



REVIEW ARTICLE

Cytogenetics of Chilean angiosperms: Advances and prospects

Citogenética de angiospermas chilenas: Avances y proyecciones

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ABSTRACT

Cytogenetic data on Chilean angiosperms have been reported since at least eight decades ago; however, much of this information is dispersed in diverse sources and is not readily available as a comprehensive document that allows having a general vision on advances and gaps in this matter. The goal of this paper is to summarize the advances and prospects on cytogenetic studies of the Chilean angiosperms based on compiled publications from 1929 to 2010. We found 78 publications supplied by four groups of Chilean researchers and some foreign specialists. Cytogenetic data have been reported for 139 Chilean angiosperm species (2.8 % of the total), which belong to 58 genera and 34 families. During 2001-2010 there was an increase in the number of publications, being available 40 reports including 95 additional species. Based on these data, we hope that such a trend can be maintained in the next decade if the current research groups and young specialists continue to be interested in the study of native plants.

Key words: chromosome banding, chromosome number, genome size, karyotype morphology.

RESUMEN

Los datos citogenéticos sobre angiospermas chilenas han sido reportados desde al menos ocho décadas atrás; sin embargo, mucha de esta información está dispersa en diversas fuentes y no está disponible como un documento completo que permita tener una visión general sobre los avances y vacíos en esta materia. El objetivo de este trabajo es resumir los avances y proyecciones sobre los estudios citogenéticos disponibles para angiospermas chilenas, basado en publicaciones recopiladas desde 1929 hasta el 2010. Nosotros encontramos 78 publicaciones aportadas por cuatro grupos de investigadores chilenos y por algunos especialistas extranjeros. Datos citogenéticos han sido reportados para 139 especies de angiospermas chilenas (2.8 % del total), las cuales pertenecen a 58 géneros y 34 familias. Durante los años 2001-2010, existió un incremento en el número de publicaciones estando disponibles 40 reportes que incluyen 95 especies adicionales. Basados en estos datos, esperamos que esta tendencia pueda ser mantenida en la siguiente década si los actuales grupos de investigación y especialistas jóvenes siguen interesados en estudiar plantas nativas.

Palabras clave: bandedo cromosómico, morfología del cariotipo, número cromosómico, tamaño genómico.

INTRODUCTION

Cytogenetics has made important contributions to the knowledge on patterns of genetic variation, phylogeny, taxonomy and evolution of plants, being recognized many other applications highly discussed in the literature (Bennett & Leitch 1997, 2005b, Lavania 2002, Singh 2003, Gregory 2005a, Hanson & Leitch 2005). As an interesting example, fossil chromosomes of the extinct Gondwanan gymnosperm *Pentoxylum*

have been found in a naturally preserved microsporangium, having a low base number like in extant members of Cycadaceae, Araucariaceae and Pinaceae (Bonde et al. 2004). Thus, the scope of cytogenetics has been extended even to the paleobotany being in this case a valuable tool to establish cyto-evolutionary relationships among extinct and living plant species.

Several authors coincide that knowing the number of species with cytogenetic studies is an important issue to evaluate the genome

diversity and plant biodiversity (Zoshchuk et al. 2003). However, it is difficult to estimate the total number of plants studied worldwide with respect to cytogenetic features due to that many old bibliographic sources are not available and interesting data may be hidden, including details on karyotype morphology and chromosome banding. In a more complete estimation, Bennett (1998) has pointed out that in ca. 25 % out of 250000 angiosperms the chromosome numbers are known, although this value can be overestimated or incorrect for several species because many of them are based on just one individual or population, and many species has been misnamed. Since that review, a significant increment in cytogenetic studies for different angiosperm groups has occurred according to available electronic databases which record 4400 species with known 2C-values and where the chromosome number is an elemental character indicative of ploidy level or aneuploidy (Bennett & Leitch 2010).

