

Gene Co-Inheritance and Gene Transfer

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The functional transfer of mitochondrial genes to the nucleus is an enigmatic feature of eukaryotic genome evolution (1). In angiosperms, functional gene transfer is characterized by periods of stasis punctuated with bursts of transfer activity, a large variance in the number of transfers among lineages, and a high frequency of recent and a dearth of ancient transfers (2, 3). Despite extensive documentation of mitonuclear gene transfer in angiosperms, there is no well-supported explanation for this “unfathomable” variation (3). To understand the variation in mitochondrial gene translocation (3) and the evolutionary forces affecting genomic transfer, we examined the association between number of functional mitonuclear gene transfer events and angiosperm reproductive mode.

When a gene moves from the mitochondria to the nucleus, its environment changes from a primarily nonrecombining, haploid, uniparentally inherited mitochondrial genome to a recombining, biparentally inherited nuclear genome. Thus, the evolutionary advantages of recombination may drive mitonuclear gene transfer, because recombination allows mitochondrial genes to escape degradation by Muller’s ratchet, the irreversible accumulation of deleterious mutations, or increases the rate of spread of advantageous mutations (4). If either of these selective forces drives mitonuclear gene transfer, more gene transfer should be observed in outcrossing taxa because they experience more effective recombination than selfing or clonal taxa.

Although selfing and clonal reproduction diminish recombination, they increase θ_{MN} , the probability that mitonuclear gene pairs in the same individual are inherited together and thus are simultaneously identical by descent. High θ_{MN} conserves mitonuclear gene combinations (5) across generations as well as nuclear gene combinations, increasing the effectiveness of selection on mitonuclear and nuclear-nuclear epistasis (6).

The opportunity for functional gene transfer

begins with the incorporation of a mitochondrial gene into a nuclear genome. The transferred gene must then acquire sequences conferring nuclear expression and sequences targeting the gene product to the mitochondrion (1). Lastly, the mitochondrial copy must be silenced or lost from the population while the nuclear copy is retained. Throughout this complex process, high θ_{MN} preserves functional gene combinations, whereas reproduction with low θ_{MN} breaks apart gene combinations, potentially uniting two nonfunctional complements.

If the process of gene transfer involves coadaptation of mitonuclear gene combinations, heritability of these combinations is necessary for a response to selection. Because adaptive function after transfer requires simultaneous genetic changes in both genomes, it is probable that co-inheritance is also essential to successful functional gene transfer (5). A positive association between co-inheritance and transfer numbers would provide support for this hypothesis.

Alternatively, mitonuclear transfer could be a neutral process, guided by random genetic drift, or an adaptive process, guided by genes with additive effects on fitness regardless of mating system. Neither of these hypotheses makes any prediction concerning the relationship between θ_{MN} and the number of transfer events.

We tested these competing hypotheses by examining the relationship between independent mitochondrial gene losses [documented in (2)] and ancestral θ_{MN} (ranked as high, intermediate, or low) across 170 angiosperm genera [see Sup-

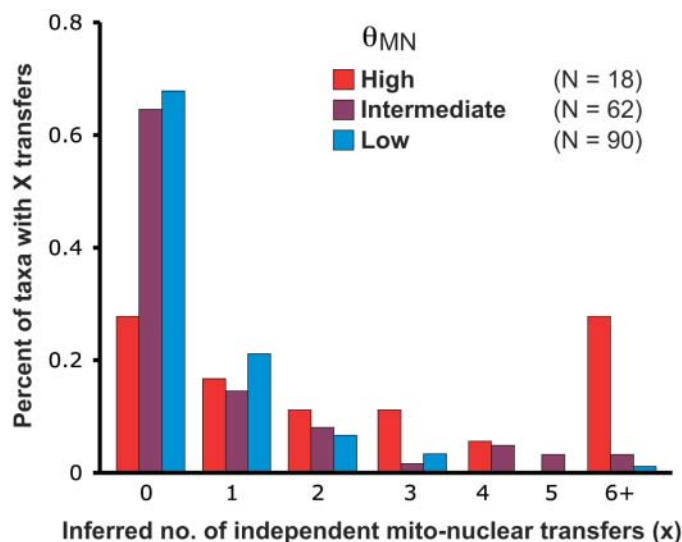


Fig. 1. Distribution of inferred number of gene transfers by θ_{MN} .

porting Online Material (SOM) text for criteria, categorization, justification, and reference of each θ_{MN}]. Adams *et al.* (2) inferred loss of essential mitochondrial genes by Southern blots but did not confirm transfer between the mitochondria and nucleus. Sequenced plant mitochondrial genomes show that most inferred losses represent true losses and that functional copies of lost mitochondrial genes are usually found in the nucleus (1, 2), with exceptions removed from our analysis (detailed in SOM text). Similarly, our inference of ancestral reproductive mode is imperfect (SOM text), and thus greater resolution of the timing of gene transfer would facilitate better inference of ancestral θ_{MN} , providing a stronger test of our hypothesis.

We found a strong, positive association between θ_{MN} and the number of functional gene transfer events (Spearman’s $\rho = 0.233$, two-tailed $P = 0.002$, Fig. 1), consistent with the prediction that gene co-inheritance facilitates functional gene transfer and opposite to predictions that suggest these advantages are due to recombination (4). The range of variation in the number of transfer events and the value of θ_{MN} within clades (fig. S1) rules out the possibility that this result is due to a phylogenetic coincidence. Furthermore, a positive association between θ_{MN} and gene transfer is consistent with the observed phylogenetic distribution of many recent but few ancient transfers; if selfing and clonal reproduction represent a “dead end” (7), gene transfer in these high θ_{MN} groups is followed by their extinction.

