

THE EVOLUTION OF SELF-FERTILIZATION IN PERENNIALS

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Submitted October 21, 1996; Revised May 16, 1997; Accepted May 21, 1997

Abstract.—Many plants are perennials, but studies of self-fertilization do not usually include features of perennial life histories. We therefore develop models that include selfing, a simple form of perennality, adult inbreeding depression, and an adult survivorship cost to seed production. Our analysis shows that inbreeding depression in adults diminishes the genetic transmission advantage associated with selfing, especially in long-lived perennials that experience inbreeding depression over many seasons. Perennials also pay a cost when selfing increases total seed set at the expense of future survivorship and reproduction. Such life-history considerations shed new light on the generalization that annuals self-fertilize more than perennials. Past research suggested reproductive assurance as an explanation for this association, but common modes of selfing offer equal reproductive assurance to annuals and perennials. Instead, perennials may avoid selfing because of adult inbreeding depression and the cost to future survivorship and reproduction.

Self-fertilization is much more common in annual than in perennial plants (Stebbins 1950, pp. 176–181). For instance, a recent survey (correcting, as much as possible, for phylogenetic dependencies) finds statistically significant differences in average selfing rates, \bar{s} , between 74 annual species ($\bar{s} = 0.64$), 47 herbaceous perennials ($\bar{s} = 0.41$), and 96 woody perennials ($\bar{s} = 0.18$) (Barrett et al. 1996). Within the Polemoniaceae, the same authors note the repeated evolutionary association between self-fertilization and an annual life history. Stebbins (1950) interprets such associations as “reproductive assurance,” with selfing in annuals selectively favored because it ensures seed production when reproductive success through outcrossing is not possible. A contrasting explanation, emphasizing the cost to perennials rather than the benefit to annuals, comes from the idea of “seed discounting” (Lloyd 1992). The seed discount is the loss of opportunity for outcrossed seed production that accompanies an increase in self-fertilization. In annuals, the seed discount is expressed within years as a trade-off between seed production through selfing and outcrossing. In perennials, Lloyd (1992) argues that a second, between year, discount also occurs when

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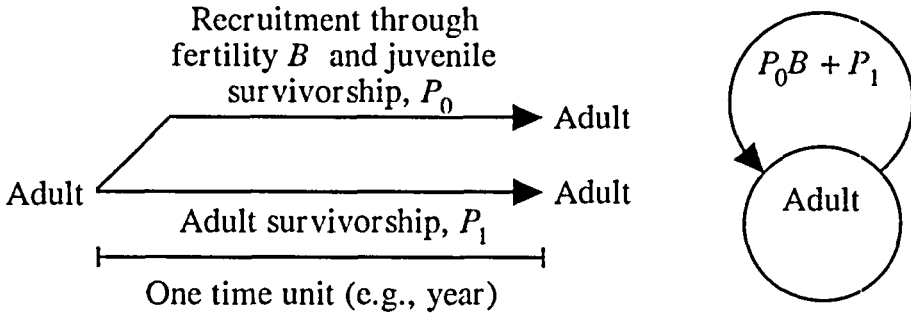


FIG. 1.—Illustration of a simple perennial life history (left) and its corresponding life-cycle graph (right).

seed production decreases survivorship and reproduction in subsequent seasons. Perennials pay a cost of reproductive assurance that annuals do not.

Do Stebbins's reproductive assurance and Lloyd's seed discounting differ in their consequences for the evolution of selfing in annuals and perennials? Theories for the evolution of selfing in annuals identify inbreeding depression (i.e., the reduced fitness of self-fertilized relative to outcrossed progeny; Charlesworth and Charlesworth 1987) as a major force maintaining outcrossing (e.g., Fisher 1941; Lloyd 1979, 1992; Lande and Schemske 1985; Holsinger 1988) but do not explicitly include perennial life histories. A handful of models address reproductive strategies in perennial hermaphrodites (Charnov et al. 1981; Waller and Green 1981; Charlesworth 1984; Kakehashi and Harada 1987; Charnov 1988; Zhang and Wang 1994; Zhang et al. 1996; Zhang and Jiang 1997), but these focus on outcrossing or asexuality. Existing theory, therefore, does not allow us to distinguish between reproductive assurance and the seed discount as explanations for the association of life history and mating system.

Here we model a perennial life history incorporating self-fertilization and inbreeding depression. The model is used to contrast the consequences of different types of seed discounting for annuals and perennials in a constant environment and to identify how perenniality and poor pollination influence the selection of selfing. In the "Discussion" section, we turn to qualitative consideration of Stebbins's reproductive assurance and Lloyd's seed discount, asking how each affects the selection of selfing in annuals and perennials. Our analysis suggests several reasons why selfing should be less common in perennial than in annual plants and argues for the importance of the seed discount and inbreeding depression rather than reproductive assurance as the selective agent responsible for this association.

MODELING POPULATION GROWTH IN PERENNIALS

In this section we develop a life-history model with overlapping generations and partial self-fertilization. Figure 1 illustrates the life history. Individuals

reach reproductive maturity after a single time period and do not alter life-history parameters (survivorship and fertility) after this point (Charnov and Schaffer 1973). The model is a caricature of a population that is neither age- nor stage-structured (Caswell 1989; Charlesworth 1994) and is not meant to be representative of the often complex life histories of plants. Table A1 summarizes important parameters of the model.

In the model of figure 1, population growth rate λ depends on recruitment of new individuals through sexual reproduction and on survivorship of adults. Adults produce B offspring who have probability P_0 of surviving a single time period (e.g., 1 yr), so that recruits enter the population at rate P_0B . Adults survive the same time period with probability P_1 . At the end of this period, both new recruits and surviving adults are capable of reproducing. In this model, the growth rate of the population is

$$\lambda = P_0B + P_1, \quad (1)$$

and the number of individuals N at time $t + 1$ is $N_{t+1} = \lambda N_t$. We define juvenile survivorship P_0 to include environmental factors (e.g., density dependent regulation of recruitment) that are external to the individual life history, whereas both fertility B and adult survivorship P_1 may depend on reproductive strategy. As noted above, the framework developed here extends to more comprehensive life histories.

