Retention of absorbed fog by Pinus thunbergii saplings under different soil drought conditions

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Research Article

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Abstract

Aim Efficient fog water utilization under soil drought conditions is important for improving the water status and growth of forest trees. However, the importance of fog water retention in tree species during drought is yet to be completely examined. The aim of this study was to examine changes in fog water retention in different organs of Japanese black pine (*Pinus thunbergii*) saplings in different drought conditions.

Methods P. thunbergii saplings were grown under different watering conditions in a glasshouse for 19 days and exposed to ^{2}H-enriched water vapor under a high relative humidity (~ 95%) for 1 h in a growth chamber with lighting. The exposed trees were harvested 48 h after the fog exposure experiment and the ^{2}H concentration of water in current needles, old needles, current branches, old branches, roots, and soil was determined.

Results Absorbed fog water was observed in the needles, branches, and roots 48 h after exposure to fog. The amount of water in the current needles, old needles, and current branches contributed by fog water was significantly higher in drought-stressed trees than in well-irrigated trees. Small amount of absorbed fog water was redistributed to the soil in well-irrigated and drought-stressed trees.

Conclusion The findings of the study indicated that more absorbed fog water is retained in drought-stressed trees than that in well-watered trees, which may improve plant water status under drought. Our results also suggest that hydraulic redistribution from the roots to the soil may occur irrespective of soil drought conditions.

Introduction

Fog is an important water source for trees in forests in fog-affected areas (Dawson and Goldsmith 2018). Fog water captured by forest crown plays an important role in the hydrological and biogeochemical cycles in forests (Prieto et al. 2012). During fog, some part of the captured fog water is evaporated, while the remaining part is directly absorbed by the plant leaves. Fog water absorption from leaf surfaces has been widely reported for various plant and tree species in several ecosystems (Dawson 1998; Burgess and Dawson 2004; Goldsmith et al. 2013; Hayes et al. 2020). Absorbed water from leaf surface contributes to improving plant water status (Boucher et al. 1995; Breshears et al. 2008; Limm et al. 2009; Limm and Dawson 2010; Dawson and Goldsmith 2018), photosynthesis, and growth (Boucher et al. 1995; Simonin et al. 2009; Eller et al. 2013; Dawson and Goldsmith 2018). However, the degree of the contribution of fog water absorption to physiological and growth responses varies among species and environmental conditions (Goldsmith et al. 2013).

The process of foliar water uptake is important for trees in arid environments, such as arid temperate coastal forests (Dawson 1998). However, foliar water uptake is also important in humid environments with higher precipitation amount, such as tropical montane clouded forests, during dry periods (Goldsmith et al. 2013; Binks et al. 2019). In temperate coastal forests, sandy soil allows rapid filtration of water into a deeper soil layer. The effects of dry soils can be more problematic for the growth and development of juvenile trees because of their relatively shallow root system. In northeastern Japan, fog occasionally occurs in summer, owing to a cool, moist air current. While the cool air current in summer usually decreases due to the decrease in solar radiation and air temperature, fog can be an important water source for juvenile trees in the forest during this season. This may be particularly crucial in the near future under the climate change scenario, when the number of days without precipitation is predicted to increase with the increase in air temperature (Kimoto et al. 2005; Oguchi and Fujibe 2012). Recently, there has been an increased attention on climate change-associated environmental stresses affecting coastal trees (Carmichael et al. 2020).

Direct foliar uptake of fog water is considered a common phenomenon in plants during fog events (Goldsmith et al. 2013; Berry et al. 2019). Foliar water uptake occurs when leaves are wet or dew is forming (Brinks et al. 2020), and it has been reported to occur in trees irrespective of well-watered or drought-stressed conditions (Burgess and Dawson 2004; Eller et al. 2016; Guzmán-Delgado et al. 2018; Lehmann et al. 2018); however, the effects of drought on foliar water absorption appear to be inconsistent in these studies. The absorbed fog water rehydrates leaf tissues and improves plant water status of drought-stressed trees (Burgess and Dawson 2004; Carmichael et al. 2020), and a part of the absorbed water is immediately incorporated into assimilates (Lehmann et al. 2018). Thus, the importance of fog water for leaf and plant water status and carbon balance of trees during drought has been widely recognized (Burgess and Dawson 2004; Breshears et al. 2008), despite a slower process of leaf rehydration via foliar absorption than that via soil water uptake (Guzmán-Delgado et al. 2018).

While most researchers have focused on foliar water uptake during drought, a few have studied the retention of the absorbed fog water in plant body after fog events. During drought, the soil water potential decreases, resulting in stomatal closure to prevent water loss through transpiration (Bond and Kavanagh 1999). After the fog events, decreased water loss under drought may help increase the retention of absorbed fog water in trees. In addition, it has been reported that the absorbed fog water can be transported to rhizosphere soil with lower water potential through the xylem of trees under drought conditions (Cassana et al. 2016). Therefore, the absorbed fog water retained in trees under different soil water potential may redistribute differently to the rhizosphere soil, providing moisturization (Dawson and Goldsmith 2018). Hence, fog water retention in drought-stressed trees could be important for understanding drought tolerant mechanism to alleviate water deficit in fog-affected areas.

Uptake and retention of tritiated water vapor in leaves have been reported in herbaceous and woody plant species, such as potato (*Solanum tuberosa*), grape (*Vitus vinifera*), and rice (*Oryza sativa*) (Belot et al. 1979; Guenot and Belot 1984; Choi et al. 2001). Guenot and Belot (1984) have shown that the half-life of a slow component of ^{3}H concentration in leaf water of grape plants was approximately 30 h, whereas a fast component had the half-life of 30 min. Thus, under well-watered conditions, the majority of absorbed water in plant leaves would be exchanged due to the flushing by transpiration stream few days after the fog events. Because soil drought causes stomatal closure and reduces root water uptake, drought-stressed plants may retain more amount of absorbed fog water in the body than well-watered plants when well-watered plants exchange the most amount of absorbed fog water. Although the amount of retained foliar absorbed water is presumably less a few days after fog events (Guenot and Belot 1984; Choi et al. 2001), the small amount of water can be valuable to alleviate water status of trees under water deficit conditions. However, increased retention of foliar absorbed water in plant body due to soil drought in fog-affected areas is not well-understood.

In the present study, the saplings of Japanese black pine (*Pinus thunbergii* Parl.), widely distributed in the coastal areas of the northeastern Japan, grown under different watering conditions were exposed to deuterium-enriched fog water; deuterium concentration in the water in trees was determined after 2 days (48 h) of fog exposure to evaluate the retention of absorbed fog water in plant body and the redistribution of the absorbed fog water to soil when the soil is dry. Based on previous studies, we selected the harvest time as it is predicted to be enough for exchanging water in well-watered trees due to transpiration (Guenot and Belot 1984). We hypothesized that more amount of absorbed fog water would be retained in drought-stressed *P. thunbergii* saplings than that in well-watered saplings at 48 h after fog exposure because soil drought reduces transpiration (Umebayashi et al. 2016). The objective of this study was to address following questions: (1) Is absorbed fog water retained in plant organs of well-watered and drought-stressed saplings at 48 h after fog exposure? (2) If so, does the retention of fog water in different organs change with soil drought conditions? (3) Is more absorbed fog water redistributed to rhizosphere soil with low water potential?

Materials And Methods

Study site and plant materials

This study was conducted at the Institute for Environmental Sciences (IES), Aomori, Japan (40° 57 N, 141° 21 E, 27 m elevation). Two- to three-year-old *P. thunbergii* saplings were grown in the field and transported to a glasshouse in the IES prior to the preliminary experiment in 2017 and soil drought treatment in 2018. The mean air temperature in the glasshouse during the preliminary experiment in 2017 and the soil drought treatment in 2018 were 23.7°C and 24.8°C, respectively.

Preliminary experiment

A preliminary experiment was conducted from early September to early October 2017 to determine the appropriate drought treatment. The trees were transplanted to 1/5000a Wagner pots (17.5 cm diameter, 20 cm tall) filled with black soil. Twenty-five trees were randomly placed in a glasshouse. Aboveground parts were harvested from five trees at 0, 3, 6, 12, and 30 days after irrigation was stopped and divided into needles and branches (including stem). Fresh plant organs were weighed and oven-dried at 60°C for more than 72 h, and the dry mass was measured. The water content in needles (NWC) and branches (BWC) was calculated on a fresh weight basis. Root samples from the pots were washed with tap water to remove soil; the dry mass was determined as described above, and the needle mass ratio (NMR, needle biomass per unit of total biomass) was calculated.

During the harvest period, soil samples were collected at two depths (0–10 cm and 10–20 cm) for further analysis. Fresh soil samples were weighed and oven-dried at 80°C for more than 48 h, and the dry mass was measured. Soil water content (SWC) was calculated on a dry weight basis. Thereafter, SWC was converted to volumetric water content (VWC) based on the bulk density of the soil measured using 100 cm^3 cylinder samples (0.75 g cm^{-3}, analyzed in Palynosurvey Co., Ltd., Japan). Soil pF was determined using a soil moisture retention model (Fink and Jackson 1973) based on the relationship between VWC and pF measured using 100 cm^3 cylinder samples (analyzed in Palynosurvey Co., Ltd.) (Fig. S1a in Online Resource 1).

Soil drought treatment

Soil drought treatment was conducted from early to late September 2018. The trees were transplanted in plastic pots (3.5 L, 18 cm diameter, 20.5 cm tall) filled with black soil, and 6-40-6 NPK fertilizer was added to the soil surface at 10 g N m^{-2}. The trees were randomly placed in the glasshouse in early August and well irrigated at intervals of a few days until the treatment began. The mean (± S.D., n = 9) diameter of the trees at 5 cm above soil surface was 5.8 ± 1.1 mm, and mean height of the trees was 25.6 ± 6.9 cm. The trees were divided into three treatments with different soil drought conditions: control treatment (well irrigated at 2–3 days interval for 19 days), low drought (LD) treatment (well irrigated at 2–3 days interval for 9 days, followed by 10 days unirrigated period), and severe drought (SD) treatment (unirrigated for 19 days). The drought duration for each group was based on the results of the preliminary experiment (see the section above).

