9 Evolution of Sexuality in Amaranths

9.1 General

The genus *Amaranthus* is unique in showing a wide range of sexuality from gynomonoecy, monoecy to dioecy and also variability in mating behaviour from self-compatibility to obligate outcrossing, i.e. from monomorphic reproductive system to dimorphic reproductive system. Bisexual flower represents the ancestral condition in angiosperm, and monoecy is considered to have been derived from bisexual condition through intermediate gynomonoecious or andromonoecious forms. Dioecy results in a division of labour between sexes and may ultimately lead to greater reproductive efficiency. A variety of hypotheses have been proposed for evolution of dioecy from hermaphroditism through monoecy, gynodioecy and androdioecy. Monoecy in the grain amaranths are supposed to have originated from the dominant cosexual form having exclusively bisexual flower through sterility mutation followed by subsequent specialisation in flower form and position. Dioecy may have evolved from monoecy through disruptive selection on male and female reproductive allocation, followed by gender specialisation ultimately leading to unisexual plants. In the case of vegetable amaranths, genetic modification in female fertility of hermaphrodite population might have resulted in the formation of bisexual member with non-functional gynoecium. Later male sterility gene might have played a role to give rise to female member. Subsequent inbreeding between these derivatives having sexual compatibility, gynomonoecious member might have originated. Monoecy in amaranths might have transmitted from cosexual species of Chenopodiaceae-Amaranthaceae alliance or Chen-Am alliance. Molecular analysis of the Caryophyllales established Chen-Am alliance as a monophyletic lineage.

9.2 Trend of Sexuality in Plants

Flowers are the most varied structure in the flowering plants. Such variability is a key factor and primarily instrumental to achieve mating success. Selective forces are responsible for origin and maintenance of sexual diversity in flowering plants. Flowering plants are mostly hermaphrodite producing bisexual flowers. Few flowering plants (−10 %) have unisexual flowers with a wide spectrum of gender strategies that involve varied combinations of female, male and hermaphrodite flowers at the plant population level. Though dioecy is widely distributed in flowering plants occurring in nearly half of all families, overall frequency of dioecious species is only 6 % (Renner and Ricklefs 1995) signifying its rare association with successful evolutionary diversification. Dioecy is commonly associated with unspecialised pollination system that involves wind, water or generalised pollinator rather than the more specialised pollinator that commonly drives floral diversification and

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reproductive isolation in many cosexual flowering plants (Johnson et al. 1998). Sexual structure can be spatially separated in a flower or can become functional at different times reducing the likelihood of self-pollination. Gradual sexual diversity has emphasised the mechanism that aimed at promoting outcrossing and reducing likelihood of inbreeding depression. Conventionally floral traits have been considered as anti-selfing mechanism that encourages cross-pollination preventing self-pollination

Strong empirical evidences indicate that bisexual flower represents the ancestral condition in angiosperm (Richard 1997; Doyle 1998; Endress 2001). Monoecy with separate male and female flowers on the same plant is considered to be derived condition from bisexual condition (Mitchell and Diggle 2005). Monoecy has traditionally been considered as originating from gynomonoecy or andromonoecy (Wilson 1979; Bawa and Beach 1981; Bertin 1982). Many research have been directed to explore the evolutionary transition giving rise to dioecious condition, i.e. male and female flowers on separate plants (Renner and Won 2001; Gleiser and Verdu 2005; Case et al. 2008). Dioecy results in a division of labour between sexes and may ultimately lead to greater reproductive efficiency (Lloyd 1982). Male and female reproductive function may be optimised through different selective processes ultimately leading to phenological dimorphism in male and female plant.

Despite seemingly complex pattern of sexual diversity in flowering plants, two broad and fundamentally distinct patterns of gender variation or sexual system have been recognised – monomorphic sexual system and dimorphic sexual system (Bawa and Beach 1981). In the former system, species bears bisexual female and/or male unisexual flowers on the same individual, leading to monoecious, gynomonoecious, andromonoecious and trimonoecious condition. In the latter system, species have dimorphic sexual system, i.e. unisexual individual such as dioecy, gynodioecy and androdioecy.

Despite the simultaneous/common occurrence of hermaphroditism and monoecy, little attention has been paid to the factors favouring evolutionary transition between these two systems. Establishment of monoecy requires specialisation in the shape, size and positioning of the male and female flower (Shmida et al. 2000). But before such specialisation, a mutant with some unisexual flowers needs to be established first. Only after the unisexual mutant is firmly established, subsequent mutation related to specialisation in flower form and position has given rise to monoecy.

Many investigations have been directed towards exploring traits leading to dioecy (Renner and Won 2001; Gleiser and Verdu 2005; Case et al. 2008). A variety of hypotheses have been proposed for evolution of dioecy from hermaphroditism through monoecy, gynodioecy and androdioecy. But not all these pathways have received the same theoretical attention. There are no well-authenticated cases of androdioecy as an intermediate stage in the evolution of dioecy and very limited evidence for the evolution of androdioecy from hermaphroditism. Two fundamental evolutionary pathways for the origin of dioecy through monoecy and gynodioecy are generally recognised. Both involve the transition from gender monomorphism to dimorphism. In the gynodioecy pathway male sterility genes spread in bisexual population, resulting in an intermediate stage that involves females and hermaphrodites. Genetic modifiers of female fertility gradually convert hermaphrodites to male resulting in dioecy. The monoecy pathway is less well investigated, assumed to involve disruptive selection on male and female allocation in monoecious population which gradually increased gender specialisation until unisexual plants originated. Monoecy has originated several times from the dominant cosexual condition in angiosperm population having exclusively hermaphrodite flower. This might have occurred through sterility mutation that produced unisexual flowers.