Analysis of the model involves identifying the life history representing an evolutionary stable strategy (ESS). Searching for an ESS rather than simple optimization is appropriate because of the frequency dependence inherent in the selection of reproductive systems (Charnov 1982; Maynard Smith 1982). Individuals adopting the ESS have a growth rate λ for which any rare variant with a different strategy has growth rate $\hat{\lambda}$ less than λ . Suppose that in a population of N individuals adopting the ESS strategy s there are $\hat{N} \ll N$ individuals adopting a slightly different strategy \hat{s} . The growth rate of the rare strategy will be maximized as it approaches the strategy of the ESS type, so that

$$\left. \frac{\partial \hat{\lambda}}{\partial \hat{s}} \right|_{\hat{s}=s} = 0. \quad (2)$$

Charlesworth (1994, pp. 190–193) suggests that this phenotypic formulation often agrees with population genetic models of life-history evolution; Charnov (1988) uses a haploid genetic model to justify maximizing λ when seeking optimal strategies in hermaphroditic plants.

Important insights into the evolution of life histories come from applying the optimality criterion (2) to the expression for population growth (1). Both recruitment and adult survivorship are functions of the life-history strategy \hat{s} , so that $\lambda = P_0B(\hat{s}) + P_1(\hat{s})$, and at the optimum

$$\lambda' = P_0B' + P_1' = 0. \quad (3)$$

The prime symbol (') indicates the partial derivative of the function with respect to the reproductive strategy, for example, $B' = \partial B(\hat{s})/\partial \hat{s}|_{\hat{s}=s}$; for notational con-

venience, terms such as $B(s)$ are written as B . If the partial derivative of population growth rate (eq. [3]) is positive for all biologically plausible values of the life-history s , selection is toward the maximum value of the life history. In mathematical terms, $\partial\hat{\lambda}/\partial\hat{s}|_{s=\hat{s}}$ is always greater than zero, and

$$P_0B' + P_1' > 0. \quad (4)$$

This condition applies to the initial increase of a rare modifier with slightly higher selfing rate than in the rest of the population.

Population Regulation

Density-dependent or density-independent processes may regulate population number. Both readily incorporate into the life history considered here.

Density-dependent population regulation requires that population size remain constant, so that the sum of recruitment and adult survivorship $P_0B + P_1 = 1$. One way of ensuring density dependence (following Charnov 1988) is to define recruitment survivorship, P_0 , in terms of fertility and adult survivorship, $P_0 = (1 - P_1)/B$. There are then $1 - P_1(s)$ opportunities for recruitment through sexual reproduction. The fraction of these opportunities accruing to a rare type adopting reproductive strategy \hat{s} , relative to the common type with strategy s , is $B(\hat{s})/B(s)$. The growth rate of the rare type becomes

$$\hat{\lambda} = (1 - P_1(s)) \frac{B(\hat{s})}{B(s)} + P_1(\hat{s}),$$

and the optimum, rewriting equation (3) to incorporate density-dependent regulation, is

$$\frac{1 - P_1}{B} B' + P_1' = 0. \quad (5)$$

Under density-independent regulation of population number, recruitment is not constrained to any particular value and growth rate equals the sum of recruitment and survivorship, $\hat{\lambda} = P_0B(\hat{s}) + P_1(\hat{s})$. The optimum solution, from equation (3) and using the relationship $P_0B + P_1 = \lambda$, is

$$\frac{\lambda - P_1}{B} B' + P_1' = 0. \quad (6)$$

Population growth rate λ is an implicit function of recruitment. Equations (5) and (6) illustrate that populations at the optimum are very similar under density-dependent and density-independent processes of regulation, differing only in the extent of juvenile mortality.

Self-Fertilization

This section outlines how population growth rate in equation (1) accommodates features of self-fertilization. We include relative fitness differences between selfed and outcrossed progeny (inbreeding depression), effects of self-

fertilization on recruitment, and consequences of seed production for adult survivorship. Inbreeding depression occurs commonly over all stages of the life history, as evidenced in a comprehensive review of empirical studies (Husband and Schemske 1996). We incorporate inbreeding depression through its effect on survivorship, although more complicated life cycles require consideration of the often substantial inbreeding depression associated with adult growth and fertility. Evidence that seed production influences adult survivorship comes from multiyear studies in species such as the orchids *Aspasia principissa* (Zimmerman and Aide 1989) or *Cypridendium acaule* (Primack and Hall 1990), where hand-pollination increases fruit set but decreases growth or reproduction in subsequent years; Calvo and Horvitz (1990) illustrate the theoretical importance of this trade-off for the evolution of reproductive strategy. Indirect support for a cost to increased fertility also comes from observation of lower seed production and growth following heavy reproduction (Stephenson 1981; Willson and Burley 1983) and apparent resource limitation of seed production following supplemental pollination (in about 40% of the studies reviewed by Young and Young 1992 or Burd 1994).

Inbreeding depression δ occurs when selfed progeny have lower fitness than outcrossed progeny (Charlesworth and Charlesworth 1987). Inbreeding depression may be specific to particular parts of the life history, for instance, because survivorship during recruitment relies on elements of the genetic repertoire that differ from those required for survivorship as an adult (Husband and Schemske 1996). We therefore introduce relative survivorship of selfed juveniles $w_j = 1 - \delta_j$ and adults $w_a = 1 - \delta_a$. Juvenile relative survivorship is the probability of juvenile survivorship of selfed progeny divided by juvenile survivorship of outcrossed progeny, and likewise for adult relative survivorship. The measures represent relative survivorship per unit of time, rather than over the entire life history (e.g., adult relative survivorship w_a might be measured over a single year, so that the relative survivorship of selfed individuals over t years as an adult is w_a^t). A rough estimate of relative fitness in outcrossing species prior to reproduction (obtained from Husband and Schemske 1996 by multiplying average relative fitnesses at the seed production, germination, and juvenile survivorship stages) is $w_j \approx 0.50$, and following reproductive maturity $w_a \approx 0.73$. The importance of relative survivorship measured per unit of time receives attention in the section on lifetime fitness measures.

