The Nucleus
https://doi.org/10.1007/s13237-026-00696-w

ORIGINAL ARTICLE

Assessing karyotype diversity and genome size in underexploited *Mimosa* L. species (Leguminosae Juss.)

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Received: 25 August 2025 / Accepted: 6 July 2026

Abstract

Mimosa L. comprises approximately 620 species of socioeconomic and environmental importance, with about half occurring in the Brazilian Cerrado. Despite this diversity, cytogenetic studies in the genus remain limited, with most restricted to chromosome counts. We investigated 11 populations of seven *Mimosa* species, focusing on the heterochromatin distribution (CMA^+ bands), and nuclear DNA content. Polysomaty was observed in root meristem cells of six species, absent only in *M. verrucosa*, in which only diploid cells were detected. Variation in the number, position, and intensity of CMA^+ bands was detected both within and among populations. The number of CMA^+ bands ranged from four in *M. caesalpiniifolia* (diploid cells) to 104 in *M. candollei* (octaploid cells), with no apparent phylogenetic pattern. Polysomatic cells generally showed a proportional increase in CMA^+ bands with ploidy level. Nuclear DNA content varied from 1C = 0.64 pg (*M. sensitiva*) to 1C = 1.55 pg (*M. arenosa*), with no correlation ($r = 0.1417$) between ploidy and DNA content. Our results, together with previous reports, indicate that polysomaty is a frequent genomic feature in *Mimosa*, likely associated with environmental adaptation, growth and development. This study represents the first intra- and interpopulation assessment of heterochromatin variation and nuclear DNA content across multiple *Mimosa* species, providing novel insights into heterochromatin dynamics and genome organization in this diverse cytogenetically understudied legume genus. This article aligns with SDG 15 (Life on Land) of the UN Agenda for Sustainable Development.

Keywords *Mimosa* · Karyotyping · Heterochromatin distribution · DNA content · Polysomaty · SDG-15 (Life on Land)

Introduction

Mimosa L., the fifth largest genus of the Leguminosae Juss., comprises over 620 species recognized for their seismonastic movements, broad distribution, and ecological adaptability [3, 28]. These species occur mainly in Neotropical regions, inhabiting equatorial, tropical and subtropical forests, Savannas (including the Brazilian Cerrado), fire-prone and arid zones, grasslands, and deserts [23]. Brazil harbors the highest diversity, with 73% of species endemic and nearly half restricted to the Cerrado [23]. *Mimosa* has multiple applications, including ornamental, medicinal, living fences, ecological restoration, and soil enrichment through nitrogen fixation [14, 32, 39]. Adaptations to fire, such as woody

Corresponding Editor: Maki Yamamoto; Reviewers: Rupali Nemgonda Chougule, Kyoko Sato.

Significance Statement: *Mimosa* exhibits remarkable diversity in constitutive heterochromatin. Additionally, polysomaty appears to be a widespread feature in the genus, potentially associated with plant growth, adaptation, and establishment. Our findings provide novel insights into nuclear DNA content and chromosome organization in *Mimosa*, offering a valuable framework for future evolutionary and genomic investigations.

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Published online: 29 July 2026

underground organs, thick bark, congested leaves, and persistent stipules, are also common [2].

Despite their ecological and economic relevance, genetic and cytogenetic studies remain scarce. DNA content has been reported only for *M. pudica* and *M. invisa* [31; https://cvalues.science.kew.org/]. Recently, *M. bimucronata* became the first species to have its genome sequenced, assembled, and annotated [14]. Chromosome counts are available for ~ 10% of *Mimosa* species [34], while fluorochrome banding with Chromomycin A3 (CMA) and 4',6-diamidino-2-phenylindole (DAPI), as well as Fluorescent *in situ* Hybridization (FISH) with ribosomal DNA (rDNA) probes, are limited to *M. caesalpiniifolia* and *M. pudica* [9, 31].

Cytologically, most *Mimosa* species are diploid ($2n = 2x = 26$), with basic chromosome number of $x = 13$ ([6]). Polyploidy occurs in ~ 25% of species and is considered a key driver of *Mimosa* evolution and speciation [20, 21]. Additionally, polysomaty, the coexistence of cells with different ploidy levels in the same organ or tissue, has also been reported in *M. bimucronata*, *M. caesalpiniifolia*, and *M. pudica* [7, 9, 24, 31].

Despite their ecological and evolutionary significance, data on DNA content and karyotype features remain largely unknown for most species, lacking a comprehensive understanding of the genome organization within the genus. Here, we present new cytogenetic data on constitutive heterochromatin (CH) patterns and genome size estimates for different populations of seven *Mimosa* species. We address the following questions: (1) Does *Mimosa* genus exhibit intra- and interpopulation variation in the number, size and position of CH bands in their karyotypes? (2) Is there a direct correlation between ploidy and DNA content in *Mimosa*? (3) Is polysomaty a common feature across the genus? Our findings provide new insights into genome dynamics and cytogenetic diversity in these understudied legumes.

