Coordinated responses of *Hemiptelea davidii* at the individual tree and stand levels
to interannual climatic variation in a water-limited area

Ke-Xin Guo\(^1,2\), Xue-Wei Gong\(^2,3,4\), Jing-Jing Guo\(^2,3,4\), Han Shi\(^2,5\), Yong-Jiao Zhou\(^2,5\),
Qian-Nan Leng\(^2,5\), Guang-You Hao\(^2,3,4^*\)

\(^1\)School of Life Sciences, Liaoning University, Shenyang 110036, China;
\(^2\)CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China;
\(^3\)Daqinggou Ecological Research Station, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China;
\(^4\)Key Laboratory of Terrestrial Ecosystem Carbon Neutrality, Liaoning Province, Shenyang 110016, China;
\(^5\)University of Chinese Academy of Sciences, Beijing 100049, China

\(^*\)Corresponding author

Phone: +86-24-83970374
Fax: +86-24-83970300
E-mail: haogy@iae.ac.cn
Abstract: Drought-associated tree mortality and forest decline have been increasingly observed across the globe due to warmer and drier climates, particularly in drought-prone environments. Understanding how forests respond to the increasing inter-annual climate variability and frequent severe drought events in the context of global change is of great significance for predicting the dynamics of forest ecosystems under future warming-drying climate scenarios. This study combined tree-ring series, xylem anatomy, wood isotope signatures, and remote sensing methods to examine the physiological mechanisms underlying the response of natural *H. davidii* forests in Horqin Sandy Land, a water-limited area in northern China to the identified severe drought events and long-term climatic variability. Our results indicated that the climatic variables related to environmental moisture conditions exert the most profound influence on the performance of the studied species, with the severe drought events significantly reducing growth vigor. The concurrent reduction in water-transporting conductivity and elevation in water-use efficiency signified the prevalence of a more conservative water-use strategy in response to severe droughts at the holistic level of the whole tree, which physiologically accounts for the increased hydraulic safety and diminished radial growth during the period. Remotely sensed vegetation indices appeared to respond less conspicuously to severe drought events relative to radial growth, xylem anatomical traits, and water use efficiency. Nonetheless, a coordinated response to climatic variability between tree canopy and individual-level performance was found over the long-term time series, implying that the adoption of a multiscale approach enhances our comprehension of the long-term forest response to climatic
variability. In short, this study highlights the role of water-related physiology in modulating the performance of *H. davidii* trees during severe droughts by adjusting xylem hydraulic functioning and tree water use efficiency.

**Keywords:** dendrochronology, remote sensing, severe drought, tree-ring xylem anatomy, xylem hydraulics, $\delta^{13}$C

1. Introduction

Numerous forests worldwide are facing high risks of decline and mortality, especially in water-limited areas due to the obvious trend of climate warming-drying (Allen et al., 2015; Hammond et al., 2022). Although warming may be beneficial to forests distributed in high-elevation and high-latitude by alleviating low-temperature limitation on tree growth, it can also exacerbate drought stress by enhancing evapotranspiration and become detrimental to trees (Ruiz-Pérez and Vico, 2020; Shi et al., 2021). In recent decades, global warming has increased the frequency, intensity, and duration of extreme droughts (IPCC, 2021), which can inhibit tree growth, lead to tree decline and death due to hydraulic failure or carbon starvation (Allen et al., 2010; Anderegg et al., 2012; Anderegg and HilleRisLambers, 2016; Kong et al., 2022). Both field observations and modeling studies have shown that forest decline and tree mortality are accelerating in water-limited regions (Liang et al., 2015; Valeriano et al., 2021). Investigating the patterns of forest responses to variation in climate variables and the underlying mechanisms are crucial in understanding and predicting how forest will
respond to ongoing climate change. Forest responses to environmental changes may differ at different scales (Brehaut and Danby, 2018; Decuyper et al., 2020). However, most studies have generally focused on investigating forest responses to climate variables at only a single scale, thereby limiting our comprehensive understanding of the influence of climate change on forests (Olano et al., 2014; Kannenberg et al., 2019b; Rahman et al., 2020). Particularly, studies involving multiple scale measurements across the same time sequence over a relatively long term are scarce and are thus keenly needed.

Dendroclimatology is one of the most widely used approaches for investigating the inter-annual changes of tree growth in response to climate variation, which can provide very valuable information for probing the influence of climate on tree performance at the individual scale (Fritts, 1976; García-Suárez et al., 2009; Cherubini, 2021). Some dendroclimatic studies indicated that warming has caused the advancement and lengthening of growing seasons, resulting in increased radial growth of trees in temperature-limited areas such as high-altitude and high-latitude regions (Bao et al., 2018; Rodriguez-Caton et al., 2021; Yang et al., 2022b). However, an extensive number of studies have reported declining radial growth of trees due to the drying effect of climate warming (Kunz et al., 2018; Zhang et al., 2021; Yang et al., 2022a). Increased warming-drying has led to a high incidence of severe droughts and the recovery of tree growth following a severe drought may depend on various factors, including the species identity, geographical location (e.g., altitude, latitude, and water table depth that mediates tree sensitivity to drought), and characteristics (severity,
frequency, and duration) of the drought events (Gao et al., 2018; Gessler et al., 2020; Bose et al., 2021). Many studies indicated that drought can adversely impact tree growth and the influence can even last for several years (Gazol et al., 2016; Kannenberg et al., 2019a).