Self-fertilization influences the number of selfed $B_s(\hat{s})$ and outcrossed $B_x(\hat{s})$ progeny recruited. Selfed progeny suffer inbreeding depression, so their contribution to recruitment is weighted by juvenile relative survivorship w_j . The fertility of an individual adopting reproductive strategy \hat{s} is then

$$B(\hat{s}) = w_j B_s(\hat{s}) + B_x(\hat{s}).$$

Selfed progeny contain two copies of the parental genome. A parent's outcrossed progeny consists of its outcrossed seeds and pollen that successfully participates in outcrossed mating; both types of outcrossed progeny contain only a single copy of the genome of the parent (Lloyd 1977). The terms $B_s(\hat{s})$ and $B_x(\hat{s})$ include these details and are developed explicitly below.

Two different aspects of adult survivorship P_1 are inbreeding depression (when the adult is itself derived from selfing) and the cost of seed production (the consequence of reproductive strategy for the adults' own survivorship). To incorporate inbreeding depression, we use the frequency of adults derived from selfing, $S(\hat{s})$ (derivation in app. B). Adult survivorship is an average of the survivorship of the $1 - S(\hat{s})$ adults derived from outcrossing and the $S(\hat{s})$ adults derived from selfing. Selfed adults survive with relative survivorship w_a , so average adult survivorship accounting for inbreeding depression is

$$(1 - S(\hat{s})) + (w_a S(\hat{s})).$$

A second component of adult survivorship P_a represents the cost of seed production. The adult survivorship cost of seed production is assumed to be independent of whether the parent is the product of selfing or outcrossing but may be a function of the parents' selfing rate if selfing increases seed production. For this reason, the survivorship cost of seed production is a function of the selfing rate and is written $P_a(\hat{s})$. Combining inbreeding depression and the cost of seed production, the expression for survivorship of adults in a population with rate of selfing \hat{s} is

$$P_1(\hat{s}) = (1 - S(\hat{s}) + w_a S(\hat{s}))P_a(\hat{s}).$$

Modifiers causing a slight increase in the selfing rate increase in frequency when $P_0 B' + P_1' > 0$ (expression [4]). In an annual life history there is no adult survivorship and only the consequences of recruitment,

$$P_0 B' = P_0 (w_j B'_s + B'_x),$$

determine the selection of selfing. The second portion of equation (4),

$$P_1' = SP_a \left[(w_a - 1 + 1/S) \frac{P'_a}{P_a} + (w_a - 1) \frac{S'}{S} \right], \quad (7)$$

reflects adult survivorship. This term applies to perennials (as does the recruitment term) and includes the adult survivorship cost of selfing (through the derivative P'_a) and the fraction of adults in the population derived from selfing (through S').

SELECTION OF SELF-FERTILIZATION IN PERENNIALS

This section develops models of competing and delayed selfing (Lloyd 1979) to illustrate different components of the seed discount. Competing selfing does not increase total seed production, but selfing reduces the number of outcrossed seeds produced within a season. This exemplifies the within-season seed discount and is relevant to both annuals and perennials. Delayed selfing increases seed production without compromising outcrossing but is costly when producing more seeds reduces survivorship in subsequent seasons. This typifies the between-season seed discount (Lloyd 1992), which is only present in perennials. Between 40% and 60% of supplemental pollination studies increase seed pro-

duction (Young and Young 1992; Burd 1994), indicating ample opportunity for enhanced female fertility through delayed selfing.

Competing Self-Fertilization

General features of competing selfing suggest several consequences of perennality. Since competing selfing does not influence total seed set, the survivorship cost of seed maturation P_a is independent of the selfing rate ($P'_a = 0$). (Competing selfing used here and defined by Lloyd 1979 differs from usage elsewhere [Lloyd 1992; Lloyd and Schoen 1992]; in the latter articles both forms of selfing provide reproductive assurance). From equation (4), selection for competing selfing occurs when

$$P_0(w_j B'_s + B'_x) + (w_a - 1)S'P_a > 0. \quad (8)$$

In annuals, there is no adult survivorship $P_a = 0$, and selection for competing selfing occurs when selfed fertility weighted by juvenile relative survivorship exceeds lost fertility through outcrossing, $w_j B'_s > -B'_x$. In perennials, adult survivorship is positive $P_a > 0$, S increases with selfing rate so that $S' > 0$, and adult relative survivorship of progeny derived from selfing w_a is usually < 1 . The term $(w_a - 1)S'P_a$ is therefore negative, making the evolution of selfing more difficult in perennials than in annuals.

Analyzing a detailed model of competing selfing (Charlesworth and Charlesworth 1979; Lloyd 1979; Charnov 1982) further illustrates the consequences of perennality. Suppose a rare individual with selfing rate \hat{s} occurs in a population with selfing rate s ; both types produce the same number $n = eo$ of seeds. The number of selfed seeds of the rare individual is $B_s(\hat{s}) = \hat{s}eo$. The outcrossed fertility of the rare individual comes from $(1 - \hat{s})eo$ outcrossed seeds, and from male gametes mating with the common type with $(1 - s)eo$ ovules available for outcrossing. Both types of outcrossed progeny contain only half the genome of the rare type (Lloyd 1976), so outcrossed fertility is $B_x(\hat{s}) = [(1 - \hat{s})eo + (1 - s)eo]/2$. Combining selfed and outcrossed fertility, incorporating juvenile inbreeding depression, and using equation (8) provides an expression,

$$P_0 B(\hat{s}) = P_0 \left(w_j \hat{s} + \frac{1 - \hat{s} + 1 - s}{2} \right) eo, \quad (9)$$

for recruitment under competing selfing.

Using the criterion in equation (4), competing selfing is selected when

$$(w_j - 1/2)P_0 eo + (w_a - 1)S'P_a > 0. \quad (10)$$

Competing selfing evolves in annuals (with $P_a = 0$) when $w_j > 1/2$ (as in Lloyd 1979). In perennials ($P_a \neq 0$), adult inbreeding depression ($w_a < 1$) means that $(w_a - 1)S'P_a$ is negative and that selection of competing selfing is more difficult than in annuals.

