Genome Size and Karyotype Studies in Five Species of *Lantana* (Verbenaceae)

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Abstract. *Lantana* species are an important component of the U.S. environmental horticulture industry. The most commonly produced and used species are *L. camara* and, on a smaller scale, *L. montevidensis*. Both were introduced to the United States from Central and/or South America. *Lantana* species native to the continental United States include *L. canescens*, *L. depressa*, *L. involucrata*, etc. and most of them have not been well exploited. This study was conducted to obtain information about somatic chromosome numbers, karyotypes, and genome size of these five species. Nuclear DNA content in these species ranged from 2.74 pg/2C (*L. involucrata*) to 6.29 pg/2C (*L. depressa* var. *depressa*). Four chromosome numbers were observed: $2n = 2x = 22$ in *L. camara* ‘Lola’ and ‘Denholm White’, $2n = 4x = 44$ in *L. depressa* var. *depressa*, $2n = 2x = 24$ in *L. canescens* and *L. involucrata*, and $2n = 3x = 36$ in *L. montevidensis*. Two basic chromosome numbers were observed: $x = 11$ in *L. camara* and *L. depressa* var. *depressa*, and $x = 12$ in *L. canescens*, *L. involucrata*, and *L. montevidensis*. Analysis of somatic metaphases resulted in formulas of $20m + 2sm$ for *L. camara* ‘Lola’ and ‘Denholm White’, $12m + 12sm$ for *L. canescens*, $44m$ for *L. depressa* var. *depressa*, $10m + 14sm$ for *L. involucrata*, and $32m + 4sm$ for *L. montevidensis*. Satellites were identified in all five species, but were associated with a different chromosome group in different species. *L. depressa* var. *depressa* had the longest total chromatin length (146.78 μm) with a range of 1.88 to 4.41 μm for individual chromosomes. The maximum arm ratio was observed in *L. canescens*, with a ratio of 2.5 in chromosome group 3. *L. depressa* var. *depressa* was the only species that had all of its centromeres located in the median region of the chromosome. The results show significant differences in nuclear DNA content, chromosome number, and karyotype among three native and two introduced *Lantana* species and will help to identify, preserve, protect, and use native *Lantana* species. The information will be helpful in assessing the ploidy levels in the genus by flow cytometry.

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estimated at \$40 million a year (Wirth et al., 2004).

The genus *Lantana* contains 129 accepted species (The Plant List, 2013). *L. camara* is the most commonly cultivated species, with hundreds of cultivars around the world (Sanders, 2012). *L. montevidensis* is also a popular species, but with a smaller scale in production. Both species originated from Central and/or South America and have been introduced to more than 60 countries and islands around the globe (Day et al., 2003). These species are known to escape cultivation and invade natural and agricultural lands through their bountiful seed production and pollination (Florida Exotic Pest Plant Council, 2019; Henderson, 1969). For example, *L. camara* in Florida has invaded natural and agricultural land, and hybridized with a native species (*L. depressa*) to the point where the native *Lantana* has become an endangered species (Florida Department of Agriculture and Consumer Services, 2018). Similarly, *L. camara* has spread widely in Australia, India, South Africa, and other countries, and has caused substantial economic and ecological damage (Day et al., 2003). In Australia alone, *L. camara* has invaded 5,000,000 ha of land throughout coastal areas of Australia (Queensland Department of Agriculture and Fisheries, 2016). *L. montevidensis* has become an aggressive weed in Australia by taking over native grasslands during periods of drought (Weeds Australia, 2011). Although it has not yet been listed as a weed of national significance like *L. camara*, it does have potential and its use is restricted (Steppe et al., 2019). Considering the invasive potential of these *Lantana* species, the environmental horticulture industry has been urged to produce and use more native and/or sterile *Lantana* species (Hammer, 2004). *Lantana* species native to the continental United States include *L. canescens*, *L. depressa*, *L. involucrata*, etc. (Sanders, 2001). The genus *Lantana* is often split into four distinct sections: *Calliorheas*, *Sarcopippia*, *Rytocamera*, and *Camara* (Briquet, 1895; Day et al., 2003). *Lantana camara* and *L. depressa* are both categorized in the *Camara* section, whereas *L. canescens*, *L. involucrata*, and *L. montevidensis* fall under the *Calliorheas* section.

Cytological studies of *Lantana* throughout the years have focused most attention on *L. camara*. Paternmann (1938) was the first to report a chromosome number for the *Lantana* genus, identifying *L. trifolia* as $2n = 48$. Since then, a range of ploidy levels have been identified in *L. camara*, from $2n = 22$ to 55 with a base number of $x = 11$ (Fedorov, 1969; Goldblatt, 1981; Natarajan and Ahuja, 1957; Ojha and Dayal, 1992; Raghavan and Arora, 1960; Sanders, 1987; Sen and Sahni, 1955; Singh, 1951; Sinha and Sharma, 1982, 1984; Spies, 1984; Spies and Storton, 1982a, 1982b; Tandon and Chandi, 1955). Both triploid ($2n = 36$) and tetraploid ($2n = 48$) cytotypes of *L. montevidensis* have been reported in Australia (Henderson, 1969). Chromosome numbers have been reported for *Lantana*

Lantana is an important ornamental because of its low-maintenance characteristics and prolific flowering. *Lantana* is also known to attract multiple species of butterflies, honeybees, sunbirds, and hummingbirds with its brightly colored flowers (Winder, 1980). The plant is commonly cultivated in containers, hanging baskets, and landscapes (Schoellhorn, 2004). *Lantana* is easy to propagate through stem cuttings and has a short production cycle, attributing to its popularity. A survey conducted by Wirth et al. (2004) reported that 19% of the Florida nurseries responding to the survey produced *Lantana*. Wholesale value of *Lantana* in Florida was

Table 1. Nuclear DNA content and karyotype summary of six lantana selections.

Species/cultivar	2C DNA (pg)	1Cx DNA (pg)	Metaphases observed	Somatic number (2n)	Basic number (n)	Ploidy level	Total karyotype length (μm)	Chromosome length, range (μm)	Satellite group
<i>Lantana camara</i> 'Lola'	3.02 ± 0.04 bc ²	1.52	40	22	11	2x	104.57 ± 1.25	3.31–6.18	7
<i>Lantana camara</i> 'Denholm White'	3.04 ± 0.03 b	1.52	42	22	11	2x	123.49 ± 2.84	4.30–6.93	7
<i>Lantana depressa</i> var. <i>depressa</i>	6.29 ± 0.01 a	1.57	33	44	11	4x	146.78 ± 1.80	1.88–4.41	6
<i>Lantana canescens</i>	2.78 ± 0.22 cde	1.39	36	24	12	2x	94.56 ± 1.56	2.13–5.59	9
<i>Lantana involucreta</i>	2.74 ± 0.25 de	1.37	40	24	12	2x	78.99 ± 3.26	1.74–5.04	9
<i>Lantana montevidensis</i>	2.96 ± 0.03 bcd	0.99	31	36	12	3x	104.50 ± 0.60	1.86–4.64	2,10

²Means followed by the same letter are not significantly different by the Tukey-Kramer honestly significant difference test at the 5% level of significance.

species native to the United States—*L. involucreta* (2n = 24, 36), *L. depressa* (2n = 22), and *L. canescens* (2n = 24) (Natarajan and Ahuja, 1957; Raghavan and Arora, 1960; Sanders, 1987)—but no information is available on their karyotypes.

Flow cytometry has been used to determine polyploidy in lantana (Czarnecki and Deng, 2009; Czarnecki et al., 2014). To interpret ploidy accurately from relative or absolute nuclear DNA contents, it is essential to understand the variation of nuclear DNA content among plant species and establish proper references (Doležal et al., 2007). Nuclear DNA content is often expressed in picograms per 2C value or picograms per somatic cell (Greilhuber et al., 2005). 2C nuclear DNA content for *L. camara* (2n = 22) was reported previously as 2.75 pg (Ohri et al., 2004). Steppe et al. (2019) reported 2C nuclear DNA content for triploid and tetraploid forms of *L. montevidensis* measuring 2.80 to 2.85 pg/2C and 3.98 pg/2C, respectively. Nuclear DNA content for other species and cultivars of lantana remains to be reported. Ojha and Dayal (1992) were the first to record chromosome measurements and classify lantana chromosomes based on size. The study classified chromosomes of *L. camara*, *L. montevidensis*, and *L. fucata* in India and used ideograms to visualize differences. Giemsa banding and fluorescence in situ hybridization have been used to analyze a tetraploid cultivar of *L. camara* (Brandão et al., 2007). However, a karyogram was not constructed and chromosome measurements were not recorded in the study, likely because of the low clarity of the chromosome spreads.

Much is known about the chromosome numbers of many lantana species, but the ability to visualize clear, well-stained metaphases has limited cytological analysis in lantana. The purpose of this study was to identify cytological features of three lantana species native to the United States and two introduced, cultivated species. The main objective was to obtain clear, darkly stained metaphase chromosome spreads of five species of lantana. Additional objectives were to produce karyotypes for each of the lantana selections and determine nuclear DNA content and its relationship with chromosome number. It is anticipated that information gathered from this study will help in the preservation of native lantana species and assist in the production of new cultivars through plant breeding.

Materials and Methods

Plant materials. Cuttings of *L. canescens*, *L. involucreta*, *L. depressa* var. *depressa*, *L. montevidensis*, *L. camara* 'Lola', and *L. camara* 'Denholm White' were taken from plants maintained at the University of Florida's Gulf Coast Research and Education Center, Wimauma, FL. Lantana plants were grown in 15-cm-diameter plastic containers filled with a commercial soilless mix (Fafard 2P mix; Florida Potting Soil, Orlando, FL). Plants were irrigated by hand daily and were fertilized with a controlled-release fertilizer (Osmocote, 15N–3.9P–10K, 5- to 6-month release at 21 °C; The Scotts Company, Marysville, OH) at 6.51 kg·m⁻³. Plants were grown under natural light in a temperature-controlled greenhouse set between 29.4 °C during the day and 21.1 °C at night.

Nuclear DNA content determination. An Accuri C6 flow cytometer (BD Biosciences, San Jose, CA) at the University of Florida's Interdisciplinary Center for Biotechnology Research, Gainesville, FL, was used to determine nuclear DNA content. The protocol suggested by Doležal et al. (2007) was followed using both rye [*Secale cereal* 'Daňkovské' (16.19 pg/2C)] and soybean [*Glycine max* Merr. 'Polanka' (2.50 pg/2C)] as internal standards. One milliliter of cold LBO1 lysis buffer (Doležal et al., 2007) was added to a petri dish at room temperature, and ≈30 mg of tender leaf tissue of lantana and either rye or soybean were chopped together using a fresh razor blade to release nuclei. The homogenate was filtered through a nylon mesh (50 μm) into a loading tube, and 50 μL of the DNA fluorochrome propidium iodide (Sigma-Aldrich; 1 mg·mL⁻¹) and RNase (Sigma-Aldrich; 1 mg·mL⁻¹) were added. The nuclei-containing solution was fed into the flow cytometer. Three biological replicates were analyzed with rye as the internal standard, and three biological replicates were analyzed with soybean as the internal standard. A minimum of 3000 nuclei were counted per run. Nuclear DNA content (in picograms per 2C value) was calculated according to Doležal et al. (2007): Sample DNA content = Nuclear DNA content of internal standard ('Daňkovské' rye or 'Polanka' soybean) × (Mean fluorescence value of sample ÷ Mean fluorescence value of internal standard). The DNA content estimations based on the two different standards were averaged together.

Chromosome counting. The cell wall degradation hypotonic method of Chen et al.

