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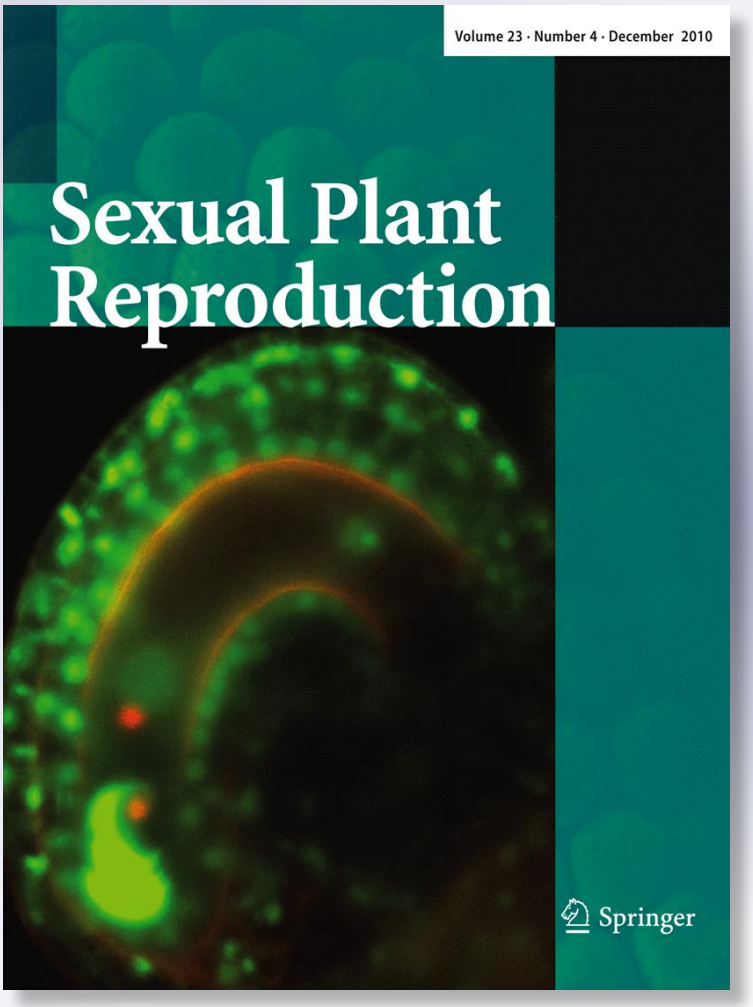

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REVIEW

Sexual and apomictic plant reproduction in the genomics era: exploring the mechanisms potentially useful in crop plants

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Abstract *Arabidopsis*, *Mimulus* and tomato have emerged as model plants in researching genetic and molecular basis of differences in mating systems. Variations in floral traits and loss of self-incompatibility have been associated with mating system differences in crops. Genomics research has advanced considerably, both in model and crop plants, which may provide opportunities to modify breeding systems as evidenced in *Arabidopsis* and tomato. Mating system, however, not recombination per se, has greater effect on the level of polymorphism. Generating targeted recombination remains one of the most important factors for crop genetic enhancement. Asexual reproduction through seeds or apomixis, by producing maternal clones, presents a tremendous potential for agriculture. Although believed to be under simple genetic control, recent research has revealed that apomixis results as a consequence of the deregulation of the timing of sexual events rather than being the product of specific apomixis genes. Further, forward genetic studies in *Arabidopsis* have permitted the isolation of novel genes reported to control meiosis I and II entry. Mutations in these genes trigger the production of unreduced or apomeiotic megagametes and are an important step toward understanding and engineering apomixis.

Keywords Apomixis · Breeding systems · Self-incompatibility · Floral traits · Model plants · Gene cloning · Quantitative trait loci · Polymorphism · Recombination

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Introduction

From ancient times, human beings have experimented with at least 3,000 species of plants for food production, of which about 150 cultivated species have entered into the world's commerce (Mangelsdorf 1966). The trend has been, however, to use fewer and fewer crop species, narrowing down to those that give the greatest return for land and labor. People are mainly fed today by 44 plant species worldwide, which vary in ploidy, haploid chromosome, genome size, life form (annual and perennial) and mating system (autogamous, inbreeding or selfing; allogamous or outcrossing; mixed mating) (Table 1). Diversity in mating systems has also been reported in some of the wild relatives of tomato, rice and wheat (Table 2). Mating systems in plant populations are influenced by genetic, demographic and environmental factors (Barrett and Eckert 1990). The genetic factors for transition from outcrossing to selfing include flower color, reduced flower size and pollen–ovule ratio, self-incompatibility (SI, genetic mechanism preventing self-fertilization), herkogamy (spatial separation of the anthers and stigma), dichogamy (separation at the time of gender expression in hermaphroditic plants), heterostyly (self-incompatibility system in which flower morphs differ in the pistil's and stamens' length), gynodiocy (or the

Table 1 Ploidy level, chromosome number, genome size, life form and mating system variations in major food crops

Common name	Latin name	Ploidy	Chromosome number	Genome size (Mbp C^{-1})	Life form	Mating system	
						Sexual	Vegetative
Cereals							
Barley	*Hordeum vulgare*	Diploid	14	5,351, 5,361 (Bennett et al. 2000)	Annual	Inbreeder	
Bread wheat	*Triticum aestivum*	Hexaploid	42	15,922, 18,817, 17,466, 17,177, 16,598, 18,431, 16,115 (Bennett and Leitch 1995)	Annual	Inbreeder	
Durum wheat	*T. durum*	Tetraploid	28	12738, 13317 (Bennett and Leitch 1995)	Annual	Inbreeder	
Einkorn wheat	*T. monococcum*	Diploid	14	5,790, 5,404, 3,860 (Bennett and Leitch 1995)	Annual	Inbreeder	
Finger millet	*Eleusine coracana*	Tetraploid	36	2,509 (Bennett and Leitch 1995)	Annual	Inbreeder	
Foxtail millet	*Setaria italica*	Diploid	18	490 (Doust et al. 2009)	Annual	Inbreeder	
Maize[a]	*Zea mays*	Diploid	20	2,605–2,798 (Bennett and Leitch 1995)	Annual	Outbreeder	
Pearl millet	*Pennisetum glaucum*	Diploid	14	2,352 (Bennett et al. 2000)	Annual	Outbreeder	
Proso millet	*Panicum miliaceum*	Tetraploid	36		Annual	Inbreeder	
Rice	*Oryza sativa*	Diploid	24	389 (IRGSP 2005)	Annual	Inbreeder	
Sorghum	*Sorghum bicolor*	Diploid	20	730 (Paterson et al. 2009)	Annual	Mixed mating	
Legumes							
Broad bean	*Vicia faba*	Diploid	12	12,985 (Zonneveld et al.2005)	Annual	Mixed mating	
Chickpea	*Cicer arietinum*	Diploid	16	1,544 (Bennett and Leitch 1997)	Annual	Inbreeder	
Common bean	*Phaseolus vulgaris*	Diploid	22	675 (Bennett and Leitch 1997)	Annual	Inbreeder	
Cowpea	*Vigna unguiculata*	Diploid	22	579 (Bennett and Leitch 1995)	Annual	Inbreeder	
Lentil	*Lens culinaris*	Diploid	14	4,053 (Bennett and Leitch 1995)	Annual	Inbreeder	
Pea	*Pisum sativum*	Diploid	14	4,246 (Bennett and Leitch 1997)	Annual	Inbreeder	
Pigeonpea	*Cajanus cajan*	Diploid	22	1,447, 1,930 (Bennett and Leitch 1995)	Annual	Mixed mating	
Soybean[a]	*Glycine max*	Diploid	40	1,061 (Bennett and Leitch 1997)	Annual	Inbreeder	
Oilseeds							
Coconut	*Cocos nucifera*	Diploid	32	3,377 (Bennett and Leitch 1997)	Perennial	Mixed mating	
Groundnut	*Arachis hypogaea*	Tetraploid	40	4,921–5,211, 5,404, 5,597–5693 (Bennett and Leitch 1997)	Annual	Inbreeder	
Oil palm	*Elaeis guineensis* and *E. oleifera*	Diploid	32	980 (Bennett and Leitch 2005)	Perennial	Controlled crosses to produce hybrids for commercial production	Negligible production from tissue culture propagation

