

Chromosome studies in the genus *Mikania* (Asteraceae)

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INTRODUCTION

Mikania is the largest genus of the tribe Eupatorieae with about 430 species distributed in the pantropics, temperate America, and Southern Africa, but with its two major diversity centers in the highlands of southeastern Brazil and the eastern foothills of the Andes from Bolivia to Colombia (King and Robinson, 1987; Holmes, 1995). The genus is widely distributed in Brazil with about 200 described species (Barroso, 1958, 1986), many of which are endemic to southern Brazil, but with a greater number of species being found in Amazon region.

The species are characterized by their capitula which is composed of four florets and an involucre composed of four phyllaries that is subtended by a subinvolucral bract. There is no variation from this basic organization, and specific differences mostly involve the type of capitulescence, size of habit, shape of organs, and plant texture (Holmes, 1995).

Until 1987 chromosome studies of the genus have been limited to chromosome counts, but such counts are available for only about 10% of the species (Gaiser, 1954; Mangenot and Mangenot, 1958; Turner, 1962; Turner *et al.*, 1967; Baquar, 1967-1968; Mitra and Datta, 1967; Sharma and Sakar, 1967-1968; Coleman, 1968; Nevlin, 1969; Powell and King, 1969; King *et al.*, 1976; Turner *et al.*, 1979; Nauman, 1981; Mathew and Mathew, 1983; Strother, 1983; Waisman *et al.*, 1984).

The first karyotype studies in *Mikania* were made by Ruas and Ruas (1987) on six species from which they suggested that there was an evolutionary trend in the genus towards the formation of aneuploid and polyploid series. In a study of ten species of *Mikania* Ruas (1989) and Ruas and Aguiar-Perecin (1997) proposed a correlation between morphological and chromosomal evolution, while an analysis of 12 cytotypes of *Mikania micrantha* by Maffei (1996) showed that the same evolutionary mechanisms that occur among species also occur at intraspecific level, results also seen in a study of two populations of *M. cordifolia* by Maffei *et al.* (1999a).

In this review, the chromosomal evolution of the genus *Mikania* is discussed based on currently available data.

KARYOLOGICAL ASPECTS

Thirty-two taxa of *Mikania* have so far been examined, including 16 different species (Ruas and Ruas, 1987; Ruas, 1989; Ruas and Aguiar-Perecin, 1997), 14 populations of *M. micrantha* (Ruas and Ruas, 1987; Maffei, 1996; Maffei *et al.*, 1998, 1999b) and two populations of *M. cordifolia* (Ruas and Ruas, 1987; Maffei *et al.*, 1999a). All the karyotypes were characterized by the presence of a secondary constriction in the long arm of chromosome 1, and Ruas and Ruas (1987), in the analysis of six species, proposed that this secondary constriction should be considered a cytological marker for the genus. In six tetraploid cytotypes of *M. micrantha* (Table I) a secondary constriction was observed in chromosomes pairs 1 and 2. In *M. sessilifolia*, a hexaploid species, this cytological marker was seen in the first three pairs of chromosomes. Ruas (1989) and Ruas and Aguiar-Perecin (1997) showed (using the silver staining methodology) that the nucleolar-organizing region is located in the secondary constriction of the long arm of chromosome 1, and it seems that this pattern has been conserved in the evolution of the karyotypes of *Mikania* as proposed by Ruas and Ruas (1987).

In all karyotypes so far examined chromosome 1 ranges in length from 2.00 to 5.20 μm and the arm ratio varies from 1.40 (*M. trinervis*) to 2.60 μm (*M. micrantha* from Praia de Ipanema, Paraná State, Brazil), which suggests that structural rearrangements such as the deletion or addition of chromatin might have occurred during the evolution of genus *Mikania*. C-banding analysis showed a large block of heterochromatin near the secondary constriction of chromosome 1 in a population of *M. micrantha* from Piracicaba (São Paulo State, Brazil), while another population of this species showed a smaller chromosome pair 1 accompanied by the total absence of heterochromatic bands. The presence or absence of heterochromatin may in part explain the variation in size observed in chromosome 1.

In all the species and cytotypes so far studied (Ruas and Ruas, 1987; Ruas, 1989; Maffei, 1996; Ruas and Aguiar-Perecin, 1997; Maffei *et al.*, 1998, 1999b) the smallest pair of chromosomes ranges in length from 0.60 to 1.50 μm and the arm ratio varies from 1.20 (*M. micrantha* from Apucarana) to 2.80 μm (*M. cordifolia* and *M. glomerata*), which suggests that structural rearrangements such as DNA

Table 1 - Origin, collection number, chromosome length (µm), karyotype symmetry, and karyotype formulas of *Mikania* species, arranged in sections according to Barroso (1958, 1986)¹.

