

Root responses of Siberian larch to different soil water conditions

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Abstract:

Decline of larch trees has been recently observed in eastern Siberia. We hypothesized that the decline might be caused by changes in soil water conditions of larch forests, especially wetting tendency due to recent climate change. Through pot experiments, we have investigated the effects of wet or dry soil water conditions on growth and abscission of roots in two larch species viz. *Larix gmelinii* that grows in boreal forests and *Larix leptolepis* that grows in temperate regions. The results showed that both the allocation of photosynthetic products to roots and the activity of roots decrease under wet conditions compared with drought conditions in *L. gmelinii*. However, the opposite results were obtained in *L. leptolepis*. The root response of *L. gmelinii* to wet conditions may be one of the causes of the recent decline in Siberian larch forests under elevated soil water conditions.

KEYWORDS *Larix gmelinii*, *Larix leptolepis*, wet conditions, fine roots, root abscission

INTRODUCTION

Larch (*Larix*) forests are the most widely distributed coniferous forest in the world (Kobak *et al.*, 1996). The distribution of 10 *Larix* species throughout the cold temperate regions of the northern hemisphere has been described (More and White, 2002). Comparing with *Pinus* or *Picea*, which have a greater number of species, the distribution of *Larix* is considered to be rather simple. Most larch forests located in eastern Siberia are dominated by *Larix gmelinii* (Dahurian larch) and *Larix cajanderi*. These regions are characterized by continuous permafrost and a continental climate, low precipitation of only about 100 mm year⁻¹, and surface soil moisture as low as 5% during the growing season of larch (Ohta *et al.*, 2008). Larch trees are known to have a shallow root system (Dem'yanov, 1980), thought to be an adaptation to severe water and temperature conditions.

Recently, soil water conditions and water balance in larch forests have changed due to the variations in annual and/or monthly precipitation in eastern Siberia (Iwasaki *et al.*, 2010; Ohta *et al.*, 2008). Iwasaki *et al.* (2010) reported that annual precipitation (from June to May) in 2005–2006, and 2006–2007, exceeded the 26-year mean of 222 ± 68 mm (mean value ± standard deviation during 1982–2008) by 185 mm and 128 mm, respectively. Also, Ohta *et al.* (2008) showed that the soil water content in eastern Siberian larch forests varied seasonally between 5% and 30% from 1998

to 2005, but reached 45% in 2006. This increasing trend in soil water content would be expected to suggest the mitigation of severe drought stress for larch trees, however, yellowing and browning of larch (*L. cajanderi*) trees was observed in a disturbed forest near Yakutsk Sakha Republic, Russia (e.g. Iwasaki *et al.*, 2010). We hypothesized that the decline might be caused by changes in soil water conditions of larch forests, especially wetting tendency.

In general, inhibition of the growth of plant roots by drought stress, among the myriad possible effects caused by changes in soil water conditions, has been reported in many plant species under various temperature conditions (e.g. Plaut *et al.*, 1996; Huang, 1999; Manes *et al.*, 2006; Torrealano and Morris, 1998). However, some plant species are able to adapt their root systems to drought conditions by increasing their root/shoot (R/S) biomass ratio (e.g. Psarras and Merwin, 2000; Nguyen and Lamant, 1989) and the branching of fine roots expressed as fine root length and specific root length (SRL) (e.g. Chiatante *et al.*, 1999; Rodrigues *et al.*, 1995; Jupp and Newman, 1987). Such plants adapt to drought conditions by increasing the surface area of roots or by branching of fine roots in order to maintain water uptake. In contrast, the response of roots to excessively wet conditions in plants that are adapted to drought conditions has not been fully investigated especially in cold regions, because humidification in cold regions has only been noticed recently.

The purpose of this study is to determine the effects of the current wetter conditions on the roots of *L. gmelinii*, a dominant, drought-tolerant tree species in eastern Siberia. The response of roots to wet conditions was detected by measuring root growth and abscission. The response of *L. gmelinii* to wet conditions was distinguished and defined by comparison to that of *L. leptolepis*, a dominant larch species in Japanese temperate forests.

