



Long-term drought modifies carbon allocation and abscisic acid levels in five forest tree species

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Background: This study analyzed the drought responses of five forest tree species grown in Korean peninsula, Korean fir *Abies koreana* (Ak), eastern white pine *Pinus strobus* (Ps), keyaki *Zelkova serrata* (Zs), tulip tree *Liriodendron tulipifera* (Lt), and Japanese elm *Ulmus japonica* (Uj). Physiological (chlorophyll, root collar diameter [RCD]) and biochemical responses (non-structural carbohydrates, proline, lipid peroxidase and abscisic acid [ABA]) of the plants grown under mild (MD) and severe drought (SD) were compared.

Results: In this study, three soil moisture regimes: control (100% precipitation), MD (60% reduction in precipitation) and SD (20% reduction in precipitation) were applied. Soil moisture content showed high water content in control site compared to MD and SD. A decline in RCD was found for Korean fir, keyaki, and tulip plants, with eastern white pine and Japanese elm showing no significant decline to the prolonged drought exposure (both MD and SD). Total chlorophyll showed a significant decline in Korean fir and tulip, with the sugar levels indicating a significant increase in Korean fir and keyaki species under SD compared to control plants. Non-significant decline in sugar level was noted for eastern white pine and Japanese elm. High accumulation of ABA, malonaldehyde and proline was noted in Korean fir, tulip, and keyaki under SD compared to control. Signs of tree mortality was only observed in Korean fir under MD (38%) and SD (43%).

Conclusions: The observed findings indicate the drought responses of five tree species. The majority of the morpho-physiological (especially mortality) and biochemical variables assessed in our study indicate superior long-term drought resistance of Ps and Uj compared to the highly sensitive Ak, and moderately sensitive Lt and Zs. The results provided will help species selection for afforestation programs and establishment of sustainable forests, especially of drought-tolerant species, under increased frequency and intensity of spring and summer droughts.

Keywords: malondialdehyde, proline, root collar diameter, sugar, tree mortality

Introduction

Under the rapidly changing global climate, drought is considered a major limitation to tree growth, species distribution and survival (Lyu et al. 2019). Droughts are predicted to increase in intensity and frequency, causing fundamental shifts in forest composition and species distribution and an increase in tree mortality (Choat et al. 2018; Jing et al. 2022; Kim et al. 2021). Understanding the tree species sensitivity to drought is therefore essential to successfully predict the ecosystem consequences of increasing drought. Water deficit primarily affects cell turgidity and stomatal aper-

ture of leaves resulting in a decrease of photosynthetic and transpiration rates and an increase in water use efficiency (Buckley 2019). In plants, water shortage leads to the excessive production of reactive oxygen species (ROS) such as $1O_2$, O_2^- and H_2O_2 , which are very reactive and lead to rapid injury to the living tissues and macromolecules (e.g. DNA, lipids, proteins and carbohydrates), eventually resulting in induced programmed cell death processes (Khaleghi et al. 2019). Photosynthesis is one of the key processes that regulate carbon fixation and metabolism. Drought stress lowers the rate of photosynthesis, and alters the distribution and metabolism of carbon in plant, leading to deplet-



ed of energy and decreased yield (Wang et al. 2018; Zhang et al. 2021a).

