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## Reconstruction of altitudinal transportation range of leaves based on stomatal evidence: An example of the Early Pleistocene *Fagus* leaf fossils from central Japan

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## ABSTRACT

Fossil plant assemblages play a critical role in paleoenvironment estimation, especially for the Cenozoic. However, the extent that the fossil assemblage reflects the source forest is difficult to estimate. The comparison between modern assemblages and their subfossil assemblages shows a significant difference, indicating that the transportation of plant organs can affect the accuracy of paleoenvironment analysis. In this study, we aim to detect leaf transport based on stomatal frequency (stomatal index and stomatal density) variation of 30 fossilized *Fagus crenata* leaves from the Sayama Formation (1.54–1.66 Ma). We distinguished the sun and shade morphotype of fossil leaves by using undulation index and calculated stomatal frequency variation of only sun fossil leaves. Considering the stomatal index variation of fossil *Fagus crenata* leaves, the paleo-pCO<sub>2</sub> variation in a warm period between 1.54 Ma and 1.66 Ma was estimated as ca. 35.0 to 39.6 pa. Based on this paleo-pCO<sub>2</sub> variation, altitudinal transportation range of the Early Pleistocene fossil *Fagus crenata* leaves was estimated at over 1000 m. We presume that leaves of *Fagus crenata* in the fossil assemblage possibly had come from a wide range of altitudes near the fossil site during the Early Pleistocene. This provides an example of altitudinal transportation of plants before their deposition, which suggests a consideration when reconstructing the palaeovegetation and palaeoclimate from fossil assemblages.

### 1. Introduction

The transportation of plant organs before their burial (Astorga et al., 2016; Steart et al., 2006) is an important process in the formation of fossil assemblage. It can affect the composition of fossil flora, which complicates the reconstruction of paleoclimates and palaeovegetation. To increase the resolution of quantitative paleoclimate analysis (Mosbrugger and Utescher, 1997; Spicer et al., 2009; Su et al., 2010; Wilf, 1997), a better understanding of plant transportation in ancient times becomes necessary.

Transportation of plant organs has been recognized in modern sedimentation of leaf, fruit/seed, and pollen assemblages by comparison with the positions of their mother plants. Investigations of the taphonomical process of modern subfossil leaf assemblages from their source forests often indicate significant differences in their composition, which

are caused mainly by wind/water-aided transportation (Astorga et al., 2016; Ozaki, 1969). Water currents transport fruits and seeds into the areas far from their mother plants (Gee, 2005; Sims and Cassara, 2009; Vassio and Martinetto, 2012), while winged seeds are transferred for an extended distance by wind (Zheng et al., 2004). Pollen transportation has been studied for a long time, in relation to the pollen source area and sedimentary basin size. The pollen assemblage commonly includes pollen that is transported between 2 and 100 km away (Prentice, 1985; Prentice et al., 1987; Sugita, 1994); Pinaceae pollen is transported for more than 500 km (Dyakowska, 1947; Szczepanek et al., 2017).

Assemblages in ancient times also exhibit evidence of the long-distance transportation of plant organs. Holocene leaf fossil assemblages in the crevasse-splay deposits in an Alabama delta show that most of the plant remains cannot be assigned to the local flