

# *Austrocedrus chilensis* (D. Don) Pic.-Ser. et Bizz. (Cupressaceae) from Chile and Argentina: monoecious or dioecious?

*Austrocedrus chilensis* (D. Don) Pic.- Ser. et Bizz. (Cupressaceae)  
de Chile y Argentina: ¿monoico o dioico?

CARMEN CASTOR<sup>1</sup>, JAIME G. CUEVAS<sup>1</sup>, MARY T. KALIN ARROYO<sup>1</sup>,  
ZARA RAFII<sup>2</sup>, RICHARD DODD<sup>3</sup> y ALEJANDRO PEÑALOZA<sup>1</sup>

<sup>1</sup>Departamento de Biología, Facultad de Ciencias, Universidad de Chile, Casilla 653-Santiago;  
<sup>2</sup>Université St. Jérôme Aix Marseille, France; <sup>3</sup>University of California, Berkeley, California 94720, USA

## ABSTRACT

Sex expression was investigated in 19 populations of *Austrocedrus chilensis*, a species previously described as monoecious, in Chile and Argentina and in Chilean herbarium material. The species was found to be dioecious throughout its range. Strong female biased sex ratios were found in three populations, but ratios did not deviate from 1:1 in other populations. Sex expression was constant over a three year period, as assessed in one site. Mean DBH was similar for males and females in three populations.

**Key words:** Dioecy, monoecy, sex ratio, cone morphology.

## RESUMEN

Se investigó la expresión del sexo en 19 poblaciones de *Austrocedrus chilensis*, previamente descrito como monoico, en Chile y Argentina y en material de herbarios chilenos. Se encontró que la especie es dioica a través de todo el rango estudiado. En tres poblaciones existen proporciones de sexo sesgadas hacia el lado femenino, mientras que en el resto no se desvían de 1:1. La expresión del sexo fue constante sobre un período de tres años evaluado en un sitio. El DAP promedio fue similar para machos y hembras en tres poblaciones.

**Palabras clave:** Dioecia, monoecia, proporción de sexos, morfología de los conos.

## INTRODUCTION

Reproductive modes in plants have been classified as hermaphroditic, monoecious and dioecious, but there are also some intermediate situations, and cases of sex change have been reported (MacArthur & Freeman 1982, Jordano 1991). Dioecy in angiosperms, and its association with pollination and dispersal syndromes and growth forms has been investigated over the last ten years (Freeman et al. 1980, Fox 1985). The spatial segregation of sexes has been observed in dioecious plants and generally has been correlated with environmental gradients like humidity (Bierzychudek & Eckhart 1988, Brunt et al. 1988). The documented variation

of sex ratios in favor of the male sex has been explained by a lower reproductive cost (Meagher 1981, Cavigelli et al. 1986), although Meagher (1981) and MacArthur & Freeman (1982), also found genetic mechanisms to explain this bias.

There have been only a few publications about reproductive modes in gymnosperms (Givnish 1980, Cavigelli et al. 1986, Brunt et al. 1988, Jordano 1991, Vasiliauskas & Aarssen 1992, Brion et al. 1993). In Cupressaceae most genera are monoecious but some like *Juniperus* and *Diselma* are dioecious (Givnish 1980, see also Jordano 1991 for an exception). Up to now, *Austrocedrus* –a monospecific genus– has been cited as being monoecious (Maldonado 1925, Givnish

1980, Hoffmann 1982, Rodríguez et al. 1983). However, over the last century, Poeppig & Endlicher (1835-1845), Endlicher (1847) and Gay (1851-1852) seem to have suspected its being dioecious. Gay's description of its "flowers being monoecious and perhaps dioecious" was ignored, whenever reproduction was mentioned, in later descriptions. Only recently has the possibility of its dioecy been considered (Brion et al. 1993).