Sucrose is a major product of photosynthesis that is synthesized by sucrose phosphate synthase (SPS). Drought conditions usually increase SPS activity, which may increase the accumulation of sucrose (Granda and Camarero 2017). Sugars, (such as glucose, fructose and sucrose), sugar alcohols (such as mannitol) and amino acids (such as proline) accumulate under drought stress conditions in different plant species and function not only as osmolytes, but also as antioxidants, helping in ROS detoxification, membrane protection and enzyme/protein stabilization, ultimately improving plant resistance against abiotic stresses (Kaur et al. 2021). Drought induces a reduction in tree growth or even mortality through hydraulic failure when water lost by transpiration exceeds the water uptake from the soil, resulting in extensive xylem cavitation (Choat et al. 2012). The relative growth of stem diameter at breast height or root collar diameter (RCD) under drought compared to the growth under optimal conditions has been used to define species drought resistance (Kono et al. 2019; Li et al. 2020). The drought resistance of a tree species depends not only on extrinsic (e.g., habitat and competition), but also on intrinsic factors (e.g., genotype and phenotype) (Fang and Zhang 2019). Abscisic acid (ABA) is critical for plant development and can redesign various physiological and biochemical signal transduction cascades in plants to cope with environmental stresses particularly drought (Muhammad Aslam et al. 2022). Abscisic acid is a prime mediator of drought and plays an important role in regulating plant growth, development, and responses to several environmental stresses (Brodrribb and McAdam 2013). Plants show a significant increase in ABA levels under drought stress, changes in expression of genes, and induction of ABA biosynthesis enzymes corresponding to mRNA level lead to enhanced ABA accumulation (Seiler et al. 2014). Thus, understanding the role of ABA-mediated drought responses in trees is critical for ensuring ecosystem balance. Quantifying the changes in various morphological, physiological, and biochemical traits of a species in relation to its drought resistance will enable a fast and efficient selection of species in the future. Therefore, we investigated the drought resistance of five tree species popular in Korea, and determined the traits that explained species drought resistance. We hypothesized that drought resistance of a tree species is associated with its morphological, physiological and biochemical traits. The objectives of the present study were to (i) quantify the species-specific drought resistance index through RCD (ii) non-structural carbohydrate balance among different species (iii) stress hormone ABA involvement in countering drought stress.

Materials and Methods

Study site and experimental design

The study was conducted for three years (2020–2023) at an experimental site on Mt. Jiri (E127°27'09" N 35°16'50", elevation 1,289 m a.s.l.) in Gurye, South Jeolla province, Republic of Korea. The mean annual temperature in the area is 13.4°C, the maximum summer temperature is ~38°C, and the average annual precipitation is 1,345.7 mm based on 1997–2018 data (Korea Meteorological Administration) (Jin et al. 2009). A frame of galvanized metal with sufficient air circulation was constructed over study plots, and transparent Plexiglas roof with 91% light transmission was installed at 3 m height. Trenches were dug around the perimeters of the study plots to reduce lateral inflow of water. Three treatments were applied: control (100% natural precipitation), mild drought (MD, 60% precipitation), and severe drought (SD, 20% precipitation) (Fig. 1). The treatments MD and SD were applied by excluding natural precipitation by opening 60% and 20%, respectively, of the Plexiglas roof area. Each treatment plot (9.0 m × 9.0 m = 81 m²) was sub-divided into 6 × 6 small cells (each cell ~1.5 m × 1.5 m), and a total of 12 seedlings of each species were transplanted in three replicated cells (each cell having 4 seedlings) at 80 cm plant-to-plant distance. During the construction of the experimental site, about 60 cm of topsoil was spread on the top to increase soil homogeneity. The soil mainly consisted of a mixture of sandstone, sand, mudstone, and gravel, with a pH of 6.5. A total of 5 plantation species comprising two conifer species: *Pinus strobus* (eastern white pine), *Abies koreana* and three broad leaved species like *Zelkova serrata*, *Ulmus japonica*, and *Liriodendron tulipifera* were selected for this study. The seedlings were grown at a pri-

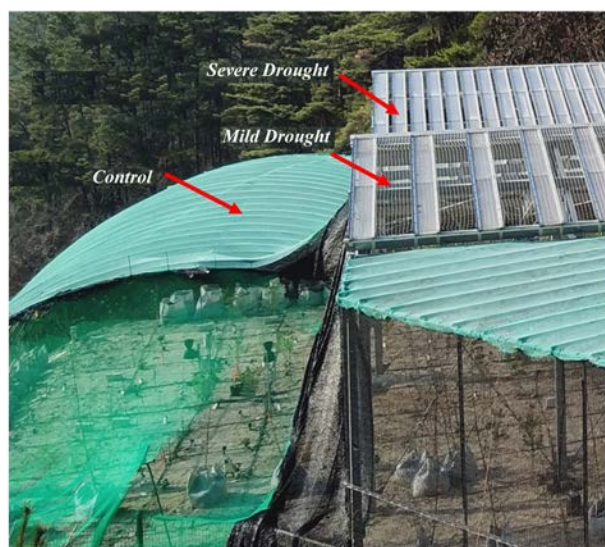


Fig. 1 Experimental site at Mt. Jiri, Gurye, Jeolla province, Republic of Korea. Different treatment plots: control (100% open), mild drought (60% open) and severe drought (only 20% open).

vate nursery, and one-year-old seedlings with similar RCD (mm) and similar height (cm) were transplanted to the experimental site. The RCD of individual tress was measured using digital calipers (MCD-6CSX; Mitutoyo Co., Ltd., Kawasaki, Japan).