Moisture sensors (ECH_2O 5TM, Meter-Group, Inc., Pullman, WA, USA) were installed vertically at the soil surface (0–5 cm depth) in the pots, approximately one month before the treatment began, to monitor the VWC of the soil. The measurement was performed at 1-min intervals during soil drought treatment. The measured values of dielectric permittivity were converted to those of VWC (VWC_{meas}) according to the formula for black soil reported by Mitsuishi and Mizoguchi (2014). Because the sensors were installed at the soil surface, a multiple regression model was applied to relate the true VWC to the VWC_{meas} and soil temperature (T_{soil}, °C) (Cobos and Campbell 2007). The temperature-corrected value of VWC (VWC_{TC}) was calculated using the following formula:

$$\mathrm{VWC_{TC}} = a \times \mathrm{VWC_{meas}} + b \times \mathrm{T_{soil}} + c$$

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where a, b, and c are the coefficients obtained for each sensor by multiple regression analysis. Then, the VWC was calculated based on the relationships between the VWC, which was measured using 100 cm^3 cylinder samples (at the 0–5 cm depth), and the VWC_{TC} (Fig. S2 in Online Resource 1). To obtain the corrected values, a pair of four or five sensors was installed in the soil in each pot under four different soil moisture conditions. Soil core samples were collected, and the VWC_{meas} and T_{soil} were recorded immediately before sampling.

To determine the moisture content of the soil and extract water from the soil in the pots at the end of the experiment, soil bags were placed in holes made by a soil sampler before irrigation on the day the treatment was started. The soil bags were cylindrical mesh bags made of fine nylon mesh (mesh size: 48 μm, 4-cm diameter, 20-cm length) and filled with sieved (2 mm sieve) air-dried black soil.

To determine variations in stem diameter, a dendrometer (DD-S, Ecomatik GmbH, Dachau/Munich, Germany) was set on the stem of each tree, except for one tree in the SD treatment, where the dendrometer was set on a branch. Variation in diameter was determined at 1-min intervals during treatment. As one of the three dendrometers in the LD treatment slipped off the stem, precise measurements could not be conducted, and thus, the data obtained during the treatment was not used in this study.

Deuterium-enriched fog exposure experiment

The fog exposure experiment was conducted using a growth chamber (1.0 × 1.0 × 1.1 m). Three trees for each soil drought treatment were exposed to deuterium-enriched fog for 1 h at a high relative humidity (RH) (> 90%) on the same day at the end of the soil drought treatment. Prior to the fog exposure experiment, the pots were covered with a zipped plastic bag and sealed with putty to prevent the direct deposition of fog water on the soil surface during the fog exposure experiment. The chamber was illuminated using three halogen lamps. Photon flux density at the top of the trees during the generation of fog in the chamber ranged from approximately 200 to 400 μmol photon m^{-2} s^{-1}. The environmental conditions within the chamber were monitored at 5-min intervals using a CO_2-temperature-humidity sensor (RTR-576-S, T&D Corporation, Nagano, Japan). During the deuterium-enriched fog exposure, CO_2 gas was added through a mass flow controller (ACE Inc., Kanagawa, Japan) at a flow rate of 3 mL min^{-1} to maintain a CO_2 concentration approximately equal to the atmospheric CO_2 concentration. The average CO_2 concentration in the chamber measured at 5 min intervals during the exposure was 417 ± 9 μL L^{-1} (mean ± S.D.; $n = 12$).

Nine trees were randomly placed in the growth chamber and exposed simultaneously to vapor of pure water or deuterium-enriched water generated by each of the two ultrasonic humidifiers (NZ-D55, Yamazen Corporation, Osaka, Japan) at a rate of 400 mL h^{-1}. After the air temperature in the chamber was stabilized, the trees were exposed to pure-water fog using humidifiers for 30 min until the RH was more than 90% to directly investigate water use during fog events. Thereafter, the trees were exposed to deuterium-enriched fog (15% deuterium oxide) by switching humidifiers at a high RH for 1 h. A circulator was used to mix the air inside the chamber. A humidity controller (HCD121, Nippo Co. Ltd., Saitama, Japan) was used to maintain the RH at more than 90% during fog exposure. Immediately after the deuterium-enriched fog exposure, the air in the chamber was ventilated using a fan, and the trees were removed from the chamber. Plastic bags and sensors were removed from the trees and pots. To collect water samples in the chamber air during the fog exposure, the air was pumped at a constant rate using a minipump (MP-Σ series, Shibata Scientific Technology Ltd., Saitama, Japan) and passed through a cold trap. Soil moisture sensors were left in the pots and dendrometers were reattached to the trees before transferring the trees to the chamber, and thus, soil VWC and diameter variation were monitored during the fog exposure experiment. The dendrometers were reset on the stem or branch prior to the fog exposure experiment, but one sensor in the LD treatment did not work properly due to the attachment of turpentine; therefore, the measurement values were not used in this study.

The trees were moved back to the glasshouse and irrigation was not applied for 48 h. The mean air temperature and RH in the glasshouse were approximately 20.0°C and 62%, respectively. We performed sampling at 48 h after exposure to focus on the retention of absorbed fog water in plant body. The incorporation of absorbed fog water into assimilates occurs immediately (Lehmann et al. 2018) and the duration of 48 h can be considered sufficient for evaporation of attached water on plant surface. Aboveground parts of the trees were harvested 48 h after the fog experiment and divided into current needles, old needles, current branches, and old branches (including stem). The bark was not removed from the branch samples. The plant organs were collected in a plastic bag and stored in a freezer at less than − 20°C until water extraction. The soil in the soil bags was collected in a plastic bag and kept in a refrigerator at approximately 2°C until water extraction. The roots were carefully removed from the pots by hand, collected in plastic bags with some soil on the roots, and then kept in a refrigerator at approximately 2°C until water extraction.

