RESEARCH ARTICLE

Drought responsiveness in two Mexican conifer species forming young stands at high elevations

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Abstract

Aim of study: To determine the response of high-altitudinal forests to seasonal drought.

Area of study: Monte Tláloc, Estado de México and Rancho Joyas del Durazno, Municipality of Río Verde, San Luis Potosí, México.

Materials and methods: In this study, we evaluate the response to drought and hydroclimate in two young Mexican conifers sampled at high elevation, correlating records of tree-ring growth and the Normalized Difference Vegetation Index (NDVI).

Main results: The results show that *Pinus teocote* and *Abies religiosa* are vulnerable to the precipitation regime and warm conditions of winter-spring. The physiological response mechanisms seem to be differentiated between the species, according to the effects of drought stress. The NDVI demonstrated the different temporal responses of the species according to their inherent physiological mechanisms in response to hydroclimatic limitations. This differentiation can be attributed to the spatial variation present in the particular physical and geographic conditions of each area. The dry and warm seasonal climates reveal *P. teocote* and *A. religiosa* to be species that are vulnerable to drought conditions. However, further evaluation of the resistance and resilience of these species is necessary, as well as disentanglement of the effects of associated mechanisms that can influence the predicted processes of extinction or migration.

Research highlights: Pinus teocote and *Abies religiosa* are vulnerable to the seasonal drought conditions. These results are of particular importance given the climatic scenarios predicted for elevated ecotones. Tree-ring widths and NDVI improved the response of radial growth to the climate, enhancing our understanding of forest growth dynamics. The response to climatic variability depends on the particular species.

Keywords: High elevation; tree-ring; ENSO; NDVI; climate-growth relationship.

Abbreviations used: Normalized Difference Vegetation Index (NDVI); Tree-Ring Width (TRw); precipitation (PP); maximum temperature (Tmax); minimum temperature (Tmin); El Niño-Southern Oscillation (ENSO); Climatic Research Unit Time-series data version 4.04 data (CRU TS v. 4.04); Standardized Precipitation-Evapotranspiration Index (SPEI); Climatic Research Unit Time-series data version 4.03 data (CRU TS v. 4.03); first-order autocorrelation (AC); mean sensitivity (MS); mean correlation between trees (Rbt); expressed population signal (EPS); Ring Width Index (RWI).

Introduction

The conifers of Mexico are present across almost their entire biogeographic range (Farjon & Styles, 1997). However, climatic variations act to modify their boundaries of distribution (Martínez-Meyer, 2005). It is well documented that trees offer unique opportunities for research at their highest limits of distribution, due to their high susceptibility to the variable climate found in these ecotones (Correa-Díaz *et al.*, 2019; Liu *et al.*, 2016).

When attempting to quantify the delay that occurs in terms of manifestation of the consequences of water shortage, tree-ring growth analysis can be complemented by vegetation indices (Vicente-Serrano *et al.*, 2016; Alcaraz-Segura *et al.*, 2008). One of the most popular of these indices is the Normalized Difference Vegetation Index (NDVI), which serves as a proxy for the productivity of the ecosystem (Babst *et al.*, 2014).

Primary reports argue that Central Mexico has been drier than preceding decades as a consequence of increased temperatures and changed precipitation regimes (González-Cásares *et al.*, 2017). Future episodes of drought are expected to become more frequent as the climate becomes warmer (Williams *et al.*, 2013). This hydroclimatic variability has triggered concern among the scientific community regarding how these ecotones will cope with climate change (Manzanilla-Quiñones *et al.*, 2020).

This region hosts representative species, such as *Abies religiosa* (Kunth) Schltdl. et Cham. and *Pinus teocote* Schiede ex Schltdl. which are currently changing in age and structure into younger stands (Santiago-García, 2020). Although previous studies that focused on old trees have reported high sensibility to climate vulnerability (Villanueva-Díaz *et al.*, 2015), there is a lack of contribution in terms of young stands at high elevations. These species also play an important role in terms of providing goods and forest environmental services to the nearby population, as well as constituting a crucial reserve for wildlife (Rzedowski, 2006). The species addressed here therefore represent a strategic opportunity to further our understanding of drought-climate responses in representative forests stands.

The elevational threshold for drought-sensitivity in these conifers could enhance our understanding of forest dynamics in high elevation forests. In this study, we conducted the first comparison of radial growth sensitivity to drought in two conifer species that form pure and young stands in high-altitudinal ecotones. In particular, we a) characterized the growth responsiveness of two species to hydroclimate, drought and the ENSO, and b) determined whether there was a relationship between tree-ring growth and NDVI values and the occurrence of seasonal drought. We hypothesized that young stands growing in sub-alpine conditions will present differential sensitivity to warm and dry winters, the ENSO circulatory phenomenon and the monthly values of NDVI.

Materials and methods

Study area and data acquisition

We sampled trees in two sites at the maximum range of their elevational distribution where these species are dominant on the studied mountain (Fig. 1, Table S1 [suppl.]). Both sites correspond to unevenly aged forest, currently under forest management, that forms young stands. While *P. teocote* forms pure stands, *A. religiosa* (Basal Area > 60%) is associated with *P. hartwegii*. The two studied species play a role of high social importance since a range of environmental goods and services are produced in these forests, directly benefitting this densely populated region. In ecological terms, these forests are also of considerable importance due to their provision of food and habitat for wildlife (Torres-Rojo *et al.*, 2016).

Given that dendrochronological studies in Mexico have been oriented mainly towards old trees or those growing in marginal conditions (Villanueva-Díaz *et al.*, 2018), we then decided to use an alternative sampling approach in order to achieve greater representativeness of forest condition (see Pollard, 1971). We therefore extracted at least two cores per tree from twenty trees using a Pressler increment borer (5 mm) at height 1.3 m above ground level. From a random and centrally located tree in the population center, the nineteen closest trees were then sampled, in a strategy adopted to more accurately characterize the population.

The studied areas are mostly fragmented due to pressures exerted from high population densities at their edges. Historically, timber logging of large trees has been the main management undertaken, although land use changes as well as livestock and agricultural activities are also practiced. Moreover, forest policies and legal regulations are continuously changing over short times. These difficulties have degraded the original forest stands, affecting species composition, age, structure and genetic load, and producing young stands with poor stocks and subsequently lower harvests (Torres-Rojo *et al.*, 2016). We argued that these young stands are currently representative of the central Mexican forests.

Dendrochronological processing and NDVI

Tree-ring cores were mounted on wooden frames with PVA glue. To facilitate observation and measurement of the tree-rings, the samples were polished using progressively coarse to fine sandpaper. Tree-ring cores of different individuals of the same species and zone were synchronized through identification of the characteristic sequences of radial growth. Tree-ring width (TRW) was measured using the VELMEX ultra-precision
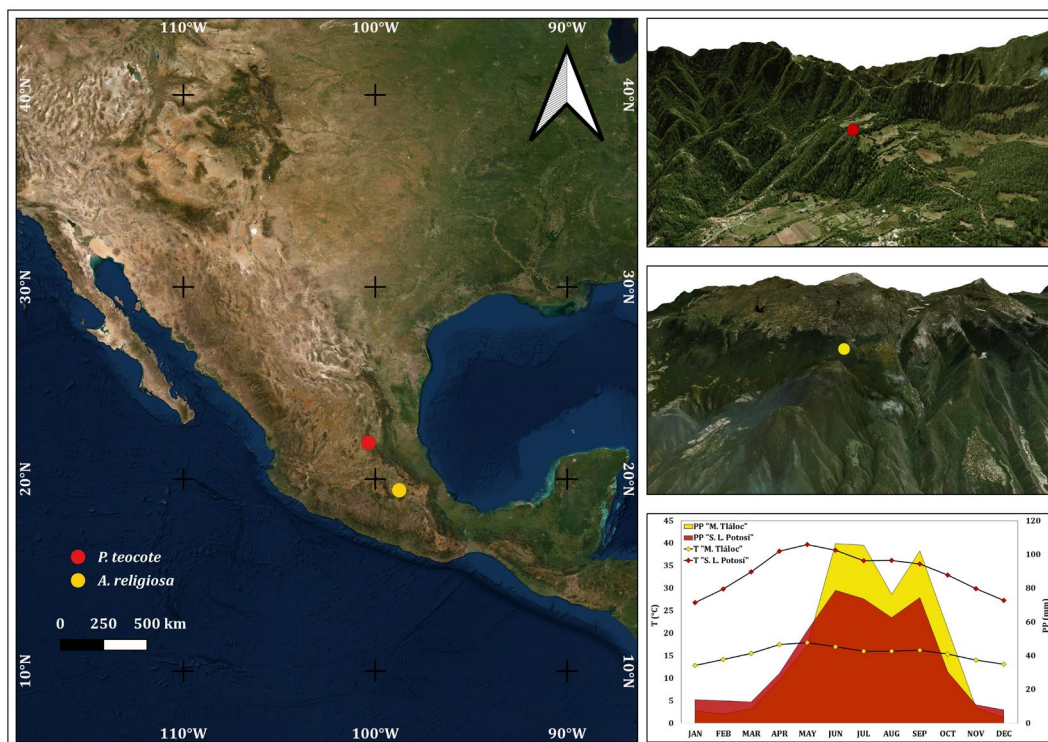
Figure 1. Study area of the two sampled sites.