Soil moisture content

Soil from all the plots was collected using a stainless-steel metal cup 3 × 3 cm (SZ metals, Seoul, Korea). Soil samples were collected at 5-cm-depth after removing the litter layer, weighed, and dried in an oven at 80°C for 72 hours before measuring the dry weight (DW). Moisture content of the soil sample was expressed in percentage according to the formula:

$$\text{Soil moisture content (SMC\%)} = (FW - DW) / DW \times 100$$

Where SMC is the soil moisture content calculated in percentage (%). FW is the fresh weight of the sample and DW is the dry weight of the sample measured.

Chlorophyll analysis

Chlorophyll content was measured based on a previously established method (Arnon 1949). Fresh leaf samples (0.5 g) were ground in liquid nitrogen and added to 10 mL of pre-chilled 80% acetone and mixed well. The mixture was centrifuged at 12,000 rpm for 10 minutes and the supernatant was collected. The supernatant was then diluted using 80% acetone and the absorbance was measured at 645 and 663 nm using acetone as blank in a ultraviolet (UV)-visible spectrophotometer (OPTIZEN 2120UV; Mecasys, Daejeon, Korea). Ten samples per treatment were used for chlorophyll analysis. Total chlorophyll content was calculated using the formula:

$$\text{Total chlorophyll} = 20.2_{(A_{645})} - 8.02_{(A_{663})} \times V / 100 \times W$$

Where V is final volume of the extract; W is FW of the sample.

Biochemical analysis

For the non-structural carbohydrates (NSC) analysis, hot air oven-dried leaves (70°C) were used. NSC analysis was performed using a previously described protocol with modifications (Li et al. 2018). In total, 0.1 g⁻¹ DW of powdered leaf samples were placed in 10 mL centrifuge tubes, and 5 mL of 80% ethanol was added. The mixture was incubated at 80°C in a water bath shaker for 30 minutes, and then centrifuged at 3,500 rpm for 10 minutes. The pellets were extracted two more times using 80% ethanol. Supernatants were retained, combined, and stored at 4°C to determine the total soluble sugar content. The ethanol-insoluble pellet was used for starch extraction. Ethanol was removed via evaporation. Starch in the residue was released

in 2 mL distilled water for 15 minutes in a boiling water bath. The solution was cooled to room temperature (22°C) and 2 mL of 9.2 M perchloric acid was added. Starch was hydrolyzed for 15 minutes and 4 mL distilled water was added to the solution following centrifugation at 4,000 rpm for 10 minutes. The pellets were extracted again using 2 mL of 4.6 M perchloric acid. Supernatants were retained, combined, and made up to 25 mL to determine starch content. The soluble sugar and starch concentrations were measured spectrophotometrically (OPTIZEN 2120UV) at 620 nm using the anthrone method, and the starch content was calculated by multiplying the glucose concentrations by a conversion factor of 0.9. Glucose was used as the standard. Ten replicates per treatment were used for NSC analysis.

Proline adjustment

Proline concentration in leaves was determined using a previously described protocol (Forlani and Funck 2020). A mixture of 0.3 g fresh leaf samples (freeze stored) and 5 mL sulfosalicylic acid was homogenized and then centrifuged at 3,000 rpm for 20 minutes. The supernatant was mixed with 2 mL glacial acetic acid and 2 mL acid ninhydrin, and the resulting mixture was boiled at 100°C for 25 minutes in a water bath. After cooling, 4 mL of toluene was added and allowed to settle. The absorbance of the extracts at 520 nm was evaluated using a UV visible spectrophotometer. Ten samples per each treatment were used for proline estimation.

Lipid peroxidation activity

Lipid peroxidation was evaluated by estimating malondialdehyde (MDA) content. MDA was measured based on a method established (Zhang et al. 2021b). A mixture of 0.5 g fresh plant material and 5 mL of 5% trichloroacetic acid was centrifuged at 12,000 rpm for 25 minutes. The supernatant was mixed with 2 mL of 0.67% thiobarbituric acid solution and heated for 30 minutes at 100°C in a water bath. Sample absorbance at 450, 532, and 600 nm was measured using a blank containing all reagents. Ten replicates per each treatment were used for lipid peroxidation analysis. MDA content in the sample was calculated using the formula:

$$C \text{ (mmol g}^{-1}\text{)} = 6.45 \times (A_{532} - A_{600}) - 0.56 \times (A_{450})$$

Where C is the concentration of the MDA content. 'A' is denoted as the wavelength set for the optical density measurements.