In addition to the traditional measurements of tree-ring width, quantitative wood anatomy and tree-ring isotope analyses have been used to gain a deeper understanding of how trees respond to climate variables (Rodriguez-Caton et al., 2021; Zhu et al., 2021). These approaches allow the investigation of tree environmental responses at a finer scale and contribute to the deciphering of physiological mechanisms underlying tree growth responses to changes in environmental variables (Pacheco et al., 2020; Puchi et al., 2021). Xylem anatomical characteristics exhibit plasticity in response to climate change, enabling acclimation to environmental changes over short and long spans of time (Fonti et al., 2010; Islam et al., 2019b; Castagneri et al., 2020). During drought events, trees may either develop larger vessels to enhance the efficiency of water transport, or produce smaller but a higher number of vessels to avoid hydraulic failure (Sperry et al., 2008; Haworth et al., 2016; Islam et al., 2019a). Analyzing wood anatomical variability along tree-ring sequences can provide valuable insights into how individual trees and species respond to changing environmental conditions (Schweingruber, 2007; Fonti et al., 2010). Moreover, the stable carbon isotope ratios ($\delta^{13}C$) of the tree rings can be used to infer the inter-annual changes of intrinsic water-use efficiency (iWUE) of trees (Farquhar et al., 1982; Martínez-Sancho et al., 2022; Xu et al., 2022a). The observed trend in iWUE generally shows an increase globally, which
can be attributed not only to rising atmospheric CO$_2$ concentrations, but also to warming and drying patterns (Saurer et al., 2014; Walker et al., 2021). Many studies have demonstrated that trees respond to water stress by decreasing stomatal conductance and increasing iWUE in drought-stressed years (Battipaglia et al., 2014; Olano et al., 2014).

Traditional techniques such as field surveys and dendrochronology often show spatial and temporal data collection constraints that can be overcome by remote sensing (Hansen et al., 2013; Liu et al., 2021). Remote sensing provides a powerful tool for investigating the patterns of changes in forest productivity and health status from forest stand to global scales (Vicente-Serrano et al., 2016; Correa-Díaz et al., 2020; Moreno-Fernández et al., 2021). These observations trace the integrated vegetation responses to environmental circumstances by means of spectral indices that concern functional processes such as Normalized Difference Vegetation Index (NDVI) quantifying vegetation greenness and Normalized Difference Moisture Index (NDMI) detecting the vegetation water contents (Tucker, 1979; Hardisky et al., 1983). Previous studies have shown that vegetation activity in most parts of China has increased in the last few decades due to climate change (Piao et al., 2006; Xu et al., 2015). Many recent studies have also shown that climate extremes have led to significant changes in terrestrial vegetation, particularly in less productive and arid ecosystems, where droughts could diminish canopy vitality (Pang et al., 2017; Hossain and Li, 2021).

_Hemiptelea davidii_ (Hance) Planch is an indigenous and dominant tree species in the southeastern part of Horqin Sand Land, a typical semi-humid area in northern China,
where the climate has relatively large inter-annual variability and the drought-induced forest decline has been frequently documented in the context of climate change. Owing to its inherent resistance to stress, there has been a growing inclination to utilize the species in developing resilient forest ecosystems within this environment characterized by limited water availability. Ascertaining the response of this native species to the interannual climatic variation and the associated physiological mechanisms contributes to the scientific utilization of the species for improving forestry sustainability and climate-smart forestry practices in this climate-sensitive and ecologically fragile area.

In this study, we employed multiscale methodologies to examine the inter-annual patterns of *H. davidii* forests’ responses to climatic variations, placing particular emphasis on the coordination and divergence of responses across distinct scales. Specifically, we utilized tree-ring analysis, xylem anatomy, stable isotope techniques, and remote sensing to investigate climate-driven inter-annual fluctuations in individual-tree and canopy level parameters as well as the responses of forests to the severe droughts that took place in 2000-2004 and 2007. Our main research questions are: (1) What are the main environmental factors determining the growth of *H. davidii* in the water-limited area? How would *H. davidii* respond to the severe drought events at different scales? (2) Would the plastic adjustments of xylem anatomical traits in *H. davidii* play a significant role in its acclimation to annual variations of water conditions? (3) Would inter-annual fluctuations in radial growth, xylem anatomical characteristics, iWUE, and spectral indices of *H. davidii* exhibit coordination?
2. Materials and methods

2.1 Study site and species description

This study was conducted in natural forests of *H. davidii* (47°07′–43°08′N, 122°59′–123°01′E) located in Tongliao, Inner Mongolia Autonomous Region, China. The forest stands are located in the southeastern part of the Horqin Sandy Land, situated within the mid-temperate sub-humid fringe area characterized by a temperate continental monsoon climate. The average annual temperature is 5.6 °C, of which January is the coldest with an average monthly temperature of -14.5 °C, and July is the hottest with an average monthly temperature of 23.5 °C (Liao et al., 2020). The average annual precipitation is approximately 400 mm with the majority occurring between June and August (Bai et al., 2008). The region is highly vulnerable to wind erosion and desertification because it is arid, windy, and rich in sand source, coupled with the influence of human activities (Liao et al., 2020). In recent decades, the climate of the study area has shown a clear warming-drying trend (Fig. S1).

*Hemiptelea davidii* (Hance) Planch is the only species of the genus *Hemiptelea* of Ulmaceae. This deciduous angiosperm tree species manifests commendable attributes, including resilience to drought and cold, and immunity to biotic stressors. Moreover, it serves as an exemplary pioneer species for sand stabilization and has been increasingly considered to be used in the establishment of protective forest ecosystems (Bao et al., 2018). *H. davidii* mainly distributes in the foothills, forest edges, and roadsides in Northeast and North China, but it does not typically form a forest community. In most
cases, it is scattered as a companion species within other forest communities (Yang et al., 2011). However, it forms unique sparse forest stands in our selected study site of the Horqin Sand Land, with tree density between 88 and 132 trees ha\(^{-1}\).

2.2 Wood sample collection and radial growth data acquisition

In August 2022, tree cores were collected across three plots in the natural *H. davidii* forests (Table 1), specially avoiding residential areas to minimize the potential effects of anthropogenic factors. All the sampling plots have similar soil and climate factors. A total of 60 trees, with each 20 trees per plot, were randomly selected and tree cores were collected at breast height (1.3 m) using an increment borer with an inner diameter of 5.15 mm. Two cores were collected in opposite directions for each tree. The collected cores were air-dried and fixed, then they were sequentially polished with 240, 600, 1000, 1500, 2000, and 3000 grit sandpaper on a wheel sander until xylem anatomical characteristics were clearly distinguished (Stokes and Smiley, 1968). Images were obtained by scanning tree cores at 1200 dpi using a scanner (Perfection V800, Epson America, Inc., Los Alamitos, CA, USA), and the tree ring width (TRW) of each ring for these cores was measured using the WinDENDRO 2022 program (Regent Instruments Canada Inc., Quebec, Canada) with an accuracy of 0.001 mm. The quality of the cross-dated series was checked using the COFECHA program (Holmes, 1983).

In addition, basal area increment (BAI) was calculated from the raw ring-width data to evaluate the radial growth of trees:

\[
BAI = \pi \times (R_i^2 - R_{i-1}^2)
\]

where \(R_i\) is the cumulative values of tree-ring width from the first year to the \(i\)th year.
Table 1 Geographical locations and stands characteristics of sample plots of natural *H. davidii* forests.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Longitude (°E)</th>
<th>Latitude (°N)</th>
<th>Altitude (m)</th>
<th>Tree height (m)</th>
<th>DBH (cm)</th>
<th>Stand density (trees ha⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>122.9780</td>
<td>43.1239</td>
<td>179.7</td>
<td>8.75 ± 2.95</td>
<td>21.50 ± 4.00</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>122.9722</td>
<td>43.1324</td>
<td>180.5</td>
<td>9.60 ± 1.70</td>
<td>20.60 ± 4.15</td>
<td>-</td>
</tr>
<tr>
<td>3</td>
<td>123.0129</td>
<td>43.1368</td>
<td>170.5</td>
<td>8.90 ± 1.70</td>
<td>20.80 ± 3.35</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>122.9832</td>
<td>43.1263</td>
<td>170.5</td>
<td>8.75 ± 2.95</td>
<td>21.50 ± 4.00</td>
<td>110</td>
</tr>
<tr>
<td>2</td>
<td>122.0091</td>
<td>43.1331</td>
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<td>14.65 ± 4.65</td>
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<tr>
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<td>123.0046</td>
<td>43.1376</td>
<td>170.9</td>
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<td>18.00 ± 7.00</td>
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</tr>
<tr>
<td>4</td>
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<td>8.30 ± 2.70</td>
<td>17.25 ± 4.25</td>
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<tr>
<td>5</td>
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<td>43.1378</td>
<td>163.5</td>
<td>7.60 ± 1.30</td>
<td>19.00 ± 5.00</td>
<td>110</td>
</tr>
<tr>
<td>6</td>
<td>123.0071</td>
<td>43.1366</td>
<td>169.2</td>
<td>9.45 ± 2.55</td>
<td>17.75 ± 2.25</td>
<td>121</td>
</tr>
</tbody>
</table>

2.3 Measurements of tree-ring xylem characteristics

Six cores, with each two cores per plot, were randomly selected and used to analyze the xylem anatomical characteristics. The surface of the pretreated cores was colored with black ink and the earlywood vessels were refilled with white chalk for optimal contrast (Martínez-Sancho et al., 2017). Digital images were captured with an inbuilt digital camera (Olympus EP50, Olympus, Münster, Germany) of LINTAB 6 system (Rinntech, Germany). The obtained digital images were analyzed ring by ring in ImageJ software (US National Institutes of Health, Bethesda, MD, USA). Considering the fact that earlywood vessels are mainly responsible for performing hydraulic functions, only the
earlywood within each ring was measured for xylem anatomical characteristics (Tyree and Zimmermann, 2002; Gea-Izquierdo et al., 2012; Zhu et al., 2021). For each ring, the diameter (d) and area (A) of all vessels (A ≥ 3000 μm²) in a defined rectangular target area (RW × L, where RW is the ring width in the sample and L is the tangent length of the annual ring) were measured using a combination of automated detection and manual editing. For each ring of each core, mean vessel area (MVA), hydraulic diameter (Dh), percentage of vessel area (PC), number of vessels (NV), vessel density (VD), theoretical hydraulic conductivity (Kh), and vulnerability index (Vx) were calculated (Islam et al., 2018; Nola et al., 2020). We normalized NV to a fixed frame with a tangential width of 2000 μm (Castagneri et al., 2020; Zhu et al., 2021). Tree-ring xylem characteristics were calculated as follows:

\[ MVA = \frac{1}{n} \sum_{i=1}^{n} A_i \]  
(2)

Where A_i is the vessel area (μm²) of the ith vessels measured.

\[ D_h = \frac{\sum d_i^5}{\sum d_i^4} \]  
(3)

Where d_i is the vessel diameter (μm) of the ith vessels measured.

\[ PC = \frac{\sum_{i=1}^{n} A_i}{RW \times L} \times 100\% \]  
(4)

Where RW is the ring width in the sample and L is the tangent length of the annual ring.

\[ K_h = \frac{10^{24} \rho \times 2000}{128 \eta l} \sum_{i=1}^{n} d_i^4 \]  
(5)

Where \( \rho \) is the density of water at 20 °C (998.2 kg m⁻³), \( \eta \) is the viscosity of water at 20 °C (1.002 × 10⁻⁹ MPa s⁻¹), d_i is the diameter of the ith vessels measured, L is the tangent length of each ring (μm), and 2000 is the tangential width (μm) of the analyzed area.
233 \[ V_x = \frac{D_h}{VD} \] (6)

2.4 Chronology establishment and evaluation

Before the dendroclimatic analyses, the ring width and xylem anatomy series were standardized using the ARSTAN program (Cook, 1985). Specifically, a cubic-smoothed spline function with a 50% frequency response cutoff equal to two-thirds of the series length was used to remove non-climatic signals to maximize the use of climatic information in the series, and the bi-weight robust mean method was used to obtain standardized chronologies for the tree-ring width index (RWI) and key stem xylem traits, i.e., MVA, and VD. To assess the quality of the chronologies, we calculated the following statistical properties (Table S1): first-order autocorrelation (AC1), mean inter-series correlation between trees (rbar.bt), signal-to-noise ratio (SNR), mean sensitivity (MS), and expressed population signal (EPS).

2.5 Calculation of carbon isotope discrimination and iWUE

We randomly selected five cores, with one or two cores per plot, for stable carbon isotope ratio analysis, and the cores were carefully separated year by year using a scalpel under a stereomicroscope (Leica ICC50, Leica Microsystems, Wetzlar, Germany). After that, the annual samples were dried in an oven until a constant mass and then grounded in a ball mill (MM400, Retsch, Haan, Germany). The carbon isotope ratios (δ13C, ‰) were determined using an isotope ratio mass spectrometer (Flash EA1112–IRMS, delta plus XP, Thermo Fisher, USA).

Farquhar and Sharkey (1982) established an equation for carbon isotope fractionation patterns in C₃ plants:
\[ \Delta^{13}C = (\delta^{13}C_a - \delta^{13}C_p)/(1 + \delta^{13}C_p/1000) \]  \hspace{1cm} (7)

Where \( \delta^{13}C_a \) and \( \delta^{13}C_p \) represent \( \delta^{13}C \) values for the atmosphere CO\(_2\) and plant samples, respectively.

The \( \Delta^{13}C \) value during CO\(_2\) fixation of C\(_3\) plants is linearly related to the ratio of intercellular CO\(_2\) concentration in the leaves (\( C_i \)) to the atmospheric CO\(_2\) concentration (\( C_a \)):

\[ \Delta^{13}C = a + (b-a)C_i/C_a \]  \hspace{1cm} (8)

where \( a \) is the diffusion fractionation coefficient of CO\(_2\) when it passes through the stomata (\( a = 4.4 \)‰), and \( b \) is the fractionation coefficient during the carboxylation of CO\(_2\) by Rubisco enzyme (\( b = 27 \)‰).

According to Fick’s Law (Farquhar et al., 1989), iWUE was calculated using \( C_i/C_a \) as follows:

\[ \text{iWUE} = A/g_s = (C_a - C_i)/1.6 = C_a(1 - C_i/C_a)/1.6 \]  \hspace{1cm} (9)

where \( A \) is the rate of CO\(_2\) assimilation by the leaves and \( g_s \) is the leaf stomatal conductance. The \( C_a \) and \( \delta^{13}C_a \) from 1994 to 2003 were obtained from McCarroll and Loader (2004). Additional data of \( C_a \) and \( \delta^{13}C_a \) (2004–2020) were obtained from the Earth System Research Laboratory of NOAA.

### 2.6 Landsat data processing and vegetation indices estimation

We established six circular plots with a radius of 17 m (Table 1) in H. davidii natural forests, with each equivalent to the area of a Landsat pixel (Moreno-Fernández et al., 2021), and used handheld GPS to obtain the coordinates of the center of the plots. Arcgis 10.6 was used to generate a 17-m-radius circular buffer as the base data for the
computation of the two key vegetation indices, Normalized Difference Vegetation
Index (NDVI) and Normalized Difference Moisture Index (NDMI). Vegetation index
data were obtained using Google Earth Engine (GEE), which is a platform designed to
efficiently acquire and pre-process large amounts of remotely sensed data (Gorelick et
al., 2017). NDVI is a greenness vegetation index that consists of the normalized ratio
of reflectance in the red (R) and near-infrared (NIR) spectral wavelengths, i.e., NDVI
= (NIR – R) / (NIR + R), and is commonly used to assess the vegetation health status
(Tucker, 1979). NDMI is a vegetation index that consists of the normalized ratio of
reflectance in the near-infrared (NIR) and middle-infrared (SWIR1) spectral
wavelengths, i.e., NDMI = (NIR – SWIR1) / (NIR + SWIR1), and is commonly used
to quantify the moisture content of the vegetation canopy (Hardisky et al., 1983).

2.7 Climate data

The climate data in this study were obtained from the CRU TS 4.06 gridded climate
dataset provided by the Koninklijk Nederlands Meteorlogisch Instituut (KNMI), with
the selected data covering the latitude and longitude regions of 43.0°–43.5°N and
122.5°–123.0°E. The downloadable data included monthly mean temperature (T_{mean}),
monthly total precipitation, and monthly self-calibrated Palmer Drought Severity Index
(scPDSI) for the period of 1950–2020 (Ning et al., 2022; Han et al., 2023). The Palmer
Drought Severity Index (PDSI) was one of the widely used integrated climatic metrics
to quantify the severity of droughts across different climates (Palmer, 1965). To address
the lack of consistency across different regions, the scPDSI model was further
developed by Wells et al. (2004). A severe drought event is defined as when the value
of scPDSI is less than −3 (Xu et al., 2022b). In the study area, the monthly mean scPDSI was less than −3 in the growing season (May–September) in 2000–2004 and 2007 (Song et al., 2017), we thus defined the droughts that occurred in 2000–2004 and 2007 as severe drought events.