Water extraction and chemical analysis

All water in the plant and soil samples was recovered by drying the samples using a cryogenic vacuum extraction system. The weights of water and dried samples were determined from the differences in the weights of the bottles before and after extraction. The hydrogen isotope ratio (δ^2H) in the water extracted from the samples and atmospheric water during exposure was analyzed using a stable isotope ratio mass spectrometer (IsoPrime 100, IsoPrime Ltd., Cheadle Hulme, UK). Because soil particles were attached on the surface of the root samples, δ^2H was corrected using the data of the weight of soil attached on the root samples, SWC, and δ^2H of the soil in each treatment.

For water samples with higher isotope ratios, the ^2H isotope ratio was analyzed using a gas chromatograph (Agilent GC 6890, Agilent Technologies, Inc., Santa Clara, CA, USA). The ^2H fraction [$x(^2H)$, in %] of the soil water was calculated from the isotope ratios using the following equation:

$$x(^2\mathrm{H}) = \frac{\left(\frac{\delta^2\mathrm{H}}{1000}+1\right)\times R_{\mathrm{VSMOW}}}{\left(\frac{\delta^2\mathrm{H}}{1000}+1\right)\times R_{\mathrm{VSMOW}}+1} \times 100 \quad (2)$$

where R_{VSMOW} is the isotope ratio of the international reference material (Vienna standard mean ocean water, VSMOW).

To compare the amount of water redistributed to the soil among the different treatments, excess atomic fraction of ^{2}H [$x^{E}(^{2}H)$, in %] in the soil water was calculated as the difference between $x(^{2}H)$ in the soil water extracted from the soil in each treatment 48 h after the fog exposure experiment and $x(^{2}H)$ in the soil water extracted from the soil in the pots that were not exposed to fog. Notably, the soil in the pots without exposure was well-watered, and thus, the effects of isotope fractionation due to drought were not excluded from the calculation. The amount of excess ^{2}H in the soil water was calculated as follows:

Amount of excess $^{2}H = x^{E}(^{2}H) / 100 \times M \times 2$ (3)

where M is the amount of water in the soil (moles of H per 100 g of dry soil) at 48 h after the fog exposure experiment in each treatment.

A simple isotope mixing model (Dawson et al. 2002) was used to determine the fraction of plant water contributed by fog water (f_F) using the following equation:

$$f_{\mathrm{F}} = \frac{(\delta_{\mathrm{P}} - \delta_{\mathrm{S}})}{(\delta_{\mathrm{F}} - \delta_{\mathrm{S}})}$$

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where δ_F, δ_S, and δ_P are the isotope values in fog water, soil water, and plant water, respectively. For the determination, the $\delta^{2}H$ values of the atmospheric water in the chamber during the deuterium-enriched fog exposure and soil water in the pots, in which saplings were grown during the treatment without the fog exposure, were used.

Statistical analysis

One-way analysis of variance (ANOVA) followed by Tukey HSD multiple comparison test was used to determine the effect of drought treatment on the NWC, BWC, and NMR of the trees; the retention rate of the fog water in each plant organ; and soil VWC 48 h after the fog exposure experiment. We also used ANOVA to test the differences in soil matric potential as well as the excess atomic fraction of ^{2}H in the soil water and amount of ^{2}H in the soil water among the treatments at 48 h after the fog exposure. Prior to ANOVA, all data were subjected to normality and homogeneity test using Shapiro-Wilk and Levene tests, respectively. All analyses were performed using R (version 3.6.3) software.

Results

Preliminary drought experiment

There was a rapid decrease in VWC of the soil between 12 and 30 days after irrigation was terminated (Table 1). The mean VWC of the soil 12 days after irrigation ranged from 0.23 to 0.25 m^{3} m^{-3} (pF: 4.0–

4.3) (Table 1, Fig. S1a in Online Resource 1), indicating that the soil moisture was near the widely used permanent wilting point of plants (–1.5 MPa equivalent to pF 4.18) (Van Genuchten 1980; Eamus and Prior 2001). Furthermore, the VWC of the experimental soil reduced to 0.09–0.14 m^3 m^{-3} (pF 5.5–6.8).

Table 1

Variations in mean (± S.D.) volumetric water content (VWC) and pF at 0–10 and 10–20 cm soil depths in the pots containing *P. thunbergii* saplings, as well as in the needle water content (NWC), branch water content (BWC), and needle mass ratio (NMR) of the trees 0, 3, 6, 12, and 30 days after irrigation in the preliminary experiment in 2017

	Soil (0–10 cm)		**Soil (10–20 cm)**		**Trees**		
Days after irrigation stopped	VWC	pF	VWC	pF	NWC	BWC	NMR
	(m^3 m^{-3})		(m^3 m^{-3})		(g g^{-1})	(g g^{-1})	(g g^{-1})
0	0.47 ± 0.06	2.0 ± 0.5	0.49 ± 0.06	1.9 ± 0.5	0.67 ± 0.01 ^{b}	0.65 ± 0.01 ^{b}	0.50 ± 0.02 ^{a}
3	0.39 ± 0.06	2.8 ± 0.5	0.40 ± 0.06	2.7 ± 0.5	0.68 ± 0.01 ^{b}	0.65 ± 0.01 ^{b}	0.51 ± 0.02 ^{a}
6	0.34 ± 0.07	3.2 ± 0.7	0.35 ± 0.07	3.1 ± 0.6	0.67 ± 0.02 ^{ab}	0.64 ± 0.02 ^{ab}	0.49 ± 0.03 ^{a}
12	0.22 ± 0.03	4.3 ± 0.4	0.25 ± 0.03	4.0 ± 0.3	0.68 ± 0.01 ^{b}	0.65 ± 0.01 ^{b}	0.51 ± 0.03 ^{a}
30	0.09 ± 0.03	6.8 ± 0.6	0.14 ± 0.02	5.5 ± 0.4	0.65 ± 0.02 ^{a}	0.62 ± 0.01 ^{a}	0.50 ± 0.03 ^{a}

