REVIEW ARTICLE

Genetics of dioecy and causal sex chromosomes in plants

SUSHIL KUMAR[1,2]*, RENU KUMARI[1,2] and VISHAKHA SHARMA[1]

[1]*SKA Institution of Research, Education and Development (SKAIRED), 4/11 SarvPriya Vihar, New Delhi 110 016, India*
[2]*National Institute of Plant Genome Research, Aruna Asaf Ali Marg, New Delhi 110 067, India*

Abstract

Dioecy (separate male and female individuals) ensures outcrossing and is more prevalent in animals than in plants. Although it is common in bryophytes and gymnosperms, only 5% of angiosperms are dioecious. In dioecious higher plants, flowers borne on male and female individuals are, respectively deficient in functional gynoecium and androecium. Dioecy is inherited via three sex chromosome systems: XX/XY, XX/X0 and WZ/ZZ, such that XX or WZ is female and XY, X0 or ZZ are males. The XX/XY system generates the rarer XX/X0 and WZ/ZZ systems. An autosome pair begets XY chromosomes. A recessive loss-of-androecium mutation (*ana*) creates X chromosome and a dominant gynoecium-suppressing (*GYS*) mutation creates Y chromosome. The *ana/ANA* and *gys*/*GYS* loci are in the sex-determining region (SDR) of the XY pair. Accumulation of inversions, deleterious mutations and repeat elements, especially transposons, in the SDR of Y suppresses recombination between X and Y in SDR, making Y labile and increasingly degenerate and heteromorphic from X. Continued recombination between X and Y in their pseudoautosomal region located at the ends of chromosomal arms allows survival of the degenerated Y and of the species. Dioecy is presumably a component of the evolutionary cycle for the origin of new species. Inbred hermaphrodite species assume dioecy. Later they suffer degenerate-Y-led population regression. Cross-hybridization between such extinguishing species and heterologous species, followed by genome duplication of segregants from hybrids, give rise to new species.

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Introduction

Species of living organisms survive, grow and multiply by adapting to different kinds of environmental changes that their respective habitats undergo, including diurnal and seasonal changes and those caused by universal physical disturbances. Various species are able to survive and evolve under the changing environments on account of the genetic variability present in the genome of their populations. Mutation and recombination are the biological (genetical) mechanisms that generate genetic variability.

The new genetic variability in the populations of each species arises in the form of mutations. There are three ways by which genetic mutations are induced. Point (frame shift and base substitution) mutations arise by errors made in the genome replication process. Genomic DNA is damaged by a variety of natural agents, including heat, ultraviolet light and ionizing radiations. It is also prone to a variety of damage at cytosines where variation in epigenetic methylation occurs. Addition mutations are induced by insertion of transposable elements in the genomic DNA. Mutations also occur by rearrangements in the genome (chromosomes). These include chromosomal fusions, deletions, translocations and inversions. The variation thus made available as mutant alleles at various loci in genome is amplified by the recombination mechanisms.

Amplification of the mutation-induced genetic variability by recombination

Species with autonomous reproductive system exist as prokaryotes and eukaryotes (figure 1). Meiosis is the principal mechanism for genetic recombination. This is possessed by eukaryotes but not by prokaryotes. The life cycle in eukaryotic species is divisible into a gametophytic (haploid) phase and a zygotic/sporophytic (diploid) phase. The process of meiosis in the sporophyte produces male and female gametophytes. The fusion product of the gametophytes of alternate sex is a zygote that grows into sporophyte. The diploid sporophyte has each chromosome in two copies, since it receives a whole set of chromosomes from each

*For correspondence. E-mail: sushil2000_01@yahoo.co.in.

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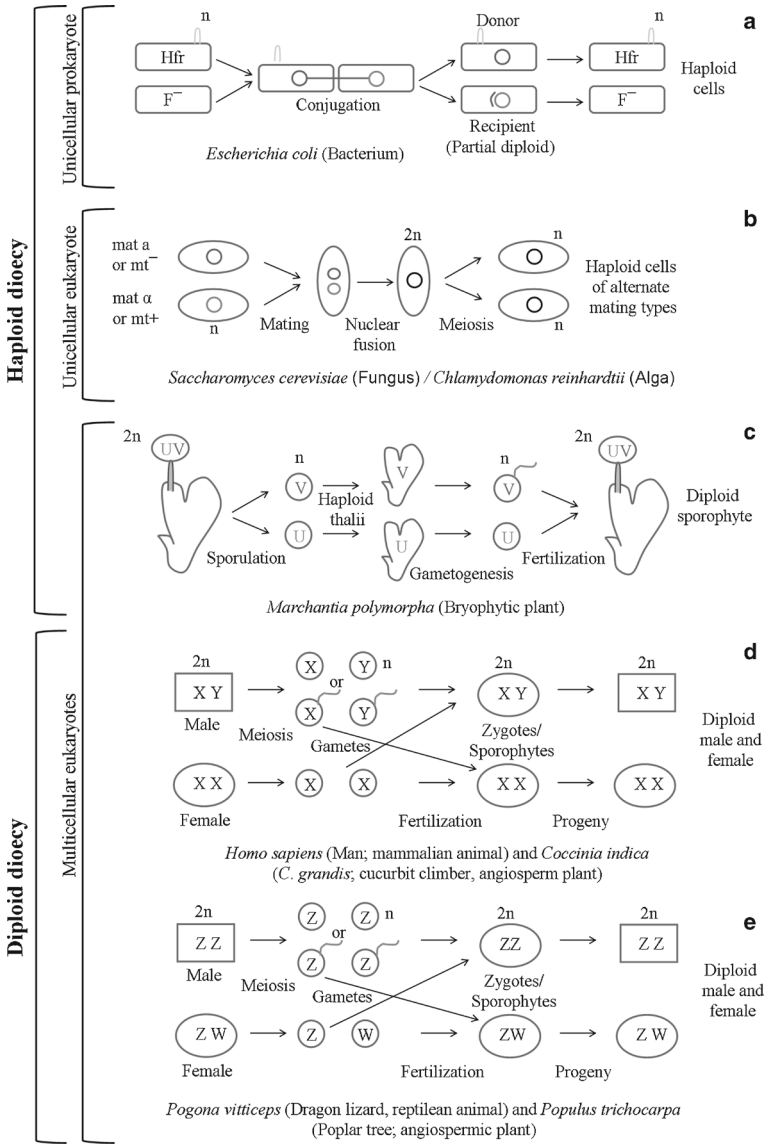

Figure 1. Examples of sexual dimorphism (dioecy) in haploid prokaryotes (bacteria), unicellular (fungi and algae) and multicellular eukaryotes (bryophytes), and diploid multicellular eukaryotes (vertebrate animals and higher plants). (a) Haploid dioecy in bacteria (Bachmann 1983); an *Escherichia coli* Hfr male cell in which the fertility factor (plasmid) F is integrated into the chromosome and F encoded pili are formed is shown mating with F^- female bacterium that lacks pili. In the mating process there is horizontal transfer of bacterial genomic DNA from Hfr to F^-. Variant F^- are formed because of the genetic recombination between the received and resident DNA sequences in F^-. (b) Haploid dioecy in unicellular eukaryotes such as the fungus *Saccharomyces cerevisiae* (Fraser and Heitman 2004; Goddard *et al.* 2005) and alga *Chlamydomonas reinhardtii* (Ferris *et al.* 2002; Kaltz and Bell 2002). Isogamous haploid cells of genetically different mating types associate such that their nuclei fuse to form diploid sporophyte which subsequently undergoes meiosis to produce haploid cells of the two mating types. The meiosis in sporophyte amplifies the allelic variation present in the genomes of the mated cells. (c) Haploid dioecy in bryophytes (liverworts and mosses exemplified by *Marchantia polymorpha* Yamato *et al*. 2007). The nuclei of cells in the haploid thalli possess a set of autosomes and a sex chromosomes. Until the reproduction has occurred female thalli are indistinguishable from male thalli. The male haploid thalli cells have V as the sex chromosomes and the sex chromosome is U in the cells of female thalli. The female gametes formed on female thallus get fertilized by sperms formed on male thallus and as a result sporophyte forms on the thallus of female. The sporophyte undergoes meiosis to produce V and U type of spores that form male and female thalli, respectively. The process of meiosis as in all eukaryotes amplifies the genetic variation. (d) Diploid dioecy in mammalian animals and angiospermic plants, exemplified, respectively by *Homo sapiens* (man; Graves 2006) and *Coccinia indica* (cucurbitaceous plant; Sousa *et al.* 2013). In these systems the males are heterogametic as they carry XY sex chromosomes besides the autosomes. Homogametic females carry XX chromosomes and autosomes. Males form meiotically two kinds of sperms, half carry X and the other half Y. The gametes formed by females are of only one kind, they carry X chromosome. Fertilization results in progenies that comprise of XY males and XX females. (e) Diploid dioecy in the vertebrate reptile *Pagona vitticeps* (dragon lizard; Ezaz *et al.* 2009a, b) animal and poplar tree plant species *Populus trichocarpa* (Hou *et al.* 2009). In these organisms the heterogametic sex is female possessing ZW sex chromosomes and autosomes. The males are homogametic by possessing ZZ sex chromosomes plus autosomes. The females meiotically produce gametes that carry Z or W sex chromosome plus a set of autosomes. Only one kind or Z type gametes are formed by the males. Fertilization results in ZZ males and ZW females.

of male and female gametes. Genetic recombination occurs during the meiotic division during reproduction via crossingover between pairs of homologous chromosomes and by independent assortment of homologous chromosomes. In the process, gametes receive new gene combinations. Based on local homologies between chromosomes, recombination also occurs during mitotic cell divisions in the growing sporophyte. However, frequency of such recombination is much lower than that occurs during meiotic cell division. Meiotic recombination, in addition to generating novel allelic combinations, also contribute to fitness of the species populations by elimination of deleterious mutations. For the recombination to be effective in releasing variability, the reproductive system in the species has to be such, as to allow outcrossing (fertilization of female gametes of an individual plant by male gametes formed on genetically distinct individuals or amphimixis) and avoid selfing (fertilization of female gametes by male gametes formed on the same individual or genetically similar individuals or automixis).

Reproductive systems that favour amplification of genetic variability

The mating systems in species of various phylogenetic groups are of two basic types (Diggle *et al*. 2011; Barrett and Hough 2012): hermaphroditism (in such systems the male organ(s) and female organ(s) are present on the same individual) and dioecism (here the maleness and femaleness are present in separate individuals). Hermaphroditism and dioecism, respectively promote automixis and amphimixis. Whereas hermaphroditism is a common feature among plants, and nonarthropod invertebrate animals, dioecism is more or less universal among the phylogenetic groups. Dioecy is of two kinds: haploid and diploid. Haploid dioecy occurs in bacteria (Lederberg and Tatum 1946; Bachmann 1983), unicellular eukaryotes (Birdsell and Wills 1996; Kaltz and Bell 2002; Ferris *et al*. 2002; Fraser and Heitman 2004) and in bryophytes that are multicellular eukaryotes (Yamato *et al*. 2007; McDaniel *et al*. 2012). In the prokaryotic unicellular bacteria, the maleness is imparted by the presence in cells of episomes such as the fertility factor F. In the F^+ bacteria, integration of F into the bacterial DNA (genome) allows this Hfr to mate with F^- bacterium and donate a copy of its genome to the recipient F^- female mating with it. When Hfr and F^- cells have different genotypes, recombination between the DNA transferred from Hfr and resident F^- DNA releases variability. There is an analogous mating mechanism, devoid of gamete dimorphism, in unicellular algae such as *Chlamydomonas reinhardtii*, fungi exemplified by *Saccharomyces cerevisiae* and flagellate animals like *Paramecium*. In such organisms, mating occurs between genetically determined mating types. Association between haploid cells of distinct mating types results in fusion of their nuclei. The diploid zygote/sporophyte subsequently undergoes meiotic division to produce cells of two mating types. The progeny from such amphimixis matings will have new genetic variants. In the dioecious bryophytic species (liverworts and mosses), the multicellular haploid male and female gametophyes comprise the major part of life cycle. Sporophyte is produced when a sessile egg born on female gametophyte is fertilized by a motile sperm formed in male gametophyte. The zygote produces a sporophyte on the female gametophyte. Meiosis in sporophyte produces male and female spores that grow into multicellular gametophytes (thalli) of the respective sex. The amphimictic matings release new variability. Pteridophytes are hermaphrodites and their chromosomes are autosomal. They are highly polyploidized. For example *Ophioglossum reticulatum* has diploid chromosome number of 1260. The polyploid nature presumably provides escape from dioecy in pteridophytes (http://floranorthamerica.org/volume/V01/Chapter12; Gorelick 2005). Dioecy in animals (insects and vertebrates) (Matsubara *et al*. 2006; Graves and Peichel 2010; Kaiser and Bachtrog 2010) and gymnospermic and angiospermic seed-producing plants (Ming *et al*. 2011; Barrett and Hough 2012; Charlesworth 2012) means that diploid male and female individuals comprise the dominant phase of life cycle. Fertilization of female gamete or sessile egg cell by sperm (motile in animals and brought in contact by pollen tube in plants), respectively produced via meiosis in the reproductive organs of female and male, forms zygote that grows into either a male or a female, because of the genetic determination of sex. Here the chances of automixing are low. The life cycles of several kinds of dioecious species are shown in figure 1.