In the case of Chilean plants, cytogenetic characters have been studied since 128 years ago, with the pioneer works of Strasburger (1882) who included some *Alstroemeria* species. Later, Whyte (1929) updated those data with new available techniques including chromosome shapes for the same species. In recent years, the number of contributions for Chilean plants has increased including a spectrum of cytogenetic characters (e.g., chromosome number, karyotype morphology, genome size, chromosome banding and FISH). Nevertheless, many reports are difficult to compile due to the dispersed sources of publication. At present, due to the high amount of information generated and its utility in genome studies, electronic databases storing cytogenetic information provide on line data and bibliography, thus representing an important resource for cytogeneticists located in different areas around the world (Goldblatt & Johnson 1979, Bennett & Leitch 2005a, Jara-Seguel & Urrutia 2011).

The growing importance to increase cytogenetic data in plants has been discussed at international workshops, and in several articles have recommended to study genomic characters of global floras or to take advantages of methodological synergy between gene sequencers and genome-size researchers (Bennett 1998, Hanson et al. 2003, Bennett &

Leitch 2005a, 2005b, Gregory 2005b, Beaulieu et al. 2010, Leitch et al. 2010, Heslop-Harrison & Schwarzacher 2011). Overall there is an agreement in that cytogenetic information is necessary to evaluate levels of genomic variation to spatial scale, helping elucidate taxonomic relationships or to understand patterns on genome size evolution and polyploidization (Soltis & Soltis 2000, Levin 2002, Bennett 2004, Bennetzen et al. 2005, Leitch et al. 2005, Murray 2005, Leitch et al. 2007, Peruzzi et al. 2009, Kraaijeveld 2010).

In this present scenario, in which the studies on genome structure and functionality are the focus of attention for biologist of different fields, has emerged the so-called post genomic era where large-scale sequencing and comparative genome analysis are routinary in many labs around the world (Pryer et al. 2002, Leitch & Leitch 2008, Greilhuber et al. 2010, Leitch et al. 2010). Thus, a new challenge has been imposed for cytogeneticists interested in studying genomic features at local or global floras. In this context, continental and insular Chilean plants, due to its high endemism (Arroyo et al. 2006), may be a reservoir of genes and genomes (including epigenetic mechanisms), and not should be excluded of that worldwide purpose. However, a first step to carry out this task is to know the state of art of cytogenetics of Chilean angiosperms, thus looking at advances and detecting gaps of information that allow to plan future researches where molecular methods should be incorporated.

The aim of this paper is to review the advances in cytogenetic studies of Chilean angiosperms, focusing in the analysis of a number of publications on the subject, taxonomic representation and geographical coverage of the plant studied, the chromosome markers analysed and its resolution to solve genomic characters of the species. Some prospects are also given.

Number of publications

Seventy eight articles on cytogenetics of Chilean angiosperms have been published since 1929 (Fig. 1). The publications on cytogenetic have increased significantly in the last decade (40 publications since 2001 to 2010), which reflects the growing interest of Chilean researchers to study cytogenetic characters of

the native flora (current Chilean researchers are shown in Table 1). In addition, there is a great interest of foreign researchers to study chromosome variation at intercontinental and insular floras (Sanders et al. 1983, Spooner et al. 1987, Sun et al. 1990, Lammers & Hensold 1992, Hanson et al. 2003, Kiehn et al. 2005, Talluri & Murray 2009). However, the growth in cytogenetic contributions has partially depended on the interest of specialized botanical journals in publishing the data. In this context, 24 articles have been published in three Chilean journals since 1954, with

21 articles within the last decade (since 2001 to 2010). Nevertheless, since 1929 the majority of the reports on cytogenetic of Chilean angiosperms were published in foreign journals, being in many cases authored by foreign cytogeneticists.

Taxonomic representation and geographical range

In our literature search found cytogenetic data for 139 Chilean angiosperm species, which belong to 58 genera and 34 families (Jara-Seguel & Urrutia 2011), i.e. 2.8 % of the total angiosperm species recognized for continental and insular Chile. However, it is possible that the number of studied species be higher to the reported here, especially on chromosome number data, due to the difficulty to compile data from old sources of publication.

The cytogenetic data compiled included only terrestrial plants, due to the lack of information for aquatic and riparian species (Hauenstein 2006, Ramírez & San Martín 2008), a pending task for the near future. On the other hand, the incomplete taxonomic knowledge of some plant groups makes difficult the identification of some species for which chromosome counts have been determined in misnamed taxa (e.g., some *Leucocoryne* species) (Araneda & Manzur 2004). Thus, systematic reviews as the Flora de Chile (Rodríguez 1995) and Libro Rojo de la Flora Nativa (Squeo et al. 2001, 2008) may play a fundamental role in updating the taxonomic knowledge, as well as in increasing data on geographic distribution, endemism and conservation status of Chilean vascular plants.

