Chromosome Numbers of Angiosperms from the Juan Fernández Islands, the Tristan da Cunha Archipelago, and from Mainland Chile[1]

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Abstract: Chromosome counts for eight native species in six genera from Juan Fernández Islands, five native species in three genera from Tristan da Cunha, and three species in two genera from mainland Chile are presented and discussed. They include the only chromosome number reports for angiosperms from Tristan da Cunha and first counts for the endemics *Robinsonia thurifera* and *Wahlenbergia larrainii* (Juan Fernández), *Agrostis carmichaelii*, *Acaena sarmentosa*, *A. stangii*, and *Nertera holmboei* (Tristan da Cunha), and for *Galium araucanum* and *Ourisia coccinea* from Chile. Counts for *Eryngium bupleuroides* and *Galium hypocarpium* differ from earlier published reports.

Isolated oceanic islands are "natural laboratories" for studying patterns and processes of evolution. In this context, knowledge about the cytological situation in endemic taxa is of special interest, because chromosome numbers often reflect speciation and radiation events on islands. However, available karyological data for plants of oceanic islands are unequally distributed, ranging from no records at all for several remote archipelagos, to comparatively high percentages (e.g., ca. 40% for species native to Hawai'i [Carr 1998, Kiehn 2005] and ca. 53% for plants from the Canary Islands and from the Bonin Islands [Stuessy and Crawford 1998]). Reported numbers in most cases are obtained from single or very few individuals and populations.

This paper aims to increase the knowledge of chromosome numbers and ploidy levels of angiosperms occurring on islands by providing first reports of chromosome numbers for angiosperms from an archipelago (Tristan da Cunha), first results for taxa not investigated before, and counts for new collections of taxa already studied. In addition, counts for three species from mainland Chile are presented.

Materials and Methods

Plant material was collected by T. F. Stuessy (Juan Fernández Islands), G.J. (Tristan da Cunha), and P. Menzel and D. Supthut (southern Chile). Field fixations of actively growing apices, young flower buds, or young flowers were made in a freshly mixed 3 : 1 solution of ethanol (96%) : glacial acetic acid (G.J., Menzel, Supthut) or in modified Carnoy's fixative (4 : 3 : 1 solution of chloroform : 96% ethanol : glacial acetic acid) (Stuessy). Fixations of root tips from plants cultivated from seeds collected in the field were made at the Botanical Garden of the University of Vienna, Austria (HBV). Somatic chromosome numbers (2*n*) were ultimately obtained from any of several tissue sources, including young flower buds, young ovaries, anthers, and root tips. Gametic number determinations (*n*) were derived from meiotic divisions of either megasporocytes or microsporocytes. In the case of root tips a pretreatment with a solution of 0.002 m 8-hydroxyquinoline (ca. 2 hr at 19–21°C followed by ca. 2 hrs at 4°C) was used before fixation in a freshly mixed 3 : 1 solution of ethanol (96%) : glacial acetic acid. The fixed material was transferred to 70% ethanol and kept at ca. 8°C before

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staining with Giemsa (after hydrolysis in 5 N HCl for 50 min at 20°C) or with Feulgen (see Kiehn 1995 for additional details on staining procedures). Hot aceto-carmine (2% solution in 45% acetic acid) was also used in some cases to intensify staining.

Exact counts could not be achieved in some instances because of limited material and/or clumping of chromosomes; chromosome numbers for these taxa are given with the range obtained. Data for each investigated collection are presented in Table 1. Voucher specimens for the chromosome number determinations have been deposited in the herbaria of the Ohio State University (OS) or at Vienna University (WU) as stated in Table 1. Permanent microscope slides from which chromosome numbers were determined are in the collection of M.K.

RESULTS AND DISCUSSION

Chromosome counts for 16 angiosperm species (28 collections) of 10 families are presented in Table 1. They comprise data for eight species (13 collections) from the Juan Fernández Islands, five species, one with two investigated forms (12 collections in total) from Tristan da Cunha, and three species (three collections) native to southern Chile.

Counts from the Juan Fernández Islands

The Juan Fernández Islands are an isolated archipelago located ca. 600 km west of the coast of Chile at a latitude of 33° S. They have never been connected to the South American mainland and harbor a unique flora with a high degree of endemism, ca. 60% of the native species and 18% of the genera (Skottsberg 1956, Stuessy et al. 1992, Marticorena et al. 1998). Three papers have reported chromosome numbers of species occurring in this archipelago (Sanders et al. 1983, Spooner et al. 1987, Sun et al. 1990). With the results presented here, cytological data for ca. 21% of the native flora of the Juan Fernández Islands are available.

APIACEAE: *Eryngium bupleuroides* is one of three endemic species of this genus on the Juan Fernández Islands (Jakubowsky and Stuessy 1999) and so far the only one investigated cytologically. Sanders et al. (1983) reported $n = 16$ for *E. bupleuroides*, a number also present in Latin American mainland species of *Eryngium* (Sanders et al. 1983, Pimenov et al. 2003). According to these data, $x = 8$ seems to be the prevalent basic number for the genus. There are several reports of polyploids, including a few counts of $n = 24$, in agreement with the report here for *E. bupleuroides* (Table 1).

According to Stuessy and Crawford (1998), *Eryngium* is one of only two potential cases of hybridogeneous speciation on the Juan Fernández Islands. Jakubowsky and Stuessy (1999) confirmed a hybridogeneous origin for *E. fernandezianum* from *E. bupleuroides* and *E. inaccessum*, a situation that had already been suspected by Skottsberg (1922).

The data presented here for *E. bupleuroides* reflect studies of all developmental stages from microsporocytes to pollen grains of nine different flowers. Most stages of meiosis showed marked irregularities; cytoplasmic bridges between microsporocytes, anaphase bridges, univalents, and restitution nuclei were abundant. In some of the irregular anaphase II divisions it was possible to count 11–25 chromosomes or chromosome fragments in different parts of the microsporocytes. Usually 15–24 chromosomes were moving together, but lagging fragments were always present. Very few normal tetrads and only a few well-formed pollen grains were observed; cells with three to six unequally sized nuclei were present instead. In all of the very few regular-looking divisions that could be counted $n = (22)–24$ chromosomes were observed. Additional cytological investigations of the genus *Eryngium* on the Juan Fernández Islands are needed to appreciate more fully the results reported here.

ASTERACEAE: The endemic genus *Robinsonia* comprises seven species (Skottsberg 1922, Marticorena et al. 1998). Chromosome numbers for two of them (*R. gayana* and *R. gracilis*) were reported and discussed by Sanders et al. (1983). Both species show a haploid number of $n = 20$. The new count of $n = 20$ for *R. thurifera* was obtained from megasporocytes. The genus *Robinsonia* is considered to be related to *Senecio*, where $n = 20$ is common (Sanders et al. 1983). The two species of *Robinsonia* investigated earlier represent two sections of the genus. Thus Sanders et al. (1983) considered speciation in the genus on the Islands to have taken place without change in chromosome number. The new result for *R. thurifera* is in accordance with this hypothesis.

CAMPANULACEAE: According to Lammers (1996) and Marticorena et al. (1998), the genus *Wahlenbergia* has five endemic species in the Juan Fernández Islands. Chromosome counts are available for two of them: *W. fernandeziana* from Masatierra and *W. masafuerae* from Masafuera. For both species $n = 11$ was counted in individuals from several populations (Sanders et al. 1983, Spooner et al. 1987, Sun et al. 1990). Our new reports revealed $n = x = 11$ (or $2n = 22$) for *W. fernandeziana* (four populations) and *W. larraini*. The latter, treated as distinct species by Ricci and Eaton (1994), has a very narrow distribution on Masatierra and is now probably extinct. However, the taxonomic status of this taxon is doubtful, because neither Lammers (1996) nor Crawford et al. (1990) nor Anderson et al. (2000) have found characters that distinguish it from *W. fernandeziana*. Because $n = x = 11$ is a basic number not known otherwise in the genus *Wahlenbergia*, chromosome numbers give no hint of geographic origin or taxonomic relationships of the species from the Juan Fernández Islands.

HALORAGACEAE: The count presented here for *Haloragis masatierrana* ($2n = 14$) is in accord with the earlier report of $n = 7$ by Sanders et al. (1983). Because the predominantly reported basic chromosome number in the family Haloragaceae is $x = 7$, our count has little bearing on questions of speciation and radiation in *Haloragis*.

LAMIACEAE: *Cuminia* is an endemic genus of the Juan Fernández Islands consisting of two clearly distinguishable species, *C. eriantha* and *C. fernandezia* (Ruiz et al. 2001). Sanders et al. (1983) reported $n = 22$ for two populations of *C. eriantha* and one population of *C. fernandezia*. The results presented here of $n = 22–24$ for *C. eriantha* and of $2n =$ ca. 44 for *C. fernandezia* are in accordance with the earlier reports and emphasize the tetraploid status of these species based on $x = 11$ (Sanders et al. 1983).

SAXIFRAGACEAE (ESCALLONIACEAE): Investigations of individuals from three different populations of the Juan Fernández Islands endemic *Escallonia callcottiae* revealed $2n = 24$ or $2n = (22–)24$, in accordance with the earlier report of $n = 12$ for this species by Sanders et al. (1983).

Counts from the Tristan da Cunha Archipelago

The Tristan da Cunha archipelago is situated in the South Atlantic Ocean, ca. 2,800 km west of South Africa and ca. 3,200 km east of South America at a latitude of 37° 15′–37° 28′ S and comprises three islands (Inaccessible, Nightingale, and Tristan da Cunha). In addition to ca. 100 species of alien flowering plants, 78 indigenous vascular plant species (37 ferns and 41 angiosperms) have been recorded for the Islands so far. Twenty-three of the angiosperm species (56%) are endemic (G.J. and M.K., unpubl. data).

The only counts of angiosperm taxa from the archipelago are those reported here, including four endemic and one nonendemic indigenous species. Together they comprise ca. 12% of the indigenous angiosperm flora. The addition of the new counts to previous reports for 20 species of ferns from the archipelago (Manton and Vida 1968) brings the proportion of indigenous vascular plant species of Tristan da Cunha that has been investigated cytologically to 32%.

POACEAE: There are five endemic species of *Agrostis* known from Tristan da Cunha. Molecular data (G.J., unpubl. data) indicate monophyly for these endemics, which all seem to be derived from *A. magellanica* subsp. *magellanica*, a species widespread in the Southern Hemisphere. Beuzenberg and Hair (1983) reported $n = 42$ for *A. magellanica* from Campbell Island, whereas Moore (1960) counted $2n = 72$ in plants from Macquarie Island (both islands south of New Zealand). Edgar and Forde (1991) mentioned $x = 7$ as the basic chromosome number for *Agrostis* and expressed doubts about the result of Moore (1960). The count presented here for *Agrostis carmichaelii* ($2n = 56$) is in accord

TABLE 1

Chromosome Numbers of Angiosperms from Tristan da Cunha, Juan Fernández Islands, and Chile

Taxon	Gametic No. (n)	Somatic No. ($2n$)	Origin[a]: Voucher (Herbarium[b])	Earlier Reports, Remarks
Apiaceae				
Eryngium bupleuroides Hook. & Arn.	(22)–24[c]	—	JF, Masatierra: *Stuessy & Crawford 11974* (OS)	$n = 16$ (Sanders et al. 1983)
Asteraceae				
Robinsonia thurifera Decne.	20	—	JF, Masatierra: *Rondanelli & Penailillo 11681* (OS)	First report
Campanulaceae				
Wahlenbergia fernandeziana (DC.) Skottsb.	—	22	JF, Masatierra: *Stuessy et al. 11735B* (OS)	$n = 11$ (Sanders et al. 1983, Spooner et al. 1987)
	—	22	JF, Masatierra: *Stuessy et al. 11735C* (OS)	
	11	22	JF, Masatierra: *Stuessy et al. 11879* (OS)	
Wahlenbergia cf. *fernandeziana*	—	22	JF, Masatierra: *Stuessy et al. 11835* (OS)	
Wahlenbergia larraini Bert. & Colla ex Skottsb.	—	22	JF, Masatierra: *Stuessy et al. 11587* (OS)	First report
Haloragaceae				
Haloragis masatierrana Skottsb.	—	14	JF, Masatierra: *Stuessy et al. 11046* (OS)	$n = 7$ (Sanders et al. 1983)
Lamiaceae				
Cuminia eriantha Benth.	22–24	—	JF, Masatierra: *Stuessy et al. 11307* (OS)	$n = 22$ (Sanders et al. 1983)
Cuminia fernandezia Colla	—	ca. 44	JF, Masatierra: *Stuessy et al. 11739* (OS)	$n = 22$ (Sanders et al. 1983)
Poaceae				
Agrostis carmichaelii J. A. Schult. & J. H. Schult.	—	56	TC, Tristan: *Jakubowsky T 344* (WU)	First report
Rosaceae				
Acaena stangii Christoph.	—	40–42	TC, Tristan: *Jakubowsky T 122b* (WU)	First report
Acaena sarmentosa (Thouars) Carm.	—	42	TC, Inaccessible: *Jakubowsky I 78* (WU)	First report
Rubiaceae				
Galium araucanum Philippi	(10–)11	—	C, IX. region: *Menzel sub MK-971105-4/1* (WU)	First report
G. hypocarpium (L.) Endl. ex Griseb. subsp. *hypocarpium*	11	—	C, IX. region: *Menzel sub MK-971105-4/2* (WU)	$2n = 44$ (M.K., unpubl. data); $n = 33$ (Huynh 1965)
Nertera granadensis (L.f.) Druce	—	42–44	TC, Nightingale: *Jakubowsky N 28* (WU)	Several reports, also as *N. depressa* Banks & Soland. ex Gärtn. (cf. Kiehn 1996)
	—	44 ± 4	TC, Nightingale: *Jakubowsky N 31* (WU)	
	—	44 ± 4	TC, Tristan: *Jakubowsky T 234* (WU)	
	—	44	TC, Tristan: *Jakubowsky T 345* (WU)	
	—	44	TC, Inaccessible: *Jakubowsky I 97* (WU)	
	—	44	TC, Inaccessible: *Jakubowsky I 85* (WU)	Originally determined as *N. depressa* f. *fimbriata* Christoph.