(0.001 microns) system. Once the measurements were completed, dating was reviewed using the program CO-FECHA, which compares the series of each tree against a master chronology for each species (Holmes, 1983). We constructed tree-ring residual chronologies for each species using TRW with the dplR library (Bunn, 2008) of the software R (R Development Core Team, 2018). By a using a negative exponential model as a standardization process, we corrected the biological and geometric growth trends. An autoregressive model was then fitted to each of these detrended series to remove the temporal autocorrelation associated with the previous year´s growth. We also calculated the expressed population signal (EPS) for the period 1985-2019, in order to determine the suitability of the species chronologies for capturing the hypothetical population signal (EPS > 0.85; Wigley *et al.* 1984).

For the NDVI, we used the global dataset taken from the Google Earth Engine (Gorelick *et al.*, 2017), through the MODIS (Moderate-Resolution Imaging Spectroradiometer) arrangement (see https://lpdaac.usgs.gov/products/mod13a1v006/). For each site, we obtained monthly values from calculation of NDVI = (NIR-R / (NIR+R), for the period 2000-2020, where NIR and R are near infrared and red values, respectively. We excluded images covered by clouds. Our approach assumed that NDVI values at the pixel level are representing the trees sampled; however, our spatial data considered coexisting tree and shrub species and the understory, which have wider seasonal dynamics.

Climate-growth relationships

Pearson correlation analysis was conducted to evaluate the responses of wood growth to the climatic variables, relating residual chronologies to the monthly variables of precipitation (PP), maximum (Tmax) and minimum (Tmin) temperature, and the El Niño-Southern Oscillation (ENSO) for the two species during the period corresponding to each chronology.

The climatological data of these sites were obtained from the Climate Explorer website (https://climexp.knmi.nl/start.cgi) and extracted at a resolution of 0.5° from the database CRU TS v. 4.04.

To compare the growth response to drought between the two species in the study sites, the Standardized Precipitation-Evapotranspiration Index (SPEI) was used (Beguería *et al.*, 2014). The data were extracted from the SPEI webpage (https://spei.csic.es/) at a resolution of 0.5° from the database CRU TS v. 4.03 with a scale of 1 to 48 months from January to December of the years of growth for both species.

Results

Pine growth patterns of studied species are presented in Table 1. *A. religiosa* presented the widest rings and also the lowest mean sensitivity. The highest coherence in growth between conspecific trees was observed in *P. teocote*. Both of these species reached an EPS that exceeded the threshold of 0.85 (Wigley *et al.*, 1984).

Table 1. Dendrochronological statistics of the sampled species considering the common interval 1985-2019.