The pF was calculated based on the relationship between VWC and pF in black soil (see Fig. S1). For trees, letters within a column indicate significant differences ($P < 0.05$, ANOVA followed by Tukey HSD test); $n = 5$, except for the NWC at 30 d, where $n = 4$

Additionally, the irrigation experiment did not significantly affect ($P > 0.05$) the NMR of the trees and needle mortality rate. However, there was a significant decrease ($P < 0.05$) in the NWC and BWC of the trees 30 days after irrigation when the soil moisture was below the permanent wilting point of plants (Table 1).

Soil drought treatment

The VWC of the control group decreased to 0.22 $m^3\ m^{-3}$ a few days after watering and recovered to approximately 0.40 $m^3\ m^{-3}$ after re-watering (Fig. S3a in Online Resource 1). Changes in soil temperature were minimal for 4 days after the treatment began and then increased (Fig. S3b in Online Resource 1), corresponding to a gradual and sudden decrease in the VWC of the SD treatment (Fig. S3a in Online Resource 1). There was a decrease in the daily average VWC of the LD and SD treatments, a few days after the last irrigation (Fig. 1a). The mean daily VWC in the control, LD, and SD treatments during the soil drought treatment was 0.30 ± 0.01, 0.28 ± 0.02, and 0.22 ± 0.02 $m^3\ m^{-3}$ (± S.D., $n = 3$), respectively.

Moreover, variations in stem diameter were influenced by variations in soil VWC. There was no significant variation in stem diameter and soil VWC, 4 days after the treatment began. Variations in the diameter of plants in the LD treatment showed a similar pattern with that of trees in the control group till 12 days and then exhibited a decreasing trend (Fig. 1b). In the SD treatments, there was a decrease in stem diameter, several days after the treatment began (Fig. 1b). Overall, in the LD and SD treatments, variations in tree diameter exhibited a trend similar to that of soil VWC (Fig. 1a, b), indicating that tree diameter was linked to soil VWC. Diurnal pattern of the diameter variations fluctuated in the SD treatment (Fig. S3c in Online Resource 1), indicating that although the trees were wilting during the drought treatment, they survived.

Deuterium-enriched fog exposure

During the pure-water and deuterium-enriched fog exposure, the air temperature and CO_2 concentration in the chamber ranged from 17.1 to 17.7°C and from 400 to 439 $\mu L\ L^{-1}$, respectively (Table S1 in Online Resource 1). The RH increased from 63–91% during the pure-water fog exposure and remained between 91% and 98% during the deuterium-enriched fog exposure (Table S1 in Online Resource 1). Thus, deuterium-enriched water exposure was performed at a high RH (> 91%). The fog was visible from the observation window of the growth chamber from the middle of the pure-water fog exposure. The δ^2H value of the atmospheric water in the chamber collected via the cold trap for 1 h throughout the deuterium-enriched fog exposure was 525,580‰ (Table S2 in Online Resource 1).

Temporal variations in soil VWC and soil temperature at the surface were minimal during the deuterium-enriched fog exposure experiment (Fig. S4a, b in Online Resource 1). However, percentage decrease in soil VWC in the control, LD, and SD treatments during the exposure period was 0.95 ± 0.10, 0.70 ± 0.78, and 0.66 ± 0.39% h^{-1} (± S.D., $n = 3$), respectively, indicating that the trees absorbed less amount of soil water during the fog treatment. Moreover, plant diameter slightly decreased in all treatments, except for one sapling in the SD treatment (Fig. S4c in Online Resource 1).

Furthermore, the mean VWC of the soil bags under control was significantly higher ($P < 0.001$) than those of under the LD and SD conditions after 48 h of fog exposure (Fig. 2a). The soil VWC (± S.D., $n = 3$) under the control, LD, and SD treatments was 0.45 ± 0.02, 0.22 ± 0.02, and 0.18 ± 0.02 $m^3\ m^{-3}$, respectively, and pF was 2.0 ± 0.1, 4.1 ± 0.2, and 4.6 ± 0.4, respectively. The soil matric potential calculated using the pF under the LD and SD treatments tended to be lower than that under control (Fig. 2b).

Distribution and redistribution of absorbed fog water

The deuterium-enriched fog exposure experiment enabled the detection of the retention of absorbed fog water 48 h after fog exposure. Using a simple isotope mixing model (Eq. 4), we evaluated the fraction of the water of each plant organ contributed by fog water (f_F) in each treatment. The f_F was the highest in the needles, followed by current branches, old branches (including stems), and roots, indicating that the needles retained more fog water (Fig. 3). There was no significant difference in the f_F values of the current and old needles (Fig. 3a, b).

The f_F in the current needles, old needles, and current branches was significantly higher ($P < 0.05$) under the LD and SD treatments than that under the control (Fig. 3a, b, c), indicating that more absorbed fog water was retained in the water-stressed trees than that in well-watered trees. Additionally, f_F in the old branches and roots was higher ($P < 0.05$) in the SD treatment than that in the control (Fig. 3d, e), indicating that the absorbed fog water remained in the old branches and roots under severe drought conditions.

