Allocation of Resources to Sex Functions in Flowering Plants

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SUMMARY

The study of allocation of resources offers the possibility of understanding the pressures of natural selection on reproductive functions. In allocation studies, theoretical predictions are generated and the assumptions as well as the predictions can be tested in the field. Here, we review some of the theoretical models, and discuss how much biological reality can be included in them, and what factors have been left out. We also review the empirical data that have been generated as tests of this body of theory. There are many problems associated with estimating reproductive resources, and also with testing how allocation of these resources affects reproductive and other components of fitness, and we assess how important these may be in allowing empirical results to be interpreted. Finally, we discuss the relevance of resource allocation patterns to the evolution of unisexual flowers, both at the level of individual plants (monoecy, andro- and gynomonoecy) and at the population level (dioecy).

1. INTRODUCTION

An understanding of the patterns of allocation of resources to different functions and structures in living organisms implies knowledge of the way natural selection acts on these functions. Therefore an important part of the study of the evolution of plant breeding systems concerns allocation to the structures and functions involved in the various stages of the reproductive process. Theoretical models of allocation to these structures enable one to incorporate interactions of plants and their environments into theories of breeding system evolution, in a disciplined and organized way. This approach complements research on the genetic advantages and disadvantages of different plant breeding systems.

When one constructs a model of allocation of reproductive resources, one tries to include all the functions and structures that can affect the numbers of progeny produced. In hermaphrodite organisms, such as most flowering plant species, this means including reproduction via both male and female functions, and including all stages of the reproductive process (Lloyd 1975; B. Charlesworth & D. Charlesworth 1978). For example, if seedlings compete with one another, the increase in the number of surviving progeny with number of seeds produced would be sharply limited, and seed number would be a poor indicator of progeny production through seeds (Lloyd 1979). Therefore, to be useful either as a conceptual framework for thinking about the costs and benefits of different reproductive functions, or to be analysed quantitatively, models of allocation must involve considerable biological realism, and include many variables with important effects on the evolution of allocation patterns. The inclusion of this degree of realism, however, causes various problems. Complex models, which take most of the important factors into account, have so many parameters that they are difficult to analyse. Alternatively, one can focus on certain effects, and construct simplified models that omit other factors. In either case, the predictions of these models are often hard to test, because species seldom differ in just the parameter of interest. For example, the prediction that plants with a certain type of pollinator should allocate more to attractive structures than those pollinated by a different type of pollinator appears to be simple and testable, until one realizes that the difference in pollination is likely to be associated with other differences, such as in the degree of self pollination, or the time of year when pollination occurs. There are thus difficult problems to be solved in the testing of allocation theories.

In this review, we start by outlining the way in which models of allocation to sex functions in hermaphrodite plant populations can be constructed and analysed. After describing simple allocation models, we review recent models with greater biological realism (i.e. more parameters). We then review the evidence that there is a single resource pool for the different reproductive functions, and the problems involved in measuring allocations and in testing the model's predictions. Finally we discuss the insight that allocation studies can give into the evolution of unisexuality.

2. THEORETICAL MODELS OF SEX ALLOCATION IN COSEXUAL PLANTS: MODELS AND METHODS OF ANALYSIS

(*a*) *Annual life cycle*

Theoretical models of sex allocation assume that the resources available for reproduction are fixed and can

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be devoted in varying amounts to different functions (reviewed by Lloyd 1987*a*, *b*). The reproductive fitness of a cosexual organism is the sum of contributions due to male and female reproduction

$$w_{\mathrm{h}} = w_{\mathrm{f}} + w_{\mathrm{m}}$$

where w_{f} is the female and w_{m} the male contribution. Assuming some genetic variation in allocation patterns due to variation at nuclear loci whose alleles act additively and have no selective effects apart from those on allocation, the relative fitnesses of different phenotypes are proportional to the numbers of gametes transmitted to progeny at the same stage in the next generation (Lloyd 1975, 1977; Charlesworth & Charlesworth 1978; Gregorius & Ross 1981). These fitnesses depend on the amounts of resources allocated, the effects on the numbers of ovules and pollen grains produced, and their success in the fertilization process and the subsequent stages of seed maturation and seedling establishment. Mating systems with both self- and cross-pollination can be modelled, as well as allocation to structures for pollinator attraction (including petals and nectar). These consume resources that could otherwise be used to produce more ovules or pollen.

The female contribution to fitness depends on the numbers of seeds and seedlings produced. Seed output depends on the proportion, F, of reproductive resources allocated to ovules, and on the allocation to attraction of pollinators, A. The probability of selfing will depend on details of the flower size and the times of maturity of the anthers and stigma, and also on the probability of pollinator visitation (Lloyd 1979). Models of allocation can include various possibilities for selfing, which may occur before pollinators visit (prior selfing), or by the agency of pollinators carrying a mixture of self and outcross pollen (competing selfing), or by self-pollination of unvisited flowers (delayed selfing). In general, therefore, we should consider selfing rates to be functions of A, $S(A)$ say (Lloyd 1987*c*). These factors can be put together (for the case when all ovules are fertilized either by prior or competing selfing, or by outcross pollen) to get an expression for the number of gametes a plant contributes through seed production:

$$O(F)\{1-S(A)+2S(A)\,(1-\delta)\}, \qquad (1)$$

where $O(F)$ is the number of ovules and δ is the inbreeding depression (the reduction in fitness of selfed, relative to outcrossed, progeny).

