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Review

Sex Chromosomes and Sex Determination in Dioecious Agricultural Plants

Olga V. Razumova [1,2,*], Oleg S. Alexandrov [1], Karina D. Bone [1], Gennady I. Karlov [1] and Mikhail G. Divashuk [1]

1 All-Russia Research Institute of Agricultural Biotechnology, 127550 Moscow, Russia
2 Tsitsin Main Botanical Garden RAS, Botanicheskaya St., 4, 127276 Moscow, Russia
* Correspondence: razumovao@gmail.com

Abstract: Unlike in animals, dioecy among flowering plants is a rare phenomenon. The vast majority of angiosperm species have a bisexual flower that combines male (androecium) and female (gynoecium) reproductive organs. However, about a quarter of species have dioecious flowers, which can be located within the same plant (monoecious) or on different plants (dioecious). The flower formation in dioecious plants is determined by various genetic mechanisms. They become more complex from the work of a single gene to the functioning of full-fledged heteromorphic sex chromosomes, which can directly affect sex differentiation or participate in the balance determination of sex (where the formation of male or female flower organs depends on the ratio of X chromosomes to autosomes, for example). In recent years, the development of sequencing techniques, bioinformatics, and molecular biology has led to an increase in interest in the sex determination mechanisms among plants. It is noteworthy that a significant number of dioecious plants have economic value. At the same time, dioeciousness often complicates the growing process. This fact increases the relevance of studies on dioecious crops. In this review, we attempt to summarize the current information on sex chromosomes and the mechanisms of sex determination in dioecious plants, concentrating on species with agricultural importance.

Keywords: dioeciousness; flowering plants; monoecious plant; dioecious plant; sex chromosomes; dioecious crops; sex determination

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1. Introduction

Dioecy is a relatively rare phenomenon in the world of angiosperms. Dioecious species make up about 5–7% of angiosperms [1–3]. The active development of bioinformatics methods, reductions in the cost of whole-genome sequencing methods, and the creation of chromosome assemblies in recent years have opened up wide-ranging opportunities for studying the mechanisms of sex determination in plants. Using new technologies, it was confirmed that dioecy arose repeatedly, in different ways, and in evolutionarily distant species [4]. The events associated with the emergence of dioecy have occurred hundreds or even thousands of times. Reverse events (a return to monoecy or hermaphroditism) have also occurred [5–7]. Consequently, it is necessary to study the sex determination mechanisms in each individual case of dioecy occurrence. Additionally, data obtained on one species cannot be interpolated to other, even phylogenetically close species. At the same time, species with dioecious flowers are quite often (about in 20% of cases) cultivated as agricultural crops [8]. The dioecy of agricultural crops must be considered in industrial cultivation. On the one hand, dioecy can be beneficial for growers, since all flowers of female plants produce fruit and the plants do not waste resources on "less profitable" male flowers. On the other hand, dioecy can create problems. For example, the sex of plants is often unknown at the juvenile stage of ontogenesis. However, growers need to know the sex of the plants so that the ratio of female to male plants is optimal for efficient pollination when setting up a nursery. In other cases, the presence of male plants in a plantation is generally unacceptable, and they must be removed before the flowering phase. Sometimes, morphological or physiological differences between plants of different sexes must be considered in the production of products from dioecious species. Thus, it is essential to have tools for the early sex differentiation of seedlings.

It has been repeatedly reported that the frequency of dioecious species occurrence varies depending on geographical conditions. It is much greater in tropical and neotropical zones than in subpolar regions. Woody and climbing forms, as well as plants with succulent fruits distributed by animals, are also more likely to be dioecious than herbaceous plants with dry fruits [9]. What environmental factors lead to the appearance of dioecious species? What evolutionary mechanisms contribute to the fixation of dioecy in some species and its culling in others? Why are these dioecious species fixed in the course of evolution? What are the benefits of separating the sexes? These questions are still debatable. It was previously believed that a mutation in two genes is required for the occurrence of dioecy. This is the "two-gene model" [10,11]. However, recent research shows that this is not the only evolutionary path. The emergence of dioecious plants is also possible with a mutation in one locus ("single-gene model"). In nature, confirmations of both the first and second models have been found [12–17]. However, such models are created on the basis of the existence of natural selection in populations. They are incorrect for dioecious crops since these have been subjected to artificial selection for a long time. Despite these difficulties, modern methods of genomics and cytogenetics have helped scientists come to an understanding of the occurrence of dioecy, at least for some species.

The occurrence of dioecy does not always lead to the formation of heteromorphic sex chromosomes [18,19]. In addition, the degree of differentiation of sex chromosomes does not always correlate with the evolutionary age of dioecy in the species under study. Therefore, it is necessary to clearly differentiate the emergence and evolution of sex determination regions and heteromorphic sex chromosomes.

In recent years, the development of technologies for high-throughput genomic sequencing, the analysis of repeatomes and proteomes, GWAS (genome-wide association studies), and other omics technologies have raised the study of wildlife to a qualitatively new and deeper level. Having obtained data on simple model objects (Arabidopsis, *Drosophila* or *C. elegans*), researchers chose economically important plant and animal species as the next candidates for more detailed studies. At the same time, researchers immediately encountered a number of problems. In the case of plants, these problems usually include huge genome sizes (for example, *Triticum aestivum* genome 1C = 17.30 pg; *Allium cepa* 1C = 17.90 pg [20]) and a large amount of non-coding DNA that, in some species, makes up 50–85% of the genome size [21,22]. Dioecious crop species have additional challenges in accurate sequencing due to differences in genotypes between male and female plants (often more than 3% of the total genome size, for example, in *Humulus japonicus* or *Rumex* spp. [23,24]), the presence of a non-recombining region in the heterogametic sex, and a pseudoautosomal region (PAR) that greatly varies in size among species [25]. Despite these difficulties, a large amount of data about the genomes of various agricultural dioecious species has been accumulated to date (Table 1).