ABA content

Freeze stored leaf samples were prepared based on a previously established protocol (Liu et al. 2012). Briefly, five replicates of each frozen leaf sample (approximately 100 mg for each replicate) were ground to a fine powder in liq-

uid nitrogen using a mortar and pestle. Each sample was weighed into a 1.5 mL tube, mixed with 750 mL cold extraction buffer (methanol: water: acetic acid, 80:19:1, v/v/v) supplemented with internal standard (10 ng $^2\text{H}^6$ ABA), vigorously shaken on a shaking bed for 16 hours at 4°C in dark, and then centrifuged at 13,000 rpm for 15 minutes at 4°C. The supernatant was carefully transferred to a new 1.5 mL tube and the pellet was remixed with 400 mL extraction buffer, shaken for 4 hours at 4°C, and centrifuged. The two supernatants were then combined and filtered using a syringe-facilitated 13 mm diameter nylon filter with a pore size of 0.22 mm (Hyundai Micro, Seoul, Korea). The filtrate was dried via evaporation under the flow of nitrogen gas for approximately 4 hours at room temperature and then dissolved in 200 mL methanol. The dissolved mixture was used for LC/MS analysis. LC/MS, SPME, and GC/MS analysis were performed at the National Instrumentation Center for Environmental Management (NICEM), Seoul National University, and Republic of Korea.

Statistical analysis

All experiments were conducted twice and the results are reported as mean \pm standard error. Data were analyzed via two-factor analysis of variance (ANOVA) using the R program (v.3.5.1). The treatment mean values were compared via Tukey's (least significance difference) test; statistical significance was set at $p \leq 0.05$. Pearson correlation coefficient was carried out among the treatments and a heat map was generated with corrplot package using the R program (v.3.5.1).

Results and Discussion

In this study, we investigated drought responses (control; MD; SD) in seedlings of five tree species to their drought resistance and survival (Fig. 1). The impact of drought stress on growth and physiology is difficult to compare among different tree species because of the complexity in variations (Lee et al. 2022a). Soil moisture content in drought-treated pots were significantly decreased compared (MD, $8.9\% \pm 0.4\%$ and SD, $4.3\% \pm 0.6\%$) to that in control pots ($13.7\% \pm 0.8\%$) (Fig. 2). Decline in SMC confirmed the occurrence of water deficit at the experiment site. Soil moisture mainly controls the rate of photosynthesis by regulating stomatal conductance (Galmés et al. 2007). The decrease of stomatal conductance caused by soil moisture stress in drought years inhibits photosynthesis and consequently light use efficiency (Tong et al. 2019). In support to this, the chlorophyll content was found to be significantly decreased in the leaves of drought treated tree species like Korean fir (MD and SD) and tulip (SD) compared to control plants (Fig. 3A). A decrease of total chlorophyll with drought stress implies a lowered capacity for

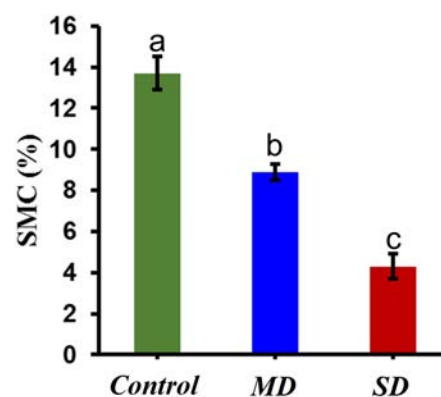


Fig. 2 Soil moisture content (SMC) measured from soil obtained treatment plots. Different alphabets represent significance in our study. Means with different alphabets denotes statistical significance at $p < 0.05$. MD: mild drought; SD: severe drought.