Geographically, the higher number of Chilean angiosperm species cytogenetically

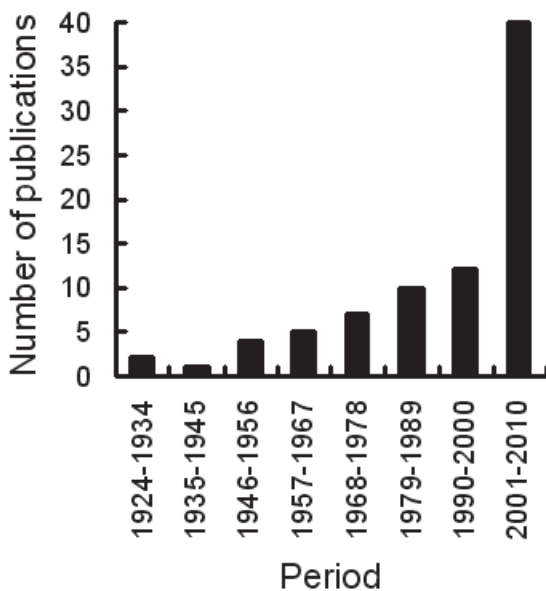


Fig. 1: Number of publications on cytogenetics of Chilean angiosperms since 1929.

Número de publicaciones sobre citogenética de angiospermas chilenas desde 1929.

TABLE 1

Chilean researchers on cytogenetics of native angiosperms.

Investigadores chilenos en citogenética de angiospermas nativas.

Name	Affiliation	Family of interest
Araneda Loreto Mansur Levi	Pontificia Universidad Católica de Valparaíso, Chile	Alliaceae, Amaryllidaceae
Baeza Carlos	Universidad de Concepción, Chile	Alstroemeriaceae, Asteraceae, Amaryllidaceae, Poaceae
Jara-Seguel Pedro	Universidad Católica de Temuco, Chile	Alstroemeriaceae, Luzuriagaceae, Philesiaceae
Palma-Rojas Claudio	Universidad de La Serena, Chile	Alstroemeriaceae, Amaryllidaceae

studied are present in a long latitudinal strip covering from 18° to 44° S, within the biodiversity hotspots. Besides, cytogenetic data for 21 % of native flora from Juan Fernández Archipelago is available (Sanders et al. 1983, Spooner et al. 1987, Sun et al. 1990, Stiefkens et al. 2001, Kiehn et al. 2005). There are data for one species from Isla de Pascua (Baeza 1996) and for species from Falkland Islands at the south edge of the Chilean Patagonia (Moore 1967). An important number of taxa are undersampled, for example those from southern Chile (> 44° S) including both continental and insular lands, as well as species that inhabit at high-altitude in the Nahuelbutan coastal ranges and Andean mountains. Efforts should be focused to the cytogenetic study of these plant groups, with special attention to local endemic taxa or to those highly specialized to their environment (e.g., parasites, xerophytes, hydrophytes, halophytes, frost resistant, carnivorous).

Chromosome number

Chromosome number is the most studied cytogenetic character for Chilean angiosperms having compiled data for 139 species, including in some cases sub-species, varieties or natural hybrids, which increased the number to 159 taxa.

Within the angiosperms the mean gametic number is $n = 16$ (Soltis & Soltis 2000) which is coincident with the mean somatic number $2n = 32$ reported for Chilean species. The minimum and maximum chromosome numbers reported for Chilean angiosperms goes from $2n = 8$ in *Hypochaeris* species to

$2n = 94$ in *Chaptalia exscapa* (Pers.) Baker var. *chilensis*, both belonging to the family Asteraceae. Besides, this family is the most studied (46 species) showing a high variation in chromosome number with 16 different $2n$ values (Jara-Seguel & Urrutia 2011). All the $2n$ number recorded for Chilean species fall within the range described for angiosperms ($2n = 4$ to $2n = \text{ca. } 640$ chromosomes, Leitch et al. 2010). Several plant families have various basic chromosome numbers, thus showing relatively high levels of cytogenetic variation. For example, cyto-evolutionary patterns have been described modifying $2n$ numbers in Alstroemeriaceae and Asteraceae including principally mechanisms of Robertsonian translocations and/or polyploidization (Buitendijk & Ramanna 1996, Weiss-Schneeweiss et al. 2003, Baeza & Schrader 2005c, Palma-Rojas et al. 2007, Baeza et al. 2007a). Nevertheless, in several families the mechanisms on numerical chromosome change are still uncertain due to the low number of studied species (Fig. 2, Table 1).