MATERIALS AND METHODS

Plant materials

Seedlings of *L. gmelinii* and *L. leptolepis* were purchased from the Forest and Wood Breeding Station in Hokkaido prefecture and the Forest Nursery Cooperative in Nagano prefecture, respectively. Mean seedling heights were 82.8 ± 1.9 cm for *L. gmelinii* and 43.5 ± 1.0 cm for *L. leptolepis*. Seedlings were planted in pots (27 cm in diameter and 30 cm in height) containing quartz sand on 21 May 2003 at the Inabu experimental forest, Nagoya University. Seedlings were grown outdoors under a rainproof roof. The annual mean, maximum, and minimum temperatures at Inabu are 11.3°C, 28.0°C, and -4.5°C, respectively. Seedlings were

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adapted to these conditions for 1 year until the start of treatment. Seedlings were watered once every 2 months during the adaptation and experimental periods with a nutrient solution of Hyponex (N/P/K = 10:3:3; Hyponex Japan) diluted 2000-fold (v/v) with water.

Water treatment

The experiment was carried out for 6 months from 24 May to 22 November 2004. For each treatment, 7 seedlings were used. For the wet treatment, 400 mL of water was supplied to seedlings every day. For the dry treatment, 400 mL of water was supplied to seedlings once a week during the initial 2 months, then the frequency was changed to once every 3 days, because the initial watering regime was too severe for *L. leptolepis* to survive. At each watering, 400 mL of stream water was supplied to a pot using an automatic watering timer (EY4200-H; Electric Industrial Co., Ltd.). Another 5 pots containing no seedlings were prepared to measure the volumetric water content of the pots for each treatment, then pot water conditions were evaluated as a pF value using a DIK-3420 Multi-Fold pF Meter (Daiki Rika Kogyo Co., Ltd.).

Measurements

(i) Gas exchange rate

Gas exchange rate was measured between 9:00 a.m. and 10:00 a.m. on 24 May, 9 June, 7 July, and 15 September 2004 using an infrared gas analyzer, CIRAS-1 (PP system). Five seedlings from each treatment were selected for measurement. The CO₂ concentration and light intensity during measurement were set to 380 $\mu\text{mol mol}^{-1}$ and 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. The dates of measurement corresponded to day 3 after watering day except for 24 May 2004.

(ii) Root elongation rate

Four seedlings were used to measure root elongation. Before treatment began, a seedling was removed carefully from a pot together with the quartz sand growing medium, and its roots were washed carefully with water. From each seedling, 5 low lateral roots (2nd or 3rd lateral root) about 2 mm in diameter were selected. The lateral roots chosen were marked with tape. The marked root was photographed with a size scale and the seedling was then carefully replanted in a pot with quartz sand. Once in a 2 month period, the marked roots of 4 seedlings were observed after removing them from their pot and washing with water, followed by replanting. Root length was determined from photographs by using image analysis software (Lia 32; Yamamoto, 2000). Root elongation rate was calculated from the difference in root lengths before and after treatment.

(iii) Root respiration rate

Root respiration rate was measured using the same seedling used for measuring root elongation (Comas *et al.*, 2000). Root samples 2 cm in length from the root tip were taken and kept cool in distilled water until measurement. Root respiration rate was measured using a Clark-type O₂ electrode (DO-24P; DKK-TOA).

(iv) Root abscission

Root abscission was determined for the same seedlings used in root elongation measurements. At the initial root observation prior to the start of treatment, all dead roots were cleaned from the sand medium. Then, each time the

seedlings were submerged in the sand medium for the wet treatment, the abscised roots remaining in the sand medium were collected by floating them to the surface in water. The collected abscised roots were then oven-dried at 80°C for 48 h to measure dry weight.

