Postprint: Ecophysiological Responses of Schima superba Seedlings from Two Provenances to Drought-Rewatering

Authors: Wang Defu, Zhao Nan, Qiu Wanbin, Sang Dongxin, Huang Guomin, Liu Wenfei, Shen Fangfang, Honglang Duan

Date: 2022-09-08T00:00:00+00:00

Abstract

Against the backdrop of global climate change, investigating the physio-ecological responses of different tree provenances to drought-rewatering will enhance our understanding of how climatic conditions in provenance origins influence tree drought resistance, thereby providing theoretical references for future forest management and operation. This study employed Schima superba from Guangdong and Fujian provenances as experimental subjects, simulated drought and rewatering conditions through potted water control, and examined the responses of hydraulic and carbon physiological traits, proline (Pro), and superoxide dismutase (SOD) to drought-rewatering in the two provenances. The results indicated: (1) Under control conditions, stem xylem water potential (Ψxylem), leaf relative water content (RWC), photosynthetic rate (Asat), and stomatal conductance (Gs) of Guangdong provenance S. superba were all lower than those of Fujian provenance. (2) Hydraulic traits, Pro, and SOD in both provenances exhibited consistent response trends to drought-rewatering, wherein Ψxylem, RWC, and Pro could recover to control levels relatively rapidly, whereas stem xylem embolism degree and SOD did not recover to control levels. (3) Leaf Asat of Fujian provenance S. superba demonstrated higher sensitivity to drought compared with Guangdong provenance, and required a longer period to recover to control levels after rewatering. (4) The recovery rate of NSC in Fujian provenance S. superba after rewatering exceeded that of Guangdong provenance. In summary, neither Fujian nor Guangdong provenance S. superba could restore embolized xylem through short-term rewatering (30 d). Although the photosynthetic rate of Guangdong provenance S. superba recovered to control levels more rapidly, its photosynthetic rate remained lower than that of Fujian provenance, and its NSC recovery capacity was inferior to that of Fujian provenance. Consequently, under scenarios of future intensified drought, the growth and survival of Guangdong provenance S. superba may face greater threats.

Full Text

Preamble

Eco-physiological responses of *Schima superba* seedlings from two provenances to drought and re-watering

WANG Defu[1,2], ZHAO Nan[1], QIU Wanbin[1], SANG Dongxin[1], HUANG Guomin[1], LIU Wenfei[1], SHEN Fangfang[1], DUAN Honglang[1,3*]

[1] Jiangxi Provincial Key Laboratory for Restoration of Degraded Ecosystems & Watershed Ecohydrology, Nanchang Institute of Technology, Nanchang 330099, China
[2] Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China
[3] Institute for Forest Resources and Environment of Guizhou, Guizhou University, Guiyang 550025, China

Abstract: In the context of global climate change, investigating the eco-physiological responses of different tree provenances to drought and re-watering will help elucidate how climatic conditions at seed origin influence drought resistance and provide theoretical references for future forest management. This study examined *Schima superba* from Guangdong and Fujian provenances, using potted seedlings subjected to controlled drought and re-watering conditions to investigate hydraulic and carbon physiological characteristics and the responses of proline (Pro) and superoxide dismutase (SOD) to drought-rewatering cycles. The results showed: (1) Under well-watered conditions, stem xylem water potential (Ψxylem), leaf relative water content (RWC), photosynthetic rate (Asat), and stomatal conductance (Gs) were lower in Guangdong provenance seedlings compared to Fujian provenance seedlings. (2) Hydraulic traits, Pro, and SOD showed consistent response patterns to drought and re-watering in both provenances, with Ψxylem, RWC, and Pro recovering rapidly to control levels, while stem xylem embolism and SOD did not recover to control levels. (3) Leaf Asat in Fujian provenance seedlings was more sensitive to drought than in Guangdong provenance seedlings, and required more time to recover to control levels after re-watering. (4) The recovery rate of NSC in Fujian provenance seedlings was higher than in Guangdong provenance seedlings. In conclusion, both Fujian and Guangdong provenances could not repair embolized xylem through short-term re-watering (30 days). Although photosynthetic rate in Guangdong provenance recovered faster to control levels, it remained lower than that of Fujian provenance, and its NSC recovery capacity was also lower. Therefore, under future scenarios of intensified drought, the growth and survival of Guangdong provenance *S. superba* may face greater threats.