Table 1. Genetic characteristics of the most agriculturally important dioecious plants species.

Species	Sex Chromosome System	Genome Sequenced *	Molecular Markers	Reference
Asparagus officinalis	XX/XY	Yes	Yes	[26]
Rumex acetosa	XX/XY1Y2	No	Yes	[27]
Spinacia oleracea	XX/XY	Yes	Yes	[28]
Cannabis sativa	XX/XY	Yes	Yes	[29]
Piper betle	unknown	No	Yes	[30]

Table 1. *Cont.*

Species	Sex Chromosome System	Genome Sequenced *	Molecular Markers	Reference
Dioscorea cayenensis subsp. rotundata	ZZ/ZW	Yes	Yes	[31]
Carica papaya	XX/XY/XY	Yes	Yes	[32,33]
Vitis vinifera	monoecious	Yes	-	-
Diospyros kaki	XX/XY	Yes	Yes	[34]
Pistacia vera	ZW/WW	Yes	Yes	[35,36]
Hippophae rhamnoides	XX/XY	No	Yes	[37]
Humulus lupulus	XX/XY	Yes	Yes	[38]
Phoenix dactylifera	XX/XY	Yes	Yes	[39]
Myristica fragrans	XX/XY	No	Yes	[40]
Actinidia chinensis	XX/XY	Yes	Yes	[41]
Ilex paraguariensis	unknown	Yes	No	-
Morella rubra	ZW/WW	Yes	Yes	[42]
Amaranthus palmeri	XX\XY	Yes	Yes	[43]

* All information about the availability of genome sequences is presented according to the NCBI website.

Here, we attempt to summarize the data available to date for a number of major cultivated dioecious crops, paying special attention to the influence of dioecious nature on the agronomic features of their cultivation (Table 2).

Table 2. Particular qualities of the most agriculturally important dioecious plants species.

Life-Forms	Species	Common Name	Part of a Plant Used by Humans	Direction of Use	What Type of Plants Are Used
Grass annual or perennial	*Asparagus officinalis*	Asparagus	Stock	Vegetable	Male or supermale
	Rumex acetosa	Sorrel	Leaves	Green crops	Male and female
	Spinacia oleracea	Spinach	Leaves	Green crops	Male and female
	Cannabis sativa	Hemp	Leaves, seeds, fibers,	Industrial, food or medicinal use	Female, male and monoecious
	Piper betle	Betel leaves	Leaves	Medicinal	Male and female
	Dioscorea spp.	Yam	Modified tubers	Food	Male and female
	Amaranthus palmeri	Green amaranth	-	Weeds	-
Woody perennial	*Carica papaya*	Papaya	Fruit	Fruit crops	Hermaphroditic
	Vitis vinifera	Grape	Fruit	Fruit crops	Only wild forms are dioecious; varieties of cultivated grapes are hermaphroditic
	Diospyros sp.	Persimmon	Fruit	Fruit crops	Female or monoecious; male needed for pollination
	Pistacia vera	Pistacia	Fruit	Nut-bearing crops	Female; male needed for pollination
	Hippophae rhamnoides	Sea buckthorn	Fruit	Berry crops, medicinal	Female; male needed for pollination

Table 2. *Cont.*

Life-Forms	Species	Common Name	Part of a Plant Used by Humans	Direction of Use	What Type of Plants Are Used
	Humulus lupulus	Hop	Fruit	Hop culture	Female; male plants are only needed for breeding to develop new cultivars
	Phoenix dactylifera	Date palm	Fruit	Fruit crops	Female; male needed for pollination
	Myristica fragrans	Nutmeg	Fruit	Cultural spices	Female; male needed for pollination
	Actinidia chinensis	Kiwifruit	Fruit	Fruit crops	Female; male needed for pollination
	Ilex paraguariensis	Yerba Mate	Leaves	Tea crops	Female and male
	Morella rubra	Chinese Bayberry	Fruit	Fruit crops	Female; male needed for pollination

2. Features of the Dioecious Crop Cultivation

2.1. Sex Chromosomes and Sex Determination in Herbaceous Crops

As a rule, vegetative parts are used in herbaceous dioecious crops, and their cultivation often does not need sexing, as in the cultivation of perennial fruit crops. However, many herbaceous dioecious plants are convenient model objects for laboratory studies. They demonstrate rapid growth and development, bloom in the first or third year, do not require large areas, and are easily introduced into in vitro cultures. Therefore, the sex chromosomes and mechanisms of sex determination in cultivated herbaceous plants have been most fully studied. Molecular sex markers for many of them have been created, although they is little demand for them in industry. At the same time, there is evidence that the male and female plants of some herbaceous crops may differ in productivity, regrowth time and technical characteristics [44].

2.1.1. Asparagus

The *Asparagus* genus includes about 200 species, among which there are hermaphroditic, dioecious, and monoecious representatives, but *Asparagus officinalis* L. has the greatest popularity in production [45]. Garden asparagus is an economically important perennial herbaceous vegetable crop that is widely grown in Asia, Europe and the Americas. The leader in production is China, and the sown area of this crop around the world is constantly increasing [46]. Juicy young shoots are used for food.

