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Biosystematic relationships among *Cajanus, Atylosia,* and *Rhynchosia* species and evolution of pigeonpea (*Cajanus cajan* (L.) Millsp.)

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Summary. Biosystematic studies encompassing morpho-cytological and electrophoretic analyses of *Cajanus cajan,* seven species of *Atylosia* and one of *Rhynchosia* revealed that *A. cajanifolia* is closest to *C. cajan,* followed by *A. lineata, A. scarabaeoides, A. sericea, A. albicans, A. volubilis, A. platycarpa* and *R. rothii,* in that order. A revision has been suggested for the taxonomic placement of the seven *Atylosia* species. Regarding the evolution of cultivated *C. cajan,* three possible alternatives have been suggested. Firstly, *C. cajan* could have evolved through gene mutation in *A. cajanifolia*; secondly, some of the *Atylosia* species and pigeonpea probably evolved from the same source; and thirdly, the pigeonpea might have developed from naturally occurring interspecific crosses of *A. lineata* and *A. scarabaeoides.*

Key words: Biosystematic relationships – Pigeonpea – Karyotype – Meiosis – Crossability – Seed protein profile

Introduction

The pigeonpea has been known by several botanical names. The earliest, *Cytisus cajan* L., was followed by *Cajan cajan* Huth, *Cajanus bicolor* DC., *C. flavus, C. indicus* Spreng., *C. luteus* Bello, and *C. pseudo-cajan* Schinz & Guill. All these names are now considered as synonyms (Thothathri and Jain 1981) of *Cajanus cajan* (L.) Millsp., the correct botanical name for pigeonpea. The name *C. indicus* was most widely used up to the mid fifties.

Cajanus cajan is the only cultivated species of the subtribe *Cajaninae* which encompasses several hundred species. *Atylosia, Rhynchosia,* and *Dunbaria* are three genera of the same tribe closely related to *Cajanus.* Research already conducted (Deodikar and Thakar 1956; Kumar and Thombre 1958; Kumar et al. 1958; Sikdar and De 1967; Reddy 1973; De 1974) suggest a close relationship between *Cajanus* and *Atylosia* and points to the need for taxonomic revision of these taxa. In the present study, work was done to formulate the biosystematic relationships of the *Atylosia* and *Rhynchosia* with *C. cajan.*

The morphology, karyotypic analysis, crossability and electrophoretic profiles of seed proteins of the cultivated species, *C. cajan,* seven species of *Atylosia,* and one of *Rhynchosia* were studied, and the species relationships and evolution of pigeonpea were worked out.

Materials and methods

The seeds of *C. cajan* cvs. 'Pant A2' and 'UPAS 120', *A. albicans* (W. & A.) Benth. (JM 2356), *A. cajanifolia* Haines (JM 2739), *A. lineata* W. & A., *A. platycarpa* Benth., *A. scarabaeoides* (L.) Benth. (ICP 7464), *A. sericea* Benth. ex Baker (ICP 7470), *A. trinervia* (DC.) Gamble, *A. volubilis* (Blanco) Gamble (JM 1984) and *R. rothii* (JM 2296) were obtained from the Genetic Resources Unit, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru (A.P.), India.

The experiments were conducted at Banaras Hindu University, Varanasi during 1977–79. Each species was characterized morphologically based on stem, leaf, flower, pod and seed characters and growth habit (Pundir 1981), and the

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similarity index of each species with *C. cajan* was calculated. Every species were examined for karyotypic features and symmetry (or asymmetry). Further, based on the extent of F1 seed production between the wild species and *C. cajan,* crossability was ascertained. Those with the highest crossability were considered closest to *C. cajan.* Also, the F1 hybrids obtained were investigated for their chromosome homology using metaphase I pairing and anaphase separation and the species were graded in order of abnormality. The hybrids were also analysed for pollen stainability and the *Atylosia* and *Rhynchosia* species were scored according to the pollen stainability of their F1 hybrids with *C. cajan.* Finally, soluble proteins were extracted in tris HCL buffer (pH 8.0) from seeds of all species and electrophoresed on 7.5% polyacrylamide gel columns in a tris glycine buffer (pH 8.3) system (Gabriel 1971). The electrophoretic pattern of each of the wild species was compared with that of *C. cajan.* The taxon with the highest number of common bands with *C. cajan* was considered the closest and those with less number of common bands were considered to be more distantly related.