(1982) was used to prepare chromosome spreads. Before 10:00 AM, vigorously growing root tips (1 cm) were excised from lantana plants and treated in 0.002 M 8-hydroxyquinoline for 3 h in the dark. Root tips were fixed in 200 μL fixative solution (3 methanol : 1 acetic acid, v/v) for at least 2 h. The fixed roots were rinsed three times in deionized water before a 1-mm section of the root tip was excised and macerated in an enzyme solution containing 2.5% cellulase and 2.5% pectinase for 2 h 30 min inside an incubator at 27 °C. Macerated root tips were washed in deionized water for 10 min and then fixed in a fixative solution (3 methanol : 1 acetic acid, v/v) for 0.5 h. Root tips were squashed in a drop of the fixative solution on a microscopic glass slide to disperse cells. The prepared slide was heated over an alcohol burner for a few seconds and stained with a 2.5% Giemsa solution for 10 min. Stained glass slides were rinsed in distilled water, air-dried, and then observed using a BX41 microscope with an Olympus Q-color 5 camera (Olympus America Inc., Melville, NY). Darkly stained and well-spread chromosomes were photographed at ×1000 magnification. A minimum of 30 cells were counted per selection.

Karyotyping and measurements. Karyograms of each cultivar/species were constructed using SmartType Karyotyper (Digital Scientific UK, Cambridge, England). Chromosome measurements were recorded from two cells per selection using ImageJ 1.52s (U.S. National Institutes of Health, Bethesda, MD). Chromosome morphology was described using the ratio of long arm length to short arm length as described by Levan et al. (1964).

Statistical analysis. Analysis of variance was performed to determine the significant differences ($P \leq 0.05$) among lantana selections in DNA content using JMP Pro 15.0.0 (SAS Institute, Cary, NC) with the Tukey-Kramer honestly significant difference procedure.

Results and Discussion

Nuclear DNA content. Nuclear DNA content calculations were consistent using both soybean and rye references. Nuclear DNA content ranged from 2.74 pg/2C (*L. involucreta*, 2n = 24) to 6.26 pg/2C (*L. depressa* var. *depressa*, 2n = 44) (Table 1). Standard deviation (SD) values for average DNA content in most of the samples were between 0.01 and 0.04 pg/2C, but the SD values in two

Table 2. Karyotype classifications of six *lantana* selections.

Species/cultivar	Chromosome pairs												Arm ratio ^y (range)
	1 ^z	2	3	4	5	6	7	8	9	10	11	12	
<i>Lantana camara</i> 'Lola'	m	m	m	m	m	m	sm	m	m	m	m		1.05–1.93
<i>Lantana camara</i> 'Denholm White'	m	m	m	m	m	m	sm	m	m	m	m		1.06–1.81
<i>Lantana depressa</i> var. <i>depressa</i>	m	m	m	m	m	m	m	m	m	m	m		1.18–1.43
<i>Lantana canescens</i>	sm	m	sm	sm	sm	m	sm	m	m	m	m	m	1.21–2.06
<i>Lantana involucrata</i>	sm	m	sm	sm	sm	m	sm	sm	sm	m	m	m	1.20–2.39
<i>Lantana montevidensis</i>	sm	m	m	sm	m	m	m	m	m	m	m	m	1.27–2.10

^zChromosome group number in karyotype.^yArm ratio = Length of the long arm ÷ Length of the short arm.

m = median region chromosomes (arm ratio, >1.0 and <1.7); sm = submedian region chromosomes (arm ratio, >1.7 and <3.0).

