

Greater hydraulic safety contributes to higher growth resilience to drought across seven pine species in a semi-arid environment

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Abstract

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Abstract

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Keywords: cavitation, drought, embolism, growth resilience, hydraulic, photosynthesis, pine, radial growth, tree-ring, xylem

Introduction

Climate-change related drought events have been observed with increasing frequency and intensity in recent decades, causing serious adverse effects on many forest ecosystems worldwide (Allen et al., 2010; Dai, 2011; McDowell et al., 2008). Widespread reductions of tree growth and increased forest decline or even mortality triggered by drought have been reported, particularly in water-limited environments (Gitlin et al., 2006; Rigling et al., 2013; Sun et al., 2019). Physiological differences among tree species can potentially lead to large interspecific variation with respect to responding to the warming-drying trend of climate change (Adams et al., 2017; Anderegg et al., 2015; Gazol et al., 2018; Zang, Hartl-Meier, Dittmar, Rothe, & Menzel, 2014). A large number of data on tree responses to droughts have been accumulated by tree-ring analyses in the past few decades, which have laid an important foundation for understanding the impacts of climatic change on forest ecosystems (Gazol, Camarero, Anderegg, & Vicente-Serrano, 2017; Lloret, Keeling, & Sala, 2011; Wu et al., 2017). However, physiological mechanisms underlying the observed patterns from tree-ring analyses are much less investigated, which limited our ability in assessing the risk of forest decline and mortality under the influence of climate change (Allen et al., 2010; Li et al., 2020b).

Tree radial growth is sensitive to annual climatic variation, especially in the water-limited environments like arid and semi-arid regions (DeSoto et al., 2020; Fritts, 1976; López et al., 2013). In general, tree radial growth decreases during droughts and recovers upon subsequent significant rainfall events, although large differences in climatic sensitivity exist among species (DeSoto et al., 2020; Fang & Zhang, 2018; Wu et al., 2017). Growth performance of different tree species in water-limited environments may strongly depend on their resistance to drought and recovering ability from climatic disturbances, which reflect species' ability in maintaining their physiological functions during and after droughts (Anderegg et al., 2013; Manrique-Alba et al., 2018). Tree sensitivity to drought stress has been found to be strongly associated with growth rate in many forest ecosystems, that is, fast-growing tree species usually have low resistance to drought stress but can recover more quickly from drought disturbances, and vice versa (Choat et al., 2012; Gazol et al., 2018; Zhang et al., 2014). A trade-off between drought resilience and growth rate across species has often been observed in water-limited environments (Gazol et al., 2017; Martínez-Vilalta, López, Loepfe, & Lloret, 2012). Characterizing growth responses of different tree species to non-lethal drought events is crucial for predicting tree growth performances and mortality risks in facing increasing climatic variability (DeSoto et al., 2020; Lloret et al., 2011; Zhang et al., 2014).

Tree-ring analysis provides a retrospective picture to characterize inter-annual variation of tree growth and its relationship with climate variables (Gazol et al., 2017; Lloret et al., 2011). The sensitivity of tree-ring growth to climate variability among species is usually presented by variations of their inter-annual ring width, which is strongly related to tree radial growth rate and resilience to drought events (Macalady & Bugmann, 2014; Taeger, Zhang, Schneck, & Menzel, 2013). Tree-ring analyses can also play an important role in characterizing tree growth rates and risks of tree mortality during and after extreme drought events (DeSoto et al., 2020; Gazol et al., 2017; Lloret et al., 2011). Recently, tree-ring analyses have been used to intuitively show interspecific difference in growth responses to drought events using three indices, i.e. tree resistance (RT), tree recovery (RC) and tree resilience (RS). Previous studies have shown that growth resilience varies greatly among species that is assumed to be influenced by the specie-specific physiological response to drought events (Anderegg et al., 2015; Gazol et al., 2017, 2018). However, studies directly linking tree-ring analyses with physiological functional traits are scarce, which hinders our ability in foreseeing tree growth decline and mortality in facing increasing drought.

Physiological functions influence tree radial growth in many aspects, including through photosynthesis rate and respiration rate, or indirectly through plant water relations (Chaves, Flexas, & Pinheiro, 2008; Hubbard, Ryan, Stiller, & Sperry, 2001). Drought-induced xylem cavitation will reduce hydraulic conductance, and thus, negatively impact on photosynthetic gas exchange and ultimately on tree radial growth (Brodribb, Holbrook, & Gutiérrez, 2002; McDowell, 2011; Rehschuh et al., 2020). Pines are known to reduce their stomatal conductance under drought stress, maintaining relatively constant minimum leaf water potentials to avoid the risk of hydraulic failure, although this unavoidably comes at a cost of reduced carbon assimilation and hence reduction in growth (McDowell et al., 2008; Meinzer et al., 2016; Tyree & Sperry, 1988). This isohydric water management strategy can contribute to avoidance or delay of catastrophic hydraulic failure due to xylem embolism; however, carbon starvation can happen and cause mortality if drought stress sustains (McDowell et al., 2008; Sala, Piper, & Hoch, 2010). Nevertheless, even among closely related pine species, interspecific variations in hydraulic architectural characteristics can exist and thus lead to different growth responses to drought (e.g. Herguido et al., 2016; Li et al., 2020a).

