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Hypotheses for the Evolution of Dioecy in Seed Plants

James D. Thomson and Johanne Brunet

Over the last decade, new hypotheses have been proposed for the evolution of dioecy in plants. Most of the selective mechanisms invoked have been suggested and supported by phylogenetic correlations. Here we review (1) the validity of the correlations (especially in light of recent critiques of the comparative method), and (2) the conformity of the proposed mechanisms to empirical data. None of the hypotheses can be flatly rejected on existing evidence, but the strength of their support varies. Future correlational studies must explicitly consider phylogeny; more importantly, such broad studies should also be supplemented by detailed studies of particular transitions to dioecy (e.g. within genera) – studies of the sort that have clarified analogous issues such as heterostyly.

Any evolutionary change that has occurred independently in numerous lineages is likely to offer insight into fundamental mechanisms of evolution. When that change is one that Darwin confessed to finding 'much difficulty in understanding'[1], it gains the stature of a central problem in biology. The evolution of dioecy from hermaphrodite ancestors is such a problem. An obvious consequence of separate sexes is the impossibility of selfing. Thus, the avoidance of inbreeding has traditionally been invoked as an important selective force in the evolution of dioecy[2–4] (despite an early caution

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by Darwin[1]). Starting about ten years ago, however, a number of alternative hypotheses have been presented[5–11]. These hypotheses usually have two parts, a correlation and a mechanism. The *correlations* are phylogenetic: dioecious taxa are more likely to exhibit fleshy 'fruits' (*sensu lato*), the woody habit, small and inconspicuous flowers, island habitats, or heterostyly. Some of these correlations date to Darwin, but most have been described only recently. The *mechanisms* typically invoke ecological circumstances that favor dioecy in ways specified by theoretical models of sexual selection and sex allocation theory.

Here, we discuss the current status of these proposals and the progress made over the last decade. We consider several pairs of correlations and mechanisms, assessing both the validity of the correlation and the adequacy of the mechanism. We do not dwell on 'pathways to dioecy' or on population genetic models[12–16], although a full interpretation of the correlations must include genetic constraints.

General difficulties with correlations

Recent critiques of the comparative method have established standards of rigor matched by few of the early papers concerning dioecy[17,18].

First, because most authors were typically concerned with only a single relationship, covariation among the 'driving' characters was usually ignored, with the risk that spurious or indirect correlations might have suggested incorrect causal relations. Muenchow[11] and Charlesworth[19] discuss this general statistical problem with particular respect to dioecy arguments.

Second, the statistical significance of phylogenetic correlations is hard to assess because of non-independence of taxa within lineages; Pagel and Harvey[18] review several recent proposals for solving this difficulty. Importantly, the 'sample size' should reflect the number of evolutionary events rather than taxa. Thus a genus containing five species, all dioecious and all woody, is properly counted as only one datum for a correlation analysis, not five. For testing a particular mechanism, the relative order in which the correlated traits originated in a lineage is also important: Donoghue[20] discusses this and other issues with particular reference to the correlation between dioecy and fleshy fruits. None of the other correlations discussed below have received this level of scrutiny. Ideally, testing for correlation of traits requires mapping those traits
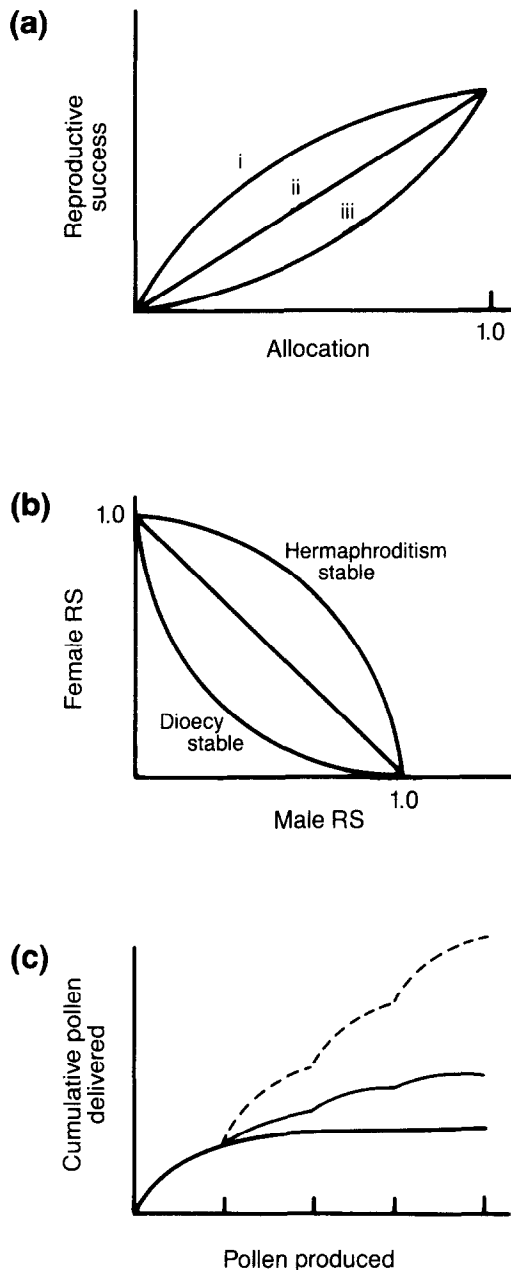
(a)