### 2.8 Data analysis

Long-term trends of annual climatic variables ($T_{\text{mean}}$, precipitation, and scPDSI) were evaluated using linear regression analysis. Interannual variability of annual ring-width indicators, stem xylem traits, and spectral indices were quantified by calculating the coefficient of variation (CV) and plasticity index (PI, $[(\text{maximum}−\text{minimum})/\text{maximum}]$) (Table 2). Pearson correlation analyses were performed to analyze the relationships between the climatic variables ($T_{\text{mean}}$, precipitation, and scPDSI) and the tree-ring width index (RWI), key stem xylem traits (MVA, VD), iWUE, and canopy vegetation indices (NDVI, NDMI) over the common period (1994–2020), using a sliding window of 3 months. Pearson correlation analysis and principal component analysis (PCA) were used to explore potential relationships between RWI, stem xylem traits, iWUE, and canopy vegetation indices. The significance threshold for all analyses was set at $P < 0.05$. Since the inverse of the vulnerability index represents hydraulic safety, we inverted $V_x$ in the PCA and Pearson correlation analyses. All statistical analyses were performed in R Ver.4.2.0 (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria).
Table 2 List of tree-ring measurements, tree-ring anatomical traits, and spectral indices in the study.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Trait</th>
<th>Units</th>
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</thead>
<tbody>
<tr>
<td>TRW</td>
<td>Tree ring width</td>
<td>mm</td>
</tr>
<tr>
<td>BAI</td>
<td>Basal area increment</td>
<td>mm²</td>
</tr>
<tr>
<td>RWI</td>
<td>Tree-ring width index</td>
<td></td>
</tr>
<tr>
<td>MVA</td>
<td>Mean vessel area</td>
<td>µm²</td>
</tr>
<tr>
<td>Dₜ</td>
<td>Hydraulic diameter</td>
<td>µm</td>
</tr>
<tr>
<td>PC</td>
<td>Percentage of vessel area</td>
<td>%</td>
</tr>
<tr>
<td>NV</td>
<td>Number of vessels</td>
<td>-</td>
</tr>
<tr>
<td>VD</td>
<td>Vessel density</td>
<td>mm²</td>
</tr>
<tr>
<td>Kₜ</td>
<td>Theoretical hydraulic conductivity</td>
<td>kg m MPa⁻¹ s⁻¹</td>
</tr>
<tr>
<td>Vₛ</td>
<td>Vulnerability index</td>
<td>-</td>
</tr>
<tr>
<td>iWUE</td>
<td>Intrinsic water-use efficiency</td>
<td>µmol mol⁻¹</td>
</tr>
<tr>
<td>NDVI</td>
<td>Normalized difference vegetation index</td>
<td>-</td>
</tr>
<tr>
<td>NDMI</td>
<td>Normalized difference moisture index</td>
<td>-</td>
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</tbody>
</table>

3. Results

3.1 Inter-annual variation in individual-tree and canopy level parameters

Radial growth of *H. davidii* trees showed relatively large inter-annual variation and obvious ontogenetic effects as indicated by the chronologies of TRW and BAI (Fig. 1). The TRW ranged from 1.5 to 2.9 mm with values during the drought years (i.e. 2000–2004 and 2007) substantially lower than the normal years before and after the drought (Fig. 1a). Overall, BAI increased with tree age with very low values during the initial
life stage before ca. 10 years old (111-155 mm\(^2\)), quickly increased to maximum values
at ca. 20 years old (1183-1258 mm\(^2\)), and then sharply decreased and maintained at
around 600-700 mm\(^2\) thereafter (Fig. 1b). Both TRW and BAI recovered sharply in 1
year after the severe drought was relieved (Fig. 1).

**Fig. 1** Inter-annual variation in tree-ring width (a, TRW) and basal area increment (b, BAI) in three plots. The gray shaded area of the figure highlights the severe drought events that occurred from 2000 to 2004 and in 2007.

Radial growth and tree-ring xylem traits showed synchronization in terms of inter-
annual variability (Fig. 1, 2). Tree-ring xylem anatomical traits had smaller ontogenetic
effects and less overall inter-annual variation than radial growth (Table S2). However,
they exhibited a noteworthy response during severe drought events (Fig. 2). MVA, \(K_h\),
and \(V_x\) exhibited low values during the initial years and stabilized at relatively high
levels after 2005 (Fig. 2a, b, d). The trend of inter-annual variation of VD was the
opposite of MVA, \(K_h\), and \(V_x\) (Fig. 2c). All stem xylem traits showed considerable
responses to the two severe drought events of 2000-2004 and 2007. Specifically, MVA, $K_h$, and $V_x$ decreased to lower values, while VD increased to higher values in 2000-2004 and 2007 (Fig. 2). However, after drought recovery, they all promptly recovered to their previous levels (Fig. 2). Among all the measured stem xylem traits, $K_h$ exhibited the highest coefficient of variation (Table S2). The inter-annual variation of iWUE overall synchronized with inter-annual changes of MVA, $K_h$, and $V_x$ (Fig. S2). It attained higher values during severe drought stressed years compared to the normal years before and after the dry years and gradually increased to high values when tree growth decreased after 2012.

Fig. 2 Inter-annual variation in mean vessel area (a, MVA), vessel density (b, VD), hydraulic diameter (c, $K_h$), and vulnerability index (d, $V_x$) of *H. davidii* in the study
area. Shading in the time series display the standard error of the chronology (n = 6). The gray shaded area of the figure highlights the severe drought events that occurred from 2000 to 2004 and in 2007.

The two studied canopy spectral indices showed relatively limited synchronization with inter-annual changes in tree-ring width and stem xylem traits, and they were less responsive to the severe drought-stressed years relative to the ring-width and stem xylem parameters. NDVI and NDMI also showed clear contrasts before and after 2012, i.e., both NDVI and NDMI remained at substantially higher levels after 2012 compared to the previous stage (Fig. 3).