Evidence that chloroplast-to-nuclear gene transfers, movement of nuclear genes among chromosomes, or movement of genes between hosts and vertically transmitted endosymbionts are associated with higher θ would further support our hypothesis. Overall, these findings and predictions demonstrate that the heritability of gene combinations provides a predictive framework for the evolution of genome architecture.

References and Notes

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SOM Text

Fig. S1

References

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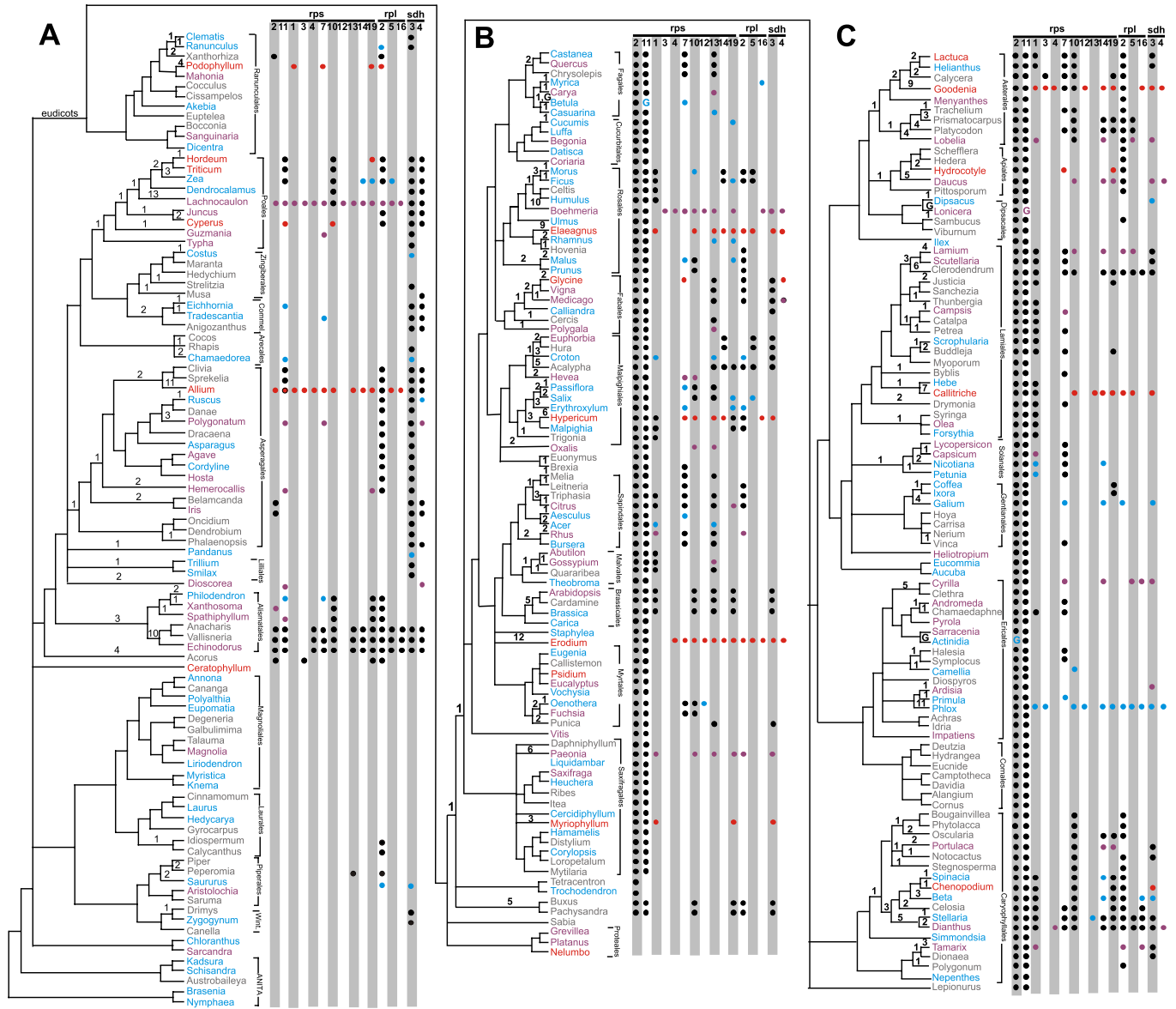
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SOM Text

Fig. S1

References



S1- Appendix 1: Gene losses, θ_{MN} , and justification for each classification across genera.

High (H) θ_{MN} genera are composed of species that primarily reproduce by selfing and/or vegetative propagation, and for which this mode of reproduction is probably ancestral.

The intermediate (I) θ_{MN} group consists of genera with mixed mating systems, or with a moderate frequency of both sexual and vegetative reproduction, and for which a mixed reproductive mode is probably ancestral. Low θ_{MN} (L) groups are predominantly self-incompatible, dioecious, or display other methods that enforce outcrossing. In some cases our inference of mating system is necessarily limited by either a dearth of extant species diversity in a genus, or by limited sampling of mating system across a genus.

Furthermore, it is possible in some cases that shared reproductive mode between species within a genus represents analogy rather than homology.

* A rosid which includes loss of *Rps13* (not accompanied by functional transfer of the mitochondrial gene (*S1*, *S2*)).

† Includes loss of *Rps7*, a nuclear copy of *Rps7* has not been found (*S1*).

