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# Acclimation and adaptation of leaf photosynthesis, respiration and phenology to climate change: A 30-year *Larix gmelinii* common-garden experiment

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ABSTRACT

Acclimation and adaptation of leaf physiology and phenology to climate change have attracted substantial attention from forest ecology and global change science communities, but partitioning these two components in situ is challenging especially for adult trees. Here, we examined seasonal variations in leaf photosynthesis, respiration and phenology of Dahurian larch (*Larix gmelinii*) trees that were originated from six provenances and grown in a common garden for 30 years; and we partitioned these variations into genetic adaptation and phenotypic acclimation. Our results showed that both area-based maximum net photosynthetic rate ($P_{max\text{-}a}$) and dark respiratory rate ($R_d$) differed significantly among the provenances, and co-varied with leaf nitrogen concentration and the environmental factors of the seed-source sites, which provides evidence for genetic adaptation of the leaf physiology to climate change. However, the leaf phenology (i.e., leaf unfolding and shedding) of the six provenances converged in the common garden, and was correlated with the local temperature, suggesting phenotypic acclimation of the leaf phenology to local habitat. The provenance differences in the $P_{max\text{-}a}$ and $R_d$ varied with the growing stages, suggesting that measuring time at different growing stages can affect the comparison of the $P_{max\text{-}a}$ and $R_d$ among the provenances. The temporal patterns of the $P_{max\text{-}a}$, $R_d$ and their correlations with the seasonal changes in the local temperature were indicative of a consistent thermal acclimation, but the magnitude and direction of the acclimation varied with temporal scale and provenance. The trees originated from cold habitats tended to have less thermal acclimation of $P_{max\text{-}a}$ and $R_d$ to local temperature, implying that the trees from the cold edge of the larch range likely exhibit less responses to climate warming. Collectively, the acclimation and adaptation of the leaf physiology and phenology of Dahurian larch to climate change are of significance in managing and modeling responses of this important species in the Eurasian boreal forests to climate change.

## 1. Introduction

Global climate change has the potential to alter forest ecosystem function and structure (Gunderson et al., 2000), which is projected to threaten the survival of sensitive tree species and lead to local extinction or range migration (Soja et al., 2007; Shuman et al., 2011). Such effects of climate change on tree survival, growth and development are mainly determined by the phenotypic acclimation and genotypic adaptation of tree ecophysiology (Oleksyn et al., 1998a; Walther et al., 2002; Cleland et al., 2007; Kremer et al., 2012). Partitioning these two components, therefore, is critical to understanding the underlying mechanisms of tree responses to climate change, and provides a theoretical framework for predicting vegetation distribution under global change scenarios. Leaf photosynthesis (*P*) and respiration (*R*) play vital roles in the material cycle and energy flow of forest ecosystems, and thus their responses to climate change have attracted substantial attention from forest ecology and global change science communities (Reich et al., 2015; Aspinwall et al., 2016; Heskel et al., 2016; Reich et al., 2016). Previous studies on acclimation and adaptation of *P* and *R* to climate change are mostly for seedlings (Reich et al., 1998; Gunderson et al., 2000; Bresson et al., 2011; Reich et al., 2016); and partitioning these components and exploring the underlying drivers remain challenging especially for adult trees in natural settings.

Common-garden experiment is an effective approach to detecting acclimation or adaptation of trees to climate change in natural settings. Planting provenance trees from different climates in the same common garden and investigating their *P* and *R* differences among the provenances are conducive to understanding their responses to climate

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**Table 1**
The geographic and climatic conditions of the common garden experiment of the six provenances of Dahurian larch and their seed-source sites, and current characteristics of the trees.*

| Provenance (code) | Lat (°N) | Long (°E) | Alt (m) | MAT (°C) | MAP (mm) | MAE (mm) | MACT (°C) | AI | LMA (mg·cm$^2$) | DBH (cm) | H (m) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Tahe (TH) | 52.19 | 124.22 | 357 | −2.30 | 467 | 971 | 1671 | 1.76 | 7.92b | 18.5b | 14.10b |
| Genhe (GH) | 50.62 | 121.95 | 980 | −0.50 | 466 | 1100 | 1298 | 2.20 | 8.59ab | 19.0b | 14.50b |
| Zhongyangzhan (ZYZ) | 50.45 | 125.20 | 230 | 0.58 | 482 | 1370 | 1780 | 2.43 | 9.17a | 17.4b | 13.47b |
| Sanzhan (SZ) | 49.62 | 126.80 | 160 | −0.29 | 535 | 1126 | 1650 | 1.84 | 8.60ab | 20.6ab | 15.40ab |
| Wuyiling (WYL) | 48.67 | 129.42 | 300 | −0.49 | 570 | 1043 | 1851 | 1.60 | 7.94b | 23.8a | 17.80a |
| Hebei (HB) | 47.55 | 130.42 | 120 | 2.60 | 554 | 1238 | 2456 | 1.86 | 8.23b | 23.6a | 17.27a |

* Meteorological data of the seed-source sites (means between 1974 and 2005) were obtained from the local long-term meteorological stations established by the State Forestry Administration of China. Lat: latitude; Long: longitude; Alt: altitude; MAT: mean annual temperature; MAP: mean annual precipitation; MAE: mean annual evaporation; MACT: mean annual cumulative temperature ≥10 °C; AI: mean growing season aridity index; LMA: leaf mass per area; DBH: tree diameter at breast height; H: tree height. The different lowercases in the columns of LMA, DBH and H denote significantly different groups among the provenances ($\alpha = 0.05$).