light harvesting. Since the production of ROS is mainly driven by excess energy absorption in the photosynthetic apparatus, this might be avoided by degrading the absorbing pigments (Herbinger et al. 2002). On the other hand, a non-significant decline was observed for keyaki plants under SD, whereas an increase in chlorophyll levels were noted for eastern white pine and Japanese elm species under both MD and SD, respectively. This increase was high in eastern white pine under SD treatment (Fig. 3A). This increase denoted the chlorophyll stability during drought in these two species, which might be a promising criterion for drought resistant trait selection (Kim et al. 2022). Drought stress (SD) significantly decreased RCD in Korean fir and tulip under both MD and SD conditions (Fig. 3B). This decrease was high in tulip compared to other tree species and control (Fig. 3B). No any significant changes in RCD was found for eastern white pine and Japanese elm, tree species, whereas a significant decline was observed in keyaki only under SD treatment (Fig. 3B). Our results corroborate the findings of Kono et al. (2019), who reported that stem diameter was a more sensitive indicator of drought resistance than other parameters (Kono et al. 2019).

Plants incur lipid peroxidation in response to various abiotic stress, which leads to the destruction and protein lysis of the cell membrane system, thereby impairing plant photosynthesis and respiration, causing the death of plant cells in severe cases (Janků et al. 2019). Malondialdehyde is one of the final products of polyunsaturated fatty acid peroxidation in the cells; for this reason, it is a widely used and reliable marker for determining the degree of injury to a stressed plant (Morales and Munné-Bosch 2019). The more the plant is damaged, the higher it's MDA content. That is to say, plants will generate ROS under abiotic or biotic stress conditions, thereby impairing the production of biomolecules, such as lipids, proteins, and nucleic acids, which increases the MDA content. In consistent with this, a significant increase in MDA content was observed in leaves of all the drought-treated plants (Fig. 3C). The increase was