(b)

(c)

Fig. 1. Sex allocation theory.

(a) 'Fitness gain curves' specify the consequences for reproductive success of varying levels of allocation of resources to male or female functions. One such curve describes male function and a second describes female function. Gain curves may be decelerating or saturating (i), linear (ii) or accelerating (iii).

(b) Male and female curves combine to yield a fitness set diagram showing male–female trade-offs on reproductive success (RS). Above the diagonal, hermaphrodites are favored; their fitness exceeds that of either type of unisexual. Below the diagonal, dioecy is the ESS. Generally, accelerating gain curves for either or both sexes will tend to produce fitness sets favoring dioecy. *Redrawn from Ref. 27.*

(c) Pollen packaging (following Ref. 44). The heavy line indicates a saturating male success relation based on the amount of pollen delivered to stigmas, as a function of the amount of pollen presented. The heavy line shows the expected relation for a single pollinator visit when all the pollen is presented simultaneously. If pollen is presented simultaneously and there are multiple visits (four in the figure), the later visits may transfer some of the pollen remaining after the first visit (light solid line), raising the gain curve slightly. If, however, pollen is presented in four separate aliquots, each visit may repeat the steep portion of the basic gain curve (dashed line), resulting in a nearly linear gain curve overall.

onto an accurate cladogram[21], which is a far tougher problem than assembling a contingency table.

Third, the data are fragmentary, and seriously biased toward temperate floras[6]. Patterns vary among floras and taxa[11]. New discoveries and compilations may change the existing picture; worse, spurious conclusions may arise from carelessly lumping heterogeneous data sets (Simpson's paradox)[23].

Arguments from allocation theory

The concept of the evolutionarily stable strategy (ESS)[24] has had a fundamental role in the recent re-examination of dioecy, by specifying conditions in which male- and female-sterile individuals could (sequentially) invade populations of hermaphrodites and supplant them. To simplify greatly, these phenotypic models involve so-called 'gain curves' that specify the reproductive success that a hermaphrodite will obtain for a certain level of resource investment in male and female reproduction (see Fig. 1). These models have numerous variations, extensions and caveats – ably discussed by the Charlesworths[25,26], Charnov[27] and Lloyd[28]. However, what is relevant here is that any process that produces an accelerating fitness gain for increased investment, whether through male or female function, is a candidate mechanism for the evolution of dioecy. Furthermore, as Charlesworth[26] points out, anything that pushes saturating curves toward linearity – even if the ESS for sex allocation is still hermaphroditism – would ease the evolution of dioecy through other selection pressures.

Dioecy and the avoidance of selfing

Willson's characterization[5] of the inbreeding depression hypothesis as an overused, uncritical 'kneejerk response' stimulated Thomson and Barrett[4] to restate a correlation first described by Baker[2,3]: they argued that negative associations between physiological self incompatibility (SI) and dioecy occurred at both familial and generic levels, suggesting that dioecy seldom evolved when selfing was prevented by other means. Willson[29] (as well as Bawa[7] and Givnish[9]) attacked this argument on several grounds. Giv-

nish compiled 2 × 2 contingency tables that he interpreted as showing no such correlations. As an early attempt in this area at statistical quantification of proposed correlations, Givnish's analysis has received considerable attention.

In calling for more detailed examinations of particular dioecious taxa and their congeners, Baker[30] questioned the validity of several of the published accounts of the co-occurrence of dioecy and SI within genera. Charlesworth's extremely detailed reanalysis[19] concludes that the available evidence simply does not permit a firm conclusion, although she tentatively supports Baker's original contention, based on the relatively 'low frequency of dioecy in families known to have SI'. The question must still be regarded as open, due particularly to inadequate characterizations of 'SI' for most taxa. Indeed, it is quite difficult to distinguish 'late-acting incompatibility'[31] from early zygote breakdown caused by inbreeding depression, although the consequences of these phenomena are very different[32]. Furthermore, 'SI' is often incomplete or 'leaky'[29], allowing substantial selfing under certain conditions. Conversely, 'self compatible' (SC) plants may show 'cryptic self incompatibility'[32], giving them high outcrossing rates. Thus, reports of 'SI' or 'SC' do not necessarily convey much information, and even if they did, no one has yet tried mapping these associations on cladograms (as discussed above).

Another charge leveled at the outcrossing hypothesis is that dioecy should not evolve in SC taxa due to inbreeding depression, because habitual selfers show little depression[33]. However, many SC species are highly outcrossed, due to mechanisms such as dichogamy and herkogamy (spatial and temporal separation, respectively, of male and female functions); in particular, it has been suggested (G.E. Muenchow, PhD thesis, University of Colorado, 1985) that dioecy may evolve when a deterioration in pollination service abruptly raises the selfing rate in a previously outcrossing (but SC) species, revealing accumulated deleterious recessive alleles in the homozygous condition. Such deterioration has been proposed in the evolution of dioecy

in *Aralia* (Fig. 2): small, short-lived clones can maintain outcrossing through synchronous dichogamy (as in the andromonoecious *A. hispida*), but such synchrony would be hard to maintain in very large, old, fragmented clones (the dioecious *A. nudicaulis*)[34].

Fleshy fruits

Three characters appear to be correlated with dioecy and each other in a complicated tangle: woodiness, fleshy fruits, and small, inconspicuous or 'greenish'[11] flowers. We summarize the data in Table 1 and the proposed evolutionary mechanisms in Fig. 3. Bawa[6] and Givnish[8], in discussing simple correlations of dioecy and fleshy fruits, argued that vertebrate frugivores, particularly 'specialists', might forage in ways that provided disproportionate dispersal to individuals with large crops of fruit, thus yielding an accelerating female gain curve – a condition favoring dioecy, and one that would not hold for dry-fruited abiotically dispersed plants (hypothesis 1, Fig. 3). Support for both the correlation and the proposed mechanism is equivocal. Muenchow[11] and Fox[22] independently examined covariation of these character states, concluding that direct correlations of dioecy with fleshiness are weak in the angiosperm floras they examined. Both found stronger associations of dioecy with inconspicuous flowers; Muenchow in particular discounted the causal role of dispersal. In the Cape flora, Steiner[35] found complex interactions of dispersal and pollination: in biotically pollinated taxa, fleshy fruits did occur with dioecy, but this correlation did not occur in abiotically pollinated groups. Although Fox accepted Givnish's report of a dispersal correlation for gymnosperms, Donoghue[20] has cast some doubt on even the gymnosperm analysis. In the only published application of cladistically conservative correlations relevant to this area, he uses Maddison's test[21] to indicate that dioecy has evolved significantly more often in animal-dispersed gymnosperm lines, but only if apparently simultaneous origins of the two characters in the cladogram are always assumed to represent 'fleshiness first, dioecy second'. If simultaneous

appearances are discounted, significance vanishes. Again, there is insufficient information to resolve the question.

