Polar Science 10 (2016) 160–166

Contents lists available at ScienceDirect

Polar Science

journal homepage: http://ees.elsevier.com/polar/

Response of larch root development to annual changes of water conditions in eastern Siberia

Chisato Takenaka [a,*], Mie Miyahara [a], Takeshi Ohta [a], Trofim C. Maximov [b]

[a] Graduate School of Bioagricultural Sciences, Nagoya University, Nagoya 464-8601, Japan
[b] Plant Ecological Physiology & Biochemistry Laboratory Institute for Biological Problems of Cryolithozone of Siberian Division of Russian Academy of Sciences, 41 Lenin Ave., Yakutsk 678891, Russia

ARTICLE INFO

Article history:
Received 5 August 2015
Received in revised form
4 February 2016
Accepted 15 April 2016
Available online 19 April 2016

Keywords:
Larch
Soil water content
Root distribution
Memory effect

ABSTRACT

Eastern Siberia is characterized by continuous permafrost, and has recently been exposed to the effects of climate change. Larch, which is the dominant tree species, has been subject to major environmental changes including fluctuations in soil water content. The purpose of this study was to clarify the responses of mature larch tree roots to changes in soil water conditions. We established a treatment plot in a larch forest, and artificially changed the soil water conditions by covering the ground surface with a vinyl sheet, and from 2004 to 2006 monitored root development through root windows. The vinyl sheet maintained high levels of soil water content, even though the ambient conditions varied from dry in 2004 to wet in 2005 and dry in 2006. In the treatment plot the plants adapted to the wet conditions by decreasing vertical root development. In contrast, roots of plants in the control plot developed to the subsurface layer, even in 2005, and did not develop vertically in 2006 despite the drought. We conclude that larch adapted to the annual changes in soil water content by changing the vertical distribution of roots, and that this reflected a memory effect.

1. Introduction

The effects of climate change on forest ecology has been the subject of much research by forest scientists, who have focused on aspects including drought stress caused by global warming, increased CO_2, and waterlogging resulting from hydrological changes related to climate change. In these studies the physiological responses of trees to various environmental changes have been widely investigated (e.g., Saxe et al., 2001; Way and Oren, 2010; Anderegg et al., 2013; Stinziano and Way, 2014). Eastern Siberia is located in a continuous permafrost region where low levels of precipitation and extremely cold conditions characterize the continental climate; boreal forests termed light taiga dominate this region. Large annual fluctuations in the water balance in eastern Siberian forests have recently been reported (Ohta et al., 2008). Iwasaki et al. (2010) investigated forest decline in eastern Siberia during 2007, and concluded that elevated soil water content caused by high levels of precipitation had a negative effect on larch trees. Ohta et al. (2014) measured the water balance changes in the eastern Siberian larch forest over 14 years (1998–2011), and classified these years into three categories based on the annual precipitation: normal (1998–2000, 2009–2011); dry (2001–2004); and wet (2005–2008). Thus, the forests of eastern Siberia can be considered ecosystems sensitive to climate change.

Larch is a dominant tree species in eastern Siberian forests. The soil water content in this area is highly variable, and characterized by high moisture content (approximately 40%) during the permafrost melting season, and extremely low content (up to 5%) during mid summer (Ohta et al., 2008). The water content is affected by precipitation, but also by the thawing depth of the permafrost. Ohta et al. (2008) reported a major change in the mean maximum permafrost thaw depth, from 127.0 cm in 1998–2003 to 182.7 cm in 2004–2006. Thus, it is assumed that larch trees have developed specific strategies to survive extreme changes in water conditions during the growing season and annually.

To counteract drought stress under extreme water conditions, plants have various generalized root adaptation strategies, including increased root biomass ratio (Psarras and Merwin, 2000), the formation of branching or fine roots (Jupp and Newman, 1987; Rodrigues et al., 1995; Chiatante et al., 1999), and the development of deeper root systems to access higher levels of soil moisture at

* Corresponding author.
E-mail address: chisato@agr.nagoya-u.ac.jp (C. Takenaka).

http://dx.doi.org/10.1016/j.polar.2016.04.012

depth (Molyneux and Davies, 1983; Tsuji et al., 2005). These strategies are very important in enabling plants to obtain water under drying conditions. However, most of the studies noted above were conducted on herbaceous plants or small tree saplings. Niinemets (2010) reviewed the response of forest trees at various stages of maturity (from saplings to mature plants) to various stresses, and showed that the responses depend on the tree age and size. It is important to understand the strategies that mature trees use to cope with serious soil water stress, as this will enable assessment of the effects of climate change on forest ecosystems. However, little information is available because of the difficulties associated with the study of mature trees, relative to saplings, seedlings, and grasses. In addition, most studies on the responses of plants to various stresses have been conducted over only one growth season (e.g., Niinemets and Keenan, 2014). However, to assess the effects of climate change on plants it is important to understand their long-term (exceeding several growing seasons) physiological response to various stresses in situ. Knowledge on the response of mature trees to wet conditions in eastern Siberia would be valuable, but is currently lacking. Based on pot experiments involving seedlings of *Larix gmelinii*, which is a common tree species in eastern Siberia, we found that the allocation of photosynthetic products to roots decreased under wet conditions (Miyahara et al., 2011). Therefore, we hypothesized that in eastern Siberia the root system of mature larch trees adapts to wet rhizosphere conditions, enabling survival under major changes in soil water conditions.