Materials and methods

Plant material

We analyzed two populations of *M. verrucosa* Benth., three populations of *M. caesalpiniifolia* Benth., two of *M. sensitiva* L., and one each of *M. tenuiflora* (Willd.) Poir., *M. arenosa* (Willd.) Poir, *M. candollei* R. Grether and *M. ophtalmocentra* Mart. ex Betnh. For cytogenetic analysis, at least 20 individuals were analyzed per population. Field-collected samples (*M. verrucosa* population 2 and *M. sensitiva* population 2) were deposited at Graziela Barroso herbarium (Universidade Federal do Piauí, Teresina, Brazil. Species and their provenance / voucher number are described in Table 1.

Chromosome preparation

Roots tips obtained from germinated seeds were pretreated in 3 mM 8-hydroxyquinoline for 4.5h at 17 °C, fixed in Carnoy (3:1, methanol: acetic acid, v/v), and stored at − 20 °C. Roots were digested with 4% cellulase (Onozuka R-10, Serva), 2% pectolyase (Sigma-Aldrich), and 20% pectinase (Sigma-Aldrich) for 4.5h at 37 °C. Slides were prepared following [8] protocol, and aged for three days.

CMA/DAPI banding

Slides were stained with CMA (0.5 mg mL^{-1}, 1.5h), counterstained with DAPI (2 mg mL^{-1}, 1h), mounted in glycerol/McIlvaine buffer pH 7.0 (1:1, v/v), and aged for three days before analysis [35].

Microscopy and chromosomal measurements and counting

Metaphases were acquired using Leica DM4B microscope with DF7000GT camera. Image brightness and contrast were adjusted with Adobe Photoshop CS3. Three to five metaphases per population were measured using Drawid v0.26 [15], following [12]. To identify the ploidy levels in polysomatic cells, over 50 cells were counted per population.

Genome size measurement

Genome size was estimated from leaf nuclei suspensions following [29] with minor modifications. The OTTO-I extraction buffer was modified by adding polyethylene glycol 2000 PEG. *Solanum lycopersicum* L. 'Stupické' served as the internal reference standard (1C = 1.00 pg). For each species, at least six plants were analyzed, with three replicates per plant, and more than 10,000 nuclei per suspension. Mean 1C values by species and ploidy levels ($2x$, $3x$, and $4x$) were visualized in ggplot2, with reference values for *M. invisa* [https://cvalues.science.kew.org/] and *M. pudica* [31]. Interpopulation differences (excluding *M. invisa* and *M. pudica*) were assessed by one-way ANOVA followed by Tukey's HSD, and linear regression was conducted to correlate genome size and ploidy. All analyses were performed in R v4.3.0.

Table 1 Scientific name, provenance, chromosome number (2*n*) and the ploidy levels observed in the polysomatic cells, range of chromosome size (RCS), karyotype formula (KF), haploid karyotype length (HKL), number and positon of CMA^+ bands, percentage of constitutive heterochromatin (CH %) per haploid karyotype, and genome size in 1C (pg) for 11 populations of the seven *Mimosa* species analyzed in this study

