollinations is approximately the same (Bateman 1956; Ockendon and Currah 1978; Weller and Ornduff 1989; Cruzan and Barrett 1992). The phenomenon is known as cryptic self-incompatibility. A weak self-incompatibility reaction can also lead to a reduced probability of fruit set from self-pollinated flowers that compete with outcrossed flowers (Becerra and Lloyd 1992). Not all self-compatible plants have competitively inferior self-pollen, however (Snow and Spira 1991).

Self-incompatibility is often incomplete, leading to varying degrees of seed set after artificial self-pollination (pseudocompatibility). In partially self-incompatible species (those in which the seed set is lower in selfed flowers than in separately crossed flowers), self-pollen performs poorly even in the absence of competition from cross-pollen. We therefore expect the prepotency of outcrossed pollen to be more pronounced in competition experiments with these species than in cryptically self-incompatible species. A number of studies of species with both gametophytic and sporophytic self-incompatibility systems have confirmed that compatible pollen is prepotent over partially incompatible pollen (Eenink 1982; Visser and Marcucci 1984; Bertin 1990). In pollen competition experiments on tristylous species of Pontederiaceae, Barrett and colleagues have found that legitimate pollen is prepotent over illegitimate pollen in both self-incompatible and self-compatible populations (Barrett and Anderson 1985; Cruzan and Barrett 1992).

We recommend that Darwin's term, *prepotency*, be revived to cover all the above phenomena that cause cross-pollen to succeed in fertilizing ovules more often than by chance when it competes with self-pollen. This definition applies to partially self-incompatible plants as well as to those that exhibit cryptic self-incompatibility, but it excludes postzygotic expressions of inbreeding depression. When prepotency occurs, the proportions of self- and cross-fertilization need not match those of self- and cross-pollination, even in nominally self-compatible species. Prepotency is probably an important determinant of the mating system in many species that have incomplete self-incompatibility barriers, although it may not have the ubiquity that Darwin postulated (Jones 1928).

Despite Darwin's lead, there has been no attempt to determine the degree to which prepotency limits natural frequencies of self-fertilization in self-compatible or partially self-incompatible species. This would require experiments on the timing of self-pollination as well as others on the prepotency of outcrossed pollen deposited

at various times relative to the deposition of self-pollen (Schoen and Lloyd 1992).

THE ENVIRONMENTAL CONDITIONS OF POLLINATION

The environmental conditions of pollination may cause variation in the amount of any of the modes of selfing. It has been shown in a considerable number of species that the frequency of self-fertilization varies with seasonal or weather conditions or even on different parts of a plant (Glendinning 1962; Rust and Clement 1977; Antonovics and Levin 1980; Stephenson 1982). These studies have identified ecological factors that influence the amounts of self-fertilization, such as population density or size (Stephens and Finkner 1953; Bateman 1956; Ganders 1975; Vaquero et al. 1989), but they have not attempted to explore the floral events that alter the deposition of self- and cross-pollen. Relevant factors include the temperature, light, and humidity, the time of the flowering season when a flower is produced, and the age of a flower. In general, unfavorable pollination conditions are likely to increase the amount of autogamy, both because self-pollen then competes less with cross-pollen and because the degree of temporal and spatial separation of the pollen and stigmas may decrease in flowers that develop under poor conditions or remain unopened for long periods. By comparing the frequency of self-fertilization among the fruit of individual plants, Schoen and Brown (1991) have provided evidence that selfing may be induced in environmental conditions associated with poor pollination.

In some species the environmental variation among flowers in opportunities for cross-pollination may be so extreme that some flowers have no opportunities for outcrossing as seed or pollen parents and can produce only self-fertilized offspring. Müller (1883, p. 18) stated that in some aquatic plants flowers remain closed and pollinate themselves if the water level is unusually high. Such flowers may merge into cleistogamous flowers, depending on when the arrest in development occurs. Some intermediate conditions are reviewed in Sculthorpe (1967). In some terrestrial species, such as Australasian sun orchids (*Thelymitra* species [Jones 1988]) and *Gentiana lineata* (Webb 1984), there may also be a dichotomous switch between conditions that allow flowers to open and those that do not. Previously we described this extreme of conditional self-fertilization as "induced selfing" (Schoen and Lloyd 1984). It is likely, however, that there are all degrees of environmental variation in the frequency of self-fertilization, and now we prefer to distinguish environmental effects as a general dimension of self- vs. cross-fertilization rather than a special circumstance.