Section	Origin and collection number	2n	Chromosome length		Karyotype symmetry		Karyotype formula	Authors
			Range (largest-smallest)	Haploid set	TF%	Ratio L/S		
Thyrsigerae B. Robinson								
<i>M. additicia</i> Robinson	Nova Friburgo, RJ ² FUEL 5721	34	3.31 ^{def} 1.00 ^{ab}	27.01 ^{de}	40.96 ^b	3.31 ^{def}	26m + 8sm	Ruas (1989), Ruas and Aguiar-Perecin (1997)
<i>M. hemisphaerica</i> Schultz-Bip	Viçosa, MG FUEL 1281	36	3.00 ^{efgh} 0.95 ^{ab}	29.48 ^{ale}	42.93 ^a	3.16 ^{ef}	32m + 4sm	Ruas (1989), Ruas and Aguiar-Perecin (1997)
<i>M. lanuginosa</i> DC.	Serra do Mar, PR FUEL 4500	36	4.46 ^{abc} 0.95 ^{ab}	29.94 ^{ale}	39.43 ^{abc}	4.69 ^b	28m + 8sm	Ruas (1989), Ruas and Aguiar-Perecin (1997)
<i>M. punctata</i> Gardner	Serra do Mar, PR FUEL 4496	36	4.16 ^{abcd} 0.93 ^{ab}	29.04 ^{ale}	39.51 ^{abc}	4.47 ^{bc}	24m + 12sm	Ruas (1989), Ruas and Aguiar-Perecin (1997)
<i>M. sericea</i> Hook. et Arn.	Serra do Mar, PR FUEL 4564	42	4.51 ^{abcd} 0.88 ^{ab}	35.41 ^{bc}	39.58 ^{abc}	5.63 ^a	28m + 14sm	Ruas (1989), Ruas and Aguiar-Perecin (1997)
<i>M. trinervis</i> Hook. et Arn.	Londrina, PR FUEL	36	4.00 ^{bcd} 1.10 ^{ab}	43.10 ^a	37.30 ^{bcd}	3.64 ^{de}	24m + 10sm + 2st	Ruas and Ruas (1987)
Corymbosae B. Robinson								
<i>M. cordifolia</i> Willd.	Guaíba, RS FUEL 6514	34	4.00 ^{bcd} 1.10 ^{ab}	35.30 ^{bc}	37.60 ^{bcd}	3.64 ^{de}	16m + 16sm + 2st	Ruas and Ruas (1987)
<i>M. hastato-cordata</i> Malme	Campinas, SP FUEL 0930	36+1-7Bs	3.04 ^{efgh} 0.72 ^{ab}	19.20 ^f	-	4.40 ^{bc}	26m + 8sm + 2st	Maffei <i>et al.</i> (1999a)
<i>M. involucrata</i> Hook. et Arn.	Guaíba, RS FUEL 1263	34	2.70 ^{gh} 1.20 ^a	28.65 ^{ale}	37.40 ^{bcd}	2.25 ^g	22m + 8sm + 4st	Ruas (1989), Ruas and Aguiar-Perecin (1997)
<i>M. micrantha</i> H.B.K.	Guaíba, RS FUEL 6122	36	2.88 ^{gh} 0.79 ^{ab}	22.29 ^{ef}	41.28 ^{ab}	3.64 ^{de}	24m + 12sm	Ruas (1989), Ruas and Aguiar-Perecin (1997)
	Londrina, PR FUEL 09335	72	2.00 ^h 1.50 ^a	38.10 ^{ab}	37.30 ^{bcd}	1.33 ^b	24m + 46sm + 2st	Ruas and Ruas (1987)
	Apucarana, PR FUEL 11017	72+0-2Bs	3.20 ^{gh} 0.60 ^b	26.10 ^{def}	37.30 ^{bcd}	3.90 ^{cd}	40m + 30sm + 2st	Maffei (1996)
	Foz do Iguaçu, PR FUEL 17307	72	2.60 ^{gh} 0.80 ^{ab}	23.80 ^{ef}	37.60 ^{bcd}	3.10 ^{ef}	40m + 26sm + 6st	Maffei (1996)
	Guaíba, RS ICN 44499	72	3.20 ^{efg} 0.80 ^{ab}	20.50 ^{ef}	37.00 ^{bcd}	3.90 ^{cd}	40m + 32sm	Maffei (1996)
	Itajaí, SC FUEL 17308	72	3.12 ^{efg} 1.00 ^a	27.44 ^{de}	37.42 ^{bcd}	3.12 ^{ef}	38m + 34sm	Maffei <i>et al.</i> (1998)
	Tamarana, PR FUEL 11448	72+0-2Bs	2.90 ^{gh} 0.80 ^{ab}	23.35 ^{ef}	38.50 ^{bcd}	3.60 ^{ef}	46m + 24sm + 2st	Maffei (1996)

