BRIEF COMMUNICATION

Effects of evening and nighttime leaf wetting on stomatal behavior of *Cryptomeria japonica* growing in dry soil

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Abstract

To examine the hypothesis that stomatal behavior of plants in dry soil is influenced by a slow recovery from daytime water deficit, we studied the effect of repeated wetting of leaves during evening and night in *Cryptomeria japonica* seedlings grown in dry soil. After 7 and 10 days of leaf wetting treatment the midday leaf water potential decreased and the transpiration rate increased, respectively. Therefore, we suggest that rapid recovery from daytime water deficit could weaken the water conserving stomatal behavior that adapts to drought conditions in the roots.

Additional key words: leaf water potential; photosynthesis; transpiration.

Plants in dry soil tend to maintain low stomatal conductance even if the vapor pressure deficit (VPD) is low and leaf water potential is high. This stomatal response enables plants in dry soil to maintain their water content and reduces the severity of water stress. Moreover, in response to low soil matric potential abscisic acid (ABA) is produced in roots and may be a possible signal substance that triggers the closure of stomata during soil drought (Zhang *et al.* 1987, William *et al.* 1994, Schachtman and Goodger 2008). Atmospheric humidity also influences water stress in plants and long-term exposure to low atmospheric humidity has shown to increase ABA concentrations in the roots and leaves and decrease stomatal conductance (Darlington *et al.* 1997), which mimics the stomatal behavior observed in plants growing in dry soil. The leaf water deficit that occurs during the day is generally reduced after sunset as evaporative demand reduces. However, the recovery from water deficit takes longer on the plants growing in dry soil than on those in moist soil. The low atmospheric humidity after sunset may also influence the recovery from daytime water deficit. In addition to cuticular transpiration, stomatal opening during the night has been documented in many species (Musselman and Minnick 2000). Foliar water uptake has been investigated in several conifers (Burgess and Dawson 2004, Boucher *et al.* 1995, Katz *et al.* 1989, Leyton and Armitage 1968, Stone *et al.* 1956). Although its contribution to water relations is generally considered to be small (Chaney 1981, Burgess and Dawson 2004), it is regarded as an effective water source for some conifers growing in dry soil (Breshears *et al.* 2008, Boucher *et al.* 1995, Stone 1957). Evening and nighttime leaf wetting might therefore improve recovery from water deficit by suppressing transpiration from the cuticle and stomata, and enhancing foliar water uptake.

Cryptomeria japonica, the tallest tree species in Japan, is known to grow taller where fog incidence is higher. The needles of *C. japonica* are arranged in dense spirals around the stems and are quadratic pyramid-shaped with stomata distributed on the four faces. Water is held between the needles and there is greater contact between water and stomata than in broad-leaved trees, where the stomata are distributed on the abaxial surface. Therefore, we suggest that *C. japonica* may be sensitive to atmospheric water conditions.

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Abbreviations: ABA – abscisic acid; E – transpiration rate; E_d – daily transpiration rate; P_N – net photosynthetic rate; P_{Nd} – daily net photosynthetic rate; VPD– vapor pressure deficit; Ψ_w – foliage water potential.

We propose a hypothesis that the stomatal behavior of plants in dry soil is influenced by the slow recovery from daytime water deficit. Our experiment aimed to clarify the effects of evening and nighttime leaf wetting on stomatal behavior of *C. japonica* seedlings growing in dry soil.

Three-year-old seedlings of *C. japonica* raised at the nursery of the Experimental Station at Tanashi, The Tokyo University Forests, were transplanted into 0.02 m^3 pots (0.08 m^2 sectional area, 0.25 m depth) in March 2007. The potting medium consisted of natural Andosol (surface soil). The transplanted seedlings were well watered, and after one month of transplanting they were fertilized and maintained in optimal growing conditions at the nursery for additional four months. The average height (mean ± SD, n = 24) was 0.88 ± 0.08 m.

The potted seedlings were placed under a translucent plastic roof to avoid rainfall. They were divided into two groups, moist group and dry group. Soil matric potential was monitored with a ceramic soil moisture meter (*SPAD-pF-33, Fujiwara Seisakusho Co. Ltd.*, Tokyo, Japan) and maintained at a level higher than –0.01 MPa for the moist group and between −0.63 and −0.32 MPa for the dry group by controlled watering. The intensity of soil drought was determined by a preliminary experiment in 2006.