N. holmboei Christoph.	—	40–44	TC, Nightingale: *Jakubowsky N 22* (WU)	First report
	—	(42)–44	TC, Nightingale: *Jakubowsky N 24* (WU)	
	—	44	TC, Inaccessible: *Jakubowsky I 88* (WU)	
Saxifragaceae (Escalloniaceae)				
Escallonia callcottiae Hook. & Arn.	—	24	JF, Masatierra: *Stuessy et al. 11089* (OS)	$n = 12$ (Sanders et al. 1983)
	—	(22–)24	JF, Masatierra: *Stuessy et al. 11103* (OS)	
	—	(22–)24	JF, Masatierra: *Stuessy et al. 11297* (OS)	
Scrophulariaceae				
Ourisia coccinea Pers.	8	—	C, IX. region: *Supthut sub MK-971102-2/1* (WU)	First report

[a] JF, Juan Fernández Islands; TC, Tristan da Cunha archipelago; C, Chile.
[b] OS, Ohio State University; WU, Vienna University.
[c] Meiotic divisions display many irregularities (see text).

with a basic number of $x = 7$ and represents octoploidy, which otherwise is unknown in the *A. magellanica* species alliance.

ROSACEAE: The new chromosome data ($2n = 42$; $2n = 40$–42) for *Acaena sarmentosa* and *A. stangii*, the two *Acaena* species endemic to Tristan da Cunha, are in accordance with earlier reports for the genus that show a basic number of $x = 21$ for all *Acaena* species from New Zealand (see survey in Dawson 2000). The cytological data are consistent with earlier hypotheses (Bitter 1911) and DNA sequencing data (Hibbs and G.J., unpubl. data) that link the Tristan da Cunha species to those of New Zealand.

RUBIACEAE: The proposed inclusion of *Nertera* into *Coprosma* (Heads 1996) is not supported by molecular studies (Anderson et al. 2001, Markey et al. 2004) and is, therefore, not followed in this paper. The new chromosome data for *Nertera* from Tristan da Cunha (Table 1) are in accord with $x = 11$ and tetraploidy obtained in most earlier counts for the genus (see Kiehn 1996). The only exceptions are the results for *N. setulosa* (= *Leptostigma setulosa*: $n = 20$ [Hair 1963]; $2n = 40$ [Dawson and Beuzenberg 2000]) and *N. yamashitae* ($2n = 22$ [Kokubugata et al. 1998]). Based on morphological characters and molecular data (Markey et al. 2004, unpubl. data), and the chromosome numbers for *N. setulosa* and *N. yamashitae*, placement of these two species in *Nertera* seems doubtful and deserves further study.

