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Species-specific tree growth and intrinsic water-use efficiency of Dahurian larch (*Larix gmelinii*) and Mongolian pine (*Pinus sylvestris* var. *mongolica*) growing in a boreal permafrost region of the Greater Hinggan Mountains, Northeastern China

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ABSTRACT

Increasing air temperature and atmospheric CO_2 concentrations (C_a) can profoundly affect photosynthesis and intrinsic water-use efficiency (*iWUE*). However, the response of trees in boreal permafrost regions to rapid warming and C_a increases is poorly constrained by prior research. Here, we evaluated long-term changes in growth (using regional curve standardization [RCS]) and *iWUE* of Dahurian larch (*Larix gmelinii*) and Mongolian pine (*Pinus sylvestris* var. *mongolica*) in the boreal permafrost region of northeastern China and species-specific responses to increasing C_a and temperature. From 1930–2010, RCS growth of Dahurian larch and Mongolian pine decreased, while *iWUE* increased by 25.5 and 21.1%, respectively. RCS growth of both species was negatively correlated with winter temperatures, but Mongolian pine depended most strongly on previous December to current February temperatures and Dahurian larch depended most strongly on March temperatures. Moisture conditions only weakly influenced growth.

We found similar long-term changes of tree-ring $\delta^{13}C$ in the two species. Carbon isotopic discrimination of Dahurian larch and Mongolian pine was determined mainly by growing season temperature (positive) and moisture (negative), but with different signal strengths, suggesting that stomatal conductance influenced tree-ring $\delta^{13}C$. Commonality analysis showed that RCS growth was affected mainly by temperature, but also by the combined effect (interaction) of *iWUE* and temperature. However, the contribution of *iWUE* alone was lower for Mongolian pine. Our results suggest that the increased *iWUE* caused by increasing C_a will not improve tree growth sufficiently to compensate for temperature-induced water stress. The rate of temperature increase has slowed around 1990, which would have stabilized the degree of temperature-induced water stress, and this could be helpful to tree growth recovery in the permafrost region of northeastern China.

1. Introduction

Boreal forests are vulnerable ecosystems that need to be monitored carefully to detect adverse changes in their response to the unprecedented modern rates of climate change (Babst et al., 2010). Studies of high-latitude and high-elevation forest ecosystems are important because of the forest's sensitivity to conditions in the frozen ground and alterations of the water environment caused by increasing temperatures (Rittenhouse and Rissman, 2015) and because of the forests vulnerability to regional and global climate change (Bonan, 2008). Compared with the global temperature increase of about 0.12 °C per decade from 1951 to 2012 (IPCC, 2013), the mean temperature in northeastern China's permafrost and seasonally frozen regions increased by 0.35 °C per decade from 1961 to 2012 (Wang et al., 2013). Therefore, this area is one of the areas responding most rapidly to global climate change (Sun et al., 2006). Importantly, the forests in northeastern China

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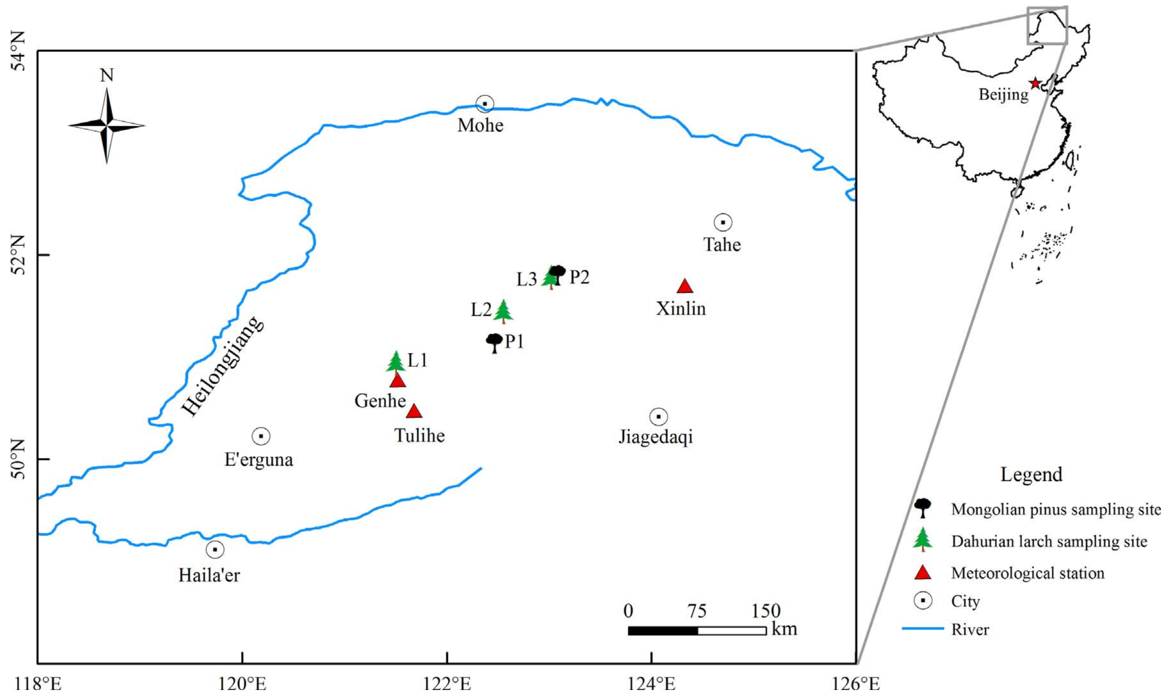