Keywords: drought-rewatering, photosynthetic traits, hydraulic traits, *Schima superba*, intra-specific differences

Introduction

Global climate change is altering future precipitation patterns, with both drought intensity and duration likely to increase (Pachauri & Reisinger, 2014). Drought stress threatens tree survival and can consequently alter community structure and function (Barros et al., 2019; Brodribb et al., 2020). Throughout their life cycle, trees frequently experience multiple drought and drought-rewatering events, and thus possess adaptive mechanisms to cope with drought conditions (Gessler et al., 2020; Duan et al., 2019). However, considerable uncertainty remains regarding whether intra-specific differences exist in the eco-physiological mechanisms underlying tree responses to drought-rewatering cycles. Therefore, under changing global precipitation patterns, studying intra-specific variation in tree eco-physiological response strategies to drought-rewatering can provide fundamental data for understanding how trees respond to drought-rewatering and for optimizing ecological models, while also offering theoretical references for future forest management.

Drought stress typically inhibits tree growth, reduces leaf water potential and photosynthetic rate, and exacerbates xylem embolism (Yan et al., 2017; Duan et al., 2019; Lü et al., 2021). Drought also induces accumulation of leaf proline (Pro) and enhanced superoxide dismutase (SOD) activity, which help alleviate damage to plant cells from water deficit (Duan et al., 2020; Sun et al., 2020). Additionally, drought stress alters non-structural carbohydrate (NSC) content. Previous studies indicate that drought effects on tree NSC depend on drought intensity and duration, with soluble sugars remaining unchanged under mild drought but increasing significantly under severe drought (He et al., 2020).

The capacity of trees to recover physiological and ecological indicators after drought stress represents an important criterion for evaluating drought adaptation. In particular, whether xylem hydraulic conductivity can recover in the short term and inter-specific differences in recovery capacity have become recent research hotspots. Studies show that leaf water potential can recover relatively quickly to control levels, whereas photosynthetic rate and xylem hydraulic conductivity recover more slowly (Duan et al., 2019; Ruehr et al., 2019). Furthermore, NSC plays a crucial role in maintaining tree hydraulic function and in the repair of stem xylem embolism, with embolism repair often accompanied by NSC consumption (Tomasella et al., 2019). Previous research has found that tree responses of photosynthetic and water physiological indicators to drought-rewatering differ not only among species but also among different distribution areas or provenances of the same species (Liu et al., 2018; Chen et al., 2019). For example, studies have shown that Fujian provenance of *Keteleeria fortunei* has greater drought resistance than Guizhou provenance (Liu et al., 2018). However, whether post-drought recovery capacity of eco-physiological indicators differs among provenances remains unclear, particularly regarding intra-specific variation in xylem hydraulic conductivity recovery.

Schima superba is a large tree species in the family Theaceae, widely distributed across southern China in provinces including Fujian, Jiangxi, Hunan, and Guangdong. It is a dominant species in subtropical evergreen broad-leaved forests and a commonly used species for afforestation and greening. Additionally, *S. superba* is an excellent fire-resistant tree that can be mixed with other species or planted alone as a firebreak. However, differences in eco-physiological responses to drought-rewatering among different provenances of *S. superba* remain unclear. Previous studies have found that plant drought resistance is related to local climatic conditions such as mean annual rainfall (Liang et al., 2019), indicating that plants possess adaptive traits to their native climate and that different provenances may exhibit varied responses to drought. Therefore, this study selected *S. superba* from two provenances with distinct climatic differences as research subjects, using pot experiments to control drought and re-watering conditions and investigate eco-physiological responses to drought-rewatering. We hypothesized that gas exchange and hydraulic traits of the two provenances would show differential responses to drought-rewatering, with the provenance from lower precipitation areas exhibiting stronger drought resistance.