Counts from Mainland Chile

RUBIACEAE: All *Galium* species considered here share a base number of $x = 11$ and are members of the group formerly treated as the genus *Relbunium* (Dempster 1990). Diploidy (Huynh 1965) and tetraploidy (Diers 1961) has been found in *G. hirsutum* Ruiz & Pavon from Peru. The widespread *G. hypocarpium* L. has been reported as a hexaploid (Peru [Huynh 1965]), a tetraploid (Costa Rica [M.K., unpubl. data]), and is here documented from Chile at the diploid level for the first time. The first report for another Chilean species, *G. araucanum* Philippi, also establishes it as a diploid. Additional cytological work on the *Relbunium* group of *Galium* would likely be highly rewarding.

SCROPHULARIACEAE: The genus *Ourisia* occurs in the mountains of New Zealand, in alpine regions of Tasmania, and throughout the South American Andes (from Venezuela to Tierra del Fuego). It comprises about 35 species (H. Meudt, unpubl. data). All 15 New Zealand species have been investigated cytologically, and all have $2n = 48$ chromosomes (Hair and Arroyo 1984). *Ourisia integrifolia* from Tasmania was reported as $2n = 32$ (Hair and Arroyo 1984). The count presented here of $n = 8$ for *O. coccinea* is the first published report for a species from the Andes and the lowest number published so far for the genus. However, H. Meudt (pers. comm.) has obtained the same number for at least one additional species of the genus from the Andes. This indicates that $x = 8$ may be the basic number for *Ourisia* and that the Andean species are diploids, whereas the Tasmanian species is tetraploid and all New Zealand species are hexaploids.

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Literature Cited

Anderson, C. J., J. H. E. Rova, and L. Andersson. 2001. Molecular phylogeny of the tribe Anthospermeae (Rubiaceae): Systematic and biogeographic implications. Aust. Syst. Bot. 14:231–244.

Anderson, G. J., G. Bernadello, P. López S., D. J. Crawford, and T. F. Stuessy. 2000. Reproductive biology of *Wahlenbergia* (Campanulaceae) endemic to Robinson