Polyploidy

Between 70-80 % of the angiosperm species are polyploids, with molecular evidence of ancient genome duplication at the base of monocots and dicots (Soltis et al. 2003, Leitch et al. 2010). Within the Chilean studied angiosperms, 20 continental species resulted to be polyploid (ca. 14 % of the studied species), whereas in endemic taxa of Juan Fernández Archipelago the level of polyploidization is estimated to be ca. 66 % (Sanders et al. 1983). As example of polyploid taxa can be mentioned the tetraploidy present

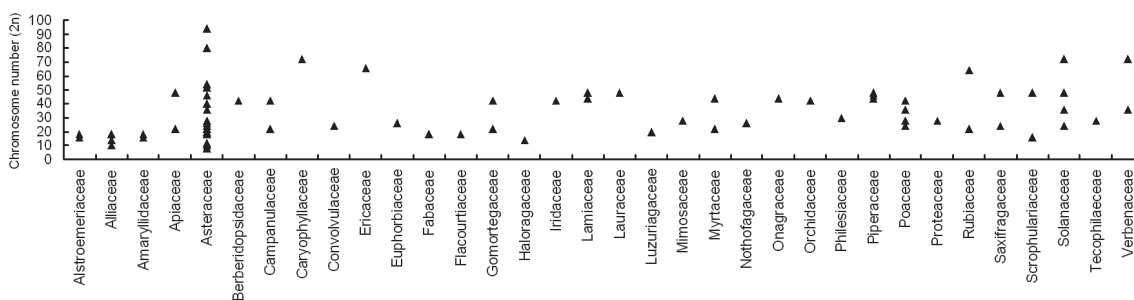


Fig. 2: Variation in chromosome number ($2n$) for each studied family of Chilean angiosperms.

Variación en número cromosómico ($2n$) para cada familia de angiospermas chilenas estudiadas.

within the families Lamiaceae ($2n = 44$, $x = 11$), Onagraceae ($2n = 42$, $x = 11$), Asteraceae ($2n = 44$, 80 ; $x = 11$, 20 ; $2n = \text{ca. } 94$) and Alliaceae ($2n = 18$, $x = 5$), and the hexaploidy present within Apiaceae ($2n = 48$, $x = 8$) (Covas & Schnack 1946, Sanders et al. 1983, Grau 1987, Kiehn et al. 2005, Talluri & Murray 2009) and Campanulaceae ($2n = 42$; $x = 7$) (Lammers & Hensold 1992). However, the highest variation in ploidy levels is present within the family Poaceae with tetra, hexa and octoploid species ($2n = 24$, 36 and 48 , respectively; $x = 6$) (Baeza 1996). The polyploidy described for Chilean Poaceae is in agreement with the estimation of that 80 % of all Poaceae worldwide described are polyploid with events of whole genome duplication dated 50-70 million years ago close to the origin of the family (ca. 89 mya) (Leitch et al. 2010). Another special case of polyploidy is that described within the Chilean endemic genus *Leucocoryne* (Alliaceae), where the tetraploid species $2n = 18$ have derived by Robertsonian translocation and chromosome duplication from cytotypes $2n = 10$ (Crosa 1988). However, many species and natural hybrids of the genus have not been cytogenetically studied as to generalize those evolutionary mechanisms to other species.