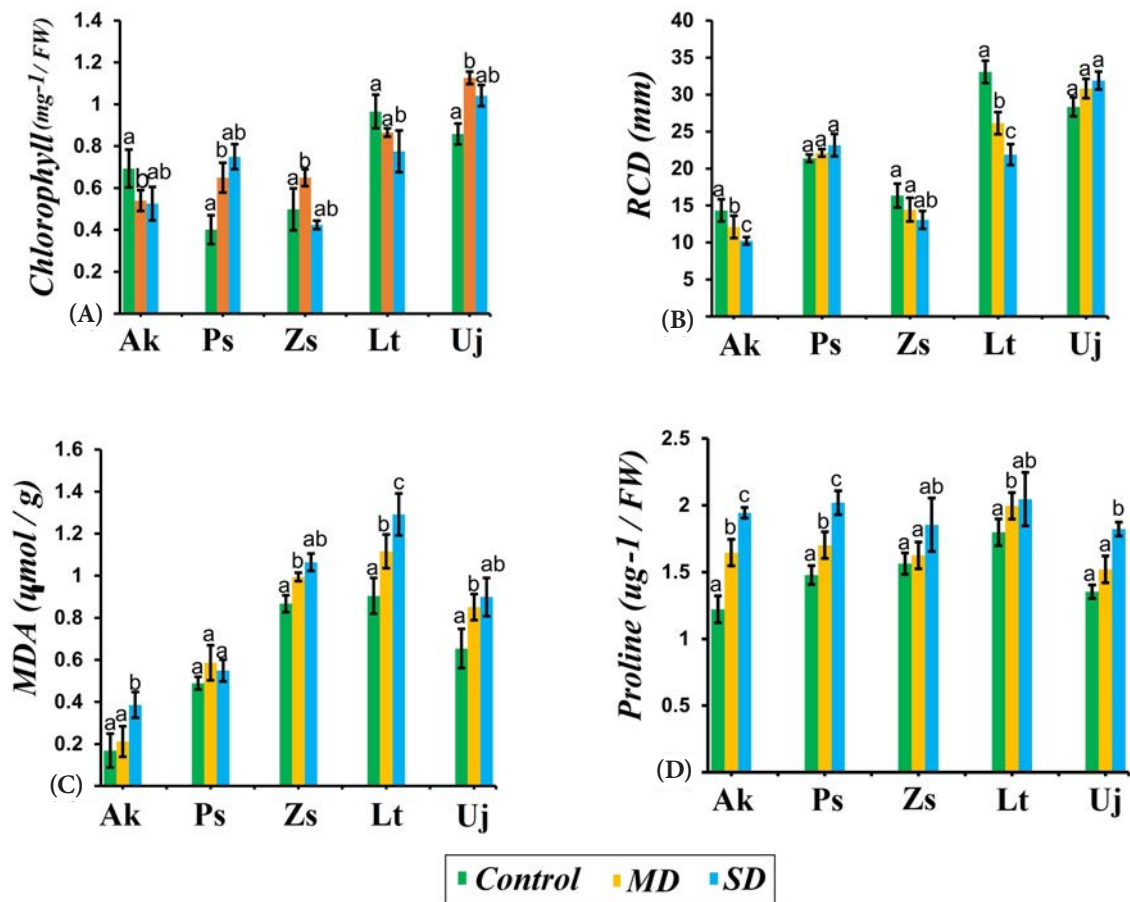


Fig. 3 Morphological and physiological responses of five Korean tree species (A) total chlorophyll content measured from the leaves of control and treatment plants (B) stem diameter studied through the RCD is shown (C) lipid peroxidase activity in leaves expose to 100%; 60% and 20% precipitation (D) variations in the free proline levels are displayed. Different alphabets represent significance in our study. Means with different alphabets denotes statistical significance at $p < 0.05$. FW: fresh weight; RCD: root collar diameter; MDA: malondialdehyde; Ak: *Abies koreana* (Korean fir); Ps: *Pinus strobus* (eastern white pine); Zs: *Zelkova serrata* (keyaki); Lt: *Liriodendron tulipifera* (tulip); Uj: *Ulmus japonica* (Japanese elm); MD: mild drought; SD: severe drought.

significant under SD treatment in Korean fir, keyaki, tulip and Japanese elm tree species, whereas a non-significant increase was observed only in eastern white pine (Fig. 3C). High increase in MDA in our results indicate an over-accumulation of ROS because of drought treatment. Excessive production of ROS has been linked to oxidative stress, which in turn has been linked to drought-induced lipid peroxidation of cell membranes.

Free proline functions as an important osmoprotectant during abiotic stress (Raza et al. 2023). A significant increase in free proline level was observed in leaves of drought-treated plants of all species compared to that in leaves of control plants under SD conditions (Fig. 3D). The increase in proline was high in Korean fir, eastern white pine, and Japanese elm under SD treatments (Fig. 3D). A significant increase under MD condition was observed in Korean fir, eastern white pine and tulip (Fig. 3). Stress-dependent accumulation of free proline plays various roles in stressed plants, such as balancing osmotic pressure, maintaining protein and cell membrane stability and scavenging ROS (Hayat et al. 2012; Meena et al. 2019). The higher proline

metabolism as seen in eastern white pine and Japanese elm species may contribute to the drought tolerant phenotype, whereas the high accumulation of free proline in Korean fir and tulip species may contribute to the protection of cell membrane from destabilization under extreme drought. Environmental stress induces proline biosynthesis in plants via signal mechanisms that involve phytohormones like ABA and several other molecules like calcium, phospholipase 6C (Fichman et al. 2015; Zarattini and Forlani 2017).

The conventional knowledge of plant response to drought stress proposes that stomatal closure occurs to prevent hydraulic failure, causing the photosynthetic uptake of carbon to diminish and in turn a reduction in carbohydrate production (Lee et al. 2022b; McDowell et al. 2008). However, unexpected accumulation of soluble carbohydrates in response to drought has been attributed to an imbalance resulting in growth being more sensitive than CO_2 to water deficits. NSCs represent major substrates in plant metabolism and have been implicated in mediating drought-induced tree mortality (Signori-Müller et al. 2021). A significant increase in soluble sugar content was observed in

drought-treated leaves Korean fir and keyaki plants with a non-significant increase observed for tulip and Japanese elm under SD condition (Fig. 4A). A possible explanation for such an increase is based on the fact that under moderate or SD, plant growth declines before photosynthesis, resulting in an excess of carbon skeletons in the form of starch, which can be directed for the breakdown in to osmolytes (Hummel et al. 2010; Vitale et al. 2011). Furthermore, soluble sugars had a greater contribution than proline in cellular osmotic adjustments in drought-stressed *Arabidopsis* (Gurrieri et al. 2020).

