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Tree age and bark thickness as traits linked to frost ring probability on *Araucaria araucana* trees in northern Patagonia

Julieta Gabriela Arco Molina[a,*], Martín Ariel Hadad[a,b], Daniel Patón Domínguez[c], Fidel Alejandro Roig[a]

[a] Departamento de Dendrocronología e Historia Ambiental, IANIGLA-CCT CONICET—Mendoza, Av. Ruiz Leal s/n, Mendoza, Argentina
[b] CIGEOBIO-CONICET—San Juan, Universidad Nacional de San Juan, Av. Ignacio de la Roza 5900 Oeste, San Juan, Argentina
[c] Área de Ecología, Facultad de Ciencias, Universidad de Extremadura, Av. Elvás s/n 06071, Badajoz, Spain

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ABSTRACT

Frost events may damage the cambium and consequently the newly produced tracheids whose cell walls have not yet completed their lignifications, leading to the formation of frost rings. This study deals with the presence of frost rings in *Araucaria araucana* trees according to cambial age and bark thickness, under the assumption that these factors may be involved in physical or physiological mechanisms that increase resistance to freezing temperatures that impact the cambial tissue. The study was conducted in northern Patagonia at two sites of contrasting geomorphology, and therefore potentially associated with a differential degree of exposure to extreme cold. Wood plus bark cores were extracted from main stems at two heights from the ground and from each of the four cardinal point directions for 30 individuals per site. A Linear Mixed Model and a Generalized Linear Mixed Model were applied in order to relate the bark thickness and the frequency of frost rings in accordance with the different sampling points on the stem. It was observed that as bark becomes thicker with cambial age, the frequency of frost rings decreases, indicating a possible thermal-induced mechanism of bark protection. Consequently, there is an increase in the presence of frost rings at the younger stages of tree life. Although the mechanisms of cold hardiness in trees can be complex, including aspects of the tree physiology, our data indicated that as tree age increases, the thickness of the bark is higher, resulting in a potential effect of isolation and passive protection against the harmful effects of frosts. This mechanism may be relevant in the ecology, conservation and management of forests faced with extreme variability in future climate and changing scenarios.

1. Introduction

Global warming in the twentieth century is considered one of the factors responsible for recent changes in the frequency and intensity of climate extremes (IPCC, 2007). Since predictions of climate change include an increase of temperature in temperate latitudes, a consequence of this phenomenon can be linked to a loss of acclimation to low growth temperatures, meaning a greater risk of frost damage during periods of active plant development (Cannell and Smith, 1986; Inouye, 2000; Augspurger, 2009). Extremely low temperatures are an important limiting factor for plant production and their distribution in large areas of the world, since two thirds of the world's landmass is annually subjected to temperatures below the freezing point (Lärcher, 2001). As low temperature stress impairs metabolic processes and dry matter production with different degrees of reversibility, frost action over plants has significant implications on the equilibrium of native vegetation, as well as high-yield crops (Lärcher, 1981). Based on these facts, it becomes relevant a better understanding of how plants may react to such potential changes induced by frosts.

Despite the fact that plants possess mechanisms to resist the effects of low temperatures on their development (e.g., cortical isolation, biochemical and enzymatic reactions, mitochondria rate respiration, increase in solute cell contents, etc.—see Lyons and Raison, 1970; Sakai and Lärcher, 1987; Hasanuzzaman et al., 2013), a freezing event may cause injuries in the cambial tissue, giving rise to two possible phenomena: (1) death of the meristems with consequent death of the plant, and (2) partial death of the cambial tissue and its regeneration after frost. Wood injuries derived

* Corresponding author. Tel.: +54 2615244231; Fax: +54 2615244201.
E-mail addresses: jarco@mendoza-conicet.gob.ar, arcojulieta@gmail.com (J.G. Arco Molina).

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by frosts were initially recognized by Rhoads (1923) as growth rings with anatomical pathologies caused by freezing temperatures, and later defined as frost rings signaled by cell morphology, shape and size that vary from the normal pattern (Kaennel and Schweingruber, 1995). Anatomically, the formation of ice crystals in the cambium zone results in freezing-altered cell wall thickness, variations in the matrix of the cellulose/hemicellulose/lignin contents and, moreover, in deformed or collapsed cells with deposits of dense material in their inner walls (Lee et al., 2007). Consequently, frost wounds in the xylem may have collateral effects in disruptions of hydraulic efficiency and risk to trigger cavitation in vessels (Sperry and Sullivan, 1992; Martínez-Vilalta and Pockman, 2002; Willson and Jackson, 2006).

Although cold or freezing stress resistance by plants comprises many different genetic, molecular and physiological features (Sakai and Lärcher, 1987; Hughes and Alison Dunn, 1996; Beck et al., 2007), there is a growing consensus that other simple characteristics may be associated to the decrease in the tree's sensitivity to frost, such as age and bark thickness (Gurskaya and Shiyatov, 2006). Total bark thickness (functional bark + rhytidome) is particularly considered to play a primary role in the thermal protection of the vascular cambium (Stöckli and Schweingruber, 1996; Treter and Block, 2004; Payette et al., 2010). In this sense, if bark thickness increases with age, the vascular cambium becomes increasingly protected against extreme colds. Several evidences indicate that most of the frost injuries are found in the rings that are close to the pith, suggesting a higher vulnerability of cambium to frost when the tree is young, and consequently its bark is still thin (Glerum, 1975; LaMarche and Hirschboeck, 1984; Stöckli and Schweingruber, 1996; Treter and Block, 2004; Gurskaya and Shiyatov, 2006; Gurskaya, 2007; Payette et al., 2010; Kidd and Copenheaver, 2014). Consequently, in tree species with age-related bark thickness, the frequency of frost rings may vary with the cambial age, that is, from juvenile to mature wood (Payette et al., 2010).