Species	No. of trees	No. of radii	No. of years	Growth-ring width (mm)	AC	MS	Rbt	EPS
P. teocote	19	38	44 ± 2	2.50 ± 0.15	0.54 ± 0.04	0.41 ± 0.01	0.59	0.97
A. religiosa	20	40	36 ± 1	4.58 ± 0.22	0.63 ± 0.04	0.26 ± 0.01	0.37	0.95

AC: first-order autocorrelation, MS: mean sensitivity, Rbt: mean correlation between trees, EPS: expressed population signal

With reference to the chronologies shown in Fig. S1 [suppl.], the two species presented similar growth patterns characterized by pointer years, in which wide rings were presented in the wet years 2010, 2004, 1997, and 1992. In contrast, narrow tree-rings were presented in the years linked to drought episodes, such as 2011, 2005, and 1998.

Both species presented significant correlations with the climatic and drought data ($p < 0.05$) (Fig. 2). Initially, for *P. teocote*, negative correlations were observed for Tmax in the months of September, October, November and December of the previous year, as well as in the period January to July of the year of growth. Positive correlations for Tmin were obtained for September and October of the previous year, including March and June of the current year. Conversely, we found a negative correlation for September in the year of growth. For the PP data, positive correlations were observed for January and the period April to July of the year of growth, as well as a negative correlation for August

in the year of growth. For the ENSO data, no significant correlation was obtained.

A. religiosa was negatively and significantly related to the Tmax data for the summer months (*e.g.* June, April, May). For the Tmin data, a positive correlation was obtained for the previous summer (June, July, August), autumn (October) and winter (December and February). Moreover, Tmin values from the early growing season during spring (*e.g.* March and April) were positively and significantly associated with radial growth. With regard to the PP values, this species had a positive correlation for March and April of the year of growth related to enhanced radial growth. With respect to the ENSO data, we found a positive association with growth during the period June to September in the year of tree-ring formation, albeit not significant.

From the SPEI values (Fig. 3), it was found that the species showed a similar correlation with the drought values: *P. teocote* presented a high correlation ($r = 0.6$) from
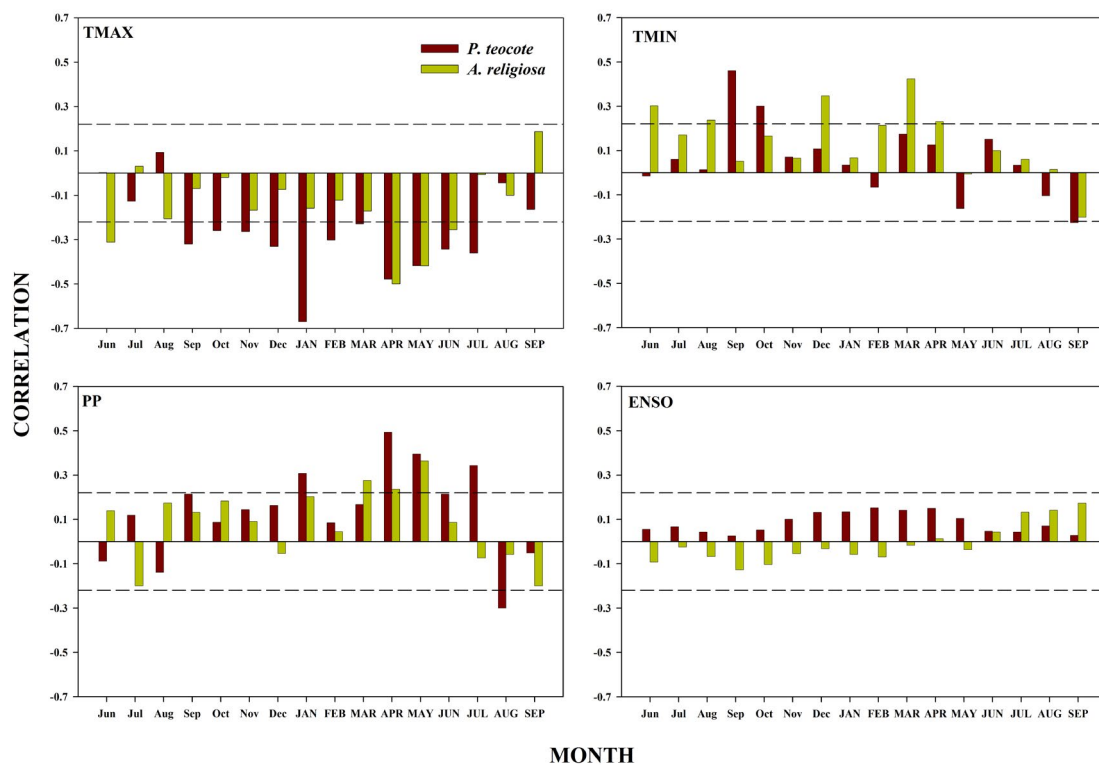