Crusoe Island (Chile). Plant Syst. Evol. 223:109–123.
Beuzenberg, E. J., and J. B. Hair. 1983. Contributions to a chromosome atlas of the New Zealand flora. 25. Miscellaneous species. N. Z. J. Bot. 21:13–20.
Bitter, G. 1911. Die Gattung *Acaena*. Vorstudien zu einer Monographie. Bibl. Bot. 74:1–336.
Carr, G. D. 1998. Chromosome evolution and speciation in Hawaiian flowering plants. Pages 5–47 *in* T. F. Stuessy and M. Ono, eds. Evolution and speciation of island species. Cambridge University Press, Cambridge.
Crawford, D. J., T. F. Stuessy, T. G. Lammers, and M. Silva. 1990. Allozyme variation and evolutionary relationships among three species of *Wahlenbergia* (Campanulaceae) in the Juan Fernandez Islands. Bot. Gaz. 151:119–124.
Dawson, M. I. 2000. Index of chromosome numbers of indigenous New Zealand spermatophytes. N. Z. J. Bot. 38:47–150.
Dawson, M. I., and E. J. Beuzenberg. 2000. Contributions to a chromosome atlas of the New Zealand flora. 36. Miscellaneous families. N. Z. J. Bot. 38:1–23.
Dempster, L. T. 1990. The genus *Galium* (Rubiaceae) in South America. IV. Allertonia 5:283–345.
Diers, L. 1961. Der Anteil der Polyploiden in den Vegetationsgürteln der Westkordillere Perus. Z. Bot. 49:437–488.
Edgar, E., and M. B. Forde. 1991. *Agrostis* in New Zealand. N. Z. J. Bot. 29:139–161.
Hair, J. B. 1963. Contributions to a chromosome atlas of the New Zealand flora. 6. N. Z. J. Bot. 1:243–257.
Hair, J. B., and M. T. K. Arroyo. 1984. Contributions to a chromosome atlas of the New Zealand flora. 28. *Ourisia*. N. Z. J. Bot. 22:357–359.
Heads, M. J. 1996. Biogeography, taxonomy and evolution in the Pacific genus *Coprosma* (Rubiaceae). Candollea 51:381–405.
Huynh, K.-L. 1965. Contribution à l'étude caryologique et embryologique des Phanérogames du Pérou. Denkschr. Schweiz. Naturforsch. Ges. 89.
Jakubowsky, G., and T. F. Stuessy. 1999. Hybridization and evolution in *Eryngium* (Apiaceae) of the Juan Fernandez Islands. Page 23 *in* Systematics Association 2nd Biennial Conference, University of Glasgow, 23–27 August 1999. Abstracts. University of Glasgow, Glasgow.
Kiehn, M. 1995. Chromosome survey of the Rubiaceae. Ann. Mo. Bot. Gard. 82:398–408.
———. 1996. Chromosomes of Rubiaceae occurring in Malesia, the Philippines, New Guinea, and the Pacific. Opera Bot. Belg. 7:249–260.
———. 2005. Chromosome numbers of Hawaiian Angiosperms: New records and comments. Pac. Sci. 59:363–377.
Kokubugata, G., S. Matsumoto, and Y. Kadota. 1998. Karyomorphological study of *Nertera yamashitae* (Rubiaceae) from Amami Island. Ann. Tsukuba Bot. Gard. 17:133–137.
Lammers, T. G. 1996. Phylogeny, biogeography and systematics of the *Wahlenbergia fernandeziana* complex (Campanulaceae: Campanuloideae). Syst. Bot. 21:397–415.
Manton, I., and G. Vida. 1968. Cytology of the fern flora of Tristan da Cunha. Proc. R. Soc. Lond. B. Biol. Sci. 170:361–377.
Markey, A. S., J. M. Lord, and D. A. Orlovich. 2004. *Coprosma talbrockiei*: An oddball sheds light on the Coprosminae. Page 6 *in* SYSTANZ General Meeting and Plant Species Radiation Workshop, Skotel, Whakapapa Village, 12–13 February 2004 (http://www.math.canterbury.ac.nz/bio/SYSTANZ/meeting/SYSTANZ_2004_programme.pdf).
Marticorena, C., T. F. Stuessy, and C. M. Baeza. 1998. Catalogue of the vascular flora of the Robinson Crusoe or Juan Fernandez Islands, Chile. Gayana Bot. 55:187–211.
Moore, D. M. 1960. Chromosome numbers of flowering plants from Macquarie Island. Bot. Not. 113:185–191.
Pimenov, M. G., M. Vasil'eva, M. Leonov, and J. V. Daushkevich. 2003. Karyotaxonomical analysis in the Umbelliferae. Science Publ. Inc., Enfield, New Hampshire.
Ricci, M., and L. Eaton. 1994. The rescue of

Wahlenbergia larrainii in Robinson Crusoe Island, Chile. Biol. Conserv. 68:89–93.
Ruiz, E., C. Marticorena, D. Crawford, T. Stuessy, F. González, R. Montoya, M. Silva, and J. Becerra. 2001. Morphological and ITS sequence divergence between taxa of *Cuminia* (Lamiaceae), an endemic genus of the Juan Fernandez Islands, Chile. Brittonia 52:341–350.
Sanders, R. W., T. F. Stuessy, and R. Rodriguez. 1983. Chromosome numbers from the flora of the Juan Fernandez Islands. Am. J. Bot. 70:799–810.
Skottsberg, C. 1922. The phanerogams of the Juan Fernandez Islands. Nat. Hist. Juan Fernandez Easter Isl. 2:95–240.
———. 1956. Derivation of the flora and fauna of Juan Fernandez and Easter Island. Nat. Hist. Juan Fernandez Easter Isl. 1:193–437.
Spooner, D. M., T. F. Stuessy, D. J. Crawford, and M. Silva O. 1987. Chromosome numbers from the flora of the Juan Fernandez Islands. II. Rhodora 89:351–356.
Stuessy, T. F., and D. J. Crawford. 1998. Chromosomal stasis during speciation in angiosperms of oceanic islands. Pages 307–324 *in* T. F. Stuessy and M. Ono, eds. Evolution and speciation of island species. Cambridge University Press, Cambridge.
Stuessy, T. F., C. Marticorena, R. Rodríguez, D. J. Crawford, and M. Silva O. 1992. Endemism in the vascular flora of the Juan Fernandez Islands. Aliso 13:297–307.
Sun, B. Y., T. F. Stuessy, and D. J. Crawford. 1990. Chromosome counts from the flora of the Juan Fernández Islands, Chile. III. Pac. Sci. 44:258–264.