Turning to mechanism, there is also little direct support for accelerating female gain curves in animal-dispersed plants. As reviewed by Flores and Schemske[36] and Denslow[37], fruit removal by vertebrates is most often a saturating or linear function of fruit production, and some reports of accelerating functions depend on statistically unreliable outliers. By indicating that avian foragers do not *generally* produce accelerating curves, these criticisms collectively weaken the dispersal hypothesis, although most of the reports concern her-maphroditic plants and generalist frugivores.

Woodiness

The analyses by Muenchow[11] and Fox[22] tend to support Darwin's correlation of dioecy and woodiness, but to different extents in different floras. Muenchow found two associations: shrubs and small trees were likely to display the syndrome of 'fleshy fruits with greenish, insect-pollinated flowers and dioecy', discussed above, whereas large trees were likely to combine dioecy and wind pollination.

The only proposed mechanisms for *direct* causal effects of woodiness on dioecy seem to involve inbreeding, especially the greater
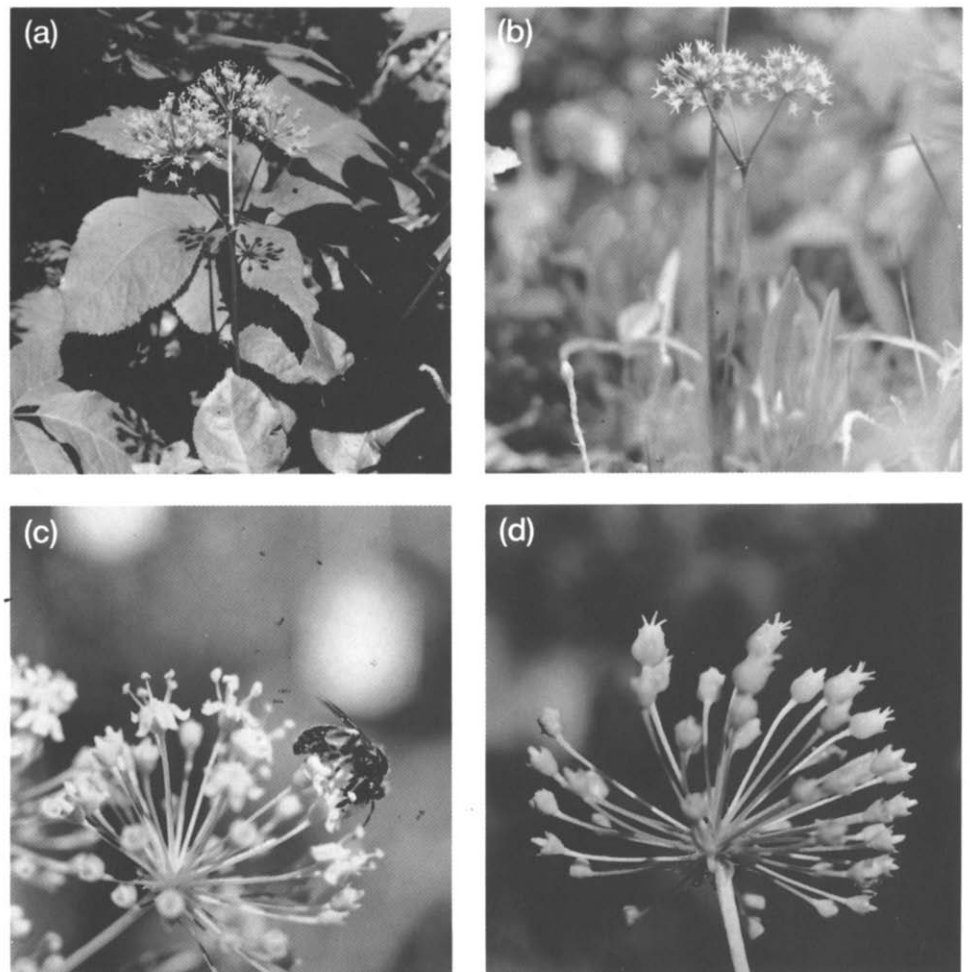