change (Reich et al., 1996; Martin et al., 2007; Frei et al., 2012). To date, however, the results from common-garden experiments are inconsistent on differences in *P* and *R* among provenances. For example, Oleksyn et al. (1998a) studied 54 provenances of Norway spruce (*Picea abies*) from eight altitudinal transects and showed that the mass-based maximum net photosynthetic rate and dark respiratory rate differed significantly among the provenances and increased with altitude of the seed origins; and these differences were suggested to be driven by the genetic adaptation to the original habitats. Similar results were found in the studies of six *Eucalyptus* provenances, five *Metrosideros polymorpha* provenances and six *Fagus sylvatica* provenances (Cordell et al., 1998; Lewis et al., 2011; Robson et al., 2012). However, Bresson et al. (2011) documented a strong phenotypic acclimation of most leaf photosynthetic parameters for 14 *Quercus petraea* provenances and 10 *Fagus sylvatica* provenances; the genetic differentiation among the provenances only accounted for 0–21% of the total phenotypic variation in the leaf photosynthetic capacity. Tjoelker et al. (2008) also reported that the difference in respiration of 20 provenances of jack pine (*Pinus banksiana*) was relatively small and largely unrelated with the climate of the seed-source origin; and they suggested that acclimation in *P* and *R* may be common and probably more important than genetic adaptation.

There are several potential reasons for the discrepancy of different studies above. First, some studies measured the *P* or *R* only once in the growing season without discussing the seasonal dynamics. Across the growing season, the leaves of temperate trees respond to the climatic seasonality by changing leaf phenology, which may have strong effects on the *P* and *R*. For example, it has been showed that the provenances from cold climates or high latitudes, when grown in a common garden, tended to bud-flush later in early growing season and shed leaves earlier in late growing season than the provenances from warm climates or low latitudes (Deans and Harvey, 1995; Mimura and Aitken, 2007; Jensen et al., 2008). It is unclear, however, whether such asynchrony of leaf phenology leads to inconsistency of the *P* and/or *R* of the provenances across the growing season. Second, previous studies often explored relationships between *P* or *R* and temperature in a common garden by mixing the data from all provenances. It remains unclear whether the responses of *P* and/or *R* to seasonal variation in temperature differ among provenances. It has been reported that tree species from the cold edge of their range exhibit more positive responses to climate warming than those from the warm edge (Reich and Oleksyn, 2008; Peng et al., 2011; Reich et al., 2015), but whether such phenomenon occurs for a specific tree species with different provenances needs to be explored.

Dahurian larch (*Larix gmelinii*) is the most important tree species in Chinese boreal forests, and is an ideal species for exploring response of trees to climate change because of its vast distribution range (Gower and Richards, 1990; Wang et al., 2001; Leng et al., 2008). To explore potential differences in the tree physiology among provenances, a common-garden experiment of six provenances of Dahurian larch was established 30 years ago at the southern boundary of its range. In this study, we measured the seasonal dynamics in the leaf *P* and *R*, phenology, and nitrogen concentration for three continuous years (2009–2011). Our specific objectives were to (1) examine the differences in the leaf *P* and *R* among the larch provenances at each growing stage across the season and partition the differences into phenotypic acclimation to the local environment and genetic adaptation to their native habitats, and (2) explore relationships between the *P* or *R* and the seasonal changes in the local temperature. We hypothesized that (1) both *P* and *R* of the provenances differed at each growing stage due to their differences in leaf phenology and nitrogen concentration (Reich et al., 1996; Oleksyn et al., 2002; Oleksyn et al., 2003; Tjoelker et al., 2008), and the differences were mainly under the genetic control (Wright et al., 2004; Reich et al., 2006); and (2) both *P* and *R* showed acclimation to the seasonal variation in local temperature, but the provenances from the cold habitats would exhibit a more positive response than those from the warm habitats (Reich et al., 2015).

## 2. Materials and methods

### 2.1. Common garden experiment and site conditions

The common garden experiment was conducted at the Maoershan Forest Ecosystem Research Station (MFERS) in northeastern China (45°24′N, 127°40′E, 300 a.s.l.). The climate is a continental monsoon climate with mean annual precipitation of 629 mm, mean annual air temperature of 3.1 °C, mean annual evaporation of 864 mm, mean annual cumulative temperature ≥10 °C of 2283 °C, and mean growing season aridity index of 1.23. The soil is dark brown soil. The experiment included six provenances of Dahurian larch across its Chinese range, i.e., Tahe (TH), Genhe (GH), Zhongyangzhan (ZYZ), Sanzhan (SZ), Wuyiling (WYL), and Hebei (HB) (Table 1). The seed-source sites of the six provenances spanned ~4° in latitude and ~5 °C in mean annual temperature.

Seeds were collected from the original sites of the six provenances in the autumn of 1980 (Yang et al., 1990), and were sown in the nursery at MFERS early in the spring of 1981. The 2-year-old seedlings of the six provenances were transplanted at a well-drained site that was located on a southwest-facing gentle mid-slope in the spring of 1983. The experimental design was randomized completely blocking design, including five blocks with a 10-m buffer in between, six plots each block with a 4-m buffer in between, and 80 trees from only one provenance each plot. The trees were planted in a 1.5 m × 2.0 m spacing. Twice thinning was conducted in 1997 and 2001, respectively, and the final spacing was 4.5 m × 4.0 m.

### 2.2. Observing leaf phenology

Since it is difficult to access the tree canopies (~18 m above the ground surface, Table 1) and labor-intensive, we sampled three representative trees for each provenance within only one block by constructing several 15-m high wooden scaffolds, and examined 5–10