This is one of the first dioecious plants in which sex determination was studied [47]. Asparagus plants are diploid, 2n = 2x = 20, and their sex chromosomes are homomorphic and do not visually differ from each other [48,49]. The female plants are homogametic and have XX chromosomes (also known as genotype mm) in their karyotype, while the male plants are heterogametic (XY\Mm karyotype). At the same time, the homogametic karyotype YY (MM), the so-called supermale, is viable, has fertile pollen, and is androdiecious in phenotype—that is, it has male and hermaphrodite flowers. The viability of the YY homozygote indicates the early stages of the dioecy evolution path with the young Y chromosome [50]. The mechanism of sex regulation in asparagus is one of the most studied among dioecious plants. A small M locus (835 kb in size) located on homomorphic sex chromosomes is responsible for sex determination in this species [12]. The development of male and female reproductive organs requires the presence of two key genes located on the sex chromosomes. These are the gene that suppresses female function (SOFF) and the gene that promotes the development and functioning of the tapetum (aspTDF1). Transcriptome analysis revealed more than 500 differently expressed genes in male and female plants [51].

Asparagus DNA methylation was studied using whole-genome BS sequencing (bisulfite sequencing) [52]. A difference was found in the DNA methylation containe d in male and female flowers. However, no difference in methylation was found in the genes responsible for the formation of flowers.

Male and supermale plants are preferred in asparagus production [44,53]. Male plants have been shown to have higher shoots per plant, increased yield, early maturity, and increased longevity [54,55]. Therefore, attempts are being made to create hybrids only consisting of male plants. They are created in ways such as the cultivation of anthers in vitro followed by dihaploidization with colchicine [56,57] and the self-pollination of andromonoecious plants. The cultivation of anthers leads to the formation of supermale plants, which are extremely rare in natural populations. In the production of asparagus, rhizomes are planted, and the sex can only be determined after flowering, which occurs in the second or third year. In this regard, the development of molecular markers, which make it possible to identify male, female, and supermale plants at the early stages of germination, seemed relevant. To determine the sex of garden asparagus, different types of markers have been developed (RAPD [56], RFLP [58], AFLP [59,60], and SSR [61]). Currently, the most interesting and relevant marker is RM17, developed by Stone et al. using whole-genome sequencing data [62]. This marker is codominant—that is, it is able to detect not only male and female but also supermale plants.

2.1.2. Sorrel

The *Rumex* genus is one of the largest in the Polygonaceae family—it has about 200 species [63,64]. Sorrel is a perennial herbaceous crop. *Rumex* spp. differ according to their economic importance. Some species (primarily *R. acetosa*) are cultivated for food consumption, while others (*R. obtusifolius*, *R. crispus*, and *R. acetosella*) are a big problem for agriculture because they are weeds in some regions of Europe, North America and Asia [65–67]. In nature, *Rumex* spp. are widely distributed in Eurasia, North America, Africa, mainly in the Northern Hemisphere. In culture, sorrel is primarily known as a traditional plant in Europe and Asia. Being adaptable to various conditions, it is widely grown throughout Russia in household plots. According to the N. I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR) classification, it is introduced into cultures, selection is carried out, and new varieties are created [68]. Some species of sorrel are used as fodder crops [69]. Additionally, sorrel species are rich in secondary metabolites, primarily flavonoids and antioxidants. Because of this, they are used in traditional medicine around the world. The use of sorrel substances to create medicines is widely studied [63,70,71].

The *Rumex* genus is one of the model groups for studying sex determination in plants [72]. Therefore, sex determination and sex chromosomes are widely studied in a number of *Rumex* species. Among these species, there are various systems for determining sex and sex chromosomes (completely hermaphroditic species, monoecious species with XY chromosomes and an active Y chromosome, and species with X:A balance sex determination, including multichromosomal species with the XY1Y2 system). Species such as *R. acetosa*, *R. acetosella*, *R. hastatalus*, and *R. suffruticosus* are dioecious and widely studied. The *R. acetosa* karyotype consists of 12 autosomes and sex chromosomes (XX in female plants and the XY1Y2 multichromosomal system in male plants) [73–76]. The sex chromosomes are the largest in the karyotype. Two Y chromosomes contain 26% of the total DNA. Sorrel Y chromosomes are heterochromatic and rich in repetitive DNA sequences [77]. In 1999, a group of tandem repeats specific to male sex chromosomes were isolated and called RAYSI (*Rumex acetosa* Y-chromosome-specific I) [78]. After that, a number of satellite DNA repeats specific for sorrel Y chromosomes were described. The repeat sequences of RAYSII and RAYSIII are AT-rich and show about 60% homology with RAYSI [73]. Repeat satDNA RAE180 is localized on two Y chromosomes and is also present on a pair of autosomes. [79]. In addition, it was shown that, in addition to satellite DNA, mobile elements played an important role in the evolution of sorrel Y chromosomes [80]. At the moment, we have not been able to find information about any differences in economically valuable traits in the male and female plants of *R. acetosa*. However, there is evidence of different morphologies in male and female plants in *R. lunaria* depending on temperature and humidity [81]. This trait can potentially affect yield, but there are no data on the economic efficiency of growing male and female plants of this crop.