Materials and Methods

1.1 Experimental Materials and Design

This experiment was conducted at the Yaohu Campus of Nanchang Institute of Technology (116°01’ 50.16’ ’ E, 28°41’ 17.12’ ’ N), which has a subtropical monsoon climate with mean annual rainfall of 1,600–1,700 mm (approximately 50% from April to June and 19% from July to September). Seeds of *S. superba* were collected from two locations: Youxi Jiufu Mountain Nature Reserve in Fujian Province (118°01 58 –118°07 16 E, 26°03 37 –26°06 59 N) and Conghua Chenhedong Nature Reserve in Guangdong Province (113°49 30 –114°01 50 E, 23°43 02 –23°48 10 N). Mean annual precipitation at the two provenances is 1,665 mm and 1,801 mm, respectively, with mean annual temperatures of 19.6°C and 22.8°C. Seeds were sown in April 2018, and seedlings were transplanted in March 2019 into 7.6 L pots (one seedling per pot) containing latosol soil. All potted seedlings were moved to a rainout shelter (20 m long × 4 m wide × 3 m high) for natural growth. The shelter roof was made of transparent PVC panels with 15% shading, and the sides were well ventilated. Before the experiment began, soil in all pots was maintained at field capacity, and weekly applications of diluted soluble nutrient fertilizer (Shi Kede Horticultural Fertilizer Co., Ltd., Wuhan; N\$ $30g\cdot L^{\{-1\}, P\{2\}O\{5\}\$\$\ 14g\cdot L}$\{-1\}, K_\{2\}O $16g\cdot L^{\{-1\}, Fe\ 0.14g\cdot L}$\{-1\}, Mn $0.06g\cdot L$^\{-1\}\$) were applied at 200 mL per pot to maintain good seedling growth.

After four months of growth, 50 healthy, uniformly sized seedlings were selected from each provenance for the experiment. Two water treatments were established: (1) Control: 20 seedlings per provenance were maintained at field capacity throughout the experiment; (2) Drought-rewatering: The remaining 30 seedlings per provenance were not watered after treatment initiation, allowing soil to dry naturally. During this period, stem xylem water potential was monitored. When water potential approached the level predicted by previous vulnerability curves to cause 88% xylem embolism (i.e., 88% loss of hydraulic conductivity, representing severe drought (Uril et al., 2013; Duan et al., 2021)), samples were harvested and stem xylem embolism was measured (see section 1.2.2). When stem xylem embolism reached approximately 88%, all seedlings were re-watered to achieve and maintain field capacity until the experiment concluded.

1.2.1 Leaf Gas Exchange Parameters

Leaf gas exchange parameters were measured using a Li-6400 portable photosynthesis system (LI-Cor, Inc., Lincoln, NE, USA). Measurements were taken between 9:00-11:00 AM on days 0, 2, 4, 5, and 6 of drought, and on days 3, 7, and 15 of re-watering. For each treatment and provenance, four seedlings were selected (one mature current-year leaf per seedling) to determine light-saturated photosynthetic rate (Asat, $\mathrm{mol} \cdot \mathrm{m}^{-2} \cdot \mathrm{s}^{-1}$), stomatal conductance (Gs, $\mathrm{mol} \cdot \mathrm{m}^{-2} \cdot \mathrm{s}^{-1}$), and transpiration rate (E, $\mathrm{mmol} \cdot \mathrm{m}^{-2} \cdot \mathrm{s}^{-1}$). An artificial red-blue light source (6400-2B) was used at 1,500 $\mathrm{mol} \cdot \mathrm{m}^{-2} \cdot \mathrm{s}^{-1}$, CO_2 concentration was set at 400 $\mathrm{mol} \cdot \mathrm{mol}^{-1}$, air temperature was controlled at (31.1\$±\$0.2)°C, and relative humidity was maintained at 60–80%.

1.2.2 Hydraulic Trait Measurements

Water Potential: Stem xylem water potential was measured at midday. Before measurement, leaves were wrapped with plastic film and aluminum foil (plastic inside, foil outside) for over 1 hour to ensure water potential equilibrium between leaves and xylem (allowing leaf water potential to represent stem xylem water potential). Leaves were then collected in sealed bags, stored in a cooler, and transported to the laboratory. Stem xylem water potential (Ψxylem, MPa) was measured using a PMS-Model 1505D digital portable plant water potential pressure chamber (PMS Instruments, Corvallis, Oregon, USA) on drought days 0, 4, 6, 7, and 9, and re-watering days 3 and 7. Four seedlings were selected per provenance and treatment (two mature current-year leaves per seedling).

Leaf Relative Water Content: After excising leaves from shoots, fresh weight was measured. Leaf petioles were then cut underwater and submerged in darkness for 12 hours. After full rehydration, leaves were removed, surface water was blotted dry, and saturated fresh weight was measured. Leaves were then oven-dried at 70°C to constant weight and dry weight was measured. Relative water content = (fresh weight - dry weight) / (saturated fresh weight - dry weight) × 100%. RWC was measured simultaneously with water potential.