According to the theory of plant ‘fast–slow’ economics spectrum, species with high water transport capability usually have low tissue density, short tissue life span and high rate of resource acquisition (Reich, 2014). Physiological functional traits associated with high rate of resource acquisition and processing are usually inversely correlated with drought resistance traits across species. Consistently, a trade-off between xylem water transport efficiency and safety against drought-induced embolism has long been hypothesized and widely observed (Brodribb, Bowman, Nichols, Delzon, & Burrett, 2010; De Guzman, Santiago, Schnitzer, & Álvarez-Cansino, 2017; Martínez-Vilalta, Prat, Oliveras, & Piñol, 2002). Although this hydraulic efficiency-safety trade-off can be weak at the global scale (Gleason et al., 2016), it has been commonly observed in specific sites (Martínez-Vilalta et al., 2002; Pockman & Sperry, 2000) and among particular taxa (De Guzman et al., 2017; Fan, Zhang, Hao, Ferry, & Cao, 2012). This trade-off can largely be attributed to biophysical constraints to xylem formation that do not allow high efficiency and high embolism resistance at the same time (Fan et al., 2012; Hao et al., 2013; Pockman & Sperry, 2000; Wheeler, Sperry, Hacke, & Hoang, 2005). Hydraulic functional traits of trees are fundamentally linked to their environmental fitness and thus may help to predict tree performances in terms of radial growth and response to drought (Reich, 2014). The combination of tree-ring analyses and measurements of hydraulic functional traits has great potential in identifying the patterns of species-specific growth performances and meanwhile revealing the underlying physiological mechanisms of such interspecific variations.

Tree growth conditions are expected to exacerbate in large areas all over the world, including vast areas of northern China, as increasingly stronger drought could be foreseen in the coming decades (Choat et al., 2018; Dai, 2011; Williams et al., 2013). In natural ecosystems, climate change is expected to induce significant shifts of population composition and forest structure since the climatic conditions may become unsuitable for some species while being more suitable for some others (Adams et al., 2017; DeSoto et al., 2020). Similarly, tree species that are commonly used for afforestation nowadays may become unsuitable in the near future due to the fast climate change (Montwé, Spiecker, & Hamann, 2014; Way & Long, 2015; Verkerk et al.,

2020). Actually, widespread and severe decline and mortality of some drought sensitive tree species widely used for creating large-scale plantations have been observed in recent years (Kang, Zhu, Li, & Xu, 2004; Liu et al., 2018; Sun et al., 2019; Tausz, Merchant, Kruse, & Samsa, 2008). Investigations on the interspecific differences in tree growth responses to drought as well as the underlying mechanisms are of great importance in forestry under the background of fast climate change (Anderegg et al., 2015; Wu et al., 2017). At the semi-arid regions of northern China, water stress is a dominant limiting factor for tree growth and survival of pine species, which are often used for creating plantations particularly in areas with sandy soil (Liu et al., 2018; Zhu, Fan, Zeng, Jiang, & Takeshi, 2003). Here, using seven pine species growing in a common environment in a typical semi-arid area with sandy soil, we tried to identify the interspecific differences in growth patterns in relation to limiting climate factors as well as to reveal the underlying physiology causing such variations particularly from the point of view of xylem hydraulics and leaf water relations. Specifically, we hypothesized that: 1) the pine species with high hydraulic conductance would have high radial growth rate considering the commonly observed positive correlation between xylem water transport efficiency and photosynthetic carbon assimilation; 2) species with characteristics related to greater resistance to drought-induced xylem embolism and leaf traits reflecting greater drought tolerance would show greater resilience to droughts during climatic extremes; 3) a trade-off between hydraulic efficiency and safety would result in greater sensitivity in tree radial growth to extreme droughts in species with intrinsically high hydraulic capacity.

Materials and methods

Study area and species descriptions

The present study was conducted in the plantations of Institute of Sand Land Control and Utilization of Liaoning Province in NE China (42°42' N, 122deg29' E; 226.5 m a.s.l.). This site is located in the southeastern part of the Horqin Sandy Land, i.e. the largest desertified land in China with a total area of over 500, 000 km². The study site has a temperate continental climate with mean annual temperature of 7.8 degC, maximum and minimum mean monthly temperature of 26.2 degC and -18.4 degC, respectively. The precipitation is strongly seasonal that on average 382 mm out of 501 mm occurs during the growing season (June to September). In this semi-arid region, vast areas of tree plantations mainly composed of *Pinus sylvestris* var. *mongolica* Litv. (Mongolian pine) trees have been created as shelter forests. However, severe decline and mortality of Mongolian pine plantations have occurred since the 1990s (Zhu et al., 2003), which may become even worse under the influence of the significant warming-drying trend caused by climate change (Fig. 1). To look for optimal afforestation species in this area, different pine species have been tested and they showed large variations in performances in terms of growth and survival. In the present investigation, we compared tree radial growth patterns and physiological traits of seven pine species growing in a common environment of tree plantations (Table 1). Sample trees for all the studied species were growing in pure stands with stand density ranging between 750 and 800 stems ha⁻¹.

Tree-ring width and basal area increment

In late August 2018, two 5 mm diameter increment cores per tree were collected at breast height for each studied species using an increment borer, and tree diameter at breast height (DBH) of each sample tree was measured. A total of 272 tree cores were sampled from 136 trees, with one or two cores per tree and the number of cores for each species ranging from 36 to 40. Tree-ring width data were obtained according to the standard procedures described by Cook and Kairiukstis (1990). Samples were air-dried, glued and mounted on wooden staves, and then polished with 400 and 600 mesh sandpaper in sequence until the tree rings were clearly visible. Tree-ring measurements were crossdated by standard dendrochronological techniques (Schweingruber, 1988) and the quality of crossdated results was validated using the COFECHA program (Holmes, 1983). To remove the inherent effect on annual increments caused by tree aging and potential disturbance signals due to forest stand development, the crossdated tree-ring width measurements were detrended using a cubic smoothing spline with 50% frequency-response cutoff equal to two-thirds of the length of each series, which was performed using the ARSTAN program (Cook, 1985). All detrended series data for each species were separately averaged to obtain tree-ring width standard chronology using

the bi-weight robust mean method (Cook & Kairiukstis, 1990).