The purpose of this paper is to determine sex expression in *Austrocedrus chilensis* based on morphological observations. The questions addressed were: 1) what is the breeding system of *A. chilensis*?, 2) if it is dioecious, what are the sex ratios of the different populations?, 3) are there significant differences in size between sexes?, 4) does the northern-most population studied by us follow the phenological pattern generally described for the species?

#### MATERIALS AND METHODS

##### *Species description*

*Austrocedrus chilensis* is a tree of xeric-mesic habitats, growing mostly on north-facing slopes (Donoso 1993) from latitudes 32° 39' S to 38° 00' S in Chile and crossing over to the Argentinian side of the Andes, where it is more abundant. In Argentina, its distribution ranges between 36° 30' S and 43° 35' S. It reappears in Chile at 44° S, and is also found in small, localized populations along the Chilean Coastal Range (Hueck 1978). Its altitudinal range is from 900 to 2200 m asl (H. Jimenénez, personal communication 1994) at its northern limit, and between 400 and 800 m in the south (Hueck 1978, Donoso 1993).

The height of *Austrocedrus chilensis* is variable, reaching up to 30 m in the Nahuel-Huapi National Park (Argentina) and becoming smaller on more xeric sites towards the east (Veblen & Lorenz 1987), in Patagonia (Veblen & Markgraf 1988) and towards its northern limit, where it only reaches around 3 m in height (Montero 1926).

On mesic sites, it forms mixed forests with *Nothofagus* spp., and as sites become more

xeric it forms pure stands, and then progressively isolated clumps (Dezzotti & Sancholuz 1991). Pollination and seed dispersal are wind mediated. Seed production is high, although cones are susceptible to insect predation, and seeds germinate easily but seedlings are prone to damage by livestock and fire (Hueck 1978).

The species' wood is appreciated for its elastic properties, and its colour (Gay 1851-1852, Rodríguez et al. 1983), but is mostly used for fence-posts, due to its resistance (Donoso 1993). In terms of its conservation, in Chile *A. chilensis* has been considered as a vulnerable species (Benoit 1989).

##### *Methods*

Sex expression was studied in 19 populations along the distributional range of *Austrocedrus chilensis* in the Chilean and Argentinian Andes Range (Table 1). The major study site was at Fundo El Romeral because the low height of the trees allowed an easy access to their reproductive branches. This enabled us to verify sex expression on whole trees. This population was studied from August 1993 to

TABLE 1

Location of study sites for *Austrocedrus chilensis*. Altitude: meters above sea level.  
CH: Chile; A: Argentina

Ubicación de los sitios de estudio para *A. chilensis*.  
Altitud: metros sobre el nivel del mar. CH: Chile;  
A: Argentina

Site	Lat. S	Long. W	Alt	Country
El Romeral	33° 48'	70° 11'	1.400	CH
San Gabriel	33° 47'	70° 15'	1.500	CH
Bellavista 1	34° 46'	70° 45'	900	CH
Bellavista 2	34° 50'	70° 45'	1.480	CH
Bellavista 3	34° 48'	70° 45'	1.000	CH
Los Maquis 1	35° 00'	70° 50'	1.100	CH
Los Maquis 2	35° 08'	70° 35'	1.100	CH
Parque Inglés	35° 13'	71° 11'	2.000	CH
Aluminé	39° 16'	70° 55'	920	A
San Martín	40° 11'	71° 20'	700	A
La Lipela	40° 49'	71° 04'	750	A
Nahuel-Huapi 1	40° 49'	71° 40'	950	A
Nahuel-Huapi 2	40° 51'	71° 31'	910	A
Nahuel-Huapi 3	40° 56'	71° 28'	860	A
Nahuel-Huapi 4	41° 04'	71° 22'	830	A
Llao Llao	41° 03'	71° 25'	860	A
El Foyel	41° 36'	71° 25'	760	A
Río Corcovado	43° 36'	71° 26'	480	A
Cerro Cóndor	43° 47'	71° 21'	860	A

January 1994. Ten branches of 40 randomly selected individuals were marked, and every three weeks, the presence and type of sexual structures, or any sign of previous cones, like characteristic scars, was registered. The individuals consistently found to be without cones were defined as vegetative. The year of ripening of open female cones was determined from their aspect, being red-brown and well conserved when they are only one year old, and grey-brown, with a scabby surface when they are two years old. Aborted female cones from previous years could be observed with relative ease. During the cone production period, female and male cones in different stages of development were collected and conserved in 70% ethanol for morphological study in the laboratory. Eighteen other populations were monitored to verify our findings along its distributional range.