(v) Total root length and root length classified by diameter

After the treatments had been conducted, three seedlings from each treatment were selected to measure total root length and root length classified by diameter. After seedling roots had been washed thoroughly, all roots, except the primary root, were cut into 20-mm lengths. The root pieces were placed on transparent film without overlapping, and images of all roots from a plant were scanned. Total root length and root length classified by root diameter were calculated from these images of the root systems using NIH Image (U.S. National Institute of Health) analysis software. Root diameter was classified into 10 classes at 0.25-mm intervals. Specific root length (SRL) was calculated by dividing total root length by root dry weight.

(vi) Root-shoot ratio

After treatments were finished (22 November 2004), all root systems were harvested, and above-ground plant parts and root systems were oven-dried at 80°C for 48 h before measuring dry weight. R/S ratios were calculated by dividing root dry weight by shoot dry weight.

Statistical analysis

Effects of treatments on each measurement were analyzed using one-way analysis of variance (ANOVA) followed by Fisher's least-significant difference (LSD) test.

RESULTS AND DISCUSSION

Figure 1 shows the change in water conditions as both volumetric water content and pF values for wet and dry treatments on day 8 when watering was conducted weekly during the initial 2 months. Volumetric water content remained constant at over 20% in the wet treatment throughout the experiment. In the dry treatment, water content decreased considerably on the 2nd day after watering and fell to about 2% by the 7th day. The soil water level in the dry treatment nearly reached pF 4.2, which is defined

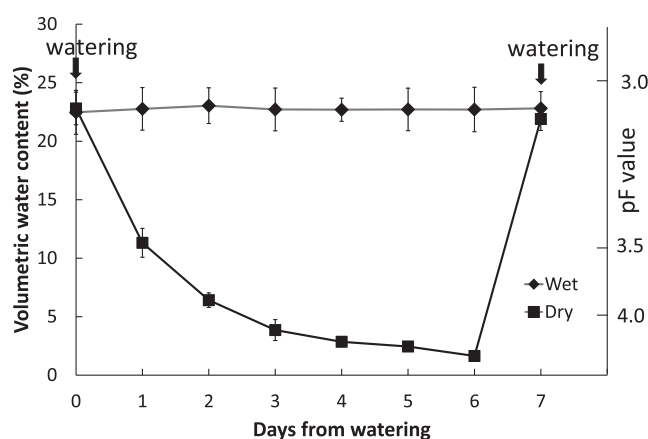


Figure 1. Volumetric water content and pF value in pots under wet or dry treatment for 8 days.

as the wilting point, and achieved the same soil water level as that observed in eastern Siberia (Ohta *et al.*, 2008).

Photosynthesis was suppressed in both species by drought conditions as shown in Figure 2. This result is a typical drought stress response caused by stomatal closure under dry conditions (Taiz and Zeiger, 2002). In our results, the decrease in photosynthesis manifested as reduction of root elongation rates as shown in Table I, particularly in *L. leptolepis*, indicating that this species is less adaptable to drought conditions. Generally, drought stress reduces root growth (e.g. Briske and Wilson, 1980; King and Bush, 1985; Stevenson and Laidlaw, 1985) as a result of suppression of

growth of the elongation zone (Dubrovsky *et al.*, 1998). The growing parts of a plant, such as meristems and the elongation zone, are much more sensitive to water stress than are its differentiated parts such as fine roots (Plaut, 1995). Therefore, reduction of the root elongation rate under the dry treatment was likely caused by suppression of root meristem activity or reduced growth of the elongation zone in the lower lateral roots.