The common statistical of tree-ring width standard chronologies including signal-to-noise ratio (SNR), expressed population signal (EPS) and all series correlation are shown in Table 1. The reliable periods of the chronologies were determined by the criterion of EPS surpassing 0.85 which were used for the subsequent climate-growth correlation analyses (Wigle, Briffa, & Jones, 1984). Mean sensitivity was calculated as a measure of growth sensitivity to climate based on the method by Speer (2010). The higher mean sensitivity value reflects greater variability in the chronologies and indicates a stronger response to inter-annual climate change (Fritts, 1976; Speer, 2010).

In order to measure the radial growth rate, the cumulative basal areas (CBA) at the same cambial age (Tognetti, Cherubini, & Innes, 2000) for each tree radius were calculated as follows:

$$CBA_i = \pi \times r_i^2 \quad (1)$$

where r_i is the cumulative tree-ring width from the first year to the i th year. Since all species showed a relatively stable growth rate (Fig. 2), we calculated the CBA at 15-year-old (CBA_{15}) of each species to compare radial growth rate at the same cambial age among the studied species.

Drought event and indices of tree resistance, recovery and resilience

The aridity index named De Martonne Index (DMI) developed by de Martonne (1926) was used to detect the drought events:

$$DMI = \frac{P}{(10+T)} \quad (2)$$

where P and T are total precipitation and mean annual temperature of the growing season (June to September), respectively.

We defined drought events as years when the DMI was less than the average annual DMI minus 1.5 standard deviations. In this way we determined drought events occurring in 1996, 2000 and 2015 (Fig. 1c). As some study species were still at the seeding stages in 1996 and 2000, only in the year 2015 the growth responses to drought event of the studied species were investigated. We calculated the tree growth responses to drought event by using the tree resistance (RT), tree recovery (RC) and tree resilience (RS) indices.

$$RT = \frac{Dr}{PreDr} \quad (3)$$

$$RC = \frac{PostDr}{Dr} \quad (4)$$

$$RS = \frac{PostDr}{PreDr} \quad (5)$$

where Dr indicates tree-ring width during the drought year (2015), $PreDr$ and $PostDr$ indicate average tree-ring width of the two years before and after 2015, respectively. We selected a period of two years before/after drought event for calculating above indices because a recent study reported that drought legacy effects on tree growth generally last for two years and most trees affected can recovery to pre-drought level within two years (Li et al., 2020b). Based on the definition of Fang and Zhang (2018), a species is considered to have high resistance if its RT is greater than 0.75, and high recovering ability if its RC is smaller than 1.25.

Stem physiological measurements

For each species, stem hydraulic conductivity was measured on eight stem segments from different healthy trees in July 2018. The long (c.a. 1 m), straight and sun-exposed terminal branches with diameter ranging from 6 to 8 mm were sampled at predawn. The end of samples was recut under water and transported to the laboratory immediately. The samples were wrapped with black plastic bag and kept the cutting end submerged in the water during transportation. Upon arrival at the laboratory, a stem segment about 15 cm in length was excised from each of the originally sampled branch. After peeling off the barks and shaving both ends of the segments with a sharp razor blade, segments were connected to a tubing apparatus consist with a 0.22 μ m filter and a 50 cm hydraulic head to allow the degassed and filtered 20 mmol L⁻¹ KCL solution

to flow through the segments. The stem native hydraulic conductivity (K_h , $\text{kg m s}^{-1} \text{MPa}^{-1}$) was calculated as follows:

$$K_h = \frac{J_v}{\left(\frac{\Delta P}{\Delta L}\right)} \quad (6)$$

where J_v (kg s^{-1}) is flow rate through the segments and $\Delta P/\Delta L$ is the pressure gradient across the segment (MPa m^{-1}).

The leaf-specific hydraulic conductivity (K_l , $10^{-4} \text{ kg m}^{-1} \text{ s}^{-1} \text{MPa}^{-1}$) and sapwood-specific hydraulic conductivity (K_s , $\text{kg m}^{-1} \text{ s}^{-1} \text{MPa}^{-1}$) of each segment were calculated as K_h divided by leaf area (LA) and sapwood area (SA), respectively. Branch segments used for the conductivity measurements were perfused by Methyl blue dye under a hydraulic head of 50 cm, the average value of dyed area of both ends of segments was determined as SA. The transverse cross-sections were scanned and the images were analyzed using ImageJ software (US national Institutes of Health, Bethesda, MD, USA) to calculate areas of stained xylems. Meanwhile, distal needles of each segment were scanned to calculate leaf area (LA) and then oven-dried at 75 °C for about 48 h to get constant dry mass to calculate leaf mass per area (LMA, g cm^{-2}). The leaf area to sapwood area ratio (LA/SA, $\text{m}^2 \text{cm}^{-2}$) of each species was calculated as LA divided by SA. The segments used for hydraulic conductivity were then used to measure wood density (WD, g cm^{-3}) by the water displacement method.

Stem hydraulic vulnerable curves were constructed using the centrifugal force method (Alder, Pockman, Sperry, & Nuismer, 1997) on six stem segments of 14.2 cm in length for each species. After measuring the native hydraulic conductivity, the segments were fixed into a high-speed centrifuge (Model 20K, Cence Instruments, Changsha, China) equipped with a customized rotor ('Sperry rotor'). The vulnerability to embolism of each segment was determined by measuring the decrease of hydraulic conductivity in response to a stepwise increase in xylem tension generated by spinning. Vulnerability curves were fitted using sigmoidal models (Fig. S1) and the pressure at 50% loss of conductivity (P_{50} , MPa) was calculated (Pammenter & Vander Willigen, 1998).

Leaf physiological measurements

Midday leaf pressures (Ψ_{md} , MPa) of each species were measured during two successive sunny days with a pressure chamber (PMS1000, Albany, OR, USA) in July 2018. Eight sun-exposed terminal twigs with each from a different tree were sampled at midday for each species (between 12: 00 and 13: 00) and then samples were sealed in small plastic bags containing moist paper towels and transported to laboratory immediately. All the samples were measured within 1 hr after excision. Hydraulic safety margins (HSM) of each species were calculated as the difference between Ψ_{md} and P_{50} .

