Tree Rings Elucidate Differential Drought Responses in Stands of Three Mexican Pines

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Abstract: Knowledge regarding the growth of trees is essential to understanding their response to predicted warmer and drier climate scenarios. We used the annual rings of three Mexican pines (Pinus montezumae Lamb., Pinus oocarpa Schiede ex Schltdl., and Pinus monophylla Torr. & Frém) to explore their drought responses. Correlation analyses showed that hydroclimatic factors differentially impact tree species in terms of the intensity and temporality. The negative influence of the maximum temperature and positive effect of the precipitation on the growth indices were notable, with P. montezumae being the most responsive species, followed by P. oocarpa and P. monophylla. The climate-growth relationships were specific and driven by the differential hydrothermal conditions across the study areas. SPEI analyses indicated that P. monophylla is better able to tolerate drought than P. montezumae or P. oocarpa, especially in recent years. The lower resilience of P. montezumae and P. oocarpa could predispose them to a higher mortality risk if warming and drying rates increase. Our findings strengthen the understanding of the responses of young Mexican stands and could contribute to the design of management strategies in the face of predicted climatic variations.

Keywords: conifers; dendroecology; drought; radial growth; tree mortality

1. Introduction

Growth rings, as paleoclimatic proxies, evidence a rise in the evapotranspiration demand and amplification of drought severity (e.g., [1,2]). For instance, the period from 2000 to 2018 was the driest 19-year span since the late 1500s in Northwestern America [3]. Recently, it was found that the occurrence of extreme drought has increased dramatically in the Southwestern U.S. over the past two decades, leading to stronger multi-year growth legacies [4]. Such recurrent and extreme mega-droughts are placing many forest tree species near the limits of their drought tolerance, thus necessitating a greater understanding of their relationships with climate. Previous studies have documented that long-term decreases in growth triggered by drought may be associated with a gradual decline in hydraulic performance coupled with depletion of carbon reserves [5–7].

These observed changes in forest dynamics are expected to have major consequences for the tree distribution and mortality, as well as for the forest functioning, composition and structure [8]. For example, there have been a number of significant changes in the distribution and functioning of coniferous forests, including the growth, mortality, and reproduction, in response to various modified rainfall regimes, increasing droughts, and significant increases in the land temperature [9,10]. These changes highlight the importance of understanding the responses of different forest species to different precipitation regimes and to current and future climatic changes [10]. However, gaps remain in our knowledge...
regarding tree responses to hydroclimatic dynamics. These findings could improve the understanding of future changes in tree species functioning, including wood formation (xylogenesis), and patterns of dominance and species distribution [11].

The complexity of geographical gradients, combined with a variety of climates, promotes high levels of biodiversity and endemism hotspots, which are a priority for ecological studies [12]. Large-scale circulation patterns have different impacts on climate elements, particularly water regimes, and act to regulate radial growth in Mexican forests [13]. Furthermore, contrasting soil moisture gradients have been shown to explain the variation in the functional responses to drought among species [14]. The contrasting environmental conditions that prevail in Mexican forests hosting a diversity of pine trees therefore present an ideal opportunity for assessing the response of forest growth to drought. Furthermore, as a consequence of pressures from logging, drought, wildfire, and other disturbances linked to climate and land-use changes [15], the structure of Mexican forests has changed toward one featuring younger stands [7].

Several authors have documented that forests in young stands show higher growth rates than forests with mature trees [16]. These differences are observed in terms of increases in the temporal and spatial ranges attributed to a range of factors [17]. Age must therefore be taken into account when evaluating tree responses to climate [18,19]. Thus, there is still a need to obtain further knowledge of the responses of different species and young trees along diverse environmental gradients in order to accurately anticipate forest responses to predicted future warmer and drier climatic conditions.

Our main objective in this study was therefore to determine the influence of climate on radial growth and to use tree rings taken from along a climatic gradient to analyze growth, focusing on young trees. We hypothesized that drought will impact the radial growth responses differentially, with a marked influence arising from hydrological regimes determined primarily by climatic variables such as increased maximum temperatures and low precipitation regimes. In this context, we assume that young species from sites with high productivity (e.g., mesic sites) will present higher responsiveness, while those from semi-arid sites will present lower sensitivity.

2. Materials and Methods
2.1. Study Area and Species Analyzed

Taking advantage of Mexico’s tree species diversity and contrasting climate variability along different environmental gradients [20], we sampled three sites dominated by three pine species distributed in three regions across Mexico (Table 1, Figure 1). These regions are characterized by contrasting drought characteristics [21] and are historically sensitive to large-scale atmospheric circulatory patterns that influence climate variability, with an impact on soil moisture [22]. Firstly, growing in a semi-arid area, *Pinus monophylla* Torr. & Frém, known as the single-leaf pinyon, is a tree of low height (6–12 m) that forms sparse forests with rounded, flat crowns [23]. It is distributed across Northwestern America, from the Western U.S. to Baja California [24]. Secondly, in an environment characterized by a temperate climate, *Pinus montezumae* Lamb., a tree species endemic to the mountainous areas of Mexico and Central America, with a moderate height (ca. 30 m) and forming valuable wood [25]. Finally, *Pinus oocarpa* Schiede ex Schltdl, a tall tree (ca. 40 m) found in the mountainous regions of Central America and Mexico, which presents a deep root system [26].
Table 1. Sampling site characteristics.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Tree Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree species</td>
<td><em>Pinus monophylla</em> Torr. &amp; Frém</td>
</tr>
<tr>
<td>Longitude °W</td>
<td>116.01295</td>
</tr>
<tr>
<td>Latitude °N</td>
<td>32.44812</td>
</tr>
<tr>
<td>Elevation (m a.s.l.)</td>
<td>1374</td>
</tr>
<tr>
<td>Region</td>
<td>Semi-arid region of the Californian Mediterranean (NW Mexico)</td>
</tr>
<tr>
<td>Sampling date</td>
<td>11 January 2022</td>
</tr>
<tr>
<td>CRU grid cell</td>
<td>32.0°, 32.5°, −116.5°, −116.0°</td>
</tr>
<tr>
<td>SPEI grid cell coordinates</td>
<td>32.5°, −116.25°</td>
</tr>
<tr>
<td></td>
<td><em>Pinus montezumae</em> Lamb.</td>
</tr>
<tr>
<td>Longitude °W</td>
<td>100.34697</td>
</tr>
<tr>
<td>Latitude °N</td>
<td>21.86355</td>
</tr>
<tr>
<td>Elevation (m a.s.l.)</td>
<td>2349</td>
</tr>
<tr>
<td>Region</td>
<td>Semi-cold and temperate sub-humid region of the Sierra Madre Oriental (central Mexico)</td>
</tr>
<tr>
<td>Sampling date</td>
<td>10 August 2020</td>
</tr>
<tr>
<td>CRU grid cell</td>
<td>21.5°, 22.2°, −100.5°, −100.0°</td>
</tr>
<tr>
<td>SPEI grid cell coordinates</td>
<td>21.75°, −100.25°</td>
</tr>
<tr>
<td></td>
<td><em>Pinus oocarpa</em> Schiede ex Schltdl</td>
</tr>
<tr>
<td>Longitude °W</td>
<td>92.90631</td>
</tr>
<tr>
<td>Latitude °N</td>
<td>16.83479</td>
</tr>
<tr>
<td>Elevation (m a.s.l.)</td>
<td>1096</td>
</tr>
<tr>
<td>Region</td>
<td>Tropical subhumid region of the Sierra Madre Centroamericana and Altos de Chiapas (SE Mexico)</td>
</tr>
<tr>
<td>Sampling date</td>
<td>21 January 2020</td>
</tr>
<tr>
<td>CRU grid cell</td>
<td>16.5°, 17.0°, −93.0°, −92.5°</td>
</tr>
<tr>
<td>SPEI grid cell coordinates</td>
<td>16.75°, −92.75°</td>
</tr>
</tbody>
</table>

**Figure 1.** Location of the study *Pinus monophylla* Torr. & Frém, *Pinus montezumae* Lamb., and *Pinus oocarpa* Schiede ex Schltdl forests in Mexico and climate diagrams. The background color scale represents the average annual rainfall in mm and the colored lines show the elevation range (m a.s.l.). In the climate diagrams the box plot represents the mean monthly precipitation, Tmin and Tmax are the mean minimum and maximum temperatures, respectively (blue lines).

