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Patterns of *Dothistroma septosporum* conidial dispersal in Colombian *Pinus tecunumanii* plantations

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Abstract

Dothistroma needle blight (DNB) caused by *Dothistroma septosporum* is one of the most important needle diseases of *Pinus* spp., especially in Southern Hemisphere plantations. In Colombia, the pathogen has caused severe outbreaks in plantations of *Pinus tecunumanii* of the low elevation population (LE). Currently, management strategies suffer from a lack of knowledge regarding the epidemiology of *D. septosporum* under tropical climatic conditions. In this study we determined the patterns of conidial dispersal and considered how climatic conditions in Colombia influence them. The study was conducted over 15 consecutive months between October 2010 and December 2011 using glass slide-based spore traps. Conidia were found on the traps throughout the year, with the peak abundance during November to January (2010) and November to December (2011). During peak conidial production, relative humidity and temperature had the greatest influence on conidial dispersal. Favourable weather conditions in Colombia, particularly rainfall, have contributed to continuous conidial production throughout the year, leading to *D. septosporum* infections all year round. This high reproductive rate as a consequence of high precipitation is in contrast to other Southern Hemisphere and Northern Hemisphere countries with more specific periods of rainfall and infection.

KEYWORDS

climate change, conidial dispersal, *Dothistroma septosporum*, *Pinus tecunumanii*

1 | INTRODUCTION

Dothistroma septosporum is one of two distinct species of *Dothistroma* that cause Dothistroma needle blight (DNB) on *Pinus* spp. and other Pinaceae hosts (Barnes et al., 2016, 2022). Repeated infections result in severe defoliation, yield reduction, tree death and economic losses (Brown, 2011; Bulman et al., 2008; Gibson, 1979). DNB is well known in the Southern Hemisphere where *D. septosporum* has caused significant damage to plantations mainly of non-native *P. radiata* (Bulman et al., 2008) as well as in natural forests and plantations of native species in the Northern Hemisphere (Adamčíková et al., 2021; Mullett et al., 2017; Piotrowska et al., 2018). Initial symptoms of DNB include yellow or tan bands on needles that develop on the upper parts of the needles while the bases remain green (Gibson, 1979). In older needles, the bands have a characteristic red to brown colour and small black stromata erupt from necrotic tissue (Gibson, 1979; Gibson et al., 1964). Generally, defoliation of second-year needles occurs approximately 1 year after infection, leaving only the current year needle flush on severely infected branches (Barnes et al., 2022; Bulman et al., 2013; Gibson, 1974).

In the late 1970s, the high demand for wood led to an increase in fast-growing *P. radiata* plantations worldwide, particularly in

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countries such as New Zealand and Chile (Aglietti et al., 2021). The climate of these areas is well-suited to plantations of this pine species but, unfortunately, also for the development of DNB (Aglietti et al., 2021; Richardson et al., 1994). A contrast between wet and dry seasons in countries with Mediterranean climate areas such as New Zealand and Chile, contributes not only to the dispersal of *D. septosporum* conidia but also to the subsequent infection (Aglietti et al., 2021; Figueroa et al., 2013). In New Zealand, two consecutive infection cycles caused by asexual conidia usually occur where there are optimal conditions of humidity (continuous wetness periods and high humidity) and temperature (day/night = 20/12°C) (Bulman et al., 2004). A first infection cycle occurs during late spring (November) and a second cycle in late summer (February), but in warmer areas of New Zealand infection can occur earlier (October) (Bulman et al., 2004). Differences in temperature and rainfall in countries where susceptible non-native *Pinus* spp. are planted strongly influence the number of infection cycles that occur in a season. In plantations, stromatal formation can occur within a short period of 5 weeks in countries like New Zealand and Kenya (Bulman et al., 2013; Gilmour, 1981). These can be substantially different to infections in Northern Hemisphere countries where typically one cycle is observed per year (Bulman et al., 2013; Peterson, 1982; Woods et al., 2016).

Dothistroma septosporum and various needle pathogens were recorded in Colombia during the 1980s (Gibson, 1979, 1980; Ivory, 1987). However, information regarding their relevance is limited, especially regarding their distribution, host range and impact (Ivory, 1987). During the course of the last 10 years, *D. septosporum* has severely affected plantations of non-native *P. tecunumanii* (Low Elevation population) and *P. oocarpa* in Colombia (Rodas et al., 2016). In this regard, *D. septosporum* has emerged as an important pathogen in Colombia where unique environmental conditions and biotic factors have increasingly contributed to disease development (Rodas et al., 2016).

In Colombia, the diverse climatic conditions and topography across different regions is typically characterized by a relatively even distribution of rainfall throughout the year (Urrea et al., 2019), particularly in areas where *Pinus* spp. are planted. The occurrence of persistent rainfall is especially favourable for needle infection by *D. septosporum* (Ivory, 1987; Woods et al., 2016). The aim of this study was to determine the months of peak conidial production in Colombia, during the initial outbreaks of the disease between 2009 and 2011, and to examine the climatic conditions that influence patterns of *D. septosporum* infection.

2 | METHODS

2.1 | Study location

Field surveys were conducted across the distribution of *P. tecunumanii* Low Elevation (LE) plantations from October 2010 to December 2011. The surveys covered three different geographic areas (North, Central and South) and nine forestry farms located in the provinces of Caldas, Cauca, Risaralda and Valle del Cauca, in Colombia (Figure 1). The total surveyed area consisted of *P. tecunumanii* LE pines of two origins (Suiza and Yucul). Subsequent to their establishment, the plantations were regularly monitored for insect pests and diseases (Rodas & Wingfield, 2020) and particularly for *D. septosporum*. *Pinus tecunumanii* LE plantations severely affected by DNB were selected to instal spore traps. These plantations included locations across the three different geographic areas (North, Central and South), as well as different ages of trees (4–7-years-old), climatic conditions and altitudes (Table 1).

2.2 | Spore trapping

In Colombia, personal observations by Rodas CA, showed that DNB symptoms appear more evident during the low-rainfall months (Colombian summer) between December to February and during the mid-year period between June and August. This is followed by heavy defoliation that becomes most obvious at the end of the low-rainfall months of January and February, and July to August, respectively. During the high-rainfall months (Colombian winter), *D. septosporum* infects the newly produced needles between February to May and September to mid-November. To measure *D. septosporum* conidial production during these periods, spore traps were installed in nine forestry farms. Each forestry farm had one compartment with ten plots and two traps were installed per plot. A total of 180 spore traps were evaluated to measure *D. septosporum* conidial dispersal (9 farms × 10 plots × 2 spore traps per plot).

Spore traps consisted of microscope slides coated with petroleum jelly similar to those used in other tree disease studies (Boateng & Lewis, 2015; Ostry & Nicholls, 1982; Swart et al., 1987). Each trap held two slides mounted horizontally with the trap side facing upwards and these were placed 1.2 m above ground level (Figure 2a). Slides in all traps were replaced every 15 days (twice per month) and evaluated from October 2010 to December 2011, corresponding to a total of 300 evaluations per farm. In order to facilitate counting the *D. septosporum* conidia, slides were stained with lactophenol cotton blue. The total number of conidia were counted across a 2 cm^2 area in the middle of the slide using a Nikon Eclipse E200 microscope at 40× magnification.

2.3 | Conidial dispersal per zone and farm

Conidial production was calculated as the mean number of conidia counted per farm and date. To consider differences in conidial production among the different geographic zones an ANOVA was used. The "zones" were included as an explanatory variable in the model and the "evaluation dates" were included as a covariable to account for repeated measures. Differences between means ($p < .05$) for the explanatory variables were tested with Tukey's HSD test. The influence of the different farms on the conidial production was analysed in the same way. The "agricolae" package of the software R 4.0.0 (R Core Team, 2020) was used to analyse conidial production.

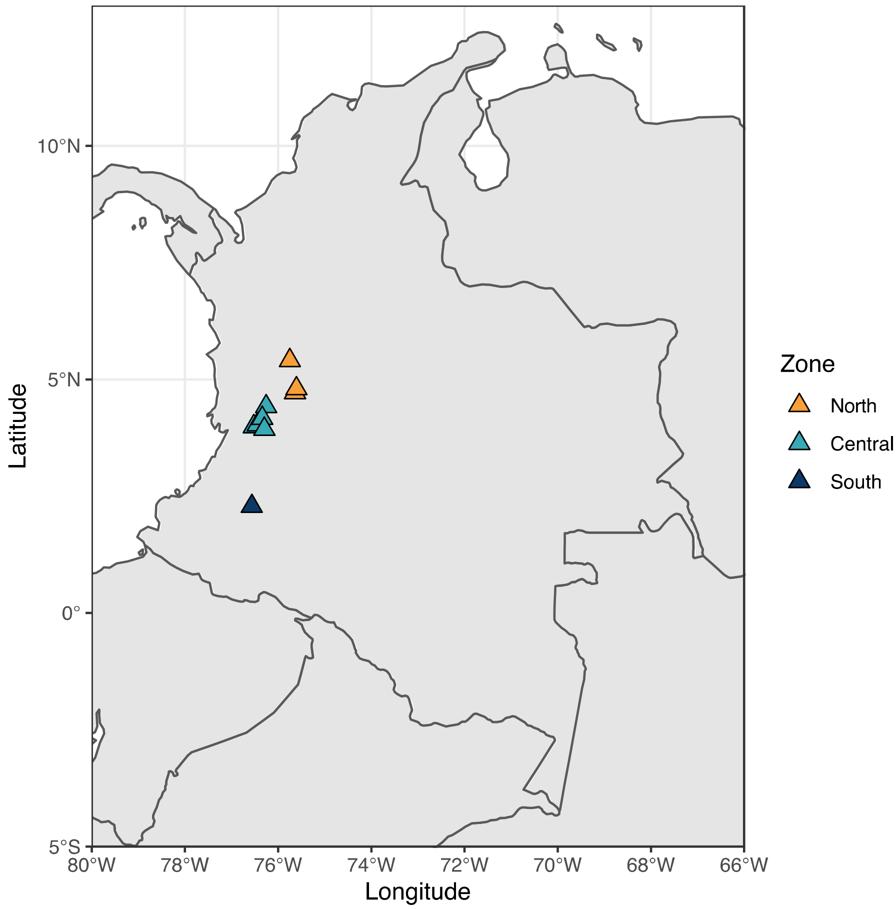

FIGURE 1 Geographic distribution of the forestry farms used for the spore traps of *Dothistroma septosporum* in Colombia located in the North, Central and South Zones, on *Pinus tecunumanii* LE.

2.4 | Relationship between conidial dispersal and environmental variables

Preliminary analyses showed that humidity and temperature were not linearly related to conidial dispersal. Therefore, a Generalized Additive Model (GAM) was used to analyse a flexible non-linear relationship between the humidity, temperature and conidial dispersal (Austin & Meyers, 1996; Guisan et al., 2002; Wood, 2006). The conidial dispersal was included as a response variable in the model. The explanatory variables included (1) rainfall (2) smooth temperature (3) smooth humidity and (4) smooth temperature by humidity. We also included the "evaluation dates" to account for repeated measures of the study design. The statistical analyses were conducted using the "mgcv" package in the software program R 4.0.0 (R Core Team, 2020). The forestry farm Tesalia was not included in the GAM because it lacked environmental variables.

3 | RESULTS

3.1 | Conidial dispersal

Dothistroma septosporum conidial dispersal in *P. tecunumanii* LE plantations occurred throughout the year in all three geographic zones that were evaluated. The peak periods of dispersal were between November and January in 2010 as well as between November and December in 2011. The months with the lowest levels of dispersal were between March and May 2011 (Figure 3). In months having high levels of rainfall, some difficulty was experienced reading slides due to traps being covered with debris.

3.2 | Conidial dispersal per zone and farm

Dothistroma septosporum conidial dispersal differed significantly between the zones ($p<.001$). The lowest level of conidia encountered was in the Central Zone, in comparison with the North and South Zones (Figure 4a). Conidial dispersal also differed significantly between the farms ($p<.001$). Analysis per farm showed that Cedral, located in the North Zone, had the highest conidial dispersal whereas Samaria, located in the Central Zone, had the lowest dispersal (Figure 4b).

3.3 | Relationship between conidial dispersal and environmental variables

Each zone had different environmental conditions during the study. For example, the North Zone had high levels of moisture and moderate temperatures with averages of Relative Humidity (RH) 83%

TABLE 1 Location of the spore traps in nine forestry farms in Colombia distributed in three different geographic areas (North, Central and South) with *Pinus tecunumanii* commercial plantations.