Furthermore, there was no significant difference in the $x^E(^2H)$ ($P > 0.05$) and excess ^2H in the soil water among the treatments (Fig. 4), suggesting that the absorbed fog water could be redistributed irrespective of soil moisture regimes.

Discussion

Consistent with our hypothesis, the retention of absorbed fog water in plant organs of drought-stressed *P. thunbergia* saplings was significantly (approximately 20 times in the current needles) higher than that in well-watered saplings at 48 h after fog exposure. The well-watered saplings possessed < 1% of the absorbed fog water. To the best of our knowledge, this is the first study to show that the retention of absorbed fog water in the trees increased under soil drought conditions. The increased amount of absorbed fog water in plant body in response to drought appears to be an important mechanism for tolerating drought stress and improve water status of the plant species growing in fog-affected areas.

Retention of absorbed fog water in plant organs

Previous studies using water isotopes showed that water vapor retention in plant leaves rapidly decreases in a few days due to water loss through transpiration and very small amount of the water is retained for several days (Guenot and Belot 1984; Lehmann et al. 2018; Choi et al. 2001). This is consistent with our results that small amount of fog water was retained in the needles, branches, and roots of *P. thunbergia* saplings 48 h after fog exposure, which is likely after water loss through transpiration. Lehmann et al. (2018) showed that the retention of water vapor was the highest in the leaf lamina followed by main veins and twig xylem. This observation is consistent with our results that the retention of the absorbed fog water was the highest in the needles, followed by current branches, and old branches irrespective of soil water conditions. Our results showed that the absorbed fog water was also retained in old branches (including stem) and roots of *P. thunbergii* saplings, suggesting that absorbed fog water can be distributed to belowground parts.

Whole-plant water transport, from leaves to stems, has been widely observed in forest trees in many ecosystems, whereas bidirectional water movement towards the branches, both from the leaves and from the soil, has rarely been reported (Goldsmith 2013). In the present study, soil moisture slightly decreased under well-irrigated conditions during the deuterium-enriched fog exposure, indicating that the trees absorbed soil water during the period. Combined with the retention of absorbed fog water in the branches 48 h after exposure, bidirectional water movement from both needle surface and roots toward branches may occur in well-irrigated trees. However, it is possible that soil water might infiltrate deeper layers from the surface where the measurements using soil moisture sensors were performed.

Changes in retention of absorbed fog water under drought

Drought-stressed *P. thunbergii* saplings consistently retained more fog water in the leaves, branches, and roots than well-irrigated saplings. The current and old needles and current branches of drought-stressed saplings retained significantly greater amount of fog water than those of well-irrigated saplings 48 h after fog exposure. During drought, soil water potential decreases, resulting in stomatal closure and reduced water loss through transpiration (Bond and Kavanagh 1999). The calculated soil matric potential in the LD and SD treatments 48 h after fog exposure was approximately − 1.5 and − 5.5 MPa, respectively. Lebourgeois et al. (1998) reported that stomatal conductance reduced near to zero when predawn needle water potential reached − 1.6 MPa in 3-year-old *P. nigra* saplings. Similarly, *P. sylvestris* showed stomatal closure to prevent the reduction of needle water potential below − 1.5 MPa (Irvine et al. 1998). These results suggest that similar retention of water in the moderately and severely drought-stressed saplings and the greater retention of water than that in well-irrigated saplings is probably because of reduced water loss through stomatal closure in both moderately and severely drought-stressed saplings. In the well-irrigated saplings, water exchange through transpiration and soil water uptake after fog exposure would decrease the retention of water in the plant organs.

There is another possible explanation for the increased fog water retention under drought due to increased fog water absorption. Eller et al. (2016) showed that the amount of absorbed fog water can increase with soil drought. In contrast, in redwood (*Sequoia sempervirens*) saplings, old leaves of well-irrigated trees absorbed more fog water than those of water-stressed trees (Burgess and Dawson 2004). Soil drought had a small effect on the amount of absorbed water in leaf lamina, main vein, and twig xylem of *Quercus robur* (Lehmann et al. 2018). The inconsistency among these studies may be related to differences in pathways of foliar water uptake, such as through cuticle, hydathodes, trichomes, stomata, and fungal hyphae (Kerstiens 1996; Burgess and Dawson 2004; Limm et al. 2009; Burkhardt et al. 2012; Fernández et al. 2014), and their contributions (Berry et al. 2019). Nevertheless, the amount of absorbed water is unlikely to influence the differences in water retention at 48 h after fogging when the majority of absorbed fog water would be lost through transpiration in well-watered conditions (Guenot and Belot 1984; Choi et al. 2001).

The severely drought-stressed saplings retained more fog water in the old branches and roots than well-irrigated saplings, unlike moderately drought-stressed saplings. The difference in the amount of retained water in the roots between severely and moderately drought-stressed saplings may be because the contribution of soil water to exchange water in the roots was lesser in the severely drought-stressed saplings. However, because it can be considered that transpiration and root water uptake rarely occurred in both moderately and severely drought-stressed saplings under low soil matric potentials in this study, the differences in the water retention in roots and old branches may be due to the differences in foliar water uptake during fog exposure because of different soil water potentials. During fog exposure, air water potential calculated using air temperature and RH based on the equation of Nobel (1999) was up to − 3 MPa, which was higher than that of the soil matric potential in the SD treatment (i.e., approximately − 5.5 MPa) but not in the LD treatment (−1.5 MPa), suggesting that a water potential gradient from the atmosphere to soil in the severely drought-stressed saplings may facilitate the transfer of absorbed fog water from leaves to belowground parts of the plants.