THE BEHAVIOR OF DIFFERENT VECTORS

The amount of selfing may also depend on the animal species that visit a particular flower. In promiscuously pollinated species with readily accessible rewards, such as many Apiaceae and Asteraceae, the diverse visitors potentially may cause widely differing frequencies of self- and cross-pollination. There have been, however, almost no studies of variation in the frequency of self-pollination caused by different visitors (Anderson and Symon 1988).

An extreme example of variation in self-pollination caused by different visitors involves long-staying "squatters," including aphids, thrips, spider mites, and nitulid beetles. The squatters are predators that eat pollen or suck plant juices and use the flowers as a protected haven. In moving around flowers, they may cause varying amounts of self-pollination, depending in part on the positions and orientations of the pollen and stigmas. Baker and Cruden (1991) demonstrated that thrips and/or aphids cause a significant amount of selfing in the course of wandering over flowers of *Ranunculus scleratus* and *Potentilla rivalis*. Squatters fly rarely or not at all, and thus cause virtually no cross-pollination. Experimental procedures that exclude mobile short-stay pollinators, such as the use of pollination bags or cages, do not remove squatters. In such experiments, any self-pollination caused by squatters will be classed as autonomous, together with the truly autonomous activities of the plants themselves and the actions of physical factors such as wind and rain. The quasi-autonomous effects of squatters can be examined by intensive pesticide treatments (Baker and Cruden 1991).

VARIATION AMONG FLOWERS ON ONE PLANT

In multiovulate ovaries, any proportion of the ovules in a single flower can be self-fertilized. Variation among flowers in the proportion of self-fertilized ovules may arise because of variation in the timing of self-pollination or from the behavior of pollinators. It is useful to distinguish between whole-flower and part-flower self-pollination. A failure to recognize interflower variation can lead to a bias in estimates of the frequency of self-fertilization (Schoen and Brown 1991).

A survey of the literature on the extent of autonomous self-fertilization

Whether the deposition of self-pollen occurs autonomously (prior, competing, and delayed selfing) or is mediated by a pollen vector (geitonogamy and facilitated selfing) affects the conditions under which self-fertilization occurs and, hence, how readily it is selected (Lloyd 1992). The traditional explanation of self-pollination as

Table 1

SEED OR FRUIT SET IN ISOLATED FLOWERS AND FOLLOWING ARTIFICIAL SELF- AND CROSS-POLLINATIONS IN 37 SELF-COMPATIBLE SPECIES

