



# *Populus pruinosa* decline in a riparian *tugai* forest on the Zarafshon River, central Uzbekistan: edaphic conditions as predisposing factors and drought as the triggering factor

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**Abstract** Ecological and anthropogenic changes have reduced the area of Central Asian riparian forests (*tugai*), involving dieback of *Populus pruinosa* Schrenk, one of the *tugai*'s principal tree species. In a *tugai* forest on the Zarafshon River, Central Uzbekistan, we investigated the role of environmental factors in *P. pruinosa* dieback by comparing one healthy and one proximate declining stand. We measured the widths of tree rings of the past 25 years (1999–2023), analyzed their carbon isotope ratios ( $\delta^{13}\text{C}$ ; 2004–2023), determined physical and chemical soil variables, and retrieved data on groundwater depths and SPEI (Standardised Precipitation Evapotranspiration Index). Over the 25-year period, radial growth did not differ between

healthy and declining trees, but tree growth of the declining stand decreased, and in the last 6 years (2018–2023), during and after 2 exceptionally dry years (2018 and 2019), radial increment was significantly smaller. Correlations between radial growth,  $\delta^{13}\text{C}$  and SPEI, indicative of drought stress, were only found in the declining stand's trees. Soil of the declining stand had a higher clay content in the subsoil (30–60 cm), higher salt concentrations in the uppermost layer (10 cm) and in the subsoil, and a lower field capacity across the entire soil profile. There was no groundwater decline during the study period. For the first time, evidence is provided that a drought spell in combination with predisposing unfavorable soil conditions can cause tree dieback in Central-Asian *tugai* forests at a relatively short distance from the water table. Our study may also contribute to initiate further research for analyzing interrelationships between hydrological, edaphic, ecophysiological and meteorological factors in dieback processes of Central-Asian riparian forests, especially in regions that are strongly underrepresented in ecological research.

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## Introduction

In Central Asian deserts and semi-deserts, riparian forests, called *tugai* or *tugay*, grow along riverbanks on floodplains at slightly elevated sites that can be flooded for certain periods of the year (Walter and Box 1983; Walter and Breckle 1994). The canopies of these forests mainly consist of the poplar species *Populus pruinosa* Schrenk (Salicaceae) and *P. euphratica* Oliv. (syn. *P. diversifolia* Schrenk) (Walter and Box 1983; Pfadenhauer and Klötzli 2014). *Populus pruinosa*

occurs from north-western China (Xinjiang) to the Caspian Sea (Kew Royal Botanical Gardens 2025) and is assessed as “near threatened” in the IUCN Red List (IUCN 2025). *Populus pruinosa* is moderately salt tolerant but less drought tolerant than *P. euphratica* (Zhai et al. 2022).

In many Central Asian regions, the survival of riparian forests is threatened by overuse for fuel, timber, and/or fodder, by decreasing groundwater due to irrigation of agricultural fields, and by severe salinization (Thomas and Lang 2021). In the longer term, the effects of climate change on regional hydrology enhance these threats as the Central Asian climate becomes warmer (Lioubimtseva and Henebry 2009; Sorg et al. 2014; IPCC 2023). A warming trend in Central Asia in 1960–2000 has been confirmed (Yu et al. 2020). Severe reductions in the areas of riparian forests due to land use changes or to alterations in the hydrological regime have been reported from north-western China (Wang et al. 1996; Feng et al. 2005; Geist 2005; Arkin et al. 2025), Kazakhstan (Rakhimzhanov et al. 2021; Dukenov et al. 2023), Tadjikistan (Vtorova et al. 1993) and Uzbekistan (Treshkin 2001; Tupitsa 2010). The Uzbek *tugai* forests are expected to be particularly affected by climate change due to ongoing reduction of their habitats (UN/ECE 2020).

In arid regions of Central Asia, the riparian forest poplar species (*P. pruinosa*, *P. euphratica*) benefit from access to groundwater (Thomas 2013; Thomas and Lang 2021). To a certain extent, these poplar species can cope with an increasing depth to groundwater upon a drop in the water table or wind-driven sand accumulation (Wang and Jia 2013) through height growth (Gries et al. 2003). However, there are limits to the growth and survival of the trees when the water table depth becomes extensive. *Populus pruinosa* grows and regenerates well at a groundwater depth up to 4 m and under low salinity (Vtorova et al. 1993), but along a transect of groundwater depths of 3.4–7.9 m that covered the range of natural *P. pruinosa* forests, hydraulic conductivity of the xylem and net photosynthesis decreased (Zhang et al. 2024). In the closely related *P. euphratica*, a decline in hydraulic conductivity due to greater water table depths resulted in a lower, more negative, leaf water potential, decreased stomatal conductance and lower radial stem growth (Gries et al. 2003).

Atmospheric drought stress can cause cavitation and embolism in the water conducting xylem (Tyree and Sperry 1989). Hydraulic failure of the xylem due to drought stress is a common occurrence in drought-induced tree mortality (Adams et al. 2017) and also a drought-stress effect on poplars of Central Asian riparian forests (Zhou et al. 2013).

Compared to hydrological conditions and drought, the effects of soil features, and physical variables in particular, have received less attention in studies on the decline of *tugai* forests. However, in an emerging riparian forest of central California, flood-induced sedimentation along riverbanks

and the development of the sediment's texture had a decisive role in the colonization by *Populus fremontii* S. Watson (Stella et al. 2011). In a *P. euphratica tugai* vegetation along the Tarim River, north-western China, soil texture decisively controlled the water supply to the roots, with a coarse texture in the topsoil being more favorable (Grashey-Jansen et al. 2014). In *P. pruinosa*, higher soil bulk density, lower porosity and increased soil salinity hampered clonal growth (Gai et al. 2020), an important mechanism for the propagation of poplars in Central Asian riparian forests (Thomas and Lang 2021). However, the interplay between meteorological and edaphic factors has not been studied in the occurrence of riparian forest decline in Central Asia.

The Zarafshon (Zeravshan) River is an 870-km-long endorheic river, one without an outflow to a sea or ocean. It rises in the mountains of North Tajikistan and seeps away in the Kyzyl Kum Desert northeast of the City of Bukhara, Uzbekistan before it reaches the Amu Darya River (Groll et al. 2015). The Samarkand section of the river, located in Central Uzbekistan, is part of its middle reaches. Here, the river has water throughout the year. Outside of settlements, farmland and industrial facilities, remnants of *tugai* forests exist with canopy layers mainly composed of the two typical *tugai* poplar species. Approximately 15 km to the north-east of the City of Samarkand and close to the Zarafshon River, the Zarafshon National Natural Park harbors extensive stands of *P. pruinosa tugai* forest. Recently, tree dieback in parts of the forest has been observed that resembled the decline of poplars in other Central-Asian *tugai* forests. As the Natural Park is protected from anthropogenic disturbances, it constitutes an ideal setting for investigating the causes of poplar dieback in a near-natural *tugai* forest in both healthy and declining stands with a similar distance to the river. In several previous studies, *tugai* stands of varying vigor have been investigated that already differed markedly in their distance to a river or to groundwater and/or in tree age (Westermann et al. 2008; Huang and Pang 2010; Aishan et al. 2013, 2015; Li et al. 2013; Thomas et al. 2017).

Against the background of these environmental factors that are involved in the decline of *tugai* forests, we aimed to test the following hypotheses: (1) drought has triggered dieback in the declining *P. pruinosa* stand at the Zarafshon River, alternatively: (2) a severe decline in the groundwater during the past ten years has triggered tree decline; (3) in the declining stand, the trees were predisposed to dieback by unfavorable edaphic conditions, in particular by high concentrations of fine particles and salt. To test these hypotheses, growth analyses were carried out using annual rings, the stable carbon isotope ratios of the tree rings determined to detect indications of drought stress, soil analyses undertaken and climate and groundwater data evaluated. The results may lead to further research for analyzing interrelationships between hydrological, edaphic, ecophysiological

and meteorological factors in dieback processes of Central Asian riparian forests.