Finally, the female contribution to fitness depends on the number of fertilized ovules matured into seeds. Two extreme situations are biologically realistic. In some plants, fruits mature after flowering and may therefore draw on a different resource pool from that available at flowering time. Because allocation models assume that there is a fixed total amount of resource for reproduction, a structure or function should be included only if changing it affects the expression of other functions. This is most likely for functions that occur simultaneously. In the case when flowering and fruiting have separate resource pools, F will be the allocation to female functions (ovaries and ovules) at the time of flowering, and the female component of fitness will have an upper limit dependent on the second resource pool (Charlesworth & Charlesworth 1987). The opposite extreme is a single resource pool for reproduction, limiting both flowering and fruiting (Lloyd 1987*c*). F is then the proportion of this amount that is used up in both stages of female reproduction. In many plants, fruits start to mature while flowers are still developing, so the reality clearly lies between these extremes. The appropriate assumptions for modelling, and for estimating the parameter F empirically, must therefore be decided according to what is most appropriate for the particular plant of interest, thus reducing the generality of the results.

Now consider male reproduction. This is necessarily competitive, since the effect of increasing pollen output on the numbers of ovules fertilized depends on the amount of pollen produced by other individuals in the population. The contribution to fitness through male function will be a function of M, the proportion of resources allocated to anthers and pollen (which equals $(1-A-F)$, because of the assumption of a fixed total amount of resource). It will also depend on visits from pollinators: the contribution to the pollen pool for outcrossing will be a function of both M and A, say $P(M, A)$. The contribution to fitness of a given phenotype through male function is therefore given by the number of ovules available to pollen in the pollen pool (which is simply the number of ovules that are not selfed), multiplied by the ratio of its pollen production to the average pollen output. We can write this fitness contribution of a particular phenotype, j, in a population with any number of allocation phenotypes designated by subscripts i and having frequencies z_i, as:

$$w_{\mathrm{m}} = \{\sum_i z_i\, O(F_i)\,[1-S(A_i)]\}\frac{P(M_j, A_j)}{\sum_i z_i\, P(M_i, A_i)}. \qquad (2)$$

Analysis of the evolution of allocation patterns based on this type of fitness equation can be achieved by searching for a set of values of allocation parameters such that, if a population existed with that set, any other slightly different values would produce a lower fitness, i.e. the fitness of the phenotype expressed by the population is higher than that of an invading rare type, so the new type will not increase in frequency. To find this evolutionarily stable strategy (ESS, see Maynard Smith 1982; Lloyd 1987*a*, *b*), the fitness equation for a particular phenotype is written as $w(\boldsymbol{a}\,|\,\boldsymbol{a}^*)$, where $\boldsymbol{a}$ refers to a vector of allocations defining a phenotype, and $\boldsymbol{a}^*$ is the vector for the population. The ESS can be found by solving for the values of the allocation parameters at which the partial derivatives of fitness with respect to the components of $\boldsymbol{a}$ are zero, and the second derivatives negative, with the derivatives evaluated with the allocation set having the values of $\boldsymbol{a}^*$ (Charlesworth & Charlesworth 1981).

Other methods of analysis derived from this fundamental method may be technically easier to use. For example, Charnov (1982) discussed the 'product rule', which applies to many allocation problems, and states that the ESS allocation parameters maximize the product of the male and female contributions to fitness.

Lloyd (1987*a*) proved a marginal value theorem stating that at the ESS allocation set the marginal gains for the functions, weighted by their reward values, are equal. Lloyd (1987*a*, *c*) has used this to solve for allocation problems in which one resource is partitioned between multiple functions. Sometimes analytical approaches may be impossible, and graphical methods may be used (see, for example, Charlesworth 1989). Charlesworth (1990) showed that the results of ESS analyses give approximately the same results as those obtained from quantitative genetic analysis, for weakly selected characters.

We must next describe how the allocations translate into the fertilities that appear in the fitness expressions. It is biologically reasonable to think that these relations should be increasing functions, but that they would rarely be linear (Charnov 1979). At least one of the male and female gain curves (and often both) will usually be saturating. This will be the case when the gain through either sex is limited by factors other than the amount of resources allocated. For example, pollen contributions to the outcrossing pollen pool will be limited by the numbers of pollinators and their capacity to carry pollen (Charnov 1979). There would therefore tend to be a diminishing returns, or saturating gain, effect for increasing pollen production. This shape of curve is also reasonable for female fertility, because seed production is often limited by resources for fruit maturation, and thus has a separate limit from that imposed by resource limits on flower and ovule production (Willson 1983). We return below to some interesting cases when one or the other curve might be accelerating.

To incorporate the shapes of the gain curves into the models, the allocations can be raised to suitable exponents. For example, to model the saturating gain for male fertility, one can raise the pollen output to a power less than 1. This method has some convenient properties for solving for allocation patterns (Charnov & Bull 1986), and is also reasonable in biological terms, although S-shaped curves would probably be more realistic (Frank 1987). Charnov & Bull (1986) and Lloyd (1989) showed that for allocations between multiple functions with this type of model in populations with no inbreeding, the ESS allocations for outcrossing populations are in the ratios of the exponents. In other words, a function with severely limited gain will tend to be allocated lower amounts of resources. Furthermore, the relative amounts of resource allocated to two functions can be deduced without considering other functions that draw on the same resource pool (Lloyd 1989).