Hermaphroditism is best exemplified by angiospermic plants (Diggle *et al*. 2011). The hermaphrodite plants are of two types: (i) those that produce perfect flowers possessing both male stamens and female carpels; and (ii) monoecious in which male flowers (stamen bearing) and female flowers (carpel bearing) are formed on the same plant on common inflorescences or distinct inflorescences. Although hermaphroditism favours automixis, there are special genetic mechanisms in hermaphrodite species to promote amphimixis. Some of these are listed in the table 1.

Frequency and spectrum of dioecious species in plant kingdom

Table 2 gives estimates of dioecy in certain phylogenetic groups of multicellular eukaryotic land plants. About 9% of the approximate 319,000 number of species have been observed to be dioecious. There is preponderance of dioecious species among bryophytes, 68% of liverworts and 57% of mosses are dioecious. None of the hornworts, lycophytes and monilophytes is dioecious. Among 1021 gymnosperm species, the frequency of dioecious species is about 36%. All cycads and gnetales, and *Ginkgo biloba* (the genus *Ginkgo* has only one species) are dioecious. In angiosperms about 5% species are dioecious in 75% of the families (or

Table 1. Reproduction systems that promote outbreeding (amphimixis) in plants.

	Name of mating system	Features	Example	Reference
1	Perfect flower sexually monomorphic hermaphroditism[a]	Prevention of self fertilization due to genetic self incompatibility (SI; gametic and sporophytic)	*Brassica rapa* (Brassicaceae)	Shiba *et al*. (2002)
2	As above	Blockage of selfing on account of style being shorter or longer than stamens (heterostyly)	*Primula sinensis* (Primulaceae)	Mather (1950)
3	As above	Avoidance of selfing via temporal asynchrony in the maturation times of anthers and stigma (dichogamy)	*Butomus umbellatus* (Butomaceae)	Bhardwaj and Eckert (2001)
4	Monoecious sexually monomorphic hermaphroditism	Dichogamy between separate male and female flowers/inflorescences borne on the same plant[b]	*Zea mays* (Poaceae)	Tanurdzic and Banks (2004)
5	Andromonecious hermaphroditism	Population has individuals bearing both female sterile and hermaphrodite flowers[b]	*Capparis spinosa* (Capparaceae)	Zhang and Tan (2008)
6	Gynomonecious hermaphroditism	Individuals in the population have both male sterile and hermaphrodite flowers[b]	*Planchonella australis* (Sapotaceae)	Mendez and Munzinger (2010)
7	Androdioecious sexual polymorphism	Out-crossing promoted by the presence in the population of male flower bearing and perfect flower bearing individuals[c]	*Schizopepon bryoniaefolius* (Cucurbitaceae)	Akimoto *et al*. (1999)
8	Gynodioecious sexual polymorphism	Promotion of out-crossing by occurrence of female flower – and perfect flower – bearing plants[c]	*Plantago maritime* (Plantaginaceae)	Nilsson and Agren (2006)
9	Dioecious sexual polymorphism	Flowers formed on individual plants of population are either male or female	*Coccinia indica* (Cucurbitaceae)	Sharma and Chattopadhyay (1991)

[a]Pollen limitation and large population structures may promote outcrossing; [b]a and self incompatibility could also operate in addition to dichogamous monoecy; [c]dichogamy, heterostyly and/or selfincompatibility could be superimposed over each of these two subdioecious systems.

Table 2. Dioecy among multicellular eukaryotic plants.

	Phylogenetic group	Total number of species described	Dioecious species			Known to possess morphological or molecularly polymorphic sex chromosomes[a]	Reference(s)
			Total number	%			
1	Bryophytes (liverworts and mosses)	22,500	13,500	62	8		Wyatt and Anderson (1984); McDaniel *et al.* (2012); Shaw *et al.* (2005)
2	Lycophytes	1,200	0	0	0		Ranker and Haufler (2008); Ming *et al.* (2011)
3	Monilophytes	12,000	0	0	0		Qiu and Palmer (1999)
4	Gymnosperms	1,021	370	36	8		Greilhuber *et al.* (2006); Ming *et al.* (2011)
5	Angiosperms	2,82,000	14,600	5	76		Renner and Ricklef (1995); Dorken and Barrett (2004); Milewicz and Sawicki (2013)
	Total	3,18,721	28,106	8.8	92		

[a]Dioecism in all the dioecious species is related to genetic differences between male and female, at atleast one locus on a pair of chromosomes. However, this polymorphism has been demonstrated in 92 plant species.

more than 200 families). About 7% of 960 angiosperm genera contain atleast some dioecious species. There are only a few angiosperm genera and families in which all the species are dioecious. There are also examples of angiosperm species in which both dioecious and nondioecious plant populations occur. Dioecy is more common in dicotyledonous families than in monocotyledonous families. Salicaceae, Manispermaceae, Myristicaceae, Moraceae, Euphorbiaceae, Urticaceae, Anacardiaceae, Moniniaceae and Cucurbitaceae are the dicotyledonous families richly endowed with dioecy. Dioecy is relatively more common in Pandanaceae, Alismataceae and Triuridaceae among monocotyledonous families. Dioecy occurs in species that have temperate, semitemperate, subtropical and/or tropical distribution. Higher plants of various habits can be placed in the following order with respect to the occurrence of dioecy: trees > herbs > climbers > shrubs (Renner and Ricklef 1995). Dioecy is more common in species that are wind and water pollinated as compared to wind and animal pollinated (Renner and Ricklef 1995). Many families possess both wind pollinated monoecious and dioecious species (Renner and Ricklef 1995). Some families have hermaphroditic monoecious, subdioecious and dioecious species, reflecting pathway of evolution of dioecy (Diggle *et al*. 2011; Ming *et al*. 2011; Barrett and Hough 2012). Dioecy, especially that associated with X and Y chromosomes, is absent or infrequent in species of the families where polyploidy is of common occurrence, such as in subfamilies Triticeae and Panicoideae of family Poaceae.

Dioecy is determined by sex chromosomes

All dioecious species have sex chromosomes, which carry genes that control development of males and females as separate individuals. Autosomes (nonsex chromosomes) contribute to this process fostered by sex chromosomes, via their participation in sex organ developmental pathways (Westergaard 1958; Matsubara *et al*. 2006; Yamato *et al*. 2007; Bergero and Charlesworth 2011; Charlesworth 2012). Sex chromosomes are linkage groups like autosomes, except that they specify inheritance of sex. Unlike in animals, only in a small number of plant species the sex chromosomes are morphologically distinguishable from each other (heteromorphic) and from autosomes. Heteromorphic sex chromosomes are microscopically distinguishable in terms of size, ratio of arms and/or stainability. The nondistinguishable sex chromosomes are called homomorphic. The main sex chromosome systems discovered in plants are listed in table 3 and depicted in figure 1. In the thallic haploid gametophytes of bryophytes, males have a very small V chromosome and females a U chromosome; males do not have U chromosome and females are devoid of V chromosome. The diploid sporophyte has both U and V chromosomes. This sex chromosome system has been demonstrated in eight bryophytes and is typical in the liverwort *Marchantia polymorpha*. In the diploid plants,

Table 3. Sex chromosomes in the diploid dioecious animals and plants where the unisexual male and female individuals have distinctive reproductive organs[a].

Heterogametic sex	Phylogenetic groups		Sex chromosome composition		Reference(s)
	Animal	Plant	Male	Female	
Male	Mammals and birds	Gymnosperms and monocot – and dicot – angiosperms[c]	XY	XX	Charlesworth and Mank (2010); Graves (2006); Graves and Peichel (2010); Renner and Ricklef (1995); Ming *et al.* (2011); Charlesworth (2013)
	Certain reptiles, amphibians, fishes and insects[b]		XY	XX	Ezaz *et al.* (2006, 2009a, b); Matsubara *et al.* (2006); Kaiser and Bachtrog (2010); Bachtrog *et al.* (2011)
Female	As above[b]	Certain dicotyledonous angiosperms[c]	ZZ	WZ	As above

[a]The sex chromosome systems of heterogametic male and female are diagrammatically illustrated in the figure 1; [b]in these groups of organisms, a species, genus or family can have two kinds of populations, those having male XY or female WZ heterogametic sexes. In some of these, the initial trigger of temperature is superimposed over the sex chromosomes in the sex determination process; [c]in a small number of haploid dioecious bryophytes sex system is heterogametic; here, female and male sex chromosomes are, respectively called V and U.

the sex chromosome systems are largely similar to those prevailing in diploid animals. The XX/XY and ZW/ZZ are the two basic sex chromosome systems present in animals and plants. In the XX/XY system, the females are homogametic XX and males are heterogametic XY; Y is the sex determining chromosome in the XX/XY system. In the other system Z is the sex determining chromosome; females are heterogametic ZW and males are homogametic ZZ. Occurrence of sex chromosomes has been demonstrated so far only in 84 higher plant species (table 2); in 57 species in terms of sex chromosome specific DNA markers and in 27 species both molecularly and cytomorphologically. The XX/XY heterogametic system is exemplified by the gymnosperm *Cycas revoluta* and angiosperm *Spinacea oleracea* and the ZW/ZZ system by the gymnosperm *Ginkgo biloba* and angiosperm *Populus trichocarpa.* Table 4 lists all the 92 plant species of 49 genera of 34 families in which sex chromosomes have been located.

Variation in the sex chromosome systems of plants

In plants, the homomorphic sex chromosomes are more common than heteromorphic sex chromosomes. It will be seen from table 4 that among the 92 dioecious species in which the presence of sex chromosomes has been established, only 27 species of 11 genera of eight families possess heteromorphic sex chromosomes. Among these, four are bryophytes of three genera of the same family, five are gymnosperms of three genera of three families and 18 are angiosperms of five genera of four families. Homomorphic sex chromosomes have been observed in 36 species of 22 genera of 16 families of angiosperms. The gymnosperm species *Pinus johannis* has homomorphic sex chromosomes.

The XX/XY sex system has been found to be present in five species of three genera of three families of gymnosperms. It is heteromorphic in four of the five gymnosperm species, except in *P. johannis.* The XX/XY system is known to occur in 46 species of 23 genera of 17 families of angiosperms. Seventeen of these angiosperm species of five genera and four families have the XX/XY system in its heteromorphic form. The WZ/ZZ sex system in heteromorphic form has been reported for the gymnosperm *Ginkgo biloba.* In angiosperms, the heteromorphic form of WZ/ZZ system has not been reported. It exists in its homomorphic form in eight species of four genera of four families of angiosperms.

In the heteromorphic sex chromosome possessing plant species, Y or V chromosome is smaller in size than X or U in the bryophyte *Marchantia polymorpha,* gymnosperm *Cycas revoluta* and angiosperm *Humulus luplus* (and certain other *Humulus* species). However, in this group, preponderantly Y chromosome is of larger size than X chromosome. Examples include the gymnosperm species of *Podocarpus* and angiosperm species of *Cannabis*, *Coccinia*, *Rumex* and *Silene*. The prime example of X/Y heteromorphism is in *Coccinia indica*, where the Y chromosome is 2.06 times larger

Table 4. Characteristics of sex determination in the model and nonmodel examples of eukaryotic multicellular dioecious plant species possessing homomorphic (molecularly distinguishable) or heteromorphic (both morphologically and molecularly distinguishable) sex chromosomes.