Cytogeographic studies on polyploid complex are scarce for Chilean plants due to that taxa have been studied at local scale for continental and insular zones (Sanders et al. 1983, Araneda & Mansur 2004, Salas & Mansur 2004, Kiehn et al. 2005). A first case has been documented for the *Lobelia tupa* L. (Campanulaceae) hexaploid complex ($n = 21$, $x = 7$, Lammers & Hensold 1992). Nevertheless, variations in ploidy levels may also be explained by evolutionary patterns to wider spatial scales, including taxa that inhabit in continental and insular zones. Such is the case of the family Poaceae whose species are mostly continental, except *Rytidosperma paschale* (Pilg.) Baeza with insular distribution in Eastern Island. All these Poaceae species are tetraploid, having $2n = 24$ chromosomes and a base number $x = 6$ (Baeza 1996).

As previously mentioned, cytogeography of Chilean plants is a field of high potential due to the Chilean long geography and climate variation along the latitudinal (from 18° to 56° S) and the altitudinal gradient from Pacific coasts to the limit of vascular vegetation in

the Andean highlands (0 to 4500 masl). In this context, the cytogeographic studies should be necessarily complemented with precise data on global positioning included within the GIS (Geographic Information Systems), thus giving accurate geo-references on distributional patterns of the populations of each species superimposed to its cytogenetic diversity, such as has been proposed by Kidd & Ritchie (2006) to phylogeographic studies.

B-chromosomes

B-chromosomes are supernumerary elements additional to the standard complement (or A-genome) which are present in ca. 1300 plants species being mostly distributed in monocots or in plants with large genomes but with low chromosome numbers (Camacho et al. 2000). For Chilean plants, B chromosomes have been reported for *Alstroemeria angustifolia* Herb. ssp. *angustifolia* (Alstroemeriaceae) (Buitendijk & Ramanna 1996) and *Lapageria rosea* R. & P. (Philesiaceae) (Hanson et al. 2003, Jara-Seguel & Zúñiga 2004), i.e., 1.8 % of the angiosperms cytogenetically studied up to now. In the present decade, although many aspects on B chromosomes in plants still remain obscure (Stebbins 1971, Trivers et al. 2004, Jones et al. 2008), several advances related with its evolution and expression of genes have been documented (Camacho et al. 2000, Leach et al. 2005). Besides, B-chromosomes have been described as promoting differences in genome size among populations (Jones et al. 2008).

Karyotypes

Data on karyotype morphology have been compiled for 45 species belonging to seven families (Alliaceae, Alstroemeriaceae, Amarillydaceae, Asteraceae, Fabaceae, Luzuriagaceae and Philesiaceae) all included within the orders Asterales, Fabales, Asparagales and Liliales (Table 2).

The first karyotype (including the first chromosome number) reported for Chilean angiosperms was obtained using histological sections of somatic tissues and from male gametophytes (Whyte 1929, Titov de Tschischow 1954, Cave 1966). Later, squash techniques have been performed on root-tip meristems treated with different anti-

mitotic reagent's, followed of fixation and stain procedures all accepted within standard methods (Singh 2003). Nomenclature to describe the chromosome morphology follows principally to Levan et al. (1964), being in many studies combined with other methods to determine karyotype asymmetry (Stebbins 1971, Arano & Saito 1980, Romero-Zarco 1986, Paszko 2006). In addition, inter-chromosomal relationships based on the ratio largest pair:shortest pair of chromosomes has provided valuable information on unimodality or bimodality of the karyotypes. Some genera of Liliales in which the karyotypes are highly asymmetric and bimodal, the largest chromosome pair are three to seven times longer than the shortest pair (e.g., *Alstroemeria*, *Lapageria*, *Luzuriaga*) (Jara-Seguel et al. 2004, Jara-Seguel & Zúñiga 2004, Baeza et al. 2010a, Jara-Seguel et al. 2010). Karyotype bimodality is a character that has been related

with a specialized kind of nuclear architecture that can be independent of the genetic status (White 1973), and some hypotheses have been proposed to explain its origin and adaptative significance (Stebbins 1971, Vosa 2005).

The karyotype morphology of species of Alstroemeriaceae, Asteraceae and Amaryllidaceae families have been the most intensively investigated in Chile, with various species and subspecies re-studied. Alstroemeriaceae is a family with ca. 200 species distributed in Central and South America. In Chile, this family comprises 38 species included within the genera *Alstroemeria*, *Bomarea* and the monotypic *Leontochir*, and in only 14 species the karyotype morphology has been described (Jara-Seguel & Urrutia 2011).