These models can be extended to include allocations to one function that may affect the success of another, for example if pollen attracts pollinators so that greater pollen output affects the chance of fertilization of the ovules, as well as the male fertility (Lloyd 1987*c*; Charlesworth & Charlesworth 1987). The selfing rate may also be a function of the male allocation (Charlesworth & Charlesworth 1981). It is also possible to study models in which functions draw on more than a single resource pool. McGinley & Charnov (1989) have done this for the problem of seed size and number. The possibility of different environments, in which the gain curves differ, has also been analysed (Charnov & Bull 1985). We will not attempt to describe these elaborations in detail here.

Another type of sex allocation model explicitly includes costs per item, such as ovules, pollen and flowers (for examples, see Cohen & Dukas 1990; Spalik 1990). Assuming that all reproductive functions, including fruiting, draw on one resource pool, so that increased allocation to flowering-time functions, such as flower numbers or attraction, reduce seed output, these models can give results about ratios of fruits to flowers (Morgan 1991), which are not possible with the kind of models described above. Constancy of the costs of the unit reproductive structures is also usually assumed (but see Schoen & Dubuc 1990).

(*b*) *Perennial life cycles*

In perennial plants with reproduction at more than one age, allocation to reproduction may affect the probability of survival to the next age class, and this can affect the sex allocation that will evolve (D. Charlesworth 1984; Charnov 1988; Kakehashi & Harada 1987). The difficulty in analysing such models is the number of parameters involved. These include the allocations to male and female functions of different age or size classes, and the effects of allocation on the transitions to the next stages. When the survival probabilities are independent of the allocations, the results are similar to those for annual life cycles (Charnov 1988). When allocation to female functions reduces survival more than male reproduction, but the effects are independent of age, allocations shift towards more male function (Tuljapurkar 1990).

These results assume that the life history is fixed, and do not allow for the joint evolution of sex allocation together with the onset and frequency of reproduction. Given the difficulty of producing general theories of life-history evolution (reviewed by B. Charlesworth 1984), it is not surprising that this even more complex problem has not been solved. Charlesworth (1990) describes a method based on quantitative genetics which is useful for this type of study of multiple allocation strategies. He used it to find ESS life histories assuming that at each age class resources may be allocated either to reproduction or to survival. Inclusion of different effects on survival of allocation to different sex functions would probably change the life histories predicted to evolve. Male reproduction probably often affects survival less than fruiting, and in many perennial plants male reproduction starts at an earlier age (or at smaller size) than female reproduction (Godley 1964; Meagher 1982). Inclusion of these sex differences into models of sex change with size has been strikingly successful in predicting the behaviour of such plants (Policansky 1981; reviewed by Charnov 1982). Investment per offspring may also evolve to be higher in harsh environments (Kawano 1981). If this happens, it will be important to take it into account in the theory. It would certainly be valuable to have more data on between-population variation within species, especially species occupying a range of habitats.

3. EVIDENCE FOR LIMITED POOLS OF RESOURCES

A major assumption, explicitly underlying theoretical models of sex allocation, is that there is a fixed amount of some resource which is available for reproductive functions alone, and which can be split up in various possible ways among the different reproductive functions (see Partridge & Sibly, this symposium). This assumption is applied strictly only in models that assume an annual life cycle. In perennials, there is also the possibility for unused resources from one reproductive episode to be used for growth and to increase survival to the next breeding season. The idea of limiting pools of resources is an old one and seems intuitively reasonable, and is a basic assumption of models of life-history evolution (see Partridge & Sibley, this symposium). Darwin considered this to be a fundamental property of biological systems, which he referred to as 'compensation' and viewed as producing an increase in the amount or size of one structure when another is reduced, for example an increase in female fertility in male-sterile plants (see, for example, the discussion in Darwin 1877, p. 280; Stauffer 1975). In the recent literature, this type of effect is usually referred to as a 'trade-off'.

Strangely, the empirical support for this principle is not very extensive (Antonovics 1980). It is important to distinguish between the concept of gender specialization in terms of allocation of more resources to one sex function than to the other, and the fact that the dependence on the fertility of other individuals in reproduction by outcrossing causes an inverse relation between the realized male and female reproductive success of different individual plants in a population (Robbins & Travis 1986). Here, we are concerned with differences in the resources devoted to different functions, and the extent to which those functions can be developed. For example, do plants with bigger than average petals tend to have fewer ovules, or smaller seeds?

A difficulty in these types of studies is that several factors that affect overall plant 'quality' can induce positive correlations between such phenotypes as the number of flowers and their size, with low quality plants having low values of the different measured characters. These factors include age effects, genetic differences between populations, different degrees of inbreeding (if the characters show inbreeding depression so that some plants will tend to have low values for independent characters), and environmental heterogeneity (B. Charlesworth 1984, 1990). Thus, although negative phenotypic correlations certainly suggest trade-offs, they are unlikely to be found in real organisms. This is a well-known problem in studying trade-offs (Bell & Koufopanou 1986).