Based on the various similarity scores, the species were arranged in descending order of their affinity with *C. cajan.* Considering that the species lower down the rows under each character column would show increasing dissimilarity with *C. cajan,* an arbitrary dissimilarity score for each species was obtained by summing the score of the species in the different columns. The species with the minimum total score should be closest to *C. cajan* and the ones with maximum total score should have the least affinity.

Results and discussion

Table 1 gives the closeness of *Atylosia* and *Rhynchosia* species to *C. cajan* as judged by their morphological, cytological, crossability and F1 pollen stainability behaviors as well as protein electrophoretic patterns.

Atylosia cajanifolia was most similar to *C. cajan* based on the gross morphology scores whereas *A. trinervia, A. lineata, A. sericea, A. scarabaeoides, A. albicans, A. platycarpa, A. volubilis* and *R. rothii,* in that order, were increasingly dissimilar.

The karyotype asymmetry index of *C. cajan* was analogous to those of *A. cajanifolia, A. volubilis* and *R. rothii. Atylosia lineata, A. scarabaeoides, A. sericea* and *A. platycarpa* had similar asymmetry scores which were higher than those of the above species. *Atylosia albicans* had the highest karyotypic asymmetry. Five of the eight wild species produced viable F1 hybrids with *C. cajan,* whereas *A. platycarpa, A. volubilis* and *R. rothii* failed to cross with *C. cajan.* Of the five viable crosses, the crossability of *C. cajan* was best with *A. lineata,* followed by that with *A. trinervia, A. cajanifolia, A. albicans* and *A. scarabaeoides.*

The F1s of *C. cajan* with *A. cajanifolia* and *A. trinervia,* showed regular meiosis. Meiotic abnormalities in the F1's (such as univalents at metaphase I and laggards at anaphase I) increased progressively when *C. cajan* was crossed with *A. scarabaeoides* and *A. albicans* (Pundir 1981). Pachytene chromosome analysis of F1 hybrids when *C. cajan* was crossed with *A. scarabaeoides, A. sericea* and *A. lineata* revealed that of the eleven bivalents, eight were homologous in the first and second hybrid, and nine in the third (Reddy 1981 a, b, c).

Based on the number of seed protein bands and RF values, *A. cajanifolia* and *A. scarabaeoides* were similar to *C. cajan. Atylosia lineata, A. sericea* and *A. albicans* had 10 bands each, identical to 10 of the 11 bands of *C. cajan.* The dissimilarity was greater with *A. platycarpa* and *A. volubilis.* The most distinct species was *R. rothii,* which had only five of its eight protein bands similar to *C. cajan* (Fig. 1).

Putting the scores of individual species together, *A. cajanifolia* emerged as the species most closely related to *C. cajan,* followed by *A. lineata, A. scarabaeoides, A. sericea, A. albicans, A. volubilis, A. platycarpa* and *R. rothii.*

Atylosia trinervia could not be studied for karyotypic details and seed protein profies and thus its

Table 1. Affinities of *Atylosia* and *Rhynchosia* species to *Cajanus cajan.* Order of affinity: *A. cajif.* – *A. lin.* – *A. scar.* – *A. ser.* – *A. albi.* – *A. volub.* – *A. platy.* – *R. rot.*