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Table 1 - Continued

Section	Origin and collection number	2n	Chromosome length		Karyotype symmetry		Karyotype formula	Authors	
			Range (largest-smallest)	Haploid set	TF%	Ratio L/S			
<i>M. micrantha</i> H.B.K.	Alfredo Guedes, SP FUEL11446	36	2.50 ^{gh}	0.70 ^{ab}	21.80 ^{ef}	37.70 ^{bcd}	3.40 ^{def}	26m + 10sm	Maffei (1996)
	Campinas, SP FUEL09331	36+6-7Bs	2.30 ^{gh}	0.70 ^{ab}	20.80 ^{ef}	39.80 ^{bce}	3.20 ^{def}	26m + 10sm	Maffei (1996)
	Esirela do Norte, SP FUEL11447	36+0-1Bs	5.20 ^a	1.00 ^{ab}	32.50 ^{bcd}	37.50 ^{bcd}	5.00 ^{ab}	22m + 14sm	Maffei (1996)
	Joinville, SC FUEL14725	42	3.50 ^{bcddef}	0.80 ^{ab}	32.20 ^{bcd}	35.20 ^d	4.40 ^{bc}	26m + 14sm + 2st	Maffei (1996)
	Petrópolis, RJ UEC26183	36	2.90 ^{gh}	0.90 ^{ab}	25.00 ^{def}	36.40 ^{cd}	3.30 ^{def}	22m + 12sm + 2st	Maffei (1996)
	Piracicaba, SP FUEL09334	36+4-14Bs	2.70 ^{gh}	0.90 ^{ab}	23.60 ^{ef}	38.30 ^{bcd}	3.20 ^{def}	20m + 16sm	Maffei (1996)
	Praia Grande, SP FUEL09334	36+0-7Bs	2.40 ^{gh}	0.70 ^{ab}	19.90 ^f	38.30 ^{bcd}	3.50 ^{def}	26m + 10sm	Maffei (1996)
	Praia de Ipanema, PR FUEL17306	36	4.40 ^{abcd}	1.00 ^{ab}	31.30 ^{cd}	36.10 ^{cd}	4.50 ^{bc}	24m + 12sm	Maffei (1996)
	Guaíba, RS FUEL6120	36	2.95 ^{gh}	1.04 ^{ab}	28.02 ^{ale}	42.61 ^a	2.84 ^g	34m + 2st	Ruas (1989), Ruas and Aguiar-Perecin (1997)
	Guaíba, RS FUEL4172	68	4.40 ^{abcd}	1.30 ^{ab}	38.90 ^{ab}	39.30 ^{bce}	3.38 ^{def}	40m + 26sm + 2st	Ruas and Ruas (1987)
Spicato-Racemosa Baker <i>M. sessifolia</i> DC.	Serra do Caeté, PR FUEL4099	108	3.49 ^{cdef}	0.89 ^{ab}	26.52 ^{def}	41.33 ^{ab}	3.72 ^{de}	88m + 20sm	Ruas (1989), Ruas and Aguiar-Perecin (1997)
	Globosae B. Robinson <i>M. glomerata</i> Spreng.	36	4.00 ^{bcd}	0.90 ^a	29.90 ^{ale}	30.90 ^e	4.45 ^{bc}	12m + 22sm + 2st	Ruas and Ruas (1987)
<i>M. laevigata</i> Schultz Bip.	Guaíba, RS FUEL3366	38	4.40 ^{bce}	0.80 ^{ab}	38.20 ^{ab}	39.40 ^{bce}	5.50 ^a	20m + 18sm	Ruas and Ruas (1987)
	Section not identified <i>Mikania</i> sp.	34	3.72 ^{bcd}	1.00 ^{ab}	28.67 ^{ale}	38.96 ^{abcd}	3.72 ^{de}	24m + 10sm	Ruas (1989), Ruas and Aguiar-Perecin (1997)

¹Means within each column followed by different letters are significant at the 5% probability level by the Tukey test. ²The abbreviations of the localities correspond to Brazilian states: RJ, Rio de Janeiro; PR, Paraná; RS, Rio Grande do Sul; SP, São Paulo.

amplification or the deletion of small portions of chromatin and pericentric inversions may have occurred in this chromosome pair during karyotype evolution (Table I).