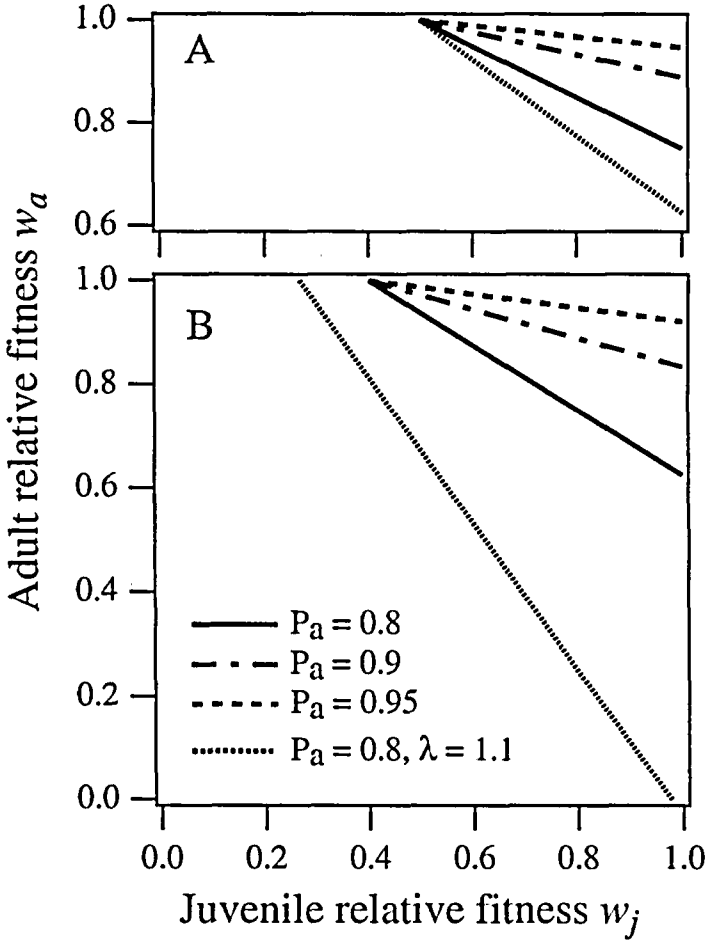


FIG. 2.—The evolution of selfing in initially outcrossing perennials. The population with growth rate $\lambda = 1.1$ is growing rapidly; the remaining populations undergo density-dependent regulation (i.e., $\lambda = 1$). For each scenario, selection for selfing occurs above the line. *A*, Competing selfing. *B*, Delayed selfing, with 100 ovules o available, a fraction $e = 0.25$ outcrossed, the gain exponent $\gamma = 0.4$, and k chosen so adult survivorship equals that in the legend. (See table A1 for parameter definitions.)

Figure 2A shows critical values of juvenile and adult relative survivorship under specific assumptions of adult survivorship and mode of population regulation. Numerical values for $S(\hat{s})$ are from equation (B1); the numbers of ovules available o and fertilized e do not need specification because P_0 and P_a subsume their influence. Perenniality dramatically reduces values of relative survivorship favoring competing selfing, especially with high adult survivorship. Growing populations somewhat reduce the consequences of adult relative survivorship. This is because the average age, and therefore cumulative effect of adult in-

breeding depression, in growing populations is less than that in constant-sized populations (Charlesworth 1994, pp. 194–196).

Delayed Self-Fertilization

Delayed selfing (Lloyd 1979) occurs after outcrossing and without pollinator intervention. Outcrossed fertility B_x is independent of selfing rate so that $B'_x = 0$. Adult survivorship $P_a(\hat{s})$ decreases with selfing ($P'_a < 0$) because more seeds require maturation. Combining these ideas with equation (4), delayed selfing evolves when

$$w_j P_0 B'_s + SP_a \left[(w_a - 1 + 1/S) \frac{P'_a}{P_a} + (w_a - 1) \frac{S'}{S} \right] > 0. \quad (11)$$

In annuals ($P_a = 0$), delayed selfing enhances recruitment and is favored whenever juvenile relative survivorship w_j exceeds 0 (as in Lloyd 1979). Perennials balance enhanced recruitment against adult survivorship costs of inbreeding depression and the between-season seed discount. The term

$$SP_a \left[(w_a - 1 + 1/S) \frac{P'_a}{P_a} + (w_a - 1) \frac{S'}{S} \right]$$

reflects these costs. Considering the sign of each component shows that this term is negative, provided $w_a < 1$. Further analysis using expression (B1) shows that greater adult survivorship P_a usually increases costs of adult inbreeding depression and the seed discount. Perenniality decreases the selective advantage of delayed selfing, with greater perenniality having larger effect.

Lloyd (1979) suggests an explicit model of delayed selfing. Outcrossed fertility B_x equals the number of ovules o multiplied by the fraction fertilized through pollinator activity e , $B_x = eo$. Selfing of the remaining ovules, $(1 - e)o$, occurs at rate \hat{s} in the rare individual, so $B_s(\hat{s}) = (1 - e)o\hat{s}$. Recruitment is thus $P_0[w_j(1 - e)o\hat{s} + eo]$. From equation (11), selection for Lloyd's delayed selfing occurs when

$$w_j P_0 (1 - e) o + SP_a \left[(w_a - 1 + 1/S) \frac{P'_a}{P_a} + (w_a - 1) \frac{S'}{S} \right] > 0. \quad (12)$$

Figure 2B shows conditions favoring delayed selfing. Calculations in the figure require the adult survivorship cost of seed production, the fraction of adults derived from self-fertilization, and the mode of population regulation. We assume that adult survivorship costs follow $P_a(\hat{s}) = 1 - k[(B_s(\hat{s}) + B_x(\hat{s}))/o]^\gamma$, so increasing the fraction of ovules matured as seed $(B_s(\hat{s}) + B_x(\hat{s}))/o$ decreases adult survivorship. Minimum survivorship (equal to $1 - k$) occurs when all ovules mature as seed. The parameter γ determines the relation between seed maturation and adult survivorship. When $\gamma < 1$, the survivorship consequence of each additional seed is less than that of the preceding seed. In outcrossing populations only one-fourth of flowers typically mature as fruit (Sutherland and

Delph 1984), and this represents an appropriate value for e ; little guidance is available for other parameter values.

In annuals, delayed selfing is always favored, but in perennials it is selectively advantageous for only a small range of relative survivorship (fig. 2B). Even without adult inbreeding depression ($w_a = 1$), delayed selfing is only favored when juvenile relative survivorship w_j exceeds 0.4. This is because of the adult survivorship cost of additional seed production. (The value 0.4 is for the specific parameters used in the figure, rather than a general property of the model.) Delayed selfing evolves more easily in growing than in constant-sized populations and evolves in long-lived perennials only when there is very little adult inbreeding depression (fig. 2B).

