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Arbuscular mycorrhizal infection in two morphological root types of *Araucaria araucana* (Molina) K. Koch

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ABSTRACT

Araucaria araucana (Molina) K. Koch is a conifer distributed in the Andean-Patagonian forests in the south of Argentina and Chile. The main objective of this work was to relate the different root classes appearing in *A. araucana* to mycorrhizal behavior. Samples were collected in three different sites in the Lanín National Park (NW Patagonia, Argentina). Two different root classes were present in *A. araucana*: longitudinal fine roots (LFR) and globular short roots (GSR). Both had extensive mycorrhizal arbuscular symbiosis (AM) and presented abundant hyphae and coils in root cells, a characteristic of the anatomical *Paris*-type. Dark septate fungal endophytes were also observed. Values of total AM colonization were high, with similar partial AM% values for each root class. Seasonal differences were found for total and partial colonization, with higher values in spring compared to autumn. Regarding the percentage of fungal structures between root classes, values were similar for vesicles and arbuscules, but higher coil percentages were observed in GSR compared to LFR. The percentages of vesicles increased in autumn, whereas the arbuscule percentages increased in spring, coinciding with the plant growth peak. Results show that both root classes of *A. araucana* in Andean-Patagonian forests are associated with AM fungi, which may have ecological relevance in terms of the importance of this symbiosis, in response to soil nutrient-deficiencies, especially high P-retention.

Key words: longitudinal fine roots, globular short roots, seasonality, *Paris*-anatomical type, dark septate fungal endophytes, P-soil deficiency

RESUMEN

Infección por micorrizas arbusculares en dos tipos de raíces de *Araucaria araucana* (Molina) K. Koch. La conífera *Araucaria araucana* (Molina) K. Koch se encuentra distribuida en los bosques Andino-Patagónicos de Argentina y Chile. En este trabajo se relacionaron las diferentes clases morfológicas de raíces presentes en la especie con el comportamiento micorrícico. Las muestras fueron tomadas en tres sitios del Parque Nacional Lanín (NO de Patagonia, Argentina). Se observaron dos clases diferentes de raíces: raíces finas longitudinales (RFL) y raíces cortas globulares (RCG). Ambas clases presentaron una importante simbiosis micorrícico-arbuscular (MA), con abundante desarrollo de hifas intracelulares y rulos, característico del tipo anatómico *Paris*. También se observaron hifas marrones septadas. Los valores totales de colonización MA fueron altos, con porcentajes parciales similares en cada clase radicular. Se encontraron diferencias estacionales en los porcentajes de infección (totales y parciales), con valores mayores en primavera comparados con los de otoño. Los porcentajes de estructuras fúngicas presentes en cada clase radicular fueron similares para vesículas y arbúsculos, pero se observaron mayores valores de rulos en las RCG que en las RFL. Los porcentajes de vesículas aumentaron en otoño, mientras que los de arbúsculos lo hicieron en primavera, en coincidencia con el pico de crecimiento vegetativo de los árboles. Los resultados muestran una fuerte asociación simbiótica MA con *A. araucana* y su relevancia en términos ecológicos en respuesta a la deficiencia de nutrientes en el suelo, en especial, a la alta retención de fósforo.

Palabras clave: raíces finas longitudinales, raíces cortas globulares, estacionalidad, tipo anatómico *Paris*, hifas marrones septadas, fósforo.

INTRODUCTION

Araucaria araucana (Molina) K. Koch, family Araucariaceae, grows in the NW Andean-Patagonian forests between 36° 45´ and 40° 23´ S (south of Argentina and Chile), and between 600-800 and 1800 m a.s.l. It can be found mostly on volcanic soils in pure stands or in mixed forests (with *Nothofagus pumilio* or *Nothofogus antarctica*). *A. araucana* is distributed across a wide range of high annual precipitations, from more than 4000 mm in Chile (western limit) to 1100 mm in Argentina (eastern limit). It is a highly fire-adapted species, occurring in an area where fires have long been caused by volcanic activity and by humans since the early Holocene (34).