2.2. Field Sampling and Dendrochronological Methods

Field data collection was performed by selecting a central tree (with a diameter > 20 cm at a height 1.3 m from the ground) in each stand dominated by each of the selected species.
The 19 trees found closest to this focal tree were then also sampled. Selected individuals were apparently healthy. For the collection of growth cores, at least 2 radial increment cores were taken from each tree with increment borers (of diameter 5 mm).

In the laboratory, the cores were air-dried and mounted on wooden racks with polyvinyl glue. These samples were then gradually polished using sandpaper, from coarse to fine, until the tree rings were clearly visible for dating and subsequent measurement. Once cross-dating was completed, the total ring width was measured to the nearest 0.01 mm using a Velmax measuring system (Bloomfield, NY, USA). The cross-dating quality of the measured tree-ring series was quantitatively checked using the statistical software COFECHA (Version 6.06P) [27].

Subsequently, a negative exponential model was fitted to the tree-ring widths to obtain standardized and detrended ring width indices, preserving the year-to-year growth variability. In this way, we generated a residual chronology, which is appropriate for hydroclimatic studies [28]. The obtained residual ring-width indices were then averaged on an annual basis for each site using a robust bi-weight mean. Detrending was conducted using the dplR package [29]. Finally, descriptive statistics were calculated for the ring-width series (TRW) of each of the sampling sites. These included first-order autocorrelation (AC), which measured the year-to-year growth persistence, the mean sensitivity (MS), which measured the relative change in width between consecutive rings, the mean correlation of individual series of ring-width indices (RBT), and the expressed population signal (EPS), a statistic quantifying the strength of the mean sites series (chronology) compared to that of an infinitely replicated series [30]. Mann–Whitney tests were also used to compare the mean tree age, ring width, AC, and MS among species.

2.3. Climate Growth Relationships

Monthly climate variables of the maximum, minimum, and mean temperature (°C), and precipitation (mm) (Tmax, Tmin, Tmean, Precc, respectively) were obtained at a spatial resolution of 0.5° from the CRU database v. 4.07 [31] for the period 1962–2022 from the Climate Explorer webpage (http://climexp.knmi.nl/, accessed on 10 January 2024) [32]. Climate diagrams were drawn for each site using these data. Climate Explorer was also used to calculate the spatial or field correlations between the cumulative precipitation from January to May (CRU climate data) and the species’ series of ring-width indices.

To evaluate the climatic influence on the ring-width growth of the evaluated species, the Pearson correlation coefficients between the monthly climate variables and the mean series of ring-width indices were calculated with a significance level of 95% (α ≤ 0.05) using a window from June of the previous year to September of the following year. We selected the best replicated period of climate and tree-ring data (1985–2019) using the EPS, with a minimum threshold value of 0.85 as a criterion for consistency in the chronologies [30]. This was performed using the treeclim R package, Version 4.3.3 (The R Project for Statistical Computing, Vienna, Austria) [33].

As a strategy to strengthen the relationship of growth with the drought duration and intensity, we calculated the standardized precipitation-evapotranspiration index (SPEI) [34]. The necessary data were obtained from the website of SPEI (https://spei.csic.es/, accessed on 10 January 2024) at a resolution of 0.5° and a temporal scale that covered 1 to 48 months, corresponding to the period of January to December.

3. Results

3.1. Growth Variables

The growth patterns of the study species correspond to young stands representative of many current Mexican forests (Table 2, Figure A1). We used Mann–Whitney tests as a non-parametric test to compare the sample means. The chronology with the greatest extension corresponded to P. monophylla (59 years), which showed the highest mean age (54 years) and the lowest growth rate (0.92 mm), while P. montezumae had the shortest chronology
(34 years) and the widest tree rings (3.70 mm). The best-replicated series corresponded to *P. monophylla*, with the highest RBT and EPS values, while the *P. oocarpa* series presented the lowest internal coherence, as indicated by its presentation of the lowest RBT and EPS values. *P. monophylla* also presented the highest growth variability between consecutive rings (MS), while *P. oocarpa* showed the highest year-to-year persistence in growth (AC).

Table 2. Dendrochronological statistics of the sampled species.

