Coexisting responses in tree-ring $\delta^{13}C$ to high-latitude climate variability under elevated CO_2: A critical examination of climatic effects and systematic discrimination rate changes

Samuli Helama [a,*], Laura Arppe [b], Joonas Uusitalo [b], Hanna M. Mäkelä [c], Markku Oinonen [b], Kari Mielikäinen [d]

[a] Natural Resources Institute Finland, Rovaniemi, Finland
[b] Laboratory of Chronology, Finnish Museum of Natural History, University of Helsinki, Finland
[c] Finnish Meteorological Institute, Helsinki, Finland
[d] Natural Resources Institute Finland, Vantaa, Finland

A B S T R A C T

Dendroclimatic methods may quantify a factor or factors affecting $\delta^{13}C$ fractionation and thus help to reveal the signals archived in dendroisotope records over the long term. Gathering evidence suggests a repertoire of limitations for photosynthesis to occur, with an increasing possibility that more than one external factor may control the assimilation rate and thus the tree-ring $\delta^{13}C$ variations. Here we show that such a situation conceivably describes the tree-ring $\delta^{13}C$ data from northern timberline and further illustrate the use of dendroclimatic analyses in separating the coexisting signals in dendroisotope data. While the assimilation rate was primarily controlled by a photon flux, thereby allowing the tree-ring $\delta^{13}C$ to provide a proxy for past variations in irradiance, there was some evidence that also a temperature signal is directly present in the tree-ring $\delta^{13}C$ data, not merely as a function of an indirect correlate reflecting its interplay between sunshine/cloud cover. Over the period common to all instrumental records (1971–2011), both the sunshine hours and global radiation influenced the $\delta^{13}C$ from mid-June to mid-July, whereas the mean maximum temperatures (T_{MAX}) showed an impact on $\delta^{13}C$ from mid-July to mid-August. We assume that these climatic associations represent mainly non-stomatal limitations to assimilation rate. Possibly, this response may involve the mesophyll conductance to CO_2 transfer from intercellular spaces to chloroplasts, a factor found previously to pose a temperature responsive limitation to photosynthesis. After correction for the Suess effect, the $\delta^{13}C$ chronology exhibited a long-term decline attributable to discrimination rate changes under elevated atmospheric CO_2 concentration. We make a methodological contribution by comparing the various methods available from literature for estimating the magnitude of this bias in the $\delta^{13}C$ chronology. The robustness of the results indicated that this data shortcoming is not critical but can be corrected. The method inter-comparisons yielded very similar results, near the previously suggested change in discrimination of 0.0073‰ per ppmv CO_2. We recommend comparative assessments of discrimination rate change to be combined with dendroclimatic analysis.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

Reconstructions of past climate variability using the proxy data of biological (paleontological) origin may suffer from various sources of uncertainty. First, the proxy records are typically calibrated against the instrumental climate variables conventionally recorded at meteorological stations, however, these variables may not represent the climatic factors to which the organism providing the proxy are sensitive. Second, most of the organisms, including trees (Fritts, 1976), may be responsive concurrently to many variables, although a limited number of these will usually predominate. Third, the biological proxy data may be contaminated by non-climatic disturbances and physiological and age-related effects arising from ontogeny and ageing of individual organisms. The increasing use of tree-ring based stable isotope data to address

a wide range of environmental and late Quaternary research questions (McCarroll and Loader, 2004; Robertson et al., 2008) calls for better understanding of the elements that contribute to uncertainties in these records. For stable carbon isotopes, the $^{13}C/^{12}C$ ratio in plant carbon ($\delta^{13}C$) is commonly described using a classical model (Farquhar et al., 1982; Francey and Farquhar, 1982) as a function of $\delta^{13}C$ of CO_2 in the ambient air ($\delta^{13}C_{ATM}$), diffusional fractionation (a), carboxylation fractionation (b), and the ratio between the concentrations of CO_2 in intercellular spaces (c_i) and in the air (c_a) as follows:

$$\delta^{13}C = \delta^{13}C_{ATM} - a - (b-a)c_i/c_a \qquad (1)$$

Thus the factors decreasing c_i, such as deficit in moisture leading to stomatal closure, increase $\delta^{13}C$, whereas the factors increasing c_i/c_a, for example low light intensity, decrease $\delta^{13}C$. In this way the model shows the photosynthesis to be limited by the stomatal conductance on one hand and the rate of the photosynthetic machinery on the other. And herein lies the climatic significance of tree-ring $\delta^{13}C$ archives. The more limited the photosynthesis is by either one of these factors, the higher is the value of that tree-ring $\delta^{13}C$ data to inform about past variations in that variable. At sites where moisture availability rarely causes stomatal closure, the $\delta^{13}C$ fractionation may be attributed predominantly to CO_2 assimilation rate, such conditions commonly prevailing at the northern timberline (Young et al., 2010, 2012; Seftigen et al., 2011). In its simplified form the model (Eq. (1)) however ignores the influence of any additional factor on fractionation. In addition to stomatal conductance, photosynthesis may be limited by the mesophyll conductance as the CO_2 must diffuse not only through stomatal openings but from the site of intercellular spaces to the sites of carboxylation. Already Farquhar et al. (1982) presented a model for a situation where the concentration of CO_2 at the sites of carboxylation (c_c) is considerably less than c_i described as

$$\delta^{13}C = \delta^{13}C_{ATM} - a - (b-a)c_i/c_a + b\left((c_i - c_c)/c_a\right) \qquad (2)$$

where increase in $(c_i - c_c)/c_a$ occurs with increase in CO_2 assimilation rate. The photosynthetic limitation imposed by mesophyll conductance has recently been highlighted and shown to be commonly of similar magnitude as stomatal limitation (Flexas et al., 2008, 2012; Warren, 2008).