Scientific name	Provenance/Voucher number	2*n*	RCS µm (*n*)	KF (*n*)	HKL µm (*n*)	CMA bands	CH %	1 C DNA(pg)
Mimosa verrucosa pop. 1	Aroazes, Piauí (−6.193356, −41.896406)/ TEPB0033159	2x = 26	2.15–4.21	11 M + 2SM	40.14	2 T + 4I + 20Peri	22.04	0.82 ± 0.17
M. verrucosa pop. 2	Amarante, Piauí (-6.23917, −42.851)/-	2x = 26	1.70–3.23	13 M	31.91	2 T + 4I + 20Peri	22.87	-
M. caesalpiniifolia pop. 1	Tatajuba, Ceará (−2.851798, −40.691787)/−	–	–	–	–	–	–	0.78 ± 0.07
M. caesalpiniifolia pop. 2	NEMA/ UNIVASF seed bank/-	2x = 26	1.79–3.76	13 M	34.98	2 T + 2 Peri	4.28	-
		4x = 52	1.52–3.06	13 M	30.09	4 T + 4Peri	2.82	-
M. caesalpiniifolia pop. 3	UFDPAR seed bank/-	2x = 26	1.85–3.12	13 M	32.01	2 T + 2Peri	4.18	-
		3x = 39	1.55–2.82	13 M	28.54	4 T + 2Peri	5.04	-
		4x = 52	1.26–2.56	13 M	24.83	4 T + 8Peri	4.83	-
M. candollei	Campo Maior, Piauí (−4.82828, − 42.1695)/-	4x = 52	1.34–2.85	11 M + 2SM	25.22	2 T + 50Peri	27.26	1.11 ± 0.07
		8x = 104	1.57–3.24	9 M + 4SM	28.84	4 T + 100Peri	27.60	-
M. ophtalmocentra	NEMA/UNIVASF seed bank/-	2x = 26	2.48–3.37	13 M	36.65	4 T + 12 Peri	8.70	0.77 ± 0.770000 0.73 ± 0.05
		4x = 52	1.65–3.11	13 M	30.95	8 T + 24Peri	9.83	-
M. arenosa	NEMA/UNIVASF seed bank/-	3x = 39	1.78–3.04	13 M	30.06	ca. 10 T + 2Peri	6.4	1.55 ± 0.08
		4x = 52	2.48–4.36	13 M	41.58	ca.14 T + 4Peri	5.47	-
M. tenuiflora	(Embrapa Meio-Norte, Piauí, Brazil)/JP3	2x = 26	1.39–2.55	13 M	24.85	2 T + 2Peri	8.20	1.53 ± 0.11
		3x = 39	1.41–2.77	13 M	26.36	ca. 16 T + 4Peri	7.23	-
		4x = 52	1.53–2.77	13 M	27.10	ca.14 T + 6Peri	7	-
M. sensitiva pop. 1	Campo Maior, Piauí (− 4.82828, −42.1695)/-	2x = 26	1.80–2.84	5 M + 8SM	29.47	2 T + 24Peri	17.16	0.64 ± 0.04
		4x = 52	1.50–2.71	13 M	26.75	4 T + 48Peri	20.75	-
		8x = 104	1.58–3.20	5 M + 8SM	30.06	8 T + 96Peri	15.63	-
M. sensitiva pop. 2	Altos, Piauí (−5.03991, − 42.4613)/ TEPB0033158	2x = 26	1.83–3.18	13 M	31.30	2 T + 2Peri	8	-
		4x = 52	1.56–3.36	13 M	31.08	4 T + 4Peri	5.11	-

NEMA/ UNIVASF = Núcleo de Ecologia e Monitoramento Ambiental/ Universidade Federal do Vale do São Francisco. UFDPAR = Universidade Federal do Delta do Parnaíba

M = metacentric; SM = submetacentric

I = Interstitial position; Peri = pericentromeric position; T = terminal position

Results

Karyotyping and polysomaty

All analyzed species exhibited basic chromosome number of $x = 13$, with symmetrical karyotypes and small meta- and submetacentric chromosomes. Six species displayed polysomaty, with diploidy as the lowest level in their endopolyploidy series, except for *M. arenosa* and *M. candollei*, a triploid and tetraploid species, respectively (Table 1; Fig. 1). *Mimosa arenosa* exhibited triploid and tetraploid cells in the same root tip tissue, whereas *M. candollei* presented tetraploid and octaploid cells. Only *M. verrucosa* was exclusively diploid. Intrapopulation variation in polysomaty was observed in *M. caesalpiniifolia* and *M. sensitiva*. Population 2 of *M. caesalpiniifolia* displayed diploid and tetraploid cells, while population 3 additionally exhibited triploid cells (36% of the analyzed cells). In *M. sensitiva* population 1 diploid, tetraploid, and octaploid cells were detected, with octaploid cells accounting for over 23% of total cells analyzed (Table 1, Fig. 1). Finally, *M. ophtalmocentra* exhibited diploid and tetraploid cells in its meristematic tissue, while *M. tenuiflora* showed three ploidy levels: diploid, triploid and tetraploid cells. The chromosome numbers and

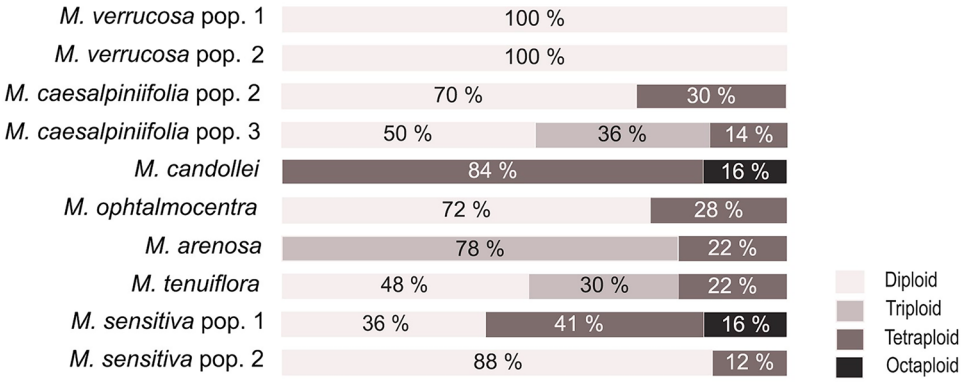

Fig. 1 Percentage of diploid, triploid, tetraploid and octaploid polysomatic cells in root meristems of different *Mimosa* populations

polysomatic series observed in each analyzed population are detailed in Table 1, and Figs. 1, 2 and 3.