## Materials and methods

### Study site and sampling

Sampling was conducted in a *P. pruinosa* forest of the Zarafshon National Natural Park close to the shore of the Zarafshon River, Central Uzbekistan. The Natural Park was established in 1975, but the area was covered with a typical riparian forest earlier. The climate is warm-temperate with hot and dry summers (Csa type according to Köppen; cf. Kottek et al. 2006; Fig. S1 of the Supplementary Material). Besides *P. pruinosa* saplings, the woody understory contains *Tamarix hispida* Willd. and *T. ramosissima* Ledeb. (Tamaricaceae), *Elaeagnus angustifolia* L. and *Hippophaë rhamnoides* L. (Elaeagnaceae), *Berberis integerrima* Bunge (syn. *B. iliensis* Popov; Berberidaceae), *Crataegus turkestanica* Pojark. (Rosaceae), *Clematis orientalis* L. (Ranunculaceae), *Sophora* L. sp. (Fabaceae) and the introduced *Maclura pomifera* (Raf.) C.K. Schneid. (syn. *M. aurantiaca*; Moraceae). The soil surface is densely covered with grass, including conspicuous tufts of *Tripidium ravennae* (L.) H.Scholz (syn. *Erianthus ravennae* [L.] P.Beauv.). There are also numerous specimens of *Colchicum kesselringii* Regel (Colchicaceae), a species that is listed as “declining” in the Republic’s Red Book (Red Book of the Republic of Uzbekistan 2019). On the sampling dates, there were no signs of flooding.

Long-term meteorological data are unavailable in Uzbekistan. Thus, mean monthly precipitation and temperature data were obtained from the Climatic Research Unit (CRU) TS3.10 datasets (Harris et al. 2014; Central Uzbekistan). Values of the Standardised Precipitation Evapotranspiration Indices (SPEI; Vicente-Serrano et al. 2010) were used as an indicator of the intensity of dry conditions at the study site. They are calculated with the Penman–Monteith approach and were retrieved on a monthly basis from <https://spei.csic.es/database.html> (Beguería et al. 2010; last accessed on November 07, 2024).

The study site consisted of healthy *P. pruinosa* forest and portions with several declining trees and dead trees.

Signs of pests or disease were not present in the trees. For this study, one stand of approximately 2 ha of the healthy forest and one of about 1 ha of the declining portion were selected that exhibited a homogeneous structure and were representative of the respective forest parts with regard to canopy height, stand density and fraction of declining trees. The distance between the healthy and the declining plots was 620 m on average. The declining trees, which only occurred in small numbers in the healthy stand, exhibited considerable defoliation and twig loss. From both stands, ten trees were randomly chosen for sampling (healthy stand: eight trees at N 39°40.03′, E 67°5.60′, 719 m a.s.l., two trees at N 39°39.98′, E 67°5.70′, 720 m a.s.l.; declining stand: 10 trees at N 39°40.25′, E 67°5.37′, 716 m a.s.l.). The elevation of the river shore (in direct distance to the study plots) was 713–716 m a.s.l. The elevations were retrieved from Google Earth Pro (last accessed on April 1, 2025) as that data can be considered more accurate than GPS data measured with a mobile device on one single occasion in the field. The distances of the sample locations to the river were approximately 700 m for the healthy and about 800 m for the declining stand. The location of the study plots is shown in Fig. S2 of the Supplementary Material.

Height, diameter at breast height (*dbh*: 1.3 m above ground) and height/diameter ratio (*h/d*) of the selected trees did not differ significantly between the healthy and the declining stand (Table 1). In autumn 2023, after the cessation of the growth period, two increment cores were taken from each tree with a 5-mm-diameter Haglöf borer at breast height from the eastern and the western side of the stems. We restricted the number of cored trees to ten per stand type to keep the amount of destructive sampling in the Natural Park to a minimum. In their pioneering work, Fritts and Swetnam (1989) stated that chronologies from ten trees fulfill the requirements for adequate chronologies, at least for non-mesic sites (see also Speer 2010). More recently, ten trees or less have been found sufficient for analyzing growth and stable carbon isotope ratios in broadleaved trees from different forest ecosystems, including *P. euphratica* (e.g., He et al. 2005; Härdtle et al. 2013a, 2013b; Walter et al. 2016; Duan et al. 2025). The core samples were fixed on cardboard and kept dry until further processing in the Geobotany Department of Trier University.

**Table 1** Features of the stands and sampled trees ( $n=10$  per stand; means  $\pm 1$  SE) at the *Populus pruinosa* site on the middle reaches of the Zarafshon River, Central Uzbekistan

| Stand category | Number of healthy (ind ha <sup>-1</sup> ) | Number of declining (ind ha <sup>-1</sup> ) | Tree height (m) | <i>dbh</i> (cm) | <i>h/d</i> (m m <sup>-1</sup> ) |
|----------------|-------------------------------------------|---------------------------------------------|-----------------|-----------------|---------------------------------|
| Healthy        | 620                                       | 80                                          | 8.1 $\pm$ 0.6   | 25.8 $\pm$ 1.5  | 31.4 $\pm$ 1.7                  |
| Declining      | 60                                        | 550                                         | 8.0 $\pm$ 0.5   | 22.5 $\pm$ 1.3  | 36.0 $\pm$ 1.8                  |

*dbh* diameter at breast height (1.3 m), *h/d* height/diameter ratio. The morphological variables did not differ significantly between the two stand types (*t*-test; cf. **Statistical analyses** section).

Monthly data on groundwater depth were obtained from Samarkand Hydrogeologic Station, Samarkand, for groundwater well #11 (N 39°40.76', E 67°6.92'; 725 m a.s.l.) for the 2010–2022 period. The distance of the well was approximately 2300 m to the healthy plots, 2400 m to the declining stand and 2700 m to the river shore. The study plots were situated between the well and the river. The location of the well is indicated in Fig. S2 of the Supplementary Material.

To determine soil morphology and soil type, one soil profile per stand was made down to the gravelly C horizon at 35–37 cm depth. From each stand, five soil samples were taken in September 2024 with soil augers from three layers of depth (0–10 cm, > 10–30 cm, > 30–60 cm) and layer- and stand-wise pooled to give one bulk sample per soil layer and stand.

### Tree-ring analyses and stable carbon isotope ratios

One core of each tree was used for measuring tree-ring widths after smoothing by cutting the uppermost 0.5 mm with a microtome (Swiss Federal Research Institute WSL, Birmensdorf, Switzerland). The tree-rings were measured using a stereo microscope (Carl Zeiss, Jena, Germany), connected to a moveable object table (Lintab 5, RinnTech, Heidelberg, Germany) interfaced directly with a computer for measurements to the nearest 0.01 mm. The oldest measurable ring had been formed in 1980, but ring series that were coherent in all trees started in 1999. Therefore, this year was selected as the starting point in calculating the increments in diameter growth. However, one tree of the healthy stand and up to nine trees (in 2023) of the declining stand had not formed rings in the most recent years (Tables S1–S3 of the Supplementary Material). The values of the growth variables were set to zero in those cases and were not considered in calculating correlations with  $\delta^{13}\text{C}_{\text{corr}}$  and with climate variables. To eliminate age effects, the individual tree-ring chronologies were detrended on the basis of regional curve standardization (RCS; Esper et al. 2003) with a moving average of ten years using TSAP-Win Scientific software (version 4.64; RinnTech). We added the mean of the respective trend series as an offset to the individual values to make all values positive (Lang et al. 2015). These ring-width data are named “indexed ring widths” hereafter. In addition, by assuming a circular perimeter of the stem, we calculated the annual basal area increment (BAI), which is suitable for removing age-related growth trends (Biondi and Quedan 2008; Speer 2010). The BAI was computed from the trees' original ring widths by year-wise subtracting the stem cross-sectional area of year  $t-1$  from year  $t$  (cf. Speer 2010):

$$\text{BAI} = \pi \left( (dbh/2 - B)_t^2 - (dbh/2 - B)_{t-1}^2 \right) \quad (1)$$

where  $dbh$  is the stem diameter at breast height and  $B$  the bark thickness. To calculate the inner cross-sectional areas, annual ring widths were subtracted year-wise from the stem radii ( $(dbh/2 - B)$ ), proceeding step-wise from the last sampling year (2023) to the earliest one.