A tendency toward karyotype asymmetry was observed in all species (Table I), with *M. glomerata* displaying the most asymmetric karyotype of all the species so far studied, having a TF% value of 30.90 and a ratio longest:shortest of 4.45 (Ruas and Ruas, 1987).

CYTOTYPES OF *M. MICRANTHA*

Fourteen cytotypes of *M. micrantha* were studied, all from different localities in Brazil (Ruas and Ruas, 1987; Maffei, 1996; Maffei *et al.*, 1998, 1999b); seven were diploid, six with $2n = 2x = 36$ and one with $2n = 2x = 42$, while six were tetraploid with $2n = 4x = 72$. In all the cytotypes of *M. micrantha* chromosome pair 1 was the most inconstant, showing variation in both size and structure. The largest chromosomes were in cytotypes from Estrela do Norte (São Paulo State) and Praia de Ipanema (Paraná State), which also had the largest haploid sets (Table I). The population from Praia Grande (São Paulo State) had the smallest chromosomes and haploid length. This difference in chromosome size occurred in all the chromosome pairs, reflecting a gain or loss of genetic material (Maffei, 1996; Maffei *et al.*, 1999b). Two other cytotypes (from Alfredo Guedes and Campinas), both with $2n = 36$, showed the same karyotype formula and similar haploid sets but they differed slightly in their arm-ratio values, which were probably modified by inversions (Maffei, 1996; Maffei *et al.*, 1999b). Similar conclusions can be reached for the analysis of the six tetraploids with $2n = 4x = 72$ chromosomes, of which the population from Londrina showed the largest haploid set, with most of the variation between the tetraploids being represented by centromeric shifts. The differences observed among the cytotypes of *M. micrantha* do not seem to be related to adaptive variables, since populations occupying similar environments bear distinct karyotypes.

KARYOTYPE EVOLUTION

Chromosome studies show a regular aneuploid series with $x = 17, 18, 19, 20$ and 21 in the genus *Mikania* (King *et al.*, 1976; Robinson and King, 1977; King and Robinson, 1987; Ruas and Ruas, 1987; Ruas, 1989; Ruas and Aguiar-Perecin, 1997; Maffei *et al.*, 1998, 1999a,b), with aneuploidy seeming to be an important component of chromosomal evolution in this genus.

In addition to aneuploidy, polyploidy is common in *Mikania*, with Ruas and Ruas (1987) having described two polyploid species, *M. viminia* ($2n = 4x = 68$) and a cytotype of *M. micrantha* with $2n = 4x = 72$, while five other cytotypes of *M. micrantha* with $2n = 4x = 72$ were described by Maffei (1996) and Maffei *et al.* (1998, 1999b). Ruas (1989) and Ruas and Aguiar-Perecin (1997) reported a hexaploid species, *M. sessilifolia* with $2n = 6x = 108$; the

karyotype of this species showed 18 subsets of chromosomes, each of them having three pairs of morphologically similar chromosomes, suggesting autopolyploid origin. *M. micrantha* has populations with $2n = 34, 36, 38, 40, 42$, and 72 chromosomes (Powell and King, 1969; King *et al.*, 1976; Turner, 1977; Strother, 1983; Waisman *et al.*, 1984; Ruas and Ruas, 1987; Maffei, 1996; Maffei *et al.*, 1998, 1999b) while *M. cordifolia* has aneuploid cytotypes with $n = 17, 18$, and 19 (Gaiser, 1954; Powell and King, 1969; Ruas and Ruas, 1987; Robinson *et al.*, 1989; Maffei *et al.*, 1999a). *M. cordata* and *M. capricorni* have counts of $n = 17$ and 18 (Coleman, 1968) and *M. pachyphylla* has counts of $n = 17, 18$, and 20 (Nevlin, 1969). These results demonstrate that aneuploid series and polyploidy are common at both the interspecific and intraspecific levels in the genus *Mikania*.