Zone	Province	Forestry farm	Coordinates		m.a.s.l.	Rainfall[a]	Provenance planted[b]	Date planted	First report of *Dothistroma septosporum*
			Latitude	Longitude					
North	Caldas	Argentina	5°24′20″N	75°44′55″W	2355	3150	Suiza LE	December 2005	July 2008
	Risaralda	Cedral	4°42′57″N	75°38′15″W	1909	4346	Yucul LE	October 2006	November 2008
	Risaralda	Tesalia	4°48′15″N	75°36′31″W	1949	4082	Suiza LE	December 2005	July 2008
Central	Valle del Cauca	Alaska	4°03′24″N	76°25′09″W	1854	2712	Yucul LE	December 2005	June 2008
	Valle del Cauca	Concha	4°00′46″N	76°25′24″W	1715	2276	Yucul LE	July 2004	June 2008
	Valle del Cauca	Esmeralda	4°03′27″N	76°25′53″W	1976	1571	Yucul LE	December 2005	June 2008
	Valle del Cauca	Samaria	4°01′47″N	76°26′30″W	1680	2276	Suiza LE	October 2007	June 2008
	Valle del Cauca	Unión_C	4°25′13″N	76°15′24″W	2104	2902	Yucul LE	August 2006	May 2009
South	Cauca	Unión_S	2°17′04″N	76°33′56″W	2695	3102	Suiza LE	December 2004	February 2009

[a]Average rainfall presented from October 2010 to December 2011.
[b]Seed orchards only from Low Elevation (LE).

and temperature (T°) of 17°C. In contrast, the Central Zone had an average RH of 79.7% and T° of 20.2°C; and the South Zone had an average RH of 80% and T° of 14.5°C, with more marked changes between dry and wet seasons. In terms of precipitation, the annual average rainfall was higher in the North Zone ($\bar{x}$: 3859.3 mm), followed by the South Zone ($\bar{x}$: 3102 mm) and the Central Zone ($\bar{x}$: 2347.4 mm). The Colombian winter months presented a higher rainfall average than the summer months (Figure 3).

The generalized additive model (GAM) showed that conidial dispersal was influenced by humidity, temperature and the interaction between these environmental variables (Table 2a). Dispersal was higher where temperature and humidity were lower, but this trend was not linear (Figure 5). Conidial dispersal was not significantly influenced by rainfall ($p < .001$) (Table 2b). The rainfall during the winter and summer months did not influence conidial dispersal, because the environment was oversaturated with moisture during the collections of the slides for conidial count (Table 2b). As an example of this, in months where the rainfall was registered lower than 76 mm, the relative humidity remained at a minimum of 65% or higher (data not shown).

4 | DISCUSSION

This is the first study to examine the patterns of *D. septosporum* conidial production and infection in Colombia under tropical environmental conditions on a commercially propagated species such as *P. tecunumanii* LE. An important outcome was that *D. septosporum* conidia are dispersed throughout the year in Colombia in different forestry zones. This was consistent with the fact that the areas studied have all-year rainfall and conditions suitable for continuous conidial production and thus infection potential. These results suggest that multiple asexual generations of the pathogen cause repeated new infections, contributing to the high levels of disease that have been observed in Colombian plantations (Rodas et al., 2016; Rodas & Wingfield, 2020).

Temperature and relative humidity were the key drivers resulting in the release of conidia throughout the year with the highest peaks between the end of the high-rain months and the beginning of the low-rain months (Colombian winter to summer). *Dothistroma septosporum* conidial production is conducive in the three zones as optimal temperatures are above 10°C (Dvorak et al., 2012). Other studies have shown that under greenhouse conditions, a combination of day and night temperatures (20/12°C) with continuous moisture, greatly favour the incidence of DNB (Gadgil, 1974).

The temperature and the increase in humidity and precipitation due to the La Niña phenomenon in Colombia during this time (Rodas et al., 2016) has favoured development of *D. septosporum* in commercially propagated plantations of *P. tecunumanii* LE. The continuous rain splash and rolling mist clouds (Figure 2b) most likely also facilitated the dispersal and spread of the conidia of *D. septosporum* (Gibson et al., 1964; Mullett et al., 2016) to neighbouring trees and possibly other areas in the country where pines are grown. Through artificial inoculations and field observations, the formation of