The stable carbon isotope ratios  $^{13}\text{C}/^{12}\text{C}$  ( $\delta^{13}\text{C}$ ; ‰) of the tree rings were determined by the Department of Geobotany, Trier University, according to Loader et al. (1997) in  $\alpha$ -cellulose extracted from the other core taken from each target tree. From the healthy stand, only eight out of the ten trees sampled could be used for  $\delta^{13}\text{C}$  analyses due to the lack of sufficient material. The individual tree rings were dissected year-wise with a scalpel from the sampling year 2023 back to 2004. For those years which covered a representative time span of the last two decades, the material was sufficient to construct coherent  $\delta^{13}\text{C}$  time series. Each tree ring (or cut pieces in cases of wider rings) was placed in a separate Teflon bag, marked, sealed, and subjected to a successive and repeated sodium hydroxide/sodium chlorite treatment (Ho et al. 2020). The  $\delta^{13}\text{C}$  ratios of the extracted and dried cellulose were measured with an isotope ratio mass spectrometer (DeltaV Advantage, Thermo Fisher Scientific, Waltham, MA, USA) against IAEA standard cellulose with a precision of 0.05‰. To account for the negative temporal trend in the atmospheric  $\delta^{13}\text{C}$  in  $\text{CO}_2$  due to continuing anthropogenic fossil fuel combustion, the  $\delta^{13}\text{C}$  values of the tree rings were corrected (hereafter,  $\delta^{13}\text{C}_{\text{corr}}$ ) according to McCarroll and Loader (2004) by year-wise subtracting correction values from the raw data (from 2023 backwards) on the basis of a list of recent atmospheric  $\text{CO}_2$  concentrations issued by NOAA ([https://gml.noaa.gov/webdata/ccgg/trends/co2/co2\\_mm\\_gl.txt](https://gml.noaa.gov/webdata/ccgg/trends/co2/co2_mm_gl.txt); accessed on September 19, 2024).

### Soil analyses

Physical and chemical soil analyses were conducted in the Department of Soil Science, Faculty of Biology, National University of Uzbekistan, Tashkent. The particle sizes were assigned to the following classes (Kachinsky 1965; Sadovski and Ivanova 2020): > 0.25 mm, 0.25 – > 0.1 mm, 0.1 – > 0.05 mm, 0.05 – > 0.01 mm, 0.01 – > 0.005 mm, 0.005 – > 0.001 mm,  $\leq 0.001$  mm. To make the classification of the major texture classes similar to the internationally used standard, we attributed the classes of > 0.25 – > 0.05 mm particle size to the sand fraction, the classes of 0.05 – > 0.005 mm to silt, and  $\leq 0.005$  mm to the clay fraction. In addition, the soil bulk density and the field capacity were determined.

Chemical soil analyses included measurements of pH (measured in  $\text{H}_2\text{O}$  and KCl), the concentrations of humus, total nitrogen (N), and water-soluble nitrate-N ( $\text{NO}_3^-$ -N) as well as the determination of the carbon:nitrogen (C:N) ratios. In addition, the concentrations of the following

water-soluble ions that are most important for assessing salinity were determined: carbonate ( $\text{CO}_3^{2-}$ ), hydrogen carbonate ( $\text{HCO}_3^-$ ), chloride ( $\text{Cl}^-$ ), sulfate ( $\text{SO}_4^{2-}$ ), calcium ( $\text{Ca}^{2+}$ ), magnesium ( $\text{Mg}^{2+}$ ), and sodium ( $\text{Na}^+$ ). We estimated the soil water potential at field capacity generated by salt ( $\Psi_{\text{Salt}}$ ) from the water content and the concentrations of soluble salts:

$$\Psi_{\text{Salt}} = c \cdot R \cdot T (\text{MPa}) \quad (2)$$

where  $c$  is the concentration of all measured salt ion charge equivalents in the water at field capacity,  $R$  the universal gas constant, and  $T$  the temperature (set to 293.15 K). The  $\Psi_{\text{Salt}}$  values indicate the theoretical minimum soil water potential at field capacity, under the assumption that all water-soluble inorganic salts are dissolved in the soil water but ignore the soil matric potential. Since in current ecophysiological literature, water potentials are given as negative values when they deviate from zero, we provide the  $\Psi_{\text{Salt}}$  values with a negative sign although they just are rescaled concentrations according to Eq. 2. Such negative values also make comparisons with values of leaf water potentials from trees more comprehensible.

## Statistical analyses

The results are means  $\pm$  1 standard error (SE) if not indicated otherwise. Differences in the investigated variables between the two stand types were tested for significance with SigmaPlot for Windows version 13.0, Build 13.0.0.83 (Systat Software, Inpixon, Palo Alto, CA, USA). Tests on significant deviations from normality were conducted with the Shapiro–Wilk test, and on deviations from variance homogeneity with the Brown–Forsythe test. Differences in the values of tree morphology between the stand types were determined with  $t$ -tests, as the respective data sets passed the above-stated tests on deviations from normality and variance homogeneity. In cases of non-significant deviations from homogeneity of variances, we tested differences between the stand types in their time courses of indexed tree-ring widths, BAI and  $\delta^{13}\text{C}_{\text{corr}}$  using repeated measurement analysis of variance (rmANOVA) of SigmaPlot’s General Linear Model (GLM) package. In cases of significant deviations from variance homogeneity, year-wise mean values were calculated from the trees of each stand type, and the difference between the stands across years was tested for significance with paired  $t$ -tests in the case of non-significant deviations of those mean values from a normal distribution, or with the paired  $U$ -test if the data sets differed significantly from normality. Time courses of the growth variables,  $\delta^{13}\text{C}_{\text{corr}}$ , SPEI and groundwater distances were tested on significant trends using the Mann–Kendall trend test ( $\tau$ -value) of the R-package ‘trend’ and the ‘sens.slope’ function (Pohler

2023). Pearson correlation coefficients were calculated between the growth variables and  $\delta^{13}\text{C}_{\text{corr}}$  as well as between these variables and SPEI, provided that the residuals did not differ significantly from normality as determined with the Shapiro–Wilk test. Otherwise, the non-parametric Spearman correlation test was applied. Additional correlations were computed between growth variables and  $\delta^{13}\text{C}_{\text{corr}}$  on the one hand and temperature, precipitation, and SPEI on the other. For these correlations, temperature and precipitation values of the individual months of the current year were considered (except for October, November and December, which could not affect the current year’s growth increment) as well as the values of late winter (January–March), spring (April–June), summer (July–September), growing season (April–September), the entire year and the preceding winter (October–March). One-tailed correlation tests were conducted when one-sided expectations could be formulated, as was the case, e.g., for SPEI. To detect breakpoints (slope changes) in the time courses of the investigated variables, we applied the ‘strucchange’ package of R and used the recursive cumulative sum (Rec-CUSUM) as the test statistic (Zeileis et al. 2024). Effect sizes of the statistical tests ( $\eta^2$ ) were calculated according to <https://www.psychometrica.de/effektstaerke.html>. The statistical power of the respective tests was taken directly from the software output or computed with G\*Power (3.1.9.7) (Faul et al. 2007) using  $f$ -values derived from the  $\eta^2$  values (Cohen 1988).

## Results

### Growth and stable carbon isotope ratios

Over the entire period of the growth analyses (1999–2023), neither the indexed tree ring widths nor the BAI differed significantly between the healthy and the declining stands (Table 2). However, trees in the declining stand showed decreasing growth during this time period and in the years 2018–2023, when growth of trees dropped in both stands, growth of the trees from the declining stand was significantly weaker (Fig. 1, Table 2). In the indexed ring widths and BAI of the declining stand’s trees, a significant breakpoint was detected in 2018 ( $S > 1.04$ ;  $P < 0.025$ ), when growth started to decline more steeply for the rest of the study period. No breakpoint was found in the growth curves of trees in the healthy stand.