Fig. 1. Micrographs ($\times 1000$) of somatic chromosomes observed in *lantana* root-tip cells stained in Giemsa. (A) *Lantana camara* 'Lola'. (B) *Lantana camara* 'Denholm White'. (C) *Lantana canescens*. (D) *Lantana involucrata*. (E) *Lantana montevidensis*. (F) *Lantana depressa* var. *depressa*. Scale bar = 10 μ m.

samples (*L. canescens* and *L. involucrata*) were much greater (0.25 pg) (Table 1). The 2C DNA content of *L. montevidensis* differed by only 0.05 pg from the amount reported by Steppe et al. (2019). Nuclear DNA content for *L. camara* differed from the previous report by Ohri et al. (2004) by ≈ 0.25 pg. This difference could be a combination of a different cultivar being used and, in the previous report, 2C DNA content was calculated from 4C DNA. This is the first report of nuclear DNA content for 'Lola', 'Denholm White', *L. canescens*, *L. involucrata*, and *L. depressa* var. *depressa*. Based on the ploidy level (discussed later), the nuclear DNA content per monoploid (1Cx) ranged from 0.99 to 1.57 pg (Table 1). The variation observed in the 1Cx value among *lantana* species highlights the importance of using a reference sample from the same species when inferring ploidy level based on flow cytometer results or relative nuclear DNA contents.

Chromosome counting. Before this study, root-tip squashing followed by acetic car-

mine staining was the primary method for observing *lantana* chromosomes (Czarnecki and Deng, 2009; Natarajan and Ahuja, 1957; Ojha and Dayal, 1992; Sanders, 1987). Although this method produced *lantana* metaphases clear enough for chromosome counting, it rarely resulted in *lantana* metaphases with a sufficient resolution or clarity for identifying major chromosomal features, such as centromeres, arms, and satellites, and for constructing reliable karyotypes. The cell wall degradation hypotonic method (Chen et al., 1982) used in this study produced many *lantana* metaphase spreads with excellent clarity. Major features of *lantana* chromosomes were clearly recognized (Fig. 1). It was relatively easy to produce dozens of metaphases with well-spread, darkly stained chromosomes for each sample in the five *lantana* species.

Examination of 222 metaphases revealed four chromosome numbers in these *lantana* species ($2n = 22, 24, 36$, and 44) (Table 1). In this study, the diploid version of *L. involucrata* ($2n = 24$) was observed, confirming the chromosome number reported by Sanders (1987). The triploid cytotype of *L. montevidensis* was observed with a chromosome number of $2n = 36$, as previously reported by Henderson (1969). Chromosome numbers of *L. camara*, *L. canescens*, and *L. depressa* var. *depressa* also confirmed previous reports. These samples showed two base numbers ($x = 11$ or 12), with $x = 11$ in *L. camara* and *L. depressa* var. *depressa*, and $x = 12$ in *L. canescens*, *L. involucrata*, and *L. montevidensis*.

It is interesting to note that *L. canescens*, *L. involucrata*, and *L. montevidensis* have a higher chromosome base number (12 vs. 11) but lower 1Cx values (0.99–1.39 vs. 1.52 pg) compared with *L. camara* 'Lola' and 'Denholm White' and *L. depressa* var. *depressa*. This may suggest that some chromosomes of *L. canescens*, *L. involucrata*, and *L. montevidensis* (in section *Calliorheas*) contain less DNA compared with their counterpart chromosomes in *L. camara* and *L. depressa* var. *depressa* (in section *Camara*).

Karyotyping. The *lantana* root-tip cell metaphases prepared in this study allowed clear identification of centromeres and satellites. Classification of chromosome groups by centromere location and relative size and further classification of groups by size yielded clear karyograms for each selection (Fig. 2). Chromosome satellites (secondary

constrictions) were observed in each selection, but the group number of chromosomes bearing satellites varied, making them useful landmarks for identification of each species (Fig. 2, Table 1). The length of satellites ranged from 0.44 μ m in *L. involucrata* to 1.30 μ m in *L. camara* 'Denholm White', with an average length of 0.80 μ m. Both cultivars of *L. camara* had one satellite on each chromosome in group 7. *L. canescens* and *L. involucrata* also had a distinguishable satellite on each chromosome in one group, but chromosome sizes placed them in group 9. *L. depressa* var. *depressa* had a satellite on each of the four chromosomes in group 6 of the karyogram.