Table 1 continued

Common name	Latin name	Ploidy	Chromosome number	Genome size (Mbp C^{-1})	Life form	Mating system	
						Sexual	Vegetative
Rapeseed	*Brassica napus*	Tetraploid	76	1,351 (Bennett and Leitch 1997)	Annual	Mixed mating	
Sunflower	*Helianthus annuus*	Diploid	34	2,895, 3,377, 3,860 (Bennett and Leitch 1995)	Annual	Outbreeder	
Root and tuber crops							
Cassava	*Manihot esculenta*	Diploid	36	772 (Bennett and Leitch 1997)	Perennial	Outbreeder	Vegetative propagation[d]
Potato	*Solanum tuberosum*	Tetraploid	48	1,715, 1,774 (Bennett et al. 2000)	Annual	Outbreeder	Vegetative propagation[d]
Sweet potato	*Ipomoea batatas*	Tetraploid Hexaploid	60	1,447, 1,737, 2,219, 2509 (Bennett and Leitch 1997)	Perennial	Outbreeder	Vegetative propagation[d]
Yam	*Dioscorea* ssp.	Tetraploid	80	675, 868, 2,316 (Bennett and Leitch 1997)	Perennial	Outbreeder	Vegetative propagation[d]
Vegetables							
Cabbage	*Brassica oleracea*	Diploid	18	868 (Bennett and Leitch 1997)	Annual	Outbreeder	
Cauliflower	*Brassica oleracea*	Diploid	18	868 (Bennett and Leitch 1997)	Annual	Outbreeder	
Carrot	*Daucus carota*	Diploid	18	482 (Bennett and Leitch 1995)	Annual	Outbreeder	
Cucumber	*Cucumis sativus*	Diploid	14	868 (Bennett and Leitch 1997)	Annual	Outbreeder	
Egg plant	*Solanum melongena*	Diploid	24	1,158 (Bennett and Leitch 1995)	Annual	Inbreeder	
Garlic	*Allium sativum*	Diploid	16	15,633 (Bennett and Leitch 1997)	Perennial	Controlled crosses	Vegetative propagation[d]
Lettuce	*Lactuca sativa*	Diploid	18	2,605, 2,702 (Bennett and Leitch 1995)	Annual	Outbreeder	
Onion	*Allium cepa*	Diploid	16	15,826 (Bennett and Leitch 1997)	Annual	Outbreeder	
Pepper	*Capsicum annuum* *Capsicum baccatum* *Capsicum chinense* *Capsicum frutescens*	Diploid	24	3,254, 3,293, 3,342, 3,381 (Moscone et al. 2003)	Annual	Inbreeder	
Pumpkin	*Cucurbita pepo*	Diploid	40	386 (Bennett and Leitch 1997)	Annual	Outbreeder	
Spinach	*Spinacia oleracea*	Diploid	12	965 (Bennett and Leitch 1995)	Annual	Outbreeder	
Tomato	*Solanum lycopersicum*	Diploid	24	950 (Barone et al. 2008)	Annual	Inbreeder (self-compatible) to outbreeder (gametophytic self-incompatibility)	
Turnip	*Brassica rapa*	Diploid	20	529 (Johnston et al. 2005)	Annual	Outbreeder	
Fruits							
Apple	*Malus* ssp.	Diploid, Triploid	34, 51	699–810 (diploid) and 762–827 (triploid) (Tatum et al. 2005)	Perennial	Controlled crosses	Vegetative propagation[d]
Banana and plantain	*Musa* ssp.	Triploid	33	579 (Bennett and Leitch 1995)	Perennial	Controlled crosses	Vegetative propagation[d]
Grape	*Vitis vinifera*	Diploid	38	504 (Vilasco et al. 2007)	Perennial	Mixed mating	Vegetative propagation[d]

Table 1 continued

Common name	Latin name	Ploidy	Chromosome number	Genome size (Mbp C^{-1})	Life form	Mating system	
						Sexual	Vegetative
Orange[b]	*Citrus sinensis*	Diploid	14	386 (Bennett and Leitch 1995)	Perennial	Controlled crosses	Vegetative propagation[c,d]
Papaya	*Carica papaya*	Diploid	18	372 (Arumuganathan and Earle 1991)	Annual	Mixed mating[c]	
Sugary crops							
Sugar beet	*Beta vulgaris*	Diploid	18	868 (Bennett and Leitch 1997)	Annual	Outbreeder	
Sugarcane	*Saccharum officinarum*	Octaploid	64	3,724 (Bennett et al. 2000)	Perennial	Outbreeder	Vegetative propagation[d]

[a] Modern maize and soybean arose through an ancient allotetraploid event and subsequent diploidization of the genome (Krishnan et al. 2001; Schnable et al. 2009)

[b] Interspecific and intergeneric hybrids are propagated and selected through nucellar embryony (one form of apomixis)

[c] Trioecious with three sex forms (male, female and hermaphrodite flowers)

[d] Commercial production by vegetative propagation, however, natural outcrossing exists or controlled crosses possible to generate new strain for vegetative production. Genome size expressed in million base pair (Mbp), 1 picogram (pg) = 965 Mbp (Arumuganathan and Earle 1991)

dimorphic breeding system in which male sterile individuals coexist with hermaphroditic individuals), pollen viability (longevity) and stigma maturity (Barrett and Eckert 1990; Cruden 2000; Dudley et al. 2007; Goodwillie et al. 2009). Seed crops are sexually propagated. The root and tuber crops are vegetatively propagated; however, controlled crosses are possible to produce hybrids from which the clones could be vegetatively propagated commercially.

Inbreeding and outcrossing are the two major forms of sexual reproduction. Apomixis, or asexual clonal reproduction through seeds, presents a major potential to agriculture as it would enable the fixation of genotypes of interest (e.g., hybrid vigor), permit true seed production for vegetatively propagated crops, and speed up breeding programs and responsiveness to changing environments.

The genomics research approach has advanced considerably in some crops; for example, maize, rice and sorghum genomes have been sequenced (IRGSP 2005; Paterson et al. 2009; Schnable et al. 2009). Of the several model plants for studying mating system evolution, *Arabidopsis thaliana* (the inbreeder) and *Mimulus guttatus* (the outbreeder) genomes have been sequenced (AGI 2000; Ganko et al. 2009), tomato (*Solanum lycopersicum*) genome (euchromatic region) sequencing has advanced considerably (Mueller et al. 2009), while sequencing the outbreeder *Arabidopsis lyrata* has been initiated (JGI 2008).

This review is focused on the floral traits associated with variation in mating systems, models for dissecting the molecular bases of differences in mating system evolution, how mating system and recombination affect molecular evolution, mapping and cloning of genes associated with autogamy, gene expression regulating mating systems and genomics of asexual seed reproduction through apomixis.

Floral traits associated with evolution of mating systems

The transition from outcrossing (allogamy) to selfing (autogamy) occurred many times independently among the angiosperms (Stebbins 1970; Wyatt 1988). Changes in floral traits, including loss of self-incompatibility and heterostyly, reduction in flower size and pollen–ovule ratio, herkogamy and the timing of self-pollination are associated with the transition from outcrossing to selfing and are discussed elsewhere (reviewed in Armbruster et al. 2002; Tang et al. 2007; Valejo-Marín and Barrett 2009). The evolutionary transition from diploid to polyploidy has also been reported to affect changes in mating systems (Barringer 2007; Husband et al. 2008). We summarize below the floral traits associated with variation in mating systems in model and crop plants, which have demonstrated potential to unravel the genetic and molecular basis

Table 2 Floral traits associated with mating system variations in wild relatives of some of the agriculturally important crops

Species	Mating system	Floral traits associated with different mating system	Reference
Genus: *Lycopersicon*			
Lycopersicon cheesmani, *L. parviflorum* and *L. esculentum*	Autogamy (self-compatible, SC)	Slightly exerted (flush or recessed with respect to the anther cone) stigma leads to selfing	Chen and Tanksley (2004)
L. chilens, *L. hirsutum*, *L. pennellii* and *L. peruvianum*	Obligate allogamy (self-incompatible, SI)	Highly exerted stigma leads to cross-pollination	
L. peruvianum (LA4125)	Selfer (self-compatible)	Small and pale flowers and spontaneous fruit set	Graham et al. (2003)
L. pimpnellifolium	Facultative allogamy	Outcrossing highly correlated with flower size and to a lesser extent with the degree of stigma exertion	Rick et al. (1978)
L. chmielewski	Facultative allogamy (self-compatible, SC)	Differences in flower size and stigma exertion; stigma of larger flowers are strongly exerted (leading to cross-pollination), while those of smaller flowers have slightly or not at all exerted stigma (leading to self-pollination)	Rick et al. (1976)
Genus: *Oryza*			
Oryza sativa f. *spontanea* and *O. perennis* subsp. *balunga*	Partial outcrossing	Anther and stigma length, and percentage of exerted stigma associated with outcrossing	Virmani and Athwal (1973)
O. perennis	Partial outcrossing	Anther length, longevity of pollen grains, longer time interval from flowering to pollen emission, length of stigma and style promote outcrossing	Oka and Morishima (1967)
O. rufipogon	Partial outcrossing	Pistil, stamen and glume traits (length, width and length–width ratio) relate to increased outcrossing	Uga et al. (2003)
O. nivara	Inbreeder	Smaller and upright anthers become dehiscent immediately after the flower opens	Grillo et al. (2009)
Genus: *Triticum*			
Triticum urartu and *T. monococcum*	Inbreeder	Not described	Haudry et al. (2008)
Genus: *Aegilops*			
Aegilops speltoides	Outbreeder	Not described	Haudry et al. (2008)
Genus: *Secale*			
Secale cereale	Outbreeder	Not described	Haudry et al. (2008)

of mating system variation and possibly use that knowledge to alter mating system in other crops.