From 2004 through to 2023, the  $\delta^{13}\text{C}_{\text{corr}}$  ratios of trees from the declining stand increased and were significantly higher (less negative) than the ratios of trees of the healthy stand (Fig. 2, Table 2, Table S4). The year-wise averaged  $\delta^{13}\text{C}_{\text{corr}}$  ratios were significantly correlated with the indexed tree-ring widths and BAI in the trees of the declining stand ( $P < 0.001$ ; Fig. 3), but not for those of the healthy stand

**Table 2** Results of statistical tests on significant differences and trends between *Populus pruinosa* trees of the healthy and the declining stand

| Variable                                              | Number of trees per stand |           | Statistical test                 | Statistical parameter    | <i>P</i>                   | Effect size $\eta^2$  | Statistical power ( $\alpha=0.05$ ) | Result                  |
|-------------------------------------------------------|---------------------------|-----------|----------------------------------|--------------------------|----------------------------|-----------------------|-------------------------------------|-------------------------|
|                                                       | Healthy                   | Declining |                                  |                          |                            |                       |                                     |                         |
| Indexed ring width, 1999–2023                         | 10                        | 10        | rmANOVA                          | $F=3.013$                | 0.100                      | 0.143                 | 0.269                               | —                       |
| Indexed ring width, 2018–2023                         | 10                        | 10        | rmANOVA                          | $F=34.907$               | <b>&lt; 0.001</b>          | <b>0.660</b>          | <b>&gt; 0.999</b>                   | <b>+ healthy</b>        |
| Trend indexed ring width 1999–2023                    | 10                        | 10        | Mann–Kendall                     | $z=0.163$<br>$z=-3.62$   | 0.870<br><b>&lt; 0.001</b> | 0.001<br><b>0.524</b> | 0.500<br><b>&gt; 0.999</b>          | —<br><b>\ declining</b> |
| BAI, 1999–2023                                        | 10                        | 10        | Paired <i>t</i> -test (2-tailed) | $t=-1.956$               | 0.062                      | 0.100                 | 0.467                               | —                       |
| BAI, 2018–2023                                        | 10                        | 10        | rmANOVA                          | $F=11.529$               | <b>0.003</b>               | <b>0.391</b>          | <b>0.866</b>                        | <b>+ healthy</b>        |
| Trend BAI, 1999–2023                                  | 10                        | 10        | Mann–Kendall                     | $z=-1.518$<br>$z=-4.227$ | 0.129<br><b>&lt; 0.001</b> | 0.092<br><b>0.715</b> | 0.857<br><b>&gt; 0.999</b>          | —<br><b>\ declining</b> |
| $\delta^{13}\text{C}_{\text{corr}}$ , 2004–2023       | 8                         | 10        | Paired <i>t</i> -test (2-tailed) | $t=-8.735$               | <b>&lt; 0.001</b>          | <b>0.722</b>          | <b>&gt; 0.999</b>                   | <b>+ declining</b>      |
| Trend $\delta^{13}\text{C}_{\text{corr}}$ , 2004–2023 | 8                         | 10        | Mann–Kendall                     | $z=0.357$<br>$z=2.239$   | 0.721<br><b>0.025</b>      | 0.006<br><b>0.251</b> | 0.502<br><b>&gt; 0.999</b>          | —<br><b>/ declining</b> |

Significant values are printed in bold

+ higher mean value in the named stand, \ significantly decreasing trend, / significantly increasing trend. —, no significant difference or trend

( $P>0.385$ ). No breakpoints were found for the  $\delta^{13}\text{C}_{\text{corr}}$  ratios of trees from the healthy or the declining stand.

### Climate variables and correlations with growth and stable isotope ratios

Over the study period, the minimum SPEI values of the year showed a significant decrease and annual SPEI amplitudes, a significant increase, both indicating a climate trending towards drier conditions (Fig. 4). No significant breakpoints were detected in the time courses of the SPEI variables, but the year 2018, when the declining stand's trees started to grow significantly less, (cf. Figure 1), and the subsequent year were particularly dry. In *P. pruinosa* trees of the declining stand, BAI was positively correlated with monthly minimum and average SPEI of the year and negatively with the annual SPEI amplitudes (Fig. 5). In these cases, we used one-tailed significance tests as we could expect a decrease in growth with lower SPEI values and with larger annual SPEI differences. No significant correlations between growth and SPEI were found in trees of the healthy stand.

Likewise,  $\delta^{13}\text{C}_{\text{corr}}$  of trees of the declining stand was positively related to the annual amplitude of monthly SPEI values and negatively to the annual average SPEI values (Fig. 6), whereas there were no significant correlations between  $\delta^{13}\text{C}_{\text{corr}}$  and SPEI in trees of the healthy stand.

The growth variables derived from trees of the declining stand were more sensitive to average monthly temperature values and precipitation sums than the similar variables

of trees in the healthy stand. The indexed tree-ring width and the BAI of the declining stand's trees were negatively related to mean temperatures of July, the July–September period and to the annual mean temperature; their BAI was also negatively correlated with the average temperature of the growing season (April–September). In contrast, trees of the healthy stand showed no significant relationships of their indexed tree-ring widths with temperature, but their BAI was negatively correlated with mean March temperatures. With regards to precipitation, the only significant and negative correlation was between indexed tree-ring width and the precipitation of May in the trees of the declining stand. All correlation coefficients with their *P*-values are provided in Table S5 of the Supplementary Material.

In trees of the healthy stand,  $\delta^{13}\text{C}_{\text{corr}}$  values were positively correlated with spring temperatures of individual months (April, May, June) as well as with temperatures of the period April–June and of the entire growing season (April–September), but negatively with winter temperatures (January, January–March, preceding October–March). They were also negatively correlated with spring precipitation (April, April–June) and all of the growing season (April–September) as well as with the precipitation of the preceding year. In trees of the declining stand,  $\delta^{13}\text{C}_{\text{corr}}$  was positively related to summer temperatures (July–September) and to precipitation in March and May (Table S5).

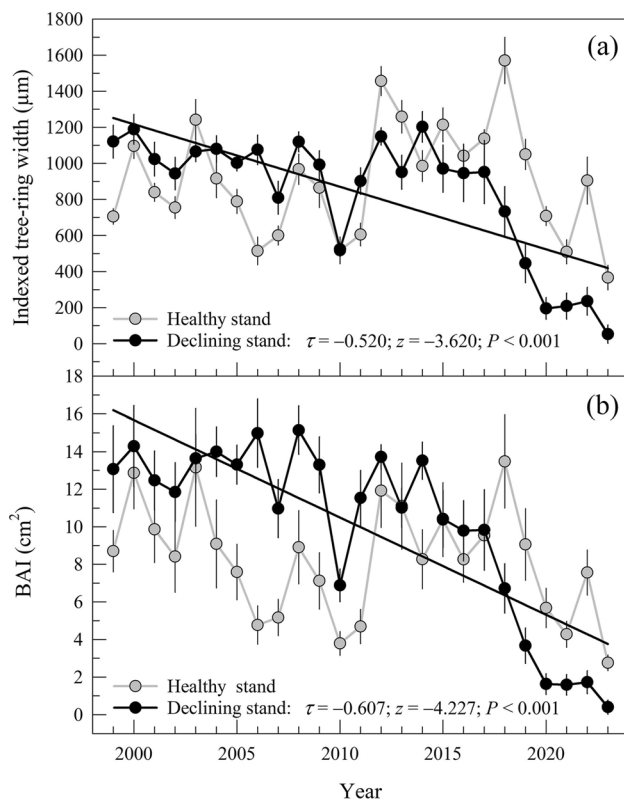


**Fig. 1** **a** stand-wise averaged indexed tree-ring width and **b** basal area increment (BAI) for each ten trees of the healthy and the declining *Populus pruinosa* stands from 1999 through 2023. Over the period, growth variables did not differ significantly between stands. For 2018–2023, indexed tree-ring width and BAI were significantly higher in the healthy stand. Black lines show significantly decreasing trend in trees of the declining stand (Mann–Kendall trend tests;  $\tau$ , Mann–Kendall’s tau-value)