Fig. 2. Inflorescences of dioecious and hermaphroditic species of North American *Aralia* (Araliaceae). In the dioecious *A. nudicaulis*, a forest-floor species that forms large clones by rhizomatous growth, plants are either male (a) or female (b). In contrast, plants of the weedier, smaller-cloned *A. hispida* are hermaphroditic, alternating male and female phases several times during a season. All flowers produce pollen upon opening (c); some of them later gain female function, as the styles elongate after the petals and stamens have been shed (d). Female flowers of the dioecious species also produce petals and rudimentary anthers, both of which are shed before the flowers are receptive, one of several indications that dioecy is a derived condition in this genus. Both species have small, numerous, greenish flowers, fleshy fruits, and are perennial – all traits phylogenetically correlated with the incidence of dioecy.

opportunities for geitonogamy (pollen transfer between flowers of a plant) offered by larger plants[11]. Although it is true that some large plants prevent geitonogamy by synchronized dichogamy, breakdowns in intraplant synchrony (as in clonal, non-woody *Aralia*, above[34]) may provide the abrupt increases in selfing that are proposed to incur strong inbreeding depression (hypothesis 4, Fig. 3). In shrubs of the synchronously dichogamous, monoecious, *Ricinocarpos pinifolius* (which is self compatible and does show inbreeding depression), observed breakdowns in synchrony were all attributable to single branches that had gone out of phase[38]. Conceivably, a greater

physiological autonomy of stems makes asynchronies more frequent in shrubs than in trees.

The elevated incidence of dioecy in perennial herbs may have similar foundations, but there appear to have been no systematic attempts to ascertain whether dioecy is more common in perennials whose growth forms predispose them to geitonogamy. Geitonogamy, although frequently invoked in evolutionary arguments, remains poorly studied empirically.

Floral syndrome and pollinator type

The correlation most strongly supported by Muenchow[11] and Fox[22] is between dioecy and the floral syndrome, variously de-

scribed as small, inconspicuous or greenish flowers. Here, we have a strong correlation in search of a mechanism. Bawa[6,39], who discovered this relationship, proposed one model based on accelerating male success curves. In this view, the plants are served by small generalist insects, especially bees, and these insects are particularly sensitive to flower number. Female-sterile plants that reallocated resources to make large displays of staminate flowers would more than compensate their loss of seed production through increased pollen donation (hypothesis 3, Fig. 3).

Although the correlation appears sound, there is limited support for this causal mechanism. First, in one

Table 1. Summary of three characters proposed by recent authors to be correlated with dioecy

Character	Level of analysis	Type of association	Flora examined	Other correlations controlled for	Reference
Woodiness					
	Species	Positive	The Carolinas, USA	No	Conn et al.[47]
	Species	Positive	California, USA	No	Freeman et al.[48]
	Species and genus	Positive	Puerto Rico and Virgin Islands	No	Flores and Schemske[36]
	Species	Positive	Alaska, California, Northeastern USA	Yes	Fox[22]
	Genus	Positive	Northeastern USA and California	Yes	Muenchow[11]
	Genus	Negative with Restionaceae; positive without	Cape flora of South Africa	Yes	Steiner[35]
Pollination					
(wind)	Species	Positive	California, USA	No	Freeman et al.[48]
(wind)	Genus	Positive	Northeastern USA and California	Yes	Muenchow[11]
(wind)	Species and genus	Positive	Cape flora of South Africa	Yes	Steiner[35]
(small bees)	Species	Positive	Dry forest of Costa Rica	No	Bawa[6]
(small flowers)	Species and genus	Positive	California	Yes	Fox[22]
(greenish flowers)	Genus	Positive	Northeastern USA and California	Yes	Muenchow[11]
(small flowers, unspecialized pollinators)	Species	No statistical testing	Tropical forest	No	Bawa and Opler[39]
Fleshy fruits					
	Species and genus	Positive	Puerto Rico and Virgin Islands	No	Flores and Schemske[36]
	Species, genus, family	Positive	–	No	Givnish[8]
	Genus	Positive	Northeastern USA and Alaska	Yes	Fox[22]
	Species	None			
	Species and genus[a]	Positive	Cape flora of South Africa	Yes	Steiner[35]
	Genus	None to weak positive	Northeastern USA and California	Yes	Muenchow[11]
	Species	Positive	Dry forest of Costa Rica	No	Bawa[6]
	Species	Variable[b]	–	Cladograms	Donoghue[20]