To date, most published studies are at the purely phenotypic level (see, for example, Stanton & Preston, 1988; MacNair & Cumbes 1990). The problems can be minimized by correcting for size differences, which should be good indicators of environmental quality and of levels of inbreeding, but this is not always done. It would be better to include estimation of genetic correlations, which should uncover negative relations, if these exist. A practical alternative for the study of some kinds of trade-offs involves manipulation experiments. Horvitz & Schemske (1988) allowed randomly chosen individuals of a tropical herb species either to set fruit by open pollination, or supplemented pollination so that more fruits than normal developed. This treatment difference had no detectable effect on survival or on flowering in the subsequent year, suggesting that there was no trade-off between fruiting and survival in the species studied.

The evidence for trade-offs in reproductive characters is well reviewed by Goldman & Willson (1986). In a few perennial species, negative correlations between heavy fruit production and growth have been convincingly shown (Eis *et al.* 1965; Rohmeder 1967; Jing & Coley 1990). In some dioecious species female plants grow more slowly than males (Meagher 1982; Sakai & Sharik 1988), but the differences are not always in this direction (Grant & Mitton 1979). Females also often flower less frequently than males (see Ornduff 1987) and may experience greater mortality, although there have been few studies in natural populations (Savage & Ashton 1983; Meagher 1982) and results in the opposite direction have also been found (Dawson *et al.* 1990). Meagher (1982) showed that the sex differences in size occur only after reproduction has occurred, which is evidence that they are due to the energetic burden of fruiting, as should be the case if they are really reflections of allocation differences, but most studies do not include such evidence.

Another type of evidence for resource limitation of one function when another related function is exercised at a high level comes from some well-known negative size-number relations. Seeds from fruits with many seeds are usually smaller than those from few-seeded fruits, and plants with many fruits tend to have smaller ones (Snow & Snow 1988). Similar differences have been found between species with different seed sizes (Kawano 1981), and in pollen sizes between males and hermaphrodites of two subdioecious species (with males having larger pollen (McKone & Webb 1988)). These relations seem likely to be the results of allocation differences. We will not discuss size-number relations further in this review, as they have recently been reviewed by Lloyd (1989). Trade-offs between reproductive structures have rarely been studied (Stanton & Preston 1988). Evidence that producing more ovules entails a cost in terms of lower pollen output, or that having large petals tends to lead to fewer ovules, is badly needed.

4. MEASURES OF ALLOCATION

Measures of allocation are involved in testing both the assumptions of allocation models and their predictions, but there are some difficulties with these estimations. The problems of using dry weight as an estimator of allocation to different functions have been emphasized (Lovett-Doust & Cavers 1982; Goldman & Willson 1986; McGinley & Charnov 1989). Because of differences in the composition of different structures (e.g. in their nitrogen and phosphorus contents), dry weights do not correctly estimate total allocations of resources to different structures (Lovett-Doust & Harper 1980). However, the problems may not be as severe as has been assumed. An allocation model specified in terms of dry weights could be tested if one had estimates of the gain curves in a particular population, based on individuals differing in the biomass of their reproductive structures. The allocation pattern for the population could then be compared with the model's predictions (in the same units). It may also be reasonable to assume that the relations between dry weight and allocations to different functions are similar in different individuals of the same species, and in closely related species, and to use dry weights to compare patterns of allocation to different functions. This assumption could be tested.

It is important to note here that the type of allocation model described above assumes that there is variation in the proportions of reproductive resources allocated to different functions, but that the total quantity of resources is fixed. In reality, plants will differ in the total amount of resources available for reproduction. This introduces a problem for studies of gain curves. The curves estimated in field studies represent the relations between the absolute amounts of resources devoted to different functions and the contributions to fitness, whereas the theoretical allocation models are expressed in terms of the proportions of the total resources. As for studies of trade-offs discussed above, it may be possible to take this into account by scaling by some measure of plant quality, such as plant size.

It may thus often be best to estimate allocations by manipulation experiments in which differences in plant quality that may affect total quantities of resources available for reproduction can be avoided, or else explicitly included in the experimental design. Silvertown (1987) estimated the cost of male function in units of plant growth, in a manoecious cucumber species, by measuring the growth of plants whose male flower buds were removed, compared with intact plants (and also by comparing the effects on growth of removing just female, or both male and female flowers). The cost of female flowers, in the same units, was estimated by removal of female flowers (and also by comparing plants whose male flowers were removed with plants with all flowers removed). Whether the growth differences were measured as number of nodes formed, or as dry weights, the results were similar: plants with male flowers removed grew by amounts similar to plants with no flowers removed, and plants with female flowers removed grew no bigger than plants with both male and female buds removed. These consistent results suggest that the cost of male flowers is slight, even though their dry weights were not, and that the cost of female functions (flowers and fruits) was the major cost of reproduction. This is not surprising, because this is a plant with large fruits (owing in part to human selection for large size). The experiment therefore confirms other evidence that, when allocation to fruit maturation is included in female allocation, female functions consume more than male functions.

