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# Chromosome studies in *Turnera* (*Turneraceae*)

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The genus *Turnera* is one of the most important genera of the *Turneraceae* comprising more than 100 species grouped in 9 series (Urban, 1883) which are distributed largely in tropical and subtropical areas of the Americas.

At least 34% of all species have been karyologically investigated. Chromosome numbers have been reported for 35 species (Raman and Kesavan, 1964; Hamel, 1965; Barrett, 1978; Barrett and Shore, 1980; Arbo and Fernández, 1983; Fernández, 1987; Solís Neffa and Fernández, 1993) but the karyotypes of only 21 have been described (Solís Neffa and Fernández, 1993; Solís Neffa, 1996).

The basic chromosome number x = 7 was found in the *Salicifolieae*, *Stenodictyae*, *Mycrophyllae* and *Leiocarpae* series and is clearly the most common, x = 5 was found in the *Turnera* (= *Canaligerae*) series and x = 13 in the *Papilliferae* (Fernández, 1987).

Cytological investigation has shown the occurrence of diploid to decaploid populations, that may be autopolyploids as well as allopolyploids (Raman and Kesavan, 1964; Barrett, 1978; Arbo and Fernández, 1983; Shore and Barrett, 1985; Fernández, 1987). From these studies it is apparent that polyploidy has played an important and sometimes dominant role in speciation within the genus. However, chromosome rearrangements may be involved in the karyotype evolution of some species (Solís Neffa and Fernández, 1993; Solís Neffa, 1996).

Chromosome studies have been particularly detailed in the *Turnera* series, focusing on taxonomy and phylogenetic relationships. Since 1982 a controlled crossing program within this series has been carried out and several interespecific hybrids obtained and, as a result of cytogenetic studies, the genomic relationships of some species have been analyzed (Fernández and Arbo, 1989, 1990, 1993a,b, 1996; Fernández, 1997).

In this article we provide a review on the karyology of the whole genus for a better understanding of the chromosomal evolution of *Turnera*.

## POLYPLOIDY

Polyploidization has long been recognized as an important process in plant evolution. In the genus *Turnera,* 59% of the population analyzed have polyploid origin, ranging from tetraploids to decaploids (Table I), with tetraploids and hexaploids more or less common and octoploids and decaploids rare (Table II).

Published counts together with our unpublished data reveal intraspecific polyploidy in several widespread species, some of which contain populations with 2x or 4x cytotypes, while *T. grandiflora* possesses 2x and 8x cytotypes. *T. sidoides* (x = 7) includes 5 subspecies that are known to be comprised of different ploidy levels, from 2x to 8x (Fernández, 1987), which makes it possible to conclude that *T. sidoides* is a polyploid complex.

Autopolyploidy is apparently less frequent than allopolyploidy, but some workers suggest that the occurrence of autopolyploidy may have been underestimated (Soltis and Riesberg, 1986): of the polyploid species of *Turnera* about 35% are autopolyploids.

Autopolyploids are usually considered to be recognizable by multivalent chromosome configuration during meiosis metaphase, while the chromosomes of allopolyploids are assumed to pair into bivalents during meiosis. Most natural polyploids, however, fall somewhere in between these two extremes in genome constitution, combining more or less well-differentiated genomes of closely related species. The terms auto-, allo- and segmental allopolyploids refer to the combination of fully homologous, non-homologous and partly homologous chromosome sets (Greilhuber and Ehrendorfer, 1988).

Data on meiotic behavior obtained from the *T. sidoides* complex (x = 7) showed high levels of multivalent formation with quadrivalents, hexavalents and octavalents, in 4x, 6x and 8x cytotypes, respectively, characterizing them as autopolyploids (Fernández, 1987). Among tetraploid species of *Turnera* series (x = 5)*,* tetravalents were found in all cells of *T. subulata*, *T. scabra* (Figure 1) and *T. krapovickasii*, chromosome-pairing analysis showing an autotetraploid origin. *T. grandiflora* possesses 2x and 8x cytotypes, with the diploid showing regular pairing while the other cytotype behaved like an auto-octoploid since it showed octavalent formation (Figure 1).