Genus	Total Losses	θ_{MN}	Independent Losses	Notes. (<i>Reference(s)</i>)
<i>Abutilon</i>	3	I	0	<i>A. theophrasti</i> (the species in (S1)) is a selfer (S2) however, on the whole the genus is protandrous and outcrossing. (S3)
<i>Acer</i>	4*	L	2*	“Duodichogamy (a sequence of male–female–male flowering) has been proposed as the breeding system of the ancestors of the genus <i>Acer</i> , based on the breeding system of the unique sister group <i>Dipteronia</i> (de Jong, 1976). Heterodichogamy (a breeding system with two reciprocal morphs: male first- and female first-flowering individuals) also appeared in the earliest members of the genus <i>Acer</i> (Gleiser & Verdú, 2005). The ancestral populations were then invaded by unisexual forms (males and females) giving rise to polymorphic breeding systems (Fig. 1). This invasion of unisexual forms resulted in the dioecious condition of derived species (de Jong, 1976; Gleiser & Verdú, 2005). It must be noted that geitonogamy is avoided in this genus by a temporal segregation of the sexual phases (dichogamy).” (S4)
<i>Actinidia</i>	1	L	0	Dioecious genus, infrequent vegetative reproduction. (S5)
<i>Aesculus</i>	3†	L	1†	Generally outcrossing, although geitonogamy may occur (S6). H_O did not differ from H_E in <i>A. turbinata</i> (S7) (S6, S7)
<i>Agave</i>	2	I	0	SC, deficiency in heterozygotes suggests high selfing (<i>A. lechuguilla</i>). (S8)
<i>Akebia</i>	0	L	0	Monoecious, SI (<i>A. quinata</i>). (S9)
<i>Allium</i>	15†	H	11†	Clonal reproduction is the primary mode of reproduction throughout the genus. When sexual, they are SC, but generally outcrossing. (S10-S12)

<i>Andromeda</i>	3 [†]	I	0	<i>A. polifolia</i> is homogamous, and self-fertile. Bagged flowers set seed. Small genus. (S13)
<i>Annona</i>	0	L	0	Dichogamous (S14)
<i>Arabidopsis</i>	7 [*]	I	0	> 90% selfing rate in wild <i>A. thaliana</i> (S15). SI is common in the Brassicaceae, and probably ancestral. <i>A. thaliana</i> 's close relative, <i>A. lyrata</i> (Diverged about 5 mya) is SI (S16). We assign an intermediate θ_{MN} to <i>Arabidopsis</i> , since <i>A. thaliana</i> (the species in (S1)) has presumably been SC for some time, but is derived from an outcrossing ancestor. (S15, S16)
<i>Ardisia</i>	3	I	1	SC, delayed automatic autogamy common. (S17)
<i>Aristolochia</i>	0	I	0	Bisexual flowers, protogynous, most species SC, but some SI. (S18)
<i>Asparagus</i>	2	L	0	<i>A. officinalis</i> dioecious, <i>A. densiflorus</i> monoecious SI. (S19)
<i>Aucuba</i>	2	L	0	Dioecious genus. (S20)
<i>Begonia</i>	2	I	0	Monoecious, SC. Genetic data in <i>B. socotrana</i> suggest the species is predominantly outcrossing (S21). There is a slight deficiency of heterozygotes in <i>B. sutherlandii</i> (S22). There is a deficiency of heterozygotes in <i>B. dregei</i> , <i>B. homonyma</i> (S23). (S21-S23)
<i>Beta</i>	9	L	3	SI common, although some species (ie <i>B. macrocarpa</i>) are SC and highly selfing, this is most likely a derived trait. <i>B. vulgaris</i> (the species in (S1)) is SI. (S24, S25)
<i>Betula</i>	2 [†]	L	1 [†]	Monoecious, herkogamous. H_O is not different than H_E in <i>B. pendula</i> (S26). Comments in (S27) suggest high levels of outbreeding across the genus. (S26, S27)
<i>Boehmeria</i>	12 ^{†*}	I	10 ^{†*}	Monoecious, SC, agamospory common. (S28, S29)
<i>Brasenia</i>	0	L	0	Dichogamous, wind pollinated. (S30)
<i>Brassica</i>	7 [*]	L	0	SI is common in the genus and most likely ancestral, and predates the split between <i>Brassica</i> and <i>Raphanus</i> . (S31)

<i>Bursera</i>	4 ^{†*}	L	0	Generally dioecious, although apomixis and hermaphroditism also occur. Dioecy probably ancestral. (S32)
<i>Calliandra</i>	3	L	0	For most populations of <i>C. calothyrsus</i> H _O is not different than H _E , although there is an insignificant deficiency of heterozygotes. Incomplete gametophytic SI system observed. (S33)
<i>Callitriche</i>	10	H	7	"Geitonogamy is predominant in <i>Callitriche</i> (e.g. Schotsman, 1985; Philbrick and Anderson, 1992) and is promoted by the proximity of stamen and style in adjacent flowers, either aerial or submersed. A unique form of geitonogamy ('internal geitonogy', IG) occurs in aerial and submersed flowers of seven <i>Callitriche</i> species (Philbrick and Anderson, 1992; Philbrick and Bernardello, 1992)." (S34)
<i>Camellia</i>	3	L	1	Both <i>C. sinensis</i> and <i>C. japonica</i> are outcrossers. (S35, S36)
<i>Campsis</i>	4 [†]	I	1 [†]	<i>C. radicans</i> is an "out-crossed plant is pollinated mostly by hummingbirds" (S37), but it also reproduces vegetatively. This is the species in (S1), and one of three in the genus. (S37)
<i>Capsicum</i>	4 [†]	I	1	Most species SC with some selfing, although <i>C. cardenasii</i> is SI; however, SI is probably ancestral, and the timing of the loss of SI is unresolved. (S38, S39)
<i>Carica</i>	2	L	0	Most species unisexual and dioecious, although some are monoecious or hermaphroditic. (S40)
<i>Carya</i>	3 [*]	I	1 [*]	Monoecious, dichogamous with incomplete temporal separation on a plant. Self-pollination probably common in <i>C. ovata</i> and <i>C. tomentosa</i> . (S41)
<i>Castanea</i>	4 ^{†*}	L	0	SI (<i>C. sativa</i> (S42)), H _O is not different than H _E , F _{IS} is not different than 0 (<i>C. crenata</i> (S43)). H _O is not less than H _E for any of the five species (<i>C.</i>