Populations polymorphic for different sex morphs may offer an opportunity to estimate allocations to male and female functions. Gynodioecious species have male-sterile individuals in populations. Preventing pollination in female or hermaphrodite plants leads to an increased number of flowers. If there is a cost of male functions, the cost per flower will be less for female than hermaphrodite flowers. If the resources not used by fruits can be used to make more flowers, female plants prevented from fruiting should make more flowers than hermaphrodites. In an experiment with paired sibling plants of *Silene vulgaris*, this did indeed happen, so that in this species there appears to be a measurable cost of male structures (D. Charlesworth, unpublished observations).

Ross & Gregorius (1983) used the principle of trade-offs to estimate proportions of resources allocated to different functions, for populations in which individuals with differing allocations occur. For each phenotype in such a population, the cost per seed (r_f) multiplied by the number of seeds (ϕ) added to the cost per pollen grain (r_m) multiplied by the number of pollen grains (μ) should equal the total amount of reproductive resources (assumed to be fixed). Thus, for two phenotypic classes of individuals, there are two equations which could be solved for the two unknown quantities, allocation to seeds ($R = r_f \phi$) and to pollen:

$$\left.\begin{aligned} r_f \phi_1 + r_m \mu_1 &= 1 \\ r_f \phi_2 + r_m \mu_2 &= 1 \end{aligned}\right\} \qquad (3)$$

For *Leavenworthia crassa*, using data of Lloyd (1965) from two flower colour morphs, the estimated allocations to female functions were 0.57 and 0.65. Two *Lupinus nanus* flower colour forms studied by Horovitz & Harding (1972) gave estimates of 0.67 and 0.76. These results are limited by the assumption that the total amount of resources is the same for all plants.

In gynodioecious populations there is known to be genetic variation at loci affecting sex functions (this may also exist in cosexual species, but the evidence for genetic variation in sex functions in these is tenuous). Atlan *et al.* (1990) used between-family variation of plants from populations having different frequencies of female plants, to detect negative correlations for the numbers of germinable seeds and pollen grains per flower, scaled to correct for differences in plant size. Their results suggest trade-offs between pollen and seed output. In addition, the data provide estimates of the cost per seed, in units of numbers of pollen grains. The values for the two sets of plants studied were 1330 and 4770, respectively. Alternatively, a plant producing no pollen could produce 2.4–2.6 times as many seeds as one that did produce pollen, a value close to the observed difference between females and hermaphrodites in this species.

5. PREDICTIONS OF ALLOCATION MODELS

In reviewing the results of allocation models, we will focus attention on the patterns they predict, rather than on quantitative predictions of amounts of resources that should be allocated. Although the theoretical models generate quantitative predictions of allocation amounts, given assumptions about the values of the parameters involved, there is in reality little possibility for testing them quantitatively. Firstly, as just discussed, it is difficult to measure allocations to different functions. In addition, no model includes all possible parameters of importance, and it is impossible to measure all parameters. It is, however, possible to predict patterns of allocation differences. Comparative data may therefore be adequate for testing the predictions of sex allocation theory, because if one has enough data the values of the parameters of interest should often be uncorrelated with the values of other parameters (Queller 1984).

Many results of allocation theory were reviewed by Charnov (1982), who stressed the similarity to sex-ratio theory for dioecious species. The chief results that have been obtained may be summarized as follows.

1. Allocations to male and female functions will be unequal when the gain in the contribution to fitness differs for equal proportionate increases in allocation to the two different sex functions, i.e. the gain curves are nonlinear (Charnov 1979). Despite the difficulty in measuring allocations, it appears highly likely that this prediction is fulfilled in plants.

2. With selfing, plants are expected to allocate less to male functions, because with fewer ovules available for the outcrossing pollen pool to fertilize, resources expended on pollen gain less in terms of fitness (Charlesworth & Charlesworth 1981). It is well documented that selfing species produce small amounts of pollen (Cruden 1977; Schoen 1982; Preston 1986; Vasek & Weng 1988; Cumaraswamy & Bawa 1989).

3. Allocation to attractive structures may be high in outcrossers, but is expected to be low in selfing populations (Charlesworth & Charlesworth 1987; Lloyd 1987*c*), in agreement with many observations of small flower sizes of self fertilizing plants (Ornduff 1969; Schoen 1982; Cruden & Lyon 1985; Ritland & Ritland 1989). When, however, both cross- and self-fertilization are mediated by pollinator visits (e.g. when selfing occurs by pollination between flowers on the same plant), attraction can still be important in selfers (Lloyd 1987*c*). Allocation to attractive structures should also be high when pollinators are limiting and competition occurs for insect or animal visits. This may be hard to test, because this situation can also select for smaller flower size and autogamous self-fertilization (reproductive assurance), but the case of alpine and arctic flowers, which appear highly attractive for pollinators (Kevan 1972), may be relevant here.

4. In wind-pollinated plants, loss of a large fraction of the pollen should produce a roughly linear male gain curve (with a low ratio of number of ovules fertilized per pollen grain produced, so that increasing pollen output would increase male success proportionately, but see Burd and Allen (1988)). In contrast, the limited pollen-carrying capacity of pollinators should cause a decelerating gain with pollen production, in animal-pollinated species. Allocation to pollen is thus expected to be higher in wind-pollinated than animal-pollinated species. If pollen of wind-pollinated species has similar, or even considerably smaller, costs per grain compared with pollen of animal-pollinated species, high pollen output is expected. Wind-pollinated plants are indeed known to produce 'an enormous quantity of pollen' (Darwin, 1877, p. 281). The sole study of the male gain curve in a wind-pollinated plant suggests an initially accelerating gain, possibly levelling off at very high male allocation (Schoen & Stewart 1986). For animal-pollinated plants, there is so far only slight evidence for decelerating gain curves (Thomson & Thomson 1989; Young & Stanton 1990).