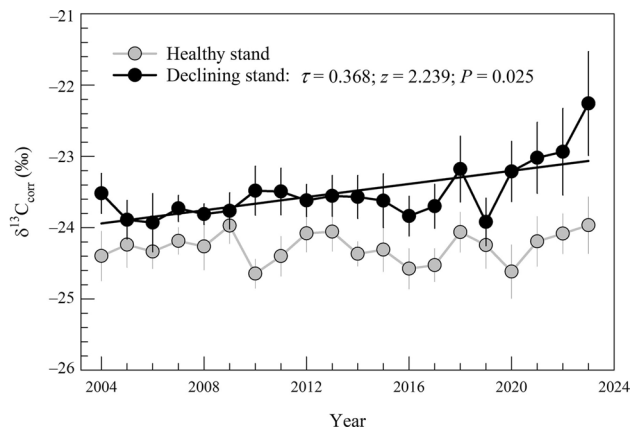


**Fig. 2** Stand-wise averaged  $\delta^{13}C_{corr}$  ratios in trees of the healthy ( $n=8$ ) and the declining ( $n=10$ ) stands near the shore of the Zarafshon River from 2004 to 2023. Across the period,  $\delta^{13}C_{corr}$  ratios were higher in the declining stand. The black line indicates increasing trend in the trees of the declining stand (Mann–Kendall trend test;  $\tau$ , Mann–Kendall’s tau-value)

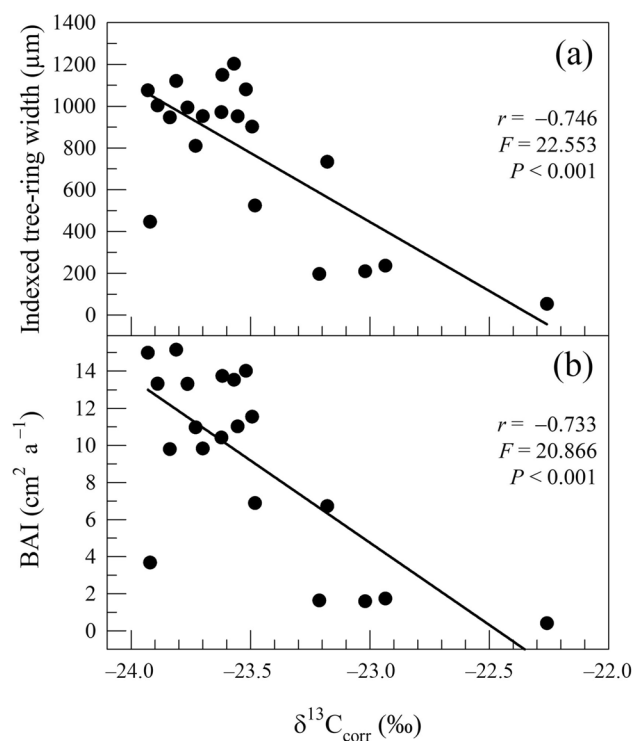


**Fig. 3** Significant correlations in the *Populus pruinosa* trees of the declining stand between the year-wise averaged  $\delta^{13}C_{corr}$  ratios and **a** the indexed tree-ring widths, and **b** the basal area increment (BAI).  $r$ , Pearson correlation coefficient

### Soil analyses and groundwater depths

The soil of the study area is a salt-influenced alluvial Fluvisol with an xC horizon of coarse fluvatile gravel intermixed with fine material. In the healthy stand, the soil shows an Ah-xC profile, in which the dark-gray Ah horizon of sandy-clayey to silty loam extends down to approximately 37 cm. In the declining stand, the clayey-loamy Ah horizon in the upper 14 cm turns into a sandy-loamy Ah/Bv horizon at > 14–35 cm depth, under which the xC horizon lies. The declining stand had a substantially higher clay content in the C horizon and a lower field capacity across the entire profile. Soil bulk density increased slightly from the uppermost layer to the subsoil and was only marginally higher in the healthy than in the declining stand. The results of the physical features of the individual sampling depths are shown in Table 3.

Concentrations of total nitrogen were low in both stands, but  $NO_3^-$ -N levels were moderately high and peaked in the upper 10 cm soil layer in the healthy stand, where humus content also was generally high. C:N ratios were relatively low but highest in the subsoil of the declining stand (Table S6).

The  $pH_{H_2O}$  values were in the alkaline range in all depths of both stands. In the healthy stand, they decreased from 7.8 in the uppermost 10 cm to 7.5 in the subsoil and were 7.6

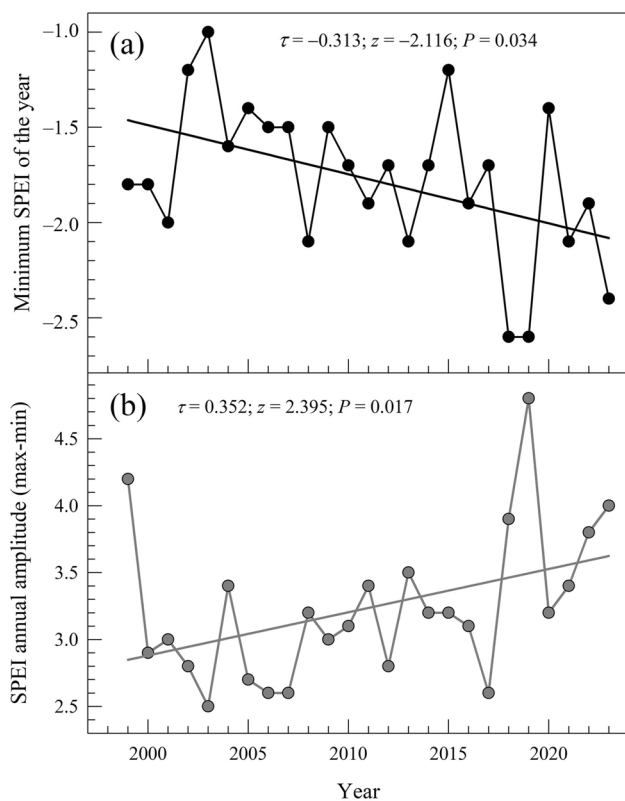
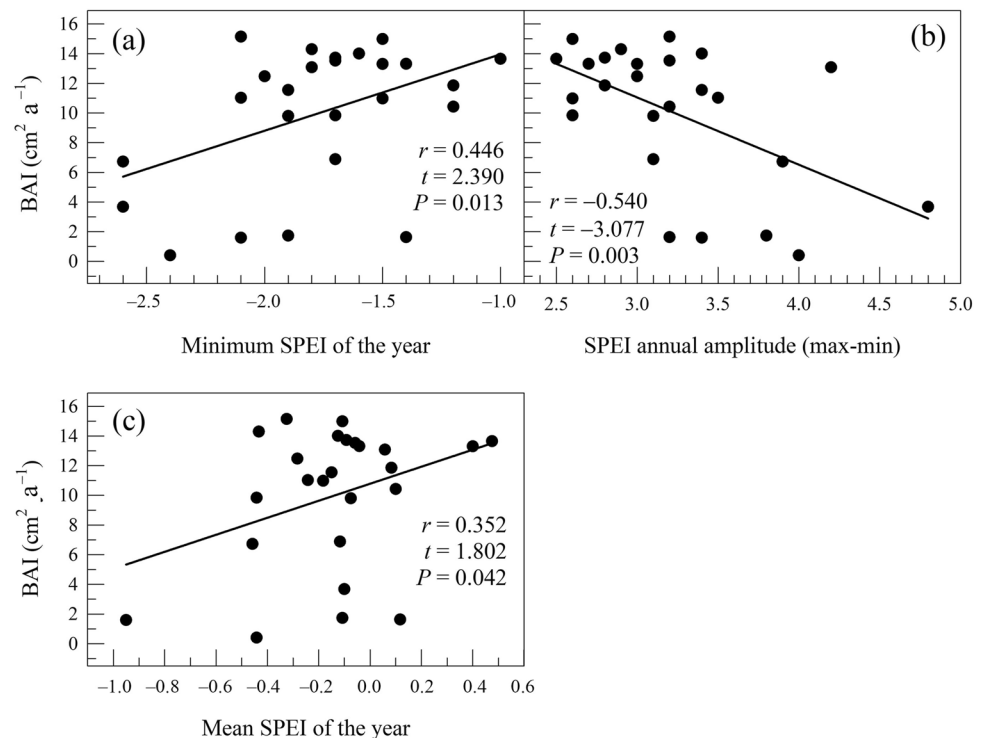


**Fig. 4** Temporal trends of **a** annual minimum Standardised Precipitation Evapotranspiration Index (SPEI) and **b** the annual SPEI amplitude during the 25 years of the study period (1999–2023). Straight lines show significant SPEI trends (Mann–Kendall trend tests;  $\tau$ , Mann–Kendall's tau-value)

**Fig. 5** Significant correlations (one-tailed) in *Populus pruinosa* of the declining stand between basal area increment (BAI) and **a** the annual monthly minimum of the Standardised Precipitation Evapotranspiration Index (SPEI); **b** the annual SPEI amplitude (monthly maximum–minimum) and **c** the mean annual SPEI.  $r$ , Pearson correlation coefficient



across all soil layers of the declining stand. The  $\text{pH}_{\text{KCl}}$  values were higher than  $\text{pH}_{\text{H}_2\text{O}}$  by 0.3–0.4 units.

