Pachytene Analyses in Cajanus cajan, Atylosia lineata and Their Hybrid

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Cytological studies on the two closely allied genera, Cajanus (Pigeonpea, Red gram) and Atylosia has been so far confined to somatic karyotypes only (Deodikar and Thakar 1956, Kumar et al. 1958, Sikar and De 1967). In a previous report we (Reddy and De, in press) critically analysed the somatic karyotypes of Cajanus and Atylosia with a view to throw some light on the phylogenetic aspects of these two genera. However, the interpretation of relationship between different species and genera from the study of the mitotic chromosomes alone is not enough. Since the pioneering work of McClintock (1929) on Zea mays, the utility of pachytene chromosomes in phylogenetical studies has been widely appreciated and well documented (Gottschalk 1954, 1972, Gottschalk and Peters 1956, Venkateswarulu 1960, 1972, Magoon et al. 1964). Hence the present study on the pachytene chromosomes of Cajanus, A. lineata and their hybrid was undertaken. The pachytene chromosomes of two allied species of Atylosia viz., A. sericea and A. scarabaeoides and their hybrids with Cajanus will be dealt in future publications.

Materials and methods

For pachytene analysis, the flower buds of Cajanus, A. lineata and their hybrid were fixed in propionic acid and ethanol mixture (1: 3) with the acid component saturated with ferric acetate. The buds were kept overnight in fixative and then the anthers were stained in 1% propiono carmine.

The chromosome lengths were measured from the camera lucida drawings using a piece of thread. The chromosome length was measured in mm and then converted to microns. Those fractions of mm which were less than 0.5 mm were neglected (except in the case of heterochromain where it is recorded as 1.0 μ) and those fractions with 0.5 mm or more were read as 1.0 mm for the sake of convenience. The length of the individual chromosomes presented in the table represent the mean length obtained from a minimum of 10 cells.

Observations

Pachytene karyomorphology of the parents

All the pachytene chromosomes of Cajanus and A. lineata belong to the differ-
entiated type. The unstained centromeres are clearly flanked by proximal dark staining heterochromatic regions (HC) and distal light staining euchromatic regions (EC).

On the basis of length, the entire pachytene complement of both the species can be divided into 3 groups—long (50.0 μ and above) medium (49.0 μ to 30.0 μ) and short (below 30.0 μ). All the chromosomes are identifiable on the basis of relative length, length of the arms, position of centromere, nucleolar association and the amount and distribution of HC and EC. The chromosomes were numbered in order of their decreasing length.

*Cajanus cajan*

The complement comprises 2 median, 6 submedian and 3 subterminal chromosomes. The length of the bivalents ranges from 61.0 μ to 22.2 μ. The total chromatin length measures 415.7 μ, of which 28.2 per cent is heterochromatic. Chromosomes I and II belong to long group, chromosomes III to VIII to the medium group and chromosomes IX to XI to the short group. The data on the mean total length and arm ratio of the individual bivalents are summarised in Table I and the idiosogram is given in Fig. 21.

The characteristic features of each bivalent are detailed below:

Chromosome I (Figs. 1A and 1B) is the longest of the complement and the HC (12.0 μ) of the long arm appears as two chromatic groups separated by a light staining region. One third of the short arm is made of HC (8.3 μ). The HC of this chromosome is not as deeply stained as that of the other chromosomes.

Chromosome II (Figs. 2A and 2B) is submedian and the HC (1.0 μ) of long arm is much shorter than that of the short arm and consists of a single macronucleomere by which it is easily recognized. The HC of short arm (10.0 μ) can be divided into two parts. The proximal part is compact and consists of 3 chromomeres of which middle one is barrel shaped. The distal part is faintly stained and consists of 4 to 5 small inconspicuous and widely separated chromomeres.

Chromosome III (Figs. 3A and 3B) is submedian and both long and short arms consist of nearly equal amounts of HC (long arm 4.6 μ; short arm 4.0 μ). The long arm consists of 4 chromomeres of which proximal one is the biggest and barrel shaped. The HC of the short arm occupies about one-fifth of its length and consists of 5 chromomeres which appear in two groups. The proximal group consists of 3 distinct chromomeres followed by the distal group of 2 chromomeres which are closely appressed.