Figure 2. Climatic correlations of the monthly variables of precipitation (PP), maximum (Tmax) and minimum (Tmin) temperature, and the El Niño-Southern Oscillation (ENSO) with the growth-ring residual width index (RWI) for the two conifer species. The horizontal dashed and dotted lines indicate the 0.05 significance levels. Months of the previous and current years are abbreviated using lower and upper case letters, respectively.
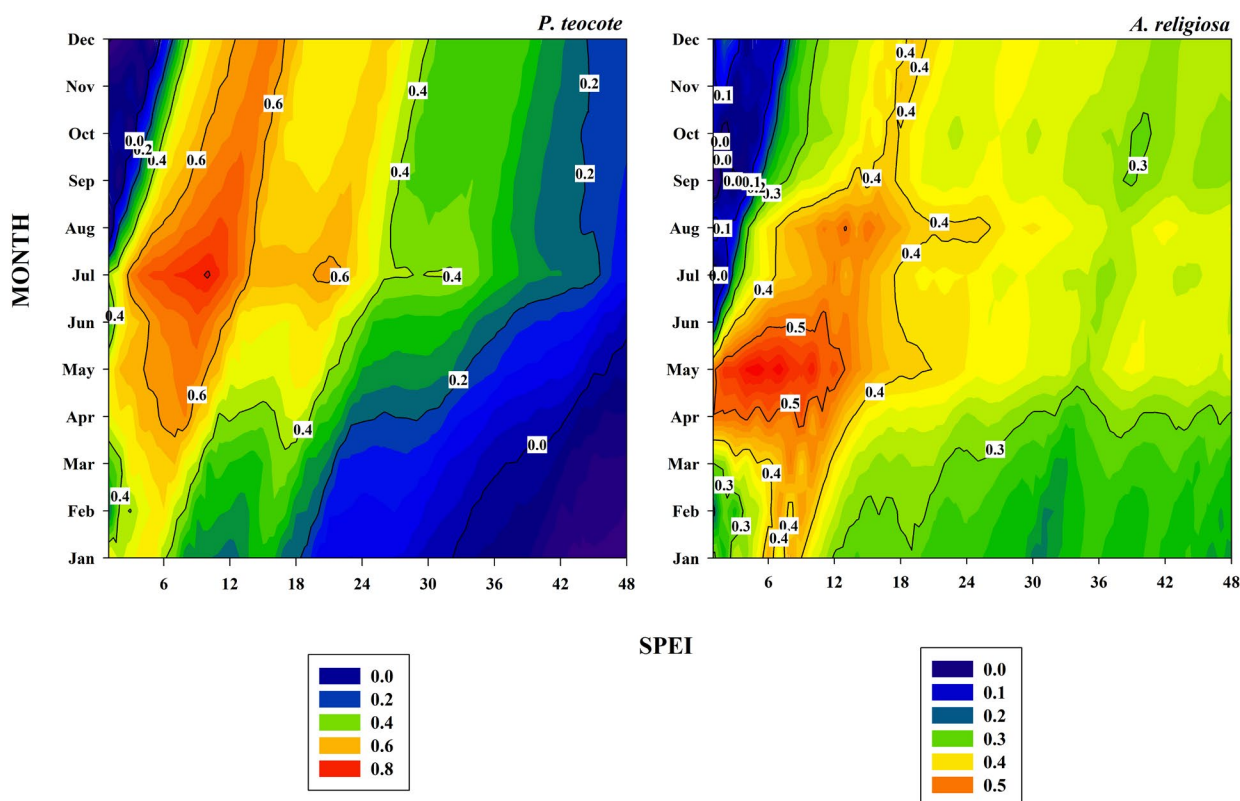
Figure 3. Growth-SPEI associations. Pearson correlation coefficients calculated between the SPEI drought index and the chronologies. Correlations were calculated considering 1- to 48-month resolutions (x-axes) and from January to December (y-axes). Significant correlations at the 0.05 level correspond to r > 0.30 or r < -0.30.