One of the key regions for development of dendroclimatic $\delta^{13}C$ data and long chronologies lies in northern Fennoscandia. The progress of dendroisotope work on *Pinus sylvestris* has proceeded in this area by producing $\delta^{13}C$ records from living and subfossil samples (Sonninen and Jungner, 1995, 1996), constructing an increasing number of living-tree site $\delta^{13}C$ chronologies (McCarroll and Pawellek, 1998), analyzing their signal strength and the multiple climatic effects on $\delta^{13}C$ variations (McCarroll and Pawellek, 1998, 2001; Hilasvuori et al., 2009; Gagen et al., 2007, 2008, 2011; Loader et al., 2013), comparing $\delta^{13}C$ records with other dendroclimatic proxy records (McCarroll et al., 2003, 2011), utilizing various statistical tests and approaches to build centennial and even millennium-long chronologies from living tree and subfossil $\delta^{13}C$ series (Gagen et al., 2007, 2008, 2011, 2012; Young et al., 2010, 2011, 2012), and finally using these proxy records for reconstructing the past climate variability (Gagen et al., 2007, 2011; Hilasvuori et al., 2009; Young et al., 2010, 2012; Loader et al., 2013). While the earlier papers made use of tree-ring $\delta^{13}C$ data as temperature-sensitive proxy records (Gagen et al., 2007; Hilasvuori et al., 2009), a more complex perspective of $\delta^{13}C$ data is now signifying its past variability either as proxy of cloud cover (Gagen et al., 2011; Young et al., 2012), sunshine and/or irradiation (Loader et al., 2013; Young et al., 2010). Assimilation rate has been assumed to occur under the influence of photon flux (Hari et al., 1981), the sunlight related parameters thus controlling the $\delta^{13}C$ variations. However, the influence of mesophyll conductance has not been previously

addressed as a factor of importance for the $\delta^{13}C$ proxy. It is noteworthy that temperature is one major source of variation in mesophyll conductance even for tree species and habitats where stomatal conductance is unrelated to temperature (Warren and Dreyer, 2006). Possibly, such a situation may prevail in northern Fennoscandia.

Apart from climatic factors, the variations of $\delta^{13}C$ in tree rings are driven by natural and manmade changes in atmospheric environment. In contrast to subtle naturally undulating isotopic composition of $^{13}CO_2$ through much of the Holocene, the anthropogenic change towards depleted ratios (more negative $\delta^{13}C$) over the course of the past two centuries is reflected in tree-ring $\delta^{13}C$ records (i.e. Suess effect) and forms a subject of correction with existing methodology (McCarroll and Loader, 2004; Leuenberger, 2007). Another, more debated issue arises from the elevated concentration of atmospheric CO_2, which may change the rate by which the plant discriminate against the heavy isotopes of carbon present in the atmosphere and available to the tree. This situation is more of a problem with a presumption that the discrimination rate changes may not be unique to tree species and habitat. Studying the $\delta^{13}C$ variation in tree rings of trees from arid environments, Feng and Epstein (1995) derived a response of the $\delta^{13}C$ to the atmospheric concentration of 0.02‰ per ppmv CO_2. A somewhat different response of 0.0073 per ppmv CO_2 was obtained by Kürschner (1996), his results thus being suggestive of a more subtle change in plant physiology and of less sizeable distortion over the recent end of the $\delta^{13}C$ chronology under elevating CO_2. So far there appears no consensus as for the suggested values. Clearly, the plant physiological responses to elevated CO_2 may not yet be fully understood. In the context of dendroisotopic analysis, there appears more than one available method for removing the non-climatic trend from the $\delta^{13}C$ chronology (McCarroll et al., 2009; Treydte et al., 2009). In some studies, the $\delta^{13}C$ chronology has been corrected by both of the suggested factors of correction (i.e. 0.0073 and 0.02‰ per ppmv CO_2) (Szymczak et al., 2012; Kern et al., 2013), although this approach results in alternative, hypothetical $\delta^{13}C$ chronologies that bifurcate systematically with elevating CO_2. We anticipate that such an approach may actually lead to subjective decisions as to whether one of the alternative scenarios proves a suitable model for assessing the recent trends in $\delta^{13}C$ chronologies. Dealing with the added uncertainty and complexity of the data, particularly over the recent decades, is especially troublesome considering a purpose of paleoclimatology to place the recent climatic trends in the context of past, natural variability. In northern Fennoscandia, the corrections for CO_2 concentration effects have been briefly compared for tree-ring $\delta^{13}C$ data from northern Sweden (Loader et al., 2013). The two independent methods (McCarroll et al., 2009; Treydte et al., 2009) were shown to give markedly similar results (Loader et al., 2013) when their dendroclimatic adjustment (Treydte et al., 2009) was accomplished by the discrimination change of 0.09‰ per ppmv CO_2, obtained using the July–August temperature as a reference instrumental variable. Soil moisture variables were not included in this testing as the $\delta^{13}C$ fractionation in these northern pines may be attributed predominantly to non-stomatal limitations (Young et al., 2010, 2012). Sunshine variables were not tested either, even though sunshine was actually suggested providing a more direct explanation for $\delta^{13}C$ variations in that data, the summertime sunshine hours/global radiation explaining much of the variance ($r^2 = 0.72$) in the short record (1984–1997) of photosynthetically active radiation (Loader et al., 2013).

Despite these dendroclimatic advances in analyzing the $\delta^{13}C$ data, there is a need for additional investigations in the same region, the northern Fennoscandia, with opportunities critically important for developing climate-sensitive $\delta^{13}C$ chronologies. First, the existing $\delta^{13}C$ chronologies make use of subfossil pinewood recovering the tree-ring based $\delta^{13}C$ variability roughly for the past