After four weeks of induced drought, we set up three plots, dry-cont and dry-mist plots from the dry group and moist-cont plot from moist group on 3 August, 2007. Each plot consisted of eight seedlings, *i.e.*, two seedlings per pot in four pots. The soil in the pots was covered with a plastic sheet to avoid spray and mist. Each plot was enclosed by a plastic sheet with top and bottom openings for ventilation. During measurements, the potted seedlings were moved to an open site. For the dry-mist plot, the shoots of the seedlings were initially wetted with a sprayer and misted with a humidifier for 90 min beginning at 17:30. The seedlings were then misted with a humidifier for three 30-min periods through the night at 21:00–21:30, 0:00–0:30, and 3:00–3:30. During the experimental period between 3 and 15 August, 2007, the mean ± SD of VPD were 2.5 ± 0.5 kPa between 10:00 and 14:00, 1.4 ± 0.2 kPa between 18:00 and 20:00, and 0.2 ± 0.1 kPa predawn. The mean midday temperature and photosynthetic photon flux density (10:00–14:00) were 32.9 ± 1.3 °C and 1570 ± 150 μmol m^{-2} s^{-1}, respectively.

Diurnal change in net photosynthetic rate (P_N) and transpiration rate (E) was measured with a portable photosynthesis system (*LI-6400, Li-Cor Inc.*, Lincoln, NE, USA) on day 0, immediately before mist treatment, and on days 3, 5, 7, 10, and 12. The rates were expressed on leaf dry mass basis. The CO_2 concentration in inlet air was maintained at 370 ppm. Air temperature and relative humidity in the chamber were approximately similar to ambient conditions, except in the early morning when the ambient VPD was very low. Predawn and midday (11:30–13:30) water potentials (Ψ_w) were measured on the same days as the P_N measurement using a pressure chamber (*Model 3000, Soilmoisture Equipment Corp.*, Santa Barbara, CA, USA) (except for Ψ_w for moist-cont on days 0 and 3).

Predawn Ψ_w was similar to soil matric potential and there were no differences between dry-cont and dry-mist plots. The midday Ψ_w of the moist-cont plot was higher than those of the dry-cont and dry-mist plots (Fig. 1). The midday Ψ_w of dry-cont and dry-mist plots did not differ before day 5, but after day 7, Ψ_w of the dry-mist plot was significantly lower than that of the dry-cont plot (Fig. 1, Welch's t-test, p<0.05). Daily transpiration rate (E_d) and daily net photosynthetic rate (P_{Nd}) in the moist-cont were higher than those of the other two plots throughout the experiment. E_d in the dry-mist plot on days 10 and 12 were 24 % (Fig. 1, Welch's t-test, p=0.06) and 28 % (p=0.04) more than in the dry-cont plot, respectively. For P_{Nd} , the same effect as for the mist treatment was shown, but the differences between the two plots were not significant (Fig. 1). We obtained similar results in a preliminary experiment in 2006.