LIFETIME FITNESS MEASURES

Further insight into the selection of self-fertilization in perennials comes from considering the total number of genes, or "lifetime genetic success," an individual transmits to the next generation. The concept of lifetime genetic success is distinct from lifetime reproductive success because it accounts for the differential genetic representation of alleles in selfed individuals. An individual with adult survivorship $P_1(\hat{s})$ per time period has a life expectancy of $P_0[\lambda - P_1(\hat{s})]^{-1}$ time periods, for reasons analogous to those outlined in appendix B. Each time period results in transmission, through reproduction, of $B(\hat{s})$ genes, so that lifetime genetic success is

$$B(\hat{s})P_0(\lambda - P_1(\hat{s}))^{-1}. \quad (13)$$

Inspection shows this to be a simple rearrangement of equation (1), so the condition for the selection of self-fertilization, equation (4), requires that the derivative of lifetime genetic success with respect to life-history strategy \hat{s} , evaluated when $\hat{s} \approx s$, exceeds zero. That is, selection of self-fertilization occurs when a more selfing type has higher expected lifetime genetic success than a less selfing type. Results in figure 2 can thus be rephrased in terms of lifetime genetic success.

Competing Self-Fertilization

When selfing rate does not influence adult survivorship through the between-season seed discount, selection of self-fertilization requires that

$$B'_s w_j P_0 (\lambda - w_a P_a)^{-1} > -B'_x P_0 (\lambda - P_a)^{-1}.$$

The term $P_0(\lambda - P_a)^{-1}$ to the right of the inequality is the life expectancy (discounted for population growth) of an outcrossed individual, whereas the term $w_j P_0(\lambda - w_a P_a)^{-1}$ to the left of the inequality is the (discounted) life expectancy of selfed individuals. The terms B'_x and B'_s describe how the change in reproductive strategy influences genetic transmission through outcrossing and selfing, respectively. The condition for the selection of selfing modes with only the within-season seed discount is that gains in lifetime genetic success in selfed individuals offset losses in lifetime genetic success through outcrossed individual.

Casting results for Lloyd's model of competing self-fertilization into terms of lifetime genetic success exemplifies the principle outlined in the previous paragraph. With the definitions of $B_s(\hat{s})$ and $B_x(\hat{s})$ used in equation (9), competing self-fertilization is selectively advantageous when

$$2w_jP_0(\lambda - w_aP_a)^{-1} > P_0(\lambda - P_a)^{-1}. \quad (14)$$

The term $w_jP_0(\lambda - w_aP_a)^{-1}$ to the left of the inequality is the life expectancy of individuals produced through self-fertilization, while the term on the right is the life expectancy of outcrossed individuals. The factor of 2 represents the genetic transmission advantage associated with this mode of selfing. The inequality states that selection of competing self-fertilization occurs when the life expectancy of selfed individuals exceeds one-half the life expectancy of outcrossed individuals. The lines in figure 2A partition parameter values into those that satisfy condition (14) and those that do not.

Delayed Self-Fertilization

Increased selfing must enhance lifetime genetic success for selection to favor selfing modes influencing adult survivorship through the between-season seed discount, such as delayed selfing. This criterion can be algebraically complicated, but some insight comes from considering the selection of a selfing variant in an initially outcrossing population, assuming Lloyd's detailed model of delayed selfing and density-dependent regulation. Under these circumstances, delayed selfing is selectively advantageous when

$$w_jP_0(1 - w_aP_a)^{-1} > \gamma P_0(1 - P_a)^{-1}.$$

The term on the left of the inequality, $w_jP_0(1 - w_aP_a)^{-1}$, represents the benefits delayed selfing provides in terms of lifetime genetic success through selfed progeny. The term on the right is, less transparently, the cost of delayed selfing. Opting for delayed selfing reduces longevity and the opportunity for production of outcrossed progeny. The γ term reflects the decrease in longevity, and $P_0(1 - P_a)^{-1}$ the lost life expectancy of outcrossed progeny. The lines in figure 2B translate this lifetime fitness criterion into relative survivorship requirements per time period.

SELECTION OF SELFING IN POOR POLLINATION ENVIRONMENTS

How does opportunity for reproductive assurance influence the threshold relative fitness required to favor selection of selfing? Answering this involves solving the threshold equation (i.e., $\lambda' = 0$; eq. [3]) for relative survivorship w_j or w_a , and taking the derivative of these solutions with respect to the rate of facilitated pollination e . When the derivatives are positive, decreasing facilitated pollination (i.e., poorer pollination environment) decreases the relative survivorship required for selection of selfing. The following focuses on initially outcrossing populations, on the specific models of selfing in figure 2, and on density-dependent population regulation.

Competing Self-Fertilization

The level of facilitated pollination e does not influence the selection of competing selfing in annuals because the derivative of the threshold equation $w_j = 1/2$ (from eq. [10]) with respect to e is zero.

Poor pollination environments make selection of competing selfing less likely in perennials. The equation of the threshold (i.e., eq. [10]) is $\lambda' = (w_j - 1/2)(1 - P_a) + (w_a - 1)S'P_a$ and, using equation (B1) to determine S' , we find

$$\frac{\partial w_j}{\partial e} = \frac{1 - w_a}{2(1 - P_a)^2} \frac{\partial P_a}{\partial e},$$

and

$$\frac{\partial w_a}{\partial e} = \frac{1 - w_a}{P_a(1 - P_a)} \frac{\partial P_a}{\partial e}.$$

The sign of both equations is determined by the derivative of adult survivorship with respect to level of pollination, $\partial P_a / \partial e$. This derivative is negative when decreased pollination reduces resources required for seed maturation and results in increased adult survivorship P_a . Qualitatively, poor pollination environments decrease adult survivorship costs of seed production, increasing longevity and amplifying fitness differences between selfed and outcrossed progeny. The declining value of selfed progeny increases the relative survivorship required for the selection of competing selfing.

Delayed Self-Fertilization

Delayed selfing is always favored in annuals (eq. [12]), provided facilitated pollination $e < 1$.

