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On sex allocation and selfing in higher plants

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On sex allocation and selfing in higher plants

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Summary

Sex allocation (male allocation/female allocation) as a function of selfing rate is studied in the wild rice *Oryza perennis*. Using dry weight measures, the male/female ratio is linearly related to the selfing rate. This linear relationship may have a fairly radical interpretation in terms of current sex allocation theory. It suggests that the intermediate selfing rates are themselves maintained by a form of frequency dependence. In particular, the linearity suggests: (i) the relative fitness of a selfed versus outcrossed offspring decreases with increased selfing; (ii) in equilibrium, a selfed offspring is approximately half as fit as an outcrossed offspring; (iii) the frequency dependence, being the opposite of that proposed in most selfing models, may result from the same forces thought to be involved in the maintenance of sex itself, and (iv) the position of the fitted line contains information about the plant's use of wind pollination for male reproduction. It suggests that wind shows much less mixing of pollen than previously assumed, and/or that there are severe morphological constraints on pollen presentation. The above interpretations are clearly speculative and tentative. Possible problems in the analysis, and some alternatives for data interpretation are discussed.

Keywords: Plant breeding systems; sexual reproduction; mixed ESS.

Introduction

Sex allocation refers to the evolution of sex ratio in dioecious species, time (and order) of sex change in sequential hermaphrodites and the allocation of resources to male versus female functions in simultaneous hermaphrodites (Charnov, 1982). These problems share common features of frequency dependence of fitness (Fisher, 1930), and the phenotypic equilibrium, the ESS of Maynard Smith (1982), may often be shown to satisfy a certain general optimality principle (Charnov, 1979a, 1982, 1986; Charnov and Bull, 1986). Sex allocation theory is thus the characterization of these evolutionary equilibria. Simultaneous hermaphrodites, which include most higher plants, provide some of the most interesting comparative material. Several formal models for sex allocation versus selfing rate predict that increased selfing selects for relatively less resource input to the male function (Maynard Smith, 1978; Charnov 1979b, 1980, 1982; Charlesworth and Charlesworth, 1981). As a qualitative prediction, plant data of several sorts show the expected pattern (Charnov, 1979b, 1982; Lemen, 1980; Lovett Doust and Cavers, 1982; Schoen, 1982; Quellar, 1984; Cruden and Lyon, 1985). Indeed, in a recent comprehensive and critical review of plant paternal strategies, Bertin (1987) concluded that " . . . of all the predictions reviewed in this paper, the only one that I feel is well supported is the tendency for male allocation to decrease as selfing becomes more prevalent."

The most precise sex allocation–selfing data are those of Schoen (1982) for *Gilia achilleifolia* (Polemeniaceae). All six populations studied showed intermediate selfing rates and the relative allocation to male function showed an almost perfect negative linear relation (Schoen, 1982;

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Charnov, 1982). His relation is shown as the dotted line on Fig. 1. In this paper, I will discuss sex allocation–selfing data for a wind pollinated grass. The data are as precise as Schoen's and they also show a negative linear relationship. After presentation of the data, I will suggest why the linearity may be an important pattern.

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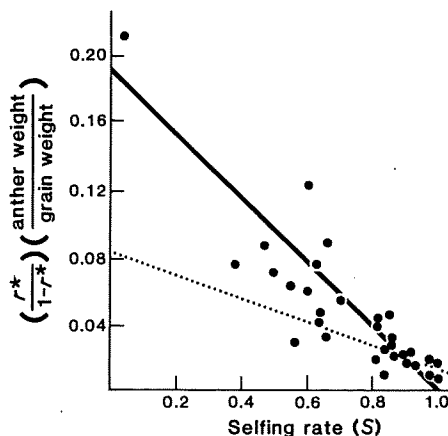lation (Schoen, 1982;

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Figure 1. Relative male/female investment ($\frac{r^*}{1-r^*}$; here total dry anther weight/total dry grain weight) versus proportion of seeds which are selfed (S) for 31 varieties of the wild rice *Oryza perennis*. $y = 0.19 - 0.19x$; $r^2 = 0.71$. The dark line is the best fit functional regression. The dotted line is the $r^*/(1-r^*)$ versus S relation for *Gilia achilleifolia* (Schoen, 1982). The methods used to estimate selfing rates for the rice varieties are detailed in Oka and Chang (1961, Table 2), Morishima *et al.* (1963, Table 4), and Oka and Morishima (1967).

Wild Rice

The plant is the perfect-flowered wild rice *Oryza perennis* (Poaceae), which is distributed throughout the tropical countries of the world. Depending upon habitat, it may be perennial or annual (or intermediate). Thought to be the progenitor of cultivated rice, *O. sativa*, it has been widely studied with respect to life history, growth and various allocation strategies (Oka and Chang, 1961; Morishima *et al.*, 1963; Oka and Morishima, 1967; Oka and Sano, 1981; Sano and Morishima, 1982; Oka, 1983; Morishima *et al.*, 1984). In the course of this work, Oka and Morishima estimated selfing rates, total dry anther weight per flower, and total dry grain weight per flower for many strains, collected from Asia, Oceania, America and Africa. References to the detailed methods are given in the caption to Fig. 1. Many populations show intermediate selfing rates; in general, the annuals are more selfed than the perennials. Drs H. I. Oka and H. Morishima have kindly provided the sex allocation and selfing data for 31 strains of this rice, including three highly selfed cultivars. The data are given in Fig. 1 and show a very strong, negative, linear relationship. Including the one wholly outcrossed strain, the functional regression (or reduced major axis; Ricker, 1973) is $y = 0.19 - 0.19x$ (correlation coefficient = -0.84, sample size = 31). Excluding this outcrossed strain reduces the correlation, as expected, to -0.73, but the functional relation is almost unchanged; $y = 0.17 - 0.16x$.

Discussion

The rice line of Fig. 1 raises a number of issues, with respect to both methods and theory. For the first part of this discussion, I shall assume that the sex allocation measures for rice are adequate; later I shall discuss alternatives. Firstly I shall present a brief review of formal sex allocation theory.

For an outcrossed simultaneous hermaphrodite, if m refers to an individual's reproductive gain through male function, and f the same through female function, the ESS allocation is that which maximizes the product of $m \cdot f$ (Charnov et al., 1976; Charnov, 1979b, 1986; Charnov and Bull, 1986). This model allows no self-fertility, but the extension to allow some degree of selfing is relatively straightforward (Charlesworth and Charlesworth, 1981; Charnov 1982). Let S = the selfing rate, or proportion of seeds which are selfed (assuming that virtually no pollen is used in selfing); $1-S$ proportion of the seeds are randomly mated, and let $1-\delta$ = fitness of selfed progeny, compared to a fitness of 1 for outcrossed progeny. The new ESS is to find m and f so as to maximize the product (Charlesworth and Charlesworth, 1981; Charnov, 1982).

$$m^a \cdot f^b \quad (1)$$

where $a = 1-S$ and $b = 1+S\,(1-2\delta)$.

In order to use Equation 1 to predict the ESS sex allocation, we further need to specify how m and f change as resource is shifted from male to female (or vice versa) function. An equation form which is particularly useful is

$$m \propto r^n \quad (2a)$$

and

$$f \propto (1-r) \quad (2b)$$

where r is the proportion of reproductive resources given to male function. In Equation 2 we assume that the gain through seeds is strictly proportional to the resources put into seeds; the reproductive gain through pollen depends upon n, a shape parameter. If $n < 1$, there are diminishing reproductive returns for resources put into pollen. Fig. 2 shows the effect of various n
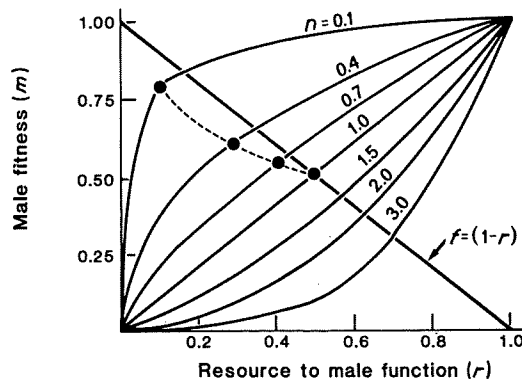

Figure 2.   If r is the proportion of resources given to male function, male fitness is given by $m = r^n$. This graph shows the male fitness (the *male gain curve*) for various values of n. Female fitness is assumed to be proportional to resource input into seeds of $f = 1 - r$. The solid circles show the ESS allocation to male function (r^*) for four values of n. The faster the saturation of male fitness (i.e., the smaller n), the smaller is the ESS r^*. (n must be < 1 for hermaphroditism itself to be stable relative to dioecy.)

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values. While the model assumptions in Equation 2 are not the only ones possible, they allow exploration of a wide range of shapes for the male gain relation ($m \propto r^n$) by changing only a single parameter (n).