Some other predictions about allocation patterns can be made by considering the shapes of male gain curves. Queller (1984) suggested that species with pollinia, or with clumped pollen, should have low pollen : ovule ratios. The main reason for this prediction is that when all the pollen from a flower is transferred to a single recipient there will be a more sharply limited gain curve for increased pollen amounts per flower.

Recently, several new models have been studied. Because increased pollen production may increase selfing we should not treat selfing rates as fixed parameters of our allocation models, but should allow them to vary in the same way as other features of the breeding system. There is a small amount of empirical support for an effect of male allocation on selfing rates (Schoen *et al.* 1986), but such data are difficult to obtain. Such differences help to maintain intermediate selfing rates in populations, rather than their evolving to the extremes of total outcrossing or total selfing (D. Charlesworth & B. Charlesworth 1978, 1981; Gregorius 1982). As many plant populations may have intermediate selfing rates (reviewed by Baker 1959; but see Schemske & Lande 1985; Barrett & Eckert 1990), this possibility is worth serious attention. Holsinger (1991) recently suggested that pollen removal from flowers during pollinator visits that cause selfing may decrease the contribution to the outcrossing pollen pool. Holsinger showed that this 'pollen discounting' (which has generally been thought to be an unimportant phenomenon, see Piper & Charlesworth (1986)) tends to maintain intermediate selfing rates as evolutionarily stable states. It may be hard to imagine how removal of the small amounts of pollen that are needed for self fertilization of flowers could significantly reduce male fertility in outcrossing, but it appears quite realistic when pollinators must align themselves accurately in relation to the flower, and pollen is placed on a specific part of their body. Then if that part comes in contact with the flower's stigma before the pollinator leaves and causes selfing, it must also cause a substantial reduction in the amount of pollen remaining to be transported to other stigmas. This interesting mode should certainly stimulate more field work on pollen discounting.

Another situation in which allocation to the two sex functions might be expected to differ is when there are two populations with pollen flow mostly in one direction, so that the pollen in one sub-population is diluted by pollen coming into it from the other. One might expect the population receiving the most pollen from the other sources to evolve lower male allocation and greater femaleness. However, Kirkpatrick & Bull (1987) showed that this is incorrect. Because the female contributions to fitness are not affected, assuming that pollen supply does not limit female fertility, the evolutionary outcome depends only on the male contributions. Equation (2) above shows that it is not absolute, but relative, male fertilities that matter, so that both sub-populations will be subject to the same selection on male function.

In a plant whose flowers develop in a sequence, the male and female contributions to fitness are each due to the sum of contributions from flowers at each of the stages in the sequence, and these contributions may differ so that pollen from different flower stages has different opportunities for siring offspring. If the stages differ in the ratios of numbers of ovules available in potential mates to the amount of pollen produced by the competitors for the pollen pool for those ovules, there can be selection for differences in sex allocation in flowers of the different stages (Brunet 1991). Various factors could produce differences in the ratios. In protandrous plants, where the anthers of each flower mature before the pistils, flowers produced early will have a low ratio of available ovules to pollen competing for them, compared with later flowers. This is expected to select for female-biased allocation patterns in the early flowers (Darwin 1877, p. 283; Pellmyr 1987), and the models of Brunet confirm that this selection pressure indeed operates. This interesting result remains true with partial selfing and when, as in the models discussed above, the male and female fertilities are nonlinear functions of the allocations. It is testable empirically, and does indeed appear to occur (Thomson 1989; Brunet 1991; Spalik & Woodell 1991). Moreover, the tests involve comparisons of flowers on inflorescences of individual plants. Therefore the different stages are comparable in the sense that there is no possibility that comparisons will be vitiated by differences in inbreeding coefficients between parental plants, or by environmental differences.

6. SEX ALLOCATION AND THE ADVANTAGES OF UNISEXUALITY

One of the most interesting aspects of the study of allocation to reproductive functions is the light this may shed on the evolution of unisexuality. Consideration of expected allocation patterns should give insight into the ecological conditions most favourable for the evolution of unisexuality. These considerations have led several workers to attempt quantitative estimates of allocation parameters (see, for example, Silvertown 1987), and have motivated study of the shapes of the gain curves for male and female fertility in plants. Even without quantitative estimates of the amounts or proportions of resources allocated to reproductive functions, we might still be able to deduce what situations would make the loss of one sex function most probable, and thus generate testable predictions. These might concern the evolution of unisexual flowers within plants, i.e. the evolution of monoecy or of andro- or gynomonoecy, or the evolution of entirely unisexual individuals, i.e. the evolution of gyno- or androdioecy and dioecy.