Leaf osmotic potential at zero turgor (π^0) and at full turgor (π^{100}) were obtained from the leaf pressure-volume (P-V) relations (Tyree & Hammel, 1972). The branches c.a. 1 m in length of each species were sampled at predawn, and transported to laboratory in dark plastic bags with the ends of branches immersed in water. After a 2 h rehydration, the terminal shoot samples were cut off and used for determining the P-V relations. The mass of saturated terminal shoot was measured using an analytical balance (CPA 225D, Sartorius Inc., Germany). The mass and water potential of the samples were measured periodically during a slow dehydration process. Samples were over-dried at 70 for 48 hr to measure the dry mass at the end. The P-V curves were fitted using a computer program by Schulte and Hinckley (1985).

In August 2018, the stomatal conductance (g_s , $\text{mol m}^{-2} \text{s}^{-1}$) and net CO_2 assimilation (A) were measured using a LICOR-6400 gas exchange system (LI-COR, Lincoln, NE, USA) equipped with a 6400-05 conifer chamber (Lincoln, Nebraska, USA) between 0900 and 1030 hours. The measurements were conducted on mature and fully developed sunlit needles of eight south-facing trees of each species at 400 ppm reference CO_2 and 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density. The humidity, temperature and photosynthetic active radiation of leaf chamber were set as ambient conditions. After gas exchange measurements, needles fit in the leaf chamber were excised and measured their area back in the laboratory. Then gas exchange needles were dried and weighed to determine their dry mass. The net photosynthetic rate per leaf area (A

a , $\mu\text{mol m}^{-2}\text{s}^{-1}$) and net photosynthetic rate per mass (A_m , $\mu\text{mol g}^{-1}\text{s}^{-1}$) were calculated as A divided by leaf area and leaf dry mass, respectively. The intrinsic water use efficiency of photosynthesis (WUE_i) was calculated as the ratio of A to g_s for each twig measured.

Statistical analysis

The correlations between functional traits (K_s , A_m , WD, HSM and π^0) and radial growth resilience indices (RT, RC and RS), growth rate (CBA_{15}), and relationship between mean sensitivity and CBA_{15} were evaluated by linear regression analyses. One-way analysis of variance (ANOVA) was used to test the differences in functional traits among studied species using the SigmaPlot 12.5 software (Systat Software, Inc., San Jose, CA, USA). Pearson's correlation coefficients between functional traits, growth resilience indices, mean sensitivity and CBA_{15} were also calculated.

Results

Under a common environment of the tree plantations, the seven pine species exhibited relatively large variations in trunk radial growth rate. Across a cambial age sequence of 15 years, the cumulative basal area of all the seven pine species exhibited linear relationships with age but the rate of increment showed relatively large interspecific differences (Fig. 2). The cumulative basal area at cambial age of 15 years (CBA_{15}) varied more than two folds among the studied species, i.e. ranged from 83.9 cm^2 in *P. tabuliformis* to 209.1 cm^2 in *P. sylvestris*. Similarly, the standardized tree-ring width chronologies of the seven studied species showed that there were relatively large variations in climate sensitivity of the annual tree-ring growth with the mean sensitivity ranged from 0.21 in *P. koraiensis* to 0.33 in *P. tabuliformis* (Table 1). Moreover, our tree-ring analyses showed that radial growth of the seven species showed substantial interspecific differences in responding to the extreme drought event happened in 2015, i.e. with values of the drought resistance index ranged from 0.54 in *P. densiflora* to 1.33 in *P. koraiensis* and the drought resilience index ranged from 0.51 in *P. densiflora* to 1.30 in *P. koraiensis*. All the studied species showed relatively low recovering ability after the extreme drought stress with the recovery index mostly lower than 1.25 (Table 1; Fig. 3).

The leaf mass based maximum photosynthetic rate (A_m) ranged from $0.0124 \mu\text{mol g}^{-1} \text{s}^{-1}$ in *P. koraiensis* to $0.0194 \mu\text{mol g}^{-1} \text{s}^{-1}$ in *P. sylvestris* (Table S1; Fig. 4a), sapwood-specific hydraulic conductivity (K_s) and leaf-specific hydraulic conductivity (K_l) ranged from $0.92 \text{ kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ and $1.05 \times 10^{-4} \text{ kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ in *P. koraiensis* to $1.32 \text{ kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ and $3.73 \times 10^{-4} \text{ kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ in *P. densiflora*, respectively (Fig. 4b). There is a significant positive correlation between K_s and A_m across the seven studied pine species ($P < 0.05$, Table S2; Pearson correlation). All the studied species showed relatively large hydraulic safety margins (HSM) ranging from 0.88 MPa in *P. densiflora* var. *zhangwuensis* to 1.29 MPa in *P. koraiensis* (Fig. 5a). Interspecific variation in wood density (WD) among the studied species overall showed a consistent order with that of HSM (Fig. 5a, b) that leads to a significant positive correlation between the two parameters ($P < 0.05$, Table S2; Pearson correlation). The order of interspecific variation in leaf level traits related to drought tolerance, as measured by leaf turgor loss point (π^0), showed different patterns with that of stem traits related to hydraulic tolerance to drought (Fig. 5a-c), which resulted in non-significant correlations across species between leaf and stem traits relevant to drought tolerance (Table S2).

Our results showed that tree drought resistance and resilience indices calculated from tree-ring analyses overall exhibited strong coordination with stem and leaf physiological traits related to drought tolerance (Fig. 6a-f). RT and RS were both positively correlated with WD ($P < 0.01$; Fig. 6a, d), HSM ($P < 0.05$, $P = 0.115$; Fig. 6b, e), and π^0 ($P = 0.069$ and 0.038 ; Fig. 6c, f). Contrastingly, both RT and RS showed significant negative correlations with functional traits pertinent to xylem hydraulic efficiency and leaf photosynthetic carbon assimilation (Fig. 7a-d). We found that tree radial growth rate as reflected by CBA_{15} has a strong negative correlation with growth sensitivity to inter-annual climate variability calculated from tree-ring analysis ($P < 0.05$; Fig. 8).