	Phylogenetic rank and family	Species	2n Chromosome number (M/F or M : F :: male : female)	Sex chromosomes homomorphic (HOM) or heteromorphic (HET) and if HET which one larger (L) or smaller (S)	Sex chromosome composition		Whether YY (males) or WW (females) viable (yes or no)	Estimated age of sex chromosomes (million years)	Whether dioecy abundant in		Comment(s)	Reference(s)
					Female	Male			Genus (yes/no)	Family (yes/no)		
A	B	C	D	E	F	G	H	I	J	K	L	M
	Bryophytes / liverworts											
1	Hepaticeae	*Frullania dilatata*	16, 17	HET (b)	X1X2 (haploid, H)	Y (H)	NA[d]	(b)	Yes	Yes	In bryophytes the multicellular plants are haploid gametophytes. The sporophyte borne on female gametophyte represents the diploid phase. The male determining chromosome labelled here as Y has also been called V and X given the lable U, in liverworts and mosses.	Temsch *et al*. (2010); McDaniel *et al*. (2012)
2		*Marchantia polymorpha*[a]	18	HET (Y=S)	X (H)	Y (H)	NA		Yes	Yes		Okada *et al*. (2000, 2001) Fujisawa *et al*. (2001); Ishizaki *et al*. (2002); Yamato *et al*. (2007); Allen (1930); McLetchie and Collius (2001)
3		*Sphaerocarpus donnellii*	14	HET	X (H)	Y (H)	NA		Yes	Yes		
		S.autinii	14	b	X (H)	Y (H)						
		S. texanus	14	HET	X (H)	Y (H)						
	Mosses											
4	Ditrichaceae	*Ceratodon purpureus*[a]	26		X (H)	Y (H)	NA		No	No		McDaniel *et al*. (2007) McDaniel (2005)
5	Orthotrichaceae	*Nyholmiella obtusifoli*[c]	36									Milewicz and Sawicki (2013)
6		*Pseudocalli-ergon trifarium*[c]										Korpelainen *et al*. (2008)
	Gymnosperms											
7	Cycadaceae (Cycad)	*Cycas revoluta* and *C. circinalis*	24	HET (Y=S)	XX	XY			Yes	No		Segawa *et al*. (1971): Gangopadhyay *et al*. (2007)
8	Lamiaceae	*Encephalartos natalensis*	18									Prakash and Staden (2006)
9	Ginkgoaceae	*Ginkgo biloba*[a]	24	HET (W=L)	WZ	ZZ	No				Only one species is known.	Chen *et al*. (1987); Wang *et al*. (2011); Lan *et al*. (2008); Liao *et al*. (2009)

Table 4 (*contd*)

	Phylogenetic rank and family	Species	2n Chromosome number (M/F or M : F :: male : female)	Sex chromosomes homomorphic (HOM) or heteromorphic (HET) and if HET which one larger (L) or smaller (S)	Sex chromosome composition		Whether YY (males) or WW (females) viable (yes or no)	Estimated age of sex chromosomes (million years)	Whether dioecy abundant in		Comment(s)	Reference(s)
					Female	Male			Genus (yes/no)	Family (yes/no)		
A	B	C	D	E	F	G	H	I	J	K	L	M
10	Podocarpaceae	*Podocarpus macrophyllus*[a]	37, 38	HET (Y=L)	$X_1X_1X_2X_2$	X_1X_2Y						Hair and Beuzenberg (1958); Hizume *et al*. (1988)
		P. longofoliolatus	37, 38	HET (Y=L)	$X_1X_1X_2X_2$	X_1X_2Y						
		P. elatus	37, 38	HET (Y=L)	$X_1X_1X_2X_2$	X_1X_2Y						
11	Pinaceae Angiosperms	*Pinus johannis*	24	HOM	XX	XY			No	No		Flores-Renteria *et al*. (2013)
12	Piperaceae	*Piper longum*	52						Yes	Yes		Banerjee *et al*. (1999); Manoj *et al*. (2005)
13	Myristicaceae	*Myristica fragrans*	24									Shibu *et al*. (2000)
14	Dioscoreaceae	*Dioscorea tokoro*	20	HOM	XX	XY			Yes	Yes	Type I abortion of sexual organs, following initiation of their primordia, in unisexual flowers.	Martin (1966); Terauchi and Kahl (1999)
		D. floribunda	40	HOM	XXXX	XXYY						Diggle *et al*. (2011)
15	Asparagaceae	*Asparagus officinalis*[a]	20	HOM	XX	XY	Yes				In this system *MM* are supermales, *Mm* are males and *mm* are females. Commercialy, male stems are preferred on account of their better growth.	Loptien (1979); Biffi *et al*. (1995); Jiang and Sink (1997); Reamon-Buttner *et al*. (1998); Spada *et al*. (1998); Gao *et al*. (2007); Ming *et al*. (2011); Deng *et al*. (2012);
16	Arecaceae	*Phoenix dactylifera*[a]	36	HOM	XX	XY	Yes		Yes	Yes	Dioecy evolved in distant past; however, PAR is maintained. Commercially useful sex linked markers to distinguish male	Siljak-Yakovlev (1996); Younis *et al*. (2008); Al-Dous *et al*. (2011); Diggle *et al*. (2011) Al-Mahmoud *et al*. (2012); Cherif *et al*. (2013) Rai and Singh (2013)
		P. rupicola	36									

Table 4 (*contd*)

Phylogenetic rank and family	Species	2n Chromosome number (M/F or M : F :: male : female)	Sex chromosomes homomorphic (HOM) or heteromorphic (HET) and if HET which one larger (L) or smaller (S)	Sex chromosome composition		Whether YY (males) or WW (females) viable (yes or no)	Estimated age of sex chromosomes (million years)	Whether dioecy abundant in		Comment(s)	Reference(s)
				Female	Male			Genus (yes/no)	Family (yes/no)		
A	B	C	D	E	F	G	H	I	J	K	L	M
16											and female plants are available. Type I abortion of sexual organs occurs at various stages of their development following their initiation in unisexual flowers	
17		*Borassus flabellifer*	32	HOM								George *et al.* (2007)
18	Poaceae	*Buchloe dactyloides*	36	HOM	XX	XY				No	Dioecy evolved long ago and PAR has been maintained	Zhou *et al.* (2011)
19		*Poa trivialis*	56						No	No		Renganayaki *et al.* (2005)
20		*Distichlis spicata*								No		Eppley *et al.* (1998)
21	Proteaceae	*Leucodendron xanthocomus*	26	HOM	XX	XY	Yes		Yes	No	More vegetative growth occurs in males than in females; males produce 20 times more flower than females.	Harris and Pannell (2010); Midgley (2010)
22	Vitaceae	*Vitis vinifera*	38	HOM	XX	XY			Yes		Three alleles of a single gene confer dioecy	Costantini *et al.* (2008); Marguerit *et al.* (2009)
23	Rosaceae	*Fragaria virginiana*[a]	56	HOM	WZ	ZZ		0.5–2.2	Yes	No	Population consists	Ahmadi and Bringhurst (1991); Ashman (2003);
		F. chiloensis	56	HOM	WZ	ZZ					of males,	Spigler *et al.* (2008,
		F. elatior	21	HOM	WZ	ZZ					females,	2010, 2011);
		F. moschata	42	HOM	WZ	ZZ					hermaphrodites	Goldberg *et al.* (2010);

Table 4 (*contd*)

Phylogenetic rank and family	Species	2n Chromosome number (M/F or M : F :: male : female)	Sex chromosomes homomorphic (HOM) or heteromorphic (HET) and if HET which one larger (L) or smaller (S)	Sex chromosome composition		Whether YY (males) or WW (females) viable (yes or no)	Estimated age of sex chromosomes (million years)	Whether dioecy abundant in		Comment(s)	Reference(s)
				Female	Male			Genus (yes/no)	Family (yes/no)		
A	B	C	D	E	F	G	H	I	J	K	L	M
23											and neuters. Unlike in *F. virginiana* which is subdioecious, *F. chiloensis* is dioecious and its sex chromosomes are different. Autosomes are also involved in sex determination. Type I abortion of sexual organs in unisexual flowers.	Diggle *et al*. (2011)
24	Elaegnaceae	*Hippophae rhamnoides*	22, 24						Yes			Persson and Nybom (1998); Sharma *et al*. (2010)
25	Cannabaceae	*Cannabis sativa*[a]	20	HET (Y = L)	XX	XY	Yes		Yes	Yes	The balance of X chromosome(s) to autosomes or X: A ratio also governs the sex determination. Sexual organ abortion in unisexual flowers occurs before initiation of stamen or carpel primordia (Type 2)	Sakamoto *et al*. (1995, 1998, 2000, 2005); Mandolino *et al*. (1999); Peil *et al*. (2003); Diggle *et al*. (2011)
		C. indica	20	HET (Y = L)	XX	XY						
		C. ruderalis	20	HET (Y = L)	XX							

Table 4 (*contd*)

Phylogenetic rank and family		Species	2n Chromosome number (M/F or M : F :: male : female)	Sex chromosomes homomorphic (HOM) or heteromorphic (HET) and if HET which one larger (L) or smaller (S)	Sex chromosome composition		Whether YY (males) or WW (females) viable (yes or no)	Estimated age of sex chromosomes (million years)	Whether dioecy abundant in		Comment(s)	Reference(s)
					Female	Male			Genus (yes/no)	Family (yes/no)		
A	B	C	D	E	F	G	H	I	J	K	L	M
26		*Humulus lupulus*[a]	20	HET (Y = S)	XX	XY					X : A ratio is also involved in the governance of sex determination	Ono (1955); Polley *et al.* (1997); Seefelder *et al.* (2000); Karlov *et al.* (2003); Danilova and Karlov (2006); Grabowska-Joachimiak *et al.* (2006, 2011); Jakse *et al.* (2008); Kim *et al.* (2008); Divashuk *et al.* (2011); Alexandrov *et al.* (2012)
		H. l. var *cordiflorus*	40	HET (Y=S)	$X_1X_1X_2X_2$	$X_1X_2Y_1Y_2$			Yes	Yes		
		H. japonicus	21, 20	HET (Y = S)	XX	XY_1Y_2	No					
		H. yunnanensis	21, 20	HET (Y = S)	XX	XY_1Y_2	No					
		H. acetosa	17, 16	HET (Y = S)	XX	XY_1Y_2	No					
27	Moraceae	*Ficus fulva*	28							Yes		Tracey *et al.* (2004)
28	Cucurbitaceae	*Bryonia dioica*	20	HOM	XX	XY	No	~ 10	No	No	Sex is also influenced by environment	Volz and Renner (2008); Oyama *et al.* (2009, 2010)
		Coccinia indica[a]	24	HET (Y = L)	XX	XY	No	3–6	Yes	No	XY, XXY and XXXY are all males; Type 1 abortion of sexual organs in unisexual flowers	Kumar and Viseveshwaraiah (1952); Roy and Roy (1971); Diggle *et al.* (2011); Holstein and Renner (2011); Holstein (2012); Sousa *et al.* (2013)
30		*Ecballium elatrium*	18	HOM	XX	XY	Yes		No	No	Monoecious and dioecious plants are inter-convertible	Galan (1946); Westergaard (1958); Costich and Meagher (1992);
31		*Trichosanthes dioica*	22		XX	XY	No		Yes	No	As above	Patel (1952); Kumar *et al.* (2008)
		T. kirilowi	22									
		T. japonica	22									
		T. multiloba	22									
		T. ovigera and *T. cucumervides*	22									

Table 4 (*contd*)

Phylogenetic rank and family	Species	2n Chromosome number (M/F or M : F :: male : female)	Sex chromosomes homomorphic (HOM) or heteromorphic (HET) and if HET which one larger (L) or smaller (S)	Sex chromosome composition		Whether YY (males) or WW (females) viable (yes or no)	Estimated age of sex chromosomes (million years)	Whether dioecy abundant in		Comment(s)	Reference(s)
				Female	Male			Genus (yes/no)	Family (yes/no)		
A	B	C	D	E	F	G	H	I	J	K	L	M
32	Datiscaceae	*Datisco cannabina*	22	HOM	WZ	ZZ	Yes				Type 2 sexual organ abortion in unisexual flowers	Wolf *et al*. (2001); Diggle *et al*. (2011)
33	Euphorbiaceae	*Mercurialis annua*	16	HOM	XX	XY			No	No	Dioecy in this system is also controlled by environment (temperature)	Pannell (1997a, b); Yang *et al*. (1998); Khadka *et al*. (2002, 2005); Pannell *et al*. (2004); Pannell (2008) Obbard *et al*. (2006); Elze and Pannell (2011); Sanchez-Vilas *et al*. (2011)
34		*Uapaca kirkiana*	26									Mwase *et al*. (2007)
35	Salicaceae	*Populus trichocarpa*[a]	38	HOM	WZ	ZZ		~ 1	Yes	Yes	It is thought that the origin of sex chromosomes in *P. trichocarpa* and *P. tremuloides* was independent. Type 2 sexual organ abortion in unisexual flowers	Paolucci *et al*. (2008); Yin *et al*. (2008); Hou *et al*. (2009); Pakull *et al*. (2009); Tuskan *et al*. (2012)
		P. tremuloides	38	HOM	XX	XY						
		P. alba	38	HOM								
		P. tomentosa	38	HOM								
36		*Salix viminalis*	38	HOM	WZ	ZZ						Alstron-Rapaport *et al*. (1998); Gunter *et al*. (2003); Semerikov *et al*. (2003); Yin *et al*. (2008); Diggle *et al*. (2011)
37	Burseraceae	*Commiphora wightii*	26									Samantaray *et al*. (2010)
38	Anacardiaceae	*Pistacia vera*	32								Sex distinguishing commercial DNA markers are available	Hormuza *et al*. (1994); Yakubov *et al*. (2005); Ehsanpour *et al*. (2008)
39	Caricaceae	*Carica papaya*[a]	18	HOM	XX	XY	No	0.5–7	Yes	Yes	In this system Mm are males, mm are females	Hofmeyr (1938); Sondur *et al*. (1996); Parasnis *et al*. (1999, 2000);

Table 4 (*contd.*)