Chromosome size ranged from 1.26 µm (*M. caesalpiniifolia* population 3, 4*x*) to 4.36 µm (*M. arenosa*, 4*x*) (Table 1). Similarly, haploid karyotype length ranged from 24.83 µm (*M. caesalpiniifolia* population 3) to 41.58 µm (*M. arenosa*). The common karyotype formula was 13 M, except for *M. verrucosa* population 1 (11 M + 2SM), *M. candollei* (11 M + 2SM and 9 M + 4SM), and *M. sensitiva* population 1 (5 M + 8SM).

Constitutive heterochromatin distribution

Heterochromatin data are novel for *M. verrucosa*, *M. candollei*, *M. ophtalmocentra*, *M. arenosa*, *M. tenuiflora* and *M. sensitiva*. The number and position of CMA^+ bands are summarized in Table 1, Figs. 2 and 3. All populations exhibited a strong terminal $CMA^{++}/DAPI^-$ band on the short arm of a chromosome pair, likely corresponding to the nucleolus organizer region (NOR). Additional CMA^+ bands occurred mainly at terminal and pericentromeric chromosomal regions, with different signal intensities. Strong pericentromeric bands were seen in *M. verrucosa*, *M. candollei* and *M. sensitiva* population 1, while small and barely visible terminal and pericentromeric bands were found in the other species (see inserts on Fig. 2). Only *M. verrucosa* exhibited interstitial bands (Fig. 2a). No $DAPI^+$ bands were detected.

GC-rich bands ranged from four (*M. caesalpiniifolia*, 2*x*) to 104 bands (*M. candollei*, 8*x*) (Figs. 2b', 3a, b, c), corresponding to 4.18–27.6% of CH, respectively. No intra-population CH variation was observed in *M. verrucosa* (Fig. SI1; Fig. 2a). Conversely, *M. sensitiva and M. caesalpiniifolia* showed intra-population differences (Fig. 3). Overall, polysomatic cells within the same population generally showed a proportional increase in CMA^+ bands with ploidy, except in *M. arenosa* and *M. tenuiflora* (Table 1, Figs. 2 d–d', e–e'').

Genome size

We generated unpublished nuclear DNA content for seven *Mimosa* species. 1C-values ranged from 0.64 pg in *M. sensitiva* (2*x*) to 1.55 pg in *M. arenosa* (3*x*), representing a 2.42-fold range (Table 1, Fig. SI2). Linear regression indicated weak association between genome size and ploidy ($r = 0.1417$). Species clustered into four groups: (a) *M. sensitiva*, *M ophtalmocentra*, *M. caesalpiniifolia;* (b) *M. verrucosa*; (c) *M. candollei*, (d) *M. tenuiflora*, and *M. arenosa* (Fig. 4).

Discussion

The identification of chromosome number, size, morphology, and the distribution of heterochromatic regions is fundamental for understanding systematics and evolution of plant species, helping to explore the genetic diversity trends of taxa [38]. Cytogenetic characterization in *Mimosa* is, however, challenging due to their small chromosomes and limited available information. Here, we provide new information for seven poorly studied species, including the first report of a triploid karyotype in *M. arenosa*, previously described as diploid [6].

Comparative cytogenetics by fluorochrome banding is a powerful tool for distinguishing karyotypes with similar chromosome number and morphology, being successfully applied in different plant groups, such as *Citrus* [22] and *Ipomea* [11]. We found great intra- and interpopaulation CH variation, indicating that CMA^+ heterochromatin evolved as a rapid and dynamic process within *Mimosa*, which may reflect different evolutionary trajectories. The presence of few heterochromatic blocks has been associated with a plesiomorphic condition, whereas large or numerous blocks are considered apomorphic [30]. In this context, the consistently low number of heterochromatic blocks in *M. caesalpiniifolia* likely represents an ancestral condition [9, 38], suggesting