The purpose of this study was to clarify the responses of roots of mature larch trees to changes in soil water conditions, particularly to the wet conditions caused by permafrost thaw. To achieve this we made field observations over several years in a dedicated plot in a larch forest in which the soil water conditions were changed artificially by covering the ground surface with a vinyl sheet. We monitored the root development through a root window set in the rhizosphere of a mature larch tree.

2. Materials and methods

2.1. Site description and study plot

The study was conducted in the Spasskaya Pad experimental forest (62°15′18″ N, 129°37′08″ E) of the Institute for Biological Problems of Cryolithozone, Russian Academy of Sciences. The forest is located near Yakutsk City, Sakha Republic, Russia. This region is characterized by continuous permafrost, and the depth of the active permafrost layer during summer fluctuates from approximately 1.2 m deep (for example in 2006) to > 2.0 m deep (for example in 2007). Soil in this area comprises clay mixed with sand layers. The forest stand is dominated by the larch species *Larix cajanderi* Mayr., which is closely related to *Larix gmelinii* (Abaimov, 2010). In this area the tree density is approximately 840 trees ha^{-1}, the mean stand height is 18 m, and the mean tree age is approximately 180 years old. The understory vegetation comprises *Vaccinium vitis-idaea* and *Arctous erythrocarpa*. The mean annual temperature and precipitation are −10.2 °C (1961–1990) and 260 mm (1998–2006; S.D. 82 mm), respectively (Ohta et al., 2008).

During August 2003 we established two plots (15 m × 11 m each) in a flat area. One plot acted as a natural control, and the other as a treatment plot in which the ground surface was covered with a vinyl sheet to artificially induce changes in the soil moisture. In each plot three target trees were chosen for observation of root development. In the treatment plot we dug a trench of 50 cm depth around the plot, and inserted vinyl sheets into the trenches to prevent the lateral intrusion of water. The soil moisture in each plot was measured at 10 cm, 50 cm, and 80 cm depths from June to the beginning of August in the years 2004, 2005, and 2006, using a time domain reflectometry (TDR) sensor (sensor: EC-10; logger: Em5; Decagon Devices, Inc.). A calibration conversion was applied to the TDR data to provide volumetric water content values.

2.2. Observation of roots

We established root windows for each of three target trees in each plot to enable observation of the growth of larch roots (Fig. 1). A hole was dug 1 m from the larch trunk, and a cross section was cut toward the target larch tree (1 m wide × 50 cm deep). The depth of the cross section was based on the results of Kajimoto et al. (2003), who studied the root system of *L. gmelinii* in central Siberia. To observe the larch root system we fixed a transparent polyethylene terephthalate board to the cross section surface. The cross section was periodically photographed using a digital camera. To prevent water inflow, the observation holes were filled with sandbags, which were removed during the observation times. During July and September 2005 the roots abutting the root window were evaluated based on the total root length and the branching index (BI), where BI = (total root length − total length of primary root)/total length of primary root (Morita and Collins, 1990). To quantify the root growth angle we counted the number of roots and their elongation angle, relative to the horizontal. These data were calculated from the root window images in 2005 using a free software (LIA32; Yamamoto, 2005).

2.3. Root sampling

We collected root samples using a core sampler (5 cm diameter, 30 cm length). A soil core was taken 50 cm from the trunk of the larch tree in the middle of July 2004, 2005, and 2006. We choose sampling points where there was no understory vegetation. Six cores were taken in each plot in each year. Each soil core was divided into two depth layers (surface layer: 0–10 cm; subsurface layer: 10–30 cm), and the root material in each layer was separated from the soil.

2.4. Evaluation of the distribution of larch roots

Following careful separation of larch roots from those of other plants, and washing using an ultrasonic cleaner, the larch root samples from each layer were weighed to determine the root mass density. After 2005, the root length was determined from a scaled photograph, using LIA32 (Yamamoto, 2005). The root length density in each layer was calculated as the total root length per unit volume of soil. Following measurement of the root length, the root samples were placed in liquid nitrogen and stored in a freezer for transport to Japan for abscisic acid (ABA) analysis.

2.5. Analysis of root abscisic acid

The ABA content was determined using a modification of the standard method described by Hirai (1994). A total of 1.0 g of frozen root sample obtained from the surface layer was ground and homogenized in 50 ml of ice-cold 80% acetone containing 10 mg of 2,6-di-t-butyl-4-methyl phenol (as an antioxidant; Milborrow and Mallaby, 1975) and 0.1 g polyvinylpyrrolidone. The homogenized sample was filtered through a No. 5C filter, and the filtrate was purified to an ABA-like substance according to Hirai (1994). The ABA was quantified using a Shimadzu HPLC (pre-column: Shin-Pack GRD-ODS; separation column: STR ODE-II; detector: UV–VIS SPD-10A at 254 nm; analyzer: CTO-10A). A mixture of 0.1% phosphate and methanol (65:35) was used as the eluent solution, using a flow rate of 1.0 mL/min at 40 °C. The measurements were replicated three times.