Drought stress not only elicits sugar accumulation but also facilitates the breakdown of storage sugars (like starch) into soluble sugars (like sucrose, glucose, fructose, etc.) leading to a decrease in the water potential of the cell, a smart strategy for taking up limited moisture present in the soil (Camisón et al. 2020). In relation to this, a significant decrease in starch content was observed in leaves of Korean fir and keyaki plants (SD) compared to the control plants (Fig. 4B). On the other hand, a non-significant increase was observed in starch content for all eastern white pine and Japanese elm species. Starch is usually a long-term carbon reserve in plants. The decrease in starch reserves in Korean fir and keyaki species denotes the steady supply of carbon and energy, when these plant lack normal photosynthesis (chlorophyll dysfunction in our study). In the same way, the steady accumulation of starch in eastern white pine and Japanese elm denotes an unshuffled supply of carbon and energy (chlorophyll increase in our study) under SD conditions. Adjustments of starch degradation occur under changing photoperiods or in response to an abiotic stress to ensure optimal carbon supply for continued growth (Stitt and Zeeman 2012).

Drought commonly triggers an increase in ABA, which regulates plants abiotic stress tolerance by controlling the hydraulic conductivity via stomatal closure (Carvalho et al. 2021). Abscisic acid concentrations in drought-treated Korean fir, keyaki and tulip plants showed a significant in-

crease under SD conditions compared to that in control plant (Fig. 5). A non-significant increase in ABA content was noted in eastern white pine under SD conditions than the control (Fig. 5). This increase in absolute ABA concentration in all the species was not related to drought resistance in our study; instead, the species with a larger increase was more sensitive to drought, which is in agreement with a previous study (Bhusal et al. 2021). Correlation analysis indicated a positive correlation existing in eastern white pine and Japanese elm between the RCD and ABA levels (Fig. 6). These positive correlated variables provided a valuable information on a possible genetic network associated with ABA signaling in countering drought tolerance. Further investigations are required to identify the major element of the network that can significantly regulate all the other components making these two species drought resistant in natural forest. Tree mortality assessment identified Korean fir as the only tree species showing mortality signs under drought treatment (MD, 38%; SD, 43%) (data

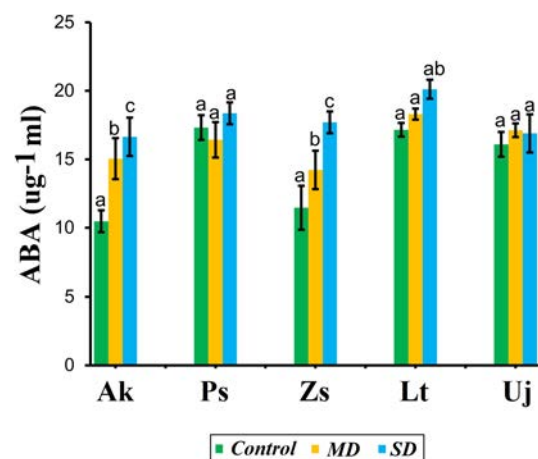


Fig. 5 Abscisic acid (ABA) contents in the five Korean tree species under different drought treatments ($p < 0.05$). Different alphabets represent significance in our study. MD: mild drought; SD: severe drought; Ak: *Abies koreana*; Ps: *Pinus strobus*; Zs: *Zelkova serrata*; Lt: *Liriodendron tulipifera*; Uj: *Ulmus japonica*.