It has sometimes been argued that when a cosexual plant has a high allocation to one sex function there should be the possibility for large gains to unisexual forms through the other sex (Givnish 1980). For example, if fruits are expensive, males could acquire large amounts of resources for increased pollen production. An accelerating gain for allocation to pollen might then permit the invasion of cosexual populations by males (see Bawa 1980). But this does not take into account that a high allocation to female function implies that the male gain is not strongly accelerating. It is therefore preferable not to use arguments of this kind, but to consider separately the invasion by female and male phenotypes. By finding the ESS allocation pattern of a cosexual phenotype, one can ask whether the increase in fitness of male or female phenotypes would be sufficient to allow them to invade the cosexual ESS population (Charlesworth & Charlesworth 1981; Charlesworth 1984). Such models can include the possibility of partial self fertilization in cosexual plants, as the avoidance of inbreeding is another factor that may be important in breeding-system evolution (B. Charlesworth & D. Charlesworth 1978).

(*a*) *Does evolution of unisexuality involve re-allocation of resources from one sex function to benefit the other?*

It seems likely that re-allocation of resources plays a major role in the evolution of dioecy. Darwin (1877, p. 279) suggests, for the evolution of dioecy: '...if a species were subjected to unfavorable conditions from severe competition with other plants, or from any other cause, the production of the male and female elements and the maturation of the ovules by the same individual, might prove too great a strain on its powers, and the separation of the sexes might then prove highly beneficial'.

Is there evidence for such processes in species that are evolving towards dioecy, such as sub-dioecious and gynodioecious species? We have considered gynodioecy above. Even when outcrossing is performed by hand, females of *Thymus vulgaris* produce more fruits per flower and more or larger seeds than hermaphrodites (Assouad *et al.* 1978). Such differences cannot be the result of inbreeding effects on the seeds of hermaphrodites. These data therefore suggest that hermaphrodites allocate more to male than to female reproduction. Further evidence comes from sub-dioecious plants. In these, females are generally quite constant in their sex phenotype, but the plants with male function often range from hermaphrodites with substantial seed set to individuals that are functionally nearly completely male (Westergaard 1958; Webb 1979). Once gynodioecy is present in a population, there will be selection for the cosexual morph to specialize in greater male function (B. Charlesworth & D. Charlesworth 1978; Charlesworth 1989). Unless there are trade-offs between male and female function, however, (e.g. if these functions had separate resource pools) increased male function need not involve loss of fruit-producing ability. The loss of female functions which occurs in the evolution of the males of sub-dioecious species is therefore evidence for a common resource pool for male and female functions. It would be very interesting to have more data on sub-dioecious populations, particularly studies of the genetic correlation between male and female functions among the plants having male function (Sakai & Weller 1991).

Femaleness may sometimes evolve without major re-allocation of resources, at least at the level of flowers. In several dioecious species, hermaphrodites have large anthers containing pollen, giving the appearance of androdioecy, but the pollen is either non-functional, or else the anthers do not dehisce during the time that stigmas are receptive (reviewed by Charlesworth 1984; see also Liston *et al.* 1990; Kawakubo 1990; Schlessman *et al.* 1990). However, females could gain extra resources if their flowers produced much less pollen, as in *Solanum* (Anderson 1979) or fewer stamens as in *Eugenia* (van Wyk & Dedekind 1985), or if there were many fewer flowers (Anderson & Symon 1989). Similar data come from species that are dioecious but in which flowers of the two sexes are morphologically similar ('cryptic dioecy'). There is usually some degree of reduction in the gynoecia of males, sometimes merely absence or reduction of the ovules, and the anthers of the females may differ only slightly from those of males (Mayer 1990; Kevan *et al.* 1990). Some re-allocation has thus probably occurred. Males may also have more flowers than females (Kevan *et al.* 1990), as is also common in many dioecious species (reviewed by Lloyd & Webb 1977). It would be interesting to have quantitative measures of the allocation to reproductive structures in the two sexes of cryptically dioecious species.

(*b*) *Theoretical results*

Charnov *et al.* (1976) first showed that the shape of the curve relating male and female contributions to fitness (which in turn depends on the relations between allocation to the two sex functions and these two contributions) can determine the stability of dioecious populations to invasion by hermaphrodites or other cosexes that can reproduce as both male and female. When the relation is bowed outwards, hermaphroditism can invade, whereas accelerating gains for the contribution of one sex to fitness may explain the evolution or maintenance of dioecy (Charnov 1982; Lloyd 1982). Although invasion by cosexes may be prevented by the presence of inbreeding depression, even when the shape of the male–female curve is decelerating (see below), this curve may nevertheless help us gain understanding of when dioecy is most likely to be maintained (Charlesworth & Charlesworth 1981). Many treatments of the evolution of dioecy concentrate on verbal arguments suggesting how various factors will affect the male–female gain curve (Thomson & Brunet 1990).

For example, the female gain curve depends strongly on the dispersal of seeds. Animal dispersal may sometimes cause an accelerating relation between allocation to female functions and female fertility, because individuals with few fruits would be little visited whereas those with many fruits would disperse many seeds (Bawa 1980; Givnish 1980), or because of wider dispersal of animal-dispersed seeds, generating less competition between sibling seedlings (Lloyd 1980). There is an association between animal dispersed fruits and dioecy, although other possibilities exist for this correlation (Muenchow 1987), and there is no clear evidence for an accelerated gain in fruit removal with increased fruit amounts present on plants (Denslow 1987). Similar arguments have been made for attraction of animal pollinators. If pollinators prefer plants with the largest floral displays, this could lead to an accelerating gain for male allocation (Bawa 1980). Queller (1983) showed that there is indeed a strong advantage in male fertility (as estimated by removal of pollinia) in *Asclepias exaltata*. Better tests of the shape of the male gain curve require estimates of the numbers of seeds actually produced through male function. A recent study of the same species, using this type of data, has found no evidence for an accelerating curve (Broyles & Wyatt 1990).

