

EVOLUTION OF SEXUALITY IN *AMARANTHUS* SPECIES

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Abstract

The genus *Amaranthus* is unique in its matting behaviour ranging from self-compatibility to obligate out-crossing also from monomorphic to dimorphic sexual system. The members included in the subgenus *Acnida* are exclusively dioecious. But members included in the other two subgenera *Amaranthus* and *Albersia* are monoecious showing varying degree of self-compatibility. Transition from monoecy to dioecy in amaranths might have achieved through establishment of mutant with some unisexual flower followed by specialization in the shape, size and positioning of male and female flower ultimately leading to phenological dimorphism in male and female plant. Both the grain and vegetable amaranths have different centre of origin, unique process of domestication and distinct evolution of sexuality.

Amaranthus L. is a cosmopolitan genus of herbs of Amaranthaceae, distributed worldwide but particularly in the hot humid tropics and temperate regions of the globe. Genus *Amaranthus* tentatively includes 70 species (Iamónico 2012) of which 40 are considered native to America. Among the American species 10 are dioecious, found in North America and remaining 46 are monoecious.

This genus is nomenclaturally and taxonomically critical both for its morphological variability and hybridization. Sauer (1967) made a taxonomic and geographic survey of grain amaranths and their relatives employing morphological features and designated two subgenera - *Acnida* (which included the dioecious species) and *Amaranthus* (which included the monoecious species). Mosyakin and Robertson (1996) recognized three subgenera - *Acnida*, *Amaranthus* and *Albersia* on the basis of their inflorescence and floral features. Subgen. *Acnida* included the monoecious species while *Amaranthus* and *Albersia* included monoecious species.

Selective forces are responsible for origin and maintenance of sexual diversity in flowering plants. Flowering plants are mostly hermaphrodite producing bisexual flowers. A 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, but overall frequency of dioecious species is only less than 6% (Renner and Ricklefs 1995) signifying its rare association with successful evolutionary diversification. Dioecy is the rare breeding system among angiosperms. It may effects the ability of a lineage to avoid extinction or encourage speciation. Gradual sexual diversity has emphasized the mechanism that aimed at promoting out-crossing and reducing likelihood of inbreeding depression. Conventionally floral traits have been considered as anti-selfing mechanism that encourages cross pollination preventing self-pollination.

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Bisexual flower represent the ancestral condition in angiosperm (Endress 2001). Monoecy is considered to have derived from bisexual condition (Mitchell and Diggle 2005) through intermediate gynomonocious or andromonocious forms (Bawa and Beach 1981). Only after the unisexual mutants are firmly established through sterility mutation, subsequent mutations related to specialization in flower form and position has given rise to monoecy (Shmida *et al.* 2000). Dioecy results in a division of labour between sexes and may ultimately lead to greater reproductive efficiency (Lloyd 1982). 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. 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. 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 specialization until unisexual plants originated.

The genus *Amaranthus* is unique in showing wide range of sexuality from gynomonocoe, monoecy to dioecy also variability in mating behaviour from self-compatibility to obligate out-crossing i.e., from monomorphic to dimorphic reproductive system. Monoecy is the predominant phenomenon in amaranths. Grain amaranths are exclusively monoecious, vegetable amaranths are predominantly monoecious with exception. A new gynomonocoe 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 showed structural gynomonocoe with rudimentary gynoecium and provided a clue regarding origin of monoecy through intermediate sexual system. It can be presumed that monoecy in amaranths might have originated from co-sexual species of Chenopodiaceae-Amaranthaceae alliance or Chen-Am alliance. The Chen-Am alliance is of world-wide distribution, comprising 2400 species. The alliance is noted for the evolution of C₄ photosynthesis, halophytism, xerophytism and a variety of breeding system. The close relationship of Chenopodiaceae and Amaranthaceae has been recognized based on core floral formula consisting of 5 tepals, 5 stamens and 2 - 3 carpels (Herskovitz 1989). Molecular analysis of the Caryophyllales (Cuenoud *et al.* 2002) established the Chen-Am alliance as a monophyletic lineage.

Broadly speaking, the genus *Amaranthus* shows three types of mating system viz. (a) obligate out-crossing in dioecious species, (b) relatively greater out-crossing in monoecious member of sect. *Amaranthus* and (c) relatively greater self-pollination in member of sect. *Blitopsis* and sect. *Pyxidium*. Dioecious species are confined to a small area in North America (Sauer 1957). 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 optimization 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 i.e., structurally gynomonocoe member. Later male sterility gene might have played a role to give rise female member. Subsequent inbreeding between these derivatives having sexual compatibility, gynomonocoe member must have originated (Fig. 1).