Family	Species	Seed or fruit set			Self-compatibility Index	Nature of data ^a	No. of stamens	Floral symmetry ^b	Reference
		Isolated flowers	Self-pollination	Cross-pollination					
Acanthaceae	<i>Justicia galapagana</i>	32	24	21	1.14	a	2	Z	McMullen (1987)
Araliaceae	<i>Panax quinquefolium</i>	37	43	31	1.19	b	5	A	Schlessman (1985)
Asteraceae	<i>Crepis tectorum</i>	61	68	78	.86	a	5	A	Andersson (1989)
Balsaminaceae	<i>Impatiens capensis</i> -CH fls ^c	0	79	78	0	a	5	Z	Schemske (1978)
Balsaminaceae	<i>I. pallida</i> -CH fls ^c	0	90	92	0	a	5	Z	Schemske (1978)
Boraginaceae	<i>Tournefortia psilostachya</i>	25	81	81	.31	a	5	A	McMullen (1987)
Cactaceae	<i>Opuntia phaeacantha</i>	19	40	39	.49	b	Many	A	Osborn et al. (1988)
Caprifoliaceae	<i>Linnaea borealis</i>	35	67	67	.52	a	4	A	Barrett and Helenurm (1987)
Caryophyllaceae	<i>Stellaria pubera</i>	5	90	94	.05	a	10	A	Motten (1986)
Commelinaceae	<i>Tinantia anomala</i>	4.4	4.4	4.0	1.10	c	6	A	Simpson et al. (1986)
Euphorbiaceae	<i>Caperonia palustris</i> ^d	10	80	67	.15	a	Ramirez and Brito (1990)
Fabaceae	<i>Aeschynomene pratensis</i>	23	69	76	.91	a	10	Z	Ramirez and Brito (1990)
Fabaceae	<i>Astragalus lonchocarpus</i>	3	22	19	.16	a	10	Z	Karron (1989)
Fabaceae	<i>Desmodium barbatum</i>	31	65	69	.45	a	10	Z	Ramirez and Brito (1990)
Iridaceae	<i>Iris cristata</i>	10	78	75	.13	a	3	A	Motten (1986)
Lamiaceae	<i>Hyptis dilatata</i>	37	59	63	.59	a	4	Z	Ramirez and Brito (1990)
Lobeliaceae	<i>Lobelia cardinalis</i> ^c	4	100	100	.04	a	5	Z	Johnston (1990)
Lobeliaceae	<i>L. siphilitica</i> ^c	2	100	100	.02	a	5	Z	Johnston (1990)
Melastomataceae	<i>Desmoscelis villosa</i>	27	41	54	.50	a	5	A	Ramirez and Brito (1990)
Orchidaceae	<i>Calopogon tuberosus</i>	0	87	83	0	a	2	Z	Firmage and Cole (1988)
Orchidaceae	<i>Cypripedium acaule</i>	0	100	100	0	a	2	Z	Barrett and Helenurm (1987)
Orchidaceae	<i>Encyclia cordigera</i>	0	78	88	0	a	2	Z	Janzen et al. (1980)
Orchidaceae	<i>Platanthera citaris</i>	0	91	85	0	a	2	Z	Robertson and Wyatt (1990)
Orchidaceae	<i>P. stricta</i>	0	98	90	0	a	2	Z	Patt et al. (1989)
Oxalidaceae	<i>Oxalis montana</i>	32	100	100	.32	a	5	A	Barrett and Helenurm (1987)
Papaveraceae	<i>Argemone aurantiaca</i>	0	168	143	0	c	Many	A	Schneider and Nichols (1984)
Papaveraceae	<i>Sanguinaria canadensis</i>	94	89	94	1.00	a	8 to 12	A	Motten (1986)
Pyrolaceae	<i>Chimaphila umbellata</i>	11	75	75	.15	a	10	A	Barrett and Helenurm (1987)
Pyrolaceae	<i>Pyrola secunda</i>	63	94	100	.63	a	10	A	Barrett and Helenurm (1987)
Ranunculaceae	<i>Hepatica americana</i>	100	100	100	1.00	a	Many	A	Motten (1986)
Ranunculaceae	<i>Isopyrum biernatum</i> ^c	0	57	50	0	a	Many	A	Melampy and Hayworth (1980)
Ranunculaceae	<i>Thalictrum clavatum</i>	66	96	97	.68	a	Many	A	Melampy and Hayworth (1980)
Rosaceae	<i>Crataegus crus-galli</i>	2	12	15	.79	a	10	A	Dickinson and Phipps (1986)
Scrophulariaceae	<i>Mazus miquelii</i>	0	85	91	0	a	4	Z	Kimata (1978)
Solanaceae	<i>Capsicum frutescens</i>	23	44	36	.64	a	5	A	McMullen (1987)
Solanaceae	<i>Solanum rostratum</i>	0	57	57	0	b	5	A	Bowers (1975)
Xyridaceae	<i>Xyris laxifolia</i>	40	84	67	.60	a	3	A	Ramirez and Brito (1990)

^a a = % fruit set; b = % seed set; c = raw seed numbers/flower.^b A = actinomorphic; Z = zygomorphic.^c Reported as dichogamous.^d Unisexual flowers.

