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IAWA Journal 39 (2), 2018: 209–220

Trabeculae in Patagonian mountain cypress (*Austrocedrus chilensis*) associated with *Phytophthora austrocedri* infection

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Accepted for publication: 26 January 2018 – Available online: March 2018

ABSTRACT

Phytophthora austrocedri is a straminipilous (heterokonta) organism that causes mortality of *Austrocedrus chilensis*, an endemic Cupressaceae from the Patagonian Andes forest in temperate South America. This soil pathogen colonizes and kills the roots and extends up to the stem causing necrosis of cambium, phloem and xylem ray parenchyma. An anatomical study of affected tissues was conducted in order to better understand the process of pathogen colonization and tree response. It was found that tracheids of the xylem of affected trees showed large numbers of trabeculae, both rod- and plate-shaped. The occurrence of these structures was clearly associated with the necrotic lesion area, since the trabeculae were rare in healthy tissues above the necrotic lesion. Trabeculae occurred in a variety of arrangements: solitary or in long files, single, double or triple. Our results could indicate that trabeculae proliferation in tracheids of *A. chilensis* trees is induced by the stress generated by the *P. austrocedri* invasion. Whether this is triggered by a nonspecific stress response or in direct response to the pathogen remains to be tested.

Key words: Forest disease, Patagonia, root pathogens, stress response, softwood, wood anatomy.

INTRODUCTION

Mountain cypress, *Austrocedrus chilensis* (D. Don) Pic.Serm. & Bizarri (Cupressaceae) is the most widely distributed of the 6 endemic conifers in Patagonia (Argentina). As pure forest or mixed with *Nothofagus* spp. it covers about 141,000 ha in Argentina (Bran *et al*. 2002) and 45,000 ha in Chile (CONAF 1997), being an important economic and ecological resource for the region.

As it is a dominant or co-dominant species, it defines forest structure and dynamics. Therefore, its mortality may have great ecological effects, altering forest structure and functionality, microclimate, and ecosystem processes (Ellison *et al*. 2005; Loo 2009).

DOI 10.1163/22941932-20170?203
Published by Koninklijke Brill NV, Leiden

Phytophthora austrocedri is a soil pathogen that causes mortality of *A. chilensis* which was, until recently, its only known host. In 2011 *P. austrocedri* was found in the UK to cause mortality of *Juniperus communis*, and susceptibility has also been reported in other species of the Cupressaceae such as *J. virginiana, Thuja occidentalis, T. plicata, Calocedrus decurrens, Chamaecyparis lawsoniana, Sequoiadendron gigantum*, and the native *Fitzroya cupressoides* and *Pilgerodendron uviferum* (Vélez *et al*. 2014). *Phytophthora austrocedri* colonizes and kills the roots and goes up into the stem causing necrotic lesions in the inner bark. External symptoms include bright yellow to red foliage, defoliation and resin exudates in the lower part of the bole, associated with the necrotic lesions in the inner bark (Greslebin & Hansen 2010).

The genus *Phytophthora* includes many well-known plant pathogens causing a wide variety of diseases including blight, stem and twigs canker, dieback, and root rot. The pathogen kills cambium and phloem causing inner bark discoloration and necrosis frequently accompanied with resinous or tarry exudates. Erwin and Ribeiro (1996) claimed that *Phytophthora* spp. were mostly unable to successfully colonize and inhabit secondary xylem. However, there are other reports of xylem invasion in natural and artificially infected trees (Smith *et al*. 1997; Brown & Brasier 2007; Oh & Hansen 2007; Parke *et al*. 2007; Collins *et al*. 2009; Greslebin & Hansen 2010; Vélez *et al*. 2012).