The species identification of *Alstroemeria* genus has been controversial and based principally in morphological characters (Muñoz-Schick & Moreira-Muñoz 2003). Karyotype

TABLE 2

Families of Chilean angiosperms for which karyotype morphology has been described. m, metacentric; sm, submetacentric; st, subtelocentric; t, telocentric. (Karyotype details of each family can be found in Jara-Seguel & Urrutia 2011).

Familias de angiospermas chilenas para las cuales se ha descrito la morfología del cariotipo. m, metacéntrico; sm, submetacéntrico; st, subtelocéntrico; t, telocéntrico. (Detalles del cariotipo de cada familia pueden ser revisados en Jara-Seguel & Urrutia 2011).

Order/Family	Number of genera	Chromosome number (2n)	Karyotype morphology
Asterales			
Asteraceae	11	8, 10, 12, 20, 22, 24, 26, 28	50-100 % of m-sm chromosomes; symmetry or asymmetry can be combined with unimodality or bimodality according to genus.
Asparagales			
Alliaceae	1	10, 14, 18	60-77 % of m-sm chromosomes; bimodal.
Amaryllidaceae	3	16	87 % of m-sm chromosomes or 75 % of t chromosomes according to genus; symmetry or asymmetry can be combined with bimodality.
Liliales			
Alstroemeriaceae	3	16, 18	37-62 % of m-sm chromosomes; asymmetry can be combined with unimodality or bimodality according to genus.
Luzuriagaceae	1	20	90 % of m-sm chromosomes; asymmetry combined with bimodality.
Philesiaceae	1	30	60 % of m-sm chromosomes; asymmetry combined with bimodality.
Fabales			
Fabaceae	1	18	100 % of m-sm chromosomes; symmetry combined with unimodality.

studies may serve to elucidate the taxonomy of the genus (in addition to both molecular and morphological studies). For instance, through karyotype morphology was possible to confirm *Alstroemeria graminea* Phil. within *Alstroemeria* (Jara-Seguel et al. 2004) thus rejecting its inclusion within the monotypic genus *Taltalia* as proposed by Bayer (1998). In another example, a close cytogenetic relationships among the monotypic *Leontochir ovallei* Phil. and *Bomarea* species has been described based in karyotype morphology (Palma-Rojas et al. 2007), being consistent with the synonymy previously described among *Leontochir* and *Bomarea* [Syn. *Bomarea ovallei* (Phil.) Rav.] (Hofreiter 2006). In addition, all *Alstroemeria* species are characterized by the presence of a conservative karyotype being asymmetric and bimodal, and where only *A. ligtu* L. has more uniform chromosome sizes (Buitendijk & Ramanna 1996). However, intra-specific variation in karyotype morphology has also been found within the complex *A. hookeri* Lodd., which is superimposed with geographical distribution of the studied subspecies (Baeza et al. 2010c). In *Bomarea* and *Leontochir* the karyotypes are less asymmetric and uniform in chromosome size compared with *Alstroemeria* (Palma-Rojas et al. 2007). Besides, *Alstroemeria* species have a high potential as ornamental plants, and artificial inter-specific hybrids and their Chilean and Brazilian parents have also been evaluated on the basis of karyotype morphology with a high probability to establish genome relationships among them (Buitendijk & Ramanna 1996) In the case of the cosmopolitan family Asteraceae, 927 species are in the Chilean flora (Marticorena 1990) and the karyotype morphology has been described for 14 species. At present, karyotype evolutionary trends among intra-continental and/or inter-continental taxa have been interpreted for the genera *Hypochaeris*, *Haplopappus*, *Grindelia*, and *Chaetanthera* using different methods (Weiss-Schneeweiss et al. 2003, Baeza & Schrader 2005a, 2005b, 2005c, Baeza & Torres-Díaz 2006, Baeza et al. 2006). For example, for New World members of *Grindelia* and *Haplopappus* their evolution has not been accompanied by large karyotype changes, although small chromosomal rearrangement have occurred and differences exist in base number and asymmetry level (Baeza &

Schrader 2005b). In the case of *Hypochaeris*, general uniformity of their karyotypes and a stable chromosome number ($2n = 8$) have been described for South American species including Chilean taxa, but differences in location of secondary constriction and chromosome size were observed (Weiss-Schneeweiss et al. 2003). Secondary constrictions and NOR location are characters well differentiated among four groups recognized within *Hypochaeris* genus (Weiss-Schneeweiss et al. 2003). Other less studied genus is *Chaetanthera* which is native to South America, and their six Chilean species present asymmetric karyotypes which can vary in level according to its altitudinal distribution (Baeza et al. 2005c, Baeza et al. 2010b).

