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Growth and physiological responses of larch trees to climate changes deduced from tree-ring widths and $\delta^{13}C$ at two forest sites in eastern Siberia

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Abstract

Tree-ring chronologies of ring width and stable carbon isotope ratios ($\delta^{13}C$) over the past 160 years were developed using living larch trees at two forest sites, each with different annual precipitation, in eastern Siberia: Spasskaya Pad (SP) (62°14′N, 129°37′E); and Elgeeii (EG) (60°0′N, 133°49′E). Intrinsic water-use efficiency (iWUE) was derived from tree-ring $\delta^{13}C$. The physiological responses of the larch trees to climate varied between these sites and over time. Ring widths correlated negatively with summer temperatures at SP, where summer precipitation is lower than at EG, probably due to temperature-induced water stress. Since the 1990s, however, the negative effect of warming has been more severe at EG, where the productivity of larch trees is higher than at SP. A greater reduction of larch tree growth and higher increase rate of iWUE at EG reflects greater temperature-induced water stress, which is incident to the larger forest biomass. Our results suggest that effect of increase in atmospheric CO_2 on larch tree growth is not sufficient to compensate for temperature-induced water stress on larch growth in eastern Siberia and differences in precipitation and forest productivity largely affect the larch tree response to changing climate in eastern Siberia.

Keywords: Eastern Siberia; Taiga; Tree-ring; Carbon isotope; Water-use efficiency

1. Introduction

Boreal forests occupy 17% of the earth's terrestrial ecosystems and store over 30% of terrestrial carbon (Kasischke, 2000), which greatly contributes to the global carbon cycle. The boreal forests in eastern Siberia, called taiga, consist of deciduous conifer larch

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and cover an area of 8.51 × 10^6 km^2, representing about 70% of the world's boreal forests (Kasischke, 2000; Food and Agriculture Organization, 2001). The study of boreal forest ecosystems is important, because of its sensitivity and vulnerability to regional and global climate changes (Bonan, 2008).

Dendroecological analysis is useful for studying the response of a forest ecosystem to a changing environment (Nikolaev et al., 2009; Sidorova et al., 2008, 2009). For the high-latitude northern forests, such studies focused largely on growth responses of trees to warm-season temperatures (e.g., D'Arrigo and Jacoby, 1993). On the other hand, a number of recent studies has shown a reduced sensitivity of tree growth to rising temperatures at least since 1960s (e.g., Wilson et al., 2007; D'Arrigo et al., 2008).

According to the physiology of trees, it is rather reasonable to consider that tree growth is controlled both by soil moisture and air temperature. Barber et al. (2000) suggested that temperature-induced drought might limit tree growth under the limited availability of soil moisture, using North American white spruces. Several other studies have also reported a decreasing trend in recent tree growth (e.g., Dulamsuren et al., 2010) and an increase in drought-related forest mortality in high-latitude regions (e.g., van Mantgem et al., 2009). Those suggest that droughts are related to warming temperatures. In eastern Siberia, dendroecological studies revealed a significant positive correlation between growth of larch trees and soil moisture content (Kagawa et al., 2003; Nikolaev et al., 2009). To the contrary, Iwasaki et al. (2010) reported that high soil moisture content caused browning and discoloration of larch needles in the summer of 2007.

The expected change in regional precipitation is still unclear, although the future climate projections by IPCC (2007) show an increase in average global precipitation. It is also uncertain whether increased precipitation enhances tree growth under the warming climate, especially in dry regions including eastern Siberia. Significant reduction in tree growth was reported for the regions where precipitations decrease with warming, e.g., Alaska (Barber et al., 2000; Wilmking et al., 2004), the Iberian Peninsula (Andreu et al., 2007; Sarris et al., 2007; Andreu-Hayles et al., 2011) and Mongolia (Dulamsuren et al., 2010). However, tree growth has not yet been well studied in dry regions like eastern Siberia.

Stable carbon isotope ratios ($\delta^{13}C$) in tree-rings have been used to show tree responses to changing environments (e.g., Saurer et al., 2004; Sidorova et al., 2008, 2009). Generally, tree-ring $\delta^{13}C$ reflects humidity and the availability of soil water (McCarroll and Loader, 2004). Intrinsic water-use efficiency (iWUE) is an indicator of internal regulation of carbon uptake and water loss in plants, and defined as the ratio of photosynthesis (A) to stomatal conductance for water vapor (g), which represents that transpiration is solely controlled by stomatal conductance without any atmospheric control. The iWUE can also be estimated from $\delta^{13}C$ values.

A number of studies has suggested that iWUE from tree-ring $\delta^{13}C$ is useful in investigating carbon–water relationship in plants (e.g., Saurer et al., 2004; Klein et al., 2005; Silva et al., 2009; Gagen et al., 2011; Nock et al., 2011; Andreu-Hayles et al., 2011; Linares and Camarero, 2012; Battipaglia et al., 2013). In addition, it should be noted that these studies mostly reported an increase in iWUE in the 20th century.

One of the major cause for the increase in iWUE can be the elevation in atmospheric CO_2 concentration (C_a). Recently, the elevated C_a (e.g., Keeling et al., 1995) has induced a change in carbon–water relationships, resulted in the changes in physiological responses of trees. Higher C_a can lead to higher carbon assimilation rate (CO_2 fertilization effect) and/or can save water by reducing stomatal conductance (g) (Field et al., 1995). The process of water saving is considered to result in the increase in iWUE. This formulation was supported by laboratory experiments (Ceulemans and Mousseau, 1994; Ainsworth and Long, 2005). However, natural ecosystems are more complicated so that iWUE can be affected by factors other than atmospheric CO_2 concentration (Saurer et al., 2004; Silva et al., 2009; Andreu-Hayles et al., 2011; Linares and Camarero, 2012; Battipaglia et al., 2013).

A tree-ring width and $\delta^{13}C$ study at Iberian pine forests (Andreu-Hayles et al., 2011) showed that stomatal conductance (g) was reduced due to low water availability, which also caused iWUE higher than expected solely from the increase in C_a. However, Linares and Camarero (2012) reported that the recent severe drought caused a decrease in iWUE improvement rate at a decayed fir (*Abies alba*) forest in northeast Spain, where the condition of the trees had reached a physiological threshold of adaptive capacity for drought. These studies suggest that changes in tree physiology are triggered by climate changes, and may vary depending on the species and/or environment. Additionally, McDowell et al. (2002, 2006) pointed out that responses of trees to the climate variation differ according to forest types and/or biomass productivity. To sum up, changes in iWUE are probably related to water budget in a forest. Therefore, although the recent