A lot of investigations have been done on the gynodioecy, but till date little attention has been given to monoecy pathway. It is not clearly resolved whether the transition is determined solely by selection or quantitative genetic variation governing sex allocation or whether major male sterility genes are also having a role. A recent molecular phylogenetic study (Renner and

Won 2001) provides convincing evidence of multiple origins of dioecy from monoecy in the primary Neotropical shrub family Siparunaceae. It is very vital to determine the circumstances under which selfing rate increased resulting in inbreeding depression in ancestral cosexual population. Such condition facilitates the spread of unisexual variants that favour outcrossing. A link between origin of gender dimorphism and conditions that promote inbreeding depression might occur through the action of polyploidy. Chromosome doubling in plants can result in the inhibition of self-incompatibility leading to self-compatibility (Chawla et al. 1997) providing opportunities for self-fertilisation. Molecular phylogeny in North American *Lycium* (Solanaceae) indicates that gender dimorphism has evolved only in species that are polyploid and self-compatible but their close relatives are diploid and self-incompatible. Such pattern also found to have originated independently in South African species of *Lycium.* Polyploidy might have acted as a trigger for the evolution of gender dimorphism (Miller and Venable 2000). Large plant size might be another condition that can potentially lead to gender dimorphism (de Jong and Klinkhamer 1994). In plant species with large stature (like shrubs and trees), a considerable amount of selfing can occur due to the presence of many open flowers on a plant at the same time leading to inbreeding depression. Recent marker gene analysis of the clonal aquatic plant *Sagittaria latifolia* offers evidences that indicate that geitonogamous selfing and strong inbreeding depression have influence in evolutionary transition from monoecy to dioecy (Dorken et al. 2002). Population of both sexual systems occur together in this species making it an excellent model for studying the evolution of combined versus separate sexes.

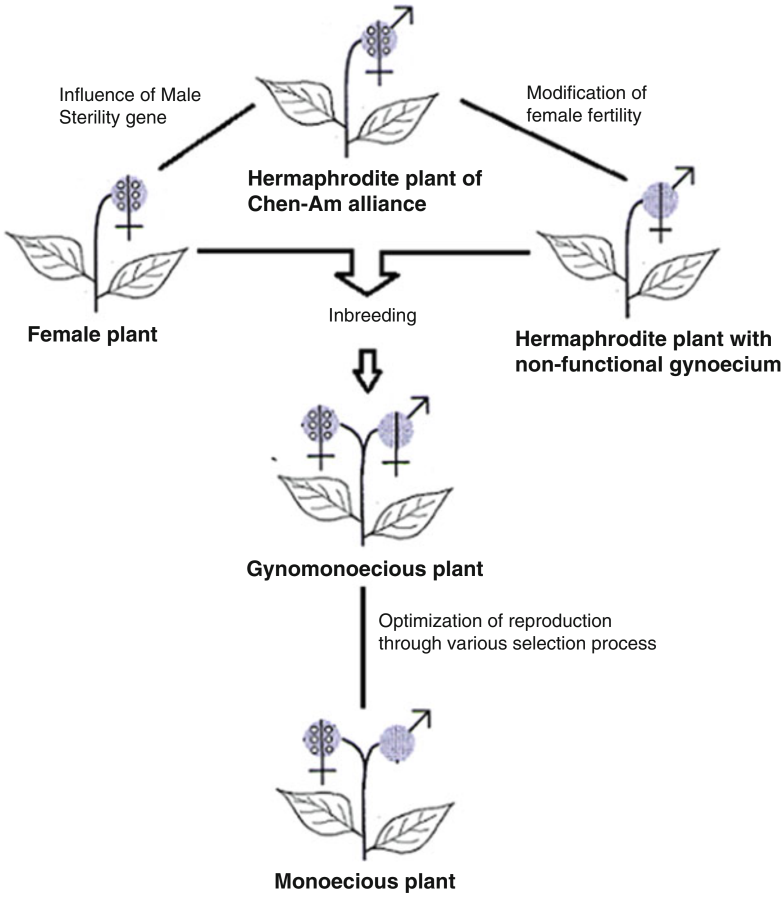
9.3 Sexuality in Amaranths

The genus *Amaranthus* is unique in mating behaviour ranging from self-compatibility to obligate outcrossing, i.e. from monomorphic reproductive system to dimorphic reproductive system. It shows a wide range of variability in sexuality from gynomonoecy, monoecy to dioecy. Dioecy is the rare breeding system among angiosperm. It may affect the ability of a lineage to avoid extinction or encourage speciation. Monoecy is the predominant phenomena in amaranths. Grain amaranths are exclusively monoecious, while vegetable amaranths are predominantly monoecious with exception. It would be logical to presume that both grain and vegetable amaranths were evolved and domesticated in their respective centre of origin from their weed progenitor having wide range of variability in sexuality ranging from monoecy to dioecy.