Table 2

SEED OR FRUIT SET IN ISOLATED FLOWERS AND FOLLOWING ARTIFICIAL SELF- AND CROSS-POLLINATIONS IN 29 PARTIALLY SELF-INCOMPATIBLE SPECIES

Family	Species	Seed or fruit set			Auto-fertility Index	Self-compatibility Index	Nature of data ^a	No. of stamens	Floral symmetry ^b	Reference
		Isolated flowers	Self-pollination	Cross-pollination						
Araceae	<i>Dieffenbachia longispatha</i> ^c	4	21	46	.09	.46	<i>a</i>	...	A	Young (1986)
Boraginaceae	<i>Cordia alliodora</i>	11	15	66	.17	.23	<i>a</i>	5	A	Opler et al. (1975)
Boraginaceae	<i>C. lutea</i>	0	2	9	0	.22	<i>a</i>	5	A	McMullen (1987)
Brassicaceae	<i>Cardamine angustata</i>	3	8	30	.10	.27	<i>a</i>	6	A	Motten (1986)
Capparidaceae	<i>Capparis flexuosa</i>	4	11	16	.23	.66	<i>a</i>	Many	A	Zapata and Arroyo (1978)
Euphorbiaceae	<i>Croton hirtus</i>	25	41	97	.26	.42	<i>a</i>	...	A	Ramirez and Brito (1990)
Fabaceae	<i>Astragalus limifolius</i>	10	20	40	.25	.50	<i>a</i>	10	Z	Karron (1989)
Fabaceae	<i>A. pectinatus</i>	0	2	10	0	.20	<i>a</i>	10	Z	Karron (1989)
Fabaceae	<i>Mimosa camporum</i>	8	56	82	.10	.68	<i>a</i>	...	A	Ramirez and Brito (1990)
Flacourtiaceae	<i>Prockia flava</i>	0	10	54	0	.19	<i>a</i>	...	A	Zapata and Arroyo (1978)
Gentianaceae	<i>Frasera carolinensis</i>	18	31	47	.38	.66	<i>a</i>	4	A	Threadgill et al. (1981)
Gesneriaceae	<i>Sinningia</i> sp.	5	15	36	.14	.42	<i>a</i>	2	Z	Ramirez and Brito (1990)
Hypericaceae	<i>Vismia baccifera</i>	19	16	35	.54	.46	<i>a</i>	Many	A	Sobrevilla and Arroyo (1982)
Lamiaceae	<i>Hyptis conferta</i>	2	11	42	.05	.26	<i>a</i>	4	Z	Ramirez and Brito (1990)
Liliaceae	<i>Erythronium umbilicatum</i>	6	10	86	.07	.12	<i>a</i>	6	A	Motten (1986)
Mayacaceae	<i>Mayaca sellowiana</i>	16	42	58	.28	.72	<i>a</i>	3	A	Ramirez and Brito (1990)
Melastomataceae	<i>Graffenrieda latifolia</i>	0	20	67	0	.30	<i>a</i>	5	A	Sobrevilla and Arroyo (1982)
Musaceae	<i>Heliconia psittacorum</i>	0	17	64	0	.27	<i>a</i>	...	Z	Ramirez and Brito (1990)
Myrtaceae	<i>Myrcia fallax</i>	28	10	37	.76	.27	<i>a</i>	Sobrevilla and Arroyo (1982)
Myrtaceae	<i>Syzygium cormiflorum</i>	18	37	73	.25	.51	<i>b</i>	Many	A	Crome and Irvine (1986)
Ochnaceae	<i>Sauvagesia rubiginosa</i>	7	38	60	.12	.63	<i>a</i>	Ramirez and Brito (1990)
Ochnaceae	<i>Ludwigia nervosa</i>	19	40	67	.28	.60	<i>a</i>	5	A	Ramirez and Brito (1990)
Paeoniaceae	<i>Paeonia californica</i>	.3	1.4	4.5	.07	.31	<i>c</i>	Many	A	Schling (1976)
Polygalaceae	<i>Securidaca scandens</i>	13	13	21	.61	.63	<i>a</i>	...	Z	Zapata and Arroyo (1978)
Rubiaceae	<i>Diodia multiflora</i>	33	43	78	.42	.55	<i>a</i>	4-10	A	Ramirez and Brito (1990)
Rubiaceae	<i>Palicourea petiolaris-pin</i>	1	33	59	.02	.56	<i>a</i>	4-10	A	Sobrevilla and Arroyo (1982)
Rubiaceae	<i>Psychotria costularia</i>	17	42	81	.21	.52	<i>a</i>	4-10	A	Sobrevilla and Arroyo (1982)
Tiliaceae	<i>Luehea seemannii</i>	0	29	42	0	.69	<i>a</i>	Many	A	Haber and Frankie (1982)
Xyridaceae	<i>Xyris savanensis</i>	17	32	81	.21	.40	<i>a</i>	3	A	Ramirez and Brito (1990)