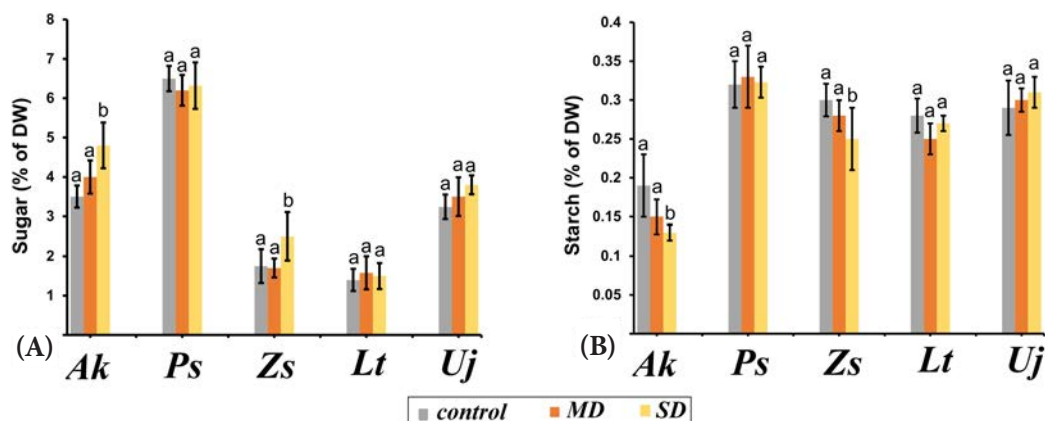


Fig. 4 Non-structural carbohydrate contents ([A] sugar and [B] starch) are shown as percentages based on the leaf DW. Different alphabets represent significance in our study. DW: dry weight; MD: mild drought; SD: severe drought; Ak: *Abies koreana*; Ps: *Pinus strobus*; Zs: *Zelkova serrata*; Lt: *Liriodendron tulipifera*; Uj: *Ulmus japonica*.

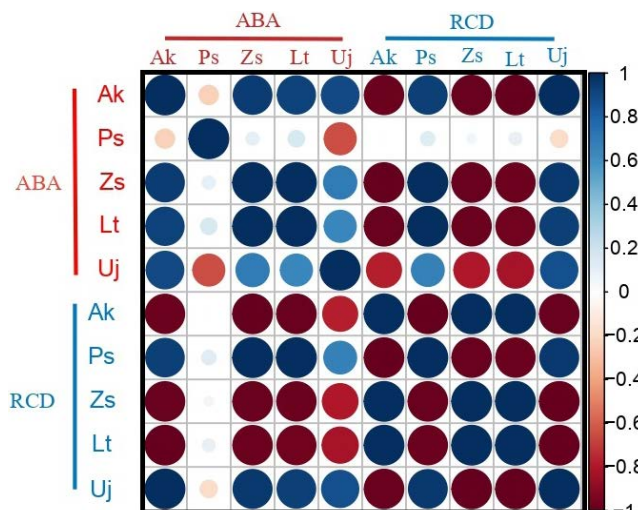


Fig. 6 Heat map showing the correlation coefficient between ABA × RCD under drought treatments among the five Korean tree species. ABA: abscisic acid; RCD: root collar diameter; Ak: *Abies koreana*; Ps: *Pinus strobus*; Zs: *Zelkova serrata*; Lt: *Liriodendron tulipifera*; Uj: *Ulmus japonica*.

not shown). Occurrence of plant mortality only in Korean fir indicates the extremity of drought in this forest tree species. Together, our results resemble the characteristic behavior of these forest tree species in natural habitats. For instance, tree mortality of *A. koreana* seedlings under drought in our study can be seen as an extension of their sensitive survival ability under natural conditions (endangered), similarly a moderate drought resistance under MD of *Z. serrata* seedlings can be foreseen to their susceptible nature under natural habitat.

Conclusions

Regional climate projections predict more frequent and severe water shortages, implying that rooting depth will become an ever more decisive trait for promoting seedling establishment and safeguarding reforestation and afforestation efforts. Selecting drought resistant tree species is critical to plantation establishment success and this first comparison of five locally important tree species in Korean peninsula therefore makes an important contribution to forestry decision making in this region. The majority of the morpho-physiological (especially mortality) and biochemical variables assessed in our study indicate superior long-term drought resistance of eastern white pine and Japanese elm compared to the highly sensitive Korean fir, and moderately sensitive tulip and keyaki. There is certainly large genotypic variation in drought-related traits of all the five species, but the mechanism by which two species namely eastern white pine and Japanese elm become resistant and Korean fir's high sensitivity to SD is of interest and thus motivates follow-up research on plant health

status and stand development for an extended period of time after outplanting.

Abbreviations

ROS: Reactive oxygen species
 PCD: Programmed cell death
 SPS: Sucrose phosphate synthase
 RCD: Root collar diameter
 ABA: Abscisic acid
 MD: Mild drought
 SD: Severe drought
 FW: Fresh weight
 DW: Dry weight
 NSC: Non-structural carbohydrates
 UV: Ultraviolet
 MDA: Malondialdehyde
 NICEM: National Instrumentation Center for Environmental Management
 SMC: Soil moisture content

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Authors' contributions

UC and HSK designed the experiment. UC performed the field, laboratory experiments, and wrote the manuscript. SB and KK assisted with laboratory experiments. WH, ARH, and YSL assisted with field experiments. ARH and HSK received research funding.

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Availability of data and materials

Not applicable.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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