**Fig. 3** Inter-annual variation in normalized difference vegetation index (a, NDVI) and
normalized difference moisture index (b, NDMI) of *H. davidii* in the study area. The gray shaded area of the figure highlights the severe drought events that occurred from 2000 to 2004 and in 2007. The thin lines in the graph represent repeated samples (n = 6) and the thick line represent the mean of the samples.

3.2 Climatic effects on individual-tree and canopy level parameters

Climate factors governing environmental moisture conditions had significant impacts on radial growth, tree-ring xylem anatomical traits, iWUE, and canopy spectral indices of the *H. davidii* trees (Fig. 4). RWI generally showed a positive correlation with precipitation but had a negative correlation with $T_{\text{mean}}$ and the correlations were particularly strong for the months of the current year growing season. The RWI exhibited significant negative correlations with the seasonal $T_{\text{mean}}$ for the current year May to July (MJJ) and July to August (JJA). Contrastingly, RWI exhibited positive correlations with both the seasonal mean precipitation and the seasonal mean scPDSI. Specifically, RWI showed significant positive correlations with the seasonal mean precipitation during the current year in April through August and the seasonal mean scPDSI during the current year in March through October (Fig. 4). MVA and VD exhibited significant negative and positive correlations, respectively, with seasonal $T_{\text{mean}}$ during the current year January to March (JFM) and December of the previous year to June of the current year (dJF–AMJ). The iWUE demonstrated a significant positive correlation with seasonal $T_{\text{mean}}$ during the previous year in July–September (jas), the current year in March–July (MAM–MJJ) and July–September (JAS), and no significant correlations were detected for MVA, VD, and iWUE with precipitation or...
scPDSI (Fig. 4). Seasonal average precipitation during April–June (AMJ) and seasonal average scPDSI in May–October (MJJ–ASO) were found to have significant positive impacts on NDMI, while no such significant influence was observed for NDVI (Fig. 4).

Fig. 4 Results of correlation analyses between key seasonal (3 months) climate variables (T\text{\textsubscript{mean}}, Precipitation, scPDSI) and tree-ring width index (RWI), tree-ring anatomical (MVA, mean vessel area; VD, vessel density), intrinsic water-use efficiency (iWUE), and spectral indices (NDVI, normalized difference vegetation index; NDMI, normalized difference moisture index) from previous May–July (mjj) to current August–October (ASO). Asterisks indicate significant correlations at P < 0.05 level.
3.3 Interrelationships among radial growth, stem xylem traits, iWUE, and spectral indices

The results of the principal component analysis (PCA) based on the 12 parameters showed that principal component 1 and 2 (PC1 and PC2) explaining 49.5% and 22.2% of the total variation, respectively (Fig. 5). Stem xylem traits representing higher hydraulic efficiency (MVA, $D_h$, NV, PC, and $K_h$) were all distributed on the positive side of PC1 (Fig. 5 and Table S3), whereas the xylem traits related to hydraulic safety (VD and $1/V_x$) distributed on the negative side of PC1 (Fig. 5 and Table S3). iWUE and TRW were the main contributors to PC2 and distributed on the positive and negative sides of the PC2 axis, respectively (Fig. 5, S3). Notably, there were coupled relationships between individual-scale and canopy-scale tree performances, with both NDVI and NDMI exhibiting linear positive correlations with BAI and $K_h$ ($P < 0.05$; Fig. 6).
Fig. 5 Results of the Principal Component Analysis (PCA) for the measured 12 parameters of *H. davidii* during the period 1994–2020. See Table 1 for abbreviations.

![Figure 5](image)

Fig. 6 Linear regressions between normalized difference vegetation index (NDVI), normalized difference moisture index (NDMI) and (a, c) basal area increment (BAI), (b, d) theoretical hydraulic conductivity ($K_h$) of *H. davidii* during the period 1994–2020. The statistics of the regression are given and the shaded area indicate the 95% confidence interval.

![Figure 6](image)

4. Discussion

4.1 Water is the predominant controlling factor for tree performances

Climatic variables that represent environmental water availability are the overarching controlling factors for the tree growth performance measured at both individual and
stand levels. At the individual scale, we found a positive correlation between RWI and precipitation as well as scPDSI, which is consistent with tree growth-climate relationships observed in other water-limited areas (Kunz et al., 2018; Yang et al., 2022a; Han et al., 2023). Trees rely on water for photosynthesis and nutrient absorption, which are essential for their growth and development (Steppe et al., 2015; Zhang et al., 2018). During years with relatively abundant precipitation, trees can benefit from ample soil moisture and the resultant increase in water availability, resulting in improved water-transporting efficiency, tree water status, photosynthetic rates, and thus increased growth potential (Teodoro et al., 2021). Therefore, trees in areas characterized by water scarcity may display increased tree-ring widths during years when the environmental water deficit is temporarily alleviated (Li et al., 2021). The scPDSI that integrates the ability of soil water supply and the intensity of evapotranspiration is proportional to the environmental water availability (Xu et al., 2022b). During periods of low precipitation and scPDSI, the water supply may fail to meet the transpiration demands, causing water stress and lower stomatal conductance. Consequently, the limited availability of water constrains photosynthesis, leading to reduced rates of plant growth as reflected by smaller tree-ring width (Rahman et al., 2019; Correa-Díaz et al., 2020).

In addition, the negative effect of temperature on radial growth indirectly corroborates the critical role of environmental water availability in determining tree growth performance. In areas with temperature limitations, such as high latitude or altitude areas, higher temperatures can have a significantly positive impact on tree growth (Yang et al., 2017; Ruiz-Pérez and Vico, 2020). However, in moisture-limited
areas, higher temperatures can intensify evapotranspiration, leading to reduced water availability (Zhang et al., 2021). Under water-limited conditions, temperature directly influences cell division, elongation, and differentiation processes, thereby affecting secondary stem growth in trees (Fonti et al., 2007). Elevated temperatures inhibit these processes, leading to slower cellular growth and reduced tree-ring width (Pritzkow et al., 2014; Jing et al., 2022). Furthermore, extremely high temperatures may enhance tissue respiration, reducing the net assimilate accumulation and resulting in insufficient carbohydrates for the structural growth of trees, ultimately leading to a smaller tree-ring width (Zhang et al., 2018).