Model plants

The genera *Mimulus* (Phrymaceae family), *Leptosiphon* (Polemoniaceae family), *Leavenworthia* (Brassicaceae family) and *Clarkia* (Onagraceae family) show tremendous variability in reproduction system (both between and within populations). Their selfing evolved frequently and could be of recent origin, which provides a means for studying variation during evolution of mating systems. In *Mimulus*, an outbreeder such as *M. guttatus* has larger flowers, more distinct anther–stigma separation and higher pollen ovule ratio than the inbreeder *M. platycalyx*. Variations in floral traits are also reported among outbreeders in *Mimulus*. For example, pollination in *M. lewisii* is mediated by bees, whereas it is hummingbirds that facilitate cross-pollination in *M. cardinallis*. Both species differ in floral traits: *M. lewisii* has large flowers low in anthocyanin and

carotenoid pigments, and inserted anther and stigma, whereas *M. cardinalis* has nectar-rich flowers high in anthocyanins, and exerted anthers and stigmas (Lin and Ritland 1997; Schemske and Bradshaw 1999). Furthermore, an allele substitution at a flower locus produces pollinator shift in *Mimulus*. The locus *YELLOW UPPER* (*YUP*) controls the presence or absence of yellow carotenoid pigments in the petals of pink-flowered *M. lewisii*, which is pollinated by bumblebees, and its red-flowered species *M. cardinalis,* which is pollinated by hummingbirds. Bradshaw and Schemske (2003) evaluated near isogenic lines (NIL) in which the *YUP* allele from each species is substituted into the other. The *M. cardinalis* NIL with the *M. lewisii YUP* allele shows dark pink flowers and receives 74-fold more bee visits than the wild type, whereas *M. lewisii* NIL with the *M. cardinalis yup* allele shows yellow–orange flowers and receives 68-fold more hummingbird visits than the wild type. These results demonstrated a shift in pollinator preference caused by a single major mutation. The species in genus *Leptosiphon* differ in floral traits associated with variation in mating systems. The selfing species such as *L. bicolor* have smaller corolla lobes, corolla tubes, stigma lobes, anthers and reduced stigma–anther separation than the outcrosser *L. jepsonii* (Schemske and Goodwillie 1996). Selfing in *Clarkia* is associated with genetically determined stigma maturation rates, which affect the degree of herkogamy and protandry, both contributing to autogamy (Dudley et al. 2007).

Cardamom (*Elettaria cardamomum*), a highly priced spice, is native to the Western Ghats of southern India. Both the wild and cultivated cardamom are self-compatible and there are no reproductive barriers between the two populations. Domestication has brought about significant changes in vegetative and reproductive traits and a shift in effective pollinators from native solitary bees (*Megachile* sp. and two species of *Amegilla*) to social bees (*Aphis dorsata*, *A. cerana* and *Trigona iridipennis*). The shift in pollinators seems to be due to the availability of a large number of flowers for prolonged periods in cultivated cardamom that can attract and sustain social bees, rather than due to co-evolution of the flower and the pollinator (Kuriakose et al. 2009).

Species of *Collinisia* and *Tonella*, the two sister genera of self-compatible annuals that constitute tribe *Collinsieae*, show extensive variation in floral size and morphology and in patterns of stamen and style elongation at anthesis. They are therefore a good model system for the study of developmental and morphological traits influencing mating system. Using a nuclear ribosomal ITS phylogeny, independent contrasts and phylogenetically corrected path analysis, Armbruster et al. (2002) showed that large-flowered taxa maintain herkogamy early in anthesis by differential elongation of staminal filaments, which positions each of the four anthers at the tip of the "keel" upon dehiscence, whereas small-flowered taxa do not show this pattern of filament elongation. The styles of large-flowered taxa elongate late in their 2–5-day anthesis, resulting in late anther–stigma contact and delayed self-pollination. Anther–stigma contact and self-pollination occur early in anthesis in small-flowered species or populations. Thus, the researchers found complex co-variation of morphological and developmental traits, as a result of multi-trait adaptation for early selfing and high levels of autogamy, delayed selfing and high levels of outcrossing or intermediate levels of outcrossing.

Crop plants

Tomato (*Solanum lycopersicum*; formerly known as *Lycopersicum esculentum*) and its wild relatives are ideal species for the study of floral variation associated with changes in mating system. This group consists of 14 closely related species or subspecies including the domesticated tomato, and also covering the full range of mating systems, i.e., from allogamy (obligate cross-pollination, enforced by gametophytic self-incompatibility) through facultative allogamy (self-compatible but with a wide variation in cross-pollination) to autogamy (obligate self-fertilization). Variations in mating systems in this species are largely influenced by self-incompatibility, flower size and degree of stigma exertion. Large flowers and highly exerted stigmas lead to cross-pollination, while small flowers with slightly exerted stigmas or not at all exerted stigmas lead to self-pollination (Rick 1984, 1987; Rick et al. 1976, 1978; Soost 1958; Chen and Tanksley 2004; Roselius et al. 2005; Moyle 2008). Variations in floral traits have also been associated with outcrossing in rice and barley. For example, anther and stigma length, percentage of stigma exertion, pollen grain longevity, time interval from flowering to pollen emission and glume traits (length, width and length/width ratio) are associated with outcrossing in some accessions of the wild rice species, *Oryza perennis*, *O. nivara* and *O. rufipogon* (Oka and Morishima 1967; Virmani and Athwal 1973; Uga et al. 2003; Grillo et al. 2009), while in barley it is the anther extrusion, as well anther and stigma size, which relates to increased outcrossing (Abdel-Ghani et al. 2005). Clearly, more research is needed to explore variation for floral traits associated with outcrossing, e.g., stigma exertion, anther and stigma separation, anther extrusion or pollen grain longevity, among others. Such variation may provide a means for modifying the breeding system in some of the agriculturally important crops.

Dissecting molecular basis of mating system evolution in model plants

Arabidopsis thaliana has a small diploid genome, a rapid reproductive cycle and an autogamous nature. This species is also a prolific seed producer and its genome has been fully sequenced (AGI 2000). It diverged from its close relative *A. lyrata* about 5 million years ago. The two species differ in mating system and life form: the self-compatible, annual *A. thaliana* ($2n = 10$) is an inbreeding species with bigger floral organs, fruits and higher seed set than the self-incompatible, perennial outbreeding species *A. lyrata* ($2n = 16$). The genes of the two species share a high degree of sequence similarity. Both are amenable to hybridization; however, *A. thaliana–A. lyrata* hybrids are pollen sterile. In contrast, backcrosses with either parent have been successful in establishing advanced backcross populations, which could be a useful resource for mapping and cloning of genes associated with mating system differences in this species (Nasrallah et al. 2000; Bomblies and Weigel 2007).

Tomato and its wild relatives are another model for studying the molecular basis of mating system differences, as its wild species have great diversity in mating systems ("Crop plants"). Tomato is a diploid species ($2n = 12$) with a rather small genome (950 Mb), a short life cycle, and possesses a wide array of genetic and genomic resources. It is amenable to genetic transformation, ease in making controlled pollination and hybridization, and is a prolific seed producer. An international consortium of ten countries is engaged in sequencing the tomato genome and it is expected that high quality reference euchromatic tomato sequences will be available to researchers by 2010 (Mueller et al. 2009). Tomato is also one of the first species in which significant inroads have already been made toward understanding the genetic and molecular basis of quantitative trait variation (Tanksley and Fulton 2007; Moyle 2008).

The wildflower genus *Mimulus* is another model system that is being used to elucidate the genetics of speciation, inbreeding depression, mating system evolution, ecological adaptation and cytological patterns of evolution (Wu et al. 2007). The species are self-compatible and genetically highly variable. Their interspecific crossing barriers range from complete to virtually nonexistent. Many *Mimulus* species are clonally propagated, show a short life cycle (6–12 weeks) and are easy to emasculate and pollinate. The species are prolific seed producers. There are substantial advances in developing genomic resources of *Mimulus*, including expressed sequence tags (EST), bacterial artificial chromosome (BAC) libraries, highly polymorphic gene-based markers, genetic maps, integrated genetic and physical maps, and seed stocks (http://www.mimulusevolution.org). More recently, 321 Mb of its genome (430 Mb) that contain ~42,000 genes has been sequenced (Ganko et al. 2009). Phylogenetically, *Mimulus* is well placed for broad comparative genomic research across the diversity of flowering plants, based on its relatedness to other model systems for floral development (*Antirrhinum*) and to crop plants with well-developed genomic resources (*Solanum*, *Helianthus* and *Lactuca*) and to *Arabidopsis*.

Mating system and recombination affecting molecular evolution

Mating systems and recombination have significant impact on molecular evolution in plants. The genomes of organisms vary in their rates and patterns of molecular evolution, including base composition, protein evolution, and insertion and deletion in non-coding DNA (reviewed in Wright et al. 2002). A few studies comparing nucleotide diversity in closely related species of *Arabidopsis* differing in mating systems revealed contrasting patterns of nucleotide variation: lower nucleotide diversity was found at the alcohol dehydrogenase (*Adh*) locus in *A. lyrata* than in *A. thaliana* (Savolainen et al. 2000). Although no differences either in protein evolution rate or codon bias occurred between *A. thaliana* and *A. lyrata*, consistently smaller intron sizes were found in *A. thaliana* than *A. lyrata*, and higher major codon uses were found for low-biased genes in *A. lyrata* (Wright et al. 2002). *Leavenworthia* (Brassicaceae) has breeding systems ranging from self-incompatible to almost strict selfing. Liu et al. (1998) reported no variation in DNA sequence polymorphism among the alleles of the *Adh* locus sampled within inbreeding populations of *L. uniflora* and *L. crassa*, whereas they reported high diversity in alleles from populations of the outcrosser *L. stylosa*, and in self-incompatible *L. crassa* populations. When portions of the *cytosolic phosphoglucose isomerase* (*PgiC*) gene in *Leavenworthia* were sequenced, Liu et al. (1999) reported low sequence diversity in sequences of intron 12 in selfers (*L. uniflora* and *L. torulosa*), but high diversity in self-incompatible *L. stylosa* and moderate diversity in *L. crassa* with partial or complete self-incompatibility.