There may also be sex-specific limits to reproductive success. Some structures (such as a brood pouch for the young of some animals) may have to be produced for any reproductive success to be possible. These costs limit the gain a unisexual form can obtain (equivalent to a diminishing returns gain curve), so that hermaphroditism will be stabilized (Heath 1977). Frank (1987) made the useful distinction between such 'fixed costs' (independent of the number of progeny) and 'packaging costs' that represent the minimum amount of resources that must be invested per progeny. In plants, these packaging costs include pedicels to support the fruits (which it is reasonable to count as female reproductive functions of the maternal plants). These pedicels would also bear the flowers, so that in hermaphroditic species, part of these costs contribute to male function (Lloyd 1989), but in monoecious species one could assign them to male and female functions separately, according to the numbers of flowers of the two sexes and the costs of the two kinds of supporting pedicels. If there are shared reproductive costs that contribute to both sex functions, this should tend to stabilize hermaphroditism. This suggests that allocation to attraction might also stabilize hermaphroditism, and Morgan (1991) has shown, by studying the conditions for stability of a cosexual form to invasion by females, that this is true. This may explain why dioecy is associated with small, inconspicuously coloured flowers (Bawa 1980). Hermaphroditism is also stabilized when the costs attributable to the two sex fertilities come from somewhat different resource pools, because hermaphrodites can then fulfill both functions, i.e. the male–female gain curve should show diminishing returns. One might therefore expect more dioecious species among plants that ripen seeds and fruits over a period of time after flowering has finished.

It is important to remember that since it is the degree of acceleration of the male versus female curve (together with the inbreeding effects) that determines the stability of dioecy to invasion by cosexual forms, an accelerating gain curve for one sex does not guarantee the instability of dioecy, because the other gain curve could be decelerating and make the overall curve unfavourable for the invasion. As discussed above, decelerating curves seem biologically realistic for many plants, at least at the upper part of the allocation range.

Other types of unisexuality may be viewed as allocation biases. Andromonoecy (with individual plants having both hermaphrodite and male flowers) and gynomonoecy (hermaphrodite and female flowers) are biases towards male and female functions, respectively. Among a group of related species (in which the cost per pollen grain, and per unit mass of fruits, should be similar) female bias in allocation, including andromonoecy, should occur in species with the most expensive fruits, and this is indeed found (Bertin 1982; Whalen & Costich 1986). However, the question of why these plants produce female-sterile flowers, rather than simply maturing fruits from few flowers, has not yet been answered. It seems likely that hermaphroditism may be a 'bet-hedging' strategy in the face of unreliable pollination of flowers. The similar problem of gynomonoecy has also not been solved, nor has the difference in the frequncy of these two breeding systems been satisfactorily explained. Gynomonoecy is known from at most 12 families, whereas andromonoecy is widespread. Perhaps the higher allocation of reproductive resources needed for fruiting than flowering more readily permits the evolution of male- than of female-biased allocation at flowering time.

7. CONCLUSIONS

The theory of sex allocation has made a number of interesting predictions, and these have been confirmed in several cases. There is still a need for more empirical data, both for testing the validity of the assumptions that are made in the models, and for finding out whether such ideas as those about gain curves in plants with different ecologies are correct. A particularly valuable type of study would involve estimation of genetic corelations between different reproductive functions. To show trade-offs between different functions, one must show that there is a negative genetic correlation, not merely a phenotypic correlation (Rose & Charlesworth 1981). Without such data, the theoretical basis for the predictions of sex allocation models is weak. Sub-dioecious species would be particularly favourable for such studies, because of the plants with male function in such populations are known to show variability for levels of female function (Delph & Lloyd 1991).

Another important type of data includes studies of the relations between allocation to (or biomass in) different reproductive structures, and the reproductive success generated. There have so far been only a few studies of the gain curve for success through pollen production, in relation either to flower number (Schemske 1980; Schoen & Stewart 1986; Piper & Waite 1988, but see Snow 1989) or attractiveness to pollinators (Bell 1985), and such studies rarely include effects on female fertility that could be used to estimate both male and female gain curves. Part of the reason for the small number of studies is that there is difficulty in estimating male success. Estimates based on numbers of visits by pollinators to flowers, or even on removal of pollen, may not be accurate if there is a nonlinear relation between pollen removed and pollen deposited on the stigmas of other plants, or numbers of seeds sired. Inaccuracy of possibly large magnitude may be common, as shown by Broyles & Wyatt (1990) in a study of *Asclepias exaltata*, in which paternity of seeds could be determined using electrophoretic markers. Even with some inaccuracy, however, such studies are badly needed. Studies of the relation between fruit production and contributions to the progeny in the next generation are also needed. Without these types of information, we cannot assess the plausibility of the ideas that have been proposed for the selective pressures involved in the evolution of dioecy and other forms of unisexuality, and our understanding of breeding system evolution will remain incomplete.

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