Surprisingly, delayed pollination in perennials is less likely in poor pollination environments. The partial derivatives of relative survivorship w_j and w_a satisfying the threshold equation (12) are

$$\frac{\partial w_j}{\partial e} = -\frac{(1 - w_a)\gamma^2}{ke^{1+\gamma}},$$

and

$$\frac{\partial w_a}{\partial e} = -\frac{(w_j - \gamma)e^{\gamma k}}{e(1 - e^{\gamma k})^2}.$$

Adult inbreeding depression $w_a < 1$ makes both equations negative (for the model in fig. 2, $\partial w_a / \partial e$ is negative when the curve for the threshold lies within $0 < w_a < 1$, which requires $w_j > \gamma$). Qualitatively, reproductive assurance is offset by survivorship costs of offspring production and the decreased value of selfed progeny due to effects of greater longevity mentioned above.

DISCUSSION

Reproductive Assurance and Selection of Outcrossing in Perennials

Reproductive assurance is not needed to explain an association between selfing and annuality. Competing selfing requires pollinators and so does not of-

fer reproductive assurance, but it is difficult to evolve in perennials because of the repeated costs of adult inbreeding depression. Delayed selfing offers reproductive assurance, but to both annuals and perennials. The association between this mode of selfing and life history arises because of the cost of adult inbreeding depression and the between-year seed discount in perennials, rather than reproductive assurance. Poor pollination environments do not enhance reproductive assurance in annuals (Lloyd 1979) and, surprisingly, magnify the fitness consequences of selfing for perennials (fig. 2). Perenniality generates an association between life history and selfing, without any necessary role for reproductive assurance.

Reproductive assurance is often couched in terms of temporal variation in pollinator abundance (e.g., Lloyd 1980), whereas we assume a constant environment. Several studies of hermaphroditic reproductive character evolution in variable environments (Charnov 1988; Tuljapurkar 1990) provide a context for the evolution of selfing. These studies maximize the geometric mean of fitnesses in each environment, so that conditions for the evolution of selfing in variable environments may lie between the conditions at the extremes of environmental variation. This suggests that environmental variation does not alter the qualitative conclusion that the consequences of perenniality rather than reproductive assurance generates an association between selfing and life history.

Lloyd (1980) asks about reproductive success of annuals versus perennials after one good and one bad pollination year. Using a geometric mean fitness for the annual and an arithmetic mean fitness for the perennial, Lloyd finds that the fitness of the annual is more affected by environmental variation than the fitness of the perennial. Unfortunately, geometric fitnesses are appropriate for both annuals and perennials (Tuljapurkar 1982), so that Lloyd's conclusion is not correct.

Lifetime Fitness

In the case of competing selfing illustrated in figure 2, outcrossing is favored when relative survivorship, w_j and w_a , are considerably larger than the value of one-half that characterizes the threshold relative fitness required for the maintenance of outcrossing in annuals (Lloyd 1979). Considering lifetime genetic success, rather than survivorship per time period, resolves this apparent contradiction. The condition in expression (14) can be rewritten as

$$1 - \frac{w_j P_0 (\lambda - w_a P_a)^{-1}}{P_0 (\lambda - P_a)^{-1}} < \frac{1}{2}. \quad (15)$$

The fraction to the left of the inequality is the ratio of the life expectancies of selfed to outcrossed individuals, and one minus this quantity represents lifetime inbreeding depression. Life expectancies are appropriate measures of fitness of selfed and outcrossed individuals because, under the competing model of selfing, fertility is not influenced by mode of reproduction. Measuring the fitness of selfed and outcrossed individuals over their entire life, rather than over a sin-

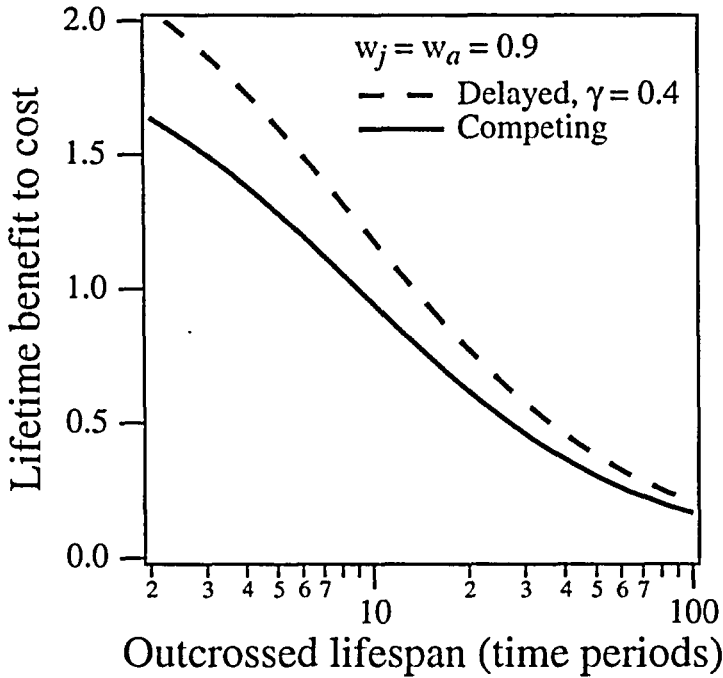


FIG. 3.—Lifetime ratio of benefit to cost of self-fertilization as a function of outcrossed adult life expectancy $(1 - P_1)^{-1}$, under competing and delayed self-fertilization in a population undergoing density-dependent regulation ($\lambda = 1$). Selfing is selectively advantageous when the ratio exceeds 1. For competing selfing, the benefit-to-cost ratio is $2w_j(1 - w_a P_a)^{-1} / (1 - P_a)^{-1}$; for delayed selfing, the ratio is $w_j(1 - w_a P_a)^{-1} / \gamma(1 - P_a)^{-1}$.

gle time period, recovers the familiar threshold inbreeding depression of one-half under competing self-fertilization.

It is useful to identify perennality per se as maintaining outcrossing. Greater adult survivorship (longevity) compounds the survivorship consequences accruing to selfed individuals, and the ratio of lifetime benefit to cost of producing selfed offspring decreases with increasing adult survivorship. This is illustrated in figure 3. Only when selfed individuals experience no deleterious adult survivorship consequence ($w_a = 1$) is the degree of perennality irrelevant to the selection of competing self-fertilization. The importance of perennality per se is particularly apparent when delayed selfing decreases life expectancy and the opportunity for production of outcrossed progeny. In this case, perennality extracts a cost even in the absence of inbreeding depression.