Notably, the agreement between vegetation canopy moisture status and environmental moisture availability, as shown by the positive correlation between NDMI and precipitation and scPDSI, further strengthens our argument that moisture plays a dominant role in tree performance in this water-limited region. During periods of higher precipitation, soil moisture becomes more available, and the presence of larger conduits in the water transport system ensures more effective water transport to the canopy (Islam et al., 2019a), compensating for leaf water loss due to transpiration and keeping high leaf water content and water potential (Pompa-García et al., 2021; Rowland et al., 2023). Extensive research has shown that canopy moisture status mirrors the water supply capacity of the soil (Zhang et al., 2016). Canopy moisture status is highly sensitive to drought and can be significantly reduced during extreme drought conditions (Assal et al., 2016; Moreno-Fernández et al., 2022). On the interannual scale, the sensitivity of the canopy water content to environmental moisture
conditions highlights the availability of moisture as a key limiting factor for tree performance in the region.

4.2 Plastic responses to extreme drought indicate water-related functional trade-offs

The xylem hydraulic traits of the *H. davidii* trees showed significant plasticity during severe drought events. When trees experience extreme droughts, water supplies become scarce, compelling them to take measures that enhance their hydraulic safety and avoid hydraulic failure to ensure survival (Rita et al., 2015). On the one hand, reducing the diameter of vessels can enhance embolism resistance to some extent. For instance, ring-porous species may reduce vessel diameter in the earlywood during drought conditions to decrease the risk of cavitation and diminish hydraulic conductivity, conserve water in the soil, and avoid extreme negative water potentials (Gea-Izquierdo et al., 2012; Martinez-Sancho et al., 2017). On the other hand, as vessel diameter decreases, vessel density increases, which also contribute to higher hydraulic safety (Poorter et al., 2010; Balima et al., 2020). Some angiosperm trees can produce a greater number of small vessels during severe droughts, ensuring that some vessels remain active for water transport and reducing the risk of hydraulic failure due to drought-induced embolism (Islam et al., 2019b; Nola et al., 2020). Meanwhile, adjustments in vessel diameter and density for the sake of higher hydraulic safety decreased the theoretical xylem hydraulic efficiency during severe droughts, suggesting a functional trade-off between hydraulic efficiency and safety at the individual scale. Our results clearly indicate that the studied *H. davidii* trees prioritize maintaining a secure water transport during extreme drought by modifying their vessel structure to enhance drought tolerance.
The response of trees to extreme drought was coordinated at the whole-tree level. During periods of severe droughts, trees experienced a decline in hydraulic efficiency, and an increase in iWUE, and the adjustments suggest a shift to a more frugal water-use strategy. When faced with water deficit, trees adopt various acclimation measures to reduce water transpiration and water loss, and utilize water resources more efficiently (Bréda et al., 2006; Rowland et al., 2023). Under drought conditions, trees can strictly regulate stomatal opening to minimize water transpiration while maintaining relatively high intercellular CO₂ concentrations (Farquhar et al., 1989; McDowell et al., 2008). This adjustment results in an increased relative abundance of C¹³ in the CO₂ molecules captured and fixed by the tree during photosynthesis, ultimately increasing the iWUE of the trees (Sanders et al., 2016; Correa-Díaz et al., 2020). These plastic adjustments enable trees to adapt more effectively to changes in resource availability and modify their growth strategies during severe drought conditions. The synchronized improvements in hydraulic efficiency and iWUE suggest a whole-plant level adjustment towards a more conservative strategy in facing more challenging water availability, which accounts for the reduced radial growth observed in the extreme drought years.

The canopy-level parameters were less susceptible to extreme droughts compared to the ring-width metrics and stem xylem traits. The radial growth of trees indicates individual growth response to stress, while the canopy spectral index overall represents the carbon sequestration capacity of the vegetation. Drought can cause significant changes in carbon allocation between leaves, wood formation, and carbohydrate storage.
Tree radial growth is deemed to be of diminished priority in resource allocation relative to other physiological processes, such as photosynthetic carbon assimilation. Therefore, trees may strategically prioritize ensuring a sufficient energy supply to sustain their immediate metabolic needs, as well as the maintenance of canopy tissues under stress (Camarero et al., 2015; Kannenberg et al., 2019b; Versace et al., 2020; Moreno-Fernández et al., 2022). In contrast, radial growth requires a substantial amount of resources, particularly water and nutrients, as well as energy for cell division and expansion. Consequently, during drought conditions, when resources are limited, trees tend to reduce or slow down radial growth as a way to conserve and allocate resources towards more critical functions. This resource allocation strategy makes tree radial growth highly sensitive to drought relative to carbon assimilation. Furthermore, the canopy spectral index may only undergo significant changes when the canopy experiences leaf discoloration and loss (Decuyper et al., 2020). It is possible that *H. davidii*, a relatively resistant indigenous tree species, might not experience serious damage in the canopy during the severe drought events, making it difficult to detect drought effect spectrally in this study. Consequently, the results suggest that the tree-ring technique may be a more effective method for providing early warning of tree decline and death in the context of climate change.  