Stem Xylem Embolism: Pots were placed in a water-filled bucket, and stems were cut underwater using pruning shears. The cut end was sealed with Parafilm and immediately submerged in another bucket covered with a black plastic bag. To minimize artificial embolism, samples were brought to the laboratory, where 5 cm was cut from the stem base underwater and the entire plant was covered with a black plastic bag for approximately one hour (with the stem base remaining submerged) to release xylem tension (Wheeler et al., 2013). When leaf water potential recovered to > -1 MPa, 5-10 cm stem segments were collected (Creek et al., 2018) and initial hydraulic conductivity was measured using a XYL' EM xylem embolism meter (with stems kept submerged throughout). The xylem was then flushed at 100 kPa for approximately 30 minutes until no more bubbles appeared at the cut ends, after which maximum hydraulic conductivity was measured (stems kept submerged). A 2 mM KCl solution was used for conductivity measurements and flushing, with a pressure gradient of 5.4 kPa during measurements. Embolism percentage = (maximum conductivity - initial conductivity) / maximum conductivity × 100% (Cochard et al., 2002). Embolism was measured at re-watering day 0 and day 30, using 3–4 seedlings per provenance and treatment.

1.2.3 Biochemical Indicator Measurements

Non-structural carbohydrate (soluble sugars and starch) content was determined using the anthrone method. Samples from each organ were oven-dried and ground to powder at re-watering day 0 (drought critical point) and day 30. Approximately 0.05 g was weighed into 15 mL centrifuge tubes, 4 mL of 80% ethanol was added, and the mixture was vortexed. Samples were heated in an 80°C water bath for 30 minutes, cooled, and centrifuged at 10,000 rpm for 8 minutes. The supernatant was collected in 15 mL tubes (repeated 3 times). The supernatant was used for soluble sugar determination, and the residue for starch determination (Wang, 2019). Four mature current-year leaves were selected per provenance and treatment.

Proline content was measured using the acidic ninhydrin colorimetric method (Li et al., 2000). Superoxide dismutase activity was measured using the nitroblue tetrazolium colorimetric method (Giannopolitis & Ries, 1977). Four mature current-year leaves were selected per provenance and treatment.

1.3 Data Processing

Data were first tested for normality and homogeneity of variance; if assumptions were not met, data transformations were applied. SPSS 19.0 (SPSS Inc., USA) was used for one-way ANOVA, with Duncan's method for post-hoc comparisons. Two-way repeated measures ANOVA was used to test the effects of provenance, water treatment, and time on each parameter. All results with $P < 0.05$ were considered significant. Figures were prepared using SigmaPlot 12.5, with all values presented as mean ± standard error.

Results

2.1.1 Hydraulic Traits

Analysis of Figure 1 revealed that under drought stress, leaf relative water content (RWC) and stem xylem water potential (Ψxylem) in both provenances decreased. On drought day 4, Ψxylem was significantly lower than control levels. On drought day 6, RWC was significantly lower than control levels. By drought day 9 (re-watering day 0), Ψxylem had dropped far below control levels, reaching -2.4 MPa in Fujian provenance and -2.5 MPa in Guangdong provenance. Additionally, on drought day 9, stem xylem embolism (PLC) in both Fujian (94%) and Guangdong (90%) provenances had reached approximately 88%, the critical point for initiating re-watering (Figure 4 [Figure 4: see original paper]). Under control conditions, Ψxylem and RWC in Guangdong provenance were lower than in Fujian provenance.

2.1.2 Photosynthetic Traits

Analysis of Figure 2 [Figure 2: see original paper] showed that under drought stress, photosynthetic rate (Asat), stomatal conductance (Gs), and transpiration rate (E) in Fujian provenance decreased earlier than in Guangdong provenance. From drought day 4, leaf Asat, Gs, and E (5.99, 0.06, 1.67) were significantly lower than control levels (11.64, 0.19, 3.93). In Guangdong provenance, leaf Asat, Gs, and E (0.16, 0.01, 0.27) became significantly lower than control levels (2.66, 0.03, 0.90) from drought day 6 (Figure 2). Furthermore, under control conditions, leaf Asat and Gs in Guangdong provenance remained consistently low and far below those of Fujian provenance.