2.1.3. Spinacia

Spinach is a perennial herbaceous plant of the Chenopodiaceae family. It has been cultivated for over 2000 years. In industry, vegetable spinach (*Spinacia oleracea* L.) is primarily used [82]. Two related wild-growing species (*S. tetrandra* and *S. turkestanica*) with sex chromosomes are studied and used for the breeding improvement of this species [83]. Spinach leaves are eaten fresh or cooked. Spinach is cultivated in more than 50 countries around the world, and China is the leader in production [28,84]. The karyotype of *S. oleraceae* is 2n = 2x = 12. Male plants are heterogametic [85]. Like asparagus, the spinach sex chromosomes are evolutionarily young and homomorphic [86,87], and the YY karyotype is viable. It can be formed by self-pollination of andromonoecious XY plants, resulting in supermales. There are individual monoecious genotypes [88].

Currently, the spinach genome has been sequenced, including by PacBio and Hi-C scaffolding. The sex determination region (SDR) was determined; it is located on chromosome 1 or 4 (according to other sources) [28]. It has been shown that the size of the SDR is 24.1 Mb on the Y chromosome and 13 Mb on the X chromosome. At the same time, the SDR on the Y chromosome contains inversions (14.1 Mb) and duplications (10 Mb) that are specific for male plants [89].

Studies have shown differences in morphological traits between male, female, and monoecious spinach plants. Vitale et al. (1985) showed that male and female plants significantly differ in height and the biomass of roots and the vegetative part while monoecious (cosexual) plants differ in the studied traits between both male and female plants [90]. Another study revealed differences in the response of spinach plants of different sexes (for example, in yield) when fertilized with selenium. Female plants were more productive and contained fewer heavy metals than male plants when selenate was applied. In addition, the contents of vitamin C, chlorophyll and carotenes increased in female plants [91]. Similar data showing that male spinach plants are taller than females but that females have a higher biomass were obtained in a later study. The response to biotic stress was also found to differ depending on the sex of the spinach [92].

2.1.4. Hemp

Hemp is an extremely polymorphic species of the Cannabaceae family, the only species of the monotypic *Cannabis* genus. Normally, these are dioecious plants, with the XX/XY system of sex chromosomes and the 2n = 2x = 18 + XX/XY karyotype [93]. The *Cannabis sativa* genome has been completely sequenced (including by modern PacBio methods). The genome size is 818 Mb for female plants and 843 Mb for male plants [94–97]. Transcriptome analysis has revealed sex-related genes.

Hemp is one of the oldest cultivated crops. According to some data, its domestication is estimated to have occurred 7000–10,000 years ago [98,99]. The cannabis sex chromosome system is also very ancient [18]. It is a multifunctional crop grown for oil and fiber, which are used in the manufacturing of biocomposite materials, as well as in the food and paint industries. Hemp is also widely known as a plant for medicinal use. According to some reports, more than 25,000 products are obtained from hemp [100]. Currently, hemp is considered one of the "greenest" crops. It is considered to have a negative carbon footprint—that is, more CO_2 is absorbed during its cultivation than is emitted [101]. In the middle of the 20th century, the area covered by this crop was declining, but in recent years, hemp has become increasingly popular, and its production has increased [100]. Due to the presence of addictive alkaloids in plants (primarily tetrahydrocannabinol (THC) and cannabidiol), cannabis cultivation is strictly regulated in many countries.

Hemp is one of the few annual agricultural herbaceous plants that are dioecious in nature. In addition, male and female cannabis plants differ in habit. The dioecy of hemp seriously affects its agricultural practices. Male and female plants differ in ripening time.

Female plants are leafier, have more lignified cell walls due to the better (compared with male plants) accumulation of lignin, bloom later, and stay green for longer [102]. These features lead to different levels of fiber quality when growing hemp as a textile crop. Cultivation technology requires expensive and time-consuming manual weeding. When growing hemp for oil, more female plants and fewer male pollinating plants are required. When growing female cannabis plants for medicinal purposes, pollination should not be allowed, since unpollinated flowers are characterized by a higher THC content. In this case, the presence of male plants in the population is undesirable. In this regard, the cultivation of monoecious varieties is more cost-effective [103]. The nature of hemp's monoecy is not yet fully understood. A number of studies have shown that monoecious varieties are female in their genetic nature and have an XX karyotype [104] and a genome size similar to female plants [105]. Male plants have 18 autosomes and XY chromosomes in their karyotype. At the same time, sex is determined according to the balance mechanism.

To recognize the sex of plants at any stage of cultivation, molecular genetic markers have been developed in hemp [29,106,107]. However, due to the annual nature of the culture, it seems more promising to create monoecious varieties. However, the ratio of male to female flowers in monoecious plants, as well as the sex of cannabis plants in general, is a very unstable trait. There have been cases of the appearance of flowers of the opposite sex in dioecious plants, as well as sex changes under the influence of environmental factors [108–111]. In this regard, a detailed understanding of the mechanisms of the occurrence of dioecy in hemp, as well as the potential opportunity to influence this trait, is of undoubted agronomic importance.