A. araucana as well as other native conifers such as *Austrocedrus chilensis* and *Fitzroya cupressoides* in the Patagonian region (Argentina and Chile), only have arbuscular-mycorrhizal associations (10, 11, 14-16, 19, 21). This differs from conifers in the North Hemisphere that possess ectomycorrhizae (2, 3, 31, 32), many of which have been introduced into Patagonia (e.g. *Pinus*, *Larix*, *Pseudotsuga* and *Picea*) (4, 5).

Within the Araucariaceae family, AM has been described for other species in South America and Australia (7, 23-25, 36). However, *Wollemia nobilis*, also belonging to the Araucariaceae family, has two types of mycorrhizae: arbuscular mycorrhizae (AM) and ectendomycorrhizae (23).

In the Araucariaceae and Podocarpaceae families, two root classes can occur: longitudinal fine roots and globular short roots (6, 7, 23), both colonized by mycorrhizal fungi. These dimorphic roots have been observed in several species of the Araucariaceae family such as *Araucaria angustifolia* in Brazil (7) and *Araucaria cunninghamii*, *Agathis robusta* and *W. nobilis* in Australia (23). Globular short roots (= nodules) were also observed in *A. araucana* from Chile (18, 20, 35).

Based on previous reports of AM symbiosis in *A. araucana*, and considering the existence of two different root classes in the family Araucariaceae, the main objective of this work was to relate the different root classes appearing in *A. araucana* to mycorrhizal behavior, and in particular:

1. To describe the mycorrhizal type and quantify percentages of AM root length colonization for each root class, in two seasons (spring and autumn).
2. To analyze the distribution of the characteristic AM fungal structures in each root class, in two seasons (spring and autumn).

METHODS

The study was conducted in the NW Andean-Patagonian Region of Argentina, which is dominated by native forests, growing on allophanic soils. The climate of the region has a seasonal regime with precipitations concentrated mostly in autumn-winter as rain and snow (22, 29).

Sampling sites of *A. araucana* were located in Lanín National Park, in Neuquén province. Three sites were situated along the N° 60 provincial route between 39°37´59.8´´-39°41´58.5´´ S, and 71°27´31.7´´-71°11´16.5´´ W), and were distributed on an altitudinal range from 900 to 1185 m a.s.l, and precipitations between 900 to 1300 mm/annual, with a mean annual temperature between 7.0-7.2 °C. All the analyzed stands corresponded to native forests with current minimal anthropogenic disturbance, and *A. araucana* as the dominant tree species. The understory comprised different shrubs and herbs, mainly belonging to the Asteraceae, Berberidaceae, Celastraceae, Ericaceae, Fabaceae, Lycopodiaceae, Poaceae and Rosaceae families. Sites differ in soil characteristics, understory composition and land use in the past. These factors combined with climatic conditions, especially precipitations, create a gradient from W to E (sites 1 to 3), with the higher concentrations of organic matter (OM), N, P, and a thicker understory in the W, and high pH and electrical conductivity in the E (Table 1).

At each site, 3 adult trees of similar diameter at breast height and canopy cover were chosen. Fine roots (< 2mm diameter), clearly belonging to each individual, were col-

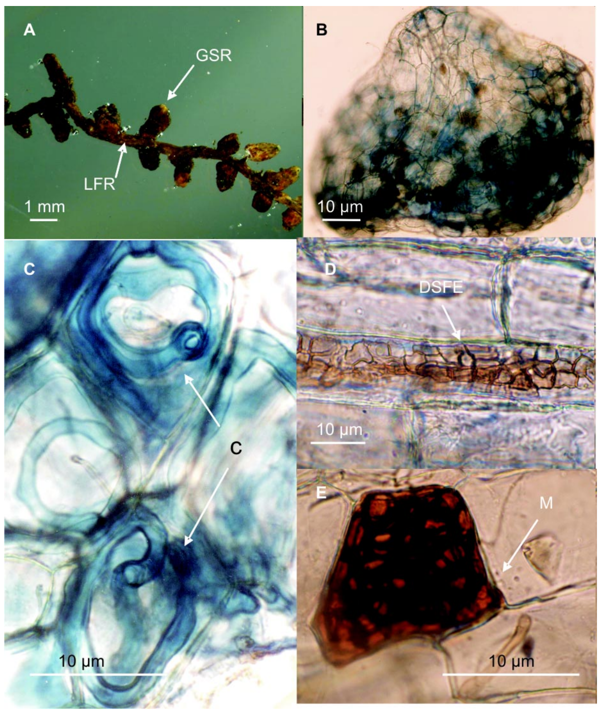

Figure 1. Dimorphic root system in *Araucaria araucana*. A: general aspect with two distinctive root classes: LFR (longitudinal fine roots); GSR (globular short roots). B: cleared globular short roots. C: Coils (C) in longitudinal fine roots. D: Dark septate fungal endophyte (DSFE) in longitudinal fine roots. E: detail of microsclerotia (M).

Table 1. Site characteristics and P level for soil and green leaves in *Araucaria araucana*. Data taken from Diehl (2006).

Site	Latitude	Longitude	Altitude m a.s.l.	Precipitation mm/annual	Soil parameters pH	EC mS/m	C (%)	N (%)	P-Olsen Mg/kg	Green leaves P (%)
1	39°37´59.8´´	71°27´31.7´´	1185	1300	5.9	56.3	8.7	0.37	58.9	0.11
2	39°36´17.7´´	71°22´10.7´´	980	900	5.9	27.1	5.4	0.26	4.9	0.07
3	39°41´58.5´´	71°11´16.5´´	900	900	6.2	18.4	2.5	0.21	3.1	0.05

lected in the amount necessary to fill a 25 ml container. Samples were taken in one year and two seasons (autumn and spring). Roots were preserved in 70% ethanol and later cleared and stained with the method of Phillips and Hayman (28). In order to quantify the percentage of root length colonized (AM%), each sample was processed under a stereoscopic microscope recording 200 root/gridline intersects, following the gridline intersect method (17). The percentage of AM root length colonization was also calculated for each of the two root classes as the percentage of intersections with colonized AM roots in fine longitudinal roots (partial AM% in LFR) or in globular short roots (partial AM% in GSR). The total AM percentage of root length colonization (total AM%) was calculated using all positive intersections (LFR+GSR) related to the total number of intersections observed.

For quantifying fungal structures (coils, vesicles, and arbuscules), 100 counts were considered for each root class, analyzing groups of 10 root pieces under optical microscope (slide method) (17).

The total AM root length colonization values were compared for different sites and seasons, using a Two Way Analysis of Variance, followed by a Pairwise Multiple Comparison Procedure. For this analysis, two factors were considered: i- site (three levels: sites 1 to 3) and ii- seasons (two levels: autumn and spring). A second Two Way ANOVA was performed to compare the partial AM root length colonization values considering the following factors: i- root classes (two levels: partial AM% in fine longitudinal roots, partial AM% in globular short roots) and ii- seasons (two levels: autumn and spring). Data were arc sine-transformed when necessary.

For the analysis of the fungal structures a One Way Analysis of Variance followed by a Pairwise Multiple Comparison Procedures were used to evaluate the distribution of each fungal structure (arbuscules, vesicles and coils %) in longitudinal fine and globular short roots in both seasons. Null hypotheses were rejected at the p <0.05 levels. The SASS program was used for all analyses.

RESULTS

A. araucana has a main root axis with fine longitudinal roots and lateral modified (globular short) roots, the latter of a small and uniform size appearing along the fine longitudinal roots. All AM structures (arbuscules, vesicles, coils and hyphae) were present in the cleared roots of all the individuals sampled. The abundant development of hyphae and coils in root cells showed that these AM belonged to the anatomical *Paris*-type. Dark septate fungal endophytes (DSF), whose melanized hyphae frequently form compact structures, microsclerotia, were also observed in all individuals, but these were not quantified (Figure 1).

A. araucana had high total AM colonization values between 72 and 91%. Significant differences in total AM% were found between seasons (P = 0.032) with the highest values in spring, but not between sites (P = 0.203) or for the interaction of the two factors (P = 0.560) (Table 2).

Both root classes in the analyzed individuals had AM colonization and the percentage of partial AM colonization in autumn and spring was also high in the range of those for total infection (Table 2). Differences between root classes (LFR and GSR) AM% were not significant (P = 0.303). However, there was a significant difference between seasons for these values (P = 0.020), being significantly lower for autumn than for spring (Table 2). The interaction between these two factors was not significant (P = 0.098).

Fungal structures tended to have higher coil percentages in globular short roots than in longitudinal fine roots, while vesicles and arbuscules had similar AM percentages in both root classes (Table 3). Significant differences were found between seasons for vesicles and arbuscules of each root class (p < 0.0001 in all cases), with higher percentages of vesicles in autumn than spring (20 vs. 3 in LFR and 19 vs. 4 in GSR), and lower percentages of arbuscules in autumn than in spring (1 vs. 6 in LFR and 1 vs. 7 in GSR), while coils had similar values in both seasons (Table 3).

Table 2. Total and partial AM percentages of root length colonization (AM%) in *Araucaria araucana*. LFR: longitudinal fine roots, GSR: globular short roots. Different letters indicate significant differences between seasons for total (capital letters) and partial (small letters) AM% (p < 0.05).

AM colonization %		Season	
		Autumn	Spring
Total		78 ± 13 B	89 ± 3 A
Partial	LFR	73 ± 15 b	90 ± 4 a
	GSR	82 ± 13	88 ± 4

Table 3. AM percentages of root length colonization (AM%) for each fungal structure in two root classes of *Araucaria araucana*. LFR: longitudinal fine roots, GSR: globular short roots. Different letters indicate significant differences between seasons for each fungal structure (p < 0.05).

Root class	Fungal structure	Season	
		Autumn	Spring
LFR	Coils	17 ± 3	14 ± 4
	Arbuscules	1 ± 1 b	7 ± 2 a
	Vesicles	20 ± 6 a	3 ± 1 b
GSR	Coils	44 ± 16	32 ± 4
	Arbuscules	1 ± 1 b	6 ± 1 a
	Vesicles	19 ± 8 a	4 ± 3 b

DISCUSSION

Arbuscular mycorrhizae are present in *A. araucana* roots, as previously observed for this species and other conifers of the region in Argentina and Chile (10, 14, 16, 18, 19, 21). In the present work, high values of total AM percentages were found, in the range of values over 80% which have been observed in other conifers in the region (9, 13, 15, 16). The high range of mycotrophy (AM colonization in all individuals, in all sites) and the elevated percentages of infection found, demonstrate the importance of this interaction. As the case had been for previously studied species of the genus *Araucaria*, *A. araucana* has a dimorphic root system with two distinctive root classes. However, as with other members of the Araucariaceae family, except for *W. nobilis*, with AM and ectendomycorrhizal colonization (23), only AM associations were found.

Generalizations about colonization patterns in AM fungi are difficult to make, because they are influenced by the host plant, the climatic and edaphic conditions, and the effects of the soil community and their interactions (24). Nevertheless, the occurrence of these high rates of colonization could be related to environmental conditions of the Andean-Patagonian forests rather than to an intrinsic characteristic of the host species. Trees in the forests sampled in this study grow in soils with high P retention and average values of available-P between 4 mg/kg in spring and 2.3 mg/kg in autumn (11). Foliar P concentration in green leaves for this species decreased from sites 1 (0.11%) to site 3 (0.05%), following the same trend of P availability in soils (Table 1). As had been considered in previous works (10, 11), P concentration in senescent leaves lower than 0.04% and N/P ratio in green leaves higher than 16, are used as the main indicators of P conservation and limitation, respectively. In *A. araucana* a P concentration in senescent leaves between 0.04 and 0.05 %, and the N/P ratio of 9.9, clearly show the lack of P limitation in this species, despite the P retention in soils (9, 10). On the other hand, *A. angustifolia* was evaluated in several native forests in Brazil, and showed lower AM% values than those found for *A. araucana* in Patagonia. Some examples for *A. angustifolia* are: 21-29% (25) and 10.7-14.7% in the cool and dry season vs. 25-40 % in the warm and rainy season (24). Only one case was observed with AM colonization (81%) similar to values in this study, but it was conducted in a greenhouse study for *A. angustifolia* seedlings inoculated with *Glomus clarum* (36).

Seasonal variations of the AM% colonization in *A. araucana*, followed a similar tendency, independently of root class (total or partial values), with the highest values in spring. Mycorrhizal seasonality was also observed in *A. angustifolia* (24), and in *Austrocedrus chilensis* (another native conifer of the Andean-Patagonian region). In *A. chilensis,* AM percentage values were higher in autumn and winter compared to spring and summer, being the autumn values significantly different from those in spring. The opposite seasonality observed in these two species could have been possibly explained by the sanitary condition of the *A. chilensis* forests: the lower values in spring and summer of *A. chilensis* corresponded to sites with sick trees affected by "*mal del ciprés*" (15). Future studies, involving more species and sites, could contribute to a better understanding of the mycorrhizal seasonality of conifers in the Andean-Patagonian forests.

The relative importance of globular short roots is unclear. Breuninger *et al*. (7) suggest that the globular short roots do not play a major role in mycorrhizal formation, based on observations of *A. angustifolia*, in which most of the mycorrhizal structures were located in the longitudinal fine roots. McGee (23) suggested that the AM colonization intensity might be related to mineral uptake rates, indicating that nodular development is a mechanism to take advantage of the capacity of mycorrhizal fungi to colonize soil without an extensive root system production. In our study, globular short roots showed equivalent AM colonization values to those from fine longitudinal roots, suggesting that both root structures play a key role in nutrient uptake. This idea is reinforced by the presence of similar amounts of arbuscules in both root classes. On the other hand, if it is considered that, as suggested by Smith and Smith (30), functional coils may replace the role of arbuscules, the fact that higher coil values in globular roots were found, suggests that the importance of this type of root may be at least equivalent to that of fine longitudinal roots. According to seasonal patterns in both root classes, in spring, arbuscules increase while vesicles decrease, suggesting a higher mycorrhizal activity coincident with the vegetative growth peak of the plants and with the increase of available P in soils (11), previously reported in this discussion.

Paris-type associations were found in *A. araucana*, and this result is in agreement with the observations for gymnosperms in general (8, 30). On the contrary, Breuninger et al. (7) classified mycorrhizal structures in *A. angustifolia* as *Arum* type. The different behaviors in the AM morphological types of *A. araucana* and *A. angustifolia* might be understood as differences in the *Araucaria* genus but, given the general evidence for gymnosperms, further studies are necessary to clarify this aspect.

The presence of dark septate fungal endophytes in *A. araucana*, as in other species in the region (9, 12), suggests the importance of this relationship in Andean-Patagonian ecosystems, and reinforces the idea that DSF seem to be more common in some particular locations with high altitude as alpine, subalpine, or cold and/or nutrient stressed ecosystems (1, 26, 27, 33).

In conclusion, considering the aspects previously discussed, this work supports the importance of the symbiosis between *A. araucana* and AM fungi in Andean-Patagonian forests and the equivalent role of both radical structures, in response to soil nutrient deficiencies, especially concerning P.

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