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Growth of *Pinus cembroides* Zucc. in Response to Hydroclimatic Variability in Four Sites Forming the Species Latitudinal and Longitudinal Distribution Limits

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Abstract: Climate change modifies the distribution and dominance of forest tree species, particularly near their distribution limits. This study used tree-ring width data for *Pinus cembroides* Zucc. at its distribution limits in Mexico and the SW USA to assess how tree populations responded to hydroclimatic variability. Indexed ring-width chronologies were built and correlated with climate and drought records at four marginal stands. We found that *P. cembroides* responds differently to climatic conditions depending on the bioclimatic and biogeographic conditions, with the forests situated in the driest area (Nuevo León) presenting the highest growth association to maximum temperatures and drought, while the forest situated in the wettest area (Puebla) was the least correlated to these hydroclimatic factors. In particular, dry and hot conditions, during the prior autumn and winter, reduced radial growth. Drought conditions could result in more vulnerable forests at the driest sites. These results advance our understanding of the radial growth responses of *P. cembroides* and similar widely distributed trees to climatic change near their biogeographical limits.

Keywords: dendroecology; drought; hydroclimate; ITRBD; radial-growth; tree-ring width

1. Introduction

Global climate change is predicted to have consequences for vegetation dynamics, causing profound changes in the distribution and mortality of trees and producing considerable alterations in forest structure, composition, and functioning [1,2]. For example, significant changes in the distribution and functioning of conifer forests (growth, mortality, reproduction) associated with altered precipitation regimes, severe droughts, and a notable increase in terrestrial temperature have recently been observed [3–5].

The natural variability of the climatic system depends, among other factors, on latitude, which determines the biogeographical frontiers or distribution limits of many trees [6]. The northern (leading edge) and southern (rear edge) distribution limits of a tree species should present different responses to climatic constraints, be it through local adaptations or by locally adjusting the phenotypic plasticity of the trees [7,8]. For example, it has been found that different pine trees face conditions of drought in different ways throughout their geographic distribution [9,10]. The vulnerability of certain trees, in terms of adaptation of their physiological functions to climatic and environmental

changes, provides an opportunity to analyze and evaluate population-level tolerance and behavior at their distribution limits [11]. Tree-ring analyses are useful tools for obtaining long-term information on growth sensitivity to climate stress through the quantification of climate-growth associations across tree distribution areas [12]. Those data improve our understanding of forest vulnerability to climate warming.

Analyses on climate-growth associations at the species' distribution limits, conducted from a dendrochronological perspective, i.e., by comparing climate and radial-growth data, generate knowledge that provides ecologists and managers with improved decision-making criteria for forest conservation [13]. In this sense, Mexico has a tremendous diversity of pines due to its climatic and topographic variation, which facilitates a biogeographic comparison of the response of radial growth to climate across the distribution ranges of specific taxa as pines [5]. For instance, *Pinus cembroides* is so widely distributed that it has a high dendrochronological application because it forms cross-datable and annual tree rings [14], and it occupies sites with different climate conditions [15], as well as diverse topographies and soil types [14,16–18]. For this reason, the wide geographic distribution of *Pinus cembroides* and its ecological amplitude provide an ideal opportunity to improve our understanding of the responses of its radial growth to hydroclimatic variability [19]. This study evaluates the association of *Pinus cembroides* to climate variables in radial growth in four sites forming the species' latitudinal and longitudinal distribution limits. By selecting such diverse biogeographical settings, we hypothesize that *P. cembroides* should present different sensitivity to climatic variables in these marginal populations; consequently, we expect to find greater sensitivity to drought conditions in the populations located at the driest sites, in this case near the easternmost distribution limit.

2. Materials and Methods

2.1. Study Species

The Mexican nut pine (*Pinus cembroides* Zucc.) is a conifer native to the mountainous zones of Mexico and Southwest (SW) USA and is distributed from the state of Puebla in Mexico to Arizona in SW USA (Figure 1a). It can reach up to 15 m in height with a diameter of 30 to 70 cm. It grows in sites with dry soils and rocky slopes or at the foot of mountains [20], and it is able to grow on steep slopes and sites with poorly developed soils. Nitrogen and phosphorous deficiencies in the soil limit the root and crown growth of *P. cembroides* [14]. This species is also able to tolerate drought, being considered very suitable for the reforestation of semi-arid regions [21]. *P. cembroides* usually occupies a transition zone between semi-arid plateaus and valleys and more mesic montane forests in areas with warm and dry climate conditions, with annual precipitation varying from 180 to 850 mm [14,22].

2.2. Study Sites and Dendrochronological Data

We obtained tree-ring width records from the International Tree-Ring Data Bank (ITRDB) [23], by searching for existing records of *P. cembroides*. This allowed us to select tree-ring chronologies from four areas (Table 1) featuring different hydroclimatic regimes and constituting the species' distribution limits (Figure 1a). These ranged from southern Arizona (Figure 1b) with an average temperature of 16.4 °C and mean annual precipitation of 450 mm, to the south of California (Figure 1c) with an average temperature of 20 °C and mean annual precipitation of 184 mm. The site in the state of Nuevo León (Figure 1d) presented a mean temperature of 24.1 °C, and a mean annual precipitation value of 660 mm, while the site in the state of Puebla (Figure 1e) was located in a zone with a mean annual temperature of 15.5 °C and mean precipitation of approximately 830 mm. These climate records were obtained using the climate research web page (<http://climexp.knmi.nl>) by extracting monthly mean temperature and total precipitation from the gridded CRU TS 4.01 database [24] at a resolution of 0.5°.