Despite suppression of root elongation rate, the R/S ratio and total root length in *L. gmelinii* tended to be greater in the dry treatment than in the wet treatment (Table I). This may be attributable to the increased development of fine branching roots in the dry treatment, which showed an increasing tendency in fine root length and SRL in Table I. Development of lateral and fine roots under drought conditions has been observed in a number of plant species (Dubrovsky *et al.*, 1998; Jupp and Newman, 1987; North and Nobel, 1994). The development of lateral roots increases the surface area of the root for water absorption. In addition, because hydraulic conductivity is higher in younger roots than in older roots (Frensch and Steudle, 1989; North and Nobel, 1992), the development of new lateral roots may increase root hydraulic conductivity. Therefore, a tendency toward increase in fine root length and SRL under drought conditions appears to contribute to drought adaptation in *L. gmelinii*.

While fine root length tended to be longer in the dry treatment in *L. gmelinii*, the degree of root abscission was significantly greater in the dry treatment than in the wet treatment (Figure 3). The opposite result was observed in *L. leptolepis* where root abscission was greater under the wet treatment than in the dry treatment. Root endodermis or exodermis is suberized by accumulation of lignin or suberin when roots are exposed to drought (Cruz *et al.*, 1992); and in general, such suberization protects roots from drought. The suberized root, however, has decreased root hydraulic conductance (Nobel, 1991) and water absorption rates as compared with new, unsuberized roots (Clackson and Sanderson, 1974). Therefore, in this experiment, the roots of *L. gmelinii* were likely suberized by drought, but these suberized roots probably abscised when new roots were produced. Such dynamics in root development could explain the high respiration rate observed under the dry treatment. Figure 4 shows that the respiration rate of roots under the dry treatment was higher than under the wet treatment in *L. gmelinii*, and that the opposite result was found in *L. leptolepis*. Furthermore, drought-induced root abscission has been suggested to reduce the possibility of water loss from the root to soil (Huang and Nobel, 1992). Thus, higher levels of root abscission in *L. gmelinii* under

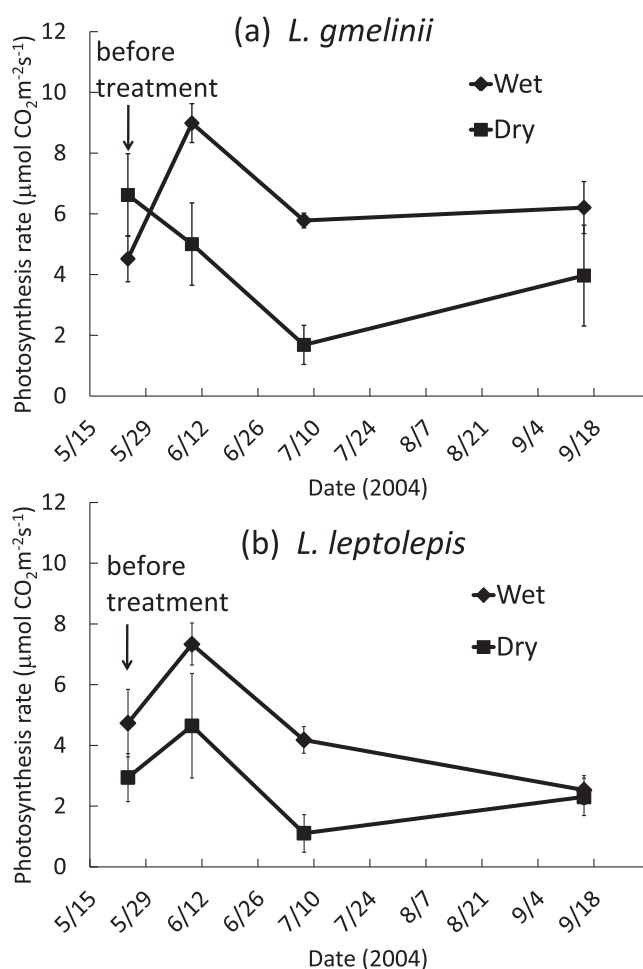


Figure 2. Photosynthesis rate of (a) *L. gmelinii* and (b) *L. leptolepis* from before the start of treatment until September.