2.2.1 Hydraulic Traits

After re-watering, Ψxylem and RWC in both provenances increased, recovering to control levels from re-watering day 3 (Figure 3 [Figure 3: see original paper]). However, Ψxylem and RWC in Guangdong provenance were significantly lower than in Fujian provenance. Provenance had significant effects on Ψxylem and RWC (Table 1). In contrast to Ψxylem and RWC, stem xylem embolism (PLC) recovered slowly. On re-watering day 30, PLC in Fujian (83%) and Guangdong (93%) provenances remained significantly higher than control levels (23% and 30%, respectively), indicating that stem xylem embolism had not recovered (Figure 4). No significant differences in PLC between provenances were observed under control or re-watering conditions at either day 0 or day 30.

2.2.2 Photosynthetic Traits

After re-watering, leaf Asat, Gs, and E in Fujian provenance showed an increasing trend, recovering to control levels by day 15 (Figure 5). In Guangdong provenance, leaf Asat, Gs, and E recovered to control levels by re-watering day 3, but showed slight fluctuations with continued re-watering (Figure 5). Overall, photosynthetic traits in Guangdong provenance recovered faster than in Fujian provenance. Provenance had significant effects on leaf Asat, Gs, and E (Table 1).

2.2.3 Biochemical Characteristics

Analysis of Figure 6 [Figure 6: see original paper] showed that after re-watering, soluble sugar (SS), starch (ST), and non-structural carbohydrate (NSC) contents in roots, stems, and leaves of Fujian provenance increased and recovered to or exceeded control levels. In contrast, SS, ST, and NSC contents in stems and roots of Guangdong provenance decreased, while leaf ST and NSC contents increased (Figure 6), but NSC contents in all organs remained significantly lower than control levels. Provenance had significant effects on leaf ST and NSC, as well as SS, ST, and NSC in stems and roots (Table 1).

After re-watering, leaf superoxide dismutase (SOD) activity and proline (Pro) content showed consistent patterns in both provenances. SOD activity gradually increased but remained significantly lower than control levels (Figure 7 [Figure 7: see original paper]). Pro content gradually decreased, recovering to control levels by day 15 (Figure 7). Provenance had significant effects on leaf Pro and SOD (Table 1).

Discussion

3.1 Physiological and Ecological Responses of Two *S. superba* Provenances to Drought Stress

Under drought stress, plant water potential and relative water content typically decrease while stem xylem embolism increases significantly (Rehschuh et al., 2020; José et al., 2018). This study found that drought stress significantly reduced stem xylem water potential and leaf relative water content while increasing stem xylem embolism in both provenances. Additionally, stomatal conductance, photosynthetic rate, and transpiration rate in *S. superba* leaves decreased with progressive drought, consistent with previous studies (Chen et al., 2019; Deng et al., 2020). However, photosynthetic rate, stomatal conductance, and transpiration rate in Fujian provenance were more sensitive to drought, decreasing earlier than in Guangdong provenance, which helps reduce water loss. The differential responses of photosynthetic physiology to drought between provenances may be related to mean annual rainfall at their origins (lower in Fujian than Guangdong), representing an adaptive strategy to local habitat conditions (Liang et al., 2019). Non-structural carbohydrates reflect plant carbon balance status (Zheng et al., 2014). During drought, when respiratory consumption exceeds photosynthetic accumulation, tree NSC decreases (McDowell, 2011), potentially leading to carbon starvation. This study found that drought significantly reduced soluble sugar, starch, and NSC concentrations in leaves, stems, and roots of both provenances, indicating negative carbon balance under drought. Among organs, NSC reduction was greatest in roots of Fujian provenance and in leaves of Guangdong provenance, suggesting drought effects on NSC vary by organ and provenance (Li et al., 2018).

When plants experience drought stress, cellular proline content typically increases to regulate osmosis and protect enzymes and proteins (Sun et al., 2020). Wang et al. (2018) found that proline content increased significantly in *Phoebe zhennan* seedlings under drought stress, and this study observed similar significant increases in leaf proline content in both *S. superba* provenances. Drought stress also increases reactive oxygen species (ROS), which adversely affect photosynthetic systems and cause lipid peroxidation and cell death (Xu et al., 2010; Sun et al., 2020). Plants counteract this by enhancing ROS-scavenging enzyme activities such as SOD to reduce damage (Xu et al., 2010; Liu et al., 2018), although some studies have found decreased SOD activity under drought (Zhang et al., 2017; Wu et al., 2017). This study found significantly reduced leaf SOD activity under drought, possibly because SOD activity in *S. superba* leaves is vulnerable to ROS damage (Wu et al., 2004; Wu et al., 2017).