The fraction of the water-soluble anions was dominated by  $\text{SO}_4^{2-}$  in the uppermost 10 cm of the soil and by  $\text{Cl}^-$  in the subsoil (> 30–60 cm) (Table 4). The predominant cations were  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  with only a small contribution of  $\text{Na}^+$ . In all soil depths, the equivalent sums of the ions were higher in the declining than in the healthy stand. This difference was particularly obvious in the uppermost soil layer and in the subsoil. According to the regional classification of saline soils (Bazilevich and Pankova 1969), the topsoil of both stands is the chloride-sulphate type and the subsoil, the chloride type; the salinity is considered moderate. However, in each soil layer, the  $\Psi_{\text{Salt}}$  values were distinctly lower in the declining than in the healthy stand.

During 2010–2022, monthly values of the groundwater distances in vicinity to the poplar stands were between 2.2 m and 3.8 m (Fig. S3). Over the years, annual mean groundwater distances showed neither temporal trends nor significant breakpoints (Fig. S4). This absence of trend and breakpoints was valid for the annual averages as well as for various months and periods of the growing season (April–September, June–September, July–September, June–July, July–August, June, July;  $\tau < 0.37$ ,  $z < 1.66$ ,  $P > 0.09$  for trends;  $S < 0.72$ ,  $P > 0.23$  for breakpoints).

**Fig. 6** Significant Spearman correlations (one-tailed) in *Populus pruinosa* of the declining stand between the stable carbon isotope ratios ( $\delta^{13}\text{C}_{\text{corr}}$ ) and **a** the annual amplitude of the Standardised Precipitation Evapotranspiration Index (SPEI), and **b** mean annual SPEI. Straight gray lines illustrate the correlation.  $\rho$ , Spearman correlation coefficient

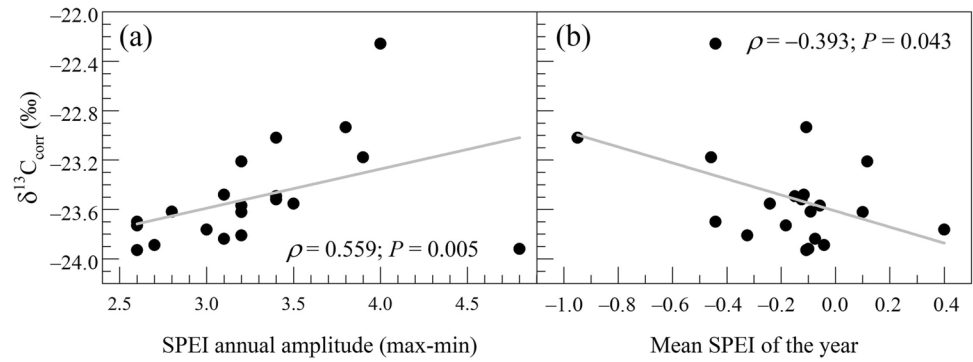


**Table 3** Physical soil features of the healthy and the declining stand at the middle reaches of the Zarafshon River, Central Uzbekistan

| Soil depth (cm)        | Sand (%) | Silt (%) | Clay (%) | Soil texture      | Soil bulk density (g cm <sup>-3</sup> ) | Field capacity (%) |
|------------------------|----------|----------|----------|-------------------|-----------------------------------------|--------------------|
| <i>Healthy stand</i>   |          |          |          |                   |                                         |                    |
| 0–10                   | 27.3     | 47.7     | 25.0     | Sandy-clayey loam | 1.3                                     | 27.5               |
| > 10–30                | 26.5     | 50.9     | 22.6     | Silty loam        | 1.4                                     | 26.8               |
| > 30–60                | 33.0     | 49.1     | 17.9     | Sandy loam        | 1.4                                     | 25.8               |
| <i>Declining stand</i> |          |          |          |                   |                                         |                    |
| 0–10                   | 26.7     | 44.7     | 28.6     | Clayey loam       | 1.3                                     | 21.6               |
| > 10–30                | 26.8     | 49.5     | 23.7     | Sandy loam        | 1.3                                     | 25.7               |
| > 30–60                | 23.0     | 45.9     | 31.1     | Clayey loam       | 1.4                                     | 23.2               |

**Table 4** Concentrations of water-soluble salt ions related to unit soil dry matter and calculated salt-generated soil water potential at field capacity ( $\Psi_{\text{Salt}}$ ) in different soil depths of the healthy and the declining *Populus pruinosa* stands

| Soil depth (cm)        | $\text{CO}_3^{2-}$ (mmol <sub>c</sub> kg <sup>-1</sup> ) | $\text{HCO}_3^-$ (mmol <sub>c</sub> kg <sup>-1</sup> ) | $\text{Cl}^-$ (mmol <sub>c</sub> kg <sup>-1</sup> ) | $\text{SO}_4^{2-}$ (mmol <sub>c</sub> kg <sup>-1</sup> ) | $\text{Ca}^{2+}$ (mmol <sub>c</sub> kg <sup>-1</sup> ) | $\text{Mg}^{2+}$ (mmol <sub>c</sub> kg <sup>-1</sup> ) | $\text{Na}^+$ (mmol <sub>c</sub> kg <sup>-1</sup> ) | Sum of ions (mmol <sub>c</sub> kg <sup>-1</sup> ) | $\Psi_{\text{Salt}}$ (MPa) |
|------------------------|----------------------------------------------------------|--------------------------------------------------------|-----------------------------------------------------|----------------------------------------------------------|--------------------------------------------------------|--------------------------------------------------------|-----------------------------------------------------|---------------------------------------------------|----------------------------|
| <i>Healthy stand</i>   |                                                          |                                                        |                                                     |                                                          |                                                        |                                                        |                                                     |                                                   |                            |
| 0–10                   | 4.3                                                      | 21.0                                                   | 36.9                                                | 50.6                                                     | 17.5                                                   | 24.7                                                   | 7.8                                                 | 162.8                                             | –1.44                      |
| > 10–30                | 11.3                                                     | 23.0                                                   | 33.0                                                | 34.3                                                     | 37.4                                                   | 25.5                                                   | 5.7                                                 | 170.2                                             | –1.55                      |
| > 30–60                | 5.0                                                      | 16.9                                                   | 34.4                                                | 9.8                                                      | 5.0                                                    | 32.9                                                   | 4.8                                                 | 108.8                                             | –1.03                      |
| <i>Declining stand</i> |                                                          |                                                        |                                                     |                                                          |                                                        |                                                        |                                                     |                                                   |                            |
| 0–10                   | 14.0                                                     | 46.1                                                   | 45.6                                                | 73.3                                                     | 22.4                                                   | 9.9                                                    | 8.3                                                 | 219.6                                             | –2.48                      |
| > 10–30                | 20.3                                                     | 3.8                                                    | 36.9                                                | 36.4                                                     | 29.9                                                   | 42.8                                                   | 9.1                                                 | 179.2                                             | –1.70                      |
| > 30–60                | 24.3                                                     | 2.6                                                    | 40.6                                                | 11.0                                                     | 24.9                                                   | 30.5                                                   | 7.0                                                 | 140.9                                             | –1.48                      |

## Discussion

### Overview

The results suggest that in the *P. pruinosa* stands, edaphic conditions (high salt and clay contents, especially in the subsoil) have predisposed the trees of the declining stand to dieback, which was ultimately triggered by two severely dry years (2018, 2019).