A detailed meiotic study of *T. grandidentata,* 2n = 4x = 20, *T. ulmifolia,* 2n = 6x = 30, and *T. orientalis,* 2n = 6x = 30 (Figure 1), showed only bivalents (Fernández, 1987). Meiosis pairing was generally regular in *T. aurelii* (2n = 8x = 40), but 18 II and 1 IV were also found. Cytological studies of hybrids between diploids and polyploids

**Table I** - Species studied.

| Species | 2n | References |
|---|---|---|
| *Salicifoliae* series | | |
| *Turnera weddelliana* Urban & Rolfe | 14 | Fernández, 1987 |
| *Stenodictyae* series | | |
| *T. macrophylla* Urban | 14 | Fernández, 1987 |
| *Leiocarpae* series | | |
| *T. nervosa* Urban | 14 | Fernández, 1987 |
| *T. pumilea* L. | 14 | Fernández, 1987 |
| *T. melochiodes* Cambess. | 14 | Fernández, 1987 |
| *T. trigona* Urban | 14 | Solís Neffa and Fernández, 1993 |
| *T. hassleriana* Urban | 14 | Fernández, 1987 |
| | 28 | Fernández, 1987 |
| *T. lamiifolia* Cambess. | 28 | Fernández, 1987 |
| *T. sidoides* L. ssp. *sidoides* | 28 | Fernández, 1987 |
| | 32, 34, 39 | Fernández, 1987 |
| *T. sidoides* L. ssp. *carnea* (Cambess.) Arbo | 14 | Fernández, 1987 |
| | 28 | Fernández, 1987 |
| | 42 | Fernández, 1987 |
| *T. sidoides* L. ssp. *integrifolia* (Griseb.) Arbo | 14 | Fernández, 1987 |
| | 28 | Fernández, 1987 |
| | 42 | Fernández, 1987 |
| | 56 | Fernández, 1987 |
| *T. sidoides* L. ssp. *holosericea* (Urban) Arbo | 28 | Fernández, 1987 |
| | 42 | Fernández, 1987 |
| *T. sidoides* L. ssp. *pinnatifida* (Juss. ex Poir.) Arbo | 14 | This paper |
| | 28 | Fernández, 1987 |
| | 42 | This paper |
| *T. opifera* Mart. | 70 | Fernández, 1987 |
| *Microphyllae* series | | |
| *T. diffusa* Willd. | 14 | Fernández, 1987 |
| *Papilliferae* series | | Fernández, 1987 |
| *T. chamaedryfolia* Cambess. | 26 | Fernández, 1987 |
| *Turnera* (= *Canaligerae*) series | | |
| *T. candida* Arbo | 10 | Solís Neffa and Fernández, 1993 |
| *T. caerulea* DC. | 10 | Fernández, 1987 |
| *T. grandiflora* (Urban) Arbo | 10 | Fernández, 1987 |
| | 40 | Fernández, 1987 |
| *T. surinamensis* Urban | 10 | Fernández, 1987 |
| *T. subulata* Smith | 10 | Fernández, 1987 |
| | 20 | Fernández, 1987 |
| *T. scabra* Millspaugh | 10 | Fernández, 1987 |
| | 20 | Fernández, 1987 |
| *T. krapovickasii* Arbo | 10 | Fernández, 1987 |
| | 20 | Fernández, 1987 |
| *T. concinna* Arbo | 10 | Fernández, 1987 |
| *T. hermannioides* Cambess. | 10 | Fernández, 1987 |
| *T. joelii* Arbo | 10 | Fernández, 1987 |
| *T. grandidentata* (Urban) Arbo | 20 | Fernández, 1987 |
| *T. arcuata* Urban | 20 | Solís Neffa and Fernández, 1993 |
| *T. angustifolia* Miller | 30 | Fernández, 1987 |
| *T. orientalis* (Urban) Arbo | 30 | Fernández, 1987 |
| *T. ulmifolia* L. sensu stricto | 30 | Fernández, 1987 |
| *T. ulmifolia var. acuta* | 30 | Solís Neffa and Fernández, 1993 |
| *T. velutina* Presl. | 30 | Solís Neffa and Fernández, 1993 |
| *T. aurelii* Arbo | 40 | Fernández, 1987 |
| *T. cuneiformis* Poiret | 40 | Solís Neffa and Fernández, 1993 |

showed partly homologous chromosomes, suggesting that polyploid species are segmental allopolyploids (Fernández and Arbo, 1990, 1993a,b).

Pollen fertility of tetraploid species of *Turnera* ranged between 59% in *T. hassleriana* (2n = 28) and 94% in *T. sidoides* ssp. *holosericea* (2n = 28). Among the autohexaploids pollen fertility varied from 67% in *T. sidoides* ssp. *integrifolia* (2n = 42) to 87% in *T. sidoides* ssp. *holosericea* (2n = 6x = 42). Pollen stainability of autooctoploids ranged from 71% in *T. grandiflora* (2n = 8x = 40) to 75% in *T. sidoides* ssp. *integrifolia (*2n = 8x = 56). Low fertility, primarily caused by multivalent formation, is known to constrain autopolyploid evolution, and selection for increased fertility may lead to cytological diploidization in polyploids (De Wet, 1980), so that the high pollen fertility in autopolyploids would correlate with the degree of diploidization observed in meiosis (Fernández, 1987).

In many autopolyploids, the cytotypes contrast in geographical distribution, an example being *T. sidoides*, which is mostly native to the Chaco Phytogeographical Domain and is spread throughout the southern regions of Bolivia and Brazil, Paraguay and Uruguay until it reaches 39ºS in Argentina and is the *Turnera* species with the most southerly distribution in the Americas (Arbo, 1986). In a preliminary analysis of the geographical distribution of the cytotypes of *T. sidoides*, greater variability was found in areas where the subspecies cohabit (Fernández, A. and Arbo, M.M., unpublished results).

Species of the *Turnera* series are mostly distributed in northern Brazil, where the 2x cytotype prevails, but in Central America and the Antilles the cytotypes are mainly 4x and 6x (Barrett, 1978; Shore and Barrett, 1985) while Paraguay has the highest levels of allopolyploids and autopolyploids and constitutes an important certer of speciation (Arbo, 1986).

## KARYOTYPE DATA AND SYSTEMATICS

Karyological information is available for 6 of 9 recognized series in the genus and so far has concentrated on species of *Turnera* series. Detailed analysis of numerical data suggests that the karyotypes of the species of the genus, although very similar, can be distinguished into differ-

**Table II** - Incidence of polyploidy in 111 populations of *Turnera* (counts made at IBONE).

| Series | 2x | 4x | 6x | 8x | 10x |
|---|---|---|---|---|---|
| *Salicifoliae* | 1 | - | - | - | - |
| *Stenodictyae* | 1 | - | - | - | - |
| *Leiocarpae* | 14 | 28 | 8 | 1 | 1 |
| *Microphylae* | 1 | - | - | - | - |
| *Papilliferae* | 2 | - | - | - | - |
| *Turnera* | 27 | 13 | 10 | 4 | - |
| Total | 46 | 41 | 18 | 5 | 1 |
| *%* | 41.44% | 36.94% | 16.22% | 4.5% | 0.9% |

ent groups, mainly in terms of mean chromosome length, type and position of satellites and karyotype asymmetry (Solís Neffa and Fernández, 1993).

Chromosomes of *Turnera* are small (2.25 µm) with mean chromosome length varying between 1.12 µm in *T. weddelliana* and 2.55 µm in *T. candida.* Species based on x = 7 generally have shorter chromosomes than species with x = 5 and x = 13.

The presence of one pair of SAT-chromosomes is quite common in the genus, although in some species 2 pairs were detected. Macrosatellites and microsatellites have been reported usually attached to the short arm of m or sm chromosomes. *T. hassleriana* is the only species with a macrosatellite located on the long arm. No satellites were observed in *T. weddelliana* and *T. melochioides*, probably due to the small size of their chromosomes (Solís Neffa and Fernández, 1993; Solís Neffa, 1996).

Most of the *Turnera* species studied have karyotypes with a low degree of asymmetry due to the predominance of m-type chromosomes (Table III), and neither highly symmetrical karyotypes, those with all m chromosomes, nor bimodal karyotypes has been observed. The asymmetry in-

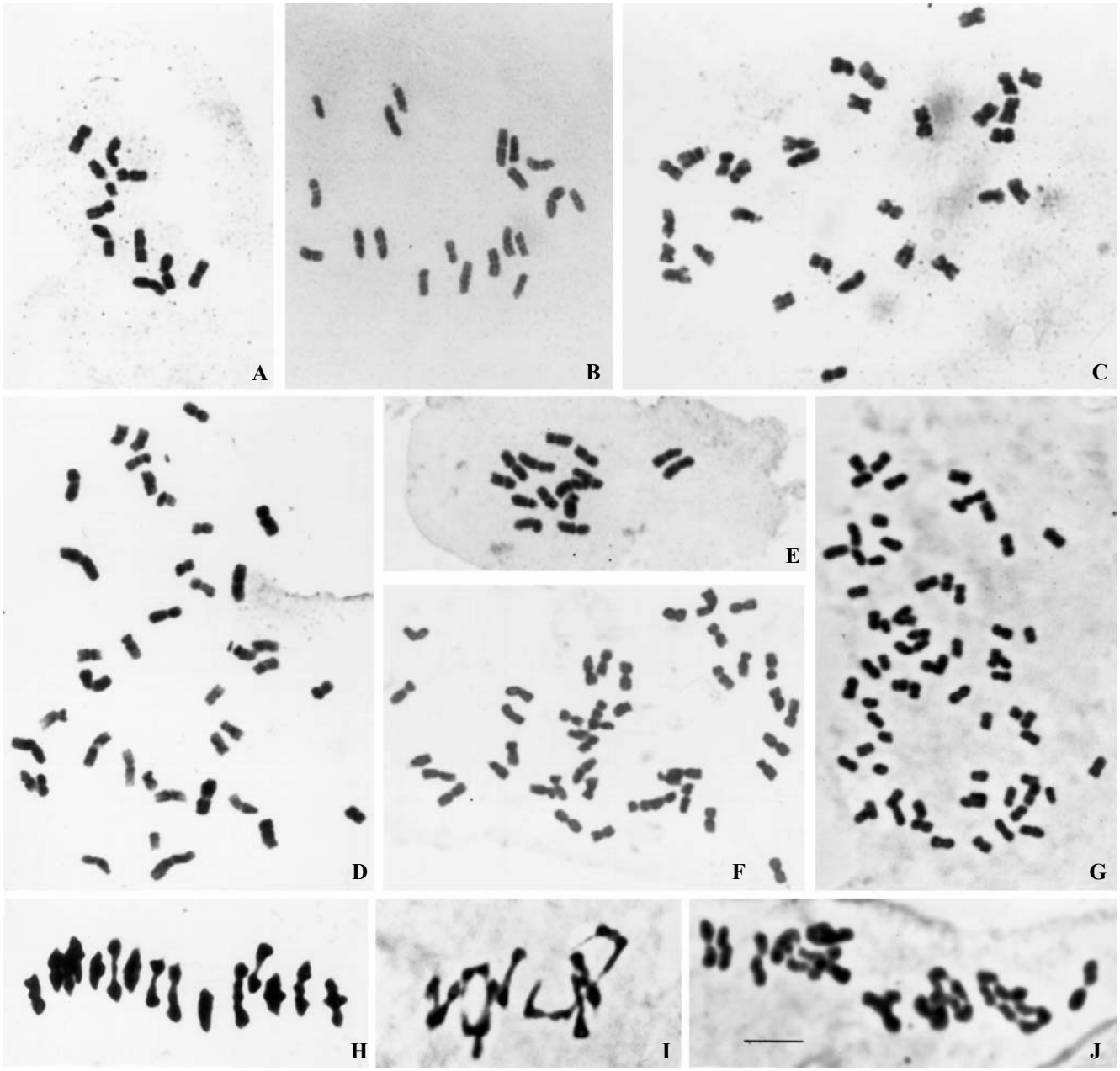


**Figure 1** - Somatic and meiotic chromosomes of *Turnera*. **A**: *T. grandiflora*, 2n = 2x = 10. **B**: *T. grandidentata*, 2n = 4x = 20. **C**: *T. ulmifolia*, 2n = 6x = 30. **D**: *T. aurelii*, 2n = 8x = 40. **E**: *T. sidoides* ssp. *pinnatifida*, 2n = 2x = 14. **F**: *T. sidoides* ssp. *integrifolia*, 2n = 6x = 42. **G**: *T. opifera*, 2n = 10x = 70. **H**: *T. ulmifolia*, 15 II. **I**: *T. scabra*, 5 IV. **J**: *T. grandiflora*, 3 VIII + 2 IV + 4II. Scale = 5 µm.