Discussion

The influence of physiological traits on tree growth rate

The significant positive relationship between xylem hydraulic conductivity and leaf photosynthetic rate indicates that there is a hydraulic-photosynthetic coordination across the studied pine species. The coordination between xylem water transport efficiency and photosynthetic rate has been widely observed in many ecosystems and among different species (e.g. Brodribb et al., 2002; Eller et al., 2017; Hao et al., 2011; Hubbard et al., 2001). The hydraulic architecture of plants determines the efficiency of water delivery along the plant water transport pathway, and controls the gas exchange of leaf stomata and hence influences the capacity of photosynthetic carbon assimilation (Tyree & Ewers, 1991; Sperry, 2000). Therefore, high hydraulic conductance and photosynthetic rate are usually linked with fast growth rate across tree species (Fan et al., 2012; McDowell, 2011).

The significant hydraulic-photosynthetic coordination, however, did not lead to high radial growth rates in tree species having greater xylem water transport efficiency and photosynthetic assimilation rate in our study. The lack of a positive correlation between instantaneous photosynthetic rate and tree radial growth rate across the studied pine species is likely related to interspecific variation in costs related to drought resistance and post-drought damage repair in drought-prone environments. Besides the carbon allocation to growth, a considerable portion of carbohydrates assimilated through photosynthesis is invested to processes not directly related to growth, such as defense against pathogens and stress tolerance (Aaltonen, Lindén, Heinonsalo, Biasi, & Pumpanen, 2016; Adams et al., 2017; Anderegg et al., 2015; Chave et al., 2009). Drought-affected pine trees would allocate more carbon to roots and construct more drought resistant but more carbon costly xylems and are usually prone to growth decline (Aaltonen et al., 2016; Eller et al., 2017; Taeger et al., 2013). Meanwhile, after the drought events, trees also need to consume more carbon to recover from the adverse effect of drought (Chave et al., 2009; O’Grady, Mitchell, Pinkard, & Tissue, 2013). The fast-growing species usually have greater capacities of xylem water transport and leaf photosynthesis, which lead to faster instantaneous carbon assimilation rate under water-sufficient conditions (Poorter et al., 2010; Schuldt et al., 2016). However, these species are usually more vulnerable to drought-induced xylem embolism even under relatively mild drought stress and are more prone to hydraulic functional damage during drought events (Brodribb & Holbrook, 2003; Martínez-Vilalta et al., 2012). Severer drought-induced damage to the plant water-transport system in species taking the “fast strategy” will limit their post-drought photosynthetic carbon assimilation, and they may require more energy input for recovery from drought events, especially in sites with drought events of high frequency (Eller et al., 2017; Skelton, Brodribb, McAdam, & Mitchell, 2017). Such costs related to recovering from drought stress may offset the beneficial effect of fast instantaneous photosynthetic carbon assimilation rate in drought-prone environments. Therefore, it may be difficult to directly linked multi-year accumulated radial growth with hydraulic traits under the relatively harsh environment, since tree species with different growth strategies may have different inter-annual growth fluctuations and growth responses to drought events.

The influence of physiological traits on tree drought resilience

Our results confirmed that inter-specific variations of radial growth responses to extreme drought event are significantly influenced by tree physiological traits pertinent to drought tolerance (Anderegg et al., 2015; Fang & Zhang, 2019; Gazol et al., 2017). Trees face more negative xylem pressures than normal during drought events that can induce serious hydraulic dysfunction through embolism formation (Anderegg et al., 2012, 2013). The conifer species with higher wood density usually have narrower tracheids and show stronger resistant to drought-induced xylem embolism (Pockman and Sperry, 2000; Montwé et al., 2014). Under the same water conditions, tree species with larger hydraulic safety margins would have lower risk of reaching P_{50} (Anderegg et al., 2012; Choat et al., 2012), which is regarded as a critical threshold of embolism formation causing catastrophic hydraulic failure in conifers (Brodribb et al., 2010; Schuldt et al., 2016). The hydraulic functions of the studied pine species with higher HSM and WD would be less likely harmed during non-lethal drought events (Anderegg et al., 2012; Santiago et al., 2018; Tyree & Sperry 1989), which would hence show lower degrees of decrease in photosynthetic carbon assimilation in face of drought and require less input for damage recovery posterior drought events. The positive correlations observed here between growth resilience to drought (RT and RS calculated from tree-ring analyses) and wood functional traits related to drought tolerance (HSM and WD) indicate the importance of hydraulic safety in guaranteeing tree growth

over relatively long periods in water-limited environments.

The positive correlation between leaf turgor loss point and growth resilience indicates that the pine species with less drought-tolerant leaves tend to show higher radial growth resistance to extreme drought event in the water-limited environment of the study site. Leaf turgor loss point can be used to predict species' capacity of osmotic adjustment and the degree of isohydry-anisohydry (Bartlett, Scoffoni, & Sack, 2014; Meinzer et al., 2016). Species with more negative leaf turgor loss points are able to resist leaf dehydration better, and thereby maintaining stomatal conductance, hydraulic conductance and photosynthetic gas exchange at lower water potentials (Bartlett et al., 2014, 2015). In contrast, species with less negative leaf turgor loss points tend to be more isohydric and enable leaves to close their stomata earlier as water potential decreases and hence can better avoid hydraulic failure during drought stress (Brodribb & Holbrook, 2003; Meinzer et al., 2016). Species with different leaf turgor loss points are linked to different capacity in regulating carbon and water balances under drought events of different duration and intensity (McDowell et al., 2008; Mitchell et al., 2013). During a drought event of high-intensity but relatively short duration, more adverse effects on tree growth would be caused by xylem embolism due to sharp decrease of water potentials in more anisohydric species than adverse effects of stomatal closure on photosynthetic carbon assimilation in more isohydric species (Manrique-Alba et al., 2018; Mitchell et al., 2013).