Surveys on *Drosophila* have consistently shown reduced levels of DNA sequence polymorphism in genomic regions experiencing low crossing over, although these same genomic regions exhibit normal amount of interspecific divergence. Naturally occurring polymorphism in tomato is positively correlated with the density of crossing over per physical length, whereas large between-species differences in DNA sequence polymorphism reflect differences in breeding systems: selfing species with much less within-species polymorphism than outcrossing species (Stephan and Langley 1998). The mating system has a highly

significant effect on the level of polymorphism, whereas recombination has only a weak effect on tomato species (Baudry et al. 2001). Furthermore, Roselius et al. (2005) demonstrated reduced nucleotide diversity in the self-compatible populations compared to the self-incompatible populations in tomato. Clearly, reduction of DNA sequence polymorphism in regions of low rates of crossing over is either due to the selective sweep (hitchhiking of neutral (or nearly neutral) variants on chromosomes bearing rare accumulation of strongly selected, favorable mutations at closely linked loci that go rapidly to fixation) or the loss of neutral or nearly neutral variants as a result of a steady elimination of linked deleterious mutations from the population (Stephan and Langley 1998).

The probability of meiotic crossing over is not a uniform function over the physical length of a chromosome region in many plants and animals. Some chromosome regions show high densities of meiotic exchanges, whereas other regions show low density or even a lack of meiotic exchanges. Gene loci in chromosome regions with low recombination rates show reduced levels of DNA polymorphism compared to chromosome regions with high recombination rates in *Drosophila* (Dvořák et al. 1998). There is a genome-wide reduction of recombination in self-fertilizing plants. Dvořák et al. (1998) compared the levels of restriction fragment length polymorphism (RFLP) at 52 single copy gene loci in chromosome regions with low recombination (centromeric regions) in wheat species differing in breeding system (five self-fertilizing and one cross-fertilizing species) and phylogenetic age in the genus *Aegilops*. They detected the highest average gene diversity in cross-fertilizing *Ae. speltoides* and the lowest in self-fertilizing *Ae. searsii*, no heterozygous loci in *Ae. bicornis*, but frequent in *Ae. sharonensis* and *Ae. longissima*. Their results suggest that the outcrossing rates vary among the self-fertilizing species. In all six species, the level of RFLP at a given locus was a function of the position of the locus on the chromosome and the recombination rate in the neighborhood of the locus. Loci in the proximal chromosome regions, which showed greatly reduced recombination rates relative to the distal regions, were significantly less variable than loci in the distal chromosome regions in all six species. Moreover, variation in recombination rates also reflected the haplotype divergence between closely related species. Loci in the chromosome regions with low recombination rates were less divergent than those in chromosome regions with high recombination rates. However, this relationship was not found among the more distantly related species. Furthermore, when investigating the effect of mating system and recombination on molecular evolution in four *Triticeae* species, two outcrossers (*Secale cereale* and *Aegilops speltoides*) and two selfers (*Triticum urartu* and *T. monococcum*), Haudry et al. (2008) found that GC content, possibly driven by biased gene conversion (bGC), was affected by mating system and recombination. Selection efficiency, however, is only weakly affected by mating system and recombination. In outcrossing lineages, selection efficiency could be reduced because of high substitution rates in favor of GC alleles. Outcrossers, but not inbreeders, would therefore suffer from a "GC-induced" genetic load.

Clearly, mating systems have the greatest influence on patterns of polymorphism. However, recombination remains one of the most important factors for crop genetic enhancement. The success of a breeding program depends on the ability of plant breeders to bring the desired alleles together into a new genotype, both by constructing desired combination of alleles on chromosomes and by designing the right combination of chromosomes. As indicated by Wijnker and de Jong (2008), recombination is therefore a critical process in plant breeding as it allows the introduction of novel allele combinations on chromosomes that can be used to breed for superior F_1 hybrids. Gaining control over increased crossover incidence, altering crossover positions on chromosomes or silencing crossover formation will allow plant breeders to effectively engineer the allelic composition of chromosomes.

Mapping and cloning of genes associated with autogamy

The switch from an outcrossing system to selfing is one of the most prevalent evolutionary trends in plant reproduction and one that has occurred repeatedly in flowering plants. However, little is known about the evolution of self-fertility and its genetic architecture. For example, *A. thaliana* switched to self-fertility as a result of mutations disrupting the self-incompatibility (SI) system controlled by the *S* locus (Koch et al. 2000, 2001; Kachroo et al. 2002). The *A. lyrata S* locus contains tightly linked orthologs of the *S-locus receptor kinase* (*SRK*) and *S-LOCUS CYSTEINE-RICH PROTEIN* (*SCR*) genes, the determinants of SI specificity in stigma and pollen, respectively, but lacks the *S*-locus glycoprotein gene. Comparative analysis of the *S*-locus region in *A. lyrata* and *A. thaliana* identified orthologs of the *SRK* and *SCR* genes and demonstrated that self-compatibility in *A. thaliana* was associated with the inactivation of SI specificity genes (Kusaba et al. 2001). *A. thaliana* ecotypes exhibit *S*-locus polymorphisms and differ in their ability to express the SI trait on transformation with *S*-locus genes derived from *A. lyrata* (Nasrallah et al. 2004). In their study, at least one ecotype (C24 containing the *SRKb-SCRb* construct) reverted to a stable, self-incompatible phenotype identical to that of *A. lyrata*. More recently, Boggs et al. (2009) identified another four *A. thaliana* accessions that revert to

full SI by transformation with *AlSRKb-SCRb*, bringing to five the number of accessions in which self-fertility was due to, and was likely caused by, *S*-locus inactivation. Analysis of *S*-haplotype organization revealed that inter-haplotypic recombination events, rearrangements and deletions have restructured the *S* locus and its genes in these accessions. Furthermore, QTL analysis revealed that the transition to inbreeding occurred due to at least two, and possibly more, independent *S*-locus mutations, and a novel unstable modifier locus contributed to self-fertility in Col-0 (Boggs et al. 2009). These ecotype differences are heritable and reflect the fixation in different *A. thaliana* populations of independent mutations that caused or reinforced the switch to self-fertility.

The degree to which the stigmas are exerted above the stamen in flowers is a key determinant of cross-pollination in many plant species. The QTL mapping approach has been used to gain insight into the genetic basis of mating system evolution. For example, using selfing and outcrossing plants derived from two contrasting natural populations of *L. pimpinellifolium*, Georgiady et al. (2002) detected major QTL (>25% phenotypic variance) for total anther length, anther sterile length and style length. Domestic tomato bears flowers with flush or inserted stigmas promoting self-fertilization, while most of its wild relatives are obligate or facultative outbreeders that bear flowers with highly exerted stigmas. Stigma exertion is a composite trait that involves interplay between the length of styles and anthers in a flower. Variation in either stamen or style length (or both) can therefore affect the degree to which the stigma surface extrudes above the anthers. Several QTL for stigma exertion have been reported in tomato, of which a major QTL, *se2.1*, was found on tomato chromosome 2. Mutation at this locus might have been involved in the evolution from allogamy to autogamy (Bernacchi and Tanksley 1997; Fulton et al. 1997; Georgiady et al. 2002). High resolution mapping at the chromosome region harboring *se2.1* QTL detected five tightly linked genes: one controlling style length (*style2.1*), three controlling stamen length (*stamen2.1*, *stamen2.2* and *stamen2.3*) and the other affecting anther dehiscence (*dehiscence2.1*), all with potential to affect stigma exertion and mating behavior. The cluster of these genes controlling various aspects of stigma exertion is reminiscent of a 'co-adapted gene complex' or 'supergenes' controlling mating behavior (Chen and Tanksley 2004). More recently, Chen et al. (2007) cloned *style2.1*, which encodes a putative transcription factor that regulates cell elongation in developing styles. The transition from cross-pollination to self-pollination was accompanied, not by change in the STYLE2.1 protein, but rather by a mutation in the *Style2.1* promoter, which led to a down-regulation of *Style2.1* expression during flower development. Major QTL was also reported for several floral traits conferring differences in mating systems in tomato (Georgiady et al. 2002; Chen and Tanksley 2004). However, both major and minor QTL contribute to floral morphology associated with mating system variation in *Mimulus* (Bradshaw et al. 1995, 1998; Lin and Ritland 1997; Fishman et al. 2002), *Leptosiphon* (Polemoniaceae) (Goodwillie et al. 2006) and *Aquilegia* species (Hodges et al. 2002).

Floral morphology associated with mating system plays an important role in sexual reproduction processes such as pollination, fertilization and seed setting in rice (Takeoka et al. 1993). The Asian cultivated rice *Oryza indica* is predominantly an inbreeder, while its ancestral wild species *Oryza rufipogon* is a partial outbreeder (Oka and Morishima 1997). There exists a wide variation for floral traits (pistil, stamen and glume) between both *Oryza* species. The outcrossing is manifested by the size of the pistil and stamen, stigma exertion and the angle of glume opening (Virmani 1994). Multiple genes control floral traits in rice: 4–7 QTL for glume length, 4–6 QTL for glume width, 1–3 QTL for length–width ratio of the filled glume and 20 QTL for anther length (Uga et al. 2003). The comparison of the locations of the QTL affecting pistil, stamen and glume positioning revealed that most QTL are located on different chromosomal regions, suggesting that phenotypic variation for these traits are primarily controlled by genes unique to each organ, while some regions that are associated with more than one organ partially affect those organs.