**4.3 Coordinated response of individual-tree and canopy scales**

On a long-term, the growth performance and response to environmental factors at the stand and individual scales exhibited coordination. The forest canopy fixes atmospheric CO₂ through photosynthesis, while tree stems use the organic matter produced by the
canopy for growth. The photosynthetic activity of the canopy determines the availability of carbohydrates for physiological processes, including radial growth, providing a physiological basis for the coordinated variation between tree-ring width and NDVI (Pompa-García et al., 2021). However, previous studies examining the relationship between tree-ring width and NDVI have shown divergent results. Some studies have found a decoupling between the two indices under drought stress and at high northern latitudes (Brehaut and Danby, 2018; Wen et al., 2021; Castellaneta et al., 2022), while our results suggest that a coordination between canopy carbon assimilation and stem radial growth over the long-term inter-annual scale. This variation in tree canopy is also coupled with adjustments in xylem hydraulic architecture at the individual tree level. Healthy and well-watered trees with high hydraulic conductivity can efficiently absorb water from the soil and transport it to the canopy, and this process contributes to the increased leaf production in the canopy, which, in turn promotes robust photosynthetic activity and higher NDVI values (Aguilar et al., 2012; Niemeyer et al., 2014; Vicente-Serrano et al., 2016). Furthermore, sufficient water supply stimulates cell division and elongation, promoting radial growth (Oliveira et al., 2008), resulting in increased trunk diameter, greater total biomass accumulation, increased leaf area index and higher NDVI values (Wang et al., 2005). The higher hydraulic conductivity and radial growth can improve tree’s ability to maintain an adequate internal water supply, which positively affects NDMI values. Fluctuations in environmental water availability contributed to coordinated inter-annual changes in xylem hydraulic traits, radial growth, and canopy spectral indices that collectively
affect synchronized changes at the individual and stand scales in terms of water status, health status, and growth.

5. Conclusions

Our results suggest that environmental moisture conditions have a leading effect on the radial growth, stem xylem characteristics, and canopy water status of the studied species in the water-limited area. Inter-annual fluctuations revealed a coordinated pattern in radial growth and key xylem anatomical traits in response to the severe drought events, while the studied canopy spectral indices were seemingly less responsive to the severe droughts. The severe drought events in 2000–2004 and 2007 resulted in decreased radial growth and reduced theoretical xylem hydraulic conductivity, but enhanced water use efficiency and hydraulic safety. Inter-annual adjustments in wood anatomical characteristics and accompanying variations in carbon isotopic imprint suggest trade-offs between hydraulic efficiency and security as well as between radial growth and water-use efficiency in the studied *H. davidii* trees. Over the studied time series, coordination exists between the tree performance at both the stand and individual levels and their response to environmental factors. These findings indicate the significance of plastic adjustments in xylem hydraulic function and water-use strategies for *H. davidii* trees in adapting to this environment with relatively strong water limitation and large inter-annual variability.

Acknowledgments

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Supplementary Materials:

Coordinated responses of *Hemiptelea davidii* at the individual tree and stand levels to interannual climatic variation in a water-limited area

Ke-Xin Guo¹,², Xue-Wei Gong²,³,⁴, Jing-Jing Guo²,³,⁴, Han Shi²,⁵, Yong-Jiao Zhou²,⁵, Qian-Nan Leng²,⁵, Guang-You Hao²,³,⁴*

¹School of Life Sciences, Liaoning University, Shenyang 110036, China;
²CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China;
³Daqinggou Ecological Research Station, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China;
⁴Key Laboratory of Terrestrial Ecosystem Carbon Neutrality, Liaoning Province, Shenyang 110016, China;
⁵University of Chinese Academy of Sciences, Beijing 100049, China

*Corresponding author

Phone: +86-24-83970374
Fax: +86-24-83970300
E-mail: haogy@iae.ac.cn
**Table S1** Characteristics of the standard chronologies of tree-ring width and wood anatomical parameters for the period 1994-2020 in the study area. RWI, tree-ring width index; MVA, mean vessel area; and VD, vessel density; AC1, first-order autocorrelation; Rbar.bt, mean inter-series correlation between trees; SNR, signal-to-noise ratio; MS, mean sensitivity; EPS, expressed population signal.

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<th>SNR</th>
<th>MS</th>
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Table S2 Temporal variation in tree-ring data, physiological parameters, and spectral indices of *H. davidii* (1994-2020). SD, standard deviation; CV, coefficient of variation; PI, plasticity index. High values of CV (≥ 0.3) and PI (≥ 0.7) are highlighted in bold.

See Table 1 for abbreviations.

<table>
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<th>mean</th>
<th>SD</th>
<th>CV</th>
<th>PI</th>
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</thead>
<tbody>
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<td>BAI (cm²)</td>
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<td>MVA (µm²)</td>
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**Table S3** Scores of tree-ring parameters, physiological parameters, and spectral indices on the principal component 1 and 2 axes in the study area (values with scores ranging from –1 to –0.3 and 0.3 to 1 are bolded).

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<td>D&lt;sub&gt;h&lt;/sub&gt;</td>
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<tr>
<td>PC</td>
<td>0.22</td>
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<tr>
<td>NV</td>
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<tr>
<td>NDMI</td>
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**Fig. S1** Trends of mean annual temperature (a, $T_{\text{mean}}$), total annual precipitation (b), and self-calibrated Palmer Drought Severity Index (c, scPDSI) for the study area, 1950–2020. The solid black lines in panel a, b, and c indicate significant changes in temperature, precipitation, and scPDSI from 1950 to 2020.
Fig. S2 Inter-annual variation in intrinsic water-use efficiency (iWUE) of *H. davidii* in the study area. Shading in the time series display the standard error of the chronology (n = 5). The gray shaded area of the figure highlights the severe drought events that occurred from 2000 to 2004 and in 2007.
**Fig. S3** Correlations of tree-ring parameters, physiological parameters, and spectral indices during the period 1994–2020. Color coding represents the correlation coefficient (red and blue represent positive and negative correlations, respectively). Asterisks indicate significant correlations at $P < 0.05$ level. See Table 1 for abbreviations.