

How common is heterodichogamy?

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The sexual systems of plants usually depend on the exact spatial distribution of the gamete-producing structures. Less well known is how the exact timing of male and female function might influence plant mating. New papers by Li *et al.* on a group of tropical gingers describe differential maturing of male and female structures, such that half the individuals of a population are in the female stage when the other half is in the male stage. This new case of heterodichogamy is unique in involving reciprocal movement of the styles in the two temporal morphs.

Most of the 250 000 species of flowering plants keep inbreeding to a minimum by genetic self incompatibility or morphological outcrossing mechanisms. Of the morphological outcrossing mechanisms, dioecy and heterostyly have received much attention, whereas others, such as androdioecy, have never been analyzed comprehensively. The recent discovery by Li *et al.*^{1–3} of an intricate outcrossing mechanism in *Alpinia*, a genus of Zingiberaceae, now highlights what is possibly the least-understood angiosperm sexual system.

Populations of *Alpinia* comprise two genetic morphs. One sheds pollen in the morning and has stigmas exposed to pollinators in the afternoon, the other sheds pollen in the afternoon and has stigmas exposed to pollinators in the morning (Fig. 1). The stigmas are brought into the 'right' position by differential growth of the style. Styles of flowers that shed pollen in the morning are initially curved upward so that their stigmas do not contact the nectar-foraging bees that pollinate *Alpinia*. At around noon, they begin to grow and curve downwards, bringing the stigmas into a position where they will contact incoming bees and receive pollen. This female stage lasts from about 4:40 pm until dark, when the flowers wilt. The reciprocal morph has styles first curved downwards, then growing and curving upwards. This system, which is reliant on temporally reciprocal morphs, is called heterodichogamy⁴, in analogy to heterostyly, which is the sexual system involving reciprocal style length morphs.

Heterodichogamy differs from normal dichogamy, the temporal separation of male and female function in flowers, in that it involves two genetic morphs that occur at a 1:1 ratio. The phenomenon was discovered in walnuts and hazelnuts^{5,6} (the latter ending a series of Letters to the Editor about hazel flowering that began in *Nature* in 1870), but has gone almost unnoticed⁷. Indeed, its recent discovery in *Alpinia* was greeted as a new mechanism, differing 'from other passive outbreeding devices, such as dichogamy...and heterostyly in that it combines some features of all of these mechanisms with the unique movement of floral parts'¹.



Fig. 1. Flower of *Alpinia bracteata* showing an upward-curved style. At around noon, this style will begin to curve downwards, bringing the stigma into a position where it will contact incoming bees and receive pollen. Photograph reproduced, with permission, from Qing-Jun Li.

A review of the literature shows that heterodichogamy is phylogenetically widespread, occurring in nine orders, 11 families, and 17 genera of flowering plants (Table 1). The system is present in six orders of core eudicot (Caryophyllales, Fagales, Malvales, Rosales, Sapindales and Trochodendrales), two orders of basal angiosperms (Laurales and Magnoliales), and in at least one monocot lineage

(Zingiberales). These figures probably underestimate the frequency of heterodichogamy. First, the phenomenon is discovered only if flower behavior is studied in several individuals and in natural populations. Differential movements and maturation of petals, styles, stigmas and stamens become invisible in dried herbarium material, and planted populations deriving from vegetatively propagated material no longer reflect natural morph ratios. The discovery of heterodichogamy thus depends on field observations. Second, many dichogamous species exhibit so-called synchronous dichogamy, the situation that flowers of an individual all mature in synchrony, with little or no overlap between carpellate and staminate stages. Completely synchronous flower development has been described from species of *Acer* (Sapindaceae), *Bomarea* (Amaryllidaceae), *Ficus* (Moraceae), *Pentagonia* (Rubiaceae), Annonaceae, Apiaceae, Araliaceae and many other genera and families^{8–10}. Such developmental synchrony among the sexual stages of flowers requires that plants are out of phase with each other for successful pollination to occur, and this is indeed the case¹¹. The factors controlling within-plant synchrony and between-plant asynchrony are poorly understood, but it is clear that time-lagged individuals in 'normal' synchronously dichogamous species do not have genetically determined morphs.