Under these assumptions, the ESS r^* is the value which maximizes (from Equation 1)

$$r^{an}\,(1-r)^b$$

(3)

Thus (as first shown in Charlesworth and Charlesworth, 1981)

$$\frac{r^*}{1-r^*} = \frac{n(1-S)}{1+S(1-2\delta)}$$

(4)

This equation has the interesting property that

$$\frac{r^*}{1-r^*} \simeq n(1-S) \qquad \text{for } 0.35 < \delta < 0.65$$

(5)

This linear relation is shown in Fig. 3. Only if $\delta \sim 1/2$ and if n does not change with S is the expected relation linear. Note also that the totally outcrossed ($S = 0$) allocation estimates the shape parameter n. Taking the linear relations of Fig. 1 seriously, we are now led to ask why $\delta \sim 1/2$ in these populations. The data present at least one other major puzzle: most populations show intermediate selfing rates.
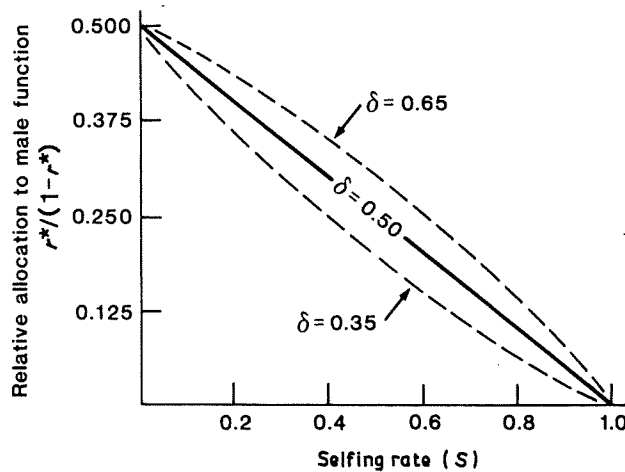

Figure 3. The ESS resource allocation to male versus female function [$r^*/(1-r^*)$] is predicted (Equation 4) to be inversely related to the selfing rate (S). The graph shows the relations for one male gain curve ($m = r^n$ where $n = 0.5$ independent of S) and three levels of inbreeding depression for selfed offspring ($\delta = 0.35$, 0.5, 0.65). Note that the intercept on the ordinate is 0.5, equal to n and that the theoretical relation is near linear for these δ values.

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As noted in Charnov (1982), the selfing model discussed here has one major difficulty when used as a sex allocation model. It takes S as a fixed value and then works out the ESS r^*. However, S is also subject to evolution, which poses a problem. The ESS S is predicted to be 1 if $\delta < 1/2$ (and zero if $\delta > 1/2$); that is, no interior equilibrium is predicted. This lack of an interior

equilibrium for the selfing rate (S) is a common feature for these population genetic models (Lande and Schemske, 1985; Holsinger, 1986). At least some plants characterized with respect to selfing rates clearly show intermediate selfing levels (Lloyd, 1979; Schemske and Lande, 1985; Aide, 1986; Holsinger, 1986), as do the two species in Fig. 1. While a transient polymorphism is possible, I would like here briefly to develop a hypothesis which allows (under some conditions) a stable intermediate value for S. Selfing has several costs and benefits (see Lloyd, 1979; Lande and Schemske, 1985 for detailed review). Genes causing selfing double their representation in selfed offspring. They also result in homozygosity, exposing deleterious recessives; that is, selfed progeny in typically outcrossed species often show inbreeding depression. While it has usually been argued that selfing rids the genome of deleterious recessive genes, resulting in a decrease in inbreeding depression ($\delta \to 0$ as $S \to 1$), I wish to propose that just the opposite may also be possible. The hypothesis is that the relative fitness of a selfed offspring may decline as the level of selfing (S) goes up (Charnov, 1982). If $\delta < 1/2$ when S is at 0, selfing will be favored. If δ goes up with S, a stable polymorphism may result if δ goes up fast enough; essentially if $\delta \to 1/2$ before $S \to 1$. It may be important to realize that $1 - \delta$ is the *relative* selfed/outcrossed fitness at each level of S. The ESS S will be near $\delta = 1/2$, but it may be different from $\delta = 1/2$ if individual genotypes with different selfing rates themselves confer different δ^s on their children (Charnov, unpublished theory).

Why might δ show this form of selfing–frequency dependence? Selfed progeny from a given parent are more alike than outcrossed progeny. The *per capita* fitness of "*offspring, all the same*" may well go down as their frequency goes up due to factors such as sib competition (Williams, 1975) or the other factors (e.g. pathogens) thought to be involved in the maintenance of sexual reproduction itself (e.g. Bell, 1982). Indeed, the model discussed here gives a mixed ESS for sexual versus asexual (= selfing) reproduction.

Making δ frequency-dependent in this way may solve both the "intermediate levels of selfing" problem *and* the $\delta \sim 1/2$ problem. In suggesting this hypothesis and interpretation of the data (Fig. 1), I also suggest great caution. Selfing is a complex phenomenon (for a comprehensive discussion see Jain, 1976) and our current population genetic models are at best rough approximations; we simply do not know if the formalism, as used here and elsewhere, captures the essential qualities of the evolution of selfing. However, at the least, the sex allocation data add a new twist to thinking about selfing, providing an easily measured character which various selfing models can address.