3.2 Physiological and Ecological Responses of Two *S. superba* Provenances to Post-Drought Re-watering

After drought re-watering, recovery of plant water status and cell turgor facilitates subsequent metabolic recovery (Ruehr et al., 2019). This study found that stem xylem water potential and leaf relative water content in both provenances recovered to control levels by re-watering day 3, indicating similar capacity for water status recovery in shoots and leaves (Yan et al., 2017). Rapid RWC recovery after re-watering suggests that the xylem maintained water transport capacity (Ruehr et al., 2019). Compared with RWC and water potential, recovery of photosynthetic rate and stomatal conductance was delayed, possibly due to inhibition by abscisic acid (Duan et al., 2020) and ethylene (Yao et al., 2020). This study also found that photosynthetic rate in Guangdong provenance recovered faster than in Fujian provenance, indicating provenance-specific differences in photosynthetic response to re-watering. The inconsistent recovery rates of leaf gas exchange parameters between provenances may be explained by several factors. First, previous studies have shown that post-drought recovery of leaf hydraulic conductance affects gas exchange recovery (Blackman et al., 2009), suggesting that differences in gas exchange recovery between provenances may be related to differences in leaf hydraulic conductance recovery. Second, abscisic acid and ethylene affect gas exchange recovery (Duan et al., 2020; Yao et al., 2020), indicating that hormonal levels may contribute to provenance differences in gas exchange recovery. Future studies should therefore examine post-re-watering changes in leaf hydraulic conductance and hormone levels (e.g., abscisic acid) to provide new mechanistic insights into inter-specific differences in plant gas exchange responses to re-watering.

After drought re-watering, plants can restore hydraulic conductivity through xylem embolism repair or by producing new xylem (Cardoso et al., 2020), though embolism repair typically requires more time than new xylem production (Brodribb et al., 2010; Martorell et al., 2014). This study found that after 30 days of re-watering, stem xylem embolism remained significantly higher than control levels in both provenances, indicating that embolism had not recovered to control levels and may require longer repair periods or recovery through new xylem production. Additionally, 30 days after re-watering, NSC in all organs of Fujian provenance gradually recovered to or exceeded control levels, while Guangdong provenance showed the opposite trend. NSC contributes importantly to post-re-watering hydraulic recovery by providing osmotic substances and energy (Tomasella et al., 2019). Therefore, the lower NSC concentration in Guangdong provenance may hinder subsequent stem xylem hydraulic recovery compared with Fujian provenance. As leaf relative water content increased after re-watering, plant osmotic regulation capacity gradually decreased (Zhou et al., 2019). This study found that leaf proline content in both provenances gradually decreased after re-watering, recovering to control levels. In contrast, leaf SOD activity gradually increased, possibly because ROS decreased after re-watering, reducing damage to SOD (Wu et al., 2004; Loreto & Becana, 2007).

This study examined changes in eco-physiological indicators (photosynthetic traits, hydraulic traits, NSC, proline, and SOD) in two *S. superba* provenances during extreme drought (approximately 88% loss of stem xylem hydraulic conductivity) and re-watering. The results indicate: (1) Both provenances responded to drought stress through stomatal closure and increased proline content; (2) Stem xylem water potential, leaf relative water content, Pro, SOD, and stem PLC showed consistent response patterns to drought-rewatering in both provenances, with stem PLC failing to recover to control levels after 30 days of re-watering; (3) Photosynthetic rate in Fujian provenance decreased earlier than in Guangdong provenance and required more time to recover to control levels after re-watering; (4) NSC recovery rate was higher in Fujian provenance than in Guangdong provenance. In conclusion, under future scenarios of intensified drought, both Fujian and Guangdong provenances cannot repair embolized xylem through short-term re-watering (30 days). Although photosynthetic rate in Guangdong provenance recovered faster to control levels, it remained lower than that of Fujian provenance, and its NSC recovery capacity was also lower. Therefore, the growth and survival of Guangdong provenance *S. superba* may face greater threats under future drought intensification.

References

BARROS FDV, BITTENCOURT PRL, BRUM M, et al., 2019. Hydraulic traits explain differential responses of Amazonian forests to the 2015 El Niño-induced drought [J]. *New Phytol*, 223(3): 1253-1266.

BLACKMAN CJ, BRODRIBB TJ, JORDAN, GJ, 2009. Leaf hydraulics and drought stress: response, recovery and survivorship in four woody temperate plant species [J]. *Plant Cell Environ*, 32(11): 1584–1595.