Chromosome IV (Figs. 4A and 4B) is median and HC of the long arm (6.6 μ) appears as two chromatic blocks. The proximal block consists of 2 closely located chromomeres followed by a block consisting of 4 to 5 small faintly stained chromomeres. The HC of short arm (5.2 μ) also appears as two chromatic

Figs. 1-7. *Cajanus cajan* pachytene chromosomes. In each pair of illustrations A is a photomicrograph (×2000) and B is an interpretive drawing. Arrows indicate position of centromere. 1A and B, chromosome I. 2A and B, chromosome II and VI. 3A and B, chromosome III. 4A and B, chromosome IV. 5A and B, chromosome V. 6A and B, chromosome VII. 7A and B, chromosome VIII.
blocks. The proximal block consists of 2 to 3 closely appressed chromomeres. The distal block consists of 4 small, closely located chromomeres.

Chromosome V (Figs. 5A and 5B) is subterminal. The HC (8.6 μ) occupies one-fourth of the length of long arm and consists of two small chromatic segments of which proximal one is flanked by 2 chromomeres. The HC (6.7 μ) of the short arm is nearly twice as long as EC and consists of 4 distinct macrochromomeres and a small distant chromatic segment. In certain cells this chromosome is attached to the nucleolus.

Chromosome VI (Figs. 2A and 2B) is submedian. The long arm is nearly twice as long as the short arm and is made of equal lengths of HC and EC. The HC (10.0 μ) of the long arm is twice as long as that of the short arm (4.8 μ).

Chromosome VII (Figs. 6A and 6B) is median. The HC (5.4 μ) of the long arm consists of 6 distinct chromomeres and EC is twice as long as HC. The HC (2.0 μ) of short arm possesses a single macrochromomere.

Figs. 8–10. Cajanus cajan pachytene chromosomes. In each pair of illustrations A is a photomicrograph (×2000) and B is an interpretive drawing. Arrows indicate position of centromere. 8A and B, chromosome IX. 9A and B, chromosome X. 10A and B, chromosome XI.

Chromosome VIII (Figs. 7A and 7B) is median and the HC (4.5 μ) of the long arm consist of 3 barrel shaped chromomeres. The HC (2.1 μ) of short arm possesses two chromomeres which are at times confluent to form a big single barrel shaped chromomere. The HC of the long arm is twice as long as that of the short arm.

Chromosome IX (Figs. 8A and 8B) is subterminal and more than one-fourth of the long arm is made of HC (5.4 μ). The HC (4.0 μ) of the short arm measures
nearly twice the length of EC. The long arm possesses 6 distinct chromomeres and in this respect this chromosome resembles chromosome VII. However, it can be readily distinguished by its arm ratio and the heterochromatic pattern of the short arm which possesses 4 distinct chromomeres as against a single chromomere in the short arm of chromosome VII.

Chromosome X (Figs. 9A and 9B) is a nucleolar organising chromosome. The nucleolus is attached to the short arm and the satellite measures approximately 4.0 μ. The HC of both long (2.2 μ) and short (2.0 μ) arms possesses 2 distinct chromomeres.

Chromosome XI (Figs. 10A and 10B) is the shortest subterminal chromosome. The HC (4.7 μ) of the long arm consists of 2 distinct chromomeres. The HC (3.3 μ) of short arm possesses a big barrel shaped chromomere followed by a smaller deeply stained chromomere.

*Atylosia lineata*

The complement consists of 2 median, 7 submedian and 2 subterminal chromosomes. The length of the bivalents ranges from 61.9 μ to 26.8 μ. The total chromatin measures 438.2 μ, of which 27.5 per cent is heterochromatic. Chromosomes I and II come under long group, chromosomes III to IX under medium group and chromosomes X and XI under short group. The data on the mean total length, arm length, arm ratio and amount of HC and EC of the individual bivalents are summarized in Table 1 and the idiogram is given in Fig. 22. The characteristic features of each bivalent are given below:

Chromosome I (Figs. 11A and 11B) is the longest of the complement. The HC (12.6 μ) of the long arm appears as two chromatic blocks separated by a light staining region. Both the chromatic blocks consist of few faintly stained chromomeres. Nearly one-third of the short arm is made of HC (9.5 μ). In most of the preparations, this chromosome is very faintly stained.

Chromosome II (Figs. 12A and 12B) is submedian and resembles chromosome I in its arm ratio. But this chromosome can easily be distinguished by the presence of a big macrochromomere in the HC (1.5 μ) of long arm. The HC (10.6 μ) of short arm appears in two blocks. The proximal block consists of 4 closely appressed macrochromomeres. The distal block consists of few faintly stained, inconspicuous chromomeres. The short arm possesses nearly equal lengths of HC and EC.

Chromosome III (Figs. 13A and 13B) is submedian. The HC (12.3 μ) of the long arm consists of a chromatic segment followed by 7 to 8 chromomeres of which first one is the biggest and barrel shaped. The chromomeres exhibit a size gradient in descending order, the chromomere located near the EC being the smallest. One-fourth of the short arm is made of HC (5.2 μ) and possesses 3 big macrochromomeres of which the first two are barrel shaped.