Phylogenetic rank and family	Species	2n Chromosome number (M/F or M : F :: male : female)	Sex chromosomes homomorphic (HOM) or heteromorphic (HET) and if HET which one larger (L) or smaller (S)	Sex chromosome composition		Whether YY (males) or WW (females) viable (yes or no)	Estimated age of sex chromosomes (million years)	Whether dioecy abundant in		Comment(s)	Reference(s)
				Female	Male			Genus (yes/no)	Family (yes/no)		
A	B	C	D	E	F	G	H	I	J	K	L	M
39											M^hm are hermaphrodites, MM, M^hM and M^hM^h are lethal; altogether it is a polygamous species. Commercially useful sex based DNA markers are available	Deputy *et al.* (2002); Urasaki *et al.* (2002); Liu *et al.* (2004); Ma *et al.* (2004); Chen *et al.* (2007); Gangopadhyay *et al.* (2007); Ming *et al.* (2008); Yu *et al.* (2008a, b); Wai *et al.* (2010); Wu *et al.* (2010); Gschwend *et al.* (2012); Wu *et al.* (2010)
40		*Vasconcellea geudotinana*	18	HOM	XX	XY						
		V. parviflora	18	HOM	XX	XY						
		V. trioecious	18	HOM	XX	XY						
		V. pulchera	18	HOM	XX	XY						
		V. cundinammar	18	HOM	XX	XY						
41	Loranthaceae	*Viscum fischeri*	21, 22	HOM	$X_1X_1X_2X_2$	X_1X_2Y					Type 2 sexual organ abortion in unisexual flowers	Barlow and Weins (1976); Diggle *et al.* (2011)
42	Polygonaceae	*Rumex acetosa*[a]	15, 14	HET (X = L)	XX	XY_1Y_2	No	15–16	Yes	No	In all Rumex species balance of X: A governs the sex. Y_1Y_2 are almost fully heterochromatic. Y is required for sex chromosome disjunction but perhaps not in sex determination. Genes for dioecy and monoecy are	Kihara and Ono (1923); Kurita and Kuroki (1970); Bartkowiak (1971); Rejon *et al.* (1994); Shibata *et al.* (1999, 2000); Rahman and Ainsworth (2004); Stehlik and Blattner (2004); Navajas-Perez *et al.* (2005a, b, 2006, 2009) Cunado *et al.* (2007); Blocka-Wandas *et al.* (2007); Mariotti *et al.* (2009); Steflova *et al.* (2013)
		R.. papillaris	15, 14		XX	XY_1Y_2						
		R. intermedius	15, 14		XX	XY_1Y_2						
		R. thyrsiflorus	15, 14		XX	XY_1Y_2						
		R. rothschildinus	15,14		XX	XY_1Y_2						
		R. suffruticosus	16	HET (X = L)	XX	XY						
		R. acetocella	14	HET (X = L)	XX	XY						
		R.. nivalis										
		R. hastatulus	15, 14 or 14	HET (X = L)	XX	XY or XY_1Y_2						

Table 4 (*contd.*)

	Phylogenetic rank and family	Species	2n Chromosome number (M/F or M : F :: male : female)	Sex chromosomes homomorphic (HOM) or heteromorphic (HET) and if HET which one larger (L) or smaller (S)	Sex chromosome composition		Whether YY (males) or WW (females) viable (yes or no)	Estimated age of sex chromosomes (million years)	Whether dioecy abundant in		Comment(s)	Reference(s)
					Female	Male			Genus (yes/no)	Family (yes/no)		
A	B	C	D	E	F	G	H	I	J	K	L	M
42											linked. Male seeds are heavier than female seeds. Type 1 abortion of sexual organs in unisexual flowers	
43	Simmondsiaceae	*Simmondsia chinensis*	26									Agrawal *et al.* (2007); Hussaini *et al.* (2011)
44	Caryophyllaceae Group A	*Silene latifolia*[a]	24	HET (X = L)	XX	XY	No	8–24	Yes	No	Haploid X plants are viable but Y plants are inviable. X gene expression is higher when Y – linked expression is lower. Type 1 abortion of sexual organs in unisexual flowers	Donnison *et al.* (1996); Di-Stilio *et al.* (1998); Zhang *et al.* (1998); Siroky *et al.* (2001); Lengerova *et al.* (2003, 2004); Moore *et al.* (2003); Smith (1964); Nicolas *et al.* (2005); Zluvova *et al.* (2005, 2007); Hobza *et al.* (2006); Bergero *et al.* (2007); Steven *et al.* (2007); Mrackova *et al.* (2008); Marais *et al.* (2008, 2011); Rautenberg *et al.* (2012); Howell *et al.* (2009a, b); Delph *et al.* (2010); Nishiyama *et al.* (2010); Diggle *et al.* (2011); Kafer *et al.* (2013)
		S. dioica	24	HET (Y = L)	XX	XY						
		S. marizii	24	HET	XX	XY						
		S. buffelii	24	HET	XX	XY						
		S. diclinis	25, 24	HET (Y = L)	XX	XY_1Y_2		5–10				
	Group B	*S. colpophylla*	24	HOM	XX	XY					Here sex chromosome evolved from a different set of autosomes than in *S. latifolia*. Type 2 sexual organ abortion in unisexual flowers	
		S. otites	24	HOM	WZ	ZZ						
		S. wolgensis	24	HOM								

Table 4 (*contd.*)

	Phylogenetic rank and family	Species	2n Chromosome number (M/F or M : F :: male : female)	Sex chromosomes homomorphic (HOM) or heteromorphic (HET) and if HET which one larger (L) or smaller (S)	Sex chromosome composition		Whether YY (males) or WW (females) viable (yes or no)	Estimated age of sex chromosomes (million years)	Whether dioecy abundant in		Comment(s)	Reference(s)
					Female	Male			Genus (yes/no)	Family (yes/no)		
A	B	C	D	E	F	G	H	I	J	K	L	M
45	Amaranthaceae	*Spinacea oleracea*[a]	12	HOM	XX	XY	Yes				Type 2 sexual organ abortion in unisexual flowers	Murray (1940); Bemis and Wilson (1953); Freeman *et al.* (1994); Ruas *et al.* (1998); Khattak *et al.* (2006); Lan *et al.* (2006); Diggle *et al.* (2011); Ming *et al.* (2011); Onodera *et al.* (2011)
		Atriplex garrettii	18	HOM	XX	XY						
		Acnida tamariscina	32	HOM	XX	XY						
46	Actinidiaceae	*Actinidia chinensis*	58	HOM	XX	XY	Yes				Occasional hermaphrodite or monoecious plants are produced. Commercially useful sex linked DNA markers are available	Harvey *et al.* (1997); Gill *et al.* (1998); Testolin *et al.* (2001); Shirkot *et al.* (2002); Fraser *et al.* (2009)
		A. deliciosa	58	HOM	XX	XY	Yes					
47	Eucommiaceae	*Eucommia ulmoides*	34									Xu *et al.* (2004); Wang *et al.* (2011)

[a]This and its sister species are included as model plants for the evolutionary analysis of dioecy and sex chromosomes; [b]empty space means that information is insufficient; [c]when the male and female plants have been distinguished by use of molecular markers, the spaces in columns D–L or E–L are usually empty for want of information; [d]NA, not applicable.

than the largest autosome and much more larger than the X chromosome.

There are variants of XX/XY system in which the X/Y chromosome is present in two copies. In the liverwort *Frullania dilata,* the female haploid gametophytes have two X chromosomes. In the gymnosperm *Podocarpus macrophyllus*, the respective sex chromosome composition of females and males is $X_1X_1X_2X_2$ and X_1X_2Y. Such sex chromosome polymorphy is also the case in the angiosperm *Viscum fischeri.* Contrastingly, there are two copies of Y chromosome in the genomes of male plants of *Humulus japonicus* (and *H. yunnanensis* and *H. acetosa*), *Rumex acetosa* (and *R. intermedius, R. papillaris, R. rothschildinus, R. tatulus* and *R. thyrsiflorus*) and *Silene diclinus.*

In some species, exemplified by *Carica papaya*, Y chromosome exists in two forms. Whereas the conventional Y form specifies maleness, the variant Y^h form renders hermaphroditism. The trioceousness of *C. papaya* is shared by *Fragaria virginiana*. In several plant species possessing the XX/XY system, sex is influenced by the ratio of X chromosomes to autosomes (*Cannabis, Humulus* and *Rumex* species). In *Rumex acetosa*, X/A ratio of 0.5 favours maleness and higher values of 1–6 favour femaleness. Interestingly, in certain genera/families the XX/XY and WZ/ZZ sex chromosome systems have cooccurrence (*Populus* and *Silene*). Whereas *Populus tremuloides* possesses XX/XY sex system, the sex in its sister species *P. trichocarpa* is governed by the WZ/ZZ system. In cucurbitaceous dioecious plants such as *Bryonia dioica* sex expression is also influenced by temperature of growth environment, maleness is favoured by high temperatures in this species.

Variety in the developmental processes for attainment of male and female unisexuality

Dioecy has evolved from hermaphroditism. The hermaphrodite flowers posses both female organ(s) gynoecium and male organs androecium. The unisexual flowers either lack the functional gynoecium or androecium. The unisexual flowers in dioecious species are divisible into two groups, type 1 and type 2 (Diggle *et al*. 2011). In type 1 flowers, both gynoecium and androecium are initiated. Subsequently, there is abortion of development of androecium in female flowers and that of gynoecium in male flowers. Abortion of organs occurs at different stages of development in the unisexual flowers of different dioecious species. The unisexual flowers of type 1 species thus demonstrate considerable variation in their structure by possessing differentially underdeveloped gynoecium or androecium. *Coccinia indica, Dioscorea tokoro, Phoenix dactylifera, Rumex acetosa, Silene latifolia* and *Vitis vinifera* exemplify type 1 species. Type 2 species produce flowers that are initiated as unisexual. In type 2 male and female flowers, the gynoecium and androecium are, respectively entirely absent. *Cannabis sativa, Populus trichocarpa* and *Spinacea oleracea* are the examples of type 2 species. Because unisexual flowers of type 1 dioecious species undergo abortion of male or female organs at many different stages of their development process (Mitchell and Diggle 2005), it is indicated that dioecy in such species must have evolved independently. Dioecy in type 2 species might have also evolved independently, because the characteristics occurs in species of many families.

Molecular basis of unisexual flower development

Considerable progress has been made towards understanding the molecular/genetic mechanisms of hermaphrodite flower development. In this regard information has been gathered on the cascades of transcriptional regulation for the initiation of flower development and combinatorial interactions between genes for the development of male and female flower organs identity and appendages in the vegetative whorls of the flower (see Krizek and Fletcher 2005 for a review). Understandably, the genetic system for the development of male and female organs must be superimposed by gene(s) that promote male or female sexual organ formation and/or suppress the formation of the organs of alternate sex. This area is beginning to be explored. In melon, it has been found that interaction between the two genes, *Cm ACS7* and *Cm W1P1*, control whether the flowers to be formed on a plant will be male, female or hermaphrodite. The expression of *Cm W1P1* in the differentiating flowers leads to carpel abortion and therefore development of only the male organs in unisexual flowers, via repression of *Cm ACS7*. In the flowers undergoing differentiation for female unisexuality, the *Cm ACS7* gene activity represses stamen development. Under environmental conditions allowing the repression of both *Cm W1P1* and *Cm ACS7*, bisexual flowers develop in place of unisexual flowers (Martin *et al*. 2009). The molecular basis of unisexual flower development in monoecious and dioecious species is an expanding area of future research.

Distinctive traits of male and female population and their effects on the survival in dioecious species

Evolution of a dioecious species from its hermaphrodite ancestral species leads to dimorphism between males and females commensurate with the roles of sexes in the survival, reproduction and evolution of the species. Dimorphism observed in dioecious plant species is much less than in animal species. The dimorphism observed between sexes of dioecious plants usually relates to morphological, physiological and life cycle traits affecting the expression of primary and secondary sexual characters. The dimorphism affects differentially the cost of production of flowers, pollination and fruit and seeds and of seed dispersal. It also affects cost of adaptation to the environmental gradients prevailing in the area of distribution of the species. These factors impact the sex ratio in dioecious species. On account of the cost of successful reproduction and adaptation to environment,

many dioecious plant species display distorted sex ratios. Male-biased sex ratios are more common than female-biased sex ratios. Pattern of expression of certain life cycle traits in male-biased and female-biased populations of dioecious plant species are shown in table 5. It will be seen that female bias is favoured by optimum environment, low cost of bioaccumulate expenditure on reproduction, heteromorphy in sex chromosomes and inviability of YY embryos.

Several above referred to traits of sex biased dioecious species and others common to all dioecious species indicate that dioecious species face a variety of challenges for their survival (Kafer *et al*. 2013). When male flowers are more attractive to pollinators than female flowers, in the season of low pollinator density seed formation will be scanty (Otto and Lenormand 2002). In dioecious species seeds are formed on only half of the population and population density will be even more strongly affected when dioecious species demonstrates male-biased sex ratio. It is perhaps for such reasons that in families that comprise of both hermaphrodite and dioecious species, the dioecious clades are species poor as compared to the sister nondioecious clades which are far richer in species composition (Heilbuth 2000; Heilbuth *et al*. 2001). The sex-biased ratios and associated traits can decrease population size, restrict distribution and thereby lower the colonization rates of dioecious species, thus harming their survival in future and leading them towards extinction. All such conditions may be responsible for short life of dioecious plant species and recurrent evolution of dioecious species in different plant families. Dioecy has been called as dead end (Kafer *et al*. 2013). Question arises what is the role of dioecy in evolution, besides avoidance of inbreeding depression.

Origin of sex chromosomes

Monosexuality or dioecy evolves from preexisting cosexuality in the form of hermaphroditism or monoecy. In plants, dioecy has evolved independently in numerous species of many families (Bachtrog *et al*. 2011; Ming *et al*. 2011). Plant possess complete sets of genes to produce gynoecium (female sex organs, carpels) and androecium (male sex organs, stamens), in the same flower in hermaphrodite and in separate flowers on the same monoecious plant. In all the species, genes for gynoecium and androecium development are distributed more or less on all the chromosomes (linkage groups) of the autosomal genomic karyotype (Kater *et al*. 2001; Honys and Twell 2004; Wellmer *et al*. 2004). However, the regulation of androecium genes and gynoecium genes is somewhat different between hermaphrodite and monoecious species (Zhang *et al*. 2005). Origin of dioecy requires occurrence of at least two mutations in cosexual species (Charlesworth and Charlesworth 1978a, b; Charlesworth 1984, 1996a, b, 2012; Rice 1984, 1986, 1987a, b, c; Negrutiu *et al*. 2001; Rice *et al*. 2008; vanDoorn and Kirkpatrick 2010). A recessive loss-of-function mutation in an androecium inducing gene of a linkage group allows abortion of androecium development (for the creation of female individuals). In the homologous linkage group a dominant gain-of-function mutation allows abortion of gynoecium development (for the creation of male individuals). Since many genes acting together control the development of androecium or gynoecium, the mutations creating males or females may affect different genes in different species such that the origin of dioecy could be different in different species (Peiffer *et al*. 2008).

The origin of males and females in the species evolving dioecy is usually sequential, because the two mutations are unlikely to occur simultaneously. When females arise first the population of species will be gynodioecious, hermaphrodites will get invaded by females. The process will open opportunities of crossing between hermaphrodites and females, allowing setting of outcrossed seeds on females, thereby increase genetic variability in species. The invasion of hermaphrodites by males (androdioecy) is thought to be less effective in enlarging the genetic variability, unless males outnumber hermaphrodites, produce pollen in massive quantities or somehow allow setting of outcrossed seeds on hermaphrodites plants. More common and easier route for dioecy appears to be via gynodioecy.

The region on the autosome pair that carries the sex limiting mutations has been termed as the sex determining region or SDR (figure 2). The SDR is initially very small due to linkage between the two mutated genes/loci

Table 5. Traits associated with distortion of sex ratios in dioecious plant species (based on the surveys described in Field *et al*. 2012, 2013; Barrett and Hough 2012; Hough *et al*. 2013).

	Trait	Male-biased population	Female-biased population
1	Habit	Woody trees and vines	Herbaceous perennials
2	Habitat	Stressful environment	Favourable environment
3	Life cycle length	Long	Short
4	Self cloning ability	High	Low
5	Flowering	Earlier and frequent	Late and rare
6	Flower number	High	Low
7	Flower bud abortion	Very low	High
8	Pollination	Biotic	Abiotic
9	Seed dispersal	Biotic	Abiotic
10	Sex chromosomes	Homomorphic; YY viable	Heteromorphic; YY inviable

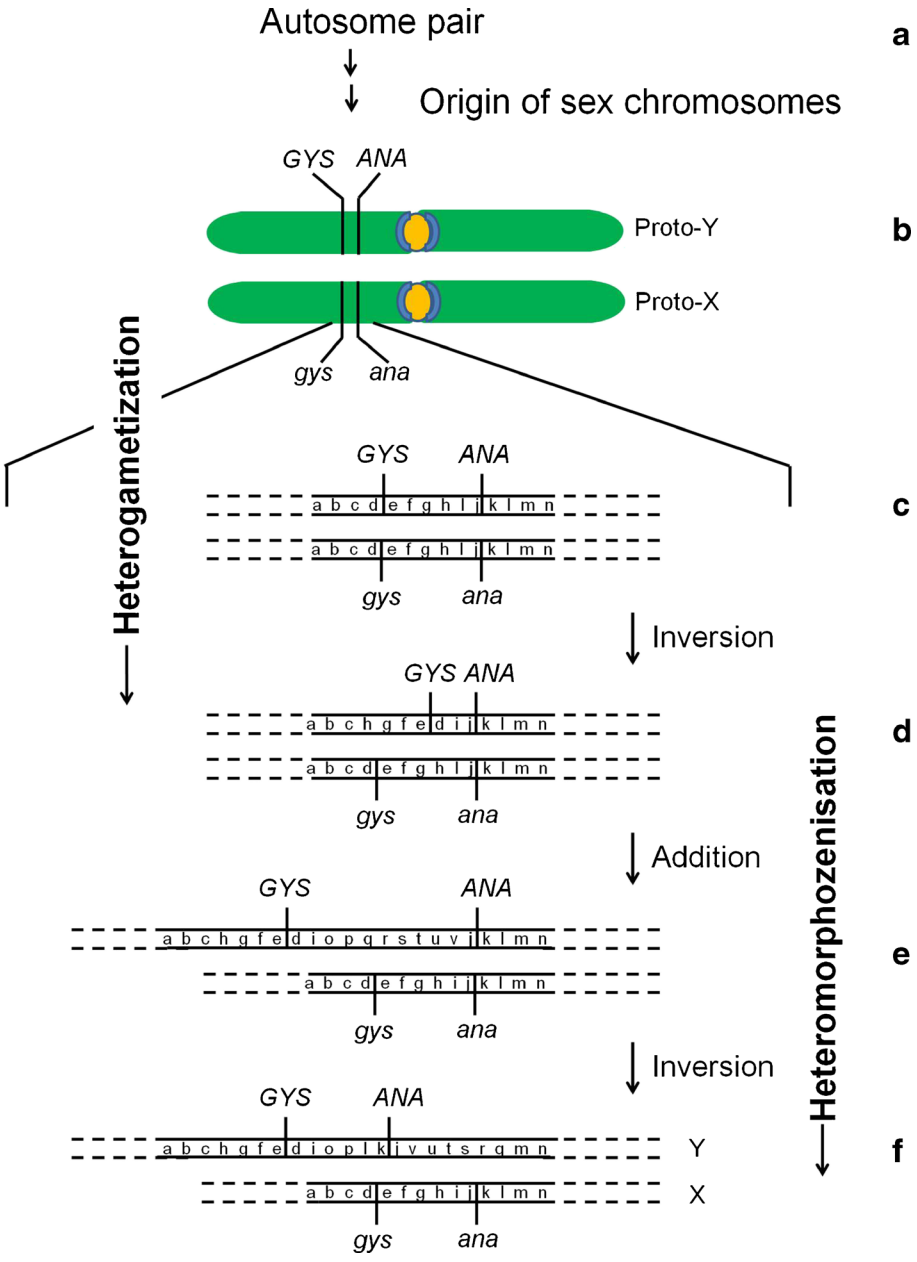

Figure 2. Diagram of the early steps in the origin of heterogametic X and Y sex chromosomes, from a pair of autosomes (a and b). The autosome pair to evolve into sex chromosomes has two linked loci called *GYS/gys* and *ANA/ana* which are shown to be located near to the centromere. The two loci comprise the proto-SDR. The autosome pair undergoes a mutation each, consecutively. If one of the pair has the mutation in *GYS*, the other has it in *ANA*. The occurrence of mutations has initiated the evolution of X and Y chromosomes and the autosome pair has now become the proto-X/proto-Y pair. The proto-X has the recessive loss-of-function *ana* mutation in the *ANDROECIUM ACTIVATOR* gene imparting the chromosome with female specificity. The proto-Y has the dominant gain-of-function *GYS* mutation such that the *GYNOECIUM SUPPRESSOR* allele imparts male specificity to the chromosome. (c) The SDR is enlarged to show homology of sequences in between and around *ANA* and *GYS* loci in the proto-X and proto-Y chromosomes (a b c. . . . . .m n). (d–f) Conversion of proto-X and proto-Y into differentiated X and Y chromosomes. (d) In the SDR of proto-Y the sequence d to h has undergone an inversion. This region is unaltered in c to din proto-X. (e) A sequence o–v has got added between i and j in proto-Y, whereas proto-X has remained unchanged. (f) Proto-Y has undergone another inversion. The sequences of proto-X and Y are now highly diverged thus obviating occurrence of recombination in this differentiated SDR. Proto-Y has evolved into Y sex chromosome and the counterpart proto-X into X chromosome. The evolution of X and Y shown here has been patterned after the origin of sex chromosomes in *Carica papaya* (Wang *et al.* 2012; Vanburen and Ming 2013). The X and Y composition in the diagrams b and c represent the sex chromosome status in *Asparagus officinalis*. Centromere in between the green chromosomes arms is shown in yellow colour.

(Bull 1983; Charlesworth 1996a, b). The maleness determining chromosome or proto-Y chromosome has the maleness inducing gene or *ANDROECIUM ACTIVATOR* (*ANA*) in its wild-type state and the dominant mutation for suppression of femaleness or *GYNOECIUM SUPPRESSOR* (*GYS*). The femaleness determining chromosome or proto-X has the androecium aborting mutation *ana* and gene(s) for femaleness development, including the *gys* allele. The tight linkage of the two loci *ANA* and *GYS* makes recombination between them rare, such that the appearance of hermaphrodite and neuters in the progeny is minimized (Lewis 1942). Except for the SDR, the proto-X and proto-Y are homomorphic and retain their autosomal structure. This method of origin of heterogametic XY system is exemplified by *C. papaya* (Yu *et al*. 2008a, b, 2007) and *Silene latifolia*. The SDR of *S. latifolia* Y chromosome has three loci essential for dioecy, *GYS* and *ANA1* and *ANA2* for early and late androecium development, respectively (Westergaard 1958; Grant *et al*. 1994a, b; Lardon *et al*. 1999).

The female heterogametic system WZ seen in *Populus trichocarpa* (Yin *et al*. 2008) and *Fragaria virginiana* (Spigler *et al*. 2008) is relatively rarer than the XY system. Female heterogamety is thought to arise from dioecious ancestors bearing the XY heterogametic system.

In some plant species, exemplified by *Bryonia dioica*, sex determination is a result of genotype–environment interaction. In *B. dioica*, an environmental trigger such as high temperature is required to induce *ANA*. Presumably, in this system *ANA* is not expressed constitutively. Dominant mutation in the promoter of *ANA* leading to constitutive expression of *ANA* is a requirement for environmental intervention, free sex determination. It has been observed in animal systems that a dominant feminizing mutation in the gene corresponding to *FYA* of plants leads to independence of ZW system from environmental effects on sex determination (Bull 1983; Valenzuela 2004; Quinn *et al*. 2007).

Development of heteromorphy between sex chromosomes

The major steps involved in the pronounced molecular and morphological differentiation of X and Y, Z and W, and U and V chromosomes are outlined in figures 2–4. These include (i) changes in the structure of SDR for the suppression of recombination in the SDR of enlarged size, (ii) accumulation of genes/alleles that favour sex limitation in X and Y chromosomes, and (iii) accumulation of deleterious gene, repeat and satellite sequences and transposable elements in SDR of Y chromosome. In the proto-X and proto-Y chromosomes (typical ones shown in figure 2) the SDR comprises of essential genetic elements for dioecy, *ANA* and *GYS* loci closely linked to each other in the pericentromeric region. Recombination between them is decreased by occurrence of sequence rearrangements in the SDR of Y chromosome. Inversion, addition and deletion events can change the sequence between and around *ANA* and *GYS* such that recombination is unlikely to occur. In the process SDR enlarges and differentiates making recombination within it untenable. However, recombination would continue to occur between X and Y chromosomes outside of SDR in the region on two arms called pseudoautosomal region (PAR). Y chromosome continues to carry many genes in their active state within and outside SDR, whereas X chromosome has almost all the genes present in ancestral autosome.

Further, differentiation of X and Y chromosomes is accelerated by two processes, one that further specializes X and Y chromosomes for their unisexual role in dioecy and second that promotes divergence of Y from X by accumulation of deleterious genetic changes. *SEXUALLY ANTAGONISTIC* (*SA*) genes/alleles are added on to X chromosome. Their presence altogether aborts androecium from females and increases fitness in females. Complementally, *ANDROECIUM POTENTIATOR* (*ANP*) genes (previously called male fertility genes M2 in relation to dioecy in animals, Charlesworth and Charlesworth 1978a, b; Charlesworth 1991) are added on to Y chromosome. The *ANP* genes have a potentiating effect on androecium development in males and increase their fitness. The *SA* and *ANP* genes initially part of different autosomes get rearranged proximal to *ANA* and *GYS* loci in SDR of X and Y by means of translocations of small size. The translocations may bring beneficial or deleterious genes linked to *SA*s and *ANP*s. Irrespectively, the presence of *SA*s and *ANP*s boosts the sex limitation gene complex on X and Y chromosomes.

SDRs of X and Y diverge also by accumulation of deleterious sequences on Y chromosome. Because its ancestor was an autosome, Y chromosomes carries many genes which are involved in diverse functions, and some genes which are essential for gametogenesis, formation of pollen and participation of pollen in double fertilization. The inessential genes may accumulate mutations making them nonfunctional. A variety of satellite sequences and repeat sequences, including transposable elements also get accumulated on Y chromosome. Intrachromosomal recombination events between repeat elements may cause enlargement, deletion and rearrangements of repeat and intervening sequences. The deleterious sequences do not get deleted from Y in the absence of recombination between SDRs of Y and X chromosomes. However, intrachromosomal recombinational rearrangements (ectopic recombination) can occur.