	Plant morphology	Karyotype symmetry	Cross-ability	F_1 meiosis	F_1 pollen stainability	Seed protein electrophoresis
Close ↑	*A. cajif.*	*A. cajif.* *A. volub.* *R. rot.*	*A. lin.*	*A. cajif.* *A. trin.*	*A. lin.*[a]	*A. cajif.* *A. scar.*
	A. trin.		*A. trin.*		*A. cajif.*	
	A. lin.		*A. ser.*[a]	*A. scar.*	*A. scar.*	*A. lin.* *A. albi.* *A. ser.*
	A. ser.	*A. lin.* *A. scar.* *A. ser.* *A. platy.*	*A. cajif.*	*A. albi.*	*A. albi.*	
	A. scar.		*A. albi.*	*A. lin.*[a]	*A. trin.*	
	A. albi.		*A. scar.*	*A. ser.*[a]	*A. ser.*[a]	*A. platy.* *A. volub.*
	A. platy.		*A. platy.* *A. volub.* *R. rot.*	*A. platy.* *A. volub.* *R. rot.*	*A. platy.* *A. volub.* *R. rot.*	
	A. volub.	*A. albi.*				*R. rot.*
Distant	*R. rot.*	–				–

[a] Source: L. J. Reddy (1981 a, b)

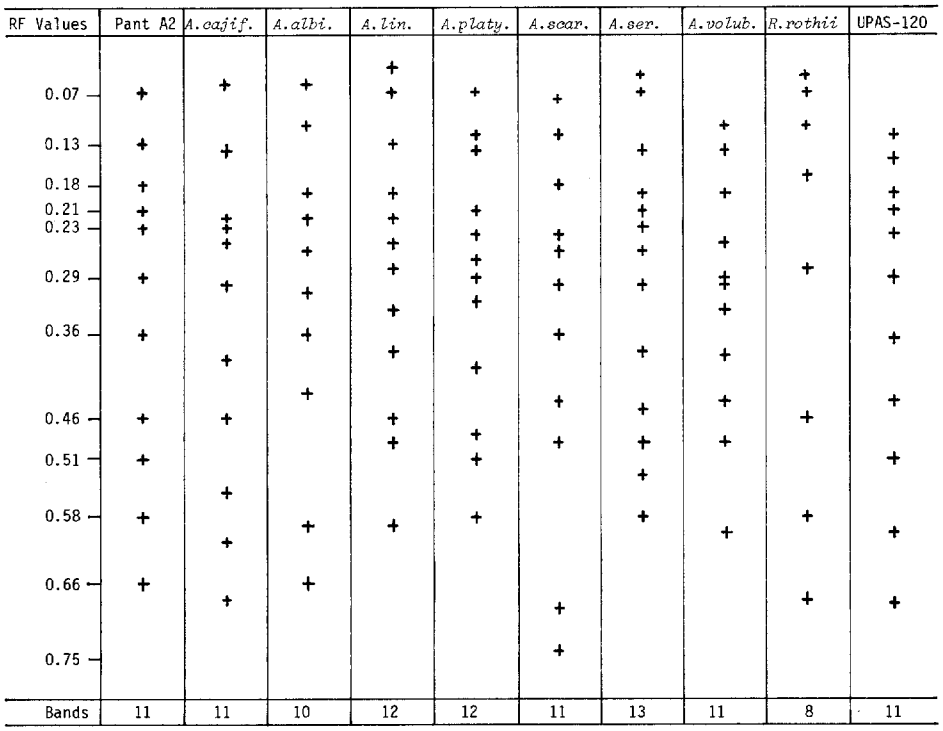

Fig. 1. Band homology in the seed protein profile of *Cajanus, Atylosia* and *Rhynchosia* species

affinity with *C. cajan* could not be fully assessed. However, based on the morphology, crossability and F1 pollen stainability scores, it can be considered a species fairly close to the cultivated species.