Chromosome IV (Figs. 14A and 14B) is subterminal. The HC (7.3 μ) of the long arm appears as two groups of 3 and 4 small chromomeres. The proximal group of 3 chromomeres is deeply stained. The HC (6.0 μ) of the short arm is slightly longer than EC.
Chromosome V (Figs. 15A and 15B) resembles chromosome IV in its HC length (7.2 μ) and size of the chromomeres of the long arm. But it can be easily recognized by its median centromere. The HC of the long arm appears in two groups, a proximal group consisting of 4 to 5 closely located chromomeres followed by a distal group consisting of 2 distinct chromomeres. The HC (5.1 μ) of short

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<th>Chromosome</th>
<th>Mean arm length in μ</th>
<th>Mean total length (μ) ± S. E.</th>
<th>Mean arm ratio (a/b)</th>
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<td>20.2</td>
<td>28.0±2.2</td>
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<td></td>
<td>*F L</td>
<td>7.0</td>
<td>18.6</td>
<td>25.6±3.9</td>
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<tr>
<td>9</td>
<td>XI C</td>
<td>5.3</td>
<td>16.9</td>
<td>22.2±2.0</td>
<td>0.31</td>
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<tr>
<td></td>
<td>XI L</td>
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<td>23.7</td>
<td>26.8±3.4</td>
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<tr>
<td></td>
<td>F L</td>
<td>4.5</td>
<td>20.1</td>
<td>24.6±4.1</td>
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Chromosomes whose homoeologues could not be identified in the hybrid.

| 10     | III C      | 19.8           | 27.8           | 47.6±5.5 | 0.71 | SM  |
| 11     | IX C       | 6.4            | 19.7           | 26.1±2.9 | 0.32 | ST  |
| 12     | VI L       | 17.5           | 18.1           | 35.6±4.1 | 0.96 | M   |
| 13     | VIII L     | 9.2            | 25.3           | 34.5±4.9 | 0.36 | SM  |

* M = Median; SM = Sub median; ST = Sub terminal.
† C = C. cajan chromosome; L = A. lineata chromosome.
* denotes nucleolar chromosome.

Figs. 11-15. Pachytene chromosomes of Atylosia lineata. In each pair of figures A is a photomicrograph (×2000) and B is an interpretive drawing. Arrows indicate position of centromere. 11A and B, chromosome I. 12A and B, chromosome II. 13A and B, chromosome III. 14A and B, chromosomes IV and XI. 15A and B, chromosome V.
arm also appears in two groups of 3 and 2 chromomeres.

Chromosome VI (Figs. 16A and 16B) is median. Both the long and short arms are constituted of nearly equal lengths of HC (long arm 3.5 μ; short arm 3.4 μ) and EC.

Chromosome VII (Figs. 17A and 17B) is submedian. The short arm measures nearly half the length of the long arm. The HC of the short arm (6.5 μ) is one and half times more than that of the long arm (2.6 μ).

Figs. 16–20. *Atylosia lineata* pachytene chromosomes. In each pair of figures A is a photomicrograph (×2000) and B is an interpretive drawing. Arrows indicate position of centromere. 16A and B, chromosome VI. 17A and B, chromosome VII. 18A and B, chromosome VIII. 19A and B, chromosome IX. 20A and B, chromosome X.
Chromosome VIII (Figs. 18A and 18B) is submedian. The HC of both the long (3.2 μ) and short (3.3 μ) arms is equal in length and possess 3 chromomeres each. Chromosome IX (Figs. 19A and 19B) is submedian. The HC of both the long and short arms is equal in length. The HC (5.3 μ) of the long arm occupies nearly one-fourth of the region and consists of 5 distinct chromomeres. The HC (5.2 μ) of the short arm possesses a barrel shaped chromomere followed by a chromatic segment.

Chromosome X (Figs. 20A and 20B) is the nucleolar organising chromosome. The
nucleolus is attached to the short arm and the satellite measures 5.6 μ. The HC (1.0 μ) of short arm consists of a single chromomere in contrast to the HC (4.7 μ) of long arm which possesses 2 big chromomeres and 3 smaller distal chromomeres.

Chromosome XI (Figs. 14 A and 14B) is the smallest subterminal chromosome of the complement and the HC of long arm measures 3.2 μ. The short arm comprises nearly equal lengths of HC and EC. The HC (1.5 μ) of the short arm possesses 2 distinct chromomeres.

