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# Branch whorls of juvenile *Araucaria araucana* (Molina) Koch: are they formed annually?

## Los verticilos de juveniles de *Araucaria araucana* (Molina) Koch: ¿son formados anualmente?

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**ABSTRACT**

The growth of *Araucaria araucana*, like that of many other conifers, is characterised by the production of a monopodial stem with branch whorls. However, the periodicity of whorl formation in this species has not been subjected to systematic study. We used growth ring counts to determine the frequency of whorl formation in sun- and shade-grown juvenile *A. araucana* in a montane forest in the Chilean coast range. Whorls were not annual in any of the 35 individuals studied, growth rings outnumbering whorls by a factor of 1.8 to 3.9. The mean interval between successive whorls was significantly shorter in sun-grown (2.1 yrs whorl$^{-1}$) than in shade-grown trees (2.6 yrs whorl$^{-1}$), suggesting a relationship with plant carbon balance. Mean distance between whorls was also sensitive to light environment. The overall result of this effect of light environment on both whorl spacing and production rate was that mean height growth rates were > 50% higher in sun-grown trees (169 mm yr$^{-1}$) than in shade-grown individuals (111 mm yr$^{-1}$). Despite the non-annual nature of whorls in the study population, whorl counts may have some potential as a non-invasive method of age estimation in juvenile *A. araucana*. In both shade- and sun-grown subpopulations, whorl number was a better predictor of stem age than were stem diameter or height.

**Key words**: Araucariaceae, conifers, dendroecology, tree growth, tree rings.

**RESUMEN**

El crecimiento de *A. araucana*, al igual que el de muchas otras coníferas, se caracteriza por la producción de un fuste monopódico y ramas en verticilos. Sin embargo, en esta especie, no se ha investigado sistemáticamente la periodicidad de la formación de los verticilos. Esta nota documenta el conteo de anillos de crecimiento para determinar la frecuencia de formación de verticilos, en árboles juveniles de *A. araucana*. Se muestrearon 17 árboles en ambientes soleados y otros 18 bajo sombra, en un bosque montano de la Cordillera de la Costa, Chile. Ninguno de los 35 individuos estudiados mostró evidencias de formación anual de verticilos, puesto que el número de anillos de crecimiento excedió al número de verticilos en 1,8 a 3,9 veces. El intervalo promedio entre la producción de verticilos sucesivos fue significativamente menor en individuos expuestos a pleno sol (2,1 años verticilo$^{-1}$) que en aquellos que crecieron bajo sombra (2,6 años verticilo$^{-1}$), sugiriendo cierta relación con el balance de carbono de la planta. La distancia promedio entre verticilos también se mostró sensible al ambiente lumínico. El resultado de este efecto del ambiente lumínico sobre tanto la tasa de producción de verticilos, como la distancia entre éstos, fue que la tasa promedio de crecimiento en altura de los individuos soleados (169 mm año$^{-1}$) excedió en > 50% a la de los individuos sombreados (111 mm año$^{-1}$). A pesar de la naturaleza no anual de los verticilos en la población estudiada, los recuentos de verticilos pueden tener potencial como un método no invasivo de estimación de edad para juveniles de *A. araucana*. Tanto dentro de las subpoblaciones soleadas como sombreadas, el número de verticilos fue mejor indicador de la edad que el diámetro o la altura del fuste.

**Palabras clave**: Araucariaceae, coníferas, dendroecología, crecimiento de árboles, anillos de crecimiento.

## INTRODUCTION

Some temperate conifers (e.g., *Pinus* spp., *Podocarpus* spp.) are known to produce annual branch whorls under normal growth conditions (e.g., O'Reilly & Owens 1989, Avery & Burkhart 1994). The annual nature of these whorls can be verified by their coincidence with cataphyll (resting bud) scars, or by checking correspondence between the number of whorls and the number of growth rings present in a given stem or branch (Lusk, in review). The accessibility of informa-

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tion afforded by this growth pattern is advantageous for ecological studies, facilitating the use of rapid and non-invasive methods for ageing and reconstructing the growth history of large seedlings and juvenile trees, and for studies of leaf demography (Ewers & Schmid 1981).