**Table III** - Karotype parameters. Chromosome numbers, ploidy level (X), karyotype formulae, mean chromosome length in µm (ML), centromeric index (CI), intrachromosomal asymmetry index ($A_1$) and interchromosomal asymmetry index ($A_2$).

| Species | 2n | X | Karyotype formulae | ML | CI | $A_1$ | $A_2$ | References |
|---|---|---|---|---|---|---|---|---|
| *T. weddelliana* | 14 | 2 | 12m + 2sm | 1.12 | 42.29 | 0.28 | 0.18 | Solís Neffa and Fernández (1993) |
| *T. pumilea* | 14 | 2 | 10m + 4sm | 1.24 | 42.82 | 0.26 | 0.21 | Solís Neffa and Fernández (1993) |
| *T. melochioides* | 14 | 2 | 10m + 4sm | 1.33 | 42.10 | 0.25 | 0.28 | Solís Neffa (1996) |
| *T. hassleriana* | 14 | 2 | 12m + 2sm | 1.83 | 43.94 | 0.22 | 0.25 | Solís Neffa and Fernández (1993) |
| *T. chamaedryfolia* | 26 | 2 | 16m + 8 sm + 2st | 1.45 | 40.82 | 0.32 | 0.20 | Solís Neffa and Fernández (1993) |
| *T. candida* | 10 | 2 | 8m + 2sm | 2.55 | 41.95 | 0.25 | 0.19 | Solís Neffa (1996) |
| *T. caerulea* | 10 | 2 | 8m + 2sm | 2.53 | 44.00 | 0.23 | 0.18 | Solís Neffa (1996) |
| *T. grandiflora* | 10 | 2 | 8m + 2sm | 2.98 | 42.82 | 0.23 | 0.17 | Solís Neffa (1996) |
| *T. grandiflora* | 40 | 8 | 32m + 8sm | 1.83 | 44.58 | 0.21 | 0.24 | Solís Neffa and Fernández (1993) |
| *T. subulata* | 10 | 2 | 8m + 2sm | 1.71 | 45.50 | 0.17 | 0.13 | Solís Neffa and Fernández (1993) |
| *T. subulata* | 20 | 4 | 16m + 2sm | 1.74 | 45.63 | 0.17 | 0.22 | Solís Neffa and Fernández (1993) |
| *T. scabra* | 10 | 2 | 8m + 2sm | 2.53 | 44.57 | 0.19 | 0.10 | Solís Neffa (1996) |
| *T. krapovickasii* | 10 | 2 | 8m + 2sm | 2.28 | 43.75 | 0.22 | 0.14 | Solís Neffa and Fernández (1993) |
| *T. krapovickasii* | 20 | 4 | 16m + 4sm | 2.02 | 44.99 | 0.19 | 0.13 | Solís Neffa and Fernández (1993) |
| *T. concinna* | 10 | 2 | 8m + 2sm | 2.52 | 44.25 | 0.21 | 0.16 | Solís Neffa and Fernández (1993) |
| *T. hermannioides* | 10 | 2 | 8m + 2sm | 2.25 | 43.99 | 0.21 | 0.12 | Solís Neffa (1996) |
| *T. joelii* | 10 | 2 | 8m + 2sm | 2.37 | 43.54 | 0.21 | 0.11 | Solís Neffa (1996) |
| *T. grandidentata* | 20 | 4 | 18m + 2sm | 2.06 | 45.58 | 0.16 | 0.20 | Solís Neffa and Fernández (1993) |
| *T. angustifolia* | 30 | 6 | 26m + 4sm | 1.88 | 44.44 | 0.21 | 0.14 | Solís Neffa and Fernández (1993) |
| *T. orientalis* | 30 | 6 | 26m + 4sm | 2.51 | 44.33 | 0.15 | 0.13 | Solís Neffa and Fernández (1993) |
| *T. ulmifolia* | 30 | 6 | 24m + 6sm | 2.32 | 42.57 | 0.23 | 0.13 | Solís Neffa and Fernández (1993) |
| *T. velutina* | 30 | 6 | 28m + 2sm | 2.38 | 44.98 | 0.18 | 0.14 | Solís Neffa and Fernández (1993) |
| *T. aurelii* | 40 | 8 | 36m + 4sm | 2.21 | 44.58 | 0.15 | 0.24 | Solís Neffa and Fernández (1993) |
| *T. cuneiformis* | 40 | 8 | 36m + 4sm | 1.36 | 44.78 | 0.20 | 0.14 | Solís Neffa and Fernández (1993) |