Stigma exertion is one of the important traits that contribute to the efficient improvement of commercial seed production in hybrid rice. More recently, Miyata et al. (2007) reported a major QTL, *qES3*, for stigma exertion located at the centromeric region on chromosome 3, contributing to about 32% of the total phenotypic variance. An NIL for *qES3* increased the frequency of the exerted stigma by 36% compared to that of Koshihikari, suggesting that *qES3* was a promising QTL for the development of a maternal line for hybrid rice.

The floral traits associated with variation in mating systems in tomato and rice led to the identification and cloning of major QTL promoting outcrossing, which may provide opportunities to alter breeding system in some crops, i.e., from predominantly inbreeding to outbreeding for the exploitation of hybrid vigor. Further research should explore such variation in crop germplasm to identify those individuals possessing traits to alter breeding systems for fixing hybrid vigor in agriculturally important crops.

Gene expression regulating mating systems

Cleistogamy is a form of mating system in flowering plants that has evolved independently a number of times and is

present in approximately 300 species in 60 plant families (Lord 1981; Campbell et al. 1983). Typically, cleistogamous plants produce two types of flowers: closed (cleistogamous, CL) flowers that require obligate self-pollination and open (chasmogamous, CH) flowers that allow for cross-pollination. CL and CH flowers can also be induced by environmental factors including light intensity, photoperiod, and water and nutrient availability (Morinaga et al. 2008).

The genus *Cardamine* (Brassicaceae) is closely related to *Arabidopsis,* having diverged from the lineage containing *A. thaliana* about 13–19 million years ago (Koch et al. 2001). *Cardamine kokaiensis* is an annual cleistogamous herb that produces individuals with both CL and CH flowers or individuals with only CL flowers. The fully sequenced genome of the *Arabidopsis* provides means for producing *Arabidopsis*-based microarrays, which are commercially available to study gene expression (Seki et al. 2002). Moreover, nucleotide sequences of several genes are well conserved between *Cardamine* and *A. thaliana* (Koch et al. 2000, 2001; Hay and Tsiantis 2006). Using chilling treatment to regulate CL and CH flowers in *C. kokaiensis* in a growth chamber and employing an *Arabidopsis*-based microarray platform, Morinaga et al. (2008) determined changes in key gene regulatory networks involved in the transition from CL to CH flowering to understand the molecular evolutionary mechanisms leading to cleistogamy. They detected 69 genes, including genes related to floral development, auxin, flowering time, cold-stress and drought-stress, which were differentially expressed between CL and CH flowers. Furthermore, semi-quantitative reverse transcriptase polymerase chain reaction (RT-PCR) validated the results for six amplified genes: three genes (*DRM1*, *SPL5* and *At4g29190* orthologs in *C. kokaiensis*) expressed lower values in CL than CH flowers, two genes (*HSP81-4* and *NMT1*) expressed higher values in CL than CH flowers, and one gene (*RD21*) was not differentially expressed between CL and CH flowers. Such results demonstrate that genetic interactions during environmental stresses are involved in the evolution of plant mating systems.

Genomics of asexual seed production through apomixis

Apomixis has evolved independently in various taxa (Savidan et al. 2001). The switch to apomixis is probably the consequence of polyploidization and/or hybridization, which appears to induce a de-regulation of developmental pathways involved in sexual reproduction (Grimanelli et al. 2001). The genus *Boechera* is an important model system for studying apomixis because of its close relationship to *Arabidopsis*. Apomixis in the *Boechera* species is of a diplosporous type, that is, the 2*n* (or unreduced) gametophyte is derived from the megaspore mother cell. Although apomixis is usually found only in polyploids, diploid *Boechera* has been shown to reproduce asexually (Kantama et al. 2007). Diploid lines contain heterochromatic (*Het*) or supernumerary chromosomes that could play a role in the apomictic phenotype. Genomic in situ studies show that these apomicts are alloploid, as they have a mixture of *B. stricta* and *B. holboellii*-like chromosomes (Schranz et al. 2006). No hybrids between *Arabidopsis* and *B. stricta* have been reported, but partial sequencing of *B. stricta* has demonstrated microsynteny between these two species, thus opening new avenues for deciphering the genetic control of apomixis and strengthening the model status of *Boechera* for apomixis research (Windsor et al. 2006). Using SuperSAGE, Sharbel et al. (2009) performed an RNA profiling comparison between ovules of diploid sexual and apomictic *Boechera* accessions and identified over 4,000 differentially expressed mRNA tags between sexual and apomeiotic ovules. Of these, 543 showed a developmental timing shift in expression correlated with apomeiosis. These data, combined with the observation that apomictic *Boechera* plants are alloploid, suggests that apomixis is a consequence of the deregulation of the timing of sexual events rather than the product of specific "apomixis" genes (Grimanelli et al. 2001).

Hieracium, a genus of daisies native to Eurasia and North America, displays both sexually and apomictically reproducing biotypes. Crosses between them yield both sexually reproducing and apomictic progeny, suggesting that their mode of reproduction is under relatively simple genetic control. Sexuality and apomixis are interrelated pathways sharing common regulatory components (Tucker et al. 2003). Apomixis in *Heracium* occurs by apospory, a developmental process characterized by three distinct deviations from sexual reproduction: avoidance of meiosis (apomeiosis) in ectopic megaspore mother cells, an avoidance of fertilization of these spores before embryo formation (parthenogenesis) and endosperm development in absence of fertilization, i.e., autonomous endospermy (Catanach et al. 2006). Using deletion mutagenesis and AFLP as a genomic fingerprinting tool, Catanach et al. (2006) reported that apomixis in *H. caespitosum* is controlled by two loci. One locus regulates events associated with the avoidance of meiosis (apomeiosis) and is designated as *loss of apomeiosis* (*LOA*) locus; the other, an unlinked locus associated with avoidance of fertilization (parthenogenesis), is designated as *loss of parthenogenesis* (*LOP*) locus. The two genomic regions identified align well with phenotypic data from the mutants: four AFLP-based SCAR markers associate themselves with *LOA* locus, while three AFLP-based SCAR markers are associated with the *LOP* locus. A BAC library from tetraploid apomictic *H. caespitosum* was further used to isolate sequences

corresponding to the *LOA* and *LOP* loci for potential use in crop improvement programs aiming to incorporate apomixis into target species. In a similar study, apomixis in daisy fleabane (*Erigeron annuus* and *E. strigosus*) was shown to be controlled by two genetically unlinked loci that regulate, independently, the formation of 2*n* female gametophytes (apomeiosis, diplospory) and autonomous seed formation, which support the hypothesis that apomeiosis and autonomous seed formation are genetically distinct (Noyes 2006). Hence, such traits can be separated and recombined to create hybrids exhibiting apomixis at near wild-type levels.

Citrus and mango are the most common apomictic crops. In these plants, maternal clones are produced through a pattern of adventitious embryony in which embryos are initiated from sporophytic cells in the ovule, such as the nucellus. Although apomixis in *Citrus* has been well characterized at the histological level (Wakana and Uemoto 1987), little information is available on its genetic control. Genetic mapping of apomixis in a cross between *Citrus volkameriana* and *Poncirus trifolicata* showed the presence of six QTL responsible for the trait (Garcia et al. 1999), which suggests that the genetic control of apomixis in *Citrus* is complex. On the other hand, polyembryony in mango (*Mangifera indica*), which is correlated with adventitious embryony (Fig. 1), is controlled by a single dominant gene (Aron et al. 1998).

A few forage grasses of commercial value, such as *Brachiaria*, *Poa* and *Panicum*, are apomictic. *Brachiaria* is the most common forage grass in tropical America (http://www.ciat.org/). *B. brizantha* reproduces through apospory, which appears to segregate as one dominant allele (Ortiz et al. 1997). *Panicum maximum* (guinea grass), an important forage grown in most tropical countries, is also aposporic and apomixis appears to segregate as one dominant allele (Savidan et al. 2001; Ebina et al. 2005). *Poa pratensis* (Kentucky bluegrass) is commonly used in lawns. While diploids are sexual, many polyploids reproduce via apospory, which appears to be linked to the presence of five QTL (Matzk et al. 2005).

Even though no major crop is apomictic, asexual reproduction occurs in wild relatives of maize (*Tripsacum*) and millet (*Pennisetum*). In diplosporic *Tripsacum* and aposporic *Pennisetum*, gametophytic apomixis is a genetically controlled phenomenon that is inherited in a simple Mendelian fashion. Interestingly, the DNA segment controlling apomixis is characterized by suppression of recombination (Conner et al. 2008; Grimanelli et al. 2001). In *Pennisetum*, this segment termed apospory-specific genomic region (ASGR) has a size in the vicinity of 50 megabases, is hemizygous and contains heterochromatin (Roche et al. 2002; Goel et al. 2003). Recently, Conner et al. (2008) sequenced and analyzed a small portion of the ASGR in *Pennisetum* and *Cenchrus*, which are two related apomictic genera, and identified 40 potentially transcribed genes: two contain sites with similarity to kinase domains and four contain domains known to bind or alter DNA, showing homology to Baby Boom (BBM) from *B. napus*. Over-expression of the latter results in ectopic formation of embryos on leaf margins (Boutilier et al. 2002). Therefore, the ASGR BBM-like proteins are credible apomixis candidate genes. Furthermore, the ASGR has a very low gene density and certain regions have microsynteny with rice and sorghum genomes, suggesting that a narrowly defined ASGR region could present genomic colinearity with rice or sorghum as a tool to assist the discovery of the apomixis genes (Conner et al. 2008).

