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Breeding system and population structure in the *Aerva javanica* complex¹⁾

By

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Introduction

The genus *Aerva* FORSKAL 1775: 8 of *Amaranthaceae* includes about twenty-nine species, which are distributed in Asia, Africa and Australia. In West Pakistan this genus is represented by four species, i. e. *A. javanica* (BURM. f.) JUSS., *A. pseudotomentosa* BLATT. & HALLB., *A. scandens* (ROXB.) WALL. and *A. lanata* JUSS. (BLATTER & HALLBERG 1919: 817, BAMBER 1916: 123 & 135). *Aerva javanica* is a widely distributed taxon and extends from Australia, Burma, Ceylon, India, Pakistan, Arabia, east and west Tropical Africa to Cape Verde Islands (HOOKER f. 1885: 727—728). In and around Karachi *A. javanica* and *A. pseudotomentosa* grow quite commonly.

The populations of *A. javanica* are quite variable morphologically, and show a kind of variation commonly present in a species complex. Populations of *A. javanica* were studied to analyse the nature and extent of morphological variation. This data was substantiated by biochemical and cytological study of the populations. The reproductive system of the various components of the complex also was taken into account.

Material and methods

Population samples were collected from the Karachi University campus. The material thus used for morphological studies was sympatric in distribution and represented naturally occurring plant populations of this area.

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For morphological studies seven criteria were used. These criteria are as follows: (I) habit, (II) length of terminal inflorescence, (III) length of lateral inflorescence just beneath the terminal inflorescence, (IV) leaf length, (V) plant length, (VI) bract length and (VII) perianth length. Metroglyphs (ANDERSON 1949: 43—48) and histograms were used to demonstrate correlations as well as population discontinuities.

Paper chromatographic method was used for biochemical analysis of free aminoacids. Fresh young leaves were ground with 80% ethanol and kept over night. After filtration the remaining debris were washed with fresh ethanol, and filtered. The two filterates were pooled and 3 parts of chloroform was added to one part of ethanol extract. After thorough

Table 1

Frequency of four types of growth habits in the University population of *A. javanica*

Habit	Number of Plants	Percentage
$\alpha 1$	16	17,53
$\alpha 2$	21	23,07
$\alpha 3$	6	6,64
$\alpha 4$	48	52,74
Total	91	99,98

shaking the resulting upper aqueous layer was removed and its volume was reduced to 1 ml. This was used as amino acid extract which was loaded as single spot on Whatman paper number 4. Chromatograms were run over night by descending method in the solvent of n- butanol: glacial acetic acid and water in a ratio of 4:1:5. The solvent front was marked with pencil and the paper was dried at room temperature. For the detection of free amino acids this paper was sprayed with 0,3% ninhydrin and the chromatogram was placed in an oven at 100° C.

For cytological studies root tips were pretreated in 8-hydroxyquinoline for 4—6 hours, and fixed in Carnoy's fixative. Squash preparations were made by fuelgen technique as given by DARLINGTON & LA COUR 1947: 156.

Observations and results

Four types of habit may be recognized within the *A. javanica* complex. These are given arbitrary symbols as 1, 2, 3 and 4 (Fig. 1). The plants of habit 1 and 2 cover comparatively larger space and their branches arise from above the level of soil. The oldest branches of 1 are opposite while they are alternate in 2 type. The plants of type 3 habit are comparatively erect but the branches originate in a similar way as in 1 and 2 types. The type 4

plants are erect, but they are different from 3 especially in bearing the branches just at the soil level. On the basis of correlation of characters *A. javanica* is divided into two populations, one including 1, 2 and 3 habits and the other only 4 type of habit. In the University population the habit 4 seems to be most common (52,74%) and 3 (6,64%) the most rare (Table 1, Fig. 1).

Frequency distribution histograms of (I) the length of terminal inflorescence, (II) length of lateral inflorescence just beneath the terminal inflores-