<table>
<thead>
<tr>
<th>Variable</th>
<th><em>P. monophylla</em></th>
<th><em>P. montezumae</em></th>
<th><em>P. oocarpa</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. of trees dated *</td>
<td>20</td>
<td>18</td>
<td>19</td>
</tr>
<tr>
<td>No. of cores dated *</td>
<td>40</td>
<td>37</td>
<td>38</td>
</tr>
<tr>
<td>Age estimated at 1.3 m (years)</td>
<td>54 ± 3 b</td>
<td>38 ± 1 a</td>
<td>37 ± 1 a</td>
</tr>
<tr>
<td>Tree-ring width (mm)</td>
<td>0.92 ± 0.05 a</td>
<td>3.70 ± 0.14 c</td>
<td>2.68 ± 0.15 b</td>
</tr>
<tr>
<td>AC</td>
<td>0.34 ± 0.03 a</td>
<td>0.35 ± 0.03 a</td>
<td>0.58 ± 0.04 b</td>
</tr>
<tr>
<td>MS</td>
<td>0.56 ± 0.01 c</td>
<td>0.40 ± 0.01 b</td>
<td>0.35 ± 0.01 a</td>
</tr>
<tr>
<td>RBT</td>
<td>0.568</td>
<td>0.534</td>
<td>0.296</td>
</tr>
<tr>
<td>EPS</td>
<td>0.981</td>
<td>0.968</td>
<td>0.918</td>
</tr>
<tr>
<td>Length of chronology (years)</td>
<td>60</td>
<td>35</td>
<td>45</td>
</tr>
</tbody>
</table>

AC, first-order autocorrelation; MS, mean sensitivity; RBT, mean correlation of individual series of ring-width indices; EPS, expressed population signal. Different lowercase letters (a, b, c) indicate significant (*p* < 0.05) differences between species according to Mann–Whitney tests. * denotes dated trees and cores.

3.2. Growth Responses to Climate

Correlation analyses showed differences in the radial growth responses to climate elements (Figure 2). Precipitation in the previous winter and the growing season (spring–early summer) has a beneficial effect on the radial growth of *P. montezumae* primarily. For *P. monophylla*, rainfall has a minimal effect on growth, as only precipitation in January of the growing year is related to the ring width, whereas, for *P. oocarpa*, rainfall was found to be a variable that is not significant for tree growth.

*Tmax* negatively affected *P. montezumae* growth from the previous autumn to the current summer and was also negatively associated with *P. oocarpa* growth in the prior late summer and current spring (Figure 2). *Tmin* showed negative correlations with *P. montezumae* and *P. oocarpa* to the current spring.

The spatial correlations showed the strong and positive responses of growth variability to the cumulative precipitation from January to May in *P. montezumae*, followed at a smaller scale in *P. oocarpa* and with an unperceived influence on *P. monophylla* (Figure 3), in agreement with the results in Figure 2. The spatial patterns of the field correlations peaked in the three distinct sampling regions located in NW, central and SE Mexico, respectively.

The species that presented the highest correlation between growth and the SPEI values was *P. montezumae*, with values of *r* = 0.7 in the months of March to July at temporal scales of 0 to 7 months. *Pinus oocarpa* presented maximum values of *r* = 0.4 for the months of April and May at temporal scales of 6 to 10 months. Finally, *P. monophylla* was less affected by changes in drought, with maximum correlation values of *r* = 0.29 for the month of January at a temporal scale of 1 month (Figure 4).
Figure 2. Correlation of the climate variables (Tmax, mean maximum temperature; Tmin, mean minimum temperature; PP, precipitation) with the series of ring-width indices of the three study species. The correlations were performed for the well-replicated common period (1985–2019). The months of the previous and current years are abbreviated in lowercase and uppercase letters, respectively. Dashed horizontal lines indicate the 0.05 significance levels.