The identification of differentially expressed genes in inflorescences of sexual and apomictic plants might allow the isolation of genes that represent candidates for the manipulation of apomixis and introduction of apomixis into sexual crops. Using differential display analysis of immature inflorescences of sexual and apomictic tetraploid genotypes of *Papsalum notatum*, Laspina et al. (2008) identified 65 candidate unigenes (34 from apomictic and 31 from sexual plants), of which 45 are functionally categorized. In silico mapping further revealed that five genes silenced in apomictic plants were clustered in a rice genomic area that was syntenic with the region governing apospory in *P. notatum* and *Brachiaria brizantha*, of which

Fig. 1 Seed of an apomictic mango (*Mangifera indica* L. var. Kensington Pride). Adventitious embryos are derived from sporophytic tissues in the ovule. Apomicts are typically polyembryonic, as seen in this example in which 11 embryos were found in one seed

two genes mapped within the set of apo-homologs in *P. notatum*. Furthermore, this research also detected that four genes controlling ploidy were among those expressed differentially between apomictic and sexual plants. Hence, several genes involved in aposporous development are also independently ploidy regulated. In diplosporous and sexual *Eragrostis curvula* genotypes, which have differing ploidy levels, Cervigni et al. (2008) detected 112 of the 8,884 unigenes sequenced from inflorescence-derived libraries showing that significant differential expression occurs in individuals with different ploidy levels or variable reproductive modes. Independent comparisons between plants with different reproductive mode (same ploidy) or different ploidy level (same reproductive mode) allowed the identification of genes modulated in response to diplosporous development or polyploidization, respectively. A group of genes were differentially expressed or silenced only in the tetraploid sex plant, presenting similar levels of expression in the tetraploid apomict and the diploid sex genotypes. Differential display analysis showed that in general, both tetraploid apomict and sex expression profiles were more related and different from the diploid sex, in both inflorescence and leaves. Although it is still not clear how many genes are involved in apomixis, the identification of several candidate genes expressed during diplosporous development (some of them mapping in regions syntenic to the locus that govern diplospory in the grasses) may contribute to a better understanding of the genetics required for further manipulation of this trait for the benefit of agriculture.

Apomixis can be used to lock in hybrid vigor or other desirable agronomic traits, as it avoids the sexual reproduction process leading to genetic variation. Fertilization-independent seed (*FIS*) genes that control autonomous endosperm development in *Arabidopsis* are also present in rice. Although the role of these genes in rice is still unclear, knockouts in rice through RNAi (RNA interference) have generated lines showing autonomous pericarp development (http://aciar.gov.au/project/CIM/2002/106). Clearly, further research will be required to understand how to trigger embryo and endosperm development in the absence of fertilization. Once this concept is demonstrated in rice, the way is open for developing apomictic cultivars of other cereals (Partners Magazine Winter 2006). More recently, Ravi et al. (2008) demonstrated that mutation of the *Arabidopsis* gene *DYAD/SWITCH1* (*SWI1*), a regulator of meiotic chromosome organization, produces a switch from reductional meiosis to a mitotic division of megaspore mother cells; thus, the alteration of a single gene in a sexual plant, whose molecular identity is known, can bring functional apomeiosis: a major component of apomixis. Moreover, d'Erfurth et al. (2009) isolated and characterized a novel gene (*OSD1*) involved in controlling entry into the second meiotic division. In *osd1* mutants, both pollen and egg cells are unreduced. These mutants do not show any somatic developmental defects and, when selfed, produce tetraploid (84%) and triploid (16%) progeny (d'Erfurth et al. 2009). As unreduced gametes are induced by the absence of a second meiotic division, recombination occurs in the *osd1* mutant. By combining this mutation with two others that affect key meiotic processes, such as recombination (*Atspo11-1*) and sister chromatid cohesion (*Atrec8*), d'Erfurth et al. (2009) were able to generate a genotype in which meiosis was totally replaced by mitosis. Such plants produced functional diploid gametes that were genetically identical to their mother. Interestingly, as pollen and egg cells are unreduced, tetraploid progeny of *osd1* mutants have a normal endosperm with two maternal and one paternal contribution. If parthenogenetic development of the unreduced egg was triggered, apomictic seed development would occur, as there are no dosage effects in the endosperm. Through the isolation of mutants that shunt meiosis I (*Dyad*) or meiosis II (*OSD1),* apomeiosis, a key element of apomixis, has been isolated. The missing component for the engineering of apomixis is the understanding and isolation of genes controlling parthenogenesis. Genetic characterization of such a trait, combined with the genes triggering apomeiosis, may permit clonal propagation through successive seed generations of crops and revolutionize agriculture.

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References

Abdel-Ghani AH, Parzies HK, Ceccarelli S, Grando S, Geiger HH (2005) Estimation of quantitative genetic parameters for outcrossing-related traits in barley. Crop Sci 45:98–105

Armbruster WS, Mulder CPH, Baldwin BG, Kalisz S, Wessa B, Nute H (2002) Comparative analysis of late floral development and mating-system evolution in tribe Collinsieae (Scrophulariceae S.L.). Am J Bot 89:37–49

Aron Y, Czosnek H, Gazit S, Degani C (1998) Polyembryony in mango (*Mangifera indica* L.) is controlled by a single dominant gene. HortSci 33:1241–1242

Arumuganathan K, Earle ED (1991) Nuclear DNA content of some important plant species. Plant Mol Biol Report 9:208–218

Barone A, Chiusano ML, Ercolano MR, Giuliano G, Grandillo S, Frusciante L (2008) Structural and functional genomics of tomato. Int J Plant Genome 2008:820274

Barrett SCH, Eckert C (1990) Variation and evolution of mating systems in seed plants. In: Kawano S (ed) Biological approaches and evolutionary trends in plants. Academic Press. Harcourt Brace Jovanovich, Publishers, New York, pp 230–254

Barringer BC (2007) Polyploidy and self-fertilization in flowering plants. Am J Bot 94:1527–1533

Baudry E, Kerdelhuè C, Innan H, Stephan W (2001) Species and recombination effects on DNA variability in the tomato genus. Genetics 158:1725–1735

Bennett MD, Leitch IJ (1995) Nuclear DNA amounts in angiosperms. Ann Bot 76:113–176

Bennett MD, Leitch IJ (1997) Nuclear DNA amounts in angiosperms—583 new estimates. Ann Bot 80:169–196

Bennett MD, Leitch IJ (2005) Plant DNA C-values database (release 4.0). http://www.rbgkew.org.uk/cval/homepage.html

Bennett MD, Bhandol P, Leitch IJ (2000) Nuclear DNA amount in angiosperm and their modern uses—897 new estimates. Ann Bot 86:859–909

Bernacchi D, Tanksley SD (1997) An interspecific backcross of *Lycopersicon esculentum* × *L.* hirsutum: linkage analysis and a QTL study of sexual compatibility factors and floral traits. Genetics 147:861–877

Boggs NA, Nasrallah JB, Nasrallah ME (2009) Independent S-locus mutations caused by self-fertility in *Arabidopsis thaliana*. PLoS Genet 5(3):e1000426. doi:10.1371/journal.pgen.1000426

Bomblies K, Weigel D (2007) Arabidopsis—a model genus for speciation. Curr Opin Genet Dev 17:1–5

Boutilier K, Offringa R, Sharma VK, Kieft H, Ouellet T, Zhang L, Hattori J, Liu CM, van Lammeren AA, Miki BL, Custers JB, van Lookeren CMM (2002) Ectopic expression of BABY BOOM triggers a conversion from vegetative to embryonic growth. Plant Cell 14:1737–1749

Bradshaw HD Jr, Schemske DW (2003) Allele substitution at a flower color locus produces a pollinator shift in monkey flowers. Nature 426:176–178

Bradshaw HD Jr, Wilbert SM, Otto KG, Schemske DW (1995) Genetic mapping of floral traits associated with reproductive isolation in monkeyflowers (*Mimulus*). Nature 376:762–765

Bradshaw HD Jr, Otto KG, Frewen BE, MvKay JK, Schemske DW (1998) Quantitative trait loci affecting differences in floral morphology between two species of monkey flower (*Mimulus*). Genetics 149:367–382

Campbell CS, Quinn JA, Cheplik GP, Bell TJ (1983) Cleistogamy in grasses. Ann Rev Ecol Syst 14:411–441

Catanach A, Erasmuson SK, Podivinsky E, Jordan BR, Bicknell R (2006) Deletion mapping of genetic regions associated with apomixis in *Hieracium*. Proc Natl Acad Sci USA 103:18650–18655

Cervigni GDL, Paniego N, Pession S, Selva JP, Diaz M, Spangenberg G, Echenique V (2008) Gene expression in diplosporous and sexual *Eragrostis curvula* genotypes with differing ploidy levels. Plant Mol Biol 67:11–23

Chen K, Tanksley SD (2004) High-resolution mapping and functional analysis of *se2.1*: a major stigma exertion quantitative trait locus associated with the evolution from allogamy to autogamy in the genus *Lycopersicon*. Genetics 168:1563–1573

Chen K, Cong B, Wing R, Vrebalov J, Tanksley SD (2007) Changes in regulation of a transcription factor lead to autogamy in cultivated tomatoes. Science 318:643–645