April to December for scales of 5 to 16 months, while for *A. religiosa*, high values of correlation ($r = 0.5$) were observed in April to June in scales of 0 to 14 months.

Graphically, patterns of correspondence were distinguished between the Ring Width Index (RWI) and the NDVI. In each case, the NDVI showed an increasing slope that simultaneously presented coherence with total growth-ring width (Fig. 4). Given that the NDVI behaves seasonally over the course of the year, Fig. S2 [suppl.] presents the significant correlations between the RWI and the monthly NDVI. A significant ($p < 0.001$) positive association was evident, but differentiated according to month and species. *Pinus teocote* presented positive correlations between the chronology and NDVI in April and July, while *A. religiosa* presented the highest positive (although not significant) value in May.

Discussion

High-elevation forests are among the most powerful "living labs" for testing the ecological and evolutionary responses of biota to geophysical influences (Körner, 1998). Here, we showed that drought acted to reduce the growth of two tree species from high elevations in central Mexico, whereas the seasonal wet climate enhanced radial growth. Specifically, warmer temperatures associated with dry episodes during the autumn and winter seasons are often related to narrow tree-rings (Villanueva-Díaz *et al.* 2018), while wet and cool winters events enhance radial growth, as reported by Gutiérrez-García & Ricker, (2019).

However, we found species-specific growth responses to hydroclimate, which are modulated by their dendrochronological potential (Table 1). Thus, *P. teocote* presents a greater relative change in ring-width index between consecutive years, which is often an indicator of high responsiveness to climate (see Fig. 2) and is in line with the findings of similar studies (Gutiérrez-García & Ricker, 2019; González-Cásares *et al.*, 2017). Furthermore, the highest coherence in growth between conspecific trees was observed in *P. teocote*, as an indicator of better growth synchrony among trees (Fritts, 1976). Indeed, this species showed more uniform growth patterns than *A. religiosa*, which can be modulated by specific-site conditions such as altitudinal range, climate type and drought tolerance, among others (Pompa-García *et al.*, 2021).