Table I. Root elongation rate, total root length, specific root length, and root/shoot ratio of *L. gmelinii* and *L. leptolepis* under wet or dry water conditions (n = 3)

Species	Treatment	Root elongation rate (cm/month)	Total root length (m)	Specific root length (m/g)	Root/Shoot ratio
<i>L. gmelinii</i>	Wet	3.75 ± 0.62	400 ± 150	20.99 ± 1.26	0.82 ± 0.15
	Dry	2.81 ± 0.25	499 ± 86	23.32 ± 0.60	1.04 ± 0.23
<i>L. leptolepis</i>	Wet	2.29 ± 0.38	307 ± 108	24.17 ± 1.00	0.70 ± 0.02
	Dry	1.19 ± 0.26*	280 ± 58	20.44 ± 2.97	0.70 ± 0.09

The mark * indicates significant difference between wet and dry conditions at $p < 0.05$.

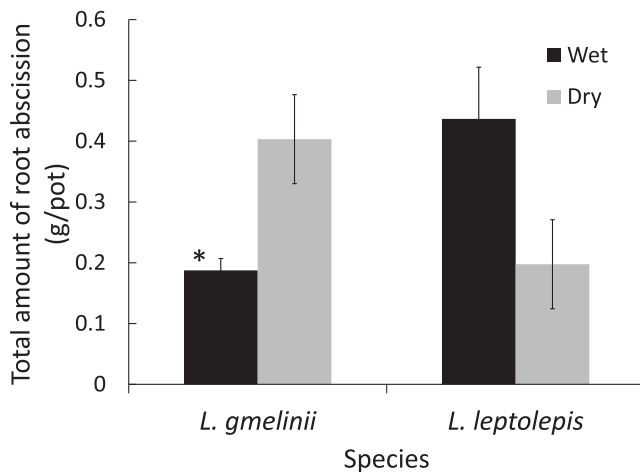


Figure 3. Total amount of root abscission during the treatment over 6 months in *L. gmelinii* and *L. leptolepis*. * indicates significant difference at $p < 0.05$ according to Fisher's LSD test.

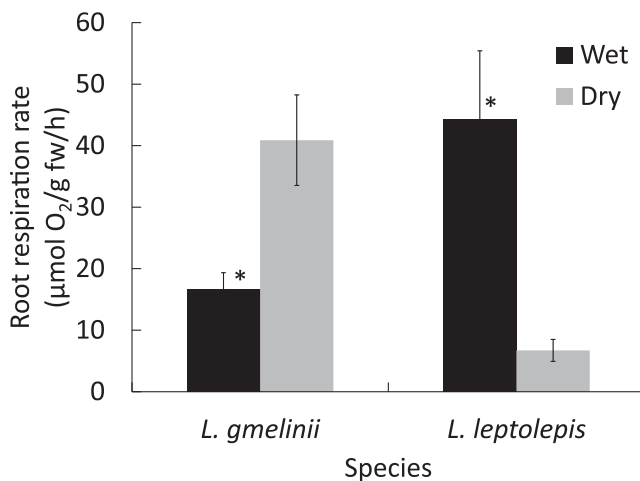


Figure 4. Root respiration rates of *L. gmelinii* and *L. leptolepis* measured on 15th July. * indicates significant difference at $p < 0.05$ according to Fisher's LSD test.

the dry treatment could be a mechanism for the plant to avoid water loss by eliminating suberized roots.