Amaranths followed the general evolutionary trend in sexuality, i.e. from monoecy to Dioecy. It can be presumed that monoecy in amaranths might have transmitted from cosexual species of Chenopodiaceae-Amaranthaceae alliance or Chen-Am alliance. The Chen-Am alliance is of worldwide distribution, comprising 2400 species. The alliance is noted for the evolution of C_4 photosynthesis, halophytism, xerophytism and a variety of breeding system. The close relationship of Chenopodiaceae and Amaranthaceae has been recognised based on core floral formula consisting of five tepals, five stamens and 2–3 carpels (Hershkovitz 1989). Molecular analysis of the Caryophyllales (Manhert and Rettig 1994; Downie and Palmer 1994; Downie et. al. 1997; Cuenoud et. al. 2002) established Chen-Am alliance as a monophyletic lineage.

The grain amaranths are grown and consumed both as green vegetable and pseudocereal. Though grain amaranths are crops of America but later they migrated to Asia and Southeast Asia, Europe and North America. Vegetable amaranths specially *Amaranthus tricolor* and *A. dubius* probably originated and domesticated in Asia and Southeast Asia (Grubben and Van Sloten 1981) and later spread throughout tropical and temperate regions of Africa, Central America and Europe by the immigrants (Martin and Telek 1979). *Amaranthus blitum* aggregate included in sect. *Blitopsis* of subgen. *Albersia*, comprising *A. blitum* and *A. emarginatus,* was studied morphometrically (Das and Iamonico 2014). *Amaranthus blitum* with two varieties are supposed to have originated and domesticated in Mediterranean

Fig. 9.1 Evolution of sexuality in vegetable amaranths



Basin, Europe and North America and *A. emarginatus* in tropical America. The member of 'blitum complex' later might have migrated to Asia, Southeast Asia and other parts of the world. *Amaranthus bengalense*, a new variant of *A. blitum*, was reported from West Bengal, India (Das and Iamonico 2014). A new gynomonoecious species *Amaranthus parganensis* Saubhik Das was discovered from Lower Gangetic Plain of West Bengal that closely resembles *A. tricolor* of sect. *Pyxidium* subgen. *Albersia* (Das 2015). The new species shows structural gynomonoecy with rudimentary gynoecia in bisexual flowers and provided a clue regarding origin of monoecy through intermediate sexual system. Dioecious species are confined to a small area in North America (Sauer 1957), though sporadic appearance has been reported from time to time (Brenan 1961). Monoecy in amaranths may have evolved from hermaphrodite Chen-Am member through various processes like spread of male sterility genes and gender modifier gene of female fertility in hermaphrodite population followed by optimisation of male and female reproductive function through different selective processes. In case of vegetable amaranths, genetic modification in female fertility of hermaphrodite population might have resulted in the formation of bisexual member with non-functional gynoecium. Later male sterility gene might have played a role in giving rise to female member. All these derivatives originated through genetic modification and have sexual compatibility. Subsequently, through inbreeding process gynomonoecious member might have originated. Monoecy is a derived condition originated from gynomonoecious condition through optimisation of male and female reproduction through different selection processes (Fig. 9.1). Further evolution of sexuality is not observed in vegetable amaranths. On the basis of available morphological and phytogeographical evidences, Mosyakin (2005) suggested that dioecy would have evolved in plants growing in open habitats such as coastal areas, river valleys, disturbed plant communities, deserts, semi-desert and prairies. It was accompanied by development of many adaptive morphological traits in some groups (perianth reduction for more successful cross-pollination through anemophily, indehiscent utricles for more successful hydro- and anemochory, etc.). Dioecious amaranths probably independently evolved from monoecious ancestor at least twice questioning the monophyly of the subgen. *Acnida* (Mosyakin 2005).

Monoecy in the grain amaranths are supposed to have originated from the dominant cosexual form having exclusively bisexual flower like most of the angiosperms through sterility mutation followed by subsequent specialisation in flower form and position. Two main evolutionary pathways for the origin of dioecy though monoecy and gynodioecy are identified, of which monoecy line might have been followed by grain amaranths. Gynodioecious pathway is not acceptable due to lack of any member with intermediate sexuality. Origin of dioecy from monoecy may have evolved through disruptive selection on male and female reproductive allocation, followed by gender specialisation ultimately leading to unisexual plants.

Increased selfing rates resulted in inbreeding depression in ancestral cosexual population. Such condition facilitates the spread of unisexual variants that favours the outcrossing. Frequent inbreeding in monoecious vegetable amaranths has resulted in a large number of morphotypes. Relatively greater self-pollination in members of sect. *Blitopsis* and members of sect. *Pyxidium* has resulted in breeding depression that favoured the spread of outcrossing. Such outcrossing might have resulted in formation of gynomonoecious member. Grain amaranths show relatively greater outcrossing forming number of variants.