Fig. 1. Map of the study region, distribution of the sampling sites, and the locations of nearby meteorological stations.

accounted for about 30% of the national land area in 2010 and stored nearly half of the national ecosystem carbon (Zhang et al., 2014; Zhang and Liang, 2014). Thus, these forests contribute greatly to the global carbon cycle (Boisvenue and Running, 2006). Moreover, climate-driven changes in their carbon balance may represent an important feedback to regional or global the climate system.

Global CO_2 concentrations have increased by 40% since pre-industrial times, with the overall mean concentration reaching 391 ppm in 2011 (IPCC, 2013), as a result of emissions from fossil fuel combustion and net changes in terrestrial emissions due to land use change. Globally, forest dynamics are expected to respond to the resulting climatic warming and increasing atmospheric CO_2 concentration, but long-term forest responses, especially in permafrost and boreal areas, are poorly understood.

Dendroecology has been widely used to study past climate change (Fritts, 1976; Chen et al., 2013; Derose et al., 2014), including extreme events (e.g. extreme drought, flooding, snowstrom, rock falls and avalanches) (Hartl-Meier et al., 2014). In addition, tree-ring widths also can be used to study shorter-term growth responses of trees to warm-season temperatures (Wilson et al., 2007) and to monitor changes in forest dynamics (Babst et al., 2010) and tree growth (Mantgem et al., 2009; Wang et al., 2012; Liu et al., 2014). Compared to tree-ring widths, tree-ring stable carbon isotope ratios ($\delta^{13}C$) have proven to be an effective tool to estimate the intrinsic water-use efficiency (*iWUE*) at sites around the world (Waterhouse et al., 2004; Silva et al., 2009; Nock et al., 2011; Liu et al., 2014). *iWUE* of trees, which represents the ratio of photosynthetic assimilation (carbon uptake) to stomatal conductance (water loss through transpiration), has been used as an indicator of carbon–water relationships in plants (Waterhouse et al., 2004; McCarroll and Loader, 2004; Liu et al., 2014; Trahan and Schubert, 2016). *iWUE* has generally increased during the 20th century, and the increase has generally been explained as a consequence of the CO_2 fertilization effect, in which increased atmospheric CO_2 concentrations (C_a) would simultaneously increase photosynthetic assimilation and at a given stomatal conductance (Saurer et al., 2004; Waterhouse et al., 2004). This means that trees could be uptake more carbon from atmospheric and less water loss through transpiration (Saurer et al., 2004; Trahan and Schubert, 2016). However, the effect of increase in atmospheric CO_2 is not sufficient to compensate for temperature-induced water stress on tree growth (Silva and Horwath, 2013; Lévesque et al., 2014; Tei et al., 2014). In addition, the nutrients (e.g. N, P, etc.) could also influence tree growth. High nutrient availability can increase water use efficiency and tree growth (Gessler et al., 2017). On the other hand, N limitation can amplify C starvation (McDowell, 2011), which can negatively impact on tree growth.

A few studies based on tree-ring widths in northeastern China indicated that the dynamics of forest growth are highly sensitive to climate change (Liu et al., 2009; Zhang et al., 2014**).** These studies revealed that the forest has been experiencing a warming environment and increasingly strong water stress (Chen et al., 2013). However, species-specific responses to increasing C_a and climatic warming have not yet been described in this region. To provide some of the missing data, we studied the responses of the two dominant species in this ecosystem: Dahurian larch (*Larix gmelinii*) and Mongolian pine (*Pinus sylvestris* var. *mongolica*). We hypothesized that against the background of climate warming, trees will face warmer winters and more intense water stress in the summer due to significant alterations of the water environment in permafrost soils and temperature-induced increases in forest transpiration. Our specific goals were (i) to compare the long-term trends in growth and *iWUE* of Dahurian larch and Mongolian pine trees, (ii) to determine the species-specific differences in the climatic factors that most strongly affected tree growth and $\delta^{13}C$ in tree rings of Dahurian larch and Mongolian pine, and (iii) to explore the possible linkages between tree-growth and *iWUE* of trees growing in permafrost regions and their responses to global warming.

2. Materials and methods

2.1. Study area and climate

The Greater Hinggan Mountains (Fig. 1) lie in a region with a typical semi-humid continental monsoon climate in northeastern China (Liu et al., 2013). In winter, dry and cold air masses enter the study area, changing to wet and warm air masses in summer, leading to distinct cold/dry and warm/wet seasons. The Xing'an–Baikal permafrost in this region is the second-largest expanse of permafrost in China,