Our findings were documented with additional information obtained through the revision of herbarium samples of the species and its synonyms. The collections reviewed belong to the Herbario de la Universidad de Concepción, the Museo Nacional de Historia Natural de Santiago and the Herbario Juan Ignacio Molina at the Universidad de Talca. These records were used in the construction of the distribution map (Fig. 1).

We calculated the sex ratio (males/females) for the 19 populations, and tested for a departure from a 1:1 ratio using a G-test for frequency analysis.

We measured the perimeters of tree trunks at breast height, and converted the measure to diameters (DBHs) in three populations: Bellavista 1, Bellavista 2, and Los Maquis 1. We analysed the differences between the sexes within each population using a Kruskal-Wallis test, and an a-posteriori Fisher's Least Significant Difference test.

## RESULTS

### *Cone morphology*

**Male cones:** in the El Romeral population male cones present a mean length  $\pm$  standard error of  $3.6 \pm 0.17$  mm, and have 12-16 fertile bracts (N = 10, in four individuals) as

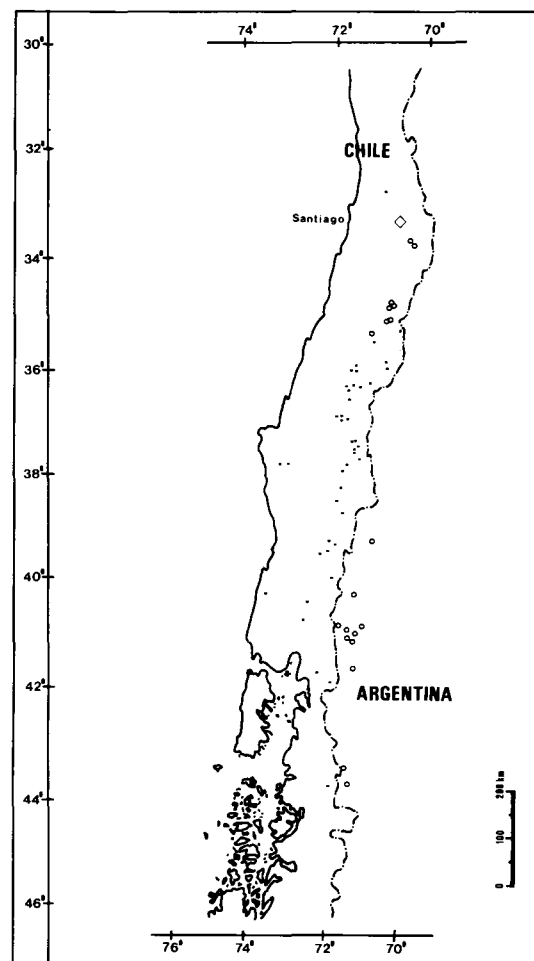


Fig. 1: Distributional range of *Austrocedrus chilensis* based on herbarium specimens at the Universidad de Concepción, Museo Nacional de Historia Natural and the Herbario Juan Ignacio Molina at the Universidad de Talca, Chile (•). Study sites considered in this paper (◦).

Rango de distribución de *Austrocedrus chilensis* a partir de información obtenida de los herbarios de la Universidad de Concepción, Museo Nacional de Historia Natural y del Herbario Juan Ignacio Molina de la Universidad de Talca, Chile (•). Sitios de estudio considerados en este artículo (◦).

measured when the cones were close to opening. The number of pollen sacs per bract is variable, but the modal value was four.