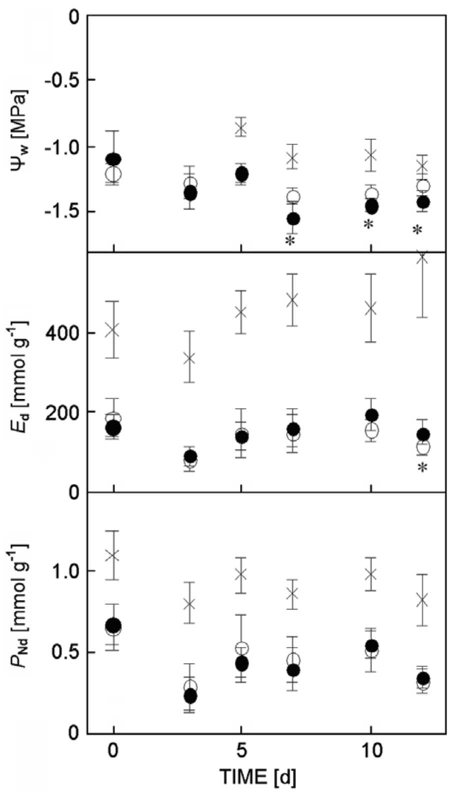

Fig. 1. Midday foliage water potential (Ψ_w), daily transpiration rate (E_d), and daily net photosynthetic rate (P_{Nd}) (7:00–16:00) of *Cryptomeria japonica* seedlings over time in three plots. Seedlings planted on moist soil were untreated (moist-cont plot, ×). Those planted on dry soil were untreated (dry-cont plot, ○) or exposed to periodic foliage wetting each day through the night (dry-mist plot, ●). Mean ± 1 SD (n = 8). * denotes statistically significant difference between dry-cont and dry-mist plots (Welch's t-test, p<0.05) for any given measure.

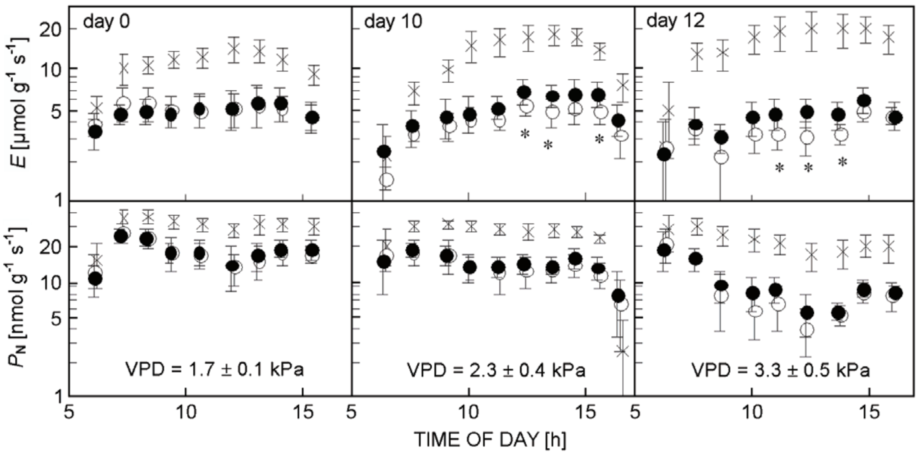

Fig. 2. Diurnal changes in transpiration rate (*E*) and net photosynthetic rate (P_N) of *Cryptomeria japonica* seedlings before (day 0) and after (days 10 and 12) mist treatment. VPD is the mean ± SD of the vapor pressure deficit between 10:00 and 14:00. The symbols are the same as in Fig. 1. Mean ± 1 SD ($n = 8$). * denotes statistically significant difference between dry-cont and dry-mist plots (Welch's *t*-test; $p<0.05$) at any given measure.

E and P_N in the moist-cont plot were higher than in the other two plots except for early morning (Fig. 2). The midday *E* in the dry-mist plot were significantly higher than those in the dry-cont plot after day 10 (Fig. 2, Welch's *t*-test, $p<0.05$), corresponding to stomatal conductance. For P_N, the same effect as for mist treatment was shown but the differences between the two plots were not significant (Fig. 2).

We showed that for *C. japonica* seedlings growing in dry soil, more than 10 days of evening and nighttime leaf wetting increased the transpiration in the middle of day, which indicates the increase in stomatal conductance (g_s). The midday Ψ_w of the dry-mist plot was lower than that of the dry-cont plot. The soil matric potential and VPD did not differ between the dry-mist and dry-cont plots. Therefore, the difference in stomatal behavior between the two plots in the middle of the day did not result from a difference in soil moisture or atmospheric humidity. Our results indicate that the water conserving stomatal behavior adaptation to dry soil is weakened by the evening and nighttime leaf wetting, maybe associate with rapid recovery from the daytime water deficit. This is the first observation of the effect of evening and nighttime atmospheric water conditions on the stomatal behavior of plants growing in dry soil.

In absorbing water from soil, tall trees must overcome large hydraulic resistance and high gravitational potential (Ryan 2006); these physical constraints may limit water absorption of leaves in a similar manner that soil dryness does. Even in moist soil, tall trees have smaller g_s and lower leaf Ψ_w than short trees (Matsuzaki *et al.* 2005). To understand how the leaves of tall trees respond to the environmental conditions, the effect of evening and nighttime atmospheric water conditions should be studied further.

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