The structures of heteromorphic Y chromosomes known in dioecious species demonstrate considerable variation in the pattern of their evolution of the kind delineated above (figures 3 and 4). *Silene latifolia* Y chromosome is much larger than its X counterpart; it has abundance of repeat elements (figure 3). In *Cycas revoluta*, X chromosome is larger than Y chromosome; its Y presumably suffered an intrachromosomal recombinational deletion (figure 3). Some populations of *Rumex acetosa* have lost Y chromosome and in them X-to-autosome ratio type of new mechanism has evolved

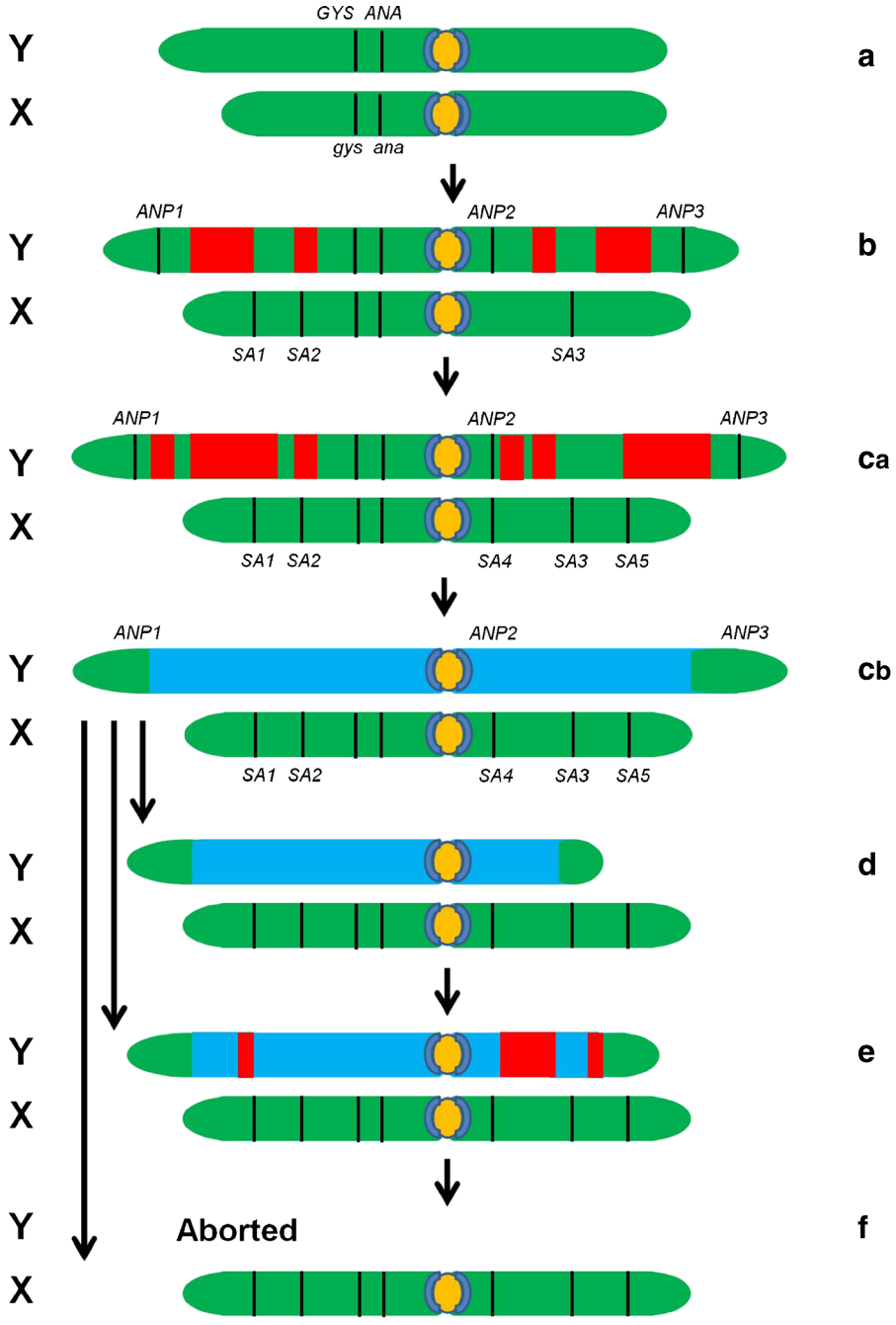

Figure 3. Diagrammatic representation of typical degenerative changes in the heterogametic Y chromosome that direct the evolution of variants of XY sex chromosome system, prevalent in some model dioecious plant species. (a) The X and Y chromosomes of the stage F of figure 2 in which SDR sequences of X and Y have extensively differentiated and therefore recombination is suppressed in the SDR. (b) The SDR in Y chromosome have enlarged by gaining repeat elements/transposons and noncoding sequences at different locations on both the arms (red colour). It has also accumulated several *ANDROECIUM POTENTIATOR* (*ANP*) alleles that are beneficial for maleness and detrimental for femaleness. The X chromosome has gained several *SEXUALLY ANTAGONISTIC* (*SA*) alleles that favour femaleness and antagonize maleness. X is relatively free of the repeat elements. (ca and cb) Whereas the structure of X is same as in b (euchromatic, green coloured), the Y has accumulated more of transposon elements and noncoding sequences on both arms which have increased its heterochromatization (shown in blue colour), saving PAR at the ends of chromosomal arms as euchromatin (green colour). ca and cb represent the X and Y heteromorphism as noted in *Silene latifolia* (table 1). (d) Ectopic recombination events between the repeat elements of same sequence have shortened the heterochromatized/degenerated SDR on both the arms of Y chromosome. Now X and Y heteromorphic such that Y is smaller than X. This condition mimics the XY system revealed in *Cycas revoluta* (table 1). (e and f) Loss of the Y chromosome. (e) The SDR of Y shown in d has acquired a translocation from an autosome (red colour) in the right arm. It has also gained homologous TE sequences on the two arms (red colour). Ectopic recombination between the homologous TEs on two arms creates a centromeric ring chromosome and an acentric rod chromosome both liable to lose during cell division(s). Y thus gets aborted. (f) X0 system is born. An example of it has been reported in some populations of *Rumex acetosa.*

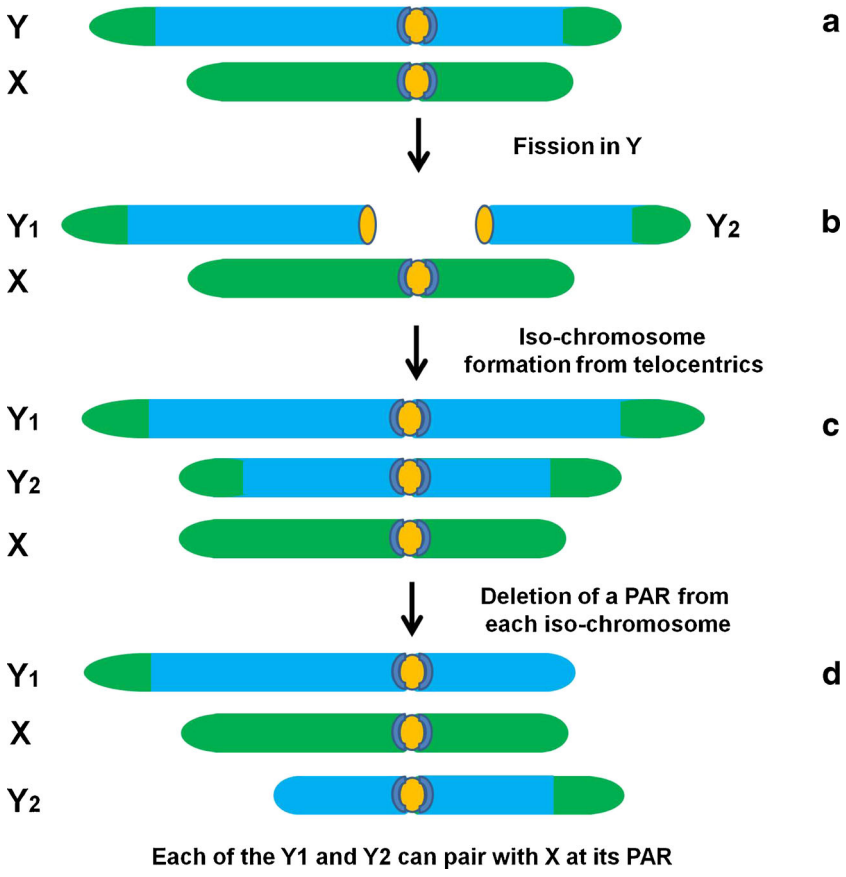

Figure 4. A possible scheme for the emergence of XY1Y2 sex chromosome system from the XY system. (a) Heteromorphic X and Y chromosome, Y is highly heterochromatized and X and Y share homology in the pseudoautosomal region (green colour at the chromosome arm ends). (b) Telocentric Y1 and Y2 chromosomes have formed by breakage of the original Y at its centromere. (c) Formation of Y1 and Y2 as isochromosomes such that the two arms have the same sequence in the centromere to telomere direction. (d) Truncation of Y1 and Y2 via deletion of a PAR from one of the arms. Now in meiosis the trivalent formed between X and two Ys will facilitate disjunction. The XY1Y2 type of heterogametic sex determination system is known in several species of *Rumex* and *Humulus* (table 1). The diagramme is a modification of that given by Vyskot and Hobza (2004) for the sex chromosome system in *Rumex acetosa.*

(figure 3; Ming *et al*. 2011). Presumably, in this system formation of a centromeric ring and an acentric chromosome due to intrachromosomal ectopic recombination has led to loss of Y chromosome. In some other populations of *R. acetosa* and in *Humulus acetosa*, two Y chromosomes have replaced the conventional Y (figure 4; Rejon *et al*. 1994; Shibata *et al*. 1999). Here, fission of Y at centromere led to formation of isochromosomes from the two arms of Y. The isochromosomes later lost segments of arms so that normal disjunction could occur at meiosis from the triad formed by X, Y1 and Y2 chromosomes from pairing between their PARs.

Degeneration in the heterogametic sex chromosomes

The Y, W, U and V chromosomes degenerate progressively from the time of their inception (until they are lost) by occurrence of loss-of-function mutations in their genes. Mutations such as base transitions, transversions, additions and deletions, insertion of repeat sequences such as transposons and deletion or rearrangement of sequences disrupt function of gene(s), in the absence of mechanisms for repair or replacement (Muller's ratchet, Muller 1964; Felsenstein 1974). The deleterious alleles do not get lost or recombined out due to suppression of recombination between X and Y, W and Z and U and V chromosomes in their SDRs. In each of the three heterogametic systems, some genes in the SDR are retained in their functional states. These include genes for pollen formation and pollen tube growth for double fertilization on Y chromosomes of angiosperms and genes for the growth of haploid thalli in U and V chromosomes of bryophytes (Lardon *et al*. 1999; Yamato *et al*. 2007). The principal reason for the degeneration of heterogametic sex chromosomes is loss of function in their genes not essential for dioecy due to suppression of recombination (Charlesworth 2009, 2012). Nonviability of YY embryos is an indication of ample Y degeneration.

Transition of XY into ZW system

The XY sex determination system can transition into WZ system. This is indicated by presence of both XY and WZ systems in different species of angiosperm genera Silene and Populus. Transition can occur readily if two conditions are met by the dioecious species to undergo XY to WZ transition (Bull 1983; Hillis and Green 1990; Mank *et al*. 2006; Kaiser and Bachtrog 2010). (i) The heterogametic Y chromosome must not have undergone high levels of degeneration. (ii) The karyotype should preferably be paleo-polyploidal. As shown in figure 5, a chromosome homologous to the ancestral X will already have *ANA* and *gys* alleles. This autosome to convert into a W chromosome will acquire a *SA* gene, if already not present, and the dominant gain-of-function mutation *GYA*. Whereas *SA* will antagonize *ANA, GYA* will antagonize *GYS* and promote the expression of femaleness (gynoecium development) in WZ females. In the transitioned system preexisting Y will serve as the Z chromosome. The WZ bearers will be monosexual females bearing gynoecium producing flowers and ZZ bearers will be males producing stamen bearing flowers. In this model, X chromosome bearing *SA*, *ana* and *gys* alleles can be directly hijacked by occurrence on it of *GYA* mutation to become W chromosome. Such transitions do not demand presence of paleo-polyploidic karyotype in the species. A new question has arisen as to whether XY to WZ transition can occur back and forth. Theoretically such transitions seem possible. If the W chromosome looses from its SDR the *GYA* allele and retains *ana*, *gys* and *SA* alleles, the W can get converted into X chromosome. → XY → WZ → XY → transitions may be a mechanism to prolong the life of dioecy in a lineage.

It is visualized that XY and WZ systems of sex determination can coexist in different populations of a species and that interbreeding between members of the XY and WZ populations will result in fertile progeny.

X1X2Y and X1X2Y1Y2 variants of XY system of sex determination

Autopolyploidization in a species already having the XY system will double the number of X and Y chromosomes like that of autosomes. Since the dosage of X: Y: autosomes in male tetraploids and X: autosomes in female tetraploids will be in conformity of corresponding diploids, sex determination in diploids and tetraploids will be identical. Two examples (table 1) known are the tetraploid variety *Cordifolius* ($2n = 40$) of *Humulus luplus* ($2n = 20$) and natural tetraploid *Dioscorea floribunda* ($2n = 40$). In Bryonia, the diploid species *B. dioica*, tetraploid species *B. marmorata* and hexaploid species *B. cretica* are all dioecious (Volz and Renner 2008). Polyploidizations in dioecious lineages alone lead to multiple presence of sex chromosomes; if dioecy arises postpolyploidization single XY pair may be responsible for maleness as in the octaploid *Rumex acetocella* (Cunado *et al*. 2007). In *Viscum fischeri*, the males and females have, respectively the genotype X1X2Y and X1X1X2X2. It is visualized that a mechanism analogous to that which made possible generation of two different chromosomes (figure 4) can also create two different X chromosomes.