Genetically determined temporal dimorphism comes in two forms. In the simplest case, flowers in the two morphs open 6, 12, or 24 h apart. For example, one morph might open flowers with receptive stigmas in the morning and shed pollen in the afternoon or the next morning (depending on species; see Table 1). The complementary morph opens flowers in the afternoon and sheds pollen the next morning or afternoon. This is the case in *Eupomatia* and Lauraceae, all of which are protogynous (female stage first), and in *Ziziphus* (Rhamnaceae), which however is protandrous (male stage first). In the second form of heterodichogamy, flowers of both morphs open simultaneously, but

Table 1. Attributes of currently known heterodichogamous flowering plants

Family	Plant species and pollinating vector	Order ^a	Sexual system flower/population	Flower ^b				Refs
				M-F separation	Morphs	Ratio	Compatibility	
Amaranthaceae (incl. Chenopodiaceae)	<i>Grayia brandegei</i> ; Wind	Caryophyllales	Unisexual/monoecious	2–3 wk	Protandrous versus protogynous	1:1	Probably SIC	17,18
	<i>Spinacia oleracea</i> var. <i>americana</i> ; Wind	Caryophyllales	Unisexual/dioecious (this variety monoecious)	24–48 h	Protandrous versus protogynous	1:1	SC	Cited in 18
Annonaceae	<i>Annona squamosa</i> ; Beetles	Magnoliales	Bisexual	c. 12 h	Protogynous, offset by 6 h	Unknown	SC	21
Betulaceae	<i>Corylus avellana</i> and other species; Wind	Fagales	Unisexual/monoecious	Several days	Protandrous versus protogynous	1:1	SIC	6,14
Eupomatiaceae	<i>Eupomatia bennettii</i> and <i>E. laurina</i> ; Beetles	Magnoliales	Bisexual	12–24 h	Protogynous, offset by 6 h	Unknown ^c	SC	22
Juglandaceae	<i>Carya illinoensis</i> and probably all <i>Carya</i> spp.; Wind	Fagales	Unisexual/monoecious	Few days	Protandrous versus protogynous	1:1	SC	12
	<i>Juglans hindsii</i> , <i>J. regia</i> , <i>J. cinerea</i> and probably all <i>Juglans</i> spp.; Wind	Fagales	Unisexual/monoecious	1 wk	Protandrous versus protogynous	1:1	SC	5,14, 20
Lauraceae	<i>Aniba rosaeodora</i> and other species; Bees	Laurales	Bisexual	6 or 12 h	Protogynous, offset by 6 h	Unknown ^c	Possibly SIC	15
	<i>Cinnamomum camphora</i> and <i>C. zeylanicum</i> ; Bees	Laurales	Bisexual	6 or 12 h	Protogynous, offset by 6 h	Unknown ^c	Possibly SIC	15
	<i>Licaria guianensis</i> and other species; Bees	Laurales	Bisexual	6 or 12 h	Protogynous, offset by 6 h	Unknown ^c	Possibly SIC	15
	<i>Mezilaurus thoroflora</i> (incl. <i>Clinostemon maguireanum</i>); Bees	Laurales	Bisexual	6 or 12 h	Protogynous, offset by 6 h	Unknown ^c	Possibly SIC	15
	<i>Persea americana</i> and <i>P. caerulea</i> ; Bees	Laurales	Bisexual	24 h	Protogynous, offset by 24 h	1:1	Possibly SIC	23,24
Rhamnaceae	<i>Ziziphus jujuba</i> (1), <i>Z. mauritiana</i> (2), <i>Z. mucronata</i> (3), <i>Z. spina-christi</i> (4); Flies and bees	Rosales	Bisexual	12 or 21 h, depending on species	Protoandrous, offset by 4 or 6 h	1:1 (unknown in species 3)	SIC (species 1 and 4)	25–28
Sapindaceae (incl. Aceraceae)	<i>Acer pseudoplatanus</i> , <i>A. saccharum</i> and other species; Insects	Sapindales	Bisexual but functionally unisexual/monoecious	24–48 h	Protandrous versus protogynous	1:1 to variable	SC	11
Thymelaeaceae	<i>Thymelaea hirsuta</i> ; Wind	Malvales	Bisexual but functionally unisexual/tri-monoecious	8–12 d	Protandrous versus protogynous	Highly variable	Unknown	16,19
Trochodendraceae	<i>Trochodendron aralioides</i> ; Flies	Trochodendrales	Bisexual	10–28 d	Protandrous versus protogynous	1:1	SC	29
Zingiberaceae	<i>Alpinia kwangsiensis</i> and other species; Bees	Zingiberales	Bisexual	6 h	Protandrous versus protogynous	1:1	SC	1–3