^a *a* = % fruit set; *b* = % seed set; *c* = raw seed numbers/flower.^b A = actinomorphic; Z = zygomorphic.^c Unisexual flowers.

a means of reproductive assurance (Darwin 1859; Müller 1883) emphasizes its autonomous nature.

We still know little about the frequency of the autonomous modes of self-pollination, however. Here we examine information pertaining to the occurrence of autonomous selfing in flowering plants. We cannot estimate the actual frequencies of autonomous self-fertilization from the published literature, since we do not know of any measurements of the natural frequency of self-fertilization that have separated the autonomous and vector-mediated modes. Nevertheless, it is possible to gain indirect information from studies that have measured seed set or fruit set in plants that have been isolated from visitors—henceforth referred to as their autofertility (Drayner 1959). An autofertility level greater than zero is a necessary prerequisite for autonomous self-fertilization, but it does not guarantee that self-fertilization will occur under natural conditions. The experimental procedures that are used to determine autofertility preclude competition with cross-pollen, but in nature cross-pollen may grow through the style more rapidly than self-pollen and reduce the amount of self-fertilization. The natural frequency of self-fertilization can be obtained only from a knowledge of the genotypes of open-pollinated seed parents and their progeny at one or more marker loci (Clegg 1980). The autofertility of isolated plants reflects the potential, rather than the actual, rate of autonomous self-fertilization.

We surveyed reports of plant reproductive biology published between 1975 and 1991 in several major botanical, ecological, and evolutionary journals. The summarized results are from 66 cosexual, predominantly hermaphrodite species. We considered only those studies reporting data on autofertility together with data on seed set and/or fruit set following artificial self- and cross-pollinations of separate flowers (tables 1, 2). The data from artificial pollinations are necessary to determine whether a given species is self-incompatible and to verify that seed set occurs in the conditions under which plants are grown. We excluded a few species that set almost no seeds following cross-pollination and a few others that exhibited significant levels of seed set after combined emasculation and bagging, an indication of apomixis. In addition, species that are completely self-incompatible or produced only occasional seeds after selfing were not considered because even if autonomous self-pollination occurred in them, there would be little or no autofertility.

We first calculated the Self-compatibility Index for each species—the average seed or fruit set after self-pollination divided by the seed or fruit set after cross-pollination (Becerra and Lloyd 1992). The index corrects the success of self-pollinations for variability in seed production caused

by variations in plant vigor, physiological limitations of seed production, or the techniques or conditions of pollination.

The Self-compatibility Indices for the 66 species range from a little above zero to more than one, with no conspicuous gaps. Thus there is no nonarbitrary boundary between partially self-incompatible and self-compatible plants. Instead, self-incompatibility must be regarded as a quantitative phenomenon (Becerra and Lloyd 1992). The values above one are presumably the result of experimental error, since there are few biological grounds for obtaining a greater seed set after self-pollination than after cross-pollination between members of the same population. Some values below one also represent random variation in populations in which separate self- and cross-pollinations are equally successful.