Redistribution of absorbed fog water to rhizosphere soil

The results of this study also indicate that the absorbed fog water was slightly redistributed to the soil in well-irrigated and drought-stressed trees. Hydraulic redistribution of water from moister to drier regions of soil through trees has been previously reported (Warren et al. 2008). The redistribution of absorbed water from the leaf surface can reach the roots and redistribute to the soil along a water potential gradient from plants to soil (Goldsmith 2013). Eller et al. (2013) indicated reverse water movement from the atmosphere to soil (including fine roots) through the xylem of *D. brasiliensis* saplings. Hydraulic redistribution has also been reported under moderate drought conditions (Hafner et al. 2017). Similarly, ^{2}H was detected in soil water recovered from the soil bags with fine mesh size in the present study, indicating that absorbed fog water from the needles of *P. thunbergii* was redistributed to the soil irrespective of soil moisture conditions. However, water loss from the soil through evaporation from the soil surface and transpiration by plants can also cause changes in the hydrogen isotope ratio in soil water (Allison et al. 1983; Lai and Ehleringer 2011). Because we did not consider the effects of isotope fractionation due to drought, further research is needed to confirm the redistribution of absorbed fog water to the soil under drought in *P. thunbergii*.

Conclusions

We found that more amount of fog water was retained in drought-stressed plants than that in well-watered plants at 48 h after fog events. Although foliar absorption is less important for plant recovery from water stress than soil water absorption (Guzmán-Delgado et al. 2018), fog water retention may contribute to alleviating plant water status of the tree species under drought when soil water is not available. Our results also suggest that absorbed fog water was slightly redistributed to the soil through the xylem irrespective of soil drought conditions. The small amount of redistributed water may be a potential water source for rhizospheric microorganisms in the soil. In near future, the number of days without precipitation is predicted to increase in northeastern Japan where fog occurs occasionally during summer (Kimoto et al. 2005; Oguchi and Fujibe 2012). Our findings of more amount of fog water retention in drought-stressed *P. thunbergii* trees and potential redistribution of the absorbed fog water to the soil suggest that the trees can use fog water as a small but important water source for tolerating drought stress in fog-affected areas.

Declarations

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Authors' Contributions

S.I. conceived and designed the research; S.I. and H.K. performed water extraction using a cryogenic vacuum extraction system; M.N. provided data on the relationships between VWC and pF of the soil; S.I. collected and analyzed the data and wrote the manuscript; all authors have read the manuscript and commented on it.

Conflict of Interest

The authors declare that they have no conflicts of interest.

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Figures

Figure 1

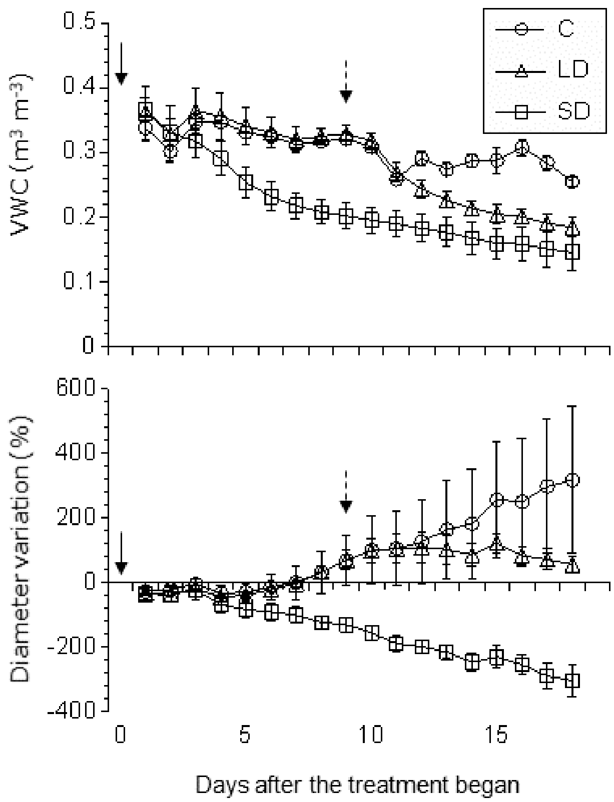

Figure 1

Diurnal variations in volumetric water content (VWC) at 0–5-cm depth (a) and percentage change in stem diameter of trees in the control (C), low drought (LD), and severe drought (SD) treatments from September 7 (day 0) to September 19, 2018 (b). The solid and broken arrows indicate the days of the final irrigation for the SD and LD treatments, respectively. The error bars denote ± SD (*n*= 3, except for the LD treatment in (b), where *n* = 2)