Age of sex chromosomes in dioecious plants

Heterogametic sex chromosomes Y and W of plants are of much recent origin than in some animals. Most ancient are the Y chromosomes of mammals that have been evolving for more than 250–300 million years ago (mya) (Skaletsky *et al*. 2003; Charlesworth 2012). Human Y chromosome is only one-third in size as compared to its counterpart X, contains only 78 genes (single or in multiple copies) and has become highly degraded (Skaletsky *et al*. 2003). The oldest Y chromosome in plants may be at least 10 times younger. Y chromosomes of some species in Silene (Bergero and Charlesworth 2011; Muyle *et al*. 2012; Rautenberg *et al*. 2012; Sousa *et al*. 2013) and Rumex (Blocka-Wandas *et al*. 2007) are estimated (Gaut 1998) to have originated less than 30 mya. The age of Y chromosomes in *Carica papaya* (Wang *et al*. 2012) and *Coccinia indica* (Holstein and Renner 2011; Sousa *et al*. 2013) have been estimated to be less than 7 mya. Plant W chromosomes are of more recent origin, less than 1 mya; exemplified by *Fragaria virginiana* (Spigler *et al*. 2008), here recombination occurs between the sex determining genes. The Y, W, U and V sex chromosomes of plants are to a degree protected against degeneration because some of their genes are required to be expressed at the gametophyte stages (Bachtrog *et al*. 2011). Despite this protective mechanism, Y chromosomes of Rumex species have undergone extensive heterochromatization and loss of function (Spielman *et al*. 2001; Navajas-Perez *et al*. 2005a, b, 2006; Cunado *et al*. 2007; Mariotti *et al*. 2009). Fact that mammalian Y chromosomes are surviving despite their origin ~250 mya means that there may be diverse mechanisms that prolong the life of Y and W chromosomes in animals and plants. Early amplification of essential genes is a mechanism of Y protection (Skaletsky *et al*. 2003). Trafficking of beneficial genes from autosomes to Y and deletion of deleterious loci from Y are identified to be two such mechanisms (Charlesworth and Charlesworth 2000; Ishizaki *et al*. 2002; Ma *et al*. 2004; Tanurdzic and Banks 2004; Bergero *et al*. 2007, 2008a, b; Yamato *et al*. 2007; Yin *et al*. 2008; Oyama *et al*. 2009; Spigler *et al*. 2010, 2011; Charlesworth 2012; Sackton and Hartl 2013; Vanburen and Ming 2013). Enlargement of PAR via translocations from autosomes may have role in providing viability and fitness to Y and W chromosomes for their long life (Carvalho 2002; Vellender and Lahn 2004; Bergero *et al*. 2007; Otto *et al*. 2011; Charlesworth 2012; Bergero *et al*. 2013).

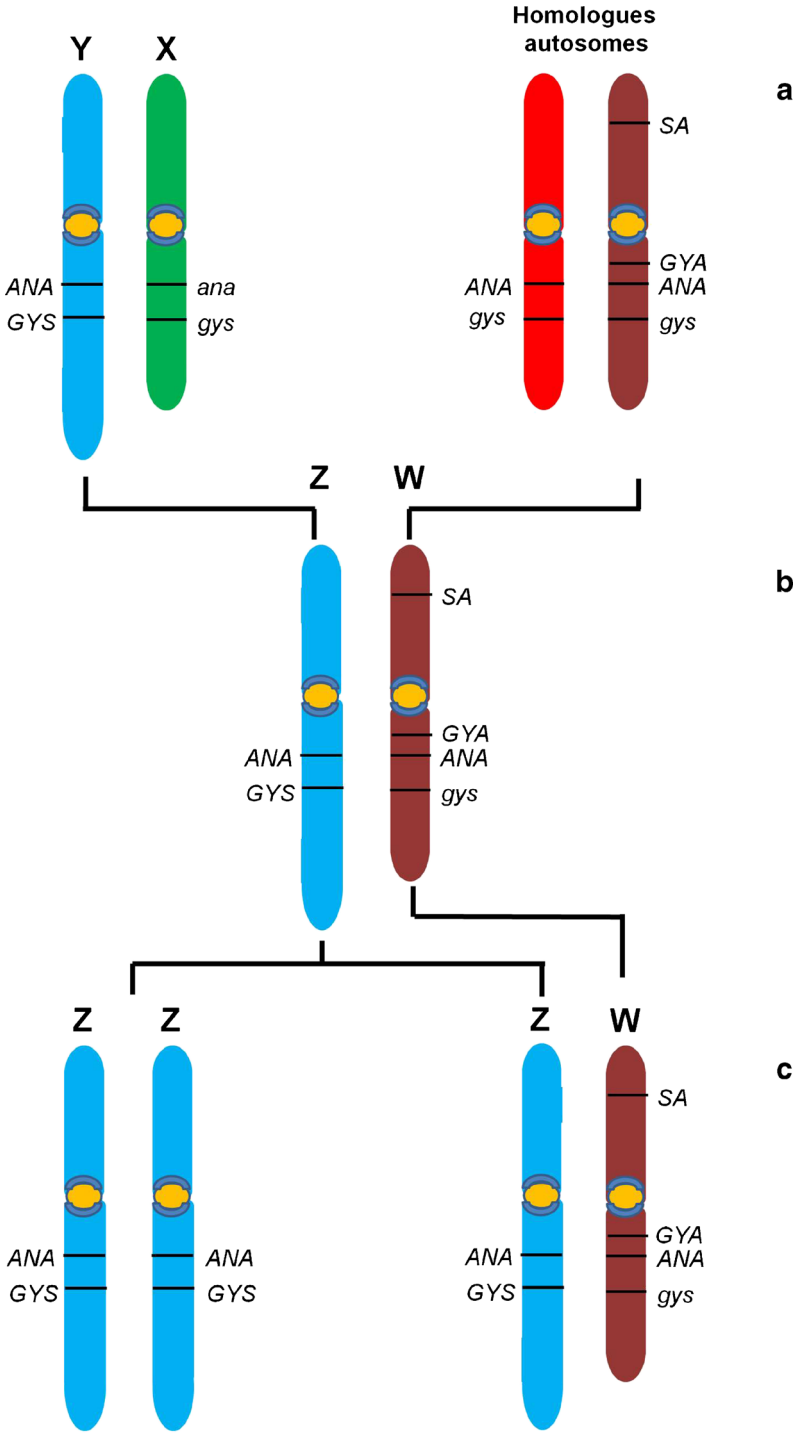

Figure 5. Delineation of a mechanism by which a XY sex determining system can transition into a WZ system. (a) On the left side an XY sex chromosome pair is shown. The Y chromosome (blue colour) carries the maleness promoting dominant alleles *ANA* and *GYS* and the X chromosome (green colour) has the *ana* and *gys* recessive alleles. On the right hand side are shown a pair of autosomes (brown colour) one number of which is to be recruited as the W chromosome (darker brown colour). Both the autosomes carry their naturally present *ANA* and *gys* alleles. The chromosome to become W acquires two more alleles, a *SEXUALLY ANTAGONISTIC* (*SA*) allele and a *GYNOECIUM ACTIVATOR* (*GYA*) allele, to become genetically tailored for promoting femaleness. The XY sex chromosomes and the autosomal chromosome pair are simultaneously present in the germline of the species undergoing XY to WZ transition. (b) The fertilization process has brought together in embryo the preexisting Y (now rechristened as Z) and the *SA* and *GYA* modified female specific chromosome now called W. The individual carrying WZ chromosomes now is a female. (c) Breeding between WZ female and XY or XZ males produces ZZ male and ZW female progeny. ZZ and WZ will now invade the population which hitherto comprised of XY and XX individuals and establish WZ system in the species. The diagram schematizes the origin of WZ heterogametic sex determining system prevailing in the genera *Populus* and *Silene* whose different species carry either XY system or WZ system of sex determination (table 1).

Lessons from the model dioecious species

At this time, relatively more information is available about the molecular genetics of dioecy in five plant species *Carica papaya, Silene latifolia, Rumex acetosa* and *Fragaria virginiana* and *Populus trichocarpus* (arranged in decreasing order of available information) than in other species. Some of the important information is summarized in table 6. Following lessons were comprehendable from the analyses of dioecy in species listed in table 6. (i) To maintain the genome of dioecious species in a condition such that recombination can continue to occur in SDR of sex chromosomes is identified as the means to keep dioecy young. It is envisaged that the species will have efficient DNA repair and meiotic recombination mechanisms and other processes that restrict invasion of genome by repeat elements, negate amplification and movement of repeat elements and allow their deletion. (ii) Maximization of the PAR in sex chromosomes via duplication of genes inherited from ancestral autosomes and translocations of genes from other autosomes, especially those that are activators of other genes borne on autosomes are also means for increasing the life of Y and W chromosomes. (iii) Features such as ploidy level, gene content of whole genome and that of autosome ancestors of sex chromosomes and nature of repeat elements that have invaded the genome at the time of inception of sex chromosomes, location of SDR on sex chromosomes and schedule and nature of mutations and sequence rearrangements that occurred in SDR are important determinants of the path that Y takes in its degradative evolution. Some paths may provide longer life to Y than others. (iv) Each dioecy has its own path of progression and life. (v) Since life of a dioecy is determinate, there is recurrent evolution of dioecy.

Correspondence between dioecious systems of animals and plants

As compared to plant kingdom, the animal kingdom is predominantly dioecious (Tanurdzic and Banks 2004). The reason for this difference is not understood. However, it will be seen from the table 7 that animal and plant dioecious species share most of the important features relating to origin and functioning of dioecy, evolution of sex chromosomes and degeneration of the heterogametic sex chromosomes. Dioecy in vertebrate animals is 300 million year old and the oldest among plants is not more than 30 million year (for reviews see Bachtrog *et al*. 2011; Charlesworth 2012). The large difference indicates that the average life of plant heterogametic sex chromosomes is rather small, perhaps about 10 million year. In both animals and plants Y and W chromosomes degenerate because of the same process, the Muller's ratchet. They lose genes inherited from ancestral autosome by various kinds of mutations in them and accumulate retrotransposons and a variety of other repeat sequences. Apparently heterogametic sex chromosome or Y chromosome degeneration occurs faster in plants than in animals. Biotic and abiotic stresses are known to lead to accumulation of repeat sequences and mutations by causing loss of cytosine methylation from genome. The transposons get induced and demethylated cytosines serve as hot spots for mutations to occur (see for a review Kumar *et al*. 2013a). Plants being sessile, they get exposed to stress much more than animals. Greater exposure to stress may be one reason for the shorter life of Y chromosome in plants. The other reasons may concern the nature of genomic karyotype and gene content of autosomes that serve as ancestors of sex chromosome. It is known that in vertebrates same autosomes have served as the ancestral chromosomes for sex chromosomes in many species of different genera (Graves 2006; Ezaz *et al*. 2006; Graves and Peichel 2010). Acquirement in *Drosophila melanogaster* Y chromosome of genes that positively regulate autosomal genes in tissue-specific manner is also a means to increase the life of Y chromosome (Sackton and Hartl 2013). Interestingly, all species of 55 genera of the plant family Salicaceae are dioecious. In the species of the genera Populus and Salix that have been studied, recombination continues to occur in the SDR (Yin *et al*. 2008; Tuskan *et al*. 2012). In species where Y continues to be young for long period, the DNA repair and meiotic recombination process may be highly proficient. Why the life of plant Y chromosomes is shorter than say primate Y chromosomes is a mystery?

Evolutionary future of dioecy

Dioecy promotes outbreeding and thereby increase in genetic variation. It supposedly arises in species suffering from inbreeding depression due to selffertilization in hermaphrodite flowers. Origin of dioecy is thought to be independent in each species (Diggle *et al*. 2011; McDaniel *et al*. 2012; Kafer *et al*. 2013). Dioecious species face extinction on account of degeneration of their heterogametic sex chromosomes (Bachtrog *et al*. 2011; Kafer *et al*. 2013). Extinction is delayed for various periods of time by means of a variety of process that allow the essential genes of SDR to remain functional and/or continuance of genetic recombination in PAR of sex chromosomes. The fossil evidence indicates that plant and animal species have gone extinct due to their maladaptation to changes in the environment of their habitat (reviewed in Kumar 2007). What happens to the dioecious species whose heterogametic sex chromosomes are undergoing degeneration, but species are not facing any destructive environmental change, is an open question? Do the dioecious species simply die out or do they hybridize with other species and pass on their genome to new species? Evolution of dioecy may be a component of the cycle: → new species → dioecious species → new species → (figure 6).

Table 6. Common and distinguishing characteristics of dioecy revealed by molecular genetic analyses of sex chromosomes in plant species of differing age of dioecy.