				<i>mollissima</i> , <i>C. seguinii</i> , <i>C. henryi</i> , <i>C. dentata</i> , <i>C. pumila</i>) examined in (S44). (S42-S44)
<i>Casuarina</i>	3*	L	1*	Flowers generally unisexual. Species monoecious, dioecious, or mixed (S45). <i>C. equisetifolia</i> and <i>C. junghuhniana</i> have low (< 0.02) inbreeding coefficients (S46). (S45, S46)
<i>Ceratophyllum</i>	0	H	0	Monoecious, selfing, and clonal reproduction predominates. (S47)
<i>Cercidiphyllum</i>	2	L	0	Two extant species, both are root sprouters. <i>C. japonicum</i> is dioecious, does not 'reproduce' clonally, but can resprout from the base, leading to a potentially long lifespan (several hundred to a thousand years). Less information on <i>C. magnificum</i> . For both species H_O is not different than H_E . (S48)
<i>Chamaedora</i>	2	L	2	Dioecious. (S49-S51)
<i>Chenopodium</i>	7	H	1	"Species of the genus <i>Chenopodium</i> are generally self-compatible and anemophilous. Flowers are small and often clustered into dense, bracteate glomerules" (S52). This floral biology probably results in high levels of selfing. In fact, <i>C. fremontii</i> is inbreeding (S53), <i>C. hircinum</i> has a deficiency of heterozygotes (S54) and <i>C. quinoa</i> is a self-pollinated crop plant (S55). (S52-S55)
<i>Chloranthus</i>	0	L	0	Bisexual, SC, but primarily insect pollinated, lower seed set upon artificial selfing than artificial outcrossing for the three species examined. (S56)
<i>Citrus</i>	7†*	I	1	SI common throughout the genus, apomixis is also common. (S57)
<i>Clematis</i>	1	L	0	Unisexual flowers, bisexual flowers, monoecy, dioecy. Generally SC, but outcrossing. (S58, S59)
<i>Coffea</i>	3	L	0	" <i>Coffea arabica</i> is predominantly self-pollinating (autogamous) and the only natural allotetraploid ($2n = 4x = 44$) species in the genus <i>Coffea</i> . The other

				coffee species are all diploid ($2n = 2x = 22$) and out crossing (allogamous) (Meyer 1965; Charrier and Berthaud 1985).” (S60)
<i>Cordyline</i>	2	L	0	SI reported for <i>C. australis</i> , <i>C. pumilio</i> and <i>C. kaspar</i> . (S61-S63)
<i>Coriaria</i>	2	I	0	Great variation in breeding systems, but most species are monoecious or hermaphroditic. SC, some autogamy. (S64)
<i>Corylopsis</i>	2	L	0	<i>C. coreana</i> has a slight deficiency of heterozygotes, nevertheless, Chung and Cheon (S65) conclude that it is an outcrosser. (S65)
<i>Costus</i>	1	L	1	SC but outcrossing, high inbreeding depression upon forced selfing. (S66)
<i>Croton</i>	6*	L	3*	Monoecious, dioecious or gynodioecious. Generally, moenoecious species are dichogamous. (S67, S68)
<i>Cucumis</i>	3*	L	1*	Flowers generally unisexual. Species monoecious, dioecious, or mixed. Protandrous, reducing probability of geitonogamy (Cucumber – <i>C. stauvus</i>). (S69, S70)
<i>Cyperus</i>	5	H	2	Clonal, weedy species comprise most of the genus. (For a representative example see S71)
<i>Cyrilla</i>	7†	I	5†	<i>C. racemiflora</i> is the only species in the genus, it is SC and geitonogamy is probably common; however a pollination vector is needed (bagged flowers do not set seed). (S72)
<i>Datisca</i>	2	L	0	Androdioecious (<i>D. glomerata</i>), dioecious (<i>D. cannabina</i>). (S73, S74)
<i>Daucus</i>	8	I	5	SC, some gynodioecy. Cultivated carrot lineages maintained by inbreeding. Wild species have mixed mating systems. (S75-S77)
<i>Dendrocalamus</i>	3	L	0	Bisexual flowers, protogynous, wind pollinated (<i>D. gigantus</i> (S78)), anemophilous (<i>D. strictus</i> (S79)). (S78, S79)
<i>Dianthus</i>	13†	I	2	Most species are hermaphroditic and SC although gynodioecy is also common. Most species outcross,