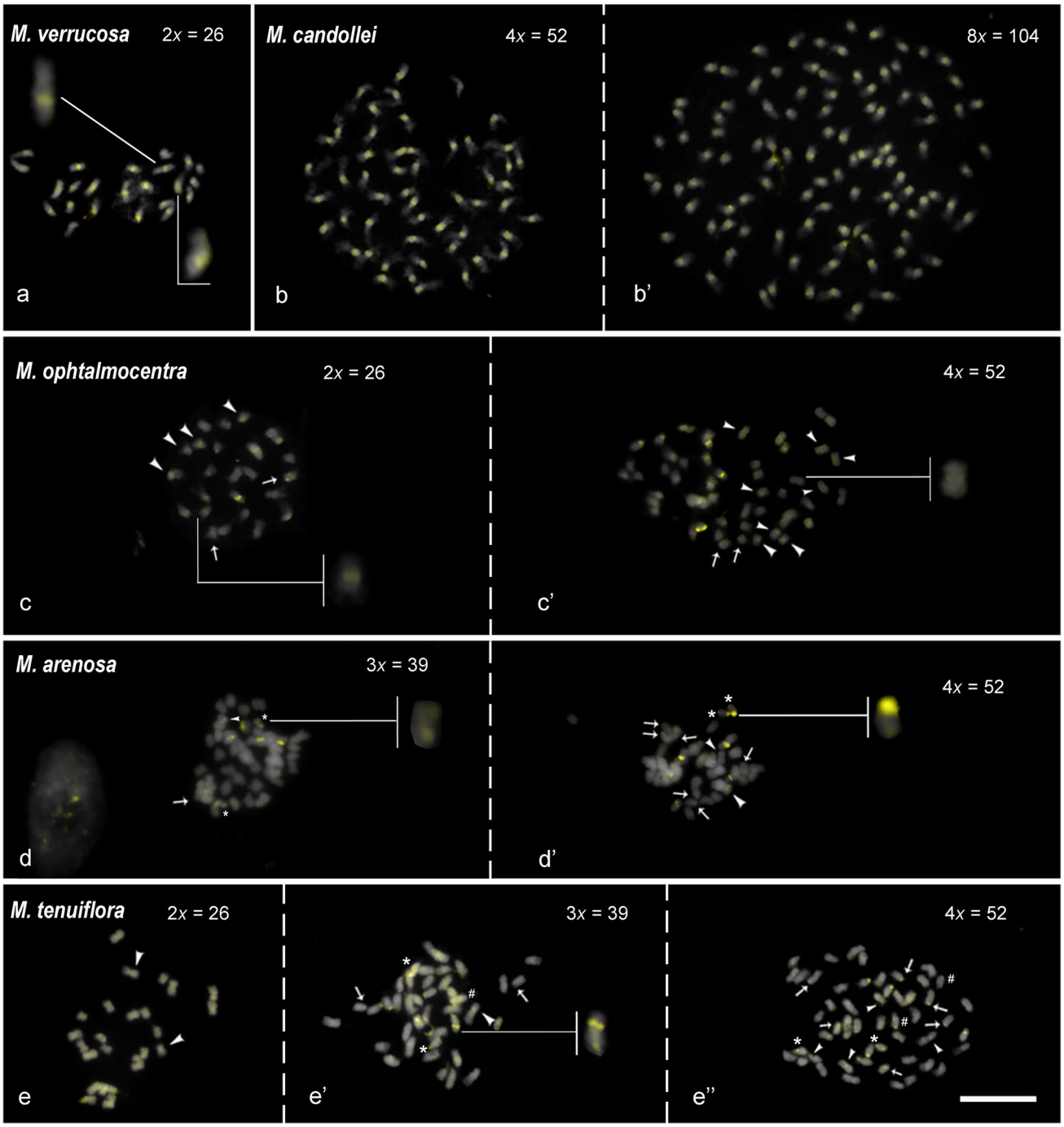

Fig. 2 Distribution of heterochromatin CMA^+ bands (yellow) across polysomatic metaphase cells from different *Mimosa* populations, with ploidy levels indicated on the right. **a** *Mimosa verrucosa*. Inserts represent one CMA^+ pair at the interstitial position; **b**–**b'**) *M. candollei*; **c**–**c'** *M. ophtalmocentra.* Inserts highlight small dot-like CMA^+ bands in pericentromeric regions. **d**–**d'** *Mimosa arenosa.* Inserts display a chromosome with two terminal bands on opposite arms: one strong CMA^{++} and another small band. This CMA pattern is identified as asterisks. **e**–**e''** *Mimosa tenuiflora*. Insert in e' shows a chromosome with two bands: one CMA^+ pericentromeric and another terminal on the long arm. This CMA pattern is identified as hashtags. Arrowheads and arrows indicate small pericentromeric and small terminal bands, respectively, difficult to detect. Bar in (**e''**) = 10 µm