### Growth, $\delta^{13}\text{C}_{\text{corr}}$ and climate

Significant differences in growth between trees of the healthy and the declining stand were only found for the last six years (2018–2023) of the study but not across the entire period (1999–2023). This suggests that a particular event triggered growth decline. Most possibly, and supporting our first hypothesis, this event was the occurrence of specific dry years of 2018 and 2019. Accordingly, in the trees of the declining stand, a breakpoint in the time series of tree-ring width and BAI was detected for 2018 that indicated a steeper decrease in those variables in and after that year than before.

However, our alternative second hypothesis of a decline in the water table as a cause of tree dieback must be rejected as no significant changes in the groundwater depth were observed before and during the dieback. On the other hand, the  $\delta^{13}\text{C}_{\text{corr}}$  ratios of the tree rings of the declining stand were higher (less negative) than those of the healthy stand's trees over the last two decades of the study period. This is indicative of a continually diminishing water supply and subsequent stress due to drought to the trees of the declining stand (Loader et al. 2007; Galle et al. 2010; Jansen et al. 2013; Metz et al. 2016; Timofeeva et al. 2017; Zhang et al. 2025), whereas under less stressful conditions or with more resilient trees, growth can be uncoupled from  $^{13}\text{C}$  discrimination during carbon assimilation (Härdtle et al. 2013a). In contrast to the same species in the healthy stand, trees of the declining stand exhibited decreasing growth and increasing tree-ring  $\delta^{13}\text{C}_{\text{corr}}$ , which was paralleled by significant trends in SPEI. This indicated a change towards drier conditions in the past 25 years of the period under investigation. This finding agrees with observations of an increase in the occurrence of hot weather and drought in Central Asia (IPCC 2023).

In the long-living evergreen *Pinus sylvestris* L. in cold regions, a “juvenile effect” of lower  $\delta^{13}\text{C}$  ratios until up to 50 years has been found (Gagen et al. 2008; Torbenson et al. 2022), whereas no such effect was detected in the deciduous *Larix decidua* Mill. (Kilroy et al. 2016), in *Quercus* spp. after the first five years (McCarroll et al. 2020), and in *Fagus sylvatica* L. (Wieland et al. 2022) from temperate regions, or the effect was not consistent (*Pinus cembra* L.; Nagavciuc et al. 2020). A possible juvenile effect has been attributed to the uptake of  $^{13}\text{C}$ -depleted  $\text{CO}_2$  by young trees growing under a dense canopy and at reduced mixing of the surrounding air (Treydte et al. 2009). However, such conditions did not prevail in the relatively sparse stands of our study sites with relatively small trees. Moreover, a juvenile effect should have been visible in the trees of both stands, which was not the case. In addition, the stands were established in the 1980s; thus, the trees of this fast-growing species were not particularly young. For these reasons, we did not correct for any juvenile effects on  $\delta^{13}\text{C}$ .

Correspondingly to the trends in growth and  $\delta^{13}\text{C}_{\text{corr}}$  of the declining stand's trees, significant correlations between tree-ring  $\delta^{13}\text{C}_{\text{corr}}$  and growth, SPEI and growth, and SPEI and  $\delta^{13}\text{C}_{\text{corr}}$  were only found for trees of the declining stand. Carbon isotope discrimination in photosynthesis is linked to water use efficiency (WUE): leaves with stomata that are less wide open will transpire less water per unit carbon fixed but  $^{13}\text{C}$  discrimination will be lower during photosynthesis, resulting in higher WUE and higher (less negative)  $\delta^{13}\text{C}$  ratios (Farquhar et al. 1989). Hence, the higher  $\delta^{13}\text{C}$  ratios in the trees of the declining stand could also be seen as an adjustment to a reduced water supply in the form of less

stomatal opening for a prolonged time during the growing season but at the expense of carbon fixation.

As the climatic conditions of both stands were similar due to their proximity, it can be assumed that the impact of drier weather conditions on trees of the declining stand has been intensified by specific site characteristics. Given the similarity of both stands in canopy height and density, the most prominent candidate for such site characteristics is the edaphic conditions.

A limitation to the interpretation of our data is the relatively large distance between the groundwater well from which the water table depths were retrieved, and the locations of the study plots. Nevertheless, our conclusion about a distinct lack of groundwater effects on the performance of the trees is justified. This is based on the absence of a decline of the groundwater level during the time of decrease in tree growth, on the close proximity of the healthy and the declining plots, the location of the plots between the groundwater well and the river that prevents underestimation of the groundwater depth in the plots, and the comparable average elevations of the plots and the well.

## Edaphic conditions

Soil samples were taken on one sampling date as we did not assume distinct changes in edaphic conditions over time: the poplar stands are located in a Natural Park established 50 years ago and have not been subjected to major anthropogenic interventions, and the stands had also been part of a typical riparian forest before the establishment of the Park. The samples can be considered representative of the respective plots due to their homogeneous structure.

The stands differed in their physical soil variables: the declining stand had a higher clay content, especially in the subsoil, and a lower field capacity. Due to stronger capillary forces, high clay contents lower soil water potential and impede water uptake through roots. In addition, the formation of fine roots, which contribute the largest part to water uptake by trees, is constrained in such soil layers. This has been found, for instance, in the deciduous tree species *Quercus robur* L., a keystone species of the hardwood riparian forests of Central and Eastern Europe and resulted in a lowered water content of the leaves (Thomas and Hartmann 1996, 1998). A comparable situation may be assumed for the declining poplar stand of the present study, but a destructive intervention to investigate root systems was not possible due to the protective status of the forest.

Soil water potential could be lowered further by higher salt concentration in the declining stand, especially in the uppermost soil layer and the subsoil. Low soil water potentials due to high salt concentrations can severely hamper water uptake (Li et al. 2023). Salt levels in the topsoil were similar to those in a healthy *P. pruinosa* stand on the Vakhsh

River in bordering South Tadjikistan (Vtorova et al. 1993) but were lower in sodium. In this study, however, we refer to the property of salt to decrease soil water potential rather than to its immediate toxicity. Generally, the more easily soluble chloride salts accumulate in the uppermost soil layer which, in the present study, is valid at least for  $\text{Cl}^-$  concentrations, they can be redissolved upon precipitation and circulate between topsoil and subsoil over the course of the year (Blume et al. 2016). Salt accumulation in the soil can be attributed to the long-term influence of river water. Although—according to measurements conducted in the recent past (Olsson and Manig 2011)—the salt concentration in the Samarkand part of the Zarafshon River is well below the critical threshold for drinking water on an annual average, salt can accumulate in the soil above river-influenced groundwater through evaporation during long periods in arid climates (Franzen 2007). Such a process is favored in climates with distinct dry and humid seasons (Schaetzl and Anderson 2005) as is at our study site. Upward movement of salt-containing soil water can even be enhanced by relatively strong capillary forces in the clay-rich soil layers.

Our calculation of  $\Psi_{\text{Salt}}$  on the basis of water content at field capacity and salt concentration can only be an approximate estimation and indicates the minimum (most negative) soil water potential under the assumption of complete dissolution of the soluble salts. However,  $\Psi_{\text{Salt}}$  becomes even more negative due to an increase in concentration by evapotranspiration. Thus, the considerably negative  $\Psi_{\text{Salt}}$  values in the declining stand (down to  $-2.5$  MPa), in combination with its higher clay content, severely impedes water uptake by the trees. In the closely related *P. euphratica* species, leaf water potential did not fall below  $-2.5$  MPa, even in the driest period of the year (Thomas et al. 2008). In *P. pruinosa*, such a minimum leaf water potential would render a continuous water uptake difficult at low soil water potentials. Such soil-born drought stress will be aggravated by atmospheric drought (low SPEI values) in the growing season. Nevertheless, easier water uptake may still be possible from the groundwater that can be tapped from 2–4 m below surface, a depth considered ideal at least for *P. euphratica* (Fan 2006; Li et al. 2013). However, in most probability, water supply is restricted in the declining stand, which is indicated by the continuously higher  $\delta^{13}\text{C}_{\text{corr}}$  ratios of the tree rings. Hence, our results support our third hypothesis of less favorable edaphic conditions in the declining stand as a predisposing factor in the dieback process.