				although geitonogamy is also probable. (S80)
<i>Dicentra</i>	0	L	0	Do not readily self-pollinate, much of the genus is SI, bee-pollinated. (S81, S82)
<i>Dioscorea</i>	2	I	2	<i>D. japonica</i> is dioecious (S83), clonal. <i>D. rotundata</i> monoecious and SC (S84). (S83, S84)
<i>Dipsacus</i>	3	L	1	"Although self-pollination appears possible, allogamous fertilization, following cross pollination by bumblebees, macrolepidoptera and other insects is the most common method of reproduction." (S85)
<i>Echinodorus</i>	10 [†]	I	0	Some SI, some SC, the SI species are highly clonal and often there is no compatibility within a population, suggesting that such populations are almost completely clonal. (S86)
<i>Eichhornia</i>	3	L	1	Tristyly, self-incompatibility ancestral. (S87)
<i>Elaeagnus</i>	11 [*]	H	9 [*]	Has deep vertical as well as shallow, nearly horizontal roots capable of sprouting, SC, with inconspicuous, (usually) perfect flowers (<i>E. angustifolia</i> (S88, S89)). <i>E. umbellata</i> readily regenerates by root after destruction of above-ground biomass. It has both perfect and unisexual flowers of both sexes on one plant, SC (S90 and references therein). (S88-S90)
<i>Erodium</i>	14 ^{+*}	H	12 ^{+*}	<i>E. rupestre</i> is SC, but is dichogamous. However, dichogamy is not synchronized within plants, and geitonogamy and bi-parental inbreeding are probably common. There is a deficiency of heterozygotes in this species. These features are probably shared with many other species in the genus (S91). Other species reproduce clonally via a crown of rosettes of leaves (S92). (S91, S92)
<i>Erythroxylum</i>	5 [†]	L	3 [†]	The genus is predominantly hermaphroditic and distylous, which is generally accompanied by SI (although some distylous <i>Erythroxylum</i> species

<i>Eucalyptus</i>	2	I	0	are SC). Dioecious species, as well as at least one agamosperous species have been reported. (S93, S94) For most species, outcrossing rates are high, and SI has been reported. Other species display moderate levels of selfing. Clonal propagation occurs. (S95, S96)
<i>Eucommia</i>	2	L	0	<i>E. ulmoides</i> is the only extant species in the genus and is dioecious. (S97)
<i>Eugenia</i>	2	L	0	'Cryptic' dioecy common in the genus. (S95)
<i>Euphorbia</i>	5	I	0	<i>E. boetica</i> is 'functionally andromonecious' dichogamous, probably minimal selfing (S98). <i>E. esula</i> is SC, and can reproduce pseudogamously, but sets greater seed set upon outcrossing (S99). <i>E. cyparissias</i> is SC but produces more seed upon outcrossing (S100). (S98-S100)
<i>Eupomatia</i>	0	L	0	Outcrossing, have staminodia that separate stigma and anthers, facilitating outcrossing these structures also attract pollinators. (S101)
<i>Ficus</i>	7	L	1	Dioecious and monoecious, monoecy and outcrossing thought to be ancestral. When monoecious, generally dichogamous but SC. (S102)
<i>Forsythia</i>	3	L	0	Heterostyly ancestral. (S103)
<i>Fuchsia</i>	4 [†]	I	0	SC, hermaphroditism, SI, gynodioecy, sub-dioecy and dioecy have all been reported in the genus. Showy flowers suggest outcrossing. However SC with some geitonogamy is probably ancestral. (S104, S105)
<i>Galium</i>	6 [†]	L	4 [†]	Generally outcrossing with H _O similar to H _E . (S106)
<i>Glycine</i>	7 ^{†*}	H	2 [†]	Wild soybean (<i>G. soja</i>) has a deficiency of heterozygotes, measures of outcrossing rates range from 2-19%. <i>G. clandestina</i> and <i>G. crytologa</i> have both open pollinated SC flowers and cleistogamous flowers. Selfing rate in <i>G. clandestina</i> is estimated to be about 70-90%. (S107, S108 and references therein)

<i>Goodenia</i>	14 [†]	H	9	“Members of the Goodeniaceae are readily distinguished by an unique floral character known as the ‘indusium’. The indusium is a cup-shaped, or two-lipped structure, located at the top of the style. Pollen collected in the indusium is carried upward by the lengthening style and is protected until it can be collected by insects. Many species also have a number of short silky hair which, when disturbed, release pollen. The stigma at this stage grows out to receive pollen from other flowers. This strange reproductive system had attracted the interest of Charles Darwin who had been able to examine and study samples of <i>Goodenia</i> , <i>Lechenaultia</i> , and <i>Scaevola</i> . These plants appeared to have a mechanism fitted for self-fertilization; challenging Darwin’s belief that beings must occasionally cross-fertilize.” (S109)
<i>Gossypium</i>	4 [*]	I	1 [*]	SC, many species are protandrous with showy, insect pollinated flowers geitonogamy possible. (S110)
<i>Grevillea</i>	0	I	0	Most species SC, although a few are SI (S111 - Table 1). Some species are highly clonal (although this is probably derived (S112)). <i>G. macleayana</i> - (S113) <i>G. caleyi</i> (S114) and <i>G. beadleana</i> (S111) are selfing. (S111-S114)
<i>Guzmania</i>	2 [†]	I	1 [†]	Deficiency of heterozygotes in <i>G. monostachya</i> . (S115)
<i>Hamamelis</i>	2	L	0	<i>H virginiana</i> (one of two species in the genus) is SI. (S116)
<i>Hebe</i>	3	L	0	Most species outcrossing, and show inbreeding depression upon selfing. Dioecy and gynodioecy also occur in the genus (derived). (S117-S119)
<i>Hedycarya</i>	0	L	0	Dioecious genus (S118)
<i>Helianthus</i>	7 [†]	L	0	Outcrossing inferred from isozyme variation in a variety of species. (S120)
<i>Heliotropium</i>	2	I	0	“The Australian <i>Heliotropium</i> species are hermaphroditic, dioecious or