Conner JA, Goel S, Gunawan G, Cordonnier-Pratt M, Johnson VE, Liang C, Wang H, Pratt LH, Mullet JE, DeBarry J, Yang L, Bennetzen JL, Klein PE, Ozias-Akins P (2008) Sequence analysis of bacterial artificial chromosome clones from the apospory-specific genomic region of *Pennisetum* and *Cenchrus*. Plant Physiol 147:1396–1411

Cruden RW (2000) Pollen grains: why so many? Plant Syst Evol 222:143–165

d'Erfurth I, Jolivet S, Froger N, Catrice O, Novatchkova M, Mercier R (2009) Turning meiosis into mitosis. PLoS Biol 7:e1000124. doi:10.1371/journal.pbio.1000124

Doust AN, Kellogg EA, Devos KM, Bennetzen JL (2009) Foxtail millet: a sequence-driven grass model system. Plant Physiol 149:137–141

Dudley LS, Mazer SJ, Galusky P (2007) The joint evolution of mating system, floral traits and life history in *Clarkia* (Onagraceae): genetic constraints vs independent evolution. J Evol Biol 20:2200–2218

Dvořák J, Luo M, Yang Z (1998) Restriction fragment length polymorphism and divergence in the genomic regions of high and low recombination in self-fertilizing and cross-fertilizing *Aegilops* species. Genetics 148:423–434

Ebina M, Nakagawa H, Yamamoto T, Araya H, Tsuruta S et al (2005) Co-segregation of AFLP and RAPD markers to apospory in guineagrass (*Panicum maximum* Jacq.). Grassland Sci 51:71–78

Fishman L, Kelly AJ, Willis JH (2002) Minor quantitative trait loci underlie floral traits associated with mating system divergence in *Mimulus*. Evolution 56:2138–2155

Fulton TM, Beck-Bunn T, Emmatty D, Eshed Y, Lopez J, Petiard V, Uhling J, Zamir D, Tanksley SD (1997) QTL analysis of an advanced backcross of *Lycopersicon peruvianum* to the cultivated tomato and comparisons with QTLs found in other wild species. Theor Appl Genet 95:881–894

Ganko EW, Clarke TH, Saunders A, Morgan A, Phillips J, Schmutz J, Lindquist EA, Barry K, Fishman L, Rokhsar D, Willis J, Vision TJ (2009) The *Mimulus guttatus* genome: a resource for comparative and evolutionary genomic studies in plants. Plant and Animal Genomes XVII Conference. 10–14 January 2009, San Diego, CA, p 208

Garcia R, Asins MJ, Forner J, Carbonell EA (1999) Genetic analysis of apomixis in *Citrus* and *Poncirus* by molecular markers. Theor Appl Genet 99:511–518

Georgiady MS, Whitkus RW, Lord EM (2002) Genetic analysis of traits distinguishing outcrossing and self-pollinating forms of current tomato, *Lycopersicum pimpinellifolium* (Jusl.) Mill. Genetics 161:333–344

GI A (2000) Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*. Nature 408:796–815

Goel S, Chen ZB, Conner JA, Akiyama Y, Hanna WW, Ozias-Akins P (2003) Delineation by fluorescence in situ hybridization of a single hemizygous chromosomal region associated with aposporous embryo sac formation in *Pennisetum squamulatum* and *Cenchrus ciliaris*. Genetics 163:1069–1082

Goodwillie C, Ritland C, Ritland K (2006) The genetic basis of floral traits associated with mating system evolution in *Leptosiphon* (Polemoniaceae): an analysis of quantitative trait loci. Evolution 60:491–504

Goodwillie C, Sargent RD, Eckert CG, Elle E, Geber MA, Johnston MO, Kalisz S, Moeller DA, Ree RH, Vallejo-Marin M, Winn AA (2009) Correlated evolution of mating system and floral display traits in flowering plants and its implications for the distribution of mating system variation. New Phytol 185:311–321

Graham EB, Shannon SM, Petersen JP, Chetelat RT (2003) A self-compatible population of *Lycopersicon peruvianum* collected from Northern Chile. CM Rick Tomato Genet Res Center 53:22–24

Grillo MA, Li C, Fowlkes AM, Briggeman TM, Zhou A, Schemske DW, Sang T (2009) Genetic architecture for the adaptive origin of annual wild rice, *Oryza nivara*. Evolution 63:870–883

Grimanelli D, Leblanc O, Perotti E, Grossniklaus U (2001) Developmental genetics of gametophytic apomixis. Trends Genet 17:597–604

Haudry A, Cenci A, Guilhaumon C, Paux E, Poirier S, Santoni S, David J, Glémin S (2008) Mating system and recombination affect molecular evolution in four *Triticeae* species. Genet Res Camb 90:97–109

Hay A, Tsiantis M (2006) The genetic basis for differences in leaf form between *Arabidopsis thaliana* and its wild relative *Cardamine hirsuta*. Nat Genet 38:942–947

Hodges SA, Whittfall JB, Fulton M, Yang JY (2002) Genetics of floral traits influencing reproductive isolation between *Aquilegia formosa* and *Aquilegia pubescens*. Am Nat 159:S51–S60

Husband BC, Ozimec B, Martin SL, Pollock L (2008) Mating consequences of polyploidy evolution in flowering plants: current trends and insights from synthetic polyploids. Int J Plant Sci 169:195–206

JGI (2008) Status of the *Arabidopsis lyrata* whole genome sequencing project. http://genome.jgi-psf.org/Araly1.info.html

Johnston JS, Pepper AE, Hall AE, Chen ZJ, Hodnett G, Drabek J, Lopez R, Price HJ (2005) Evolution of genome size in Brassicaceae. Ann Bot 95:229–235

Kachroo A, Nasrallah ME, Nasrallah JB (2002) Self-incompatibility in the Brassicaceae: receptor-ligand signaling and cell to cell communication. Plant Cell 14(Suppl):S227–S238

Kantama L, Sharbel TF, Schranz ME, Mitchell-Olds T, de Vries S, de Jong H (2007) Diploid apomicts of the *Boechera holboellii* complex display large-scale chromosome substitutions and aberrant chromosomes. Proc Natl Acad Sci USA 104:14026–14031

Koch M, Haubold B, Mitchell-Olds T (2000) Comparative evolutionary analysis of chalcane synthase and alcohol dehydrogenase loci in *Arabidopsis*, *Arabis*, and related genera (Brassicaceae). Mol Biol Evol 17:1483–1498

Koch M, Haubold B, Mitchell-Olds T (2001) Molecular systematics of the Brassicaceae: evidence from coding plastidic *matK* and nuclear *Chs* sequences. Am J Bot 88:534–544

Krishnan P, Sapra VT, Soliman KM, Zipf A (2001) FISH mapping of the 5S and 18S–28F rDNA loci in different species of Glycine. J Hered 92:295–300

Kuriakose G, Sinu PA, Shivanna KR (2009) Domestication of cardamom (*Elettaria cardamomum*) in Western Ghats, India: divergence in reproductive traits and a shift in major pollinators. Ann Appl Biol 103:727–733

Kusaba M, Dwyer K, Hendershot J, Vrebalov J, Nasrallah JB, Nasrallah ME (2001) Self-incompatibility in the genus *Arabidopsis*: characterization of the S locus in the outcrossing *A.* lyrata and its autogamous relative *A. thaliana*. Plant Cell 13:627–643

Laspina NV, Vega T, Seijo JG, González AM, Martelotto LG, Stein J, Podio M, Ortiz JPA, Echenique VC, Quarin CL, Pession SC (2008) Gene expression analysis at the onset of apomixis in *Papsalum notatum*. Plant Mol Biol 67:615–628

Lin J, Ritland K (1997) Quantitative trait loci differentiating the outbreeding *Mimulus guttatus* from the inbreeding *M. platycalyx*. Genetics 146:1115–1121

Liu F, Zhang L, Charlesworth D (1998) Genetic diversity in *Leavenworthia* populations with different inbreeding levels. Proc R Soc Lond B Biol Sci 265:293–301

Liu F, Charlesworth D, Kreitman (1999) The effect of mating system differences on nucleotide diversity at the phosphoglucose isomerase locus in the plant genus *Leavenworthia*. Genetics 151:343–357

Lord EM (1981) Cleistogamy: a tool for the study of floral morphogenesis, function and evolution. Bot Rev 47:421–449

Mangelsdorf PC (1966) Genetic potentials for increasing yields of food crops and animals. Proc Natl Acad Sci USA 55:370–375

Matzk F, Prodanovic S, Baumlein H, Schubert I (2005) The inheritance of apomixis in *Poa pratensis* confirms a five locus model with differences in gene expressivity and penetrance. Plant Cell 17:13–24

Miyata M, Yamamoto T, Komori T, Nitta N (2007) Marker-assisted selection and evaluation of the QTL for stigma exertion under japonica rice genetic background. Theor Appl Genet 114:539–548

Morinaga S, Nagano AJ, Miyazaki S, Kubo M, Demura T, Fukuda H, Sakai S, Hasebe M (2008) Ecogenomics of cleistogamous and chasmogamous flowering: genome-wide expression patterns from cross-species microarray analysis in *Cardamin kokaiensis* (Brassicaceae). J Ecol 96:1086–1097

Moscone EA, Baranyi M, Ebert I, Greilhuber J, Ehrendorfer F, Hunziker AT (2003) Analysis of nuclear DNA content in *Capsicum* (Solanaceae) by flow cytometry and feulgen densitometry. Ann Bot 92:21–29