Pachytene studies in the hybrid

In nine out of the eleven bivalents the homoeologues participating in pairing were identified in the hybrid. The synapsis in these bivalents is complete except for certain interstitial and terminal regions in a few cells. Of the remaining two chromosomes, one appears to be involved in a trivalent configuration and the other is represented by a morphologically distinct bivalent. A detailed account of the pairing behaviour of specific chromosomes of the two parents is given below. A comparative statement of the cytological values of the parents and the hybrid is given in Table 1.

Chromosome I of Cajanus pairs with the chromosome I of A. lineata. They are completely homologous as to their length, arm ratio and amount and distribution of HC. In most of the cells, this bivalent is completely paired. However, in a few cells, the distal EC region of the short arm is unpaired (Figs. 23A and 23B).

Chromosome II of Cajanus pairs with the chromosome II of A. lineata which has bigger chromomere in the long arm. This chromomere is intermediate in size in the hybrid. In a few cells, the HC of short arm was found to be partly unpaired (Figs. 24A and 24B).

Chromosome III of Cajanus pairs with the chromosome III of A. lineata. The total length, arm ratio and the HC length in the long arm of lineata chromosome are slightly more than those of Cajanus. The differences in the length of the HC of the long arm of the parents is clearly visualised in the hybrid, the excess of HC of lineata chromosome being associated nonhomologously with the EC of Cajanus chromosome (Figs. 25A and 25B).

Chromosome IV of Cajanus pairs with the chromosome V of A. lineata. Both are median chromosomes and the HC of both the arms of these chromosomes appears in two groups of chromomeres. However, the number of chromomeres forming each group differ. In Cajanus, the proximal group of long arm possesses 2 closely appressed chromomeres followed by the distal group consisting of 4 to 5 small faintly stained ones. In A. lineata, the proximal group of long arm possesses 4 to 5 chromomeres followed by the distal group consisting of 2 distinct chromomeres. Inspe
Figs. 27–33. Pachytene chromosomes of *C. cajan × A. lineata* hybrid. In each pair of figures A is photomicrograph (×2000) and B is an interpretive drawing. Arrows indicate position of centromere. 27A and B, bivalent, V⁰-IV⁸. 28A and B, bivalent, VI⁰-VI⁸. Note the HC length differences in the long arm. The excess of HC of *C. cajan* chromosome is loosely associated with EC.
of these differences, the bivalent in the hybrid is intimately paired (Figs. 26A and 26B). In a few microsporocytes non-pairing in the HC region of both long and short arms was observed.

Chromosome V of *Cajanus* pairs with the chromosome IV of *A. lineata*. Both are subterminal chromosomes. In the hybrid, the bivalent possesses slightly higher arm ratio than the parents (Figs. 27A and 27B). Occasionally, EC regions of this chromosome were unpaired.

Chromosome VI of *Cajanus* pairs with the chromosome VII of *A. lineata*. These two chromosomes differ in the length and amount of HC of the long arm. The *lineata* chromosome possesses a single macrochromomere in its long arm in contrast to a long HC region in *Cajanus* long arm. These differences in the length of HC are clearly brought out in the hybrid, the excess HC of *Cajanus* chromosome being loosely associated with EC of *lineata* chromosome (Figs. 28A and 28B). In a few microsporocytes, this bivalent appears heteromorphic in the long arm.

Chromosome VII of *Cajanus* pairs with the chromosome IX of *A. lineata*. These two chromosomes differ in their length, arm ratio and the HC pattern of short arm. Inspite of these differences, in the hybrid, this bivalent is intimately paired except in few microsporocytes where there is a failure of pairing in EC regions (Figs. 29A and 29B).

Chromosome X of *Cajanus* pairs with the chromosome X of *A. lineata*. Both are nucleolus organising chromosomes and *lineata* chromosome is slightly longer than that of *Cajanus* and they differ in the HC pattern in minor details. In the hybrid, this bivalent is completely paired except for few pairing failures in the terminal EC regions (Figs. 30A and 30B).

Chromosome XI of *Cajanus* pairs with the chromosome XI of *A. lineata*. Both are subterminal chromosomes but differ in their length and arm ratio. Inspite of these differences, the bivalent is completely paired in the hybrid (Figs. 31A and 31B). In a few microsporocytes, heteromorphism in the long arm was noticed.

The bivalents formed by the chromosomes VIII and IX of *Cajanus* and chromosomes VI and VIII of *A. lineata* could not be identified. Instead, a chromosome participating in a trivalent configuration was observed (Fig. 32). This chromosome could not be identified and its corresponding univalent was not observed. A bivalent which is morphologically distinguishable from the above chromosomes of the parents and the rest of the bivalents was observed in 3 microsporocytes (Figs. 33A and 33B). This bivalent measures 38.6 μ with an arm ratio of 0.70.