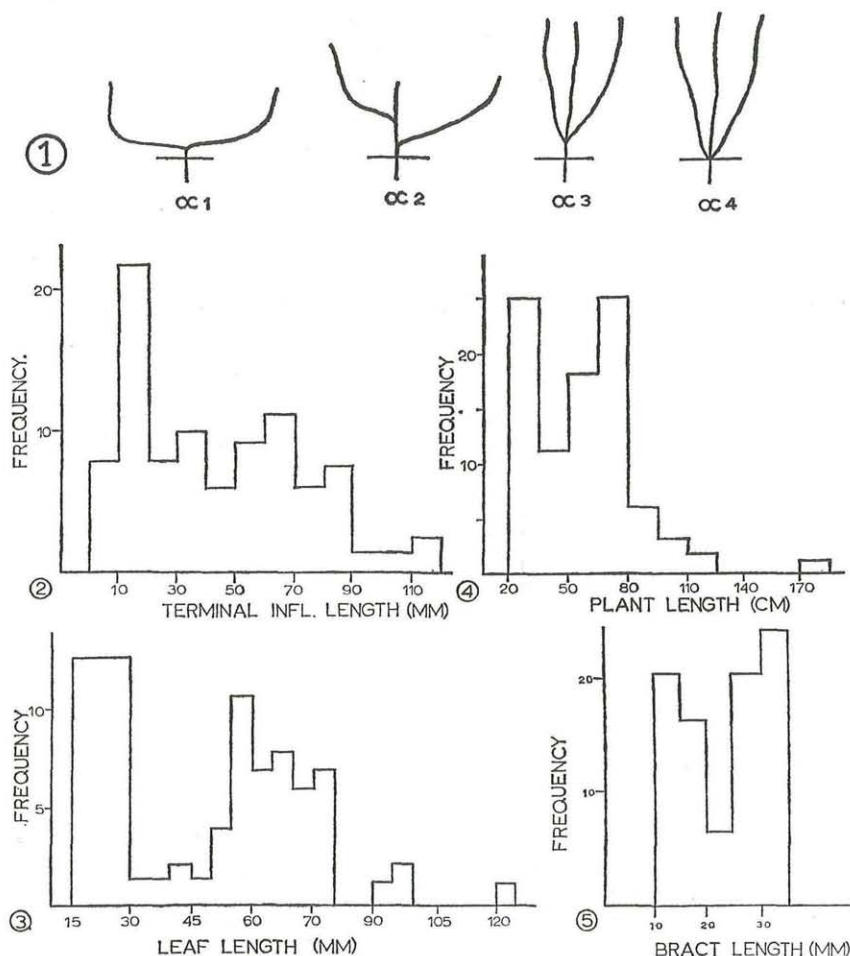


Fig. 1-5. *Aerva javanica* complex.

Fig. 1. Diagrammatic representation of four types of growth habit. — Fig. 2-5. Histograms showing population variability with respect to terminal inflorescence length (Fig. 2), leaf length (Fig. 3), plant length (Fig. 4), bract length (Fig. 5).

cence, (III) length of leaf, (IV) plant length, (V) bract length and (VI) perianth length were studied. Out of these the histograms of (I) the terminal inflorescence length (Fig. 2), (II) leaf length (Fig. 3), (III) plant