BRODRIBB TJ, BOWMAN D, NICHOLS S, et al., 2010. Xylem function and growth rate interact to determine recovery rates after exposure to extreme water deficit [J]. *New Phytol*, 188(2): 533-542.

BRODRIBB TJ, POWERS J, COCHARD H, et al., 2020. Hanging by a thread? forests and drought [J]. *Science*, 368(6488): 261-266.

CARDOSO AA, BILLON LA, BORGES AF, et al., 2020. New developments in understanding plant water transport under drought stress [J]. *New Phytol*, 227(4): 1025-1027.

CHEN MY, LI YC, WANG LB, et al., 2019. Photosynthetic responses to drought and subsequent re-watering in seedlings from two different provenances of *Quercus variabilis* Bl [J]. *Chin J Ecol*, 38(10): 2950-2958.

COCHARD H, COLL L, ROUX XL, et al., 2002. Unraveling the effects of plant hydraulics on stomatal closure during water stress in walnut [J]. *Plant Physiol*, 128 (1): 282-290.

CREEK D, BLACKMAN C, BRODRIBB TJ, et al., 2018. Coordination between leaf, stem, and root hydraulics and gas exchange in three arid-zone angiosperms during severe drought and recovery [J]. *Plant Cell Environ*, 41(12): 2869-2881.

DENG XX, SHI Z, XIAO WF, et al., 2020. Effects of drought and shading on growth and photosynthetic characteristics of *Pinus massoniana* seedlings [J]. *Acta Ecol Sin*, 40(8): 2735-2742.

DUAN HL, de Dios VR, WANG DF, et al., 2021. Testing the limits of plant drought stress and subsequent recovery in four provenances of a widely distributed subtropical tree species [J]. *Plant Cell Environ*, 45(4): 1187-1203.

DUAN HL, LI Y, XU Y, et al., 2019. Contrasting drought sensitivity and post-drought resilience among three co-occurring tree species in subtropical China [J]. *Agr For Meteorol*, 272: 55-68.

DUAN HL, WANG DF, WEI, XH, et al., 2020. The decoupling between gas exchange and water potential of *Cinnamomum camphora* seedlings during drought recovery and its relation to ABA accumulation in leaves [J]. *J Plant Ecol*, 13(6): 683-692.

DUAN HL, WU JP, LIU WF, et al., 2015. Water relations and carbon dynamics under drought stress and the mechanisms of drought-induced tree mortality [J]. *Sci Silv Sin*, 51(11): 113-120.

DUAN N, XU J, CHEN HL, et al., 2019. Effects of drought stress on phenotypic plasticity of *Cerasus humilis* [J]. *Guihaia*, 39(9): 1159-1165.

GESSLER A, BOTTERO A, MARSHALL J, et al., 2020. The way back: recovery of trees from drought and its implication for acclimation [J]. *New Phytol*, 228(6): 1704-1709.

GIANNOPOLITIS CN, RIES SK, 1977. Superoxide dismutases, 1: occurrence in higher plants [Corn, oats, peas] [J]. *Plant Physiol*, 59(2): 309-314.

HE W, LIU H, QI Y, et al., 2020. Patterns in nonstructural carbohydrate contents at the tree organ level in response to drought duration [J]. *Glob Change Biol*, 26(6): 3627-3638.

JOSÉ PP, ÓSCAR MH, EUSTAQUIO GP, et al., 2018. Cavitation limits the recovery of gas exchange after severe drought stress in Holm Oak (*Quercus ilex* L.) [J]. *Forests*, 9(8): 443-455.

LIU F, ZHOU LT, JIAANG Y, et al., 2018. Physiological response from different provenances of *Keteleeria fortunei* seedlings to drought stress [J]. *J Centr S Univ For Technol*, 38(11): 35-45.

LI HS, SUN Q, ZHAO SJ, et al., 2000. *Principle and technology of plant physiological and biochemical experiment* [M]. Beijing: Higher Education Press, 164-261.

LI W, HENRIK H, ADAMS HD, et al., 2018. The sweet side of global change-dynamic responses of non-structural carbohydrates to drought, elevated CO_2 and nitrogen fertilization in tree species [J]. *Tree Physiol*, 38(11): 11-28.

LIANG XY, HE PC, LIU H, et al., 2019. Precipitation has dominant influences on the variation of plant hydraulics of the native *Castanopsis fargesii* (Fagaceae) in subtropical China [J]. *Agr For Meteorol*, 271: 83-91.