Hydraulic dysfunction caused by extreme drought events impairs post-drought growth and results in legacy effects of drought, which have been reported to be most prevalent among pine species and in dry ecosystems (Anderegg et al., 2013, 2015; Gazol et al., 2017; Wu et al., 2017). Drought-induced xylem embolism limit water transport capability and hinder the recovery of photosynthetic rate over a relatively long period after drought events (Anderegg et al., 2013; Rehschuh et al., 2020; Skelton et al., 2017). A growing body of literature indicates that drought-induced hydraulic dysfunction in pines is nonreversible and is compensated primarily by xylem development over the next few growing seasons rather than embolism refilling (Anderegg et al., 2013; Brodribb et al., 2010; Hammond et al., 2019). Our data supported the viewpoint that hydraulic safety influences the post-drought radial growth probably through the residual effect of drought-induced hydraulic dysfunction, since the studied species with larger hydraulic safety margin tend to have higher RS, and RT. The results also indicate that physiological traits reflecting plant resistance to drought (e.g. HSM and WD) can be used as good proxies for predicting specific-specific growth response to drought events (Skelton et al., 2017; Zhang et al., 2017; Fu & Meinzer, 2018).

The trade-off between drought resilience and instantaneous flux capacity

The strong negative correlation found here between tree growth stability in facing extreme drought events (RT and RS) and physiological traits of water and carbon flux capacity (K_1 and A_m) suggests that an intrinsic fast strategy of instantaneous resource acquisition and processing are disadvantageous in drought-prone habitats, which is underlain by an association between high hydraulic efficiency and small hydraulic safety margin. Species with a fast-growing strategy usually require relatively high xylem hydraulic conductance that allow them to meet higher transpirational water demands and the maximization of photosynthetic carbon assimilation when water are readily availability; however, they tend to function with relatively small hydraulic safety margins (Gong et al., 2020; Liu et al., 2015). This renders tree species adopting a fast strategy higher risk of drought-induced xylem embolism, while greater sensitivity to hydraulic dysfunction in such species would lead to greater degrees of reductions in carbon assimilation, radial growth or even tree mortality when facing extreme drought events (Eller et al., 2017; Li et al., 2020b; Pockman and Sperry, 2000). Moreover, species that are more sensitive to drought-induced hydraulic dysfunction would require more carbon input for recovery to pre-drought conditions that would further compromise tree growth in drought-prone environments (Chave et al., 2009; O'Grady et al., 2013).

The result that tree species with lower mean sensitivity in ring growth to inter-annual climate variation have higher radial growth rate (CBA_{15}) further indicates the importance of drought resilience in determining tree growth rate expressed over a long term in water-limited environments. It has been shown that tree species with high climatic sensitivity are more prone to drought-induced mortality (Macalady & Bugmann, 2014; Ogle, Whitham, & Cobb, 2000). Similarly, growths of species with higher climatic sensitivity have

been found to be more strongly limited by inter-annual climate swings (Fritts, 1976; Macalady & Bugmann, 2014). Especially in arid and semi-arid regions, even minimal climatic fluctuations may significantly affect tree species with high climate sensitivity (Speer, 2010; Vanderwel, Lyutasarev, & Purves, 2013). Tree species with a fast strategy would be more sensitive in radial growth to variations of environmental water availability due to their intrinsically greater water demand and higher sensitivity to drought stress, which would be less advantageous in environments with persistent water deficiency (Gazol et al., 2017; Martínez-Vilalta et al., 2012). Tree species with high resource acquisition capability can have high rates of carbon assimilation and store more carbohydrates during the wet years but may not be enough to compensate for the adverse impacts of water deficiency in the dry years (Breshears et al., 2009). Therefore, our results indicate that greater resilience to drought stress, rather than high instantaneous rates of resource acquisition and assimilation, is more important in determining long-term tree growth performances in water-limited environments.

Conclusions

Results across the studied conifer species growing in a common environment of semi-arid area indicate that drought tolerance rather than efficiencies of resource acquisition are more important for tree growth as quantified by tree-ring analyses. Physiological characteristics reflecting higher resource acquisition (intrinsic instantaneous water and carbon flux capacity) showed significant negative correlations with drought resistance and resilience to extreme drought events that is underlain by an association between high hydraulic efficiency and small hydraulic safety margin. Results of this study suggest that hydraulic safety margin can be used as importance references in predicting interspecific variations in radial growth responses to drought events in water-limited environments, which would also shed light on the prediction of inter-specific variations in tree growth performances in a warming and drying world of the future.

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Conflict of Interest Statement

The authors declare no conflict of interests.

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Table 1 Basic information of the seven studied tree species, dendrochronological statistics for the standard chronologies and the growth resilience indices of 2015 drought event.

	Core number	Species code	Symbol	DBH	Dendrochronology	Dendro
					All series correlation	SNR
<i>Pinus koraiensis</i> Sieb. et Zucc.	40	Pk		26.3 ± 0.6	0.331	16.4
<i>Pinus banksiana</i> Lamb.	36	Pb		17.0 ± 0.2	0.440	22.0
<i>Pinus sylvestris</i> var. <i>mongolica</i> Litv.	40	Psm		17.9 ± 0.5	0.483	30.9
<i>Pinus tabulaeformis</i> Carriere	38	Pt		21.3 ± 0.5	0.422	23.3
<i>Pinus densiflora</i> var. <i>zhangwuensis</i>	39	Pdz		17.7 ± 0.3	0.595	48.4
<i>Pinus sylvestris</i> var. <i>mongolica</i> (Takenouchi) T.	40	Ps		19.3 ± 0.4	0.315	15.7
<i>Pinus densiflora</i> Sieb. et Zucc.	39	Pd		22.5 ± 0.5	0.507	41.1

Note: DBH, diameter at breast height; SNR, signal-to-noise ratio; EPS, expressed population signal; RT, tree resistance; RC, tree recovery; RS, tree resilience; MS, mean sensitivity. DBH values are means ±1 SE ($n = 20$)

Figure Legends

Fig. 1 (a) Annual mean temperature, (b) annual precipitation of the growing season (June to September), and (c) the De Martonne Index (DMI) reflecting environmental aridity of the study area for the period of 1970-2019. The solid line in panel a shows a significant trend of temperature increase, the dashed lines in panel b, c show the average of annual growing seasonal precipitation and DMI for 1970-2019, and the shaded area in panel c indicates the -1.5 times standard deviation of DMI. Data were from Zhangwu meteorological station located about 31 km from the study site.