[a]Biotic pollination only.
[b]Depending on treatment of simultaneous appearances of dioecy and fleshy fruits.

temperate-zone study, 'small bees' as a general class were actually less size-discriminating in choosing *Aralia* inflorescences than were larger bumble bees[40] – but bumble bees are not generally associated with dioecy. Second, as in the case of birds and fruits, relatively few studies support an accelerating relationship between pollinator visitation (or other estimates of male success) and flower number (see Thomson[41]), although again most studies involve hermaphrodites. Bawa's mechanism may well operate in the tropical systems with which he was most concerned, but alternatives should be considered. Bawa also suggested that such small pollinators might tend to stay within plants, thus fostering geitonogamy and inbreeding depression (hypothesis 2, Fig. 3).

Muenchow (PhD thesis, cited above) suggested that dioecy, shrubbiness, fleshy fruits and greenish flowers all unite in an understory syndrome associated with poor or 'slow' pollination conferred by the small, unspecialized pollinators that typify such habitats: slower delivery of outcross pollen may allow more fertilizations by self pollen, favoring dioecy through an outcrossing advantage. In Muenchow's hypothesis, fleshy fruits come along for the ride because understories are inimical to wind dispersal. This mechanism (hypothesis 6, Fig. 3) depends on particular details of pollen arrival schedules and pollen tube growth rates.

Recently, Thomson *et al.*[42] proposed a different way of looking at the 'small flower' correlation; they argue that the causal relation may not depend on smallness or inconspicuousness *per se*, but on the fact that such flowers are usually numerous. Plants that produce many flowers can engage in pollen packaging strategies[43,44] – specifically, staggering flower openings over time – that can linearize an otherwise saturating male gain curve (see Fig. 1), thus easing the way to dioecy (as proposed by Charlesworth[26]; hypothesis 5, Fig. 3). Packaging seems to enhance male function in many circumstances, according to simulation models[44]; and it is practised by many plants, but no one has systematically examined pollen packaging and dioecy.
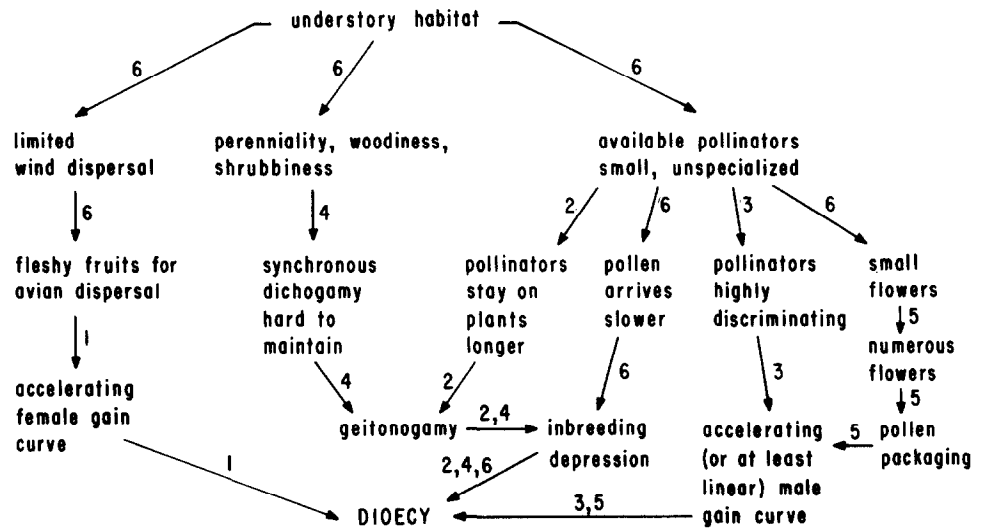
Other correlations

High frequencies of dioecious taxa on islands are not universal, and when present they almost certainly have highly indirect causes; it is quite possible that this is through the greater colonizing capability of avian dispersal, which itself seems only indirectly linked to dioecy. Correlations with insularity are especially susceptible to phylogenetic redundancy, given the frequency of post-colonization radiations. Such patterns badly need the dissection into 'independent events' of known sequence provided by the cladistic approaches.