<i>Hemerocallis</i>	2	I	2	trioecious. Predominantly, the species are hermaphroditic and the majority of these appears to be inbreeding.” (S121) Deficiency of heterozygotes in all five species examined in (S122), SC. (S122)
<i>Heuchera</i>	2	L	0	SI common throughout the genus. (S123)
<i>Hevea</i>	4 [†]	I	2 [†]	Modest levels of selfing / inbreeding. (S124)
<i>Hordeum</i>	6	H	1	98% selfed progeny in wild <i>H. vulgare ssp. Var. sponteum</i> , the progenitor of cultivated barely. Cultivated barely is the group examined in 1. (S125, S126)
<i>Hosta</i>	2	I	0	SC, some species selfing, others outcrossing. (S127)
<i>Humulus</i>	3	L	0	Hop (<i>H. lupulus</i>) is dioecious. (S128)
<i>Hydrocotyle</i>	5	H	2	Clonal reproduction predominates. (S129-S131)
<i>Hypericum</i>	11 ^{†*}	H	6 ^{†*}	<i>H. perforatum</i> is primarily apomictic with occasional selfing and outcrossing (S132). <i>H. cumulicola</i> is highly SC (S133) and shows no inbreeding depression upon selfing, suggesting high historical levels of selfing (S134). (S132-S134)
<i>Idiospermum</i>	1	I	0	Great variation in mating and breeding systems, some dioecious, some monoecious, some SC. (S135)
<i>Ilex</i>	2	L	0	Dioecious genus; however, at least one species – <i>I. leucoclada</i> is clonal. (S136, S137)
<i>Impatiens</i>	2	I	0	Most species exhibit a mixed-mating system with cleistogamy and geitonogamy; however, a few species are predominantly outcrossing. (S138-S141)
<i>Iris</i>	3	I	0	SC, some species highly outcrossing, others self with moderate frequency. (S142-S145)
<i>Ixora</i>	3	L	0	SI / outcrossing predominate. (S146)
<i>Juncus</i>	3	I	0	Clonal, weedy, produces a lot of sexual seed. (S147, S148)
<i>Kadsura</i>	0	L	0	Unisexual flowers, predominantly monoecious. (S149)

<i>Knema</i>	0	L	0	Dioecious genus. (S150)
<i>Lachocaulon</i>	16 [†]	I	13 [†]	Monoecious, SC, flowers not showy, both hermaphroditic and unisexual inflorescences. (S151)
<i>Lactuca</i>	7 [†]	H	0	<i>L. sativa</i> (the species in (S1)) is a self-fertilizing crop species, selfing common in its wild relatives. (S152, S153)
<i>Lamium</i>	9 [†]	I	4	Preponderance towards high θ in the genus. <i>L. amplexicaule</i> is cleistogamous. <i>Lamium subgenus Galbdolon</i> is clonal, although it reproduces sexually more frequently than previously thought. (S154, S155)
<i>Laurus</i>	0	L	0	Dioecious or dichogamous. (S156)
<i>Liquidambar</i>	2	L	0	Outcrossing. Ho is similar to He for the species examined by Hoey and Parks (S157). (S157)
<i>Liriodendron</i>	0	L	0	Protogynous, SC. No seed set in bagged flowers. (S158)
<i>Lobelia</i>	8	I	4	Self-compatible gynodioecious taxa. (S159, S160)
<i>Lonicera</i>	1	I	0	Outcrossing and clonal reproduction typify the genus. (S161-S163)
<i>Luffa</i>	2	L	0	Monoecious. (S164)
<i>Lycopersicon</i>	3 [†]	I	0	"Most populations of <i>L. hirsutum</i> are obligately outcrossing-a mating system strictly enforced by the gametophytic self-incompatibility system-and exhibit several features typical of outcrossers (Rick et al. 1979), including high nucleotide diversity (Miller and Tanksley 1990; Stephan and Langley 1998). In contrast, <i>L. esculentum</i> ((Solanum) <i>lycopersicum</i> , the cultivated tomato) is a domesticated, self-pollinated species with comparatively low genetic variation. The putative wild progenitor of <i>L. esculentum</i> is also predominantly selfing (Miller and Tanksley 1990; Kondo et al. 2002), and self-compatibility is thought to have preceded domestication (Rick 1995)" (S165). Data in (I) are from <i>L. esculentum</i> . Since <i>L. esculentum's</i> wild

<i>Magnolia</i>	0	I	0	progenitor was selfing, but derived from an outcrossing lineage we assign an intermediate level of θ_{MN} . (S165) Outcrossing, SC. High inbreeding depression upon selfing (although <i>M. obovata</i> is highly selfing), showy flowers, suggesting historically outcrossing groups. (S166, S167)
<i>Mahonia</i>	0	I	0	Outcrossing, clonal (<i>M. aquifolium</i>). (S168)
<i>Malpighia</i>	5	L	0	Isozyme diversity suggests outcrossing predominates in <i>M. emarginata</i> . (S169)
<i>Malus</i>	6 [†]	L	2 [†]	SI. (S170)
<i>Medicago</i>	6*	I	1	SC and high selfing is common throughout the genus, there is some SI in <i>M. sativa</i> (alfalfa). (S171-S173)
<i>Menyanthes</i>	3	I	0	<i>M. trifoliata</i> is clonal, SI. (S174)
<i>Morus</i>	7	L	1	Dioecious genus. (S175)
<i>Myrica</i>	3	L	1	<i>M. rubra</i> , <i>M. cerifera</i> and <i>M. rivasmartinezii</i> are dioecious. Unisexual flowers and dioecy common in the genus, <i>M. cerifera</i> is clonal. (S45, S176-S178)
<i>Myriophyllum</i>	5	H	3	<i>M. spicatum</i> is an invasive species that is primarily clonal (S179). Vegetative reproduction is common throughout the genus. (S179, S180)
<i>Myristica</i>	0	L	0	Dioecious genus. (S181)
<i>Nelumbo</i>	0	H	0	Reproduction primarily vegetative in <i>N. pentapetala</i> (S182) and <i>N. nucifera</i> (S182). (S182, S183)
<i>Nepenthes</i>	2	L	0	Dioecious genus. (S184)
<i>Nicotiana</i>	5 [†]	L	2	Most species SI, SC is probably derived. (S185, S186)
<i>Nymphaea</i>	0	L	0	The genus is SC, but predominantly dichogamous (S187)
<i>Oenothera</i>	5 [†]	L	1	SI found in all three sections except for sect. <i>Contortae</i> (although plants from each disjunct area of the distribution of <i>O. xylocarpa</i> should be examined for self-incompatibility) indicate that self-incompatibility was present in the common ancestor of the genus. There is a clear trend in three of the sections for evolution from self-incompatibility