Fig. 2 The change of cumulative basal area (CBA) with tree cambial age for each studied conifer species. The dashed vertical line marks the age of 15 years and the number in the upper right corner of each panel shows the CBA value at a cambial age of 15 years (CBA_{15}) for each species. Species name abbreviations are as shown in Table 1.

Fig. 3 Standardized tree-ring width chronologies (red lines) of the seven studied tree species. The blue line in each of the left panels shows the number of cores in specific years. The panels on the right show standardized tree-ring width indices during, before and after the 2015 drought event. Species name abbreviations are as shown in Table 1.

Fig. 4 (a) Net photosynthetic rate on per leaf dry mass basis (A_m) and (b) sapwood-specific hydraulic conductivity (K_s , gray bars) and leaf-specific hydraulic conductivity (K_l , black bars) of the seven studied conifer species. Error bars show 1SE ($n = 8$). Species name abbreviations are as shown in Table 1. Results of one-way analyses of variance are shown in each panel.

Fig. 5 (a) hydraulic safety margin (HSM), (b) wood density (WD) and leaf osmotic potential at zero turgor (π^0). Error bars show 1SE ($n = 18-24$ for WD, $n = 8-10$ for HSM and π^0). Species name abbreviations are as shown in Table 1. Results of one-way analyses of variance are shown in each panel.

Fig. 6 Correlations between tree drought resistance index (RT), resilience index (RS) and (a, d) wood density (WD), (b, e) hydraulic safety margin (HSM) and (c, f) leaf osmotic potential at full turgor (π^0). Horizontal error bars show $\pm 1SE$ ($n = 18-24$ for WD, $n = 8-10$ for π^0). Symbols are as defined as in Table 1.

Fig. 7 Correlations between tree drought resistance index (RT), resilience index (RS) and (a, c) leaf-specific hydraulic conductivity (K_s) and (b, d) net photosynthetic rate on per leaf dry mass (A_m). Horizontal error bars show $\pm 1SE$ for K_s and A_m , respectively ($n = 8$). Symbols are as defined as in Table 1.

Fig. 8 Correlation between the cumulative basal area at cambial age of 15 years (CBA_{15}) and mean sensitivity from tree-ring analysis across the seven studied conifer species. Symbols are as defined in Table 1.