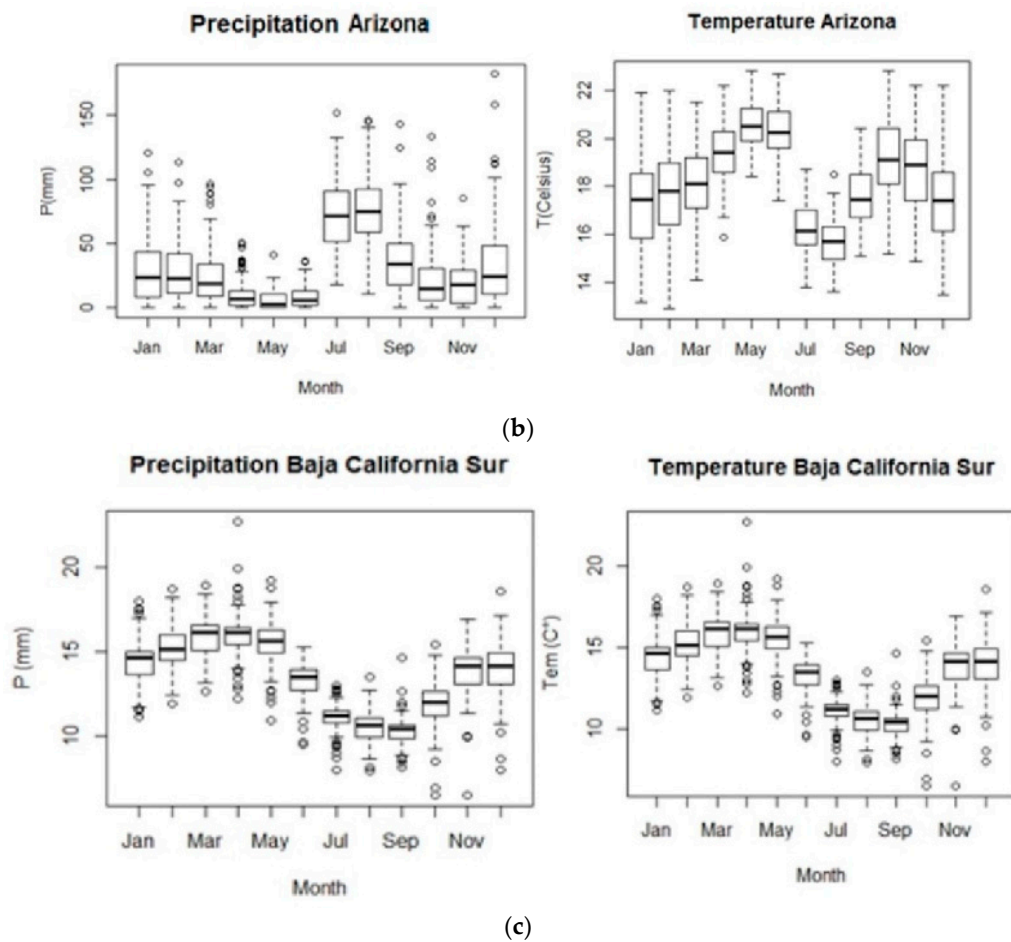
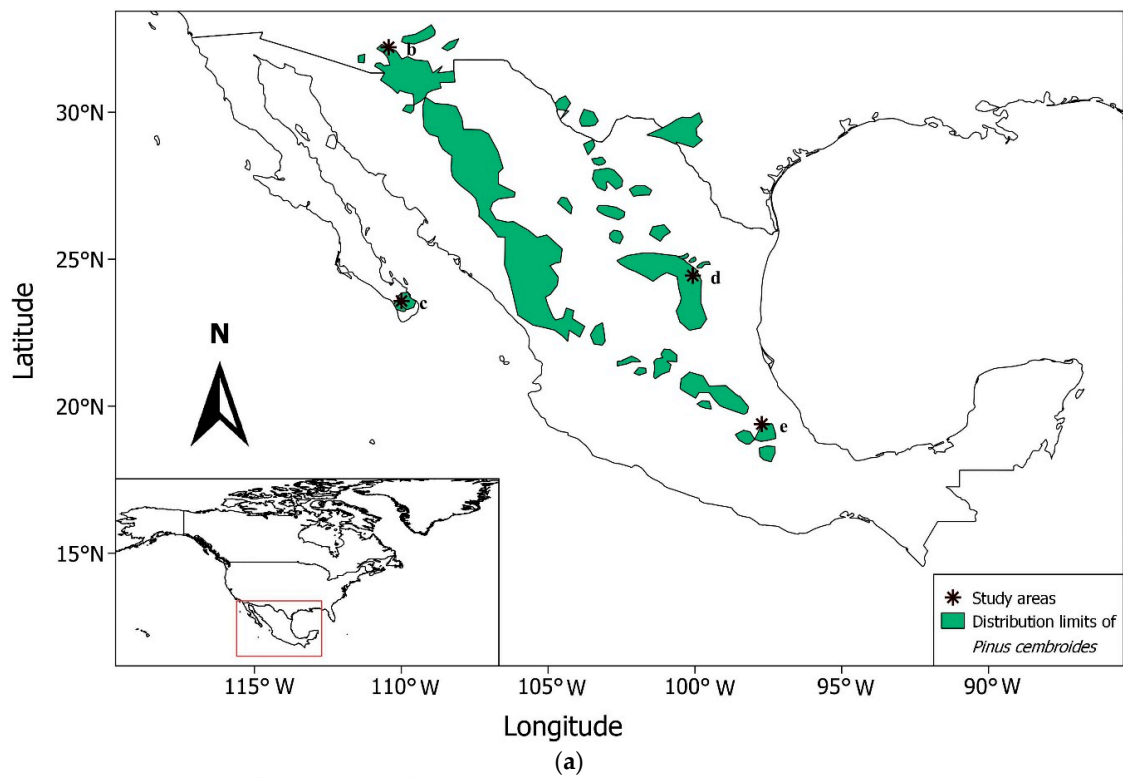


Figure 1. Cont.

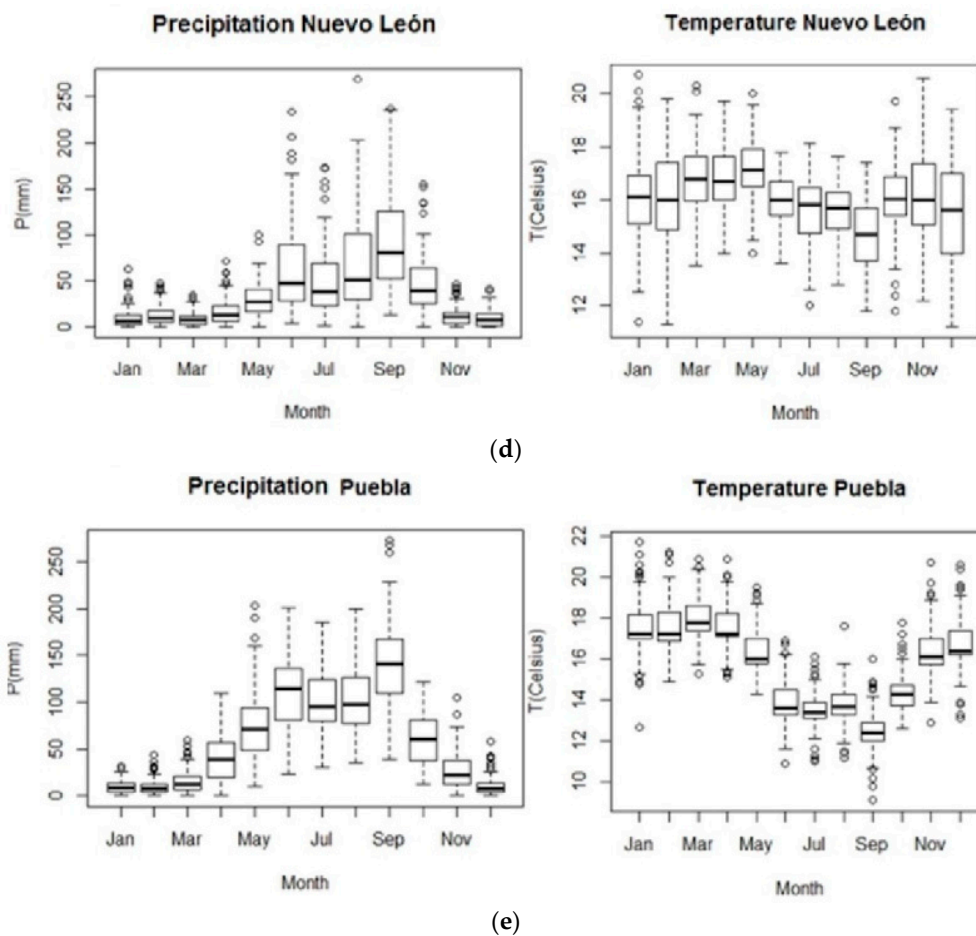


Figure 1. Map of the geographic distribution of *Pinus cembroides* and the location of the four study areas forming the species' distribution limits (a). The graphs show the distribution of monthly precipitation (P) and mean temperature (T) in these four sites: Arizona (b), California Sur (c), Nuevo León (d), and Puebla (e).

Table 1. Characteristics of the study sites. The International Tree-Ring Data Bank (ITRDB) code corresponds to the site where the tree-ring width chronology was developed.

Study site	Latitude (N)	Longitude (W)	Elevation (m a. s. l.)	ITRDB Code	Contributors
Arizona	32.21	110.43	1645	az506	J.A. Parks
California Sur	23.58	109.99	2300	mexi105	J. Villanueva
Nuevo León	24.73	100.12	1265	mexi093	J. Villanueva
Puebla	19.39	97.72	2582	mexi102	J. Villanueva

The available tree-ring width records were used to generate the corresponding indexed ring-width chronologies, except in the Arizona site, where the chronology was the only existing series. In order to eliminate biological effects and geometric trends due to widening of the stem and aging of the tree, the raw tree-ring width data were standardized and their trends eliminated with the library *dplR* [25] of the statistical software R (Version 1.0.143) [26]. Negative exponential functions were fitted to the tree-ring width data in order to obtain the residual series.

This conservative trend was used to preserve the greatest high frequency variability possible while maximizing the climate signal. Autoregressive models were adjusted to remove most of the first-order temporal autocorrelation and were averaged using biweight robust means to obtain the

mean residual series for each site. These averaged series of residual ring-width indices or pre-whitened chronologies were used in the subsequent climate- and drought-growth correlation analyses.

The statistical quality of the chronologies was assessed using the following statistics calculated over the period 1873–1987: mean and standard deviation (SD); first-order autocorrelation (AC), a measure of the year-to-year growth similarity; mean sensitivity (MS); a measure of relative year-to-year variability in width indices over consecutive rings; and the series intercorrelation or mean correlation of each individual series with the site mean series [27].

2.3. Relationships between Climate, Drought and Growth

Pearson correlation analyses were calculated to evaluate the radial-growth responses to monthly climate variables, relating the series of residual ring-width indices to mean maximum and minimum temperatures and precipitation over the common period 1901–1987. The climate data corresponded to the gridded CRU TS 4.01 database [24]. The correlations were calculated from the prior September to the current August based on previous studies [9].

In order to compare the growth responses to drought in the study sites, the drought index known as the Standardized Precipitation Evapotranspiration Index (SPEI) was used. This index measures the severity and duration of drought at several time scales, with negative and positive values indicating dry and wet conditions, respectively [28]. The SPEI data were obtained at a resolution of 0.5° using the SPEI Global Drought Monitor webpage [29], which was calculated from local instrumental climate data using the SPEI library of R [30]. The SPEI was calculated at scales of one to 28 months, from January to December of the year of growth, and correlated with the site series of ring-width indices.

Finally, the spatial relationships between the sites' chronologies and the SPEI drought values more strongly related to growth were calculated using the Climate Explorer web page (<https://climexp.knmi.nl/>) [24] and considering the region encompassing Mexico and the southern USA.

3. Results

Tree-ring widths ranged from 1.47 mm (Nuevo León) to 2.03 mm (California Sur). The dendrochronological statistics showed a higher mean sensitivity and series intercorrelation in the driest site (Nueva León), whilst first-order autocorrelation peaked in the Puebla site (Table 2). The Expressed Population Signal (EPS) was >0.85 in all sites, indicating a high coherence in growth between coexisting trees.

Table 2. Dendrochronological statistics corresponding to the raw tree-ring width data (mean; SD, standard deviation; AC, first-order autocorrelation) and the ring-width indices (MS, mean sensitivity; series intercorrelation; Rbt, mean correlation between trees; SNR, signal-noise ratio; and EPS, Expressed Population Signal). Values were calculated for the common period (1873–1987).

Study Site	Timespan	No. Series	Mean \pm SD Tree-Ring Width (mm)	AC	MS	Series Intercorrelation	Rbt	SNR	EPS
Arizona	1766–1987	*NA	*NA	*NA	*NA	*NA	*NA	*NA	*NA
Baja California Sur	1833–1997	17	2.03 \pm 0.88	0.38	0.36	0.68	0.45	7.39	0.88
Nuevo León	1597–2012	57	1.47 \pm 0.82	0.56	0.43	0.69	0.32	36.2	0.97
Puebla	1873–2008	51	1.80 \pm 1.10	0.78	0.68	0.68	0.45	27.6	0.96

* The information was not available because analyses were directly based on the residual chronology and no raw data (tree-ring width series) were accessible at the ITRDB. NA means not available.

The shortest chronology spanned from 1873 to 2008 (Puebla), whereas the longest chronology spanned from 1597 to 2012 (Nuevo León). The four chronologies showed variability during the common period (1873–1997). For instance, growth decreased during 1904, 1909, 1946, and 1960, and increased during 1911, 1919, 1958, and 1977. The periods of common growth variability were most noticeable in the 1910s, 1950s, and 1980s (Figure 2).

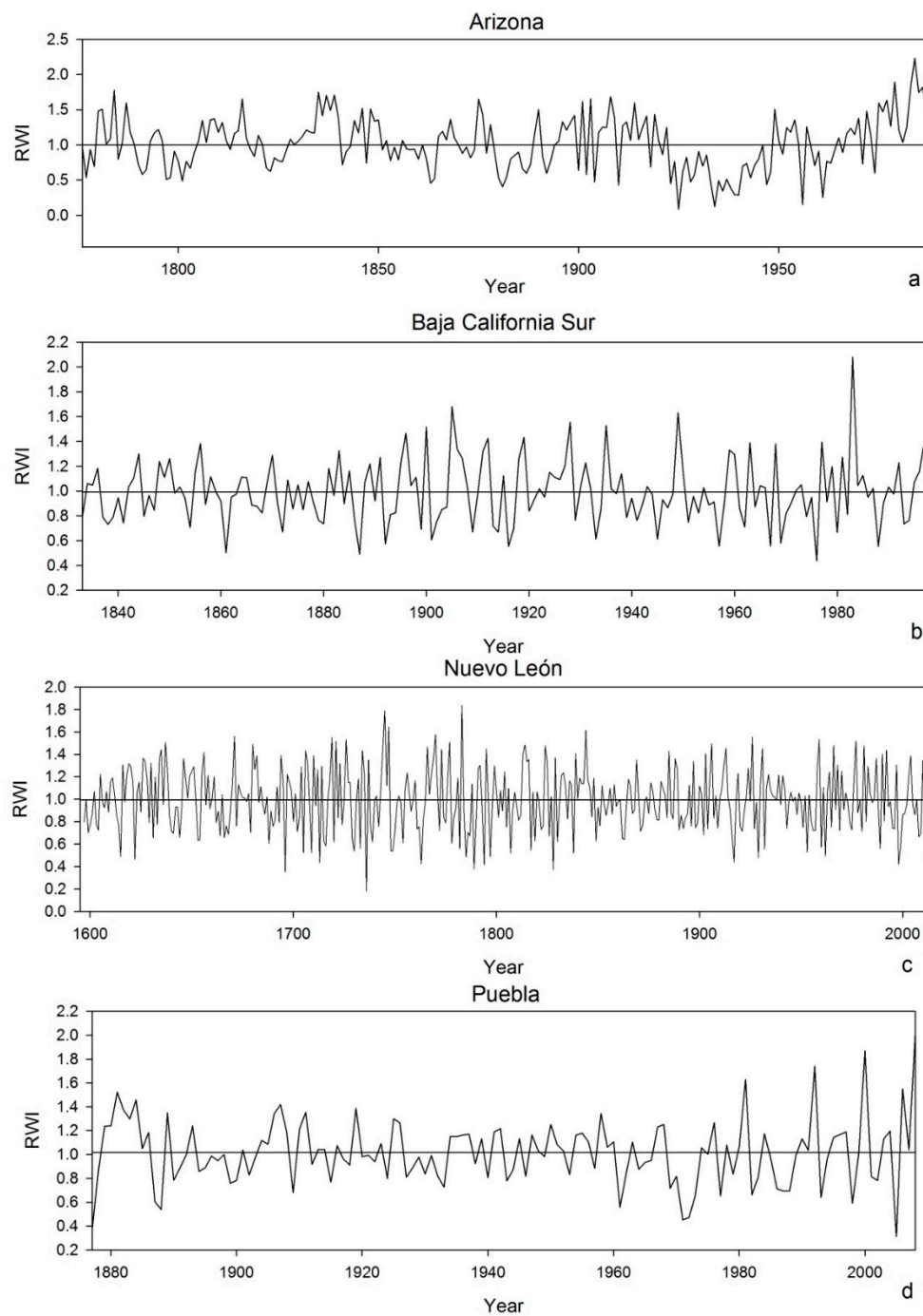


Figure 2. Residual chronologies of ring-width indices (RWI) of (a) Arizona; (b) Baja California Sur; (c) Nuevo León; and (d) Puebla. The residual chronology of Arizona was directly retrieved from the ITRDB.

The radial growth of *P. cembroides* decreased in association with high mean maximum temperatures during the prior autumn and winter (November, December) and current spring and early summer (March to June) (Figure 3). High precipitation during the previous autumn and winter (October to November) and current spring (March, May) was associated with higher ring-width indices, particularly in the driest Nuevo León site. Regarding February to June minimum temperatures, they were also negatively associated with growth in the Nuevo León site.