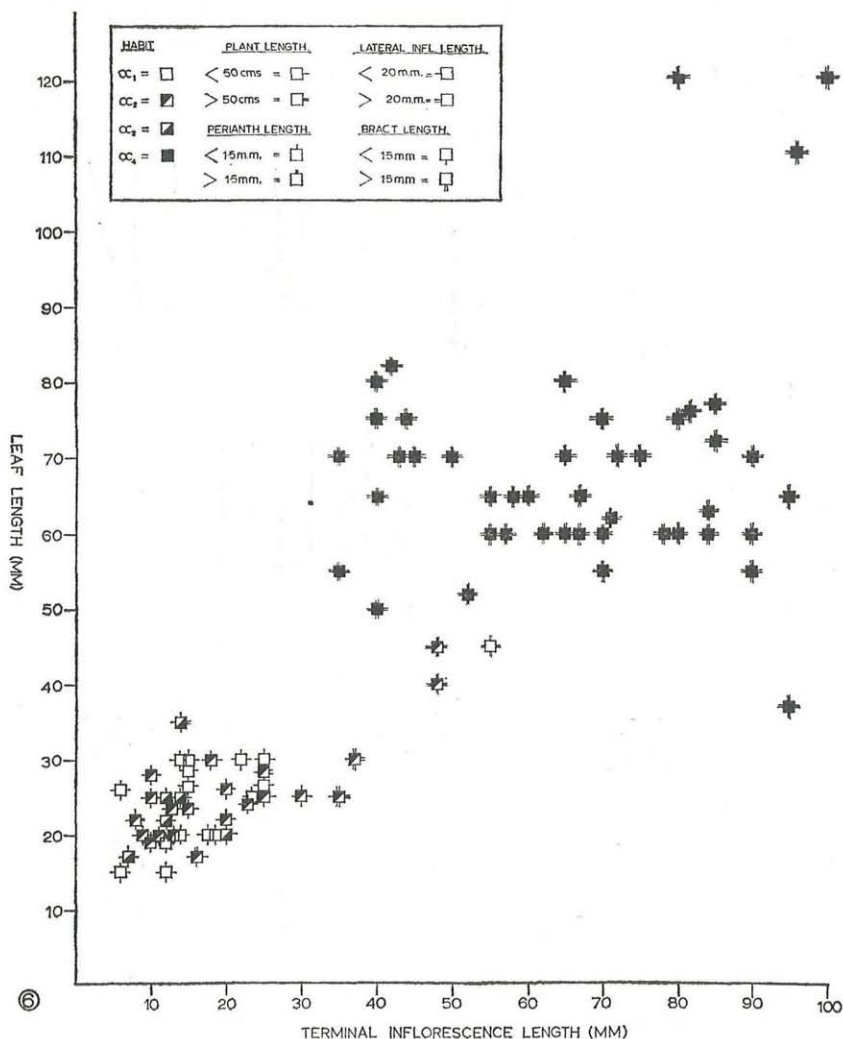


Fig. 6. Pictorialized scatter diagram showing discontinuous variation within the *Aerva javanica* complex.

length (Fig. 4), and (IV) bract length (Fig. 5) are bimodal, and indicate the possibility of the presence of two populations. A study of correlation of various characters indicates that *A. javanica* complex consists of two

morphologically distinct populations which can be differentiated from each other on the basis of habit, plant length, leaf length, length of terminal as well as lateral inflorescence and bract length (Fig. 6).

Table 2

Distribution of male and female plants of *A. javanica* complex in the world

Locality	No. male Plants	No. female Plants
Cape Verde Islands	Zero	14
Senegal	Zero	3
Morocco	Zero	1
Algeria	Zero	3
Libya	Zero	1
Sudan & Nubia	1	29
Nigeria	Zero	11
Cameroons	Zero	1
Tanganika	Zero	15
Kenya	Zero	34
Uganda	Zero	1
Ethiopia	Zero	13
Somaliland	4	27
Eritrea	2	6
Egypt and Sinai	5	30
Niger and French Niger	1	1
Sahara	2	4
Dahlak Islands (Red Sea)	2	1
Arabia	7	29
Syria	Zero	12
Socotra	Zero	2
Arabian and Persian Gulf Isls.	Zero	11
Persia	Zero	1
Afghanistan	Zero	1
West Pakistan	Zero	13
India. Delhi & Punjab	1	18
South India	Zero	13
Burma	Zero	1
Malay Islands	Zero	1
Australia	Zero	2
Total	25	299
Percentage	7,7	92,3

On the basis of these characters one can recognize the following two populations.

Population A: Habit of plant 1, 2 or 3 type, plant length usually less than 50 cm, leaf length 1,5–5,0 cm, terminal inflorescence length generally 6–37 mm, perianth length and bract length c. 1–1,5 mm.

Population B: Habit of plant is of 4 type only, plant length usually more than 50 cm, leaf length 5–12,5 cm, terminal inflorescence length 4–12 cm, lateral inflorescence length usually more than 20 mm, perianth and bract length more than 1,5 mm.

Biochemical study: The biochemical data based on chromatographic analysis of free amino acids is in accord with the morphological findings. The population A has only one free amino acid while population B has three free amino acids (Fig. 8). *A. pseudotomentosa* has one free

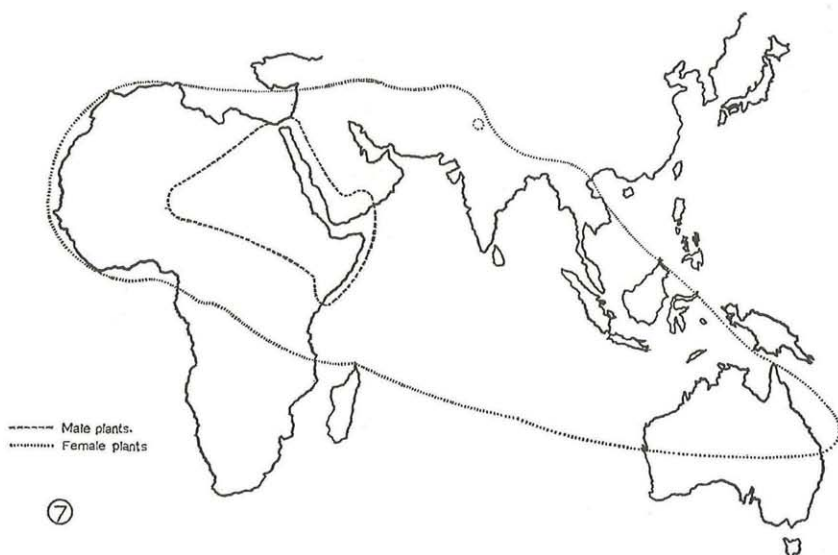


Fig. 7. Distribution of male and female plants of *Aerva javanica* complex in the world.

amino acid also, and in this respect it is similar to population A. It seems that in all of these populations one free amino acid is common.