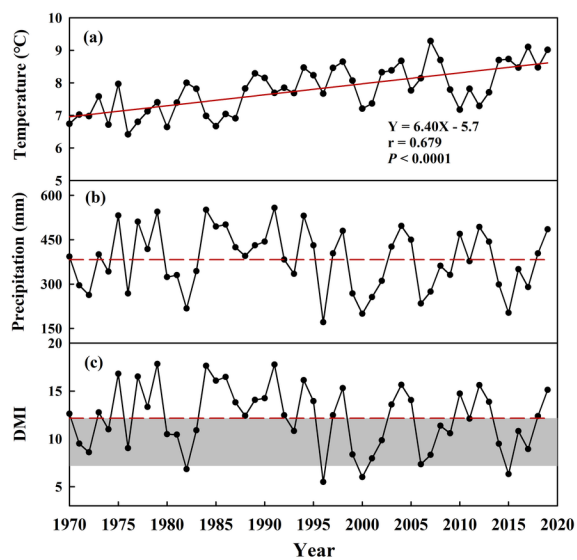


Fig. 1

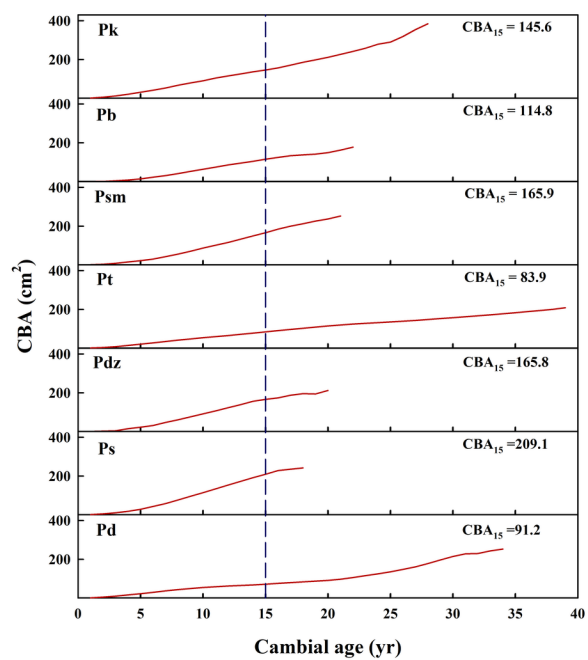


Fig. 2

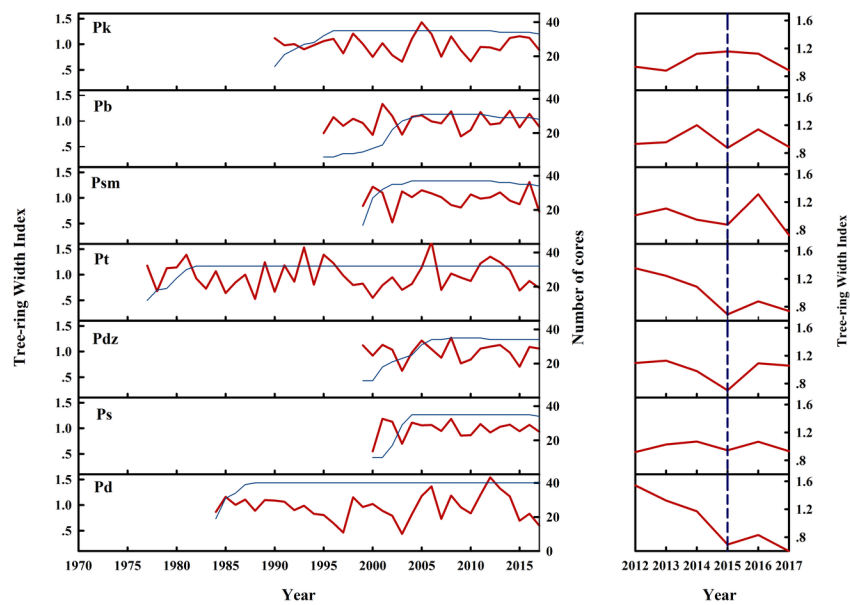


Fig. 3

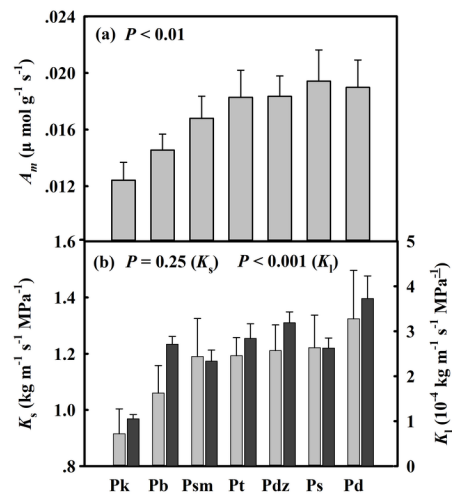


Fig. 4

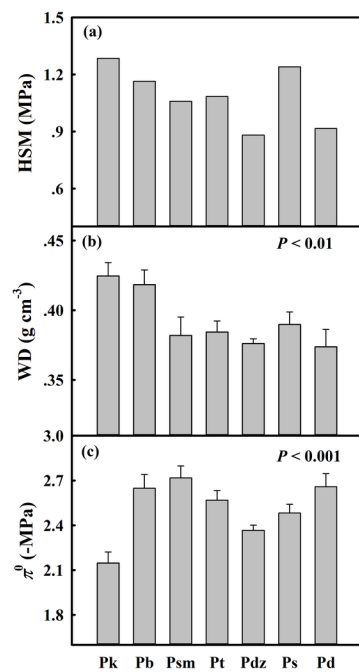


Fig. 5

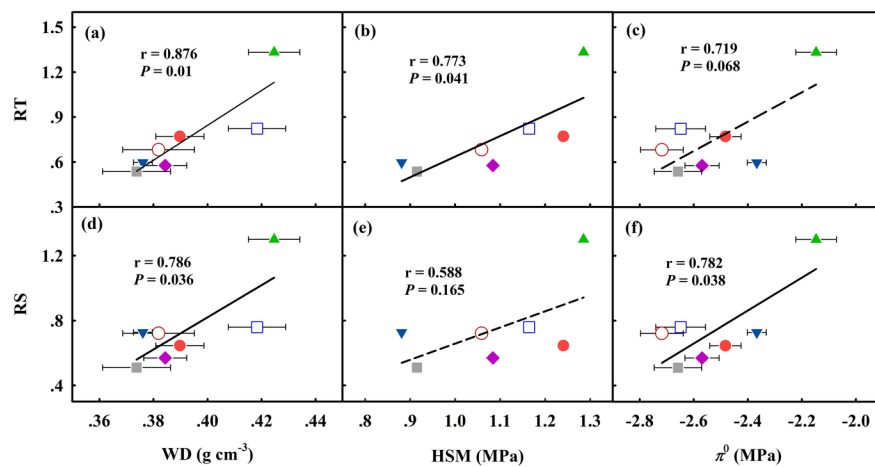


Fig. 6

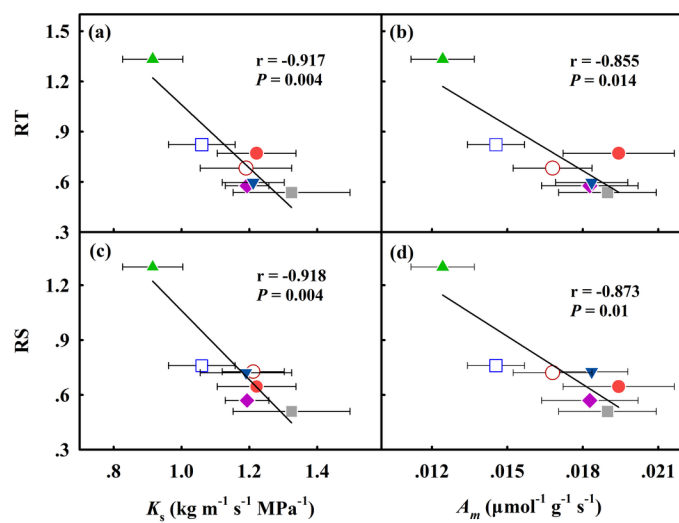


Fig. 7

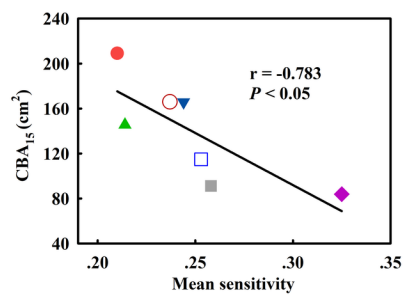


Fig. 8