To compare major segments of the self-compatibility continuum, we divided the range of Self-compatibility Indices into two groups (tables 1, 2). The 37 samples with indices greater than 0.75 are described as self-compatible. The boundary was chosen at 0.75 because its reciprocal (1.33) is close to the highest index obtained (1.39); this assumes that in plants in which separate self- and cross-pollinations succeed equally well, random variations in the actual counts of small samples are equally likely to show less frequent success of self- or cross-pollinations. The geometric mean (appropriate for dividends varying around 1.0) for the Self-compatibility Indices of the self-compatible plants is 1.02. This indicates that, on average, separate self-pollinations do just as well as cross-pollinations—although cross-pollen might still be prepotent in competition with self-pollen. There were 29 species with Self-compatibility Indices between zero and 0.75, which we describe as self-incompatible. On average, selfs succeeded 40% as frequently as crosses in this group.

For each sample we also calculated an Autofertility Index, the seed (or fruit) set of isolated plants divided by that of artificial cross-pollinations. Again the denominator removes some of the effects of variable pollinating conditions. The Autofertility Indices ranged continuously from zero to above one (tables 1, 2), indicating that all degrees of autonomous self-pollination occur.

Low levels of autofertility do not necessarily imply lack of self-pollination under natural conditions. In fact, estimations of the mating systems of several species in the tables with low Autofertility Indices reveal that they have significant amounts of natural “self-fertilization” (Mitchell-Olds and Waller 1985; Johnston 1990; Schoen and Lloyd 1992). In these species, it is likely that one of the mediated modes of self-pollination is occurring, but biparental inbreeding cannot be ruled out as an alternative explanation.

To see how autofertility is related to self-com-

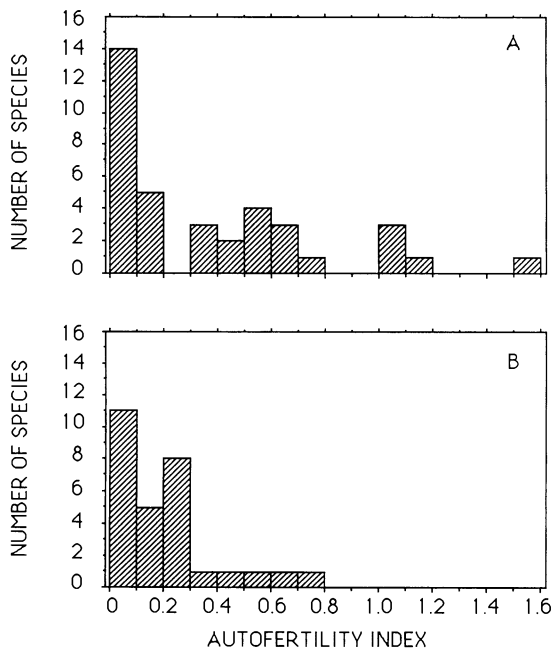


Fig. 1 The distributions of Autofertility Indices for (A) self-compatible species and (B) self-incompatible species.

patibility, we compared first the Autofertility Indices for the self-compatible and self-incompatible groups. Among the self-incompatible samples, the Autofertility Indices range from zero (six species) to 0.76 (fig. 1 B); the geometric mean of non-zero values is 18% of the potential seed set. The Autofertility Indices for the self-compatible plants range even more widely, from zero (11 samples) to 1.52 (fig. 1 A); five samples have values of one or more, and the geometric mean of non-zero values is 47%. The results indicate a significant relationship between self-compatibility and autofertility, as one would expect. The association between self-compatibility and autofertility is confirmed when the average frequencies of seed set in isolated flowers and after self-pollination are graphed against each other (fig. 2; $r = +.32$, $n = 65$, $P = .01$ when both frequencies are transformed to angles to improve the approximation to a bivariate normal distribution). The correlation between the two indices cannot be tested directly because both indices include the cross-pollination success in their computations. Furthermore, several detailed studies have shown that autofertility is correlated with the estimated selfing rate among populations of a species (Harding et al. 1974; Schoen 1982; Lyons and Antonovics 1991). In these species, at least some of the self-fertilization appears to result from the operation of one or more of the autonomous modes of selfing.