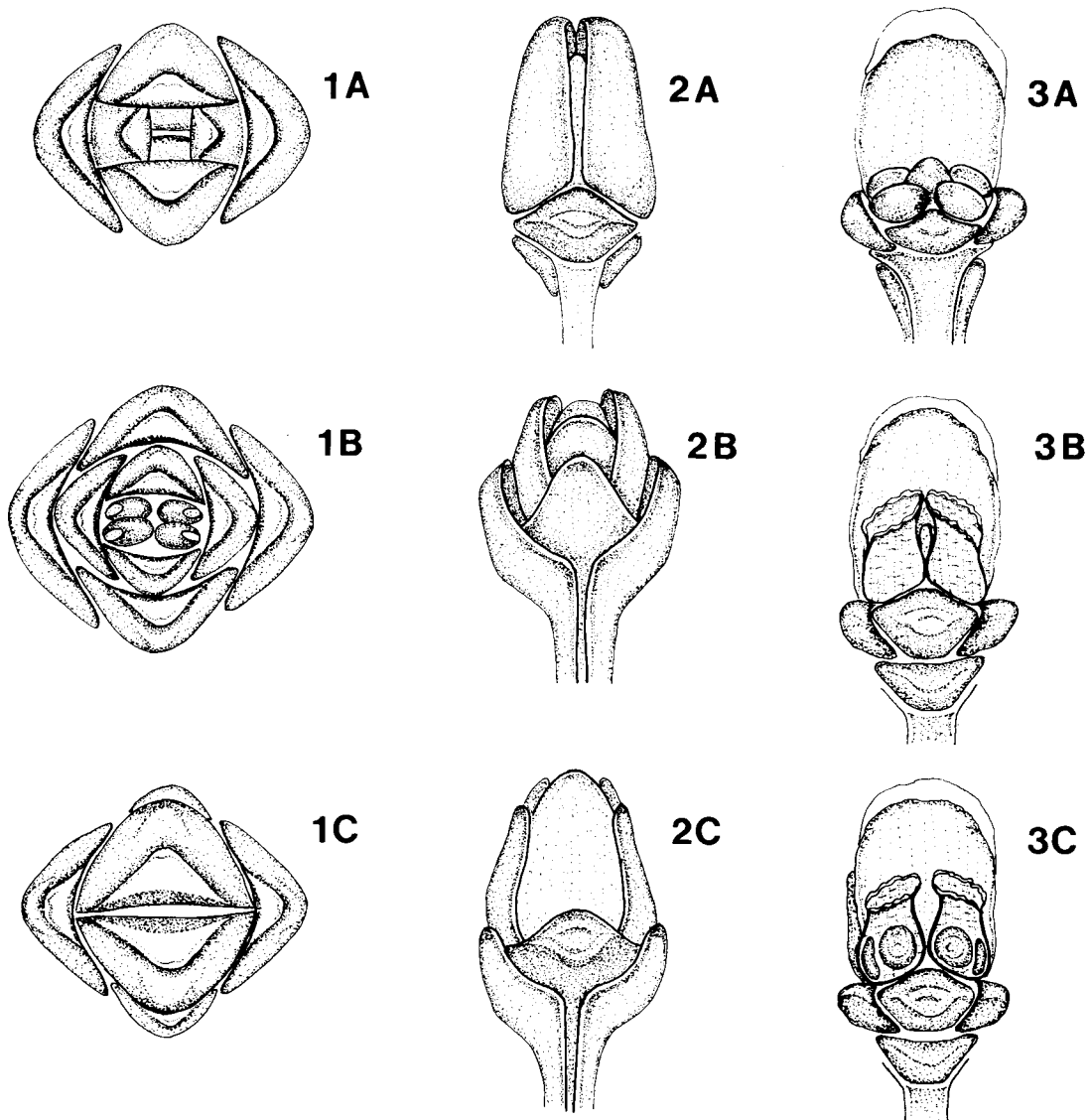
**Female cones:** in the receptive stage they are so small (less than 1 mm) and immersed in the vegetative bracts, that they can easily be overlooked. They are characterized by a small rectangular opening in the apex of the branchlets, with four small, white, veil-like integuments just visible inside. On

opening the cone, one finds four paired ovules attached to an apical tissue, forming a point between them, which withers during development (Fig. 2). The four fertile bracts form a protective covering, and seal the space where seeds develop through additional tissular growth at the margins, and halfway up the inner surface of the internal bracts. When the female cones mature in January to February (austral summer) the bracts stay green until they split open to

release seeds, then they become spongy and rapidly dry out, turning brown.