Figure 5 shows the size distribution of root lengths after 6 months of treatment in *L. gmelinii* (Figure 5a) and *L. leptolepis* (Figure 5b). Unlike *L. gmelinii*, drought conditions tended to decrease fine root length and SRL in *L. leptolepis*. Coarse root length, however, increased under the dry treatment in this species. According to Eissenstat *et al.* (2000), thick roots tend to have greater longevity than fine roots. Therefore, *L. leptolepis* may have developed thick roots with greater longevity under the dry treatment as a way of maintaining its root system. In addition, root abscission was considerably lower in *L. leptolepis* in the dry treatment than in the wet treatment. This may also be a mechanism for maintenance of the root system under drought conditions. In brief, the strategy of *L. leptolepis* under drought stress may be to maintain its root system by

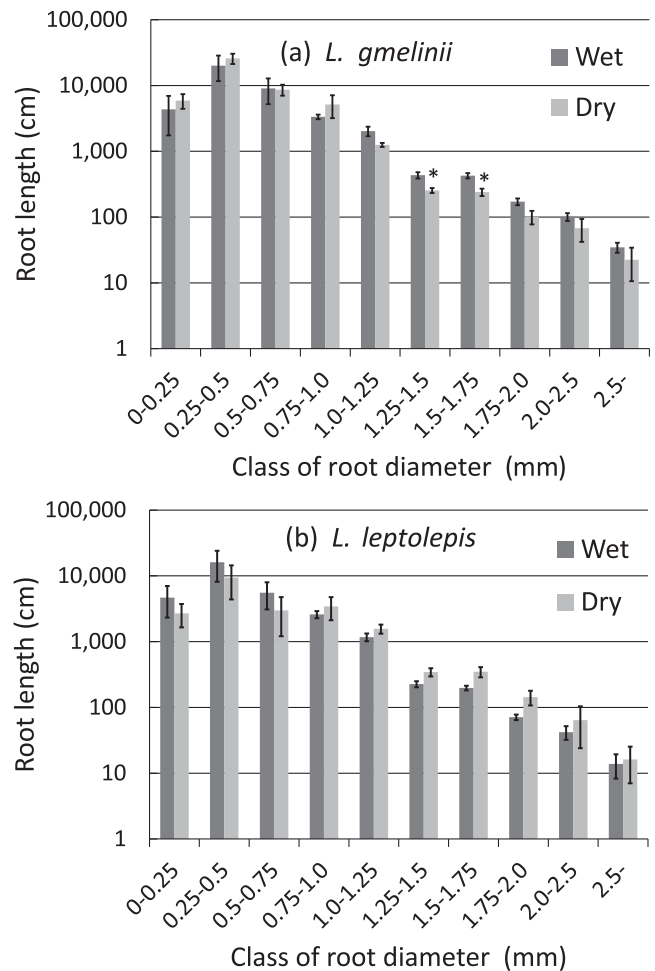


Figure 5. Root length classified by diameter for (a) *L. gmelinii* and (b) *L. leptolepis*. * indicates significant difference at $p < 0.05$ according to Fisher's LSD test.

increasing average root diameter and by decreasing root abscission.

In summary, under drought, the roots of *L. gmelinii* exhibit greater development of fine roots and a higher level of abscission, as corroborated by higher respiration than under wet conditions, even though photosynthesis decreases under the dry treatment. These results suggest that in *L. gmelinii*, both allocation of photosynthetic products to roots and root activity decrease under wet conditions compared with drought conditions, or that wet conditions constitute a stress for roots genetically adapted to drought conditions. On the contrary, *L. leptolepis* showed higher production, abscission, and respiration rates of roots under wet conditions suitable for growth in plants adapted to more temperate and wetter regions. From these opposing results in two larch species under dry and wet conditions, wet conditions are apparently less favorable for *L. gmelinii* than drought conditions. The decreased tendency of *L. gmelinii* to produce fine roots under wet conditions might have negative adaptive effects, because fine roots are also an important organ for acquisition of nutrients.

In conclusion, *L. gmelinii* adapted to dry conditions changed allocation of photosynthetic products and then

decreased fine roots under wetter soil water condition. That is, the recent elevations in soil water conditions in eastern Siberia may adversely affect the growth of larch trees, rather than the expected mitigation of water stress. It is suggested that the response of *L. gmelinii* roots to wet conditions, including decreases in respiration and production of fine roots, could be a cause of the recent decline in Siberian larch populations in eastern Siberia.

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