Breeding system: Nearly two thousand five hundred flowers in *A. javanica* populations from Karachi and West Pakistan were investigated but none of them was found to be male. The female inflorescences covered under plastic bag always produced seeds. Study of pistil for pollen or pollen tube also provided no evidence of any pollen germination in *A. javanica*, indicating that this species is an apomict. In the allied species *A. pseudotomentosa* where hermaphrodite flowers are present, both pollen tubes as well as pollen grains were observed. For a survey of male flowers in *A. javanica*, herbarium specimens from the herbaria of the University of Karachi, Gordon College, Rawalpindi, as well as Kew were studied.

The survey based on the entire range of distribution *A. javanica* (Table 2) showed 7,7 percent male plants. But out of 25 male plants scored from the entire range of distribution, 24 male plants were distributed in Africa and Arabia. This means that 96% of the male plants were recorded from Africa and Arabia. A single male plant recorded from India came from Lodhiana, while no plant with staminate flowers were recorded from Southern India, Burma, Ceylon and Australia (Table 2, Fig. 7).

Cytology: The chromosome counts in the root tip of *A. javanica* complex of both the groups showed $2n=c. 72$ chromosomes.

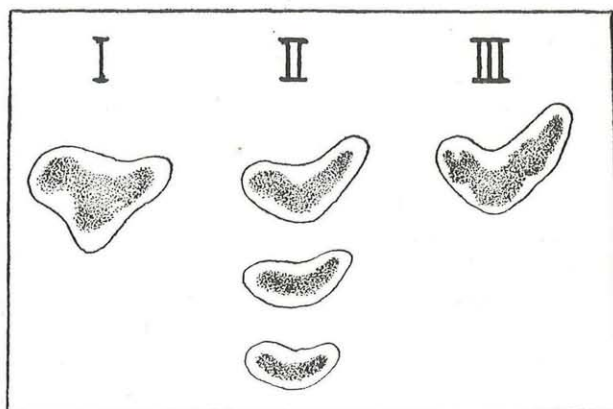


Fig. 8. Chromatographic profiles of (I) *Aerva pseudotomentosa*, (II) Population B and (III) Population A of *Aerva javanica* complex.

Discussion

Classically it was believed that apomixis is a blind alley in evolution. Experimental studies have demonstrated that facultative apomixis facilitates interspecific as well as long range hybridizations (ROSENBERG 1907: 143–170, OSTENFELD 1910: 241–285, ROLLINS 1944: 93–99, 1946: 21–30, SØRENSEN & GUDJONSSON 1946: 1–48, CLAUSEN 1954: 469–479, 1961: 87–94, HARLAN & al. 1961: 5–30, FARUQI 1963: 57–64, 1964: 280–297), hence, it is a mechanism that is helpful in the evolution of plants. Moreover, in those plant species that are pseudogamous, selection can still function on an apparently uniform clonal population producing different forms under varied environmental conditions, as pointed out for apomictic *Rubus* (HASKELL 1966: 141–151). Since *A. javanica* is an obligate apomict, the reasons presented earlier for the production of variability in apomictic plant populations do not account for the variability in this species. It was pointed out by GUSTAFSSON 1946: 1–66, that phenomenon such as mutation, autosegregation, somatic crossing over may also be responsible for

the genetic reshuffle in apomictic populations. A better understanding, however, has come from the study of those plants that reproduce by vegetative means, where several methods for chromosomal as well as cytoplasmic genetic reshuffle were pointed out (SHARMA & DAS 1954: 23—48, BREESE 1966: 51—60, HASKELL 1966: 141—151). Male plants in *A. javanica* are almost negligible, and seeds are produced in the absence of pollen, indicating that this species is an obligate apomict. According to NYGREN 1966: 131—140, obligate apomicts are quite rare in the plant kingdom.

The morphological and biochemical analysis indicate that this species includes two populations different from each other in a number of features, and moreover, each one of these populations exhibit considerable variation. The variability, therefore, is either a result of asexual segregation or it is there as a result of past segregation of a highly heterozygous sexual ancestor. Cytologically *A. javanica* is a polyploid species, thus both polyploidy and past hybridization seem to be associated with apomixis.