		Name of species and estimated age of dioecy (million years)			
	Characteristic	*Actinidia chinensis*, *Asparagus officinalis*, *Fragaria virginiana*, *Populus trichocarpa* (1-2)	*Carica papaya* (< 7)	*Rumex acetosa* (20)	*Silene latifolia* (< 30)
1	Presence of supermales, neuters and/or hermaphrodites in addition to males and females in progeny, indicating occurrence of recombination in SDR	Yes	No	No	No
2	Location of SDR near to centromere on sex chromosomes	Not known	Yes	Not known	Yes
3	Whether inversions present in SDR that suppress recombination	No	Yes	Yes	Yes
4	PAR present near to sex chromosome tips	No, PAR is extensive	No, PAR is extensive	Yes	Yes
5	Y (or W) chromosome is larger than X (or Z)	No	Yes	There are two Ys; together they are larger than X	Yes
6	Y is required both for formation of male flowers and male fertility	Yes	Yes	No, Y is required only for male fertility	Yes
7	Y has many functional genes	Yes	Yes	No	Yes
8	Level of expression of Y borne genes is lower as compared to X borne genes	Not expected	Not known	Not known	Yes
9	In Y, many genes inherited from autosome ancestor have loss-of-function mutations	Not expected	Yes	Yes	Yes
10	There is transcriptional inactivation of one X and dosage compensation	Not expected	No	Not known	Yes
11	Y is degenerated by addition of a variety of repeat elements (TE, transposable element insertions) and some of these sequences are organeller and some have no homology with any known plant DNA	No	Yes	Yes	Yes
12	Ectopic recombination within Y enlarges TE sequences as well as causes their deletion	Not expected	Yes	Not known	Yes
	References	Testolin *et al*. (1995, 2001); Harvey *et al*. (1997); Gill *et al*. (1998); Mariziani *et al*. (1999); Semerikov *et al*. (2003); Ashman (2005); Yin *et al*. (2008); Telgmann-Rauber *et al*. (2007);	Skaletsky *et al*. (2003); Liu *et al*. (2004); Ma *et al*. (2004); Yu *et al*. (2007, 2008a, b); Ming *et al*. (2008); Wu *et al*. (2010); Gschwend *et al*. (2012); Na *et al*. (2012);	Rejon *et al*. (1994); Shibata *et al*. (1999); Navajas-Perez *et al*. (2005a, b, 2006); Blocka-Wandas *et al*. (2007); Cunado *et al*. (2007); Mariotti *et al*. (2009); Steflova *et al*. (2013)	Ye *et al*. (1990); Desfeux *et al*. (1996); Vyskot *et al*. (1993); Farbos *et al*. (1999); Lardon *et al*. (1999); Filatov *et al*. (2000, 2001); Filatov and Charlesworth (2002); Uchida *et al*. (2002);

Table 6 (*contd*)

Characteristic	Name of species and estimated age of dioecy (million years)			
	Actinidia chinensis, *Asparagus officinalis*, *Fragaria virginiana*, *Populus trichocarpa* (1-2)	*Carica papaya* (< 7)	*Rumex acetosa* (20)	*Silene latifolia* (< 30)
	Paolucci *et al*. (2008); Spigler *et al*. (2008, 2010, 2011); Fraser *et al*. (2009); Tuskan *et al*. (2006, 2012); Deng *et al*. (2012)	Tenaillon *et al*. (2011); Wang *et al*. (2012); Vanburen and Ming (2013) Singh and Smith (1971)		Pritham *et al*. (2003); Filatov (2005a, b); Ironside and Filatov (2005); Laporte *et al*. (2005); Nicolas *et al*. (2005); Zluvova *et al*. (2005, 2007); Hobza *et al*. (2006, 2007); Kejnovsky *et al*. (2001); Scotti and Delph (2006); Bergero *et al*. (2007, 2008a, b, 2013); Macas *et al*. (2008); Marais *et al*. (2008); Mrackova *et al*. (2008); Rautenberg *et al*. (2012); Bernasconi *et al*. (2009); Howell *et al*. (2009a, b); Kaiser *et al*. (2009); Mariotti *et al*. (2009); Delph *et al*. (2010); Bergero and Charlesworth (2011), Chibalina and Filatov (2011); Blavet *et al*. (2012); Muyle *et al*. (2012); Blavet *et al*. (2012); Kafer *et al*. (2013) Grabowska-Joachimiak and Jochimiak (2002) Lebel-Hardenack *et al*. (2002) Rautenberg *et al*. (2010) Zluvova *et al*. (2010) Carroll and Mulcahy (1993)

Table 7. Some features noted as common among certain dioecious animals and plants[a].

Feature	Description
Evolutionary environment for the origin of dioecy in species	Paucity of genetic variability due to small population size and low mutation and or recombination rates
Genetical sex determination systems	Three types of sex determination: XY type = homogametic XX females and heterogametic XY males; WZ type = homogametic ZZ males and heterogametic WZ females; and X0 type = homogametic XX females, and single X no Y males
Origin of sex chromosomes	Inception of heterogametic sex chromosome system by occurrence of a recessive mutation for loss of maleness in the proto-X chromosome and a dominant gain-of-function mutation for the suppression of femaleness on proto-Y chromosome and thereby creation of sex determining region (SDR) on the proto-X and proto-Y chromosomes
Environmental sex determination	Maleness or femaleness determining genes regulated via an environmental cue such as high/low temperature
Subdioecy	Occurrence of males, females and hermaphrodites in populations of species because of recombination within SDR
Ancestory of sex chromosomes	Sex chromosomes arise from autosomes. Same pair of autosomes can be ancestral for species of same genus or of different genera. Different autosome pairs may be ancestoral for different populations of a species or different species of a genus
Cooccurrence of XY and ZW system	Different populations of a species can have XY and WZ systems of sex determination
Homomorphic sex chromosomes	X and Y, W and Z and U and V are called homomorphic when they have identical cytology
Heteromorphic sex chromosomes	Sex chromosomes are heteromorphic when cytological differences in morphology are present in X versus Y, W versus Z and U versus V
Heterogametic sex chromosome (Y or W) degeneration	Loss-of-function mutations of various types inactivate genes present in SDR and SDR accumulates repeat elements, including transposons, and organelle sequences (mitochondrial in animals and chloroplastic and mitochondrial in plants) in abundance, in Y, W, U and V chromosomes
Duplication of genes	Y, W, U and V accumulate essential genes in more than one copy
Pseudoautosomal region (PAR)	Regions present on X and Y and W and Z that can recombine in meiosis
Male-biased mutation rate	Because larger number of meiotic cell divisions occur in the production of pollen in plants and sperms in animals than in production of female gametes, genes have greater chance of undergoing mutation in males than in females
Sexually antagonistic mutations	It is the process by which mutations get selected on sex chromosomes; the mutations selected on Y and Z are beneficial to males and detrimental for females and those selected on X or W are beneficial to females and detrimental to males
Dosage compensation	Mechanism that allows hyper-expression of genes borne on sex chromosomes to balance the expression levels of genes borne on autosomes

[a]Evidence is provided/referred to in the following publications: Charlesworth (1996a, b, 2002, 2012); Jaarola *et al.* (1998); Miller and Venable (2000); Atanassov *et al.* (2001); Okada *et al.* (2001); Bachtrog and Charlesworth (2002); Lindholm and Breden (2002); Charchar *et al.* (2003); Bachtrog and Gordo (2004); Liu *et al.* (2004); Albert and Otto (2005); Filatov (2005a, b); Steinemann and Steinemann (2005); Bachtrog (2006, 2008a,b); Matsubara *et al.* (2006); Weeks *et al.* (2006); Bergero *et al.* (2007); Eppley and Pannell (2007); Quinn *et al.* (2007); Yamato *et al.* (2007); Wu and Xu (2003); Jamilena *et al.* (2008); Spigler *et al.* (2008, 2010, 2011); Yin *et al.* (2008); Naurin *et al.* (2009); Charlesworth and Mank (2010); Fanchini *et al.* (2010); Graves and Peichel (2010); Kaiser and Bachtrog (2010); Mank *et al.* (2010); Prince *et al.* (2010); Bachtrog *et al.* (2011); Ming *et al.* (2011); Wang *et al.* (2012); Zhou and Bachtrog (2012); Sackton and Hartl (2013); Vanburen and Ming (2013); Greilhauber and Leitch (2013); Hamilton (1967); Marin *et al.* (2000); Ohno (1967); Price (1984); Turner (2007); Charlesworth *et al.* (2005); De Bodt *et al.* (2005); Ezaz *et al.* (2005); Frajman *et al.* (2009).

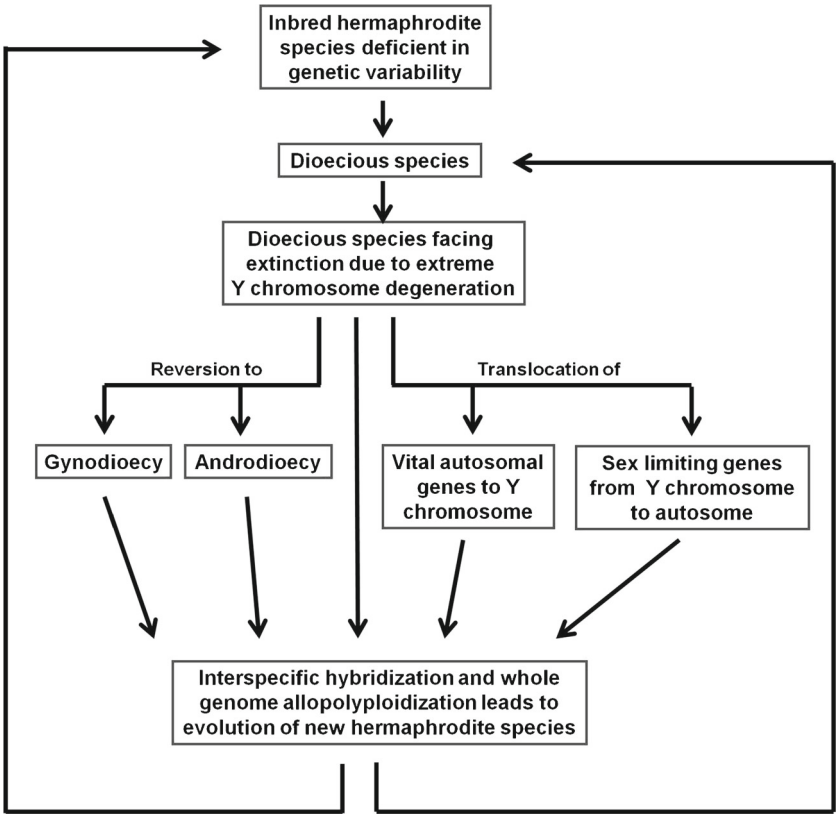

Figure 6. A scheme of the hypothesized evolutionary cycle for the sequential origin of plant species via the intermediacy of dioecy. A new species arises as a segregant from an ancestral interspecies hybrid having undergone a fertility ensuring whole genome duplication. Initially, despite the hermaphroditic sexual system, the species is rich in genetic variation. In time, genotype–environment led selections and selfing of hermaphrodite flowers cause inbreeding depression in the species. Advent of dioecy in the species brings relief in the form of increase in genetic variation because of unisexuality promoted outcrossing. A variety of mechanisms increase the life of dioecy. However, the degeneration of heterogametic sex chromosome takes the dioecious species towards extinction. Since the vitality of male sex has weakend, the females get crossfertilized with the pollen of foreign species. Successful hybrid so formed becomes the resource for the origin of one or more species. The cycle new species → dioecy → new species ensures dispensation of the degenerated chromosome(s).

Interspecific or intergeneric hybridizations followed by partial or whole genome duplication and biased retention of duplicated genes/chromosomal regions has been identified as the principal mechanism of evolution of angiosperm species and diversification of angiosperm lineages (De Bodt *et al*. 2005; Thomas *et al*. 2006; Magdum *et al*. 2013; Kumar *et al*. 2013b). The interspecies hybrids combine genomic contents of two parental species. Besides, their new genome undergo DNA demethylation due to genetic shock rendered by hybridity (reviewed in Kumar *et al*. 2013a). Genome scale demethylation allows amplification and movement of repeat elements and occurrence of all kinds of point and rearrangement mutations at the demethylated cytosine sites. Segregating populations of hybrids demonstrate considerable karyotypic variability and are therefore resources for one or more species via duplication of genomic karyotype(s) of original hybrid and/or of segregants, followed by selection for adaptation to environment and fertility. Initially, the populations of new species will be rich in genetic variation. In time, exercise of selective forces on the species may force them into dioecy. Presumably, genomes are tailored to give rise to new species via dioecy as the intermediate stage.

Applications in crop agriculture

In comparison to the hermaphrodite and monoecious species, dioecious species provide more controlled and efficient system for cross pollination to exploit hybrid vigour. Dioecy also offers possibilities of raising unisexual female or male plants in excess of the other. Since fruits are formed on female plants, production cost of fruits can be lowered by raising more female plants, by ensuring the pollination of female flowers. Another possible application is to produce seedless fruits, in crops like date palm and papaya. This will require induction of tetraploidy and a method for micropropagation of tetraploid females. Seedless fruits may form on tetraploid female plants by fertilization of their flowers with pollen from diploid males. Attempts need to be made to develop technology for seedless watermelon, pumpkin and

Benincasa hispida fruits. The means could be via crossing them with nearest dioecious species and repeated backcrossing of the unisexual segregants to the economically important species to obtain suitable male and female lines. Subsequently, tetraploid female lines could be developed for bearing the triploid fruits.

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