2.1.5. Betel

Betel (*Piper betle* L.) is a perennial evergreen dioecious vine of the Piperaceae family. This crop is economically significant for Asian countries, primarily for India, where it is one of the most important export crops [112]. Betel is grown for its leaves, which are chewed after meals and widely used in traditional medicine in the countries of Central and Southeastern Asia [113–117]. This plant also has important religious and ceremonial significance. Traditionally, this culture is vegetatively propagated [118]. Betel rarely blooms, but there have been reports of economically significant differences in the varieties of male and female plants [30]. There is very little information about the chromosome numbers and the level of ploidy of this species. The main number of chromosomes of this species is $x = 13$; however, polyploid rows are reported in this culture. Apparently, plants with a high level of ploidy are mainly grown. It was shown that female plants are tetraploid and have 52 ($2n = 4x = 52$) chromosomes in their karyotype, while male plants are triploid and have 39 chromosomes ($2n = 3x = 39$) [119]. Sex markers have been created for betel plants, mainly to accompany the breeding process, which is currently not very developed due to the complexity in the biology of the culture [30,120,121].

2.1.6. Yams

Yams (*Dioscorea rotundata*) are one of the most important crops in a number of countries, primarily in the African continent, where Nigeria, Ghana, Côte d'Ivoire, and Benin are considered leaders in the production of yams [46]. The plant is grown for the production of tubers, which are then used for food. Normally, *D. rotundata* is a dioecious species; however, cases of monoecious occurrence have been observed. Despite the huge role of this crop in African countries, the selection of this species is difficult, largely due to its dioecious nature and problems with flowering (it is predominantly a vegetatively propagated crop) [122,123]. In addition, a change in the sex of plants under the influence of the environment is repeatedly observed during the growing season, which also complicates the breeding process of this crop [124]. The identification of sex chromosomes in yams is also difficult [125]. However, using modern sequencing techniques, the ZZ/ZW sex determination system has been demonstrated [125]. In 2020, the first yam genome obtained as long reads using the Oxford Nanopore Technologies technique was presented [126].

A number of studies have shown that the yam sex determination system is apparently multigenetic and probably still evolving [122,126–128].

2.2. Sex Chromosomes and Sex Determination of Perennial Tree Crops Grown for Fruits

Most dioecious species are perennial tree crops [129]. One of the differences between perennial tree crops and annual and perennial herbaceous crops is a long juvenile period—the reproductive stage often only occurs by the age of 5–8. This feature causes difficulties in growing such plants, since most perennial tree crops are cultivated for the fruits and seeds that appear from the ovary located on the female plants. Revealing the mechanisms of sex determination and the early diagnosis of the sex of such crops are critical tasks for production and breeding. The accumulation of repetitive DNA sequences in sex chromosomes may contribute to the development of sex-associated molecular markers, which is especially important for agricultural plants with a long juvenile period. In cultures such as papaya (*Carica papaya* L.), lychee (*Litchi chinensis* Sonn.), rambutan (*Nephelium lappaceum* L.), and longan (*Euphoria longan* Steud.), the sex determination system is complex. There are not only dioecious plants but also hermaphroditic, gynodioecious, and monoecious plants in the population.

Perennial tree crops grown for their vegetative parts are also found. The production of these crops generally does not require knowing the sex of the plant. However, some agronomically important indicators for these crops (the same as those described above for annual plants) may differ depending on the sex [130].

2.2.1. Papaya

Papaya (*Carica papaya* L.) is one of the most widely studied model plant species with sex chromosomes. The genome and SDR in papaya are the most widely studied among dioecious plants. Many molecular markers have been created to identify the sex of papaya plants, the genome and transcriptome of this species have been sequenced and assembled, sex chromosomes have been observed, and gene dose compensation and sex-related epigenetic modifications have been noted [131–137]. The papaya sex chromosomes were the second to be fully sequenced after the human sex chromosomes [137]. They are evolutionarily young and outwardly practically homomorphic [11,138]. One of the features of papaya is the presence of hermaphroditic plants—in fact, it is a trioecious species, not a dioecious species. There are two types of Y chromosomes in this species. The first type is represented by the Y chromosome, which is found in male plants. The second type is represented by the Yh chromosome, which causes the hermaphroditism of flowers. At the same time, the YY, YYh, and YhYh genotypes are lethal [33,139]. The non-recombining region on the Y chromosome of papaya was formed as a result of two inversions of retrotransposons and is 8.1 Mb, while the size of the analogous region of the X chromosome is 3.5 Mb. All genes in non-recombining regions have been annotated [140]. Wild papaya is generally dioecious but cultivated as a rule of the gynodioecy cultivar [131]. It has been shown that evolutionarily hermaphroditic plants have been fixed for about 4000 years during domestication [141]. In addition to differences in the ease of cultivation (when growing hermaphroditic plants, male pollinating plants that do not produce fruits are not needed) between female and hermaphroditic plants, there is dimorphism in the shape of the fruits. Fruits from hermaphrodite flowers are more elongated and commercial producers prefer them, rejecting the more rounded fruits of female plants [137]. However, plants can change the sex of their flowers during the growing process. Hermaphroditic flowers can stop the development of carpels, turning into functionally male flowers under the influence of environmental factors such as drought or high temperatures [142–144]. Such phenomena lead to economic losses. It is necessary to create varieties that are less susceptible to environmental factors [145].

2.2.2. Vitis

Grapes are another perennial fruit species in which domestication appears to have perpetuated spontaneous monoecy. The wine grape (*Vitis vinifera* L.) is one of the most economically important fruit crops in the world. It is the third most important, after the tomato and potato, among all horticultural crops [146]. The *Vitis* genus includes about 70 species, all of which are dioecious, and only the cultivated grape *V. vinifera* ssp. vinifera is monoecious, although the wild subspecies *V. vinifera* ssp. sylvestris is also dioecious [147]. It has been shown that the emergence of hermaphroditic forms occurred about 6000–8000 years ago at the time of the domestication of wild grapes [5,148,149]. Like papaya, grapes have three sex-determining loci—Y (M) is male, X (F) is female, and Yh (H) is hermaphroditic. Unlike papaya, the HH, HM, or MM genotypes are viable in grapes. Three sex-linked grape genes (ViviPLATZ, VviFSEX, and APRT3) have been described, and the expression of each differs in hermaphroditic plants [149].