Responses to the Tmax affect growth through hydric stress (Fig. 2), as documented in similar studies (Astudillo *et al.*, 2017; Gutiérrez-García & Ricker, 2019. As expected, both species seem to have a disadvantage under warmer conditions, possibly exploiting the high temperatures to accelerate their metabolism and thus increase their
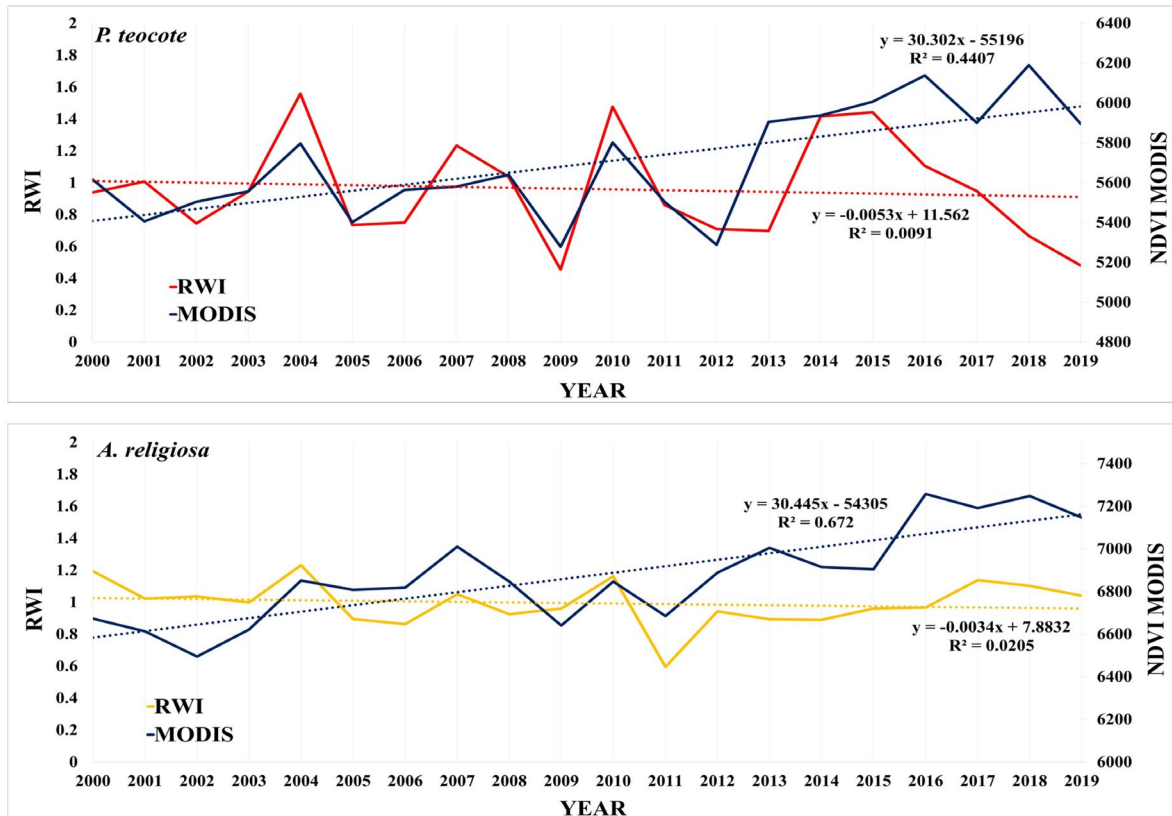
Figure 4. TRW-NDVI relationships in the two studied conifer species during the period 2000-2020.

evaporative demand. In line with a study of the species in neighboring sites (Astudillo *et al.*, 2017; Manzanilla-Quiñones *et al.*, 2020), our studies show that both *P. teocote* and *A. religiosa* seem to decline under drought conditions. It is well known that droughts are becoming more extreme and frequent, since high temperatures are driving increased evapotranspiration and reducing soil moisture (Williams *et al.*, 2013; Vicente-Serrano *et al.*, 2016). Consequently, the species addressed here are vulnerable to hydroclimate variations in face of climate change.

High previous winter precipitation, combined with cool conditions, provides moisture availability in the early growing season (*e.g.* spring), when the studied species typically begin to grow. Such hydroclimatic conditions allow moisture to penetrate the deeper layers of the soil that are important for the formation of wood, and this water is thus available for early growth during spring (González-Cásares *et al.*, 2017).

The climate of the study area is subjected to the influence of the ENSO (Villanueva-Díaz *et al.*, 2015; Gutierrez-García & Ricker, 2019), but non-significant relationships were found in our young stands (Fig. 2). Conversely, we expected that the ENSO would reflect hydroclimatic conditions for the young populations living at high elevations. It was evident that the ENSO differentially affects species subjected to similar regional climate conditions. We therefore argue that different growth sensitivities to drought could be used to infer species drought tolerances.