^aAPG classification from Ref. 30.

^bThe male (M) and female (F) function of the flowers are separated by the times indicated, and each population comprises two reciprocal temporal morphs.

SC, self-compatible; SIC, self-incompatible.

^c*Eupomatia* and *Cinnamomum* were studied in greenhouses, and natural morph ratios are therefore unknown. For the Lauraceae canopy tree species studied by Kubitzki and Kurz, extremely low densities prevented the assessment of morph ratios (H. Kurz, pers. commun.).

one morph is protogynous, the other protandrous. This is the case in walnuts, hickories, pecans and perhaps all Juglandaceae¹², hazelnuts, most maples, *Grayia*, *Spinacia*, *Thymelaea*, *Trochodendron* and, as Li *et al.* now report^{1–3}, *Alpinia*.

Evolutionarily, heterodichogamy is seen as coming from synchronous dichogamy^{11,13,14} and leading to dioecy^{8,11,13, 15–18}. Phylogenetic studies that would test either hypothesis are not yet available. Four of the 17 genera (*Acer*, *Grayia*, *Spinacia* and *Thymelaea*) contain both heterodichogamous and dioecious species or populations and could be used to study the proposed pathway (see data base of dioecious angiosperms available at <http://www.umsl.edu/~biosrenn/dioecy.pdf>).

The occurrence of 1:1 morph ratios in natural populations of heterodichogamous species suggests that a single pair of alleles controls heterodichogamy. Indeed, in walnuts and pecans^{12,14}, a dominant–recessive mendelian factor of one locus and two alleles regulates heterodichogamy. Protandry is the recessive homozygote (gg) and protogyny either the heterozygote (Gg) or dominant homozygote (GG). GG is extremely rare in nature, because heterodichogamy is almost 100% effective at precluding selfing^{12,14}. By contrast, dioecy is usually controlled by a pair of genes that are heterogametic for males and homogametic for females, or occasionally by three loci, each with two alleles¹⁹.

Contrary to earlier expectations¹⁷, most heterodichogamous taxa are insect pollinated (11 versus six wind pollinated; Table 1) and about half are self incompatible (Table 1). Heterodichogamy depends on the exact timing of floral organogenesis²⁰ and the interplay of environmental and genetic factors. Nothing is known about the physiological control of flowering in the two morphs, probably because developmental events that occur only once in a season do not lend themselves to experimental analysis. If a herbaceous species were discovered in which morphs opened and closed their flowers repeatedly, then one could do the experiments needed to establish light-cycle control. The completely unexpected discovery of heterodichogamy in Zingiberaceae^{1–3}, besides its intrinsic interest, should cause more biologists to be on the watch

for temporal behavioral dimorphisms in plants. As they say, ignorance is no excuse, it is the real thing.

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