2.2.3. Diospyros

Sex reversion from dioecious to monoecious species in *Diospyros* spp. also occurred as a result of a polyploidization event. *Diospyros* is a very large genus of the Ebenaceae family, which includes several hundred species [150]. Some species of persimmons are edible, but *Diospyros kaki* L. is of the greatest economic importance. This species is widely grown in Asia (more than 80% of world production) and Europe (about 10%) for its fruits [151]. It is an autopolyploid species with 2n = 90 or 135 chromosomes (2n = 6x; 2n = 9x; x = 15) [152]. Despite the presence of at least one Y chromosome in the karyotype, this species is usually monoecious or has completely female plants, with rare male flowers [34]. Recent studies have shown that in the dioecious diploid species *D. lotius* L. (a close relative of *D. kaki*), the *OGI* gene located on the Y chromosome is responsible for sex formation. It encodes a small RNA that targets the autosomal *MeGl* gene, regulating anther fertility in a dose-dependent manner. In polyploid species (*D. kaki,* in particular), there is an insertion of a retroelement, named Kali, in the promoter region of the *OGI* gene that prevents the synthesis of small RNA and promotes the development of monoecy. The authors do not exclude that this mutation, which led to monoecy, could also be fixed as a result of artificial selection [19].

2.2.4. Pistachio

Pistachio (*Pistacia vera* L.) is an economically significant crop for Turkey, Iran, the USA, and a number of other countries [46]. It is a dioecious plant species, where females are needed in production but male plants are needed for pollination. There are also monoecious cultivars [153,154]. From the point of view of the evolution of sex and sex chromosomes, this crop is interesting regarding the ZZ/ZW (2n = 30) system of sex chromosomes [155]—that is, the heterogametic sex of the pistachio is female, like birds or some insect species. This system of sex chromosomes is rare in plants. A recent study on sequencing and assembling the genomes of the male and female plants showed that the pistachio W sex chromosome arose from three successive inversions [156].

2.2.5. Hippophae

Sea buckthorn (*Hippophae rhamnoides* L.) is a berry crop of the Elaeagnaceae family. It is a very commercial, extremely polymorphic species with many subspecies (*Hippophae* has about six to seven species in addition to sea buckthorn) [157,158]. All plants of this genus are strictly dioecious. Sea buckthorn berries contain a large number of vitamins and biologically active substances, and they are used in fresh and cooked food. The oil is obtained from the seeds of sea buckthorn, as well as from the pulp of the fruit. It contains linoleic and linolenic acids, carotenes, fatty acids (primarily omega-3, omega-6, omega-9, and palmitoleic acids), and stearic acids. This is a multipurpose plant, the fruits of which are classified as "superfoods" [159–161]. The ability to enter into symbiosis with nitrogen-fixing bacteria and resistance to adverse environmental conditions (drought, high and low temperatures, etc.) makes sea buckthorn a promising crop for growing in poor and polluted soils, as well as for land remediation. Sea buckthorn is most widespread in Asia, including China, India, and Russia. In Europe, it is popular in Germany, Sweden, and Denmark [162]. The sea buckthorn karyotype consists of 24 chromosomes (22 autosomes and a pair of X/Y sex chromosomes) [163]. In the genome (about 2.6 pg in size), researchers have observed a uniquely large number of satellites that may turn out to be good cytogenetic markers [163–165]. The development of molecular markers to determine the sex of sea buckthorn in the early stages of cultivation has been quite successful, but our experiments have shown the unstable operation of these markers, which may be due to sea buckthorn's polymorphism [166–168]. Morphologically, male and female plants can only be distinguished by their generative buds after flowering age has been reached. At the same time, mainly female plants are needed in agricultural production. Additionally, breeding is carried out independently for male pollinating plants and female plants [169]. These facts demonstrate the need for a deeper study of the genetic determination of the sex in sea buckthorn.

The closest relatives of sea buckthorn are dioecious plants from the *Shepherdia* Nutt. genus. *Shepherdia* berries are also used as food, and these plants are a promising crop due to their decorative qualities and high contents of biological substances [170,171]. The system of sex chromosomes and sex determination in *Shepherdia* has not been widely studied.

2.2.6. Humulus

Humulus lupulus L. is a dioecious woody vine of the Cannabaceae family that is of great importance in brewing. Hops are grown for the female buds, which contain substances that create the characteristic taste, aroma and bitterness of beer. Due to the popularity of this drink, hops are cultivated on every continent except Antarctica. The hop karyotype consists of 18 autosomes and a pair of sex chromosomes (XX/XY). The Y chromosome is the smallest in the karyotype, which may indicate its degeneration and evolutionary antiquity [172–174]. In commercial cultivation, the female varieties are vegetatively propagated. A very important task is to prevent the pollination of inflorescences, since setting seeds spoils the taste of beer [175]. Hop is a wind-pollinated crop with light pollen, so just one male plant in the area can cause a lot of economic damage [176]. To prevent pollination, all male plants in a nursery and nearby wild populations must be eradicated. As a part of this procedure, molecular genetic markers are used to identify sex in the early stages of ontogenesis [38,177,178]. In hop production, seedless triploid varieties are also cultivated. They are more productive and have a high growth rate [179,180]. However, they are prone to monoecy. A more detailed study of the mechanisms of sex determination in hops could open up opportunities for influencing this trait and contribute to the creation of high-yielding barren varieties.