Moyle LC (2008) Ecological and evolutionary genomics in the wild tomatoes (Solanum sect. Lycopersicon). Evolution 62:2995–3013

Mueller LA, Lankhorst RK, Tanksley SD, Giovannoi JJ, White R, Vrebalov J, Fei Z et al (2009) A snapshot of the emerging tomato genome sequence. Plant Genome 2:78–92

Nasrallah ME, Yogeeswaran K, Snyder S, Nasarallah JB (2000) *Arabidopsis* species hybrids in the study of species differences and evolution of amphiploidy in plants. Plant Physiol 124:1605–1614

Nasrallah ME, Liu P, Sherman-Broyles S, Boggs NA, Nasrallah JB (2004) Natural variation in expression of self-incompatibility in *Arabidopsis thaliana*: implications for the evolution of selfing. Proc Natl Acad Sci USA 101:16070–16074

Noyes RD (2006) Apomixis via recombination of genome regions for apomeiosis (diplospory) and parthenogenesis in *Erigeron* (daisy fleabane, Asteraceae). Sex Plant Reprod 19:7–18

Oka H, Morishima H (1967) Variations in the breeding systems of a wild rice, *Oryza perennis*. Evolution 21:249–258

Oka H, Morishima H (1997) Wild and cultivated rice. In: Matuo T, Hoshikawa K (eds) Science of the rice plant. Genetics, vol 3. Food and Agriculture Policy Research Center, Tokyo, pp 88–111

Ortiz JPA, Pessino SC, Leblanc O, Hayward MD, Quarin CL (1997) Genetic fingerprinting for determining the mode of reproduction in *Paspalum notatum*, a subtropical apomictic forage grass. Theor Appl Genet 95:850–856

Partners Magazine Winter (2006) The hybrid vigour of sexless rice. ISBN 1031-1009

Paterson AH, Bowers JE, Bruggmann R, Dubchak I, Grimwood J, Gundlach H, Haberer G, Hellsten U et al (2009) The *Sorghum bicolor* genome and the diversification of grasses. Nature 457:551–556

Ravi M, Marimuthu MPA, Siddiq I (2008) Gamete formation without meiosis in *Arabidopsis*. Nature 451:1121–1124

Rick CM (1984) Evolution of mating systems: evidence from allozyme variation. In: Chopra VL, Joshi BC, Sharma RP, Bansal HC (eds) Genetics: new frontiers. XV International Congress of Genetics. Applied genetics, vol IV. Boker, Epping, pp 215–221

Rick CM (1987) Genetic resources in *Lycopersicon*. In: Nevins DJ, Jones RA (eds) Plant biology. Tomato biotechnology, vol 4. Alan R. Liss Inc., New York, pp 17–26

Rick CM, Kesciki E, Fobes JF, Holle M (1976) Genetic and biosystematic studies on two new sibling species of *Lycopsericon* from Interandean Perú. Theor Appl Genet 47:55–68

Rick CM, Holle M, Thorp RW (1978) Rates of cross pollination in *Lycopersicon pimpinellifolium*: impact of genetic variation in floral characters. Plant Syst Evol 129:31–44

Roche D, Conner JA, Budiman MA, Frisch D, Wing R, Hanna WW, Ozias-Akins P (2002) Construction of BAC libraries from two apomictic grasses to study the microcolinearity of their apospory-specific genomic regions. Theor Appl Genet 104:804–812

Roselius K, Stephan W, Städler T (2005) The relationship of nucleotide polymorphism, recombination rate and selection in wild tomato species. Genetics 171:753–763

Savidan Y, Carman JG, Dresselhaus JG (eds) (2001) The flowering of apomixis: from mechanisms to genetic engineering. CIMMYT, IRD, European Commission DG VI (FAIR), Mexico, D.F.

Savolainen O, Langley CH, Lazzaro BP, Fréville H (2000) Contrasting patterns of nucleotide polymorphism at the alcohol dehydrogenase locus in the outcrossing *Arabidopsis lyrata* and the selfing *A. thaliana*. Mol Biol Evol 17:645–655

Schemske DW, Bradshaw HD (1999) Pollinator preference and the evolution of floral traits in monkey flowers (*Mimulus*). Proc Natl Acad Sci USA 96:11910–11915

Schemske DA, Goodwillie C (1996) Morphological and reproductive characteristics of *Linanthus jepsonii* (Polemoniaceae), a newly described, geographically restricted species from North Carolina. Madrono 43:453–463

Schnable PS, Ware D, Fulton RS, Stein JC, Wei F, Pasternak S, Minx P, Reily AD, Courtney L, Kruchowski SS et al (2009) The B73 maize genome: complexity, diversity, and dynamics. Science 326:1112–1115

Schranz ME, Kantama L, de Jong H, Mitchell-Olds T (2006) Asexual reproduction in a close relative of *Arabidopsis*: a genetic investigation of apomixis in *Boechera* (*Brassicaceae*). New Phytol 171:425–438

Seki M, Navusaka M, Ishida J, Nanjo T, Fujita M, Oono Y, Kamiya A, Nakajima M, Enju A, Sakurai T, Satou M, Akiyama K, Taji T, Yamaguchi-Shinozaki K, Carninci P, Kawai J, Hayashizaki Y, Shinozaki K (2002) Monitoring the expression profiles of 7000 *Arabidopsis* genes under drought, cold, and high salinity stresses using a full-length cDNA microarray. Plant J 31:279–292

Sharbel TF, Voigt ML, Corral JM, Theil T, Varshney A, Kumlehn J, Vogel H, Rotter B (2009) Molecular signatures of apomictic and sexual ovules in the *Boechera holboellii* complex. Plant J 58:870–882

Soost RW (1958) Progenies from sesquidiploid F_1 hybrid of *Lycopersicon esculentum* and *L. peruvianum*. J Hered 49:208–213

SP IRG (2005) The map-based sequence of the rice genome. Nature 436:793–800

Stebbins GL (1970) Adaptive radiation of reproductive characteristics in angiosperms. I. Pollination mechanisms. Annu Rev Ecol Syst 1:307–326

Stephan W, Langley CH (1998) DNA polymorphism in *Lycopersicon* and crossing-over per physical length. Genetics 150:1585–1593

Takeoka Y, Shimizu M, Wada T (1993) Panicles. In: Matuo T, Hoshikawa K (eds) Science of the rice plant. Morphology, vol 1. Food and Agriculture Policy Research Center, Tokyo, pp 295–338

Tang C, Toomajian C, Sherman-Broyles S, Plagnol V, Guo Y-L, Hu TT, Clark RM, Nasrallah JB, Weigel D, Nordborg M (2007) The evolution of selfing in *Arabidopsis thaliana*. Science 317:1070–1072

Tanksley S, Fulton TM (2007) Dissecting quantitative trait variation—examples from the tomato. Euphytica 154:365–370

Tatum CT, Svetlana S, Biradar DP, Rayburn AL, Korban SS (2005) Variation in nuclear DNA content in *Malus* species and cultivated species. Genome 48:924–930

Tucker MR, Araujo AG, Paech NA, Hecht V, Schmidt EDL, Rossell J, de Vries SC, Koltunow AMG (2003) Sexual and apomictic reproduction in *Hieracium* subgenus *Pilosella* are closely interrelated developmental pathways. Plant Cell 15:1524–1537

Uga Y, Fukuta Y, Cai HW, Iwata H, Ohsawa R, Morishima H, Fujimura T (2003) Mapping QTL influencing rice floral morphology using recombinant inbred lines derived from a cross between *Oryza sativa* L. and *O. rufipogon* Griff. Theor Appl Genet 107:218–226

Valejo-Marín M, Barrett SCH (2009) Modification of flower architecture during early stages in the evolution of self-fertilization. Ann Bot 103:951–962

Virmani SS (1994) Outcrossing mechanisms and hybrid seed production practices in rice. In: SS Virmani (ed) Heterosis and hybrid rice breeding. Springer, Berlin, pp 79–109. ISSN 0341-5376

Virmani SS, Athwal DS (1973) Genetic variability in floral characteristics influencing outcrossing in *Oryza sativa* L. Crop Sci 13:66–67

Wakana A, Uemoto S (1987) Adventive embryogenesis in *Citrus.* I. The occurrence of adventive embryos without pollination or fertilization. Am J Bot 74:517–530

Wijnker E, de Jong H (2008) Managing meiotic recombination in plant breeding. Trends Plant Sci 13:640–646

Windsor AJ, Schranz ME, Formanova N, Gebauer-Jung S, Bishop JG, Schnabelrauch D, Kroymann J, Mitchell-Olds T (2006) Partial shotgun sequencing of the *Boechera stricta* genome reveals extensive microsynteny and promoter conservation with *Arabidopsis*. Plant Physiol 140:1169–1182

Wright SI, Lauga B, Charlesworth D (2002) Rates and patterns of molecular evolution in inbred and outbred *Arabidopsis*. Mol Biol Evol 19:1407–1420

Wu CA, Lowry DB, Cooley AM, Lee YW, Willis JH (2007) *Mimulus* is an emerging model system for the integration of ecological and genomic studies. Heredity 100:220–230

Wyatt R (1988) Phylogenetic aspects of the evolution of self-pollination. In: Gottleib LD, Jain SK (eds) Plant evolutionary biology. Chapman and Hall, London, pp 109–131

Zonneveld BJM, Leitch IJ, Bennett MD (2005) First nuclear DNA amounts in more than 300 angiosperms. Ann Bot 96:229–244