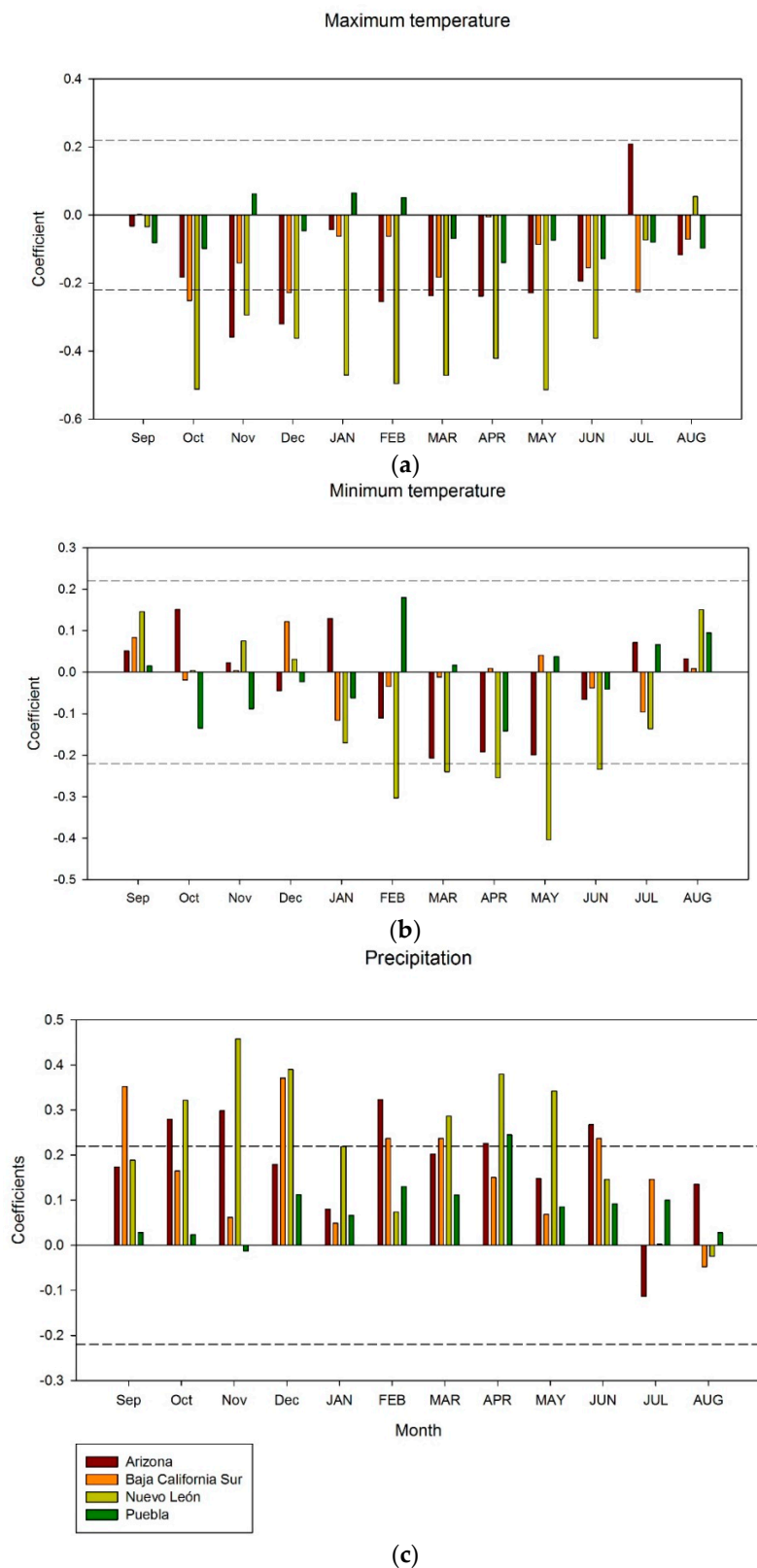


Figure 3. Climate-growth associations (Pearson correlation coefficients) of study areas with respect to the following climatic variables. Mean maximum temperature (a), mean minimum temperature (b), and precipitation (c). The months of the previous year are labeled in lower case letters and those of the current year in upper case letters. Significant correlations ($p < 0.05$) correspond to values located above ($r > 0.22$) or below ($r < -0.22$) the dashed horizontal lines.

The ring-width indices were positively correlated with the SPEI. In this regard, Nuevo León (Figure 4c) presented the highest correlation value in the month of May ($r = 0.60$) for a five to eight month long drought. The Arizona (Figure 4a) and California Sur (Figure 4b) sites presented their highest correlations values ($r = 0.50$) in July and June, respectively, for 10-month long droughts. In Puebla (Figure 4d), correlations were the lowest across all four sites ($r = 0.20$) and were found from October to December and considering 10-month long droughts.

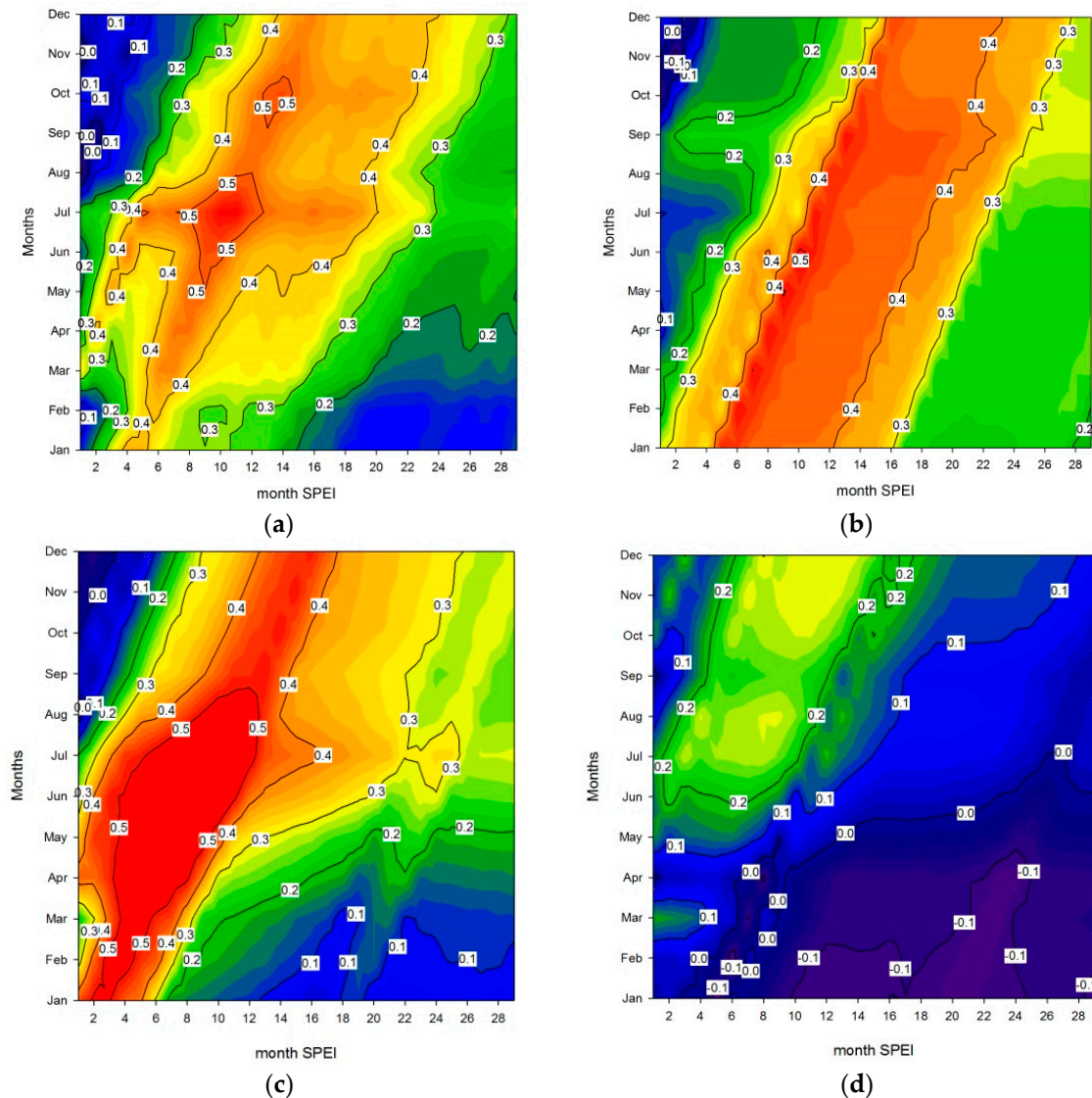


Figure 4. Correlations between the Standardized Precipitation Evapotranspiration Index (SPEI), and the residual chronologies of ring-width indices. Arizona (a), California Sur (b), Nuevo León (c), and Puebla (d). The SPEI was calculated at a scale of one to 28 months from January to December of the growth year (x axes). The Pearson correlation coefficients (r) are indicated using color scales.