Amarillydaceae, is represented in Chile by 43 species and seven genera. At present, karyotype morphology has been described only for nine species belonging to the genera *Phycella*, *Rhodophiala*, *Placea*, *Rodholirium* and *Traubia*. All five genera of Amarillydaceae studied have asymmetric karyotypes and show similar chromosome morphology with little variations (Baeza & Schrader 2004, Baeza et al. 2004, Baeza et al. 2007b, Cisternas et al. 2010).

In general, robust karyotype affinities based in quantitative and/or qualitative analyses have been established within Chilean angiosperm families, allowing in many cases accurate cyto-evolutionary and cytotaxonomic circumscriptions.

Banding and FISH methods

C-banding method has been used only for two genera of the family Alstroemeriaceae (*Alstroemeria* and *Leontochir*), with eight species studied. In *Alstroemeria* species, the haploid relative length values of the C-bands vary between 2.0 to 6.5 % (Buitendijk & Ramanna 1996, Jara-Seguel et al. 2004), whereas in the case of *Leontochir ovallei* the haploid relative length value of the C-bands was 20 % (Jara-Seguel et al. 2005). Within the genus *Alstroemeria* considerable intraspecific and interspecific variation in C-bands relative length and chromosome location of constitutive heterochromatin have been observed, being these characters additional to heterocigosity in size and location of C-bands among homologous chromosome pairs in some species (Buitendijk & Ramanna 1996). Besides, the presence of

large C-bands has been co-related with large chromosome size and high nuclear DNA content, being these characters associated with geographical distribution and climate on a latitudinal gradient (Buitendijk & Ramanna 1996, Buitendijk et al. 1997, Jara-Seguel et al. 2004).

C-banding has been an important tool to describe the genome complexity in some Alstroemeriaceae species. For this reason, and due to its low cost in reagents and the use of conventional microscopy, C-bands technique is attainable for any laboratory and could be performed in more angiosperms families, thus valuable information on genome structure and dynamics can be obtained. This information may be a fundamental knowledge to the application of other modern molecular techniques such as clonation, sequencing and *in situ* hybridization of C-heterochromatin regions or ribosomal cistrons, all focused to the understanding of phylogenetic relationships among species.

The application of fluorescent banding such as DAPI, CMA₃ and/or FISH has been an important step to study genome characters in species of the genera *Alstroemeria*, *Hypochoeris*, *Haplopappus*, *Grindelia*, *Placea*, *Rhodophiala* and *Chaetanthera* that inhabit in Chile (Kamstra et al. 1999, Weiss-Schneeweiss et al. 2003, Zhou et al. 2003, Baeza et al. 2004, Baeza & Schrader 2004, 2005a, 2005b, 2005c, Baeza et al. 2007a) with a total of 23 studied species. The available data are restricted to physical chromosome mapping of genes, specific sequences or DNA fragments within Chilean angiosperms, thus opening the way to comprehensive studies on genome affinities and dynamics (e.g., meiotic chromosome behavior, chromosome rearrangement, rDNA location), and where promising advances in the knowledge on genome structure and functionality can be obtained. Besides, in the future populational micro-identification focused to define conservation units of endangered species can be carried out, and an interesting propose on this field has been discussed by Lavania (2002).