				and mandatory out-crossing to self-compatibility and predominant autogamy. In both sects. <i>Ravenia</i> and <i>Pachylophus</i> self-compatible, autogamous species have evolved, while <i>O. primiveris</i> is apparently in a transitional state where there are mixed populations of SC and SI individuals, a situation thus far found elsewhere in the genus only in <i>O. grandiflora</i> . (S188)
<i>Olea</i>	3	I	0	<i>O. europaea</i> (the species in (S1)) is SI, clonal. (S189, S190)
<i>Oxalis</i>	4*	I	2*	Vegetative reproduction predominates in <i>O. tuberosa</i> (S191) and pentaploid <i>O. pes-carpe</i> , the diploid progenitor of these species, <i>O. pes-carpe</i> is tristylous and SI (S191). <i>O. acetosella</i> is cleistogamous and vegetatively reproducing, with occasional outcrossing. <i>Oxalis oregana</i> "spread extensively... by belowground perennating structures" (S192) <i>O. squamata</i> is a perennial tristylous species (S193). In summary there is great variability in θ_{MN} . (S191-S194) <i>P. cambessedessi</i> is SC (S195). <i>P. broteroi</i> is SC; however, seed set is lower for selfed flowers than outcrossed flowers (S196). <i>P. jishanensis</i> is SI (S197). <i>P. californica</i> is SC and geitonogamy is probably common (S198). (S195-S198)
<i>Paeonia</i>	8*	I	6*	<i>P. cambessedessi</i> is SC (S195). <i>P. broteroi</i> is SC; however, seed set is lower for selfed flowers than outcrossed flowers (S196). <i>P. jishanensis</i> is SI (S197). <i>P. californica</i> is SC and geitonogamy is probably common (S198). (S195-S198)
<i>Pandanus</i>	1	L	1	Dioecious genus. (S199)
<i>Passiflora</i>	5†*	L	1†	SI (<i>P. edulis</i> and <i>P. incarnata</i>), some vegetative reproduction in <i>P. incarnata</i> , but sexual reproduction predominates. (S200)
<i>Petunia</i>	4†	L	1	SI predominates although SC is a derived condition in some species / varieties. (S201)
<i>Philodendron</i>	5†	L	2†	Primarily unisexual flowers, most species xenogamous. (S202)
<i>Phlox</i>	13	L	11	" <i>Phlox</i> species are typically highly self-incompatible and dependent on insect pollination for reproductive

				success (Levin, 1966). One known exception is the central Texas annual <i>Phlox cuspidata</i> , which is self-compatible and sets autogamous seed (Levin, 1978). Grant and Grant (1965) stated that <i>P. superba</i> (listed as <i>P. stansburyi</i> in their treatment) is likely self-incompatible based on preliminary crossing studies in an experimental garden, and <i>P. dolichantha</i> plants grown from seed in a growth chamber set no autogamous seed" (S203). Cultivated strains of <i>P. paniculata</i> are propagated asexually. (S203)
<i>Platanus</i>	0	I	0	Monoecious, clustered, wind pollinated. (S204)
<i>Podophyllum</i>	4 [†]	H	4 [†]	SI, highly clonal (<i>P. peltatum</i> , the species in (1)). (S205-S207)
<i>Polyalthia</i>	0	L	0	Dichogamous, selfed flowers do not yield fruit. (S208)
<i>Polygala</i>	3 [*]	I	1 [*]	SC. Neither an excess nor deficiency of heterozygotes in populations of <i>P. reneii</i> (S209). <i>P. vulgaris</i> is "largely self pollinating." (S210) <i>P. paucifolia</i> produces both cleistogamous and chasmogamous flowers. (S211) (S209-S212)
<i>Polygonatum</i>	5 [†]	I	3 [†]	Weakly SI, clonal. (S213)
<i>Portulaca</i>	6	I	2	Of the three species examined in S214 two are selfing and one is weakly SI. (S214)
<i>Primula</i>	3 [†]	L	1 [†]	<i>P. elatior</i> is obligately outcrossing (S215), <i>P. sieboldii</i> is ancestrally SI, but is undergoing a loss of SI. <i>P. vulgaris</i> is SI (S216). <i>P. interjacens</i> is outcrossing (S217). <i>P. veris</i> is SI (S218). <i>P. farinosa</i> is outcrossing, while its close relatives <i>P. scotia</i> , <i>P. scandinavia</i> and <i>P. stricata</i> are autogamous (S219). (S215-S219)
<i>Prunus</i>	4	L	0	SI. (S170)
<i>Psidium</i>	2	H	0	Large deficiency of heterozygotes in wild <i>P. guajava</i> populations (S220). <i>P. firmum</i> is highly SC, and bagged flowers have 37% fruit set (S221). (S220, S221)