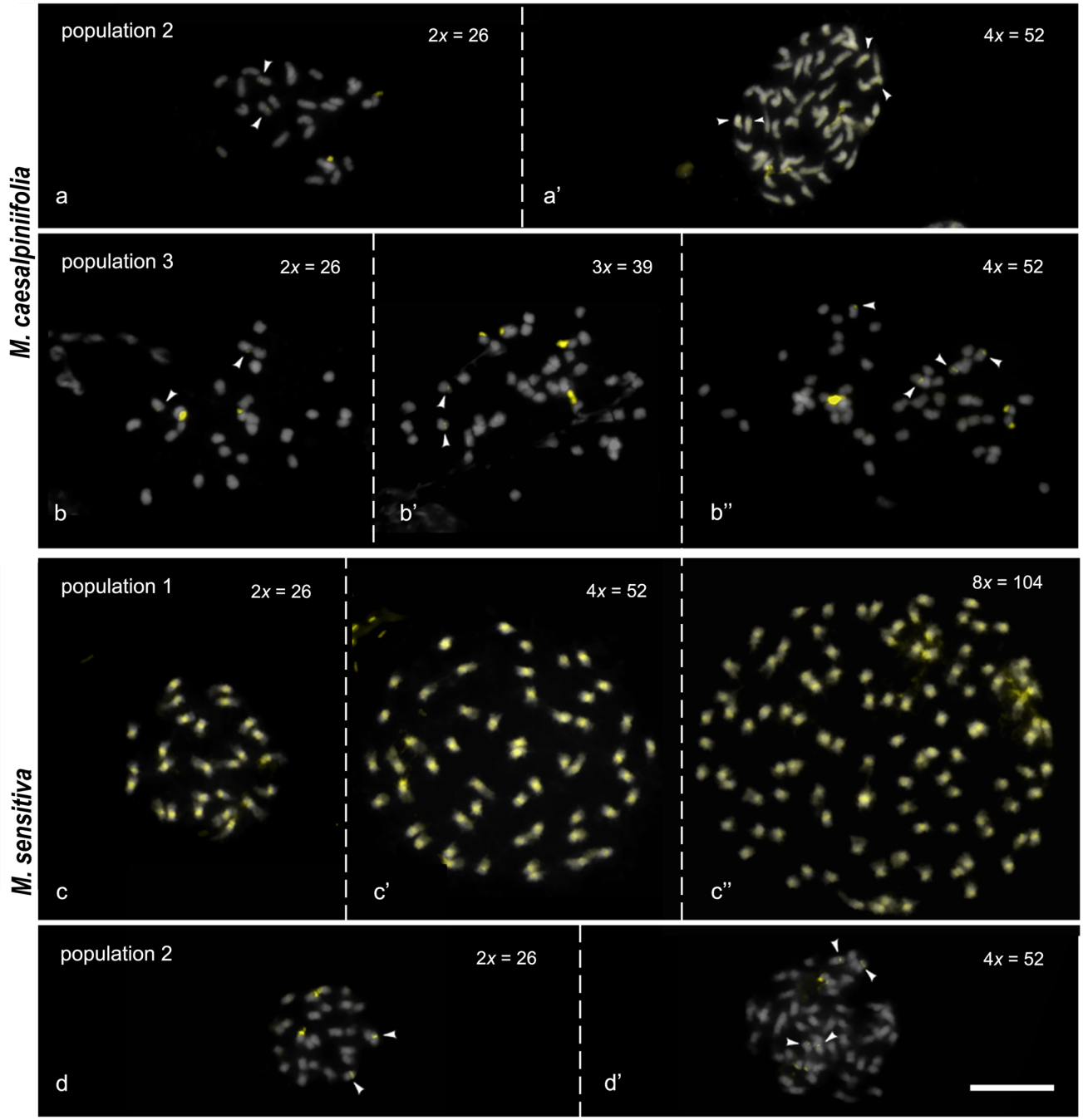

Fig. 3 CMA/DAPI banding revealed variation in CMA^+ bands (yellow) in polysomatic metaphase cells from different *M. caesalpiniifolia* and *M. sensitiva* populations, with ploidy levels identified on the right. **a**–**a'** *Mimosa caesalpiniifolia* population 2, **b**–**b''** population 3; **c**–**c''** *M. sensitiva* population 1 and **d**–**d'** population 2. Arrowheads indicate small pericentromeric bands difficult to detect. Bar in d' = 10 µm

heterochromatic stability and structural conservation in this species.

Heterochromatin distribution did not reflect *Mimosa* phylogeny. *Mimosa* is divided into five sections: *Mimadenia*, *Batocaulon, Calothamnos*, *Habbasia*, and *Mimosa* [2, 36]. Within Batocaulon (including *M. verrucosa*, *M. caesalpiniifolia*, *M. candollei*, *M. ophtalmocentra*, and *M. arenosa*), we observed contrasting patterns: *M. verrucosa* and *M. candollei* exhibited widespread pericentromeric CMA^+ bands, while *M. caesalpiniifolia* presented only four distinct bands.