dices proposed by Romero Zarco (1986) are important in that they allow the discrimination of clear differences among species (Figure 2). Asymmetry analysis has shown that *T. chamaedryfolia* of the *Papilliferae* series (x = 13) has the highest tendency towards asymmetry while *Turnera* series species (x = 5) have the smallest degree of asymmetry. Species with x = 7 showed an intermediate level of asymmetry.

Regarding series with x = 7, karyotype information is available for *Salicifoliae* and *Leiocarpae*. In the other series, only chromosome numbers have been reported. For the *Salicifoliae* series the karyotype of *T. weddelliana* has been studied (Table III), while for the *Leiocarpae* series 20% of the species have been cytologically investigated. Although *Leiocarpae* series is the largest series of the genus, chromosome numbers have been verified for only 8 species, with 2n = 2x = 14 being the most common number, the karyotypes of 4 of which have been analyzed (Table III) and are characterized by the presence of small chromosomes and a moderate degree of asymmetry.

Recently the karyotypes of the *T. sidoides* complex (x = 7) have been studied (Solís Neffa, V.G. and Fernández, A., unpublished results), and although this species belongs to the *Leiocarpae* series, it presents some unusual features (Arbo, 1985). Karyotype analysis of *T. sidoides* agrees with exomorphological data, and this species shares the basic number and the degree of karyotype asymmetry with the other species of the series but it differs in chromosome size, with the mean chromosome length more in accordance with the values for species of *Turnera* series (Solís Neffa, V.G. and Fernández, A., unpublished results). Moreover, *T. sidoides* is the only species in the *Leiocarpae* series having one pair of st-type chromosomes in its karyotype.

*Turnera chamaedryfolia* (x = 13) belongs to the monotypic *Papilliferae* series. Karyotype characteristics confirm the distinctiveness of this taxon from other *Turnera* species, not only in basic chromosome number but also in karyotype asymmetry. This may be due to the high number of sm chromosomes and the presence of one pair of st chromosome in its karyotype formula (Table III).

The *Turnera* series presents the most complex floral structure in the family and is made up of about 22 species that are divided into two groups by seminal characters (Arbo, 1986). One of the groups constitutes the *T. ulmifolia* complex while the other comprises some tropical species (Fernández and Arbo, 1989), with species of each group being genetically related to each other (Arbo and Fernández, 1987).

*Turnera ulmifolia* is a polymorphic complex and Urban (1883) recognized more than 10 varieties with yellow- and blue-flowered forms, which can be either heterostylous or homostylous. Shore and Barrett (1985) made a phenetic study based on morphological differentiation of 6 taxa; the results indicate that the complex is composed of several differentiated assemblages reproductively isolated from one another chromosomally via polyploidy, as well as genetically, via crossing barriers. These observations support the separation of the complex into several species. Most of the