Although analysis of the dependence of radial growth on stand age is beyond the scope of this study, we partially attribute the lack of influence of the ENSO on the study species to physiological processes that vary with tree age (Fritts, 1976). Photosynthetic capacity, and thus ring growth, diminishes with individual age, causing hydraulic limitation (see Carrer & Urbinati, 2015). This restriction then causes greater climatic sensitivity in older individuals than in their younger counterparts, and has usually been detected in neighboring sites (Villanueva-Díaz *et al.*, 2018). In this way, we speculate that the ENSO causes differential effects of sensitivity to the climate in adult compared to younger woodland since the former presents higher rates of evapotranspiration and the latter presents lower rates of photosynthesis. We also hypothesized those other circulatory phenomena and/or monsoon rains serve to counteract the potential effect of the ENSO by reducing drought stress in the trees.

However, not all growth processes are related simply to the ENSO. For example, aspects of the plant architecture must still be considered, including root length and crown coverage, among other contrasting traits among the age classes. Given that the forests of the region are becoming younger, these findings highlight the implications for management practices, including relative water balances since these basins supply the hydric systems of the area of influence. Here, we document that these stands are generating mechanisms of adaptation that are

different to those that have normally been reported in previous studies.

Both conifer species were negatively affected by drought (Fig. 3). The values of correlation with drought indices were observed to be high, although only for short periods, which can lead to changes in the vegetation (Vicente-Serrano *et al.*, 2016). Thus, *P. teocote* and *A. religiosa* are intolerant of high temperatures and low levels of precipitation (Fig. 2 and 3).

Previous study has been conducted with the climatic drivers of tree growth and NDVI data in the high-elevation forests of central Mexico, reporting that the mature trees presented decadence during the second half of the 20th century (Correa-Díaz *et al.*, 2019). However, studies of young stands remain scarce in this region. The young trees presented responsiveness to climatic variability, conferring greater importance to our sampling strategy and anticipating new insights in dendroecological knowledge (Pompa-García *et al.*, 2020).

The approach of linking tree-ring growth to the values of NDVI makes it clear that the trees have mechanisms of rapid response to the conditions of climatic variability (Fig. S2 [suppl.]). The correlations presented in Fig. S2 [suppl.] show that there is a lag of one or two months between the occurrence of drought and its impact on the values of greenness. In this way, the trees seek to avoid having to tolerate hydric deficit for prolonged periods (Peña-Gallardo *et al.*, 2018). However, other factors remain to be studied, including species competition, site productivity and the inclusion of other drivers, such as CO_2, nitrogen deposition, etc. The severity of fire, for example, has an effect on growth-ring width (González-Rosales & Rodríguez-Trejo, 2004).

Responses in the NDVI and chronologies differed among species, indicating a differential response among these proxies. Positive relationships were found between NDVI variability and tree ring-growth in *P. teocote*. However, in *A. religiosa*, greenness and senescence of canopies were not coupled to the timing of radial growth (Fig. S2 [suppl.]). It seems that soil moisture or cambial dynamics influence NDVI values. Therefore, better quantification of the timing of wood formation and NDVI is required in these species. Despite the fact that the TRW data have provided more sensitive metrics of forest conditions than the NDVI data (Gazol *et al.*, 2018), one of the great advantages of the NDVI is that its values can help to identify early alarm signals of the tree response to climate, which can be subsequently confirmed by analysis of tree-ring growth (Vicente-Serrano *et al.*, 2016).

The NDVI dataset often presents certain limitations in the form of cloudiness and noise from radiometric and atmospheric correction, which should be addressed in further research. For the purposes of this study, the short seasonality of coverage was sufficient, but could be limiting for future studies.

Conclusions

We found differential growth responsiveness to drought between the two studied conifer species. Although both species are vulnerable to seasonal drought, *P. teocote* was the most responsive to drought. Wet and cool winter and spring conditions enhance radial growth; however, we did not find a positive response to the ENSO. We found positive interrelationships between the tree-ring growth data and NDVI values only for *P. teocote*. The differential coupling between tree-ring growth data and NDVI is attributed to interspecies-specific responses and physical site conditions.

Given that our results show the species-specific response to climate at high elevations, they are of particular importance in the face of global warming scenarios. In terms of the forest management, this could provide technical criteria, if we consider that these forests tend to become younger as a result of selective harvesting.

Acknowledgements

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