(a) 

Figure 3. Cont.
Figure 3. Field correlations calculated by relating the residual tree-ring width chronologies of the three study species to the cumulative precipitation from January to May (0.5°-gridded CRU data): (a) *P. monophylla*, (b) *P. montezumae*, and (c) *P. oocarpa*. Asterisks denote the approximate location of the study forests and the color scales indicate the Pearson correlations.
Figure 4. Correlations between the SPEI drought index and width indices for several time scales (x-axis) and from January to December (y-axis) in *P. monophylla* (1962–2021), *P. montezumae* (1985–2019), and *P. oocarpa* (1975–2019).
4. Discussion

Retrospective quantification of the effect of drought on annual tree growth confirmed that early-warning signals have been intensifying in some areas during recent years and are differentially affecting the studied species in both spatial and temporal terms. The contrast in climates among the studied sites provided an ideal setting to assess the differences presented in terms of the drought response. This strategy has been used in similar studies [35] since the results have shown spatial and functional trends according to species traits.

Although the modern literature states that sensitivity to climate can vary with age, it is not clear whether climate sensitivity can vary with age or not (see [36]). We argue that our results are devoid of such influence, given the marginal range of average ages among the three species (~17 years), in contrast to those studies based on long-lived trees growing in limited soil moisture conditions. Furthermore, relevant studies show that tree size matters more than age when assessing the tree response to climate [19].

The species showed sensitivity to the precipitation and maximum temperature as the most important drivers of radial growth variability (Figure 2). These two variables, combined with evapotranspiration, have been linked to growth decline and have triggered tree mortality episodes [37].

The mean sensitivity (MS) of *P. monophylla* was slightly higher than that of the other species, consistent with its EPS value, meaning that this species retains a greater amount of the climatic signal, which is plausible given the arid conditions it inhabits. Interestingly, the January precipitation of the year of growth and, to a lesser extent, the Tmin of the previous July are the only variables that are significantly related to its growth. In this region, it has been documented that winter precipitation triggers growth activation when evaporation is low and soil moisture is recharged [38]. This allows the tree to store photosynthates that will be used for radial growth when the growing season begins. The minuscule correlation with the rest of the climatic variables of this species could be attributed to the physiological response of the young trees as a strategy of resilience against current hydroclimatic variations. However, further studies are required to test this hypothesis, including analysis of the microsite, xylogenesis and evaluation of resilience, recovery and resistance.

That is, far from expected, the studied individuals of *P. monophylla* show no signs of decline in the response to aridification in the SW USA [39]. For example, ref. [40] modeled drought scenarios that warn of the risk to the biogeography of forest ecosystems in the region.

In contrast, *P. montezumae* from the central temperate zone is a poorly studied species that shows sensitivity to precipitation regimes. High temperatures seem to lead to high evapotranspiration rates that mostly influence its radial growth. This puts into perspective the severe and intense droughts that have been predicted, which could result in a decline in growth in the species, including a reduction in productivity that could presage the regressive death of these stands [41].

Likewise, *P. oocarpa* in the tropical area is more influenced by the Tmax in its radial development, and less by rainfall. It seems that this species benefits from the mesic conditions in which it lives, where rainfall is not a strong limiting factor and therefore these individuals are less responsive to drought.

These results show that in mesic sites, high temperatures combined with water regimes play a dominant role in regulating growth [42]. In contrast, in semi-arid areas, individuals show less association with drought conditions. In other words, the interaction between drought and radial growth has a greater influence on young trees from central to southern Mexico. This suggests that trees living in humid conditions are more affected by the adverse events of changing temperature and precipitation patterns, which is attributed to their lower ability to withstand the initial impact of drought.

In short, *P. monophylla* appears to have no limitations when it comes to growing radially. In contrast, at sites where the rainfall is higher and the temperatures lower, the species appear to be more susceptible to abrupt climatic changes. The apparently different
adaptations of the species to local climatic variables highlight the importance of analyzing and understanding the response of forests to different geographic gradients [7].

The varied correlation of the species with drought events indicated that each species experiences differential spatio-temporal influences on hydroclimatic regimes that are related to the intensity and duration of drought [43]. This was also in agreement with the different geographical patterns of the spatial correlations between growth and winter-spring precipitation.

Changes in the precipitation and thermal regimes are the main limiting factor for the growth of the evaluated species, particularly in mesic forests. This suggests that the impacts of drought are increased in these biomes, which could in the long term lead to the movement of the distribution sites of several species to places that present different conditions [44].