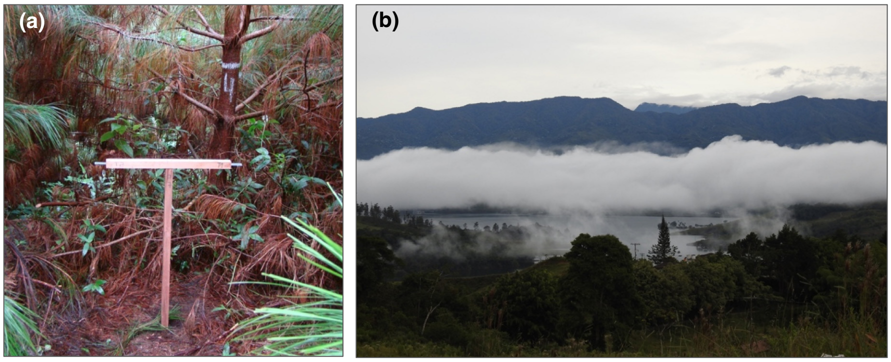

FIGURE 2 Spore trap in a *Pinus tecunumanii* LE plantation severely affected by *Dothistroma septosporum* (a). Conidial dispersal of *D. septosporum* by cloud mist surrounding *Pinus* plantations in Colombia (b).

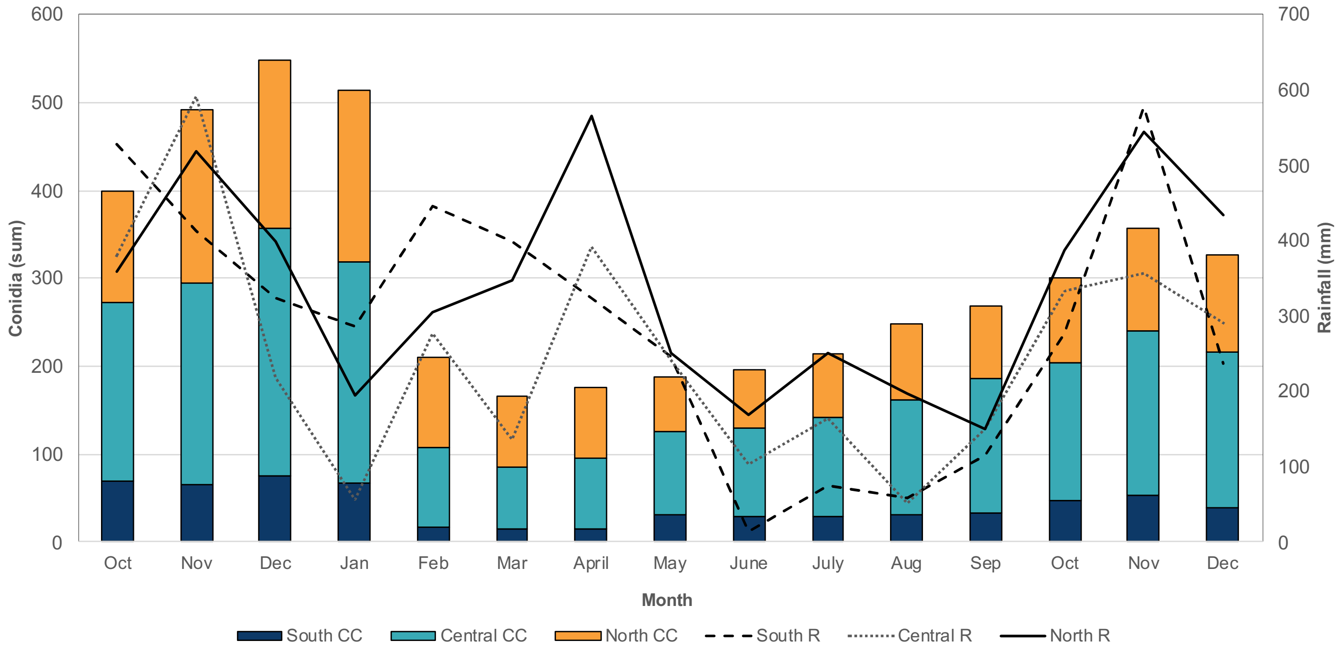

FIGURE 3 Sum of the *Dothistroma septosporum* conidia count (CC) in each of the three zones of Colombia per month evaluated (columns). The average monthly rainfall (R) (in mm) per area is represented as dotted continuous lines.