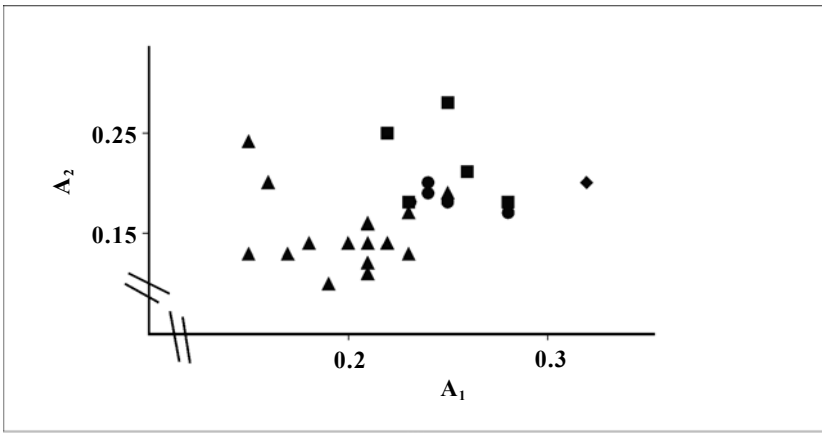


**Figure 2** - Scatter diagram of mean intrachromosomal asymmetry index ($A_1$) against mean interchromosomal asymmetry index ($A_2$) for *Turnera* species. ▲: x = 5. ■: x = 7. ◆: x = 13. ●: *T. sidoides* complex.

varieties of *T. ulmifolia* are now recognized as independent species (Backer, 1951; Arbo, 1985). Cytological data (Fernández, 1987; Fernández and Arbo 1989, 1990, 1993a) and karyotype analysis (Solís Neffa and Fernández, 1993; Solís Neffa, 1996) support this separation.

No hybrids were obtained between yellow-flowered and blue-flowered diploid species (Arbo and Fernández, 1987). They are reproductively isolated because of their different genomes; all yellow-flowered species share the same basic genome A (Fernández and Arbo, 1989), while all blue-flowered have the basic genome C (Fernández and Arbo, 1996). These species share the karyotype formula 8m + 2sm, which is considered the fundamental karyotype, nevertheless these taxa can differ by type and position of satellites, relative size of the chromosomes ($A_2$) and mean chromosome length.

## KARYOTYPE EVOLUTION IN THE GENUS *TURNERA*

In *Turnera* there are different karyotypic evolutionary trends. Considering the published chromosome numbers and the data presented here, polyploidy is quite frequent in the genus. However, aneuploidy and dysploidy are also thought to be important in the chromosomic evolution of some species.

Data suggest that x = 7 is the ancestral basic chromosome number of the genus, from which x = 5 and x = 13 could have been derived (Fernández, 1987), x = 13 being an unusual number within the genus since only one member of the genus has been identified as having this chromosome number. The origin of x = 13 probably was by reductional aneuploidy from 2n = 4x = 28.

Dysploid alteration of the basic chromosome number is usually the outcome of successive translocation, so that centromeres can be lost without damage to the plant. This brings about a reduction in chromosome number and a progressive increase in chromosome size, a mechanism which is supposed to be involved in the origin of x = 5.

Dysploid changes may also explain the remarkable differences in chromosome size and karyotype asymmetry among species with x = 7 and with x = 5. Although in many Angiosperms symmetrical karyotypes are correlated with the primitive condition of the taxa (Stebbins, 1971), the major symmetry shown by species with x = 5 is in agreement with their derived basic number and would represent a secondary tendency in chromosome evolution.

Diploid species of the *Turnera* series show the same basic haploid karyotype, although some karyotype variation occurs among the species. They may be differentiated by type and position of satellites, the relative size of the chromosomes and mean chromosome length, differences which might be the result of structural chromosome rearrangements which occurred during the evolution of this species.

Polyploidy has been correlated with a decrease in chromosome length (Stebbins, 1938) and species with autopolyploid cytotypes show karyotypes with smaller chromosomes and more symmetry than in diploids (Solís Neffa and Fernández, 1993; Solís Neffa, 1996).

## CONCLUSION

The data presented in this article suggest that there are different chromosomic evolutionary trends in *Turnera*. Cytological studies suggest that x = 7 is the ancestral basic chromosome number for the genus, from which x = 5 and x = 13 may have been derived. Although polyploidy has played an important role in speciation within the genus, aneuploidy and dysploidy have also occurred. The origin of x = 13 probably was by reductional aneuploidy, while dysploid alteration is thought to be involved in the origin of x = 5. Dysploid changes may also explain the differences in chromosome size and karyotype asymmetry among species.

Karyological data are meaningful in a systematic sense, since karyotype characteristics support taxonomic

treatment of the species which can be distinguished by their mean chromosome length, type and position of satellites and karyotype asymmetry.

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