The mode of action of *Phytophthora* in the xylem, as well as the tree's reaction to the invasion, are still poorly investigated. Parke *et al*. (2007) showed that *P. ramorum* invades the xylem, spreading radially at about 0.5 mm/day, hand in hand with the formation of tyloses in the vessels. Collins *et al*. (2009) demonstrated that infection by *P. ramorum* induces tyloses in the xylem vessels of tanoak and that the resulting occlusion of this tissue reduces the conductivity of the sapwood. Oh and Hansen (2007) found xylem colonization in one resistant seedling of *Chamaecyparis lawsoniana* after stem wound inoculation but not in other resistant or susceptible seedlings. Brown and Brasier (2007) have shown that various *Phytophthora* species can colonize and survive in tree xylem of a range of broad-leaved trees. In the case of *Austrocedrus chilensis*, Greslebin and Hansen (2010) demonstrated that *P. austrocedri* inhabits the xylem of naturally infected adult trees, by isolating the pathogen from wood, and Vélez *et al*. (2012) showed that its hyphae invade *A. chilensis* xylem through the rays and spread through bordered pits of xylem tracheids causing a reduction in the water supply of the plant.

Kino veins, tylosis, non-conducting wood, cavitation of tracheids, dry zones and resin-soaked zones have been reported associated with *Phytophthora* invasion of xylem in Jarrah, Oak and Pine trees (Tippet 1986; Davison *et al*. 1994; Parke *et al*. 2007). However, invasion mechanisms and plant responses to invasion in other tree species are still insufficiently known.

Trabeculae, according to the IAWA Softwood List (Richter *et al*. 2004), are defined as rod-like or spool-shaped parts of a cell wall which project radially across the lumen. They are intracellular bar-like structures extending radially across the tracheid lumen from tangential walls. First described by Sanio (1863, 1874) in angiosperms and by Winkler (1872) in gymnosperms, trabeculae were subsequently studied in detail by Müller (1890) and Raatz (1892) and, more recently, by many other authors such as

Butterfield and Meylan (1979), Werker and Baas (1981), Yumoto (1984), and Grosser (1986). The multilayered ultrastructure of trabeculae is very similar to the structure of the cell wall and it is continuous with it (Keith 1971; Ohtani 1977; Butterfield & Meylan 1979; Parameswaran 1979; Yumoto 1984).

In gymnosperms, trabeculae have been reported mainly in tracheids but also in epithelial cells and surrounding parenchyma of resin ducts (Grosser 1986).

The causes of trabeculae formation have been widely discussed in the literature, but at present there is no general agreement. Trabeculae have been associated with diseases, injuries, frost, or other disturbances to the cambium (Hoefert & Gifford 1967; Werker & Baas 1981; Yumoto 1984; Grosser 1986; Ohtani *et al*. 1987; Nakada & Kawamura 2002; Yaman 2007). On the other hand, some authors have considered that these structures are not related to diseases or injuries (Mameli 1913; Bärner 1937). However, most agree that trabeculae are more frequent and abundant in abnormal than in normal wood and in declining than in healthy trees.

Grosser (1986) suggested the function of trabeculae is to prevent a collapse of the tangential cell walls during local compression or tensile stress, interposing themselves as reinforcing elements between walls. Yumoto (1984) suggested that the involvement of trabeculae is of secondary nature, probably triggered by cytological events which are brought about by different factors of damage.

This study describes and evaluates the occurrence of trabeculae in xylem of *Austrocedrus chilensis* in relation to *Phytophthora austrocedri* infection in a natural forest in Patagonia, Argentina.