Nitrogen concentrations and their decrease from the surface to the subsoil are in a range typical of arid regions (West 1981). The C:N ratios and humus levels are characteristic for dark-gray soils of Central Asia (Breckle 2021), albeit the humus concentrations were lower than 3%–4% typical of Central Asian floodplain vegetation (Walter and Box 1983). However, low C:N ratios are indicative of fast mineralization

rates. It is unlikely that lower humus in the uppermost soil layer and the wider C:N ratio in the subsoil of the declining stand have critically contributed to tree growth decline as growth in both stands was similar for almost 20 years before the onset of decline.

With the alkaline pH values of the soil and its large sand fractions that facilitate good aeration under non-flooding conditions,  $\text{NO}_3^-$  may be regarded as the almost exclusive source of mineral N for plant uptake. The  $\text{NO}_3^-$  concentrations in the present study are similar to those measured in *P. pruinosa*/*P. euphratica* *tugai* stands along the Syr-Darya River, Kazakhstan (Vesselova et al. 2022). Lower soil water availability due to drought or low (strongly negative)  $\Psi_{\text{Salt}}$  values result in impeded N uptake (Gebler et al. 2005) and in lower N levels in the plants (Massonnet et al. 2024; Thomas et al. 2024). In contrast, increased salinity in hydroponics had no effect on  $\text{NO}_3^-$  uptake (Dluzniewska et al. 2007). In *P. euphratica* at the southern fringe of the Tarim Basin, dry matter-related leaf N concentrations were positively correlated with their  $\delta^{13}\text{C}$  ratios (Arndt et al. 2004). This is caused by enhanced photosynthesis through higher foliar N concentrations, which would—at comparable relative air humidity—result in lower intracellular  $\text{CO}_2$  concentrations and thereupon reduced  $^{13}\text{C}$  discrimination (Scheidegger et al. 2000). At our study site, however, tree-ring  $\delta^{13}\text{C}$ , which reflects the  $\delta^{13}\text{C}$  ratios of the leaves (Loader et al. 2007), was higher in the declining stand than in the healthy one, which—on the basis of the relationships found by Arndt et al. (2004)—would not be indicative of a lesser N supply. In general, poplars are characterized by intense internal N cycling that renders them less dependent on short-term alterations in N supply (Rennenberg et al. 2010). Floodplain forest poplars exhibit continuous growth during the growing season which makes N limitation of growth unlikely (Rennenberg et al. 2010). Although it cannot be completely excluded that a reduced supply and uptake of N is a contributing factor to poplar decline at our study site, it is improbable that it played a significant role.

### Edaphic and weather conditions as predisposing and triggering factors in the decline of *P. pruinosa*

Our results support our hypotheses that unfavorable edaphic conditions, consisting of high clay and salt contents and relatively low field capacity, predispose trees of the declining stand to dieback, which is ultimately triggered by extremely dry weather conditions. This study shows that drought in combination with unfavorable soil conditions can cause tree dieback in Central Asian *tugai* forests, even at sites with an ideal distance to groundwater (2–4 m). However, the evidence for this scenario is somewhat circumstantial as more intense measurements of soil parameters (soil water potential, soil water retention curves) and of ecophysiological

variables of the tree (e.g., sap flow, leaf water potential) were not possible due to the protective status of the forest and the limited local research facilities. Nevertheless, our conclusions are reasonable against the background of several other studies. The growth of the North American *Populus balsamifera* L., a typical component of riparian forests, showed low resistance to air-born drought stress (Marchand et al. 2025). Soil texture played a decisive role in water availability and thus, the growth and survival of riparian *P. euphratica* stands (Grashey-Jansen et al. 2014). A combination of harmful changes in the hydrological regime and salinization has been responsible for the decline of *P. pruinosa* forests in Tadjikistan (Vtorova et al. 1993). Soil salinization is also a crucial factor in the decline of *tugai* forests in Uzbekistan (Kuzmina and Treshkin 1997) and in northwest China (Peng et al. 2022). In this study, we provide evidence for the combination of edaphic conditions, including soil salinity, and atmospheric drought as causal factors in the decline of a *tugai* forest.

### Changes in the hydrological regime and riparian forest decline in Central Asia

In large parts of Central Asia, a decline in the groundwater due to intense withdrawal of water for irrigation of agricultural land has been identified as the principal cause of the dieback of riparian forests of *P. pruinosa* and/or *P. euphratica*. Reports have been published on the Tarim Basin of north-western China (e.g., Feng et al. 2005; Chen et al. 2011; Li et al. 2013), the Amu-Darya region of Uzbekistan (Treshkin 2001), and the south-eastern part of Tadjikistan (Vtorova et al. 1993). These regions are in a hyper arid or arid climate in which many perennial plants are phreatophytes, i.e., they rely partly or completely on access to groundwater (Thomas 2013). In some regions, the pressure on the hydrology of the riparian forests is also caused or intensified by the construction of embankment dikes (e.g., in the Tarim Basin; Halik et al. 2006), or by dams for reservoirs or hydroelectric power plants (Treshkin 2001). The construction of dams and reservoirs has also been responsible for the decline of riparian *P. euphratica* forests in south-eastern Kazakhstan in combination with anthropogenic pressures of recreational activities and related expansion of infrastructure as well as grazing (Rakhimzhanov et al. 2021). Dukenov et al. (2023) also consider the regulation of river flow and the subsequent decrease in the duration and intensity of flooding in combination with climate change responsible for the decline of the riparian forests.

Without question, changes in river flow and a decline in groundwater are major—and often even exclusive—causes for the decline of Central Asia's riparian forests. This has also been confirmed in our studies on *P. euphratica* stands in the Tarim Basin (e.g., Lang et al. 2016; Thomas and

Lang 2021). However, the case of the *P. pruinosa* decline discussed here differs from the previous studies in several points: (1) according to our data, the water table at our study site was not deeper than 4 m throughout the year and in the periods before, during and after the onset of tree decline. *Populus pruinosa* grows and regenerates at a groundwater depth of 4 m and under low salinity (Vtorova et al. 1993), and *P. euphratica* only shows degradation when the depth exceeds 6 m (Li et al. 2013). This makes a groundwater-related decline of *P. pruinosa* at our study site improbable, especially with regard to the proximity of the healthy and the declining stand and their similar distances to the groundwater well and to the river shore; (2) In contrast to other river courses with riparian forests, the Zarafshon River in the study region carries water throughout the year and is not regulated by dams, and floods at the study site have been observed in recent years. Hence, drastic changes in the water regime are not probable causes of the onset of tree decline in parts of the forest in 2018; (3) In contrast to the Tarim Basin, the lower Amu-Darya region and south-eastern Tadjikistan, the Samarkand region has a semi-arid climate which exerts a lower transpirational demand on the vegetation. In such areas, unusual dry spells as in 2018–2019 can present a more intense stress on trees than in arid regions where riparian forests may be better adapted to a continuously dry climate but still have access to groundwater.

Therefore, although we cannot completely exclude the possibility that changes in the hydrological regime have contributed to the *P. pruinosa* decline at our study site, the most reasonable explanation for the onset of the decline—against the background of our results and the above-stated reasons—is the combination of climatic and edaphic factors.

### Conclusion

Despite some similarities, the combination of a (semi-)arid continental climate, a continuing anthropogenic impact on the hydrological regime, a relatively low (phyto)diversity and overuse of biological resources, differentiate the unique Central Asian *tugai* forests from the riparian forests of Central Europe and (semi-)arid regions of North America that also contain poplar species as constitutive elements (Webb and Leake 2006; Thevs et al. 2008; Stromberg et al. 2010). This combination renders the *tugai* forests even more susceptible to disturbances and requires extensive protection measures. The expected warmer climate in Central Asia may further enhance the risk of poplar dieback in *tugai* forests at sites with unfavorable edaphic conditions, and of a continuing decrease in forest areas. Our study encourages the establishment of further integrative research that combines hydrology, hydrogeology, soil science, ecophysiology, and

meteorology (Wilkenning et al. 2024) to develop appropriate protection and management strategies, especially in Central Asian regions that are underrepresented in ecological research.

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**Data availability** Original data not presented in the main text are provided in the Supplementary Material.

**Declarations**

**Conflict of interest** The authors declare no conflict of interest.

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