The South American conifer *Araucaria araucana* (Molina) Koch (Araucariaceae) also produces a monopodial stem with branch whorls (Fig. 1), technically termed "pseudo-whorls" by architectural specialists (Grosfeld et al. 1999). However, in the case of *A. araucana* there is no unequivocal external evidence as to the periodicity of whorl formation, as this species, in common with others of the genus, does not produce cataphylls between successive growth periods (Griffith 1952). Observations by Grosfeld et al. (1999) imply non-annual whorl formation in heavily-shade juvenile *A. araucana*: although these authors did not systematically examine the question of whorl formation rates, they reported that the apical meristems of shaded juveniles may undergo resting phases of several years between two successive periods of extension growth. Clarification of the periodicity of whorl production in this species would require either direct monitoring, or growth ring counts in stems or branches. In this brief communication, we report a study that uses the latter approach to study whorl formation rates and associated growth traits in shaded and open-grown juvenile *A. araucana*.

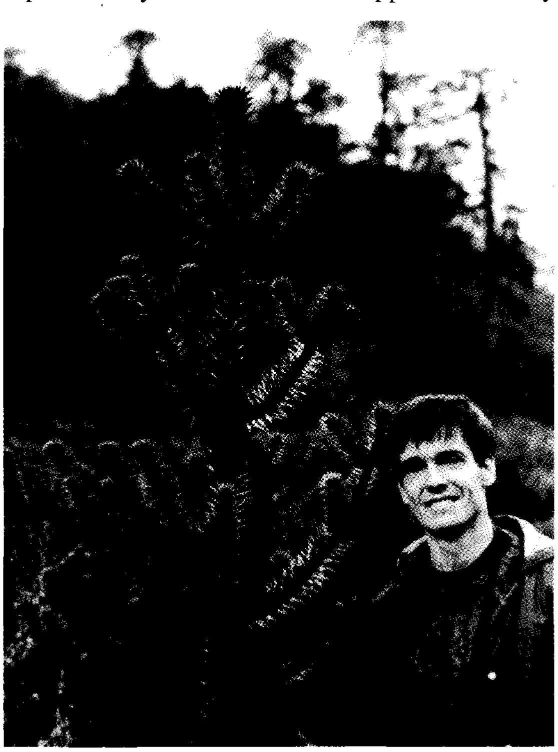

*Fig. 1.* Juvenile *Araucaria araucana*, Chilean coast range.

Arbol juvenil de *Araucaria araucana*, Cordillera de la Costa, Chile.

## MATERIALS AND METHODS

Sampling was carried out in secondary forests on the upper seaward slopes of the Cordillera de Nahuelbuta, near the locality of Don Vicente (37°41' S, 73°07'W), at an altitude of about 1,000 m a.s.l. Although *Araucaria araucana* is capable of suckering (Schilling & Donoso 1976), we sampled only individuals that appeared to be of seedling origin. Given the possibility that whorl formation rates could be influenced by light environment, we collected two data sets: one from juvenile trees growing under moderate shade beneath a stand of *Nothofagus dombeyi* (Mirb) Blume and *N. obliqua* (Mirb.) Oerst, and another from well-lit individuals trees growing in the open or on the forest margin. Data were obtained from a total of 35 randomly-selected juvenile *Araucaria araucana* (1.5-6.7 m tall), 17 of these open-grown, and 18 growing under shade. A similar range of sizes was present in both open-grown and shaded subpopulations. In order to check the correspondence between whorls and growth rings, an increment core was extracted from near the base of the stem, at a level where branch whorls had not yet been abscised (generally at 250-500 mm height). The number of whorls present above this sampling point was counted, and stem length from sampling point to apex was also measured, in order to estimate the average distance between branch whorls.

Increment cores were dried, mounted and sanded with progressively finer sandpaper in order to produce a suitable surface for ring counts. Crossdating of ring sequences *of A. araucana* in dendrochronological studies (e.g. La Marche et al. 1979, Holmes 1982, Villalba & Boninsegna 1992) provides abundant evidence that growth ring formation is normally annual in this species. Skeleton plots (Stokes & Smiley 1968) of our ring sequences provided further support for annual ring formation: 1985 and 1993 were identified as marker years, with narrow rings being produced by 83% and 75% of the trees in these years respectively.

All statistical procedures were carried out using JMP Statistical Software (SAS Institute).

## RESULTS

### *Growth patterns in sun and shade*

Stem ages at coring height ranged from 13 to 38 years. In none of the 35 trees did the number of growth rings correspond to the number of branch whorls, rings outnumbering whorls by a factor of 1.8 to 3.9 (Fig. 2). The number of rings per whorl was significantly higher on average in shade-grown trees (2.61) than in open-grown trees (2.10) (Table 1; T-test, $P = 0.0011$).

Height growth rates, and to a lesser extent, spacing between whorls, were also significantly influenced by light environment (Table 1). Average distance between whorls was ca. 25% greater in open-grown trees (351 mm) than in shade-grown individuals (282 mm) (Table 1; T-test, $P = 0.0105$). The effect of light environment on growth rates was much stronger: mean height growth rates were > 50% greater under open conditions (169 mm $yr^{-1}$) than under shade (111 mm $yr^{-1}$) (Table 1; T-test, $P < 0.0001$).

*Correlations of growth parameters with stem age*

There was a strong positive overall correlation between the number of whorls and the number of growth rings present in a stem ($R^2 = 0.43$, $P < 0.0001$) (Fig. 2). This relationship was stronger for open-grown trees ($R^2 = 0.64$, $P < 0.001$) than for shade-grown trees ($R^2 = 0.45$, $P = 0.0022$).

Stem diameter at sampling height, and stem height, were both also correlated with stem age at sampling height (Fig. 3, 4). However, both of these relationships were weaker than that observed between whorl number and stem age (Fig.

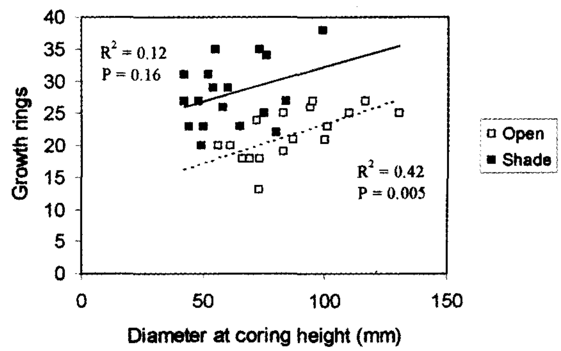


*Fig. 3.* Relationship between stem diameter at coring height and number of growth rings in juvenile *Araucaria araucana*.

Relación entre diámetro del fuste a la altura de taladraje, y el número de anillos de crecimiento en árboles juveniles de *Araucaria araucana*.

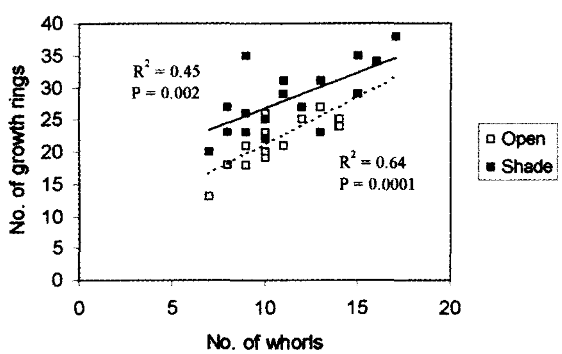


*Fig. 2.* Relationship between number of branch whorls and number of growth rings in stems of juvenile *Araucaria araucana*.

Relación entre número de verticilos y número de anillos de crecimiento en árboles juveniles de *Araucaria araucana*.

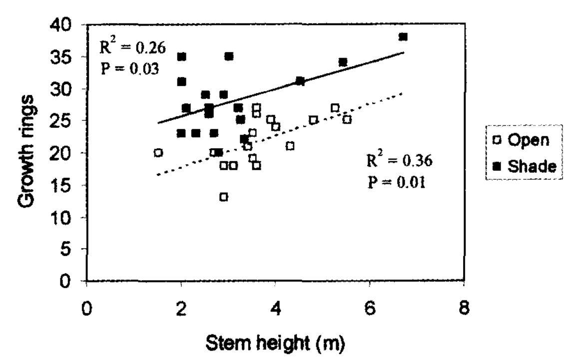


*Fig. 4.* Relationship between stem height (above coring height) and number of growth rings in juvenile *Araucaria araucana*.

Relación entre altura del fuste y el número de anillos de crecimiento en árboles juveniles de *Araucaria araucana*.

TABLE 1

Growth characteristics of juvenile *A. araucana* under shade and in the open (mean ± 1 SE)

Características del crecimiento de juveniles de *A. araucana* en ambientes de sombra y sol (promedio ± 1 ES)

| | Shade | Sun |
|---|---|---|
| Growth rings per whorls | 2.61 ± 0.13 | 2.10 ± 0.06 |
| Mean distance between whorls (mm) | 282 ± 17 | 350 ± 18 |
| Height growth rate (mm $yr^{-1}$) | 111 ± 8 | 169 ± 9 |

3, 4). In both cases, relationships were weaker for shaded trees than for open-grown individuals.

## DISCUSSION

We found that, in contrast to the growth pattern of many other temperate conifers (e.g., O'Reilly & Owens 1989, Avery & Burkhart 1994), branch whorl formation in juvenile *Araucaria araucana* does not follow a strictly annual rhythm. Even in well-lit individuals of the montane population that we studied, average intervals between successive whorls were > 1.8 yrs (Fig. 2, Table 1).

What, then, determines the periodicity of whorl formation in *A. araucana*? The significant influence of light environment on whorl formation rate (Fig. 2, Table 1), suggests that periodicity is probably linked to whole-plant carbon balance. On a montane site in the Chilean coast range, juvenile *A. araucana* apparently take at least two years to accumulate sufficient reserves to initiate the construction of a new branch whorl, especially when growing under shade (Fig. 2, Table 1). Although spanning only 3° of latitude, the geographic range of *A. araucana* encompasses wide variation in altitude (600 – 1,800 m) and precipitation (1,000 – 4,000 mm) (Veblen et al. 1995). If whorl formation rate were in fact linked to carbon balance, we would expect this parameter to vary throughout the species' range, as well as responding to fine scale variation in resource availability.

Light environment influenced not only the rate of whorl production, but also stem extension growth between successive whorls (Table 1). Mean distance between whorls was c. 25% greater in open-grown than in shaded individuals, an effect of similar magnitude to that seen on the rate of whorl production. The overall result of this effect of light environment on both whorl spacing and production rate was that height growth rates were > 50 % faster in open-grown than in shaded trees (Table 1).

Despite the non-annual nature of whorls in the study population, whorl counts may have some potential as a non-invasive method of age estimation in juvenile *A. araucana*. In both shade- and sun-grown sub-populations, whorl number was a better predictor of stem age than were stem diameter or height (Fig. 2 - 4). Site-specific relationships of whorl number to age could therefore be useful in demographic studies, enabling approximate age structure determinations without the need to obtain increment cores from all individuals. In *A. araucana*, this short-cut is most likely to be most applicable to regenerating populations on open sites, in view of the weaker relationship of whorl number with stem age under shaded conditions (Fig. 2). In much the same way, Enright (1992) was able to study the demography of the palm *Rhopalostylis* by determining the approximate relationship between stem age and the number of frond scars – with the difference that direct monitoring was required in this case, as palms do not produce growth rings

The findings of this study are strictly applicable only to the juvenile growth form. The architecture of *A. araucaria* undergoes a major change on maturation (Grosfeld et al. 1999), and we cannot rule out the possibility of different whorl formation patterns in adult trees.

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