Monoecy in grain amaranths supposed to have originated from the dominant co-sexual form having exclusively bisexual flower like most of the angiosperms through sterility mutation followed by subsequent specialization in flower form and position. Dioecy may have evolved from monoecy through disruptive selection on male and female reproductive allocation, followed by gender specialization ultimately leading to unisexual plants. Centre of origin of grain and vegetable amaranths are different, grain amaranths are native of Americas while vegetable amaranths originated and domesticated primarily in Asia and South-East Asia. As such versatility of sexual evolution is not same in both the groups.

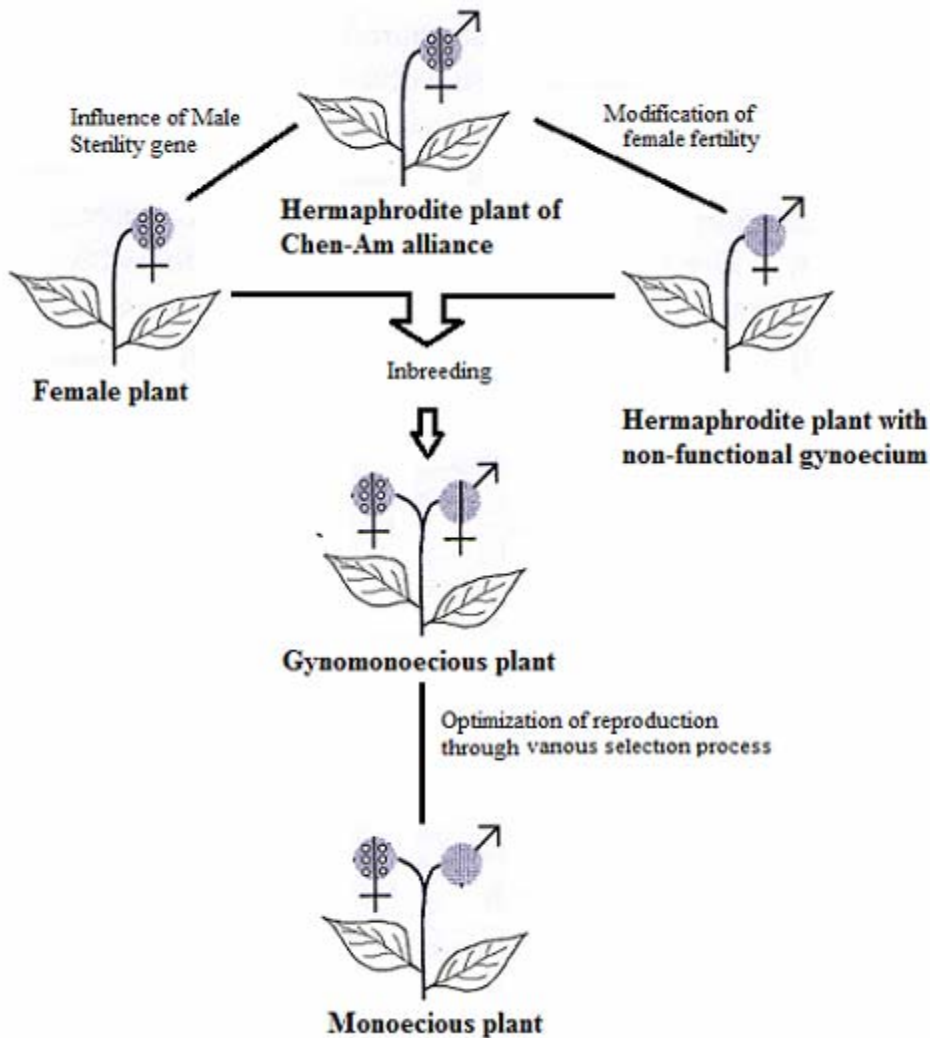


Fig. 1. Evolutionary trend in sexuality of vegetable amaranths.

Increased selfing rates resulted in inbreeding depression in ancestral co-sexual population. Such condition facilitates the spread of unisexual variants that favours the out-crossing. 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 out-crossing. Such out-crossing might have resulted in the formation of gynomonoeious member. Grain amaranths show relatively greater out-crossing forming number of variants.

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