RESUMEN

El género *Helianthus* consiste de 51 especies, nativas de América del Norte, clasificadas en cinco secciones y seis series. Comprende especies diploides, tetraploides y hexaploides, e incluye a las formas silvestres del girasol cultivado *H. annuus L.* var. *macrocarpus.* Diferentes trabajos han abordado el estudio de las relaciones filogenéticas entre las especies del género, aunque varios puntos continúan sin resolverse, particularmente el origen de las especies poliploides que son en su totalidad perennes. El objetivo general de esta tesis es contribuir al conocimiento de la historia evolutiva del género, examinando las afinidades existentes entre las especies hexaploides, *H. resinosus* y *H. tuberosus*, especies diploides anuales, y especies diploides y tetraploides perennes. Se llevaron a cabo estudios citogenéticos, clásicos y moleculares, como así también análisis con marcadores moleculares nucleares y organelares y secuencias de regiones intergénicas de cloroplasto. Las configuraciones meióticas en la progenie de la cruza *H. annuus* × *H. resinosus* incluyeron univalentes, bivalentes, trivalentes y cuadrivalentes. La ocurrencia de husos con disposición anormal en meiosis II, condujo a la formación de productos meióticos en forma de díadas y tríadas además de las tétradas normales. Como consecuencia, los granos de polen de los híbridos presentaron heterogeneidad en el tamaño, con una distribución que pone en evidencia la formación de gametos 2n no reducidos. En el caso de la cruza *H. resinosus* × *H. neglectus,* los productos meióticos se caracterizaron por la presencia de micronúcleos, adicionados a las tétradas de tamaño normal. La hibridización de cromosomas de la progenie de *H. resinosus* × *H. annuus* con sondas de ADN genómico de *H. annuus* (GISH) confirmó el nivel tetraploide de los individuos F_1 y puso en evidencia la marca de 17 cromosomas provenientes del parental *H. annuus*. En cuanto a las configuraciones meióticas, los bivalentes estaban compuestos principalmente por apareamiento autosindético de cromosomas de *H. resinosus*, aunque también se observaron apareamientos alosindéticos entre cromosomas de ambas especies parentales. Esto sugiere cierta homología parcial, que permite el apareamiento homeólogo y probablemente la recombinación. Los univalentes correspondieron a una u otra especie parental. El GISH utilizando ADN genómico de *H. annuus*, y otras especies diploides, aplicados a células mitóticas de *H. resinosus* y *H. tuberosus* mostró una señal de hibridación débil y uniformemente distribuida sobre los cromosomas de las especies hexaploides. De este modo, no fue posible detectar subgenomas en el complemento cromosómico 6x, lo que puede ser atribuido a la presencia de secuencias repetitivas comunes a las especies del género. Estos resultados rechazan la hipótesis de *H. annuus* como una de las especies diploides parentales. La única posibilidad que permite retener a *H. annuus* como candidato implica la ocurrencia de un mecanismo de homogeneización de los subgenomas a nivel de ADN repetitivo luego del evento de hibridización, lo que volvería inefectiva la técnica de GISH para detectar complementos cromosómicos originales. Las técnicas de RAPD e ISSR generaron marcadores consistentes y polimórficos. Fue posible diferenciar a las especies hexaploides, *H. resinosus* y *H. tuberosus*, de 9 diploides anuales y de 8 diploides y tetraploides perennes, y se detectaron grupos taxonómicos previamente descriptos dentro de cada sección. En nuestro conocimiento, este es el primer estudio que emplea loci microsatélites de cloroplasto (SSRcp) para el estudio de las relaciones filogenéticas entre especies de *Helianthus*. El nivel de polimorfismo de siete loci SSRcp fue alto. Las relaciones obtenidas entre especies con estos marcadores mostraron grandes discrepancias con clasificaciones previas, probablemente adjudicados a procesos como homoplasia en tamaño o transferencia diferencial de los genomas nuclear y de cloroplasto. El empleo de secuencias de una región intergénica de cloroplasto permitió la separación de las especies perennes de las anuales y esto la coloca como una técnica comparativamente más informativa. Se continúa con la secuenciación de otras regiones intergénicas a fin de incrementar la resolución de las relaciones entre las especies del género *Helianthus*.

ABSTRACT

The genus *Helianthus* consists of 51 species, native to North America, classified into five sections and six series. It contains diploid, tetraploid and hexaploid species, and includes wild forms of cultivated sunflower *H. annuus L.* var. *macrocarpus.* Several studies have addressed the study of the phylogenetic relationships among species of the genus, but a number of points remain unresolved, particularly the origin of polyploid species which are completely perennial. The general objective of this thesis is to contribute to the knowledge of the evolutionary history of the genus, examining the affinities between the hexaploid species, *H. resinosus* and *H. tuberosus*, annual diploid species, and diploid and tetraploid perennial species. Cytogenetic studies (both classical and molecular) were carried out, along with nuclear and organellar molecular marker analyses and chloroplast intergenic-regions sequencing. The meiotic configurations in the progeny of the crosses *H. annuus* × *H. resinosus* included univalents, bivalents, trivalents and quadrivalents. The occurrence of anormal spindles in meiosis II generated the formation of meiotic products like dyads and triads besides the normal tetrads. Consequently, pollen grains of the hybrids showed heterogeneity in size, with a distribution that exposes the formation of unreduced 2n gametes. In the case of cross *H. resinosus* × *H. neglectus*, the meiotic products were characterized by the presence of micronuclei, added to normal size tetrads. The hybridization of chromosomes of the progeny of *H. resinosus* × *H. annuus* with probes of genomic DNA of *H. annuus* (GISH) confirmed the tetraploid level of the F_1 and showed the mark of 17 chromosomes coming from the parental *H. annuus*. Regarding meiotic configurations, bivalents were composed mainly of autosyndetic pairing of *H. resinosus* chromosomes, although allosyndetic pairings between chromosomes of both parental species were observed. This suggests some parcial homology that allows homeologous paring and probably recombination. Univalents corresponded to one or other parental species. GISH using genomic DNA of *H. annuus* and others diploids species, applied to mitotic cells of *H. resinosus* and *H. tuberosus* rendered a weak signal of hybridization, and uniformly distributed over chromosomes of hexaploide species. Therefore, subgenomes of the 6x chromosomic complement could not be identified, which can be attributed to the presence of repetitive sequences common to the species of the genus. These results reject the hypothesis of *H. annuus* as one diploid parental species. The only possibility that allows keeping *H. annuus* as a candidate involves the occurrence of a mechanism of subgenomes homogenization at repetitive DNA level following hybridization, which would make GISH technique ineffective for detecting original chromosome complements. RAPD and ISSR techniques generated polymorphic and consistent markers. It was possible to differentiate the hexaploid species, *H. resinosus* and *H. tuberosus*, from 9 diploid annual and 10 diploid and tetraploid perennial species, and taxonomic groups previously described were detected within each section. To our knowledge, this is the first study using chloroplast microsatellite loci (SSRcp) to study the phylogenetic relationships among species of *Helianthus*. The polymorphism level of seven loci SSRcp was high. The relationships between species obtained with these markers showed large discrepancies with previous classifications, probably awarded to processes such as homoplasy in size or selective transfer of nuclear and chloroplast genomes. The use of a sequence of an intergenic region of chloroplast allowed the separation of perennial species from the annual species, and this characterizes this technique as comparatively more informative. The sequencing of other intergenic regions follows, in order to increase the resolution of relationships among species of the genus *Helianthus*.

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