The spatial correlations of the four sites with respect to the SPEI values calculated at six to 12-month long scales demonstrated that the area of Nuevo León presented the most prominent associations between that drought index and ring-width indices considering May SPEI values (Figure 5c), compared to those of the sites of Arizona (Figure 5a) and California Sur (Figure 5b). Contrastingly, in Puebla (Figure 5d), the correlation was slightly associated with December SPEI.

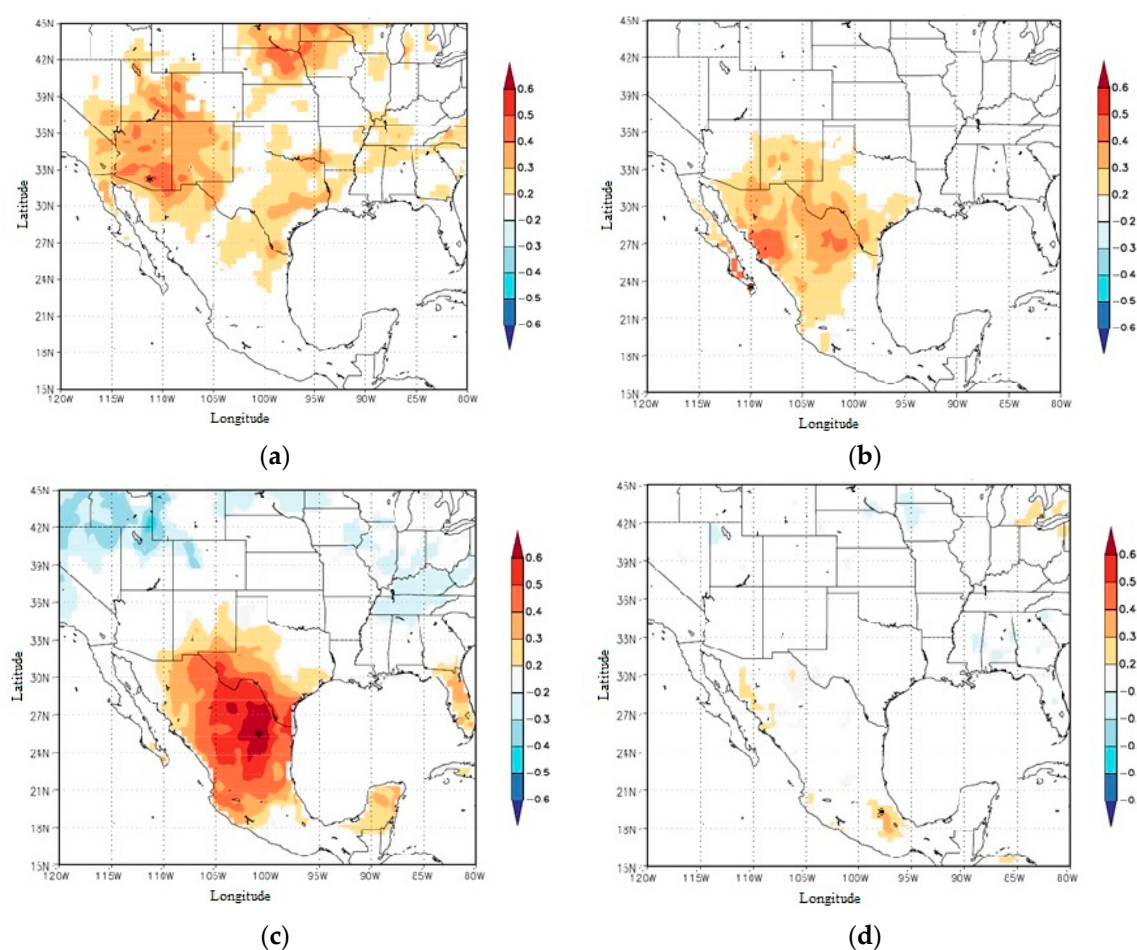


Figure 5. Spatial correlations calculated with the residual chronologies of ring-width indices at each site and the most significant growth—Standardized Precipitation Evapotranspiration Index (SPEI) correlations of each site obtained at eight-Arizona (a), eight-California Sur (b), six-Nuevo León (c), and 12-month long scales Puebla (d). The asterisk indicates the approximate location of each study area.

4. Discussion

This study employed dendrochronological techniques to conduct a comparison among four marginal populations of *Pinus cembroides* forming its distribution limits and encompassing wide bioclimatic gradients across Mexico and the SW USA, in order to determine how their radial growth related to climate conditions. As we hypothesized, the driest Nuevo León study site showed the highest growth response to low precipitation, warm temperatures, and drought, conditions which reduced growth. The suitability of *P. cembroides* for dendrochronology was adequate according to the reported dendrochronological statistics (Table 2). These statistics indicate a high common variance of tree growth patterns within each site. A common feature across all study sites was their sensitivity to the previous-winter climate conditions. This is in line with previous studies at neighboring and similar sites where growth was usually enhanced by wet and cool winter-spring conditions [31].