The association between the degrees of self-compatibility and autofertility is not unexpected.

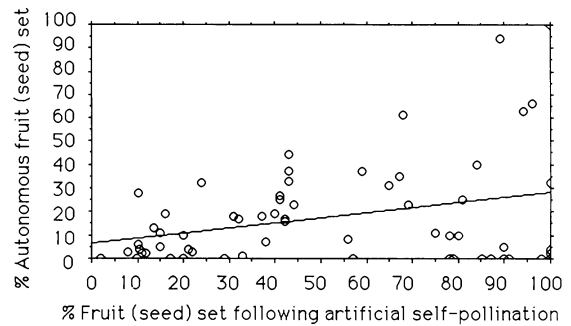


Fig. 2 The relationship between the frequencies of fruit or seed set after self-pollination and in isolated flowers among the samples of self-compatible and self-incompatible species in tables 1 and 2.

What is surprising is that this association is not stronger, as is seen in the wide ranges of autofertility in self-incompatible and self-compatible species and in the scatter in figure 2. In some self-incompatible species, the evolution of even a restricted ability of self-pollen to succeed in fertilization is sufficient to allow some autonomous selfing despite the partial incompatibility barrier. On the other hand, the range of autofertility in self-compatible species shows that complete self-compatibility, at least as evident in separate self- and cross-pollinations, does not guarantee that much, or even any, autonomous self-pollination will be possible. The degree of self-compatibility apparently is not the only factor that influences the extent of autonomous pollination.

To identify morphological and phenological factors that affect the ease of autonomous pollination, we have examined a number of features of the floral biology of the species reviewed (tables 1, 2). The species lacking autofertility altogether or having low Autofertility Indices tend to be concentrated in a few families, particularly the Balsaminaceae, Fabaceae, Lobeliaceae, Orchidaceae, and Scrophulariaceae. These families have specialized pollination mechanisms and characteristically have bilaterally symmetrical flowers, fused petals, and, in most species, relatively few stamens per flower. In most species there is a strong herkogamy mechanism separating the pollen and stigmas. The three species with unisexual flowers, *Caperonia palustris*, *Dieffenbachia longispatha*, and *Croton hirtus*, also have low Autofertility Indices. Moreover, all species reported as dichogamous have low autofertility, e.g., species of *Impatiens*, *Lobelia*, and *Isopyrum*.

At the other extreme, the species with more than 50% autofertility usually have radially symmetrical flowers, separate petals, and more than five stamens per flower (tables 1, 2). These species are likely to have less precise placement of floral parts, and this may allow less herkogamy and greater levels of autonomous selfing.

Conclusion

We have postulated that a variety of ecological, morphological, and physiological factors affect how much self-fertilization takes place in a flower and how it occurs. Some of these factors have not been examined seriously in even a single species. The effects on natural frequencies of self-fertilization of, e.g., prepotency, structural constraints, short-term environmental fluctuations, and the mode of selfing are virtually unknown. The survey of the literature confirms that the amounts of autonomous self-fertilization vary widely among species and are influenced by both the degree of self-compatibility and features of floral morphology and phenology.

The functional dimensions of self- and cross-fertilization deserve to be considered along with the currently more popular genetic factors, such as the degree of overdominance at loci causing

inbreeding depression (which is poorly known after three-quarters of a century of effort) and the amount of recombination between the viability loci and the (equally poorly known) mating system loci. We will not understand the evolution of self-fertilization properly until we know more about its functional dimensions as well as the genetic aspects. For this purpose, it is necessary to analyze the effects of these factors on the selection of self- and cross-pollination and to measure their operation in natural populations. We examine these aspects in the following two articles in this series.

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