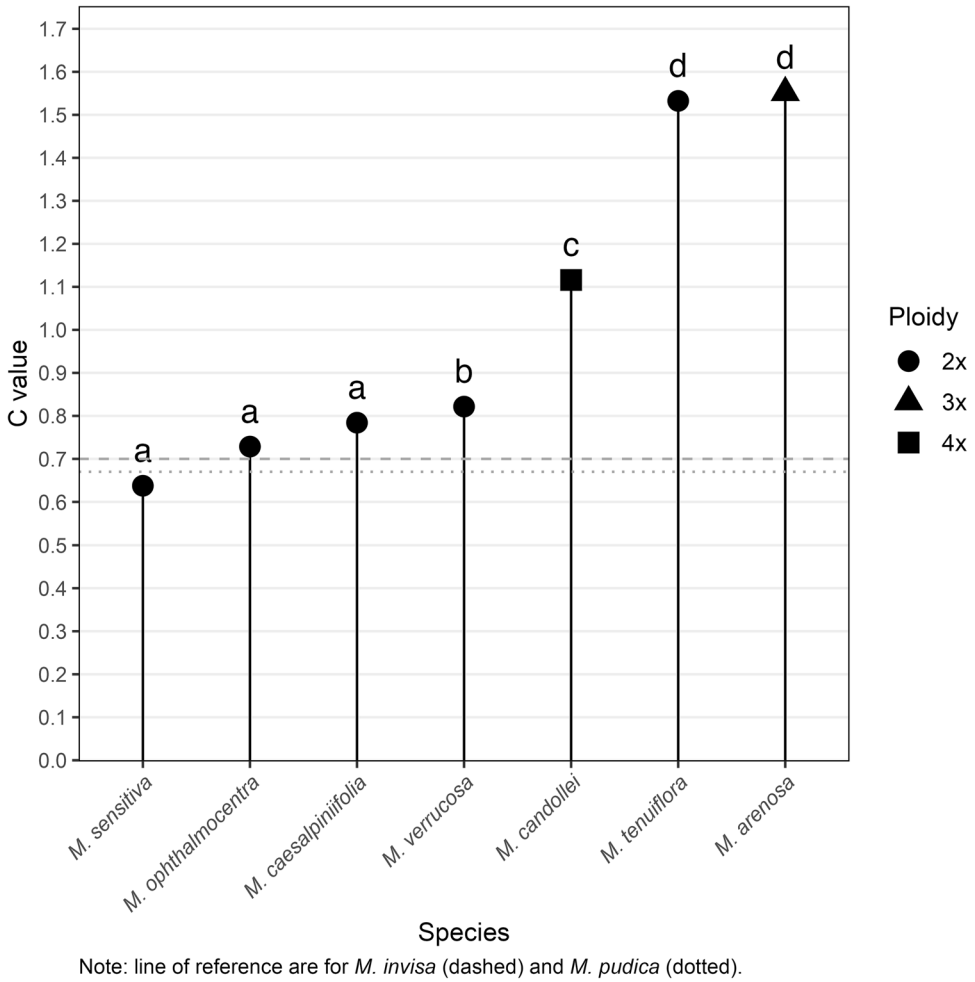

Fig. 4 Mean nuclear 1C value (pg) in *Mimosa* species, with ploidy on the right. Different letters indicate statistically significant differences (ANOVA followed by Tukey's test, $p < 0.05$)

CMA/DAPI banding can characterize heterochromatin in more detail by producing GC-rich bands and may reveal classes of repetitive DNA. Studies combining *in silico* and *in situ* repetitive DNA location across plant karyotypes have been performed. In *Cenostigma* (Leguminosae), for example, pericentromeric CMA bands colocalize with Ty3/gypsy-Athila and Ty3/gypsy-Tekay transposable elements [4]. Moreover, in the Brazilian sucupira legumes *Pterodon emarginatus* and *P. pubescens*, CMA^+ bands generally colocalize with 5S and 35S rDNA sites, besides Tekay, Athila and/or satellite DNAs [1]. In *M. verrucosa*, *M. candollei* and *M. sensitiva* population 1, the centromeres are flanked by pericentromeric CMA blocks. As centromeres are composed of centromere-specific satellite arrays and retrotransposons, these regions may be enriched with different classes of repetitive elements. Further genome skimming sequencing combined with FISH using repetitive DNA probes will help to understand the exact role behind the diversity and composition of these sequences across *Mimosa* karyotypes.