MATERIALS AND METHODS

Study area and sampling methods

Studied trees were selected in a forest area located at 43° 10' S and 71° 42' W, in the "Valle 16 de Octubre", in the province of Chubut, Patagonia, Argentina, where the disease is widely distributed. This valley includes protected areas (Los Alerces National Park), as well as farms and lands under silviculture and livestock. Symptomatic trees were examined for presence of necrotic lesions at the base of the stem. Six trees showing active necrotic lesions were selected for the study. From each tree, wedge-shaped samples of conducting tissues (bark and xylem) for anatomical studies were taken at four different heights: I) the oldest area of the lesion (tree base), II) the middle area of the lesion, III) the margin of the lesion (advancing area), IV) healthy tissues 60 cm above the margin of the lesion. As control, samples from three asymptomatic trees of the same area were taken. Control trees were chosen according to the following criteria: no or less than 25% of crown defoliation, and healthy phloem (no necrotic lesions) present at root collar. Because control trees were in an affected area and infection of roots could not be discarded, samples from three additional control trees of a healthy cypress forest were also taken. Wedge-shaped samples of conducting tissues (bark and xylem) of asymptomatic and healthy trees were taken at 50 cm height of the tree stems. A cube, approximately 1 cm wide, 1 cm long and 2 cm depth (including both conducting tissues: xylem and phloem), was obtained from the center of each sample. Slides from these cubes were obtained for optical microscopic (OM) studies.

Techniques for light microscopy

Transverse, tangential and radial sections (10 µm thick) were cut on a Leica Hn 40 sledge microtome and treated with two different staining methods: safranine-fast green combination according to D'Ambrogio (1986) and cotton blue. The cotton blue stain technique can be summarized as follows: a) bleaching with hydrogen peroxide 30% for 1.30 h, b) rinse with distilled water 3 to 4 times, c) stain with cotton blue 24 h, d) rinse with distilled water 3 to 4 times, e) mounting of sections in lactoglycerol. Ten slides of each sample in each section were stained with one of these techniques. A total of 760 slides of affected trees (5 slides × 2 stains × 4 zones of 6 affected trees) plus 180 slides of the six healthy trees were studied.

Observations were made in the last 5 annual rings with a light microscope Leica DM500 and photomicrographs were obtained with a Canon EOS Rebel T3i digital camera. Counting of trabeculae was done in radial sections (over a width of 5 annual rings and a height of 10 mm).

In order to confirm that the lesions were caused by *Phytophthora*, isolation and an ELISA test (DAS ELISA reagent set for *Phytophthora*, ADGIA Inc.) were attempted from the margin of the lesions as described in Greslebin & Hansen (2010).

A Kruskal–Wallis non-parametric analysis of variance was applied in order to analyze differences in the number of trabeculae between the different areas of the lesion. A non-parametric test was used because data did not fulfill the assumption of homogeneity of variance. The analyses were performed in INFOSTAT statistical software (Di Rienzo *et al*. 2011).

RESULTS

Healthy trees did not show trabeculae in their xylem. Not a single trabeculum was found in the 90 slides from 3 healthy trees from a healthy area, and only 3 trabeculae were found in one of the 90 slides from 3 asymptomatic trees growing next to the affected ones analyzed, while in the xylem associated with the necrotic inner bark of affected trees, all of the 760 slides from six trees analyzed showed numerous trabeculae (Table 1). In all "affected" samples analyzed the presence of *Phytophthora* in the necrotic inner bark was confirmed by isolation and/or the ELISA test. A total of 3,739 trabeculae, on average more than 600 per tree, were observed in the xylem adjacent to the necrotic lesion caused by *Phytophthora*. Healthy xylem above the margin of the necrotic lesion showed no trabeculae or a significantly (Kruskal-Wallis H: 12.87, $P = 0.0048$) lower number (Table 1). The number of trabeculae of the different areas of the lesions (margin, middle and oldest area) did not differ significantly.

Affected trees showed also a high variety of arrangements and types of trabeculae (Table 2 and 3). Both, rod- and plate-shaped trabeculae, were present. Within these two major classes, 18 different kinds of arrangement were observed in xylem associated with the necrotic lesions in the inner bark. Rod trabeculae appeared solitary, in short (Fig. 1) or long files (Fig. 2, 6) in early- and latewood; and in simple, twinned or triple (Fig. 3–5) arrangement. Plate-shaped trabeculae appeared solitary, in short (Fig. 7, 8), or long files (Fig. 9) in early- or latewood, and in simple, twinned or triple arrangement (Fig. 10).