Taxonomic revision

It is clear from the above that several of the *Atylosia* species can easily be hybridized with *C. cajan* and interspecific hybrids may occur in nature. Some of the species, such as *A. cajanifolia,* morphologically resemble *C. cajan* very closely. As such, revision of the placement of the seven *Atylosia* species studied is called for. It is suggested that while the taxonomic status of *Cajanus* and *Atylosia* may be retained, based on the closeness and following taxonomic rules of nomenclature, species like *A. cajanifolia, A. lineata, A. sericea, A. scarabaeoides* and *A. albicans* should be placed under the genus *Cajanus.* The species *R. rothii* maintains a distinct status outside the *Cajanus – Atylosia* complex. In gross morphology, *A. platycarpa* is similar to *R. aurea* but represents the genus *Atylosia* better. *Atylosia volubilis* is quite distant from pigeonpea and should be retained under the genus *Atylosia.*

Evolution of pigeonpea

On the basis of the biosystematic data obtained in this study and observations on the segregation patterns in the interspecific crosses (Pundir 1981), three possible alternatives are suggested for the evolution of cultivated pigeonpea.

1. The overall morphological, cytogenetical and biochemical similarities between *C. cajan* and *A. cajanifolia* suggest that pigeonpea has evolved through selection of gene mutations in the species *A. cajanifolia* which is recommended to be included in the genus *Cajanus* (van der Maesen 1980). The gene mutations and selection pressures under domestication underlying the evolution of the cultivated species have probably resulted in the accumulation of modifiers and differentiation of plasmon in the cultivated species. These changes render *C. cajan* as an unsuccessful seed parent (Pundir 1981) when cross pollinated with *A. cajanifolia* (though we made about 1,500 pollinations over two seasons) and thus restricting unwanted recombination in the nature. However, Reddy et al. (1980) reported that *C. cajan* set crossed seeds when pollinated with *A. cajanifolia.* The discrepancy may be due to different genotypes used in the crosses.

2. Inheritance studies of seven contrasting oligogenic characters (leaflet shape, stem colour, twining nature, pod hairiness, growth habit, presence or absence of seed strophiole and seed colour) in *C. cajan* × *Atylosia* species crosses revealed that these traits are under monogenic and digenic controls. New intermediate types were also obtained in the interspecific progenies. The segregation and recombination patterns showed

little interspecific interference. Moreover, strophiole was no longer a specific feature of *Atylosia,* earlier it had been considered the key character for differentiating *Atylosia* and *Cajanus* (Hooker 1879). Several *C. cajan* populations have now been found to possess strophioles. Perennial forms of pigeonpea growing as wild populations in Andhra Pradesh and the occurrence of *A. cajanifolia* on the Bailadilla Hills, Madhya Pradesh, India (van der Maesen 1980) indicate that the argument 'wild forms of *C. cajan* do not exist in India and the supposed place of origin only Western Ghats of India (De 1974, 1976)', are no longer tenable. Based on the present observations it may be proposed that the species of the *Cajanus-Atylosia* complex have evolved from a common gene pool. It appears that they have taken diverse evolutionary pathways and over the millenia have acquired specific morphological attributes and adaption.

3. Pigeonpea type segregants were obtained from a cross of *A. lineata* and *A. scarabaeoides* (Pundir 1981). Based on seed protein profiles of 90 pigeonpea accessions and four *Atylosia* species, Ladizinsky and Hamel (1980) indicated the polyphyletic origin of *C. cajan* from several *Atylosia* species. The present study shows a close affinity of *A. lineata* and *A. scarabaeoides* with *C. cajan.* Considering the above facts, one is tempted to consider that *C. cajan* may have had its evolution through selection of erect, vigorous, and productive plants from the segregants of the *Atylosia* interspecific cross/es (*A. lineata* × *A. scarabaeoides*?).

To settle the issue among the three possibilities of mode of evolution of *C. cajan,* additional work on ecogeographical distribution, and genetic, cytogenetic and cytoplasmic relationships is needed. Deployment of biochemical and molecular techniques may facilitate research in this area.

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