Even though some differences in chronologies across the gradient were found, general trends in ring-width variation were similar. An increased period of growth preceded by a period of low growth during the 1920s and 1950s was coincident with severe regional droughts reported in nearby ecosystems [14,18]. These similarities suggest that *P. cembroides* growth is influenced by the local hydroclimate. Nevertheless, there are some differences in climate responses between sites due to specific site variation.

As expected, we found the strongest growth association with drought in the driest site (Nuevo León) forming the easternmost distribution limit of *P. cembroides*. Short and long term responses to climatic influences and to drought in this and other pines remain to be studied from a perspective that addresses their geographic distribution.

We found discernible differences across four sites in the climate-growth relationships of *P. cembroides*, which indicates that the response of tree growth to climate changes as a function of the regional and local climatic conditions and the species biogeographic limits [31–33]. This is in accordance with the concept of differing climatic signals at different sites captured in tree-ring width data as argued before [31]. These differences could probably be attributed to specific site conditions. In other words, the unique geography, ecology, and topography of the sites sampled might induce differential genotypic or phenotypic responses [31].

As a consequence, the capacity of the response in growth to the hydroclimatic variability could be used as an indicator of forest vulnerability to drought [9], and these responses could be used to forecast growth and productivity responses to climate change [34].

Despite the fact that other studies also indicate that issues other than climatic factors, such as poor water-use efficiency and nutrient limitation, can contribute to explaining growth reductions [35,36], our results confirm that *P. cembroides* is very associated with drought and can be considered an excellent tree for dendrochronological purposes [14].

This study demonstrates that the radial growth in the study areas responds differently to the climatic conditions of each particular zone. The area of Nuevo León (Figure 3a) appears to be comparatively more sensitive to maximum temperature during the months of growth, presenting a notable negative association, while in Arizona, California Sur, and Puebla, the maximum temperature in these months had little effect on growth. This indicates that high temperatures may increase evapotranspiration, decrease water availability, and, indirectly, reduce the production rates of new tracheids [37,38].

In contrast to that found in some studies with similar pine species where the minimum temperature seems to have a positive effect on radial growth [9,39], in this study, the growth of all of the study areas was negatively related with minimum temperature, particularly over the growing season. Once again, the area of Nuevo León was prominent as the most susceptible site, coinciding with previous results [40], showing that, in some areas, warm minimum temperature may constrain radial growth by enhancing the soil water deficit during the night when growth is often most active.

Our results show that growth was favored by prior wet winter conditions in all sites and that Nuevo León is again the site showing the highest sensitivity to the variability in winter precipitation. This indicates that growth is positively related to the prior moisture conditions which can recharge soils whose water reserves were depleted in autumn [41]. Favorable winter conditions may also improve photosynthesis and increase the reserves of carbohydrates later used in the growing season [33]. These ideas agree with similar results in other studies showing a positive correlation between winter precipitation and radial growth [33,34,42]. Bickford et al. [31] also indicated that tree growth in dry areas from N. Mexico is mainly limited by low winter precipitation. Pasho et al. [37] suggested that these relationships are due to the fact that the winter precipitation contributes to the recharge of soil reserves but may also improve the formation of carbohydrates, which are later used to form the earlywood during the following growing season.

Together, these environmental conditions prior to the growing season critically influence growth and tree-ring formation [43]. High temperatures are associated with the rates of evaporation in winter, which causes a moisture deficit in the soil, reducing the production of carbohydrates and the formation of new tracheids the following growing season [44]. Accordingly, we found very marked spatial variations that indicate that *P. cembroides* responds differently to drought conditions depending on the location of the study area. In the Nuevo León, growth presents greater sensitivity to accumulated drought, as reflected by the marked association between the ring width index and the May SPEI for six-month long scales (Figure 5c).

This agrees with studies that confirm that similar forests located in dry areas demonstrate higher sensitivity to relatively long droughts [31,45]. The observed growth responses to SPEI indicate that all the *P. cembroides* populations are sensitive to drought, but at different strengths and temporal scales. The marked negative response to drought in Nuevo León makes this forest highly vulnerable to extreme climatic events, including hot droughts characterized by high temperatures and evapotranspiration rates and low precipitation values.

Previous studies have reported that large-scale atmospheric climatic patterns (El Niño-Southern Oscillation, ENSO) influence the regimes of climatic variability in the study areas by affecting the summer Monsoon [18,46]. Our results concur with this idea, particularly for the Nuevo León site, where growth showed a positive response to winter precipitation and the SPEI in central Mexico, a region affected by ENSO effects and also by fronts coming from the Atlantic Ocean [46]. For this reason, if forecasted aridification trends for central and northern Mexico are fulfilled, the easternmost populations of *P. cembroides* inhabiting dry zones such as the Nuevo León area may become vulnerable, with negative consequences for their persistence and productivity.

5. Conclusions

The dendrochronological approach adopted in this study allowed evaluating the response of *P. cembroides* radial growth to the hydroclimatic conditions at its geographic limits of distribution. The growth responses of this species in response to climate and drought varied among the four marginal populations studied, regardless of local climate conditions. Site adaptations or genotypic differences may explain these responses of local populations to site environmental variation. The driest site showed the most pronounced growth responses to low precipitation, warm conditions, and drought, conditions which reduced growth. This influence prior to the beginning of tree-ring formation could become more relevant due to the presence of warmer and drier winters, making some forests more vulnerable to climate warming and hotter droughts.

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