Abiotic pollination seems to be associated with dioecy in some temperate floras. In tropical forests, however, insect pollination prevails[6,39]. The temperate zone patterns may be, in part, indirect consequences of woodiness. Biotically and abiotically pollinated taxa show different correlations of dioecy with other variables. This area also needs further analysis, especially of the interactions among characters. The only proposed direct mechanism seems to be Givnish's suggestion[8] that wind pollination, by presenting a saturating male gain curve, allows easier invasion by male-steriles when the female gain curve is accelerating. There is no reason, however, to believe that anemophily should produce more saturating gain curves than entomophily. Some theorists assume the reverse[28]; the only two empirical measurements of male gain curves suggest saturation in both an anemophilous tree[45] and

an entomophilous herb[46], but the anemophilous curve would be considered linear except for data from a single unsuccessful donor.

Cox[10] makes a case for dioecy in *Freycinetia* evolving in response to flower-damaging bat pollinators, but the generality of such a mechanism is unknown. Dioecy has apparently evolved from heterostyly, but not often enough to produce a positive simple correlation at the family level.

Summary and prospects

The search for causes of dioecy displays both the enticements and the pitfalls of the comparative method. A cynic could view the foregoing as a muddle, a poor yield of progress for nearly a decade's debate. Few of the old or new hypotheses have been rejected. However, it may well be that most of the hypotheses are correct. Although the discussion has at times appeared to pit genetic factors against ecological factors, none of the defenders of outcrossing advantages has in fact denied a substantial role for ecological factors, and none of the proponents of ecological explanations has advised ignoring genetics. In this comparatively pluralistic atmosphere, the primary goal has been to assess the relative importance of the various selection pressures and to understand how they interact in different situations. Correlation is not much of a tool for doing this, but it is a place to start. (If the separation of sexes arises by various pathways, as seems indisputable, we will understand

correlations better by thinking of 'dioecy' as several different 'dioecies', each likely to have its own set of correlations.)

Furthermore, Bawa's[6] and Givnish's[9] attempts to attach significance levels to phylogenetic associations, although simplified, were instrumental in stimulating the improved techniques that are now becoming available for this purpose[17,18]. More studies such as Donoghue's[20] are undoubtedly forthcoming, and will allow disentanglement of some conflicting hypotheses, where sufficient data exist. Although it would be naive to hope that such approaches will produce universal consensus – witness the acrimony that pervades the field of numerical systematics in general – they can help choose among otherwise equally plausible scenarios. New compilations of data, such as Charlesworth's[19], may not settle the issues for which they were assembled, but they clarify what additional data are needed – and point out areas, such as compatibility systems, where the data are so unreliable that correlation studies may indeed be pointless.

Also, we feel that at least one general correlation/mechanism – 'fleshy fruits' – has indeed been weakened, at least as a general proposition. The correlations involve potentially confounding variables and the mechanism receives little support from general studies of frugivore behavior. In contrast, the ecological association of dioecy with small insect-pollinated flowers seems more robust, and although pollinator discrimination has not been confirmed as a causative explanation, other explanations have been put forward for testing. More knowledge of such components as geitonogamy, synchronous dichogamy, pollen presentation, par-

tial compatibility systems and inbreeding depression will be needed for such tests.

As Willson saw clearly ten years ago, the way to evaluate sex allocation predictions is to document the successes and failures of both sexes' gametes, but very few comprehensive treatments have been completed. Not only do we need further 'excruciating'[5] studies of male gain curves, we must also abandon the simplifying assumption[27] that female curves are linear. True fitness curves are so hard to specify, however, that limited progress must be expected.

As several authors have concluded[19,20,30], the next phase will also entail more detailed study of lineages in which dioecy co-occurs with hermaphroditism. We can combine statistical and molecular phylogenetic tools with a deeper understanding of ecological, physiological and genetic mechanisms, and begin mapping character state transitions to sort out the most likely selection pressures, given the unique biology of each case. With an adequate library of such cases, we should be able to establish what the repeated evolution of dioecy represents. True convergence driven by one overarching selection pressure? A small handful of pathways, each with a characteristic combination of driving mechanisms? Or a formless collection of idiosyncrasies? Given our current knowledge, the first possibility is too much to hope for, but the second is not.

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