Genome size

Genome size is a strong unifying element in biology with practical and predictive uses, having interest in other biological fields that

includes ecology, biogeography, physiology and embryology (Bennett & Leitch 1997, 2005b, Gregory 2005a, Kraaijeveld 2010, Greilhuber et al. 2010, Grover & Wendel 2010). Many authors have documented data on genome size including local and global floras of different continents, being described ca. 4400 angiosperm species (Leitch et al. 2010). In the case of Chilean angiosperms, studies on genome size have been done in only 12 species. *Alstroemeria* has been the most studied genus with seven species, varying the range of C-values between 19.9 pg in *A. pulchra* Sims. ssp. *pulchra* to 34.7 pg in *A. ligtu* ssp. *ligtu* (Buitendijk et al. 1997). It is remarkable that the C-values of *Alstroemeria* species fall within the largest genome sizes of the Plantae kingdom (Sanzo & Hunziker 1998), but are lower than the maximum 1C = 127.3 pg described within monocots (Leitch et al. 2010). On the other hand, *Lapageria rosea* R. & P. has an intermediate 1C-value of 6.8 pg (Bennett & Leitch 2005a), whereas the other Chilean genera studied up now have small C-values (*Prosopis* 1C = 0.4 pg, *Berberidopsis* 1C = 0.3 pg, and *Fuchsia* 1C = 1.46 pg) (Bukhari 1997, Bennett & Leitch 2005a, Talluri & Murray 2009) lower than the average 1C = 6.3 pg estimated for angiosperms (Leitch et al. 2005).

Prospects

The interest for the cytogenetic knowledge of plants that inhabit in Gondwanan regions has increased, and statistical reports on number of species studied have been documented for some countries and islands. In a recent compilation, Dawson (2008) has estimated that chromosome numbers for about 80 % of the indigenous vascular plant of New Zealand are known. In addition, an important compilation is also available for Paraguay where almost 313 species of its flora have been cytogenetically studied (Molero et al. 2001). For other zones of South America (Central and Eastern Brazil) and Oceania (Australia, Tasmania) despite the extensive studies on cytogenetic of plants, statistical estimations on the total number of examined species are not available (Jackson 1958, Smith-White 1959, Coleman 1982, Carvalheira et al. 1991, Watanabe et al. 1999, Forni-Martins & Martins 2000).

The current cytogenetics knowledge on the Chilean flora and especially of angiosperms

which is the most diverse (160 families and 4946 species), contrast with the situation of other Gondwanan zones. Documents storing cytogenetic information that support statistical evaluations on number of studied species are few, being replaced by electronic databases that include chromosome numbers and/or genome size of global floras (Goldblatt & Johnson 1979, Bennett & Leitch 2010), and by a recently launched database that shows a broad spectrum of cytogenetic characters of Chilean plants (Jara-Seguel & Urrutia 2011). However, on the basis of the available data, the future can be promising due to that the number of publications on cytogenetic of Chilean plants has increased greatly in the last ten years (~40 publications) with 95 additional species. We hope that this trend may be maintained in the next decade if the current research groups and young specialists follow interested in to study native angiosperms, being also necessary to include the undersampled Bryophyta, and the scarcely studied Pteridophyta and Pinophyta.

The importance of plants as base of life on earth was emphasized by Bennett (1998), thus remarking the need for more work on many basic aspects of angiosperm genomes. In the case of Chilean vascular flora, due to the species richness (5105 species) and the high level of endemism (45.8 %) have a scientific, economic and cultural value, which justify increasing the knowledge of plant genomes. Regards the species useful to man, Chile is the origin center of *Fragaria chiloensis* (L.) Mill. (Synonime *Bianca chiloensis*), *Lycopersicon chilense* Dun., *Solanum tuberosum* L. ssp. *tuberosum*, *Ugni molinae* Turcz. and *Gevuina avellana* Mol. among other species recognized as edibles, medicinals and ornamentals (Hoffmann et al. 2003, Seguel 2008). However, studies on genomic diversity are scarce for these species (except *S. tuberosum* with various studies) and for this reason in the near future the study of chromosome number, karyotype morphology, and genome size of Chilean angiosperm species should be a priority task. These data should be combined with modern cytogenetic tools (conventional and fluorescent banding, FISH and GISH techniques) (Heslop-Harrison & Schwarzacher 2011) or molecular methods (DNA sequencing, DNA fingerprint) (Campos et al. 2000) thus providing important antecedents on structure, complexity, dynamics and evolution of the genomes of Chilean plants, which can also be

applied to its conservation and/or improvement of species with economic importance. This review on Chilean angiosperms is focused to show the advances, detect gaps and prioritize needs, but future papers will record how well these expectations are met.

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