Figure 2

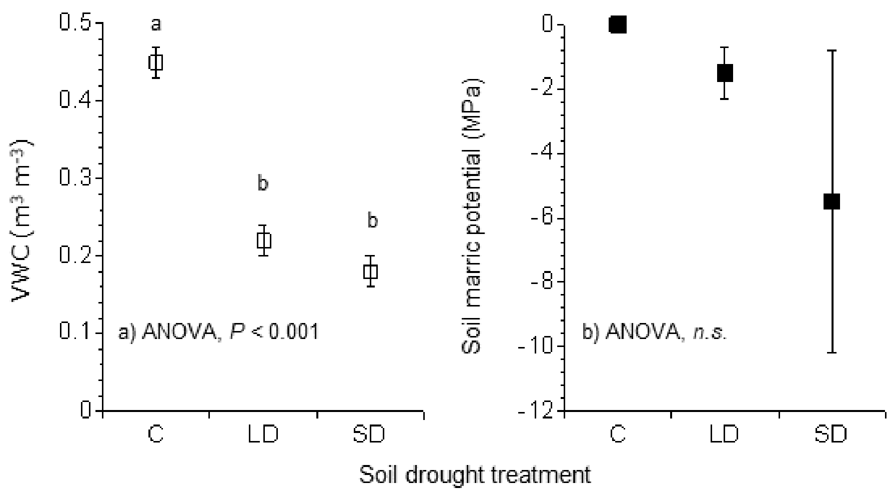

Figure 2

Volumetric water content (VWC) (a) and matric potential (b) of the soil bags of the pots containing *P. thunbergii*saplings under the control (C), low drought (LD), and severe drought (SD) treatments 48 h after fog exposure experiment. One-way ANOVA was performed for each plant organ. The error bars denote ± SD (n = 3)

Figure 3

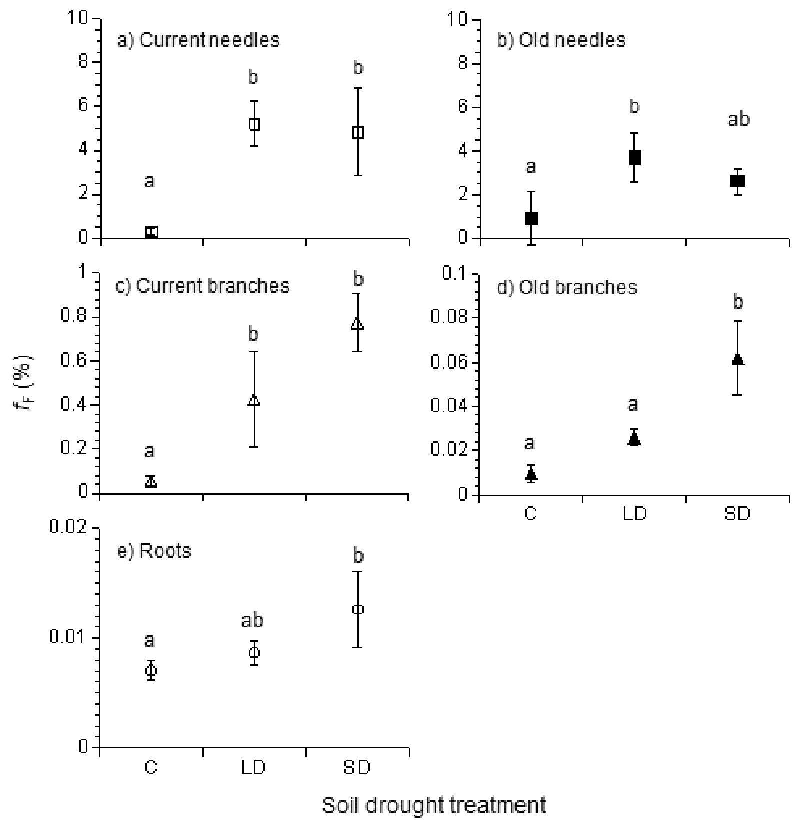

Figure 3

The fraction of water in current and old needles (a), current and old branches (including stem) (b), and roots of *P. thunbergii* saplings contributed by fog water (f_F) under control (C), low drought (LD), and severe drought (SD) treatments 48 h after fog exposure experiment (c). One-way ANOVA followed by Tukey HSD test was performed for each plant organ ($P < 0.05$). The error bars denote ± SD (n = 3)

Figure 4

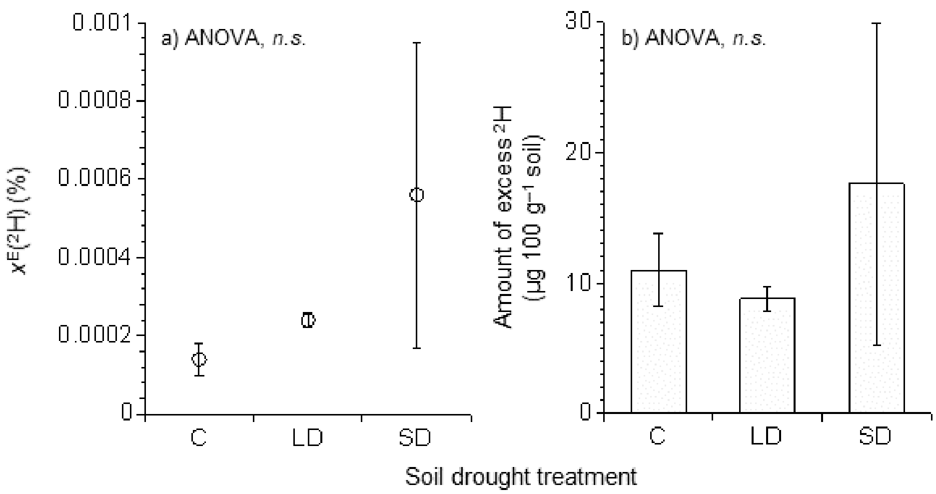

Figure 4

Excess ^2H ($x^E(^2H)$, in %) (a) and amount of excess ^2H (b) in soil water of the pots containing *P. thunbergii* saplings under the control (C), low drought (LD), and severe drought (SD) treatments 48 h after fog exposure experiment. One-way ANOVA was performed for each plant organ. The error bars denote ± SD (n = 3)

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