#### *Sex expression*

For all sites studied, we found that no tree presented both male and female structures on the same individual. All populations were therefore dioecious. This was corroborated through revision of herbarium material (Table 2), where no branch contained dif-



*Fig. 2:* Female cones of *Austrocedrus chilensis* at the pre-receptive (A), receptive (B) and (C) post-receptive stages. Samples taken from El Romeral in September 1993. 1: top view; 2: lateral view; 3: sagittal section.

Esquema de los estróbilos femeninos de *Austrocedrus chilensis* en estado pre-receptivo (A), receptivo (B) y post-receptivo (C) en El Romeral (Septiembre 1993). 1: vista desde arriba; 2: vista lateral; 3: sección sagital.

TABLE 2

Revision of herbarium material.  
 N: number of specimens; F: specimens with only female branches; M: specimens with only male branches; V: specimens with vegetative branches; F-M: specimens where male branches and female branches were together as one specimen but without physical connection between them.

Revisión de material de herbario. N: número de especímenes; F: especímenes sólo con ramas femeninas; M: especímenes sólo con ramas masculinas; V: especímenes con ramas vegetativas; F-M: especímenes donde ramas masculinas y femeninas se encontraban juntas pero sin conexión física.

Herbarium	N	F	M	V	F-M
Universidad Concepción	77	39	9	22	7
Museo Nac. Hist. Natural	39	19	6	13	1
J.I. Molina, Univ. Talca	7	3	2	2	0

ferent sexes together. All individuals from El Romeral showed a 100% constancy of sex expression from one year to another, as deduced from the reproductive structures present on the tree. For females, data can be deduced for three years, but for males the data can not be extended more than one year backwards due to the lack of visible structures.

#### *Phenology of the El Romeral population*

At El Romeral we observed that the ripening of male cones had already begun by August 1993, reaching full maturity in September releasing great amounts of pollen. After pollen dispersal, the aments soon abscised. However, under mild climatic conditions, and in protected microsites, male cones may remain on the tree from one year to the next. The scar of abscised male cones is typical, and easily recognizable for at least one year.

Female cones appeared sporadically over a much longer period, from August to December. Maximum aperture of female cones was delayed two weeks with respect to males, and lasted from mid-September to November. Different female individuals produced peak numbers of receptive cones at different times. The pollination of female strobili occurred mainly in September, and cones were fully ripe by the end of January 1994, liberating their seeds in an almost synchronous manner.

#### *Population sex ratios*

We found that for 16 out of 19 populations (Table 3), the sex ratios did not significantly vary from the expected 1:1 ratio. However, in El Romeral the sex ratio was 0.500, in Los Maquis 2 was 0.613 and in Aluminé was 0.639, all three being female biased.

#### *Sex versus diameter*

The Kruskal-Wallis test showed that, within each population, the groups (female, male and vegetative) are significantly different among themselves (Table 4, BV1:  $H = 36.166$ , BV2:  $H = 52.253$ , LM1:  $H = 38.101$ , all  $P < 0.001$ ). A Fisher's Least Significant Difference test showed that the difference is due to the vegetative class given that comparisons between males and females in each population did not show significant differences, but all comparisons with vegetative individuals were statistically different (Table 4).