LORETO NR, JAVIER RAMOS, ESTHER MG, et al., 2007. The response of carbon metabolism and antioxidant defenses of Alfalfa nodules to drought stress and to the subsequent recovery of plants [J]. *Plant Physiol*, 144(2): 1104-1114.

LÜ CY, GAO ZX, YAN Y, et al., 2021. Effects of drought-rewatering on leaf water potential of two *Dendrobium* plants [J]. *Guihaia*, 41(2): 177-182.

MARTORELL S, DIAZ-ESPEJO A, MEDRANO H, et al., 2014. Rapid hydraulic recovery in *Eucalyptus pauciflora* after drought: linkages between stem hydraulics and leaf gas exchange [J]. *Plant Cell Environ*, 37(3): 617-626.

MCDOWELL NG, 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality [J]. *Plant physiol*, 155(3): 1051-1059.

PACHAURI R, REISINGER A, 2014. Climate change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change [J]. *J Romance Stud*, 4(2): 85-88.

REHSCHUH R, CECILIA A, ZUBER M, et al., 2020. Drought-induced xylem embolism limits the recovery of leaf gas exchange in Scots pine [J]. *Plant Physiol*, 184(2): 852-864.

RUEHR NK, RÜDIGER G, STEFAN M, et al., 2019. Beyond the extreme: recovery of carbon and water relations in woody plants following heat and drought stress [J]. *Tree Physiol*, 1(8):

SUN Y, WANG C, CHEN HYH, et al., 2020. Response of plants to water stress: a meta-analysis [J]. *Front Plant Sci*, 11(4): 978-985.

TOMASELLA M, PETRUSSA E, PETRUZZELLIS F, et al., 2019. The possible role of non-structural carbohydrates in the regulation of tree hydraulics [J]. *Int J Mol Sci*, 21(1):

URIL M, PORTE AJ, COCHARD H, et al., 2013. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees [J]. *Tree Physiol*, 33(7): 672-683.

Wang DF, 2019. The effect of drought and water-logging stresses on eco-physiology of *Cinnamomum camphora* seedlings [D]. Nanchang: Nanchang Institute of Technology: 10-11.

WANG X, HU HL, HU TX, et al., 2018. Effects of drought stress on the osmotic adjustment and active oxygen metabolism of *Phoebe zhennan* seedlings and its alleviation by nitrogen application [J]. *Chin J Plant Ecol*, 42(2): 240-251.

WHEELER JK, HUGGETT BA, TOFTE AN, et al., 2013. Cutting xylem under tension or supersaturated with gas can generate PLC and the appearance of rapid recovery from embolism [J]. *Plant Cell Environ*, 36(11): 1938-1949.

WU L, LI ZH, WU JY, et al., 2017. Response of drought stress on cholorophyll content and anti-oxydant enzyme of *Cyclobalanopsis glauca* provenance clone seedlings [J]. *J Centr S Univ For Technol*, 37(6): 51-55.

WU ZH, ZENG FH, MA SJ, et al., 2004. A review of advances in active oxygen metabolism in plants under water stress [J]. *Subtrop Plant Sci*, 33(2): 77-80.

XU Z, ZHOU G, SHIMIZU H, 2010, Plant responses to drought and rewatering [J]. *Plant Signal Behav*, 5(6): 649-654.

YAN W, ZHENG S, ZHONG Y, et al., 2017. Contrasting dynamics of leaf potential and gas exchange during progressive drought cycles and recovery in *Amorpha fruticosa* and *Robinia pseudoacacia* [J]. *Sci Rep*, 7(1): 4470-4481.

YAO GQ, LI FP, NIE ZF, et al., 2020. Ethylene, not ABA, is closely linked to the recovery of gas exchange after drought in four *Caragana* species [J]. *Plant Cell Environ*, 44(2): 399-411.

ZHANG C, LI X, HE YF, C4-phosphoenolpyruvate-carboxylase-introduced rice line shows that sucrose metabolism is involved in the improved drought tolerance [J]. *Plant Physiol Biochem*, 115:328-342.

ZHENG YP, WANG HX, LOU X, et al., 2014. Changes of non-structural carbohydrates and its impact factors in trees: A review [J]. *Chin J Appl Ecol*, 25(4): 1188-1196.

ZHOU HH, FU LC, MA L, et al., 2019. Physiological characteristics of *Osmanthus fragrans* 'Boyejingui' with drought stress and rewatering [J]. *J Zhejiang A & F Univ*, 36(4): 687-696.