Since the rice is wind pollinated, n should not change with selfing level. The Y-intercept thus allows an estimate of n which makes $n \simeq 0.19$. Earlier, Charlesworth and Charlesworth (1981) and Charnov (1979b, 1982) suggested that wind pollination would show little saturation of the male gain relation; m versus r was predicted to be nearly linear, or n near 1. This would, of course, make $r^*/(1-r^*) \simeq 1$ under outcrossing. Data on wind pollinated shrubs presented by Lemen (1980) appeared to support this equal allocation. Lemen's (1980) methods have since been called into question by Willson and Ruppel (1984). They found $r^*/(1-r^*)$ values from about 0.12 to 0.4 in a wind pollinated, outcrossed ($S < 0.1$), monoecious, North American wild rice (*Zizania aquatica*). Likewise, using stamen dry weight over total reproductive dry weight to estimate r^*, Cruden and Lyon (1985) came up with r^* estimates in the range of 0.1 to 0.2 for two wind pollinated species. It would thus appear that wind pollination shows much more saturation for the male gain relation than previously suspected. Indeed, the sum total of our more precise plant data suggests that n is between 0.1 and 0.3, and will not depend strongly on the pollination system; compare the Schoen line versus the rice line in Fig. 1. Lloyd (1984) has reviewed other sex allocation data for outcrossed plants; in general, all plants give much more of their resources to female function than to male function. Under current sex allocation theory, this observation

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To this point the discussion has accepted the data (Fig. 1) and used a simple sex allocation model ($f \propto 1-r$, $m \propto r^n$). Of course, dry weight may not be a good measure of the resources traded off between male and female function (Charnov *et al.*, 1976; Willson and Ruppel, 1984; Geber and Charnov, 1986); various nutrients, or even time are other possibilities. Probably the most worrying aspect of the rice data is that the male measurement is pre-fertilization while the female (= grain) measurement is *very* much post-fertilization. Photosynthesis, post-fertilization, would appear to make resources which are simply not available for male function, at least in annuals (Geber and Charnov, 1986). It is thus possible that our model for *m* and *f* is too simple and explicit consideration of time is needed. It could also be that the sex allocation represents a compromise between the genetical interests of nuclear genes and cytoplasmic genes; this would certainly give greater female allocation than just nuclear genes (Charnov, 1982). I raise these issues to provoke further discussion. The rice data discussed in this paper, as well as Schoen's (1982) data, give good linear relations. Any theoretical construct must address the issues they raise. We have probably just begun.

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Some comments on "Sex allocation and selfing in higher plants"

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In a previous paper in this journal (Charnov, 1987) I suggested that a linear relationship between the ratio of male allocation to total seed allocation, and the proportion of seeds which are selfed, contains information about the relative fitness of selfed versus outcrossed offspring; in particular, that the selfed offspring were half as fit as outcrossed and that this may be the result of frequency dependent selection which itself stabilizes the intermediate selfing rates. All this conjecture was based on a selfing–sex allocation model proposed by Charlesworth and Charlesworth (1981). I now believe that their model itself confounds sex allocation with selection for/against selfing. Their model takes the proportion of seeds which are selfed as fixed and allows selection to adjust the proportion of resources given to pollen versus seeds. Note that under this scheme, selection can increase or decrease the proportion of reproductive resources given to selfed offspring by giving more or less to seeds. Thus the "fixed selfing rate" is not really fixed; it is adjusted through the back door by altering the sex allocation. The resulting non-linear selfing versus sex allocation graphs (see for example Fig. 3, Charnov, 1987) are themselves a result of selection using sex allocation to increase or decrease the level of selfing. A model which corrects this defect would take the proportion of reproductive resources given to selfed offspring as fixed and look at allocation to male versus female function among the outcrossed component. Assuming as before (Charnov, 1987) that the male and female gain relations do not change with the selfing rate, it is clear that the ESS sex allocation among the outcrossed resources obeys the outcrossed product theorem and is not at all related to the selfing rate. Furthermore, a plot of the ratio of pollen allocation to total seed allocation versus the proportion of seeds which are selfed will be linear, independent of the level of inbreeding depression for selfed offspring. Under this new allocation scheme, a linear sex allocation versus selfing relation (see data discussed in Charnov, 1987) contains no information about the inbreeding depression level. Of course, the new model, just as the old one, does not itself account for the maintenance of the intermediate selfing rates themselves. This puzzle still remains.

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