Intra-and interpopulation polysomaty was observed in six of the seven species, except in *M. verrucosa*. Polysomaty is reported in several angiosperms, such as sorghum [16], *Strobilanthes anamallaic* [5], and in ~ 26% of the 125 *Mimosa* taxa [7], including *M. caesalpiniifolia*. The formation of polysomatic cells in somatic tissues is mainly driven by endoreduplication. This genomic DNA duplication is caused by a specific loss of mitosis phases, generating cells with duplicated chromosome numbers, considered a putative basis for whole genome duplication and for polysomaty in plant-specific tissues [10, 19]. Moreover, polysomaty is regulated by genetic and environmental factors [37], although the exact causes of this phenomenon remain unknown.

In species with polysomaty, endopolyploid series are typically expected to follow a regular progression (2*x*, 4*x*, 8*x*, 16*x*), reflecting successive rounds of endoreduplication [17, 18]. However, deviations from this pattern were observed in some species analyzed in this study. In *M. caesalpiniifolia* (population 3) and *M. tenuiflora*, triploid cells occurred as intermediate levels, while *M. arenosa* showed only triploid and tetraploid cells, with no diploids detected, which does not confirm to the canonical endoreduplication model. These irregularities suggest that alternative mechanisms, such as incomplete/partial endoreduplication, nuclear fusion, or mitotic abnormalities, may contribute to the formation of

non-multiplicative ploidy levels [13, 17, 18]. Similar observations were reported in *M. bahamensis* and *M. dysocarpa* [7], with diploid, triploid, and tetraploid cells, indicating that irregular endopolyploidy is a common feature in the genus.

Mimosa species exhibit a broad capacity for adaptation and establishment in diverse environments, reflected in different growth patterns and genetic plasticity, which likely supports their wide distribution [2, 7, 14, 23]. *Mimosa pudica*, *M. bimucronata*, *M. caesalpiniifolia* and *M. tenuiflora* are invasive worldwide species, colonizing disturbed habitats due to rapid growth, expansion and high environmental adaptability [14, 27]. Our results, together with previous studies, indicate that polysomaty is a frequent, dynamic, and possibly transient cytological feature in *Mimosa,* likely associated with seedling development and stress adaptation [7, 21, 24, 31]. This process may enhance developmental flexibility under adverse conditions, such as prolonged dry seasons and nutrient-poor soil of the Cerrado and Caatinga biomes.

Genome size variation can result from multiple biological mechanisms, including polyploidy and repetitive DNA accumulation [25]. However, no direct correlation between nuclear DNA content and ploidy in *Mimosa* species analyzed was observed. This pattern is consistent with previous reports in *Artemisia* L. [26] and *Passiflora* L. [33]. Genome downsizing following polyploidization is a recurrent and biologically significant evolutionary process in angiosperms, often associated with the elimination of repetitive sequences, such as transposable elements, rDNA, and satellite DNA [25]. This process may account for the relatively small and homogeneous genome sizes observed in *Mimosa* species with different ploidy levels.

Conclusion

Our findings suggest genomic plasticity, dynamic evolution and recent diversification in *Mimosa*, evidenced by variation in constitutive heterochromatin, chromosome number, and frequent occurrence of polysomaty. This work advances our understanding of plant cytotaxonomy, diversification and cytogenetics diversity of the genus. Broader taxon sampling and integrative cytogenomic approaches will be essential to further elucidate the evolutionary dynamics of these legumes.

Acknowledgements The authors would like to thank "Núcleo de Ecologia e Monitoramento Ambiental—NEMA/ UNIVASF", "Projeto de Integração do Rio São Francisco com as Bacias Hidrográficas do Nordeste Setentrional -PISF" and "Ministério da Integração e do Desenvolvimento Regional—MIDR" for providing *M. arenosa* and *M. ophthalmocentra* seeds. We thank Fundação Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and Fundação de Amparo à Pesquisa do Estado do Piauí (FAPEPI) for scholarships. Finally, we thank Professor Thaís Cury de Barros for the taxonomic identification of *M. verrucosa* populations 1 and 2, *M candolleii*, *M. caesalpiniifolia* population 1 and *M. sensitiva* populations 1 and 2 collected in the field.

Author contribution MVS, MECFB, LCS, GSS: cytogenetic analysis and manuscript writing. JHS: statistical analysis. BAC, FAFS, WRC: DNA content estimation. PS, JRL, ACAL, MFC RLFG, ACBV, SM: conceived the research and manuscript writing. LVM: conceived the research, analyzed data, and wrote the manuscript. All authors read and approved the final version of the manuscript.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614). Not applicable.

Data availability Not applicable.

Declarations

Conflict of interest None declared.

Ethical approval Not applicable.

Informed consent Not applicable.

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