TABLE 3

Number of individuals of each sex and results of G-Test to check departure from a 1:1 ratio. N: total individuals studied per site; F: female individuals; M: male individuals; SR: sex ratio (M/F); P: level of significance, \*:  $P < 0.05$

Número de individuos en cada sexo y prueba de G para probar desviación de la proporción 1:1. N: total de individuos estudiados por sitio; F: individuos femeninos; M: individuos masculinos; SR: proporción de los sexos (M/F); P: nivel de significancia, \*:  $P < 0.05$

Site	N	F	M	SR	P
El Romeral	69	46	23	0.500	0.005*
San Gabriel	48	22	26	1.182	0.566
Bellavista 1	111	53	58	1.115	0.632
Bellavista 2	136	61	75	1.230	0.230
Bellavista 3	100	52	48	0.923	0.689
Los Maquis 1	50	27	23	0.852	0.572
Los Maquis 2	100	62	38	0.613	0.016*
Parque Inglés	100	42	58	1.381	0.109
Aluminé	100	61	39	0.639	0.027*
San Martín	100	52	48	0.923	0.689
La Lipela	100	54	46	0.852	0.424
Nahuel-Huapi 1	100	42	58	1.381	0.109
Nahuel-Huapi 2	100	44	56	1.273	0.230
Nahuel-Huapi 3	100	41	59	1.439	0.071
Nahuel-Huapi 4	100	52	48	0.923	0.689
Llao Llao	100	47	53	1.128	0.548
El Foyel	100	56	44	0.786	0.230
Río Corcovado	100	45	55	1.222	0.317
Cerro Cóndor	100	41	59	1.439	0.071

TABLE 4

Diameter data for Bellavista (BV1, BV2) and Los Maquis (LM1) populations. V: vegetative; F: female; M: male; N: number of individuals; DBH: diameter at breast height; SE: standard error. Different superscripts indicate differences at the level of  $P < 0.001$  (only comparisons within each population). Test: Fisher's Least Significant Difference

Información de diámetros para las poblaciones Bellavista (BV1, BV2) y Los Maquis (LM1). V: vegetativo; F: femenino; M: masculino; N: número de individuos; DBH: diámetro al nivel del pecho; SE: error estándar. Distintos superscritos indican diferencias al nivel  $P < 0.001$  (sólo comparaciones dentro de cada población). Prueba: Diferencia Significativa Mínima de Fisher

Site	Sex	N	Mean DBH $\pm$ SE (cm)
BV1	V	22	8.59 $\pm$ 0.82 <sup>a</sup>
	F	41	23.11 $\pm$ 1.81 <sup>b</sup>
	M	47	22.15 $\pm$ 1.48 <sup>b</sup>
BV2	V	48	6.72 $\pm$ 0.73 <sup>a</sup>
	F	36	23.37 $\pm$ 3.01 <sup>b</sup>
	M	43	20.98 $\pm$ 1.78 <sup>b</sup>
LM1	V	23	7.57 $\pm$ 0.82 <sup>a</sup>
	F	27	34.26 $\pm$ 2.59 <sup>b</sup>
	M	17	32.73 $\pm$ 2.30 <sup>b</sup>

## DISCUSSION

Without a careful observation *Austrocedrus chilensis* can sometimes be difficult to sex, particularly when cones are in the early stages of development. Immature male cones can be mistaken with growing vegetative apices, especially because these are compact and of a slightly rounded form. Female cones in the receptive state can easily be missed, due to their small size and hidden position among the vegetative bracts. In field observations, the pedicels where male cones have become detached can be confounded with young, aborted female cones. In the populations studied we have also found insect-formed galls modifying the form of apices, which could then easily be confounded with sexual structures. Another factor that can be misleading is the intertwining of branches from neighboring trees to such an extent that if they happen to be of different sexes one can think that one tree is expressing both sexes on separate branches. Tree height can also limit a more detailed observation. Finally, there seems to have been little attention to sexuality in most descriptions of this species. The basionym by D. Don (in

Lambert 1828) under the name of *Thuja chilensis* is rather short, and Pichi-Sermolli & Bizzarri (1978) only renamed the species giving it its present name, conserving D. Don's description. Most authors have simply copied descriptions from one another, as can be seen from a review of Poeppig & Endlicher (1835), Hooker (1843), Endlicher (1847), Gay (1851) and Maldonado (1925).

Through the revision of herbarium material we have established that it is easy to confound sexual structures at first glance on dried specimens. Particularly aborted female cones, when four to six vegetative bracts die off below the fertile bracts, can be confused with male cones. Additionally, on some herbarium samples, several branches are found together on the same specimen, but without specifying if they come from the same individual or not (Table 2). Older contributions seem especially prone to this omission, as all specimens with these characteristics, studied by us, were dated before 1958.

These considerations and the comments made by Brion et al. (1993), with respect to the misuse of the terms "monoecious" or "dioecious", when these should be used for populations and not for structures, contribute to understanding the confusion about the breeding system of *A. chilensis*. Our results are consistent with their observation that this species is dioecious and, apparently, does not present sex variation in time. This does not exclude the possibility of a very low frequency of monoeciousness, which has not yet been detected because of its rarity. MacArthur & Freeman (1982) provide a list of subdioecious taxa, where a low frequency of monoecy occurs in normally dioecious plants.

Our data on phenology at the El Romeral population confirms that the ripening of female strobili occurs from October onwards, and that seed shedding occurs from January to March (Rodríguez et al. 1983). Our observations show a slight tendency for dispersal earlier in the season due to the more northern position of this population. In male cones, peak pollen dispersal was two weeks earlier than the apparent peak for female cone receptivity. According to Stephenson & Bertin (1983), the span of male flowering

should be longer than that of females, and more male flowers or more male individuals in flower should be observed. However, the data presented here seem to contradict this tendency.

Data for El Romeral, Los Maquis 2 and Aluminé are not sufficient to hypothesize on the possible reasons for a female biased sex ratio. However, the fact that in most populations the sex ratio did not deviate from 1:1, and that male and female individuals had the same size on all three sites, apparently suggests that no differential allocation of resources takes place between sexes (Lloyd & Webb 1977).

## ACKNOWLEDGMENTS

Research was financed by Fondecyt Grant 92-1135 and Project ECOS-CONICYT B 9305. We thank Roberto Rodríguez and Clodomiro Marticorena of the Universidad de Concepción, José San Martín of the Universidad de Talca, Mélica Muñoz of the Museo Nacional de Historia Natural, Santiago and Peter Raven, Missouri Botanical Garden, for literature. Drawings were prepared by Cecilia Niemeyer. We also thank the owners of Fundo El Romeral for permission to work on their property. We appreciate the comments made by two anonymous reviewers. The English version was kindly reviewed by J.F. Hernández.

## LITERATURE CITED

- BENOIT IL, ed (1989) Red list of Chilean terrestrial flora (Part One). Corporación Nacional Forestal (CONAF), Santiago de Chile. 151 pp.
- BIERZYCHUDEK P & V ECKHART (1988) Spatial segregation of the sexes of dioecious plants. *American Naturalist* 132: 34-43.
- BRION C, D GRIGERA & P ROSSO (1993) The reproduction of *Austrocedrus chilensis* (D. Don) Florin et Bouleje. C.R. Academie de Sciences Paris. *Sciences de la vie/Life Sciences* 316: 721-724.
- BRUNT JW, MR CONLEY & GL CUNNINGHAM (1988) Sex in *Ephedra trifurcata* (EPHEDRACEAE) with relation to Chihuahuan Desert habitats. *American Midland Naturalist* 119: 137-142.
- CAVIGELLI M, M POULOS, EP LACEY & G MELLON (1986) Sexual dimorphism in a temperate dioecious tree. *Ilex montana* (AQUIFOLIACEAE). *American Midland Naturalist* 115: 397-406.
- DEZZOTTI A & L SANCHOLUZ (1991) Los bosques de *Austrocedrus chilensis* en Argentina: ubicación, estructura y crecimiento. *Bosque* 12: 43-52.
- DONOSO C (1993) Bosques templados de Chile y Argentina. Variación, Estructura y Dinámica. Editorial Universitaria, Santiago, Chile. 488 pp.
- ENDLICHER SL (1847) Synopsis coniferarum. *Sankt-Gallen* IV: 368.
- FOX JF (1985) Incidence of dioecy in relation to growth form, pollination and dispersal. *Oecologia* 67: 244-249.
- FREEMAN DC, KT HARPER & W KENT OSTLER (1980) Ecology of plant dioecy in the intermountain region of western North America and California. *Oecologia* 44: 410-417.
- GAY C (1851-1852) Historia física y política de Chile. Botánica V. Paris. 406 pp.
- GIVNISH TJ (1980) Ecological constraints in the evolution of breeding systems in seed plants: dioecy and dispersal in gymnosperms. *Evolution* 34: 959-972.
- HOFFMANN AJ (1982) Flora silvestre de Chile, Zona Austral. Ediciones Fundación Claudio Gay, Santiago, Chile. 258 pp.
- HOOKER JW (1843) Figure and description of a new species of *Thuja* from Chile. *London Journal Botany* 2: 107.
- HUECK K (1978) Los bosques de Sudamérica. Sociedad Alemana de Cooperación Técnica. 476 pp.
- JORDANO P (1991) Gender variation and expression of monoecy in *Juniperus phoenicera* (L.) (Cupressaceae). *Botanical Gazette* 152: 476-485.
- LAMBERT AB (1828) A description of the genus *Pinus*, illustrated with figures, directions relative to the cultivation, and remarks on the uses of the several species, also description of many other trees of the family of Coniferae. Second edition, Vol 2. London.
- LLOYD DG & CJ WEBB (1977) Secondary sex characters in plants. *Botanical Review* 43: 177-216.
- MACARTHUR AD & DC FREEMAN (1982) Sex expression in *Atriplex canescens*: genetics and environment. *Botanical Gazette* 143: 476-482.
- MALDONADO E (1925) Contribución al estudio de la industria maderera y bosques chilenos. *Revista Chilena de Historia Natural* 29: 70-131.
- MEAGHER TR (1981) Population biology of *Chamaelirium luteum*, a dioecious lily. II. Mechanisms governing sex ratios. *Evolution* 35: 557-567.
- MONTERO G (1926) Contribución al área geográfica del *Libocedrus chilensis*, Endl. *Revista Chilena de Historia Natural* 30: 298.
- PICHI-SERMOLLI R & MP BIZZARRI (1978) The botanical collections (Pteridophyta and Spermatophyta) of the AMF Mares - G.R.S.T.S. expedition to Patagonia, Tierra del Fuego and Antartica. *Webbia* 32: 50.
- POEPPIG E & S ENDLICHER (1835-1845) Nova genera ac species plantarum quas in regno chilensi peruviano et in terra amazonica annis mdcccxxvii ad mdcccxxxii legit Eduardus Poeppig et cum Stephano Endlicher descripsit iconibusque illustravit. *Leipzig* 3 Vol.: 17.
- RODRIGUEZ RR, O MATTHEI & M QUEZADA (1983) Flora arborea de Chile. Ediciones de la Universidad de Concepción, Chile. 408 pp.
- STEPHENSON AG & RI BERTIN (1983) Male competition, female choice and sexual selection in plants. In: Real L (ed) *Pollination Biology*: 109-149. Academic Press.
- VASILIAUSKAS SA & LW AARSSSEN (1992) Sex ratio and neighbor effects in monospecific stands of *Juniperus virginiana*. *Ecology* 73: 622-632.
- VEBLEN TT & DC LORENZ (1987) Post-fire stand development of *Austrocedrus-Nothofagus* forests in northern Patagonia. *Vegetatio* 71: 113-126.
- VEBLEN TT & V MARKGRAF (1988) Steppe expansion in Patagonia? *Quaternary Research* 30: 331-338.