There is an intimate connection between apomixis, hybridization and polyploidy (STEBBINS 1950: 380—419, CARNAHAN & HILL 1961: 1—162, FARUQI 1964: 280—297). This association may be owing to the reason that genes controlling apomixis are recessive and with the increase of ploidy level apomixis is reinforced. Similarly, through hybridization suitable combinations of genes may come together which promote apomictic mode of reproduction (POWERS 1945: 323—346, STEBBINS 1950: 380—419). On the other hand, in the genera *Bothriochloa*, *Capillipedium*, and *Dichanthium* the genes responsible for apomixis are dominant and still the known diploids are sexual and polyploids are apomictic. STEBBINS 1950: 380—419, has pointed out that hybridization promotes apomixis through the greater vigour and tolerance of a wide range of ecological conditions possessed by hybrid genotypes. CLAUSEN 1954: 469—479 argues, that facultative apomicts maintain a partial balance within themselves. Looking back into the apomictic mode of reproduction one must realize that apomixis is a stabilizing force, and for this reason in populations involving hybridization, polyploidy (STEBBINS 1950: 380—419, CLAUSEN 1961: 87—94, FARUQI 1964: 280—297) or any such forces that bring instability to populations apomixis should be favoured by natural selection.

It has been observed (Table 2, Fig. 7) that *A. javanica* possesses staminate flowers only in some restricted areas of its distribution. The male plants are distributed mainly in Arabia, Aden, Syria, Egypt, Eritrea, Somaliland, Dahlak Island, Sahara and Nigeria. But the proportion of staminate and pistillate plants is 24 to 258. A single staminate flower was scored from Western India whereas none from South India, Burma, Ceylon, Malaya and Australia. Since the apomictic mode of reproduction is derived from sexual reproduction (WINKLER 1908: 293—454, NYGREN 1966: 131—140), the sexually reproducing populations must have given rise to

populations with apomictic mode of reproduction. In view of the concentration of plants with male flowers in North East Africa and Western Arabia, and its absence in South East Asia and Australia the origin of *A. javanica* should be sought where both staminate and pistillate flowers are recorded. According to BAKER 1953: 114—145, long range dispersal of self-incompatible plants can be possible only, if it is concurrently accompanied by self-compatible breeding system. In dioecious plant species, chances of long range dispersal are extremely remote, unless it is accompanied by apomictic mode of reproduction, because the possibility of dispersal and establishment of plants of both the sexes in the same space and time is almost negligible. *Aerva javanica* is likely to have spread to other regions where staminate flowers do not occur, after the establishment of apomictic mode of reproduction.

The success of a cross fertilized plant species in nature depends upon its genetic diversity. Owing to this feature it remains potentially adapted to a changing environment (BAKER 1959: 177—191, STEBBINS 1957: 337—354, MATHER: 1966: 12—19). A self fertilized or sexually reproducing plant is quite successful in a stable environment, but in a drastically changing environment it has lesser chances of survival than the cross fertilized species. But the asexually reproducing plants after establishment colonize an area rather easily. Since *Aerva javanica* extends from Cape Verde Islands to Australia, we may conclude that this particular species, by virtue of agamospermy, has been quite successful in long range dispersal. Such a distribution in this complex is substantiated also by the fact that the seeds are associated with a woolly structure which makes it prone to be transported easily.

The biochemical studies of the two populations of *A. javanica* show one amino acid common to both the taxa. Two other free amino acids are present only in the population 'B'. In view of the principle adopted by HASKELL 1966: 141—151, in the study of flavonoid compounds of *Rubus*, the amino acid common to the population 'A' and 'B' of *A. javanica* and *A. pseudotomentosa* is ancestral. Whereas the two amino acids that are present only in the population 'B' of *A. javanica* are more likely to have evolved later.

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Summary

Experimental studies of the populations of *Aerva javanica* (BURM. f.) JUSS. from Karachi have revealed the existence of two distinct populations. This conclusion is substantiated by the correlation of morphological criteria

and biochemistry of free amino acids. Genetic diversity and wide distribution seems to be on account of apomictic mode of reproduction. Cytologically this species complex is a polyploid. It is argued that in the case of dioecious plant species which have secondarily adopted apomictic mode of reproduction, the presence of plants of the both sexes in certain regions, may also be taken as indicative of centre of origin of the taxon concerned. It is pointed out that in dioecious plants only apomictic mode of reproduction can facilitate long range dispersal.

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