2.2.7. Date Palm

The date palm (2n = 2x = 32) is one of the oldest dioecious crops. As with other crops grown for fruit, its production primarily requires female date palm plants. Males are required in smaller numbers for pollination (a ratio of 1:20 is used, i.e., one male plant pollinates 20 females). At the same time, the date palm blooms in the 5–6th year of cultivation—that is, it is not possible to morphologically detect the sex of a tree before this age. Many molecular markers have been developed to identify the sex of the date palm in the early stages of ontogenesis. The genetic mechanisms of sex determination in the date palm have been recently identified [181–185]. An association of two genes, presumably associated with sex, was found on chromosome 12 [186]. Moreover, several genome sequences of different date palm varieties have been published [187–190].

2.2.8. Myristica

Nutmeg (*Myristica fragrans* Houtt., 2n = 38 of 44, according to different communications [191]) is a tropical evergreen tree grown in Asia and Africa for its fruits. It is widely used around the world as a spice [192]. The world production of nutmeg is estimated at

139,000 tons [46]. In agricultural production, female plants are needed more. Attempts to create molecular markers have been made to identify sex in the early stages of vegetation [40,193,194]. However, sex chromosomes in *M. fragrans* have not been found.

2.2.9. Actinidia

Kiwifruit (*Actinidia chinensis* Planch.) is a plant of the Actinidiaceae family. The *Actinidia* genus includes 50–70 species [195]. Several species of kiwifruit are cultivated. The most popular are A. chinensis and A. deliciosa. A. arguta is grown in New Zealand, the USA, and some European countries, but the acreage occupied by this species is small [196]. A. kolomikta is popular in Russia in personal plots due to its winter hardiness. All species of the genus are dioecious. Morphologically, the flowers look bisexual, but female plants form flowers with sterile pollen while male plants have an underdeveloped and non-functioning pistil [197]. However, some species sometimes have bisexual flowers. Hermaphroditic flowers have been observed in A. arguta, A. chinensis, A. deliciosa, and A. eriantha Benth. [196]. Kiwifruit has only been cultivated for just over 100 years, but it has achieved great popularity around the world, and its production is about 4 million tons per year [46]. Polyploidy is widespread in species of the *Actinidia* genus [198]. Chromosomal numbers range from 2n = 58 to 2n = 174 (x = 29) [199]. Polyploidy does not appear to affect sex in kiwifruit. Male plants have at least one Y chromosome in the karyotype, and female plants have XX [200,201]. The sex chromosomes are small and homomorphic, with a small SDR [41,202]. The mechanism of sex determination has been widely studied. This mechanism is based on two genes (the Shy Girl gene (SyGI), the dominant suppressor of carpel development, and the Friendly Boy gene (FrBy), expressed in tapetum cells) [15]. Currently, the kiwifruit genome is actively being studied, and genetic maps and molecular markers are being created to aid the breeding of this crop [203–206]. However, hermaphroditism can be determined by additional genetic factors, which creates difficulties for sex determination based on molecular markers [206].

2.2.10. Ilex

Ilex L. is a large genus of dioecious plants in the Aquifoliaceae family with over 500 species [207]. *Ilex* plants are trees or shrubs, mostly found in nature in East Asia and South America. Some species are found in Europe, Africa, and Northern Australia [208]. Ilex species are grown as ornamental crops to decorate gardens or to make traditional Christmas wreaths [209,210]. The most economically significant plant of this genus is a Paraguayan holly (*I. paraguariensis* A.St.-Hil.; 2n = 40 [211]). It is widely used in a number of countries (mainly Latin America) for the manufacturing of the mate herbal tea drink. According to FAO data, the global production of mate leaves in 2020 exceeded 1,400,000 tons [46]. In this species, sexual dimorphism has been repeatedly shown in the intensity of photosynthesis, leaf area, and higher mortality of female plants. Thus, male plants have a larger leaf area than female plants, and the intensity of photosynthesis is higher in female plants, while the leaves of male plants make the taste of the drink less bitter [130,212–214]. Like *Actinidia*, *I. paraguariensis* is functionally dioecious, with morphologically hermaphroditic flowers, and one of the sexes is sterile or abortive [215]. From a genetic point of view, this species is poorly studied. Heteromorphic sex chromosomes have not been identified. Molecular markers for marker-associated selection and sex detection have been developed [216–218].

2.2.11. Chinese Bayberry

Chinese bayberry (*Morella rubra* Lour.) is widely cultivated in China for fruits. It is the only edible species of the Myricaceae family [219]. The chromosome number is 2n = 16, and the heterogametic sex is presumably female (ZW chromosome system) [220]. A comparison of the sequenced genomes of male and female plants revealed a small region (59 kb) on chromosome 8 that is specific to female plants [42]. The differential expression of some genes, presumably associated with the development of sex in this species, was also shown [221].

2.3. Sex Chromosomes and Sex Determination of Weeds

In addition to dioecious crops, there are dioecious weed and parasitic species that have negative effects on the cultivation of agricultural plants. In addition to the species of sorrel mentioned above, examples of such weeds are *Amaranthus palmeri* S. Wats. and *A. tuberculatus* (Moq.) J.D. Sauer. These weeds cause enormous damage to US agriculture. They have huge seed productivity and a high resistance to herbicides [222]. The study of the sex determination mechanisms, reproduction features, and secondary sexual characteristics of these species may open up an opportunity for crop protection in the future [223].