**Discussion**

The pachytene chromosomes of both *Cajanus* and *A. lineata* belong to the differentiated category with distinct centromeres flanked by proximal dark staining HC and distal light staining EC. The total chromatin length of *A. lineata* is more
than that of *Cajanus* by 22.5 μ. *Cajanus* possesses 2 median, 6 sub-median and 3 subterminal chromosomes and *A. lineata*, 2 median, 7 sub-median and 2 subterminal chromosomes. *Cajanus* with more of subterminal chromosomes and smaller genome length, appears to be an advanced and derived species from *Atylosia*.

On the basis of length, arm ratio, association of nucleolus and/or HC pattern 10 chromosomes viz., I, II, III, IV, V, VI, VII, VIII, X and XI of *Cajanus* correspond with chromosomes I, II, III, V, IV, VII, IX, VI, X, and XI of *A. lineata* respectively. These corresponding pairs show varying degrees of similarity. While some are exactly identical in all the morphological criteria employed in their identification some are identical only in few respects.

In the hybrid, in a number of microsporocytes, at pachytene, synopsis was found to be complete, thereby indicating a very high degree of homology between *Cajanus* and *Atylosia lineata*. These observations also indicate that the differences in the mean length and arm ratio noted in a large number of parent chromosomes do not constitute major differences between the two genera. The differences in the mean lengths of chromosomes are circumvented by reciprocal adjustments in lengths in the hybrids resulting in bivalents of intermediate length as in the case of interspecific hybrid between *Phaseolus aureus* and *Phaseolus mungo* (De and Krishnan 1966). Similar observations were made in the case of intergeneric hybrid between *Lycopersicon esculentum* and *Solanum lycopersicoides* (Menzel 1962), in the hybrid between maize and teosinte (Longley 1937) and in an interspecific hybrid between *Pennisetum typhoides* and *P. purpureum* (Pantulu 1967). The differences in arm ratio of the parent chromosomes are accommodated during pairing in the hybrid in a similar way or by indifferent pairing with respect to the position of centromeres. This may, perhaps be accompanied by non-homologous pairing near the centromeric region. To some extent, the differences in the HC of the parent chromosomes are circumvented by reciprocal adjustments in lengths in the hybrids. However, in certain cases, non-homologous association of HC of one chromosome with the EC of its homoeologue was observed. As for example, the excess of HC of chromosome III of *A. lineata* is associated non-homologously with the EC of *Cajanus* chromosome. In certain cases, where there are HC length differences between parent chromosomes, the excess of HC remained unpaired with the corresponding EC region. Thus, for example the excess of HC of chromosome VII of *A. lineata* is either loosely associated or not paired with the corresponding EC of chromosome VI of *Cajanus*.

No major structural alterations were evident from pairing behaviour in the hybrid. Two bivalents viz., IVc—VIl and XIc—XIℓ exhibit heteromorphism. Occasionally, a trivalent configuration was observed, thereby, indicating the presence of a possible duplicated segment.

The comparative analysis of the somatic karyotypes of *Cajanus* and *A. lineata* indicated that 7 chromosomes are common to *Cajanus* and *A. lineata* (Reddy and De, in press). On the basis of the direct comparison of pachytene chromosome morphology it has been found that 10 chromosomes are common to *Cajanus* and *A. lineata*. On the basis of pairing behaviour of the pachytene chromosomes of the hybrid, it is evident that 9 chromosomes are common to *Cajanus* and *A. lineata*. Hence it is concluded that *A. lineata* is very closely related to *Cajanus*. 
Summary

The individual pachytene chromosomes of the entire complement of *Cajanus cajan* and *Atylosia lineata* were identified on the basis of relative length, arm ratio, chromomere pattern and nucleolar association. The pachytene chromosomes of both the species were found to belong to the differentiated type. *Cajanus* possesses 2 median, 6 sub-median and 3 subterminal chromosomes and *A. lineata*, 2 median, 7 sub-median and 2 subterminal chromosomes. On the basis of the various criteria employed for the identification of pachytene chromosomes, 10 chromosomes were found to be common to both *Cajanus* and *A. lineata*.

In the *Cajanus × A. lineata* hybrid a considerable number of microsporocytes, at pachytene, revealed complete synapsis. This indicates a very high degree of homology between the two genera. In the hybrid, in nine out of the eleven bivalents the homoeologues participating in synapsis were identified. No major structural alterations were evident from the pairing behaviour and two bivalents exhibited heteromorphism in the hybrid. These studies indicate that indeed *Cajanus* and *Atylosia lineata* are closely related to each other.

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References


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