C-BANDING ANALYSIS

C-banding analysis has been applied in three diploid cytotypes of *M. micrantha* from Piracicaba, Campinas, and Praia Grande (Maffei, 1996; Maffei *et al.*, 1999b) and revealed a variable pattern in the amount and distribution of heterochromatin in these cytotypes. The cytotype from Piracicaba showed a large heterochromatic block near the secondary constriction of chromosome 1, and three other chromosome pairs had small centromeric bands, while another cytotype exhibited a block of heterochromatin located near the secondary constriction of the large arm of chromosome 1 and several other chromosomes showed centromeric C-bands. On the other hand, the cytotype from Praia Grande had only three pairs of chromosomes with very small centromeric bands and a total absence of heterochromatin in chromosome 1. Thus, at least for the diploid cytotypes of *M. micrantha*, difference in haploid chromosome length may reside in unique and repetitive sequences of DNA.

B-CHROMOSOMES

B-chromosomes in the genus *Mikania* were only described in four diploid and two tetraploid cytotypes of *M. micrantha* (Maffei, 1996; Maffei *et al.*, 1999b) and in one population of *M. cordifolia* from Campinas (Maffei *et al.*, 1998); variation in number of Bs among cells of the same root meristem was observed in all the plants examined, which may be explained by nondisjunction during mitotic division of the meristem cells.

Besides the variation in number from cell to cell and among cytotypes, the B-chromosomes of *M. micrantha* diverged in size (from micro-size to about $0.8 \mu\text{m}$) and morphology. Three morphological types were observed, m, sm, and st, which also varied from micro-sized in some cells to large telocentrics in other cells. A variable number of very small m type B-chromosomes were found in many cells of the Piracicaba cytotypes, which may be explained

by centromere misdivision of a single unpaired B-chromosome, giving rise to two different-sized chromosomes and further derivatives by deletion of parts of the arms. Since the B-chromosomes occurred in both littoral (Praia de Ipanema and Praia Grande) and high altitude (Petrópolis) populations of *M. micrantha* their presence was not adaptive.

C-banding in the diploid cytotypes from Piracicaba, Campinas, and Praia Grande showed heterochromatic B-chromosomes, and no detectable differences were observed in the C-band pattern between A and B-chromosomes, suggesting that there is no difference in the repetitive sequences of these two chromosome types.

MORPHOLOGICAL AND CYTOLOGICAL EVOLUTION

Lawrence (1951) suggested a series of evolutionary events to explain the origin of the different types of inflorescences found in Asteraceae. In *Mikania*, the inflorescence types are more complex than those observed in other genera of the tribe Eupatorieae, suggesting that this genus is evolutionarily advanced (Stebbins, 1977).

Five types of inflorescence are found in the genus *Mikania*, and according to Lawrence (1951) the thyrse type is the most primitive. More complex types of inflorescence such as corymbose, spicate, racemose, and glomerulate may have evolved from modifications that occurred in the thyrse type. The species with the thyrse inflorescence (section *Thyrsigerae*) correspond to about 48% of all species cited by Barroso (1958). As noted in Table I there is a high frequency of species with $x = 18$ in the *Thyrsigerae* section, supporting the hypothesis that $x = 18$ is the original basic number for *Mikania*, from which the other values (17, 19, 20, and 21) have originated by aneuploidy. These data are in agreement with the findings of Mathew and Mathew (1983). High basic numbers, such as those observed in *Mikania* ($x = 17, 18, 19, 20, 21$), are considered to have originated by aneuploidy from the basic numbers of $x = 7, 8, 9$, found in angiosperms (Grant, 1981). The analysis of species and cytotypes suggests that in the genus *Mikania* there is a correlation between chromosome numbers and inflorescence types.

CONCLUDING REMARKS

1. A secondary constriction in the long arm of chromosome 1 of all the species examined was identified as a cytological marker for the genus.

2. Analysis of the karyotypes demonstrated that chromosome rearrangements are common in the evolution of the genus *Mikania* at both the intraspecific and the interspecific level.

3. The chromosomal data obtained showed an aneuploid and polyploid series of $2n = 34, 36, 38, 40, 42, 68, 72,$ and 108, which clearly demonstrated that aneuploidy and polyploidy are common in the evolutionary trend of this genus.

4. Correlation between the inflorescence types and chromosome numbers found in the genus indicated that $x = 18$ is the primitive basic chromosome number from which the others have been derived by aneuploidy ($x = 17, 19, 20,$ and 21).

5. C-band analysis showed that a mechanism of DNA amplification or deletion of small segments of chromatin may be responsible for the variation observed in the size of chromosome 1.

6. B-chromosomes were observed in some cytotypes of *M. micrantha* and the C-band analysis demonstrated that these supernumerary chromosomes are heterochromatic. The same kind of heterochromatin was present in both A and B chromosomes.

7. Meristem cells showed variation in B-chromosome numbers, size and morphology, both in individual cells of the same plant and in different plants.

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