Life History and Mode of Self-Fertilization

The results presented here offer heuristic guides (Morgan and Schoen 1997) to the selection of self-fertilization in perennials, but the simplified life history and consideration of only two modes of selfing mean that the results are inappropriate for direct application to any particular plant species. The most general

guide is that benefits and costs measured as lifetime genetic success dictate the selective advantage of self-fertilization. Lifetime genetic success represents an accounting technique for tallying the expected number of genes that selfed and outcrossed individuals transmit. In models such as competing selfing that entail only the within-season seed discount, the selection of self-fertilization reduces to a simple assessment of whether a doubled genetic representation in selfed individuals more than outweighs the fitness consequences of decreased relative fitness and hence reduced life expectancy (eq. [14]). With delayed or other forms of selfing that alter total offspring production per time period, there is an additional accounting required to accommodate the fitness consequences of decreased parental survivorship. Specific aspects of reproductive biology may mean that the within-season seed discount is not exactly one-to-one (as occurs when, e.g., the mechanism of selfing partly reduces opportunity for outcrossing, as in Lloyd's 1979 "prior" model of selfing) or that self-fertilization alters male fertility through pollen discounting (Nagylaki 1976; Wells 1979; Holsinger et al. 1984). Such issues influence the number of adult genes transmitted to progeny (as with pollen discounting) or, indirectly, parental reproductive success as a consequence of changing resource demands of offspring maturation (as when prior selfing increases total seed production and hence decreases parental life-span). For these reasons, there is unlikely to be a simple proxy (e.g., a ratio of selfed to outcrossed life expectancies) for determining the selection of self-fertilization in perennials.

The life history in figure 1 is neither age- nor stage-classified, but the methods outlined here extend to less idealized (e.g., Sibly and Curnow 1993) or complicated life histories (Caswell 1989; Calvo and Horvitz 1990). For instance, the steps in an analysis of stage-structured populations involve developing expressions for population growth rates $\lambda(\delta)$ as a function of reproductive strategy (B_s and B_x in the model here), stage-specific survival and growth, and relative fitness consequences for selfed individuals at each stage. The expression for population growth is then subjected to the criterion for an ESS (eq. [3]) or the selection of self-fertilization (eq. [4]). Our analysis suggests that in complicated life histories selection favors self-fertilization when lifetime genetic success through selfing exceeds that through outcrossing. Developing realistic life histories may provide novel insights into the selection of self-fertilization.

Empirical Implications

A general criterion for the selection of self-fertilization is that lifetime genetic success through selfing exceeds that through outcrossing. Evaluating the selection of self-fertilization in perennials requires comprehensive life-history data and appropriate measurement of survivorship of selfed and outcrossed individuals.

Comprehensive life-history data.—Identifying the threshold for the selection of selfing in perennial life histories requires detailed information on consequences of reproductive strategy for parental reproduction through outcrossing and selfing and relative fitnesses of selfed and outcrossed individuals. Inbreeding depression measured over a limited part of the life cycle provides insufficient

information to evaluate the evolution of selfing in perennials. Instead, juvenile and adult phases need to be examined. Even this may be insufficient if adult inbreeding depression varies (e.g., decreases) over the life history, as recent studies suggest (Husband and Schemske 1996). An ideal data set would combine life table information with age- or stage-specific inbreeding depression.

When selfing provides reproductive assurance, the adult survivorship cost of seed production is important. An estimate of this cost might come from augmenting pollen loads to increase seed set and observing subsequent adult growth and reproduction. Between-year studies in orchids often identify such a cost (Calvo and Horvitz 1990), although this is not always found in other species (e.g., Bierzychudek 1981; Horvitz and Schemske 1988). Using such manipulative approaches to study life-history trade-offs (e.g., Bell and Koufopanou 1986) may not, however, identify genetic constraints important for evolution (Reznick 1985; Pease and Bull 1988; Charlesworth 1990). Also, modularity of plant construction (Watson and Casper 1984) allows response to pollen augmentation by adjusting reproductive strategy within the current season (Lubbers and Lechowicz 1989; Zimmerman and Pyke 1989), obscuring the between-season seed discount. Similar problems occur whenever multiple life-history components influence fitness (Charlesworth 1990; Houle 1991; Fry 1993). Inferences about the survivorship cost of seed production might also come from comparing reproductive strategies, as is done in dioecious species where males and females differ in growth and reproduction (Lloyd and Webb 1977). Again, though, complex trade-offs within seasons can hide between-season costs of seed production (Delph 1990).

Comparative studies may shed light on the evolution of outcrossing and perenniality. For instance, a recent molecular phylogeny supports the evolution of perenniality and outcrossing in island species of *Echium* (Böhle et al. 1996). Böhle et al. follow A. R. Wallace (1878) and suggest that perenniality reduces reproductive risk in novel environments where pollinators are rare. Our model accounts for subsequent evolution of outcrossing, since perenniality increases the costs of inbreeding depression and reproduction through self-fertilization. Another possible insight from comparative study involves the distribution of modes of selfing in annuals and perennials (Schoen and Lloyd 1992). Selfing that enhances total seed production is easier to evolve in annuals than in perennials (due to adult survivorship costs of the between-year seed discount rather than to reproductive assurance), so autonomous modes of selfing should occur more frequently in annuals. This possibility refines Stebbins's observation that annuals self-fertilize more than perennials do.

Measurement of relative survivorship.—Models of age- or stage-structured populations require that life-history parameters be measured over time intervals of equal duration (Caswell 1989): survivorship over a few weeks of germination is not directly comparable to adult survivorship measured over an entire year. Measures of relative fitness reported in the literature (summarized by Husband and Schemske 1996) are usually based on time periods of unequal duration. Calculating lifetime inbreeding depression as one minus the product of relative survivorship over periods of different duration (e.g., Husband and Schemske 1996)

implicitly assumes a life history without stage structure, as illustrated in figure 1. Since only rudimentary demographic information is available for many species, this simple life history may represent the best available solution. Realistic life histories require measures of relative fertility spanning comparable lengths of time. This does not preclude obtaining data over experimentally convenient time periods (e.g., germination experiments vs. yearly survival) and combining such data into comparable periods (Caswell 1989, pp. 45–53). Future reports of inbreeding depression in perennials should provide an explicit life-cycle graph and measures of life-history parameters over standardized periods of time.