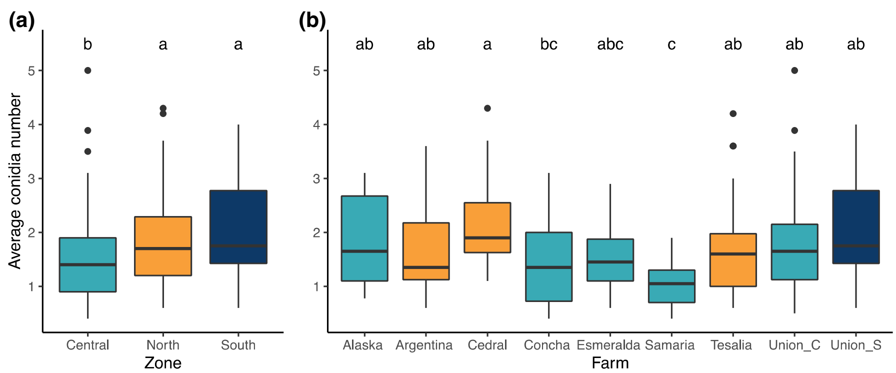

FIGURE 4 Box plots of the mean number of conidia counted in the different (a) zones, and (b) farms between October 2010 and December 2011. The shared colours correspond to zones and farms. Bars show standard errors and the different letters indicate the significance differences ($p < .05$).

D. septosporum stromata has been recorded within five to 16 weeks post-infection in different countries and on various hosts (Fraser et al., 2015; Gilmour, 1981; Woods et al., 2016). The present study has shown that in Colombia, under optimal weather conditions, *D. septosporum* could have between 2 and 10 infection cycles per year. Results of this study suggest that in tropical countries, such as Colombia, the unique climate characterized by year-round rainfall results in patterns of infection that differ from countries such as New Zealand and Chile, where rainfall occurs during discrete periods (Woods et al., 2016). Conidial dispersal and infection by *D. septosporum* is thus linked to specific months in those countries and not throughout the year as seen in Colombia.

In Colombia, the year-round dispersal of *D. septosporum* conidia constitutes a threat not only to *P. tecunumanii* LE plantations, but to

TABLE 2 Results of the generalized additive model to analyse the influence of (a) humidity and temperature (non-parametric coefficients), (b) and rainfall (parametric coefficient), on the number of conidia of *Dothistroma septosporum* calculated as the mean number of conidia counted per farm every 15 days, from October 2010 to December 2011.

(a) Non-parametric coefficients	Estimated.df	Ref.df	*F*	*p*-Value
s (Humidity)	2.245	2.865	5.262	**.003**
s (Temperature)	1.973	2.524	13.166	**<.001**
s (Humidity, Temperature)	6.649	9.197	5.647	**<.001**
s (Forestry Farm)	0.000	1.000	.000	**<.001**
s (Evaluation date):forestry farm	9.231	9.835	27.952	**<.001**
(b) Parametric coefficients	**Estimate**	**SE**	***t*-Value**	***p*(>|*t*|)**
Intercept	1.909	0.116	16.448	**<.001**
Rainfall	0.000	0.001	0.684	.495

Note: Significant *p*-values are indicated in bold.

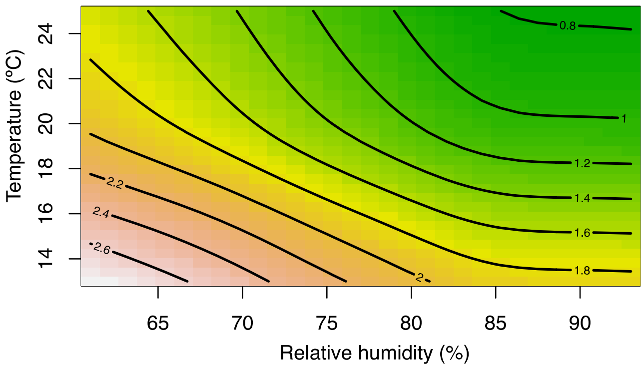

FIGURE 5 Non-linear relationship between the relative humidity (%), temperature (°C) and conidial production of *Dothistroma septosporum* in Colombia. Conidia production was calculated as the mean number of conidia counted per farm every 15 days, from October 2010 to December 2011.

other species in the country. Epidemiological studies such as the one presented here will be important to ensure long-term sustainability of these plantations. Historical data can also provide useful information about the epidemics of *D. septosporum* that have been attributed to changing climatic conditions as is the case of DNB in Canada (Watt et al., 2021; Woods, 2011; Woods et al., 2005). Furthermore, population genetic studies should be undertaken to better understand how this needle pathogen entered Colombia and how future introductions can be avoided.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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