The more frequent arrangement was in long files of trabeculae traversing earlywood (Fig. 6), and also latewood, which could include up to 52 tracheids (Fig. 11). Similarly, the plate-shaped trabeculae occurred solitary as well as in files; however, files were much shorter on average than files of rod-shaped trabeculae. Also, the different kinds of trabeculae (rods and plates) occurred close one to another or combined (Fig. 8–10). The margin of the lesion was the area with the highest variety of trabeculae arrangements. Long files of trabeculae connected with the necrotic cambium were also observed (Fig. 12).

Table I. Number of trabeculae in the last 5 annual rings of *Austrocedrus chilensis* trees affected and not-affected by *Phytophthora austrocedri*.

Tree[2]	Number of rod- and plate-shaped trabeculae in last 5 annual rings[1]			
	Healthy area	Lesion margin	Lesion middle zone	Lesion oldest zone
Diseased I	3	160	67	37
Diseased II	9	70	50	137
Diseased III	0	143	477	397
Diseased IV	3	380	407	294
Diseased V	3	170	180	170
Diseased VI	0	430	—[3]	167
Asymptomatic I	0	—	—	—
Asymptomatic II	3	—	—	—
Asymptomatic III	0	—	—	—
Healthy I	0	—	—	—
Healthy II	0	—	—	—
Healthy III	0	—	—	—

[1] Numbers of rod- and plate-shaped trabeculae result from counts of 10 radial sections per tree and per area of the lesion. Healthy area of diseased trees was 60 cm above lesion margin. In the case of asymptomatic and healthy trees only one healthy area was studied. Size of radial areas studied: width = 5 annual rings; height = 10 mm; thickness = 10 μm.

[2] Diseased trees are those that exhibit necrotic lesions caused by *P. austrocedri* at the root collar. Asymptomatic trees are those growing near the diseased ones but without symptoms of the disease (no crown defoliation and healthy tissues at the root collar). Healthy trees are those from a disease-free forest area.

[3] The short length of the lesion did not allow sampling the middle area.

Table 2. Occurrence and arrangements of rod-shaped trabeculae in *Austrocedrus chilensis* xylem associated with different areas of *Phytophthora austrocedri* damage.

Area of the lesion	Single		Twinned		Triple	
	solitary	files*	solitary	files*	solitary	long files
Healthy zone above necrotic lesion	18	0	0	0	0	0
Advancing zone (lesion margin)	317	830 (757)	17	26 (26)	3	6
Middle zone	497	567 (490)	7	13 (13)	0	0
Oldest zone	363	713 (650)	10	30 (30)	0	0

*In brackets the number of trabeculae that were present only in earlywood.

Table 3. Occurrence and arrangements of plate-shaped trabeculae in *Austrocedrus chilensis* xylem associated with different areas of *Phytophthora austrocedri* damage.

Zones	Single		Twinned		Triple	
	solitary	files*	solitary	short files*	solitary	short files
Advancing zone	83	71 (64)	0	0	0	0
Middle zone	57	40 (40)	0	7	0	3
Oldest zone	30	50 (50)	0	3	0	3

*In brackets the number of trabeculae that were present only in earlywood.

↗

Figure 1–6. Radial sections of xylem of *Austrocedrus chilensis* trees naturally infected with *Phytophthora austrocedri* showing different arrangements of rod-shaped trabeculae (stained with cotton blue). – 1: Short file of two trabeculae in adjacent tracheids. – 2: Part of a long file of trabeculae traversing early- and latewood (RF). – 3: Twinned file of trabeculae traversing earlywood (RTF). – 4: Triple short file of trabeculae (RTrF). – 5: Long files (RF) and double files (RTF) of trabeculae traversing earlywood. – 6: The most frequent arrangement of trabeculae: single file traversing earlywood.