These low growth rates and the reduced xylem production are a result of water limitation and increasing evaporative demand [45,46], potentially affecting water transport and carbohydrate availability. The continuous and progressive reduction of tree growth can be translated into an early-warming signal of increased mortality risk [37,47]. In fact, some Mexican forests are showing growth declines and alarming mortality rates linked to hotter droughts, particularly at the xeric (low elevational) limits of distribution of some tree species [48]. The growth response can also have negative values if the post-disturbance performance is lower than that prevalent during the disturbance event [49], which could lead to increased stand mortality [50]. For example, ref. [51] showed that negative effects on growth can persist beyond 1–4 years after drought and can produce legacy effects, especially in xeric sites.

The great capacity for a growth response in the face of drought demonstrated by P. monophylla represents a strategy to adapt and respond to recurrent periods of water deficit, which some authors link to a substantial plasticity in the xylem or an improved efficiency in leaf area transpiration [52]. We should also consider the great longevity of this species [23], which may confer functional advantages. Thus, this species is adapted to arid conditions with consequent functional advantages in the water-use efficiency and productivity [53]; for example, the low-density stands it forms allow it to reduce competition between trees for soil water [54]. In contrast, the other two pine species, but particularly P. oocarpa, live in mesic conditions where the soils have higher water availability and where mycorrhizae are more abundant and soils are more productive compared to xeric sites [55].

According to our findings, the growth response to drought is not only driven by site aridity, since drought has been shown to reduce growth and productivity even in non-water-limited mesic sites [56]. For instance, if dry years become more common in southeastern Mexico, where P. oocarpa grows, it could be hypothesized that this species is threatened by such aridification. However, more data on growth, photosynthesis, and carbon metabolism use should be included to better assess tree responses to drought in similar wet regions (e.g., [57]). The fundamental differences among the studied species are attributed to their drought response strategies, such as the avoidance of hydraulic failure or allocation to carbon storage, the nature of which is driven by the long-term water availability, drought severity, and soil properties [58].

As a limitation of our study, we recognize that our results are not applicable to the rest of the species cohabiting the gradients [59], since they are influenced by microenvironmental conditions, such as the intra- and inter-species competition within the site, soil properties, individual tree vigor, and ontogenetic characteristics [14,60]. We therefore suggest linking further xylogenesis analysis associated with remote sensing at the individual tree level to measure concurrent changes in the tree growth and vigor at fine spatial and temporal scales (e.g., [61]).

Although our spatial gradient contained climatically contrasting sites, we still need to improve the stand and individual scales since the number of chronologies is limited and Mexico presents a great opportunity for research from this perspective due to its high tree diversity and potential in dendro-sciences [62]. This framework would make it
possible to characterize suitable conditions to describe at finer resolution the environmental gradients for species distribution. Finally, the age of the trees studied here corresponded to young stands; however, age seems to influence the growth response of the species and further efforts in older forests should therefore be conducted to complement these analyses (see [7]).

5. Conclusions

The different responses to drought found among the three stands of young pines improved our understanding of the response of these tree species to hydroclimatic variability. Each species presented different growth strategies to cope with drought. The results allowed us to identify which species had been most impacted by drought, particularly considering the new composition of Mexican forests, which is characterized by young individuals.

The species most responsive to water availability was *P. montezumae*, followed by *P. oocarpa* and *P. monophylla*. *Pinus montezumae* and *P. oocarpa* were found to be less resilient to drought compared to *P. monophylla*, which seems to take advantage of it, possibly attributed to the physiological adaptive capacities of young trees. The maximum temperature was one of the drivers complementing the climatic influence on radial growth, especially in mesic site species. These differences could dictate the long-term growth trends and mortality risk in response to increasing aridification.

**Author Contributions:** Conceptualization M.P.-G.; methodology, M.P.-G.; validation, M.P.-G. and J.J.C.; formal analysis, E.D.V.-V. and J.J.C.; investigation, E.D.V.-V., M.P.-G. and J.J.C.; resources, M.P.-G.; data curation, E.D.V.-V. and J.J.C.; writing—original draft preparation, E.D.V.-V., M.P.-G. and J.J.C. All authors have read and agreed to the published version of the manuscript.

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**Data Availability Statement:** The data presented in this study are available on request from the corresponding author. The data are not publicly available due to privacy and legal reasons.

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**Conflicts of Interest:** The authors declare no conflicts of interest.

**Appendix A**

Figure A1.

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