3. Conclusions

Modern research on sex chromosomes and the mechanisms of sex determination in plants is focused on the identification of sex-determining genes and on the fundamental issues of the occurrence of dioecy, the evolution of sex and sex chromosomes in a separate family or a whole class of plants. As a rule, a rather limited list of model objects is studied, and the study itself (even if carried out using modern methods and omics technologies affecting the entire plant genome/transcriptome or proteome) focuses on differences in the generative sphere in male and female plants. At the same time, a significant proportion of dioecious plants are economically significant species that have been cultivated by humans for many centuries. It should be noted that their features are linked with their cultivation (Figure 1).

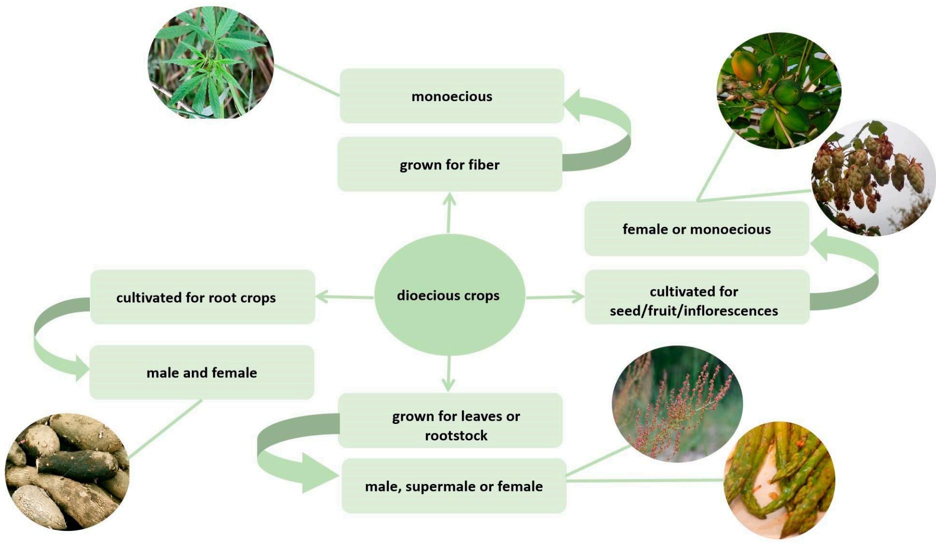

Figure 1. The use of dioecious plants depending on its sex.

According to Figure 1, dioeciousness has a greater or lesser effect on crop cultivation. It is most noticeable on fruit trees. Gardeners strive to grow as many female plants as possible due to the fact that females produce the target product. However, male plants are necessary for pollination and cannot be completely abandoned. However, the maximum effective sex ratio differs depending on the plant and the type of pollination (insect pollination or wind pollination). For example, sea buckthorn shows the best yield in a planting pattern where one mixed row of male and female plants falls between two rows of female plants (in a mixed row, male plants comprise one in five plants) [160]. The role of the pollinator in the formation of economically valuable traits cannot be directly assessed. In addition to dioecy, a long juvenile period also affects the breeding of tree crops. Half of the population during seed propagation comprises male plants. This fact leads to the loss of labor, time, and other resources that are spent on growing males before flowering. Therefore, sex detection using molecular markers is often used in the cultivation of perennial fruit crops.

Additionally, the use of monoecious and parthenocarpic forms may be relevant in such cases. At the same time, male plants are only used in the breeding of some other plants, such as hops. The pollination of industrial plantings is unacceptable. The spatial isolation of hop plantings and the early complete culling of male plants is necessary. In plants in which the vegetative part is used, the role of dioecy is not so obvious and it seems that plants of any sex can be used. However, the different maturation times of male and female plants, as in hemp, or the different yields of male and female plants, as in asparagus, can shift the interest of producers to monoecious forms or plants of a specific sex. Thus, researchers should consider the final purpose of the cultivated crop, as well as its biological characteristics in general, not only focusing on the genes for the formation of pistils or stamens. Humans have a significant impact on the entire environment, and dioecious cultures are no exception.

On the one hand, dioecious plants have been subjected to the influence of artificial selection for a long time, and many of them have gone through a "bottleneck" in their evolution and have lost some of their genotypes. On the other hand, differences between males and females are often not limited to differences in flower structure. Unlike animals, secondary sexual characteristics in plants are usually not expressed; however, individual reports demonstrate their existence. Evolutionarily, this is explained by the different reproductive costs of male and female plants. Females generally require more carbon to produce fruits and seeds, while males (especially wind-pollinated plants) need to produce larger amounts of pollen. This determines differences in not only the type of flowers but also reactions to stress, biomass, productivity, and other traits [224–228]. The significance of a number of dioecious plants for humans indicates the relevance of their in-depth study, and the economic efficiency of growing plants of a certain sex should be evaluated in accordance with the goals of growing such a crop.

Theoretically, it is also interesting to evaluate the means of possible evolution in cultivated dioecious plants (to monoecy, in particular). It is possible that humans will continue to have significant impacts on the rate and direction of evolution for many species. A deeper understanding of the evolution and sex determination of cultivated dioecious plants, together with the characteristics of cultivation, can open up new opportunities for agricultural management.

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