In the study conducted by Brandão et al. (2007), satellites were visible in *L. camara* metaphase images, but low image quality prevented karyotyping and measurements. Ojha and Dayal (1992) showed satellites in one chromosome group in a triploid, tetraploid, and pentaploid of *L. camara* examined. The study did not identify any satellites in the diploid varieties analyzed, which could be the result of low-resolution images. *L. montevidensis* had satellites in two chromosome groups. Two of three chromosomes in group 2 had satellites and one of three chromosomes in group 10 had a satellite. This phenomenon could be the result of a diploid and tetraploid cross, where the satellites on chromosome group 2 originated in the tetraploid parent, and the satellite in chromosome 10 was contributed by the diploid parent. Further investigation into the lineage of the triploid *L. montevidensis* is needed to determine the source of the satellite groups.

Chromosome measurements. The largest chromosome recorded had a length of 6.93 μ m in *L. camara* 'Denholm White' and this cultivar had the largest average chromosome length of 5.61 μ m. The smallest average chromosome length was 2.90 μ m and was found in the triploid *L. montevidensis*. It is of interest to note that *L. montevidensis* recorded the lowest nuclear DNA content per basic chromosome number (1Cx) as well. Total karyotype length was the lowest in the diploid *L. involucrata* at 78.99 μ m and greatest in tetraploid *L. depressa* var. *depressa* at 146.78 μ m. A previous study reported a range of *lantana* chromosome length of 1.37 to 4 μ m (Ojha and Dayal, 1992). These values were much smaller than those reported in this study; it remains to be determined whether different pretreatment methods and plant

Fig. 2. Karyotypes of six *Lantana* selections. (A) *Lantana camara* 'Lola'. (B) *Lantana camara* 'Denholm White'. (C) *Lantana canescens*. (D) *Lantana involucrata*. (E) *Lantana montevidensis*. (F) *Lantana depressa* var. *depressa*.

tissues used [leaf tips in Ojha and Dayal (1992) vs. root tips in our study] might have contributed to this variation. Total chromatin length provided more drastic differences between species of the same ploidy when compared with DNA content. This information could be valuable in species or cultivar identification studies where DNA content and the presence of satellites are not differentiable features.

The chromosomes have been designated according to Levan et al. (1964), i.e., median point [M, arm ratio (r) = 1.0], median region (m, $r > 1.0$ and ≤ 1.7), submedian region (sm, $r > 1.7$ and ≤ 3.0), subterminal region (st, $r > 3.0$ and ≤ 7.0), terminal region (t, $r > 7.0$), and terminal point (T, $r = \infty$). *Lantana involucrata* had the most chromosome sm groups, with more than half of its centromeres located in sm (Table 2). A recognizable feature of the *L. camara* species is the sm chromosomes in group 7 with obvious satellites, which might be useful for detecting interspecific hybrids originating from crosses involving *L. camara*. Both *L. canescens* and *L. involucrata* have many more sm chromosomes in addition to the presence of satellites. *Lantana depressa* var. *depressa* had all its centromeres located in m. The differences observed in the size and arrangement of

chromosomes in the karyotypes of these five species may suggest the variation in gene arrangement and composition that differentiates the phenotypes of these species (Stebbins, 1971). Because of the large genome size of *lantana*, sequencing data have yet to be published, but are needed to investigate the variation in gene composition of these different species. Toward this, the combination of this research with *L. camara* transcriptomes already published (Peng et al., 2019; Shah et al., 2020) may aid in future assembly and annotation of the *lantana* genome.

Our results revealed significant variation in chromosome morphology and nuclear DNA content among the five *lantana* species accessed. This is the first report of nuclear DNA content for the three U.S. native *lantana* species and the first karyotypes constructed for each species except *L. camara*. The chromosome squash protocol presented will allow for further cytological investigation into other *lantana* species and cultivars. Nuclear DNA content data will provide references for ploidy analysis of breeding lines and unknown plants.

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