Future Prospects

Genetics of fitness variation.—The models developed above assume fixed inbreeding depression during the adult phase of the life history. This is unlikely to be true. Genes expressed early in life experience stronger selection (Medawar 1946, 1952, cited in Charlesworth 1994, p. 189; Williams 1957; Hamilton 1966), so deleterious mutations affecting later life may accumulate and relative fitness decline with age. There are substantial relative survivorship deficits later in the life history (Husband and Schemske 1996), but how inbreeding depression changes with age is unknown.

Inbreeding depression is evolutionarily dynamic, probably determined by the balance between mutation and selection of deleterious alleles (Lande and Schemske 1985; Charlesworth and Charlesworth 1987; Charlesworth et al. 1991; Lande et al. 1994). Perenniality increases the number of episodes of selection and may reduce the equilibrium inbreeding depression. In contrast, the absence of a germ line in plants allows transmission of somatic mutations between generations. Cell lineages contributing gametes in older individuals experience more divisions than those in younger individuals (Klekowski 1988), increasing the mutational component of inbreeding depression. The balance between the forces of mutation and selection in perennials represents an unanswered empirical question.

Self-fertilization and reproductive strategy.—Finally, we address the evolution of selfing and perenniality without considering other elements of the reproductive strategy. Several studies investigate reproductive resource allocation in perennial hermaphrodites (Kakehashi and Harada 1987; Charnov 1988; Zhang and Wang 1994), providing a complement to our own research. Temporal deployment of resources within a single growing season (Brunet and Charlesworth 1995; Seger and Eckhart 1996) receives attention in annuals but may also apply to perennials. Important insights may arise from combining sex allocation and self-fertilization. For instance, Charlesworth (1984) modeled the evolution of sex allocation and female sterility (androdioecy), asking whether males benefit by avoiding the adult survivorship cost of seed production required by hermaphrodites. When female fertility extracts a large survivorship cost, the resource allocation to female function decreases. There is therefore little resource or survivorship advantage to be gained by specializing only in male function. This example illustrates an interaction between allocation and life-history strategies that may have a parallel for self-fertilization. Perennials may evolve to minimize

the between-year seed discount, reducing the cost of reproductive assurance. The answer to this question awaits future research.

ACKNOWLEDGMENTS

S. C. H. Barrett, D. Charlesworth, D. Schemske, J. Willis, and an anonymous reviewer provided helpful comments. Financial support for this work includes a Natural Sciences and Engineering Research Council of Canada (NSERC) post-doctoral fellowship to M.T.M., and an NSERC operating grant to D.J.S.

APPENDIX A

TABLE A1

PARAMETERS OF A PERENNIAL LIFE HISTORY WITH PARTIAL SELF-FERTILIZATION

Symbol	Definition
Life history:	
B	Combined fertility through male and female functions
P_0	Juvenile survivorship
P_1	Adult survivorship
λ	Population growth rate
Self-fertilization:	
B_s	Fertility through self-fertilization
B_x	Fertility through outcrossing
P_s	Adult survivorship independent of mating system
S	Frequency of the parental genome found in adult progeny derived from self-fertilization
w_j	Survivorship of self-fertilized, relative to outcrossed, progeny during recruitment, $w_j = 1 - \delta_j$
w_a	Survivorship of self-fertilized, relative to outcrossed, adults during a single period (e.g., 1 yr), $w_a = 1 - \delta_a$
Specific models of selfing:	
e	Proportion of ovules fertilized by external pollination vectors
k	Decrement in longevity when all ovules mature as seeds
n	Number of seeds produced by an individual
o	Number of ovules available for fertilization
s	Frequency of the parental genome in seeds derived from self-fertilization
γ	Parameter determining the shape of the relationship between the fraction of ovules matured as seeds and adult survivorship

APPENDIX B

FREQUENCY OF THE PARENTAL GENOME IN ADULT PROGENY DERIVED FROM SELF-FERTILIZATION

This appendix presents an expression for the fraction of adults derived from self-fertilization S in density-dependent and density-independent populations. In a population growing at rate λ per time period and currently of size N individuals, there were N/λ adults in the previous time period, N/λ^2 in the time period before that, and so on. The number of adults derived from self-fertilization consist of recruits from the previous time period $(N/\lambda) \times w_j P_0 B_s$, (i.e., number of adults times recruitment per capita), recruits from 2 yr previous who

also survive one time period as adults $(N/\lambda^2) \times w_j P_0 B_s \times w_a P_1$, and so on. The total number of adults derived from self-fertilization is therefore

$$(N/\lambda)w_j P_0 B_s + (N/\lambda^2)w_j P_0 B_s w_a P_1 + (N/\lambda^3)w_j P_0 B_s (w_a P_1)^2 + \dots \\ = N \frac{w_j P_0 B_s}{\lambda} \sum_{i=0}^{\infty} (w_a P_1/\lambda)^i.$$

The summation corresponds to a geometric series and has a simple closed form:

$$\sum_{i=0}^{\infty} (w_a P_1/\lambda)^i = \frac{1}{1 - w_a P_1/\lambda}$$

(e.g., Apostle 1967, p. 388) so that the number of adults derived from self-fertilization is

$$N \frac{w_j P_0 B_s/\lambda}{1 - w_a P_1/\lambda} = N \frac{w_j P_0 B_s}{\lambda - w_a P_1}.$$

Density-dependent populations have growth rate $\lambda = 1$ in this expression. The number of adults derived from outcrossing has the same form, but with relative survivorship of juveniles w_j and adults w_a replaced by 1, $NP_0 B_x/(\lambda - P_1)$. The fraction of adults derived from self-fertilization in a population adopting reproductive strategy s is the ratio of the number of adults derived from selfing to the total number of adults,

$$S(s) = \frac{w_j B_s(s)/(\lambda - w_a P_1(s))}{w_j B_s(s)/(\lambda - w_a P_1(s)) + B_x(s)/(\lambda - P_1(s))}. \quad (B1)$$

Analysis of this formula demonstrates the intuitively reasonable results that greater selfing \hat{s} increases the fraction of adults derived from selfing ($S' > 0$), and larger values of the relative survivorship of juveniles w_j or adults w_a increase S .

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Associate Editor: Douglas W. Schemske