<i>Pyrola</i>	2	I	0	Most species SC with some selfing; although in general (with the exception of <i>P. minor</i>) pollination vectors are necessary (S222). Positive F_{IS} , (0.184) was observed in <i>P. japonica</i> . (S223) (S222, S223)
<i>Quercus</i>	4 ^{†*}	I	0	Some signs of inbreeding, the highest F_{IS} (from populations of <i>Q. petraea</i> , <i>Q. robur</i> , <i>Q. cerris</i> and <i>Q. pubescens</i>) was 0.159 for <i>Q. pubescens</i> (S224). Very low levels of inbreeding in <i>Q. humboldtii</i> (S225). (S224, S225)
<i>Ranunculus</i>	2	L	1	SI predominates (S226). Asexual reproduction, both vegetative (<i>R. reptans</i> (S227)) and apomictic (polyploid species in the <i>R. auricomus</i> complex S228) occurs. (S226-S228)
<i>Rhamnus</i>	4 [*]	L	2 [*]	Dioecious genus. (S229)
<i>Rhus</i>	6 ^{†*}	I	2 [*]	" <i>Rhus</i> ... combines sexual reproduction with extensive clonal spread" (S230)
<i>Ruscus</i>	3	L	1	Dioecious or subdioecious. (S231)
<i>Salix</i>	6 [*]	L	2	Dioecious genus and Ho generally does not differ from He. One interesting exception is <i>S. silvicola</i> , which has a deficiency of heterozygotes, potentially due to bi-parental inbreeding. (S232)
<i>Sanguinaria</i>	0	I	0	Protogynous, SC, selfing. "Facultatively xenogamous" (S233 and references therein)
<i>Sarcandra</i>	0	I	0	Bisexual, protandrous flowers, insect pollinated, SC (field data from <i>S. glabra</i> one of three extant species). (S234)
<i>Sarracenia</i>	2	I	0	Outcrossing, clonal spread common. (S235-S237)
<i>Saururus</i>	2	L	2	SI common. (S238 and references therein)
<i>Saxifraga</i>	2	I	0	Outcrossing, and clonal reproduction common. (S239-S241)
<i>Schisandria</i>	0	L	0	Unisexual flowers, both monoecious and dioecious species. (S242)
<i>Scrophularia</i>	3	L	0	"In reproductive terms most <i>Scrophularia</i> species studied thus far behave as xenogams or facultative

				xenogams (Shaw, 1962; Dalgaard, 1979; Ortega-Olivencia & Devesa, 1993c). In general, autogamy is not widespread in this genus, and has been identified only in <i>S. arguta</i> Aiton on the basis of the cleistogamic flowers at the base of the stem (Masters, 1869; Ortega-Olivencia & Devesa, pers. obs.). In the remaining taxa some degree of selfing can be expected as a result of either a failure in dichogamy (e.g. <i>S. peregrina</i> L., Shaw, 1962; Ortega-Olivencia & Devesa, 1993c) or the occurrence of geitonogamy in self-compatible species." (S243)
<i>Scutellaria</i>	4 [†]	I	0	Cleistogamy and selfing common in many species; however, predominant outcrossing (but SC) is observed in other species. (S127,S244,S245)
<i>Simmondsia</i>	2	L	0	Unisexual flowers. <i>D. chinensis</i> (the species in (S1)) is dioecious. (S246)
<i>Smilax</i>	1	L	0	Dioecious. (S247, S248)
<i>Spathiphyllum</i>	4	I	1	Clonal, protogynous SC, pollination between ramets is rare but pollination between gamets may be more common. (S249)
<i>Spinacia</i>	7	L	1	<i>S. oleracea</i> (the species in (S1)) is dioecious. (S250)
<i>Staphylea</i>	2	L	0	<i>S. trifolia</i> is SI. (S251)
<i>Stellaria</i>	12	L	1	Hermaphroditic, <i>S. arencola</i> is selfing. Its progenitor, and the genus at large are primarily outcrossing. (S252)
<i>Tamarix</i>	6 [†]	I	3	All SC, variable levels of heterozygosity. (S253)
<i>Theobroma</i>	2	L	0	Incomplete SI system. Despite being partially SI wild <i>T. cacao</i> populations are generally characterized by an excess of homozygotes (S254,S255). On the other hand, <i>T. grandiflorum</i> shows no excess of homozygotes (S256). (S254-S257)
<i>Tradescantia</i>	3	L	1	Stigmatic self-incompatibility. (S258)
<i>Trillium</i>	1	L	0	Some species SI, others SC, some outcrossers, others mixed mating. Outcrossing appears to be ancestral. (S259-S264)

<i>Triticum</i>	5	H	0	H_o is less than H_e for species examined in (S265). "All wild wheats show a high degree of inbreeding". (S265)
<i>Trochodenron</i>	2	L	0	Perfect flowers, both protogynous, and protandrous morphs, both SI. Slight deficiency of heterozygotes. (S266)
<i>Typha</i>	1	I	0	Unisexual flowers, monoecious and SC. (S267, S268)
<i>Ulmus</i>	2	L	0	SI common, although some species SC. (S269)
<i>Vigna</i>	5*	I	0	Mixed mating, some cleistogamy, some species are highly selfing. (S270-S272)
<i>Vitis</i>	2	I	0	"Table grape cultivars (<i>V. vinifera</i>) are either female or hermaphroditic self compatible plants and most of the seeds produced by hermaphrodites result from selfing events." (S273)
<i>Vochysia</i>	2	L	0	All species examined as of (1994, with the exception of <i>V. ferruginea</i>) are SI. (S274)
<i>Xanthosoma</i>	5	I	1	<i>X. daguense</i> is clonal, weakly SI, monoecious, <i>X sagittifolium</i> is a clonally propagated crop plant. (S275)
<i>Zea</i>	8	L	3	"Like other <i>Zea</i> species, all of which are native to Mexico and Central America, <i>Z. diploperennis</i> and <i>Z. perennis</i> are both wind-pollinated outcrossing taxa." (S276)
<i>Zygogynum</i>	1	L	0	Outcrossing, protogynous, insect pollinated. (S277)

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