On the other hand, Schweingruber (2007) claimed that both frequency and intensity of the frost injury varies around the stem's circumference. This could be attributed to different exposures of stems to cold air or local variations of bark thickness. Moreover, the localization of the frost injury within the growth ring makes it possible to classify the frost event in relation to the growing activity (Gurskaya, 2014). In this sense, Schweingruber (2007) pointed out that frost damage at the beginning of the growth ring could indicate an extremely cold condition prior to the growing season (winter months), while frost injury on earlywood and latewood is produced during the growing season by late and early frosts, respectively (Glerum and Farrar, 1966). Although it is very unusual, two frost events in the same growth ring have also been reported (Gurskaya and Shiyatov, 2002; Hadad et al., 2012).

Among multiple applications, frost rings offer the possibility to use them as markers to successfully cross-date tree-ring series (Glerum, 1975), to estimate the degree of plant resistance to low temperatures (Gurskaya and Shiyatov, 2002), and to construct long-term extreme cold event chronologies at large geographic scales (Gurskaya and Shiyatov, 2002; Treter and Block, 2004; Gurskaya, 2007; Hadad et al., 2012). Moreover, frost rings could indicate when a large-scale atmospheric circulation and its related weather events play a role in this particular tree-growth response at local and/or regional scales (e.g., Mock et al., 2007) and when other physical phenomena, like volcanic eruptions, may be responsible for the occurrence of widespread frost events (LaMarche and Hirschboeck, 1984; Brunstein, 1996; Hantemirov et al., 2004; Salzer and Hughes, 2007, 2010).

In the Andes of Argentina between 37°20′–40°20′ SL, and from 900 to 1800 m altitude, the temperate forests of *Araucaria araucana* (Molina) K. Koch ("pehuén") spread in an ample ecological setting from the humid Andes foothills to the dry ecotone of the Patagonian steppe (Roig, 1998; Roig and Villalba, 2008). Growing under a cold temperate climate, *A. araucana* may attain centennial-to-millennial ages and a significant bark thickness development at tree maturity (Castro, 2009). It has been argued that the thickness of this bark can efficiently protect the inner living tissues (lateral cambium) from fires and other physical injury-related factors (Veblen et al., 1996; Roig and Villalba, 2008).

Recent studies reported the presence of frost-induced damages on the growth rings of *A. araucana* trees, pointing out the potential of this species to record past extreme cold events through dendrochronological techniques (Hadad et al., 2012). However, it remains poorly unknown whether there is a differential impact on frost ring formation depending on tree ontogeny and the age-related development of other tree organs, such as the bark. The hypothesis for this study is that bark thickness in *A. araucana* is age-dependent, linking this relationship to the probability that the derivative cells may be mostly exposed to different levels of frost damage when the trees are in their early stages of life. Therefore, if the increase in the bark thickness means more insulation, then the cambium may be more protected from frost as the tree ages. In this sense, a morphological traits such as the bark thickness could be an advantage to protect the vascular cambium from extreme colds during advanced stages of youth tree development, but may be inefficient during recruitment and development of new seedling generations, where plants have not yet formed an efficient bark isolation (Hantemirov et al., 2000; Gu et al., 2008). These considerations may be relevant topics in the ecology of plant communities under a global warming scenario, where more frequent and intense climate extremes, including freezing events, are expected.

2. Materials and methods

2.1. Study area

The study sites are located at the northern distribution area of the *A. araucana* forests, characterized by open woodlands intermingled by the Patagonian steppe (Golluscio et al., 1982; Schlichter and Laclau, 1998). Soils receive 500 mm of precipitation per year and the mean annual temperature is 12.4 °C. Winter months have a uniform atmospheric circulation originated from the Pacific, whereas summer has a relatively weak zonal component superimposed on the meridional gradient. Therefore, the west winds have a southerly component (west–southwest to southwest). These winds are characterized not only by their prevalence during the entire year but also by their higher seasonal speeds, particularly from October to February (summer) (Prohaska, 1976).

Temperature in our study region is the highest in Patagonia at a continental level, with harsh winters and temperate summers (Rubí Bianchi and Cravero, 2010). The relative humidity decreases from the Andes to the steppe, which causes an increase in the daily thermal amplitude in the same direction. Both conditions enhance the likelihood of frost occurrence (Bustos, 2001). This area experiences a mean annual frost-free period of 90 days (Movia et al., 1982), with December 1st as the date of the last late frost and March 21st as the date of the first early frost (Bustos, 2001). This period of frost risk, either corresponding to early or late frosts, concurs with the period of active division of the cambial cells and with the consequent growth ring formation in *A. araucana*.

The sites considered in this study represent two different topographical conditions: one is the Primeros Pinos (PP) site located in a plateau east from the mountain foothills and the second one is the Picún Leufú (PL) site located on the SE slope of the foothills of the Andes, which is more protected from western winds (Fig. 1).