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Figure 7–10. Radial section of xylem of *Austrocedrus chilensis* trees naturally infected with *Phytophthora austrocedri* showing different arrangements of plate- and rod-shaped trabeculae (stained with cotton blue). – 7: Short file of plate-shaped trabeculae. – 8: Combination of short file of rod-shaped (R) and short file of plate-shaped trabeculae (PF) in earlywood. – 9: Four different trabeculae long files: rod-shaped triple file (RTrF), rod-shaped file (RF), plate-shaped file (PF), rod-shaped twinned file (RTF). – 10: More than ten rod- and plate-shaped trabeculae files traversing earlywood.

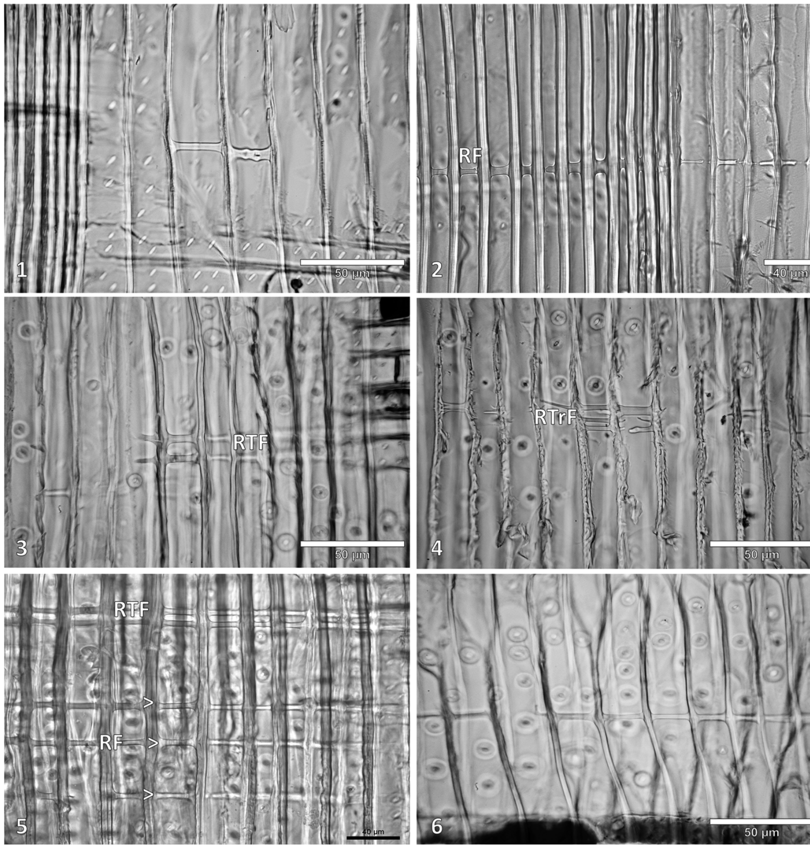

Figure
1–6

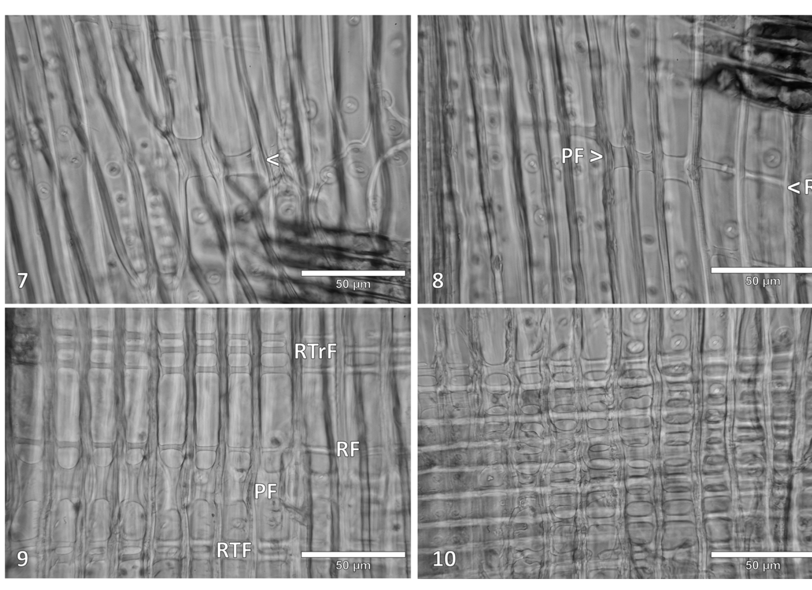

Figure
7–10

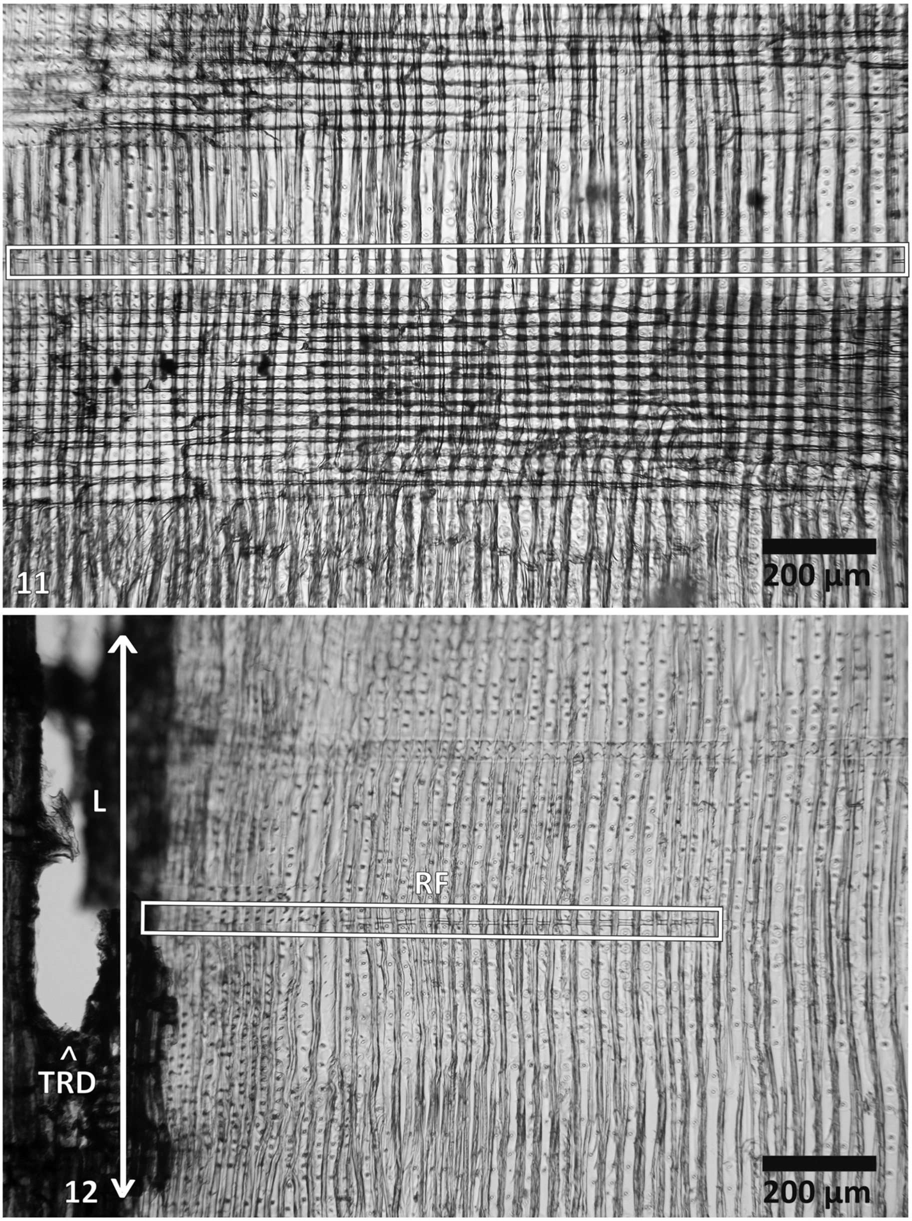

Figure 11 & 12. Radial section of xylem of *Austrocedrus chilensis* trees naturally infected with *Phytophthora austrocedri* showing different arrangements of rod-shaped trabeculae (stained with cotton blue). – 11: Long file of trabeculae traversing 52 tracheids of early- and latewood. – 12: Long file of trabeculae traversing earlywood and latewood beginning from necrotic lesion of cambium and phloem (L) near a traumatic resin duct (TRD).

DISCUSSION

The evident difference in the number and variety of trabeculae between healthy and affected Patagonian mountain cypress trees suggests that the disease leads the formation of trabeculae.

Different factors have been hypothesized as direct or indirect causes of trabeculae formation: frost (Petri 1912; Jöhnssen 1933; Fuess & Schneiders 1935; Müller-Stoll 1965), viruses (Wehrmeyer 1960; Hoefert & Gifford 1967), degenerated mitoses (Bode 1937), fungi (Jeffrey 1917; Hale 1935), injuries, wounds, compression wood and environmental stress (Werker & Baas 1981; Yumoto 1984; Grosser 1986), and other unspecified climatic factors (Raatz 1892). Yumoto (1984), based on a thorough analysis of all the evidence, concluded that these hypotheses can be explained in terms of the disturbance of cell division and proposed a hypothesis of abnormal cell division as cause on trabeculae formation. The author supported his hypothesis by pointing out the similarity between abnormal tissues induced by frost, fungal infection (*e.g.* galls), tumors, wounds, and hazel growth. All these abnormal tissues are associated with the occurrence of trabeculae, which suggest that there is a common cause responsible for their formation, and that this cause depends on the plant, not on the factor that generates the disturbance.

Coincidentally, Grosser (1986) found that trabeculae are more common in wounded and compression wood than in normal wood and that this structure occurs regularly and in great numbers in irregularly formed and arranged cells. He also concluded that its development is a consequence of disturbances in cell division, closely related to the partial collapse of the cambial cells during cell division. As irregularities may also occur in normal divisions of the fusiform initials, trabeculae can also occur in normal wood but are more frequent in wood of stressed or wounded trees. Anatomical studies of *Austrocedrus chilensis* wood made by Tortorelli (1956, 2009) and Guerra *et al.* (1994) do not mention trabeculae, but Roig (1992) and García *et al.* (2004) reported them as exceptionally present.

Yumoto (1984) and Grosser (1986) have suggested that trabeculae proliferation is brought about as a response to damage but that the mechanism that induces its formation are yet to be elucidated. Vélez *et al.* (2012) have shown that the mechanism of action of the *Phytophthora austrocedri* may involve the participation of protein effectors secreted by the pathogen which could trigger a hypersensitive reaction. The possible involvement of effectors secreted by the pathogen for stimulating trabeculae formation is a subject that deserves to be addressed in future studies.

The results of this work, based on the high frequency of trabeculae in diseased trees and the absence in healthy ones from the same area, show that trabeculae formation is clearly associated with the *Phytophthora* invasion. Whether those are triggered by a nonspecific stress response or in response to the pathogen remains to be tested.

ACKNOWLEDGEMENTS

We deeply acknowledge Dr. Beatriz Galati for acting as pre-submission reviewer of the manuscript, and Mr. and Mrs. Berwin for kindly allowing sampling in their property. This work was supported by the national agency of scientific and technical promotion of Argentina (ANPCyT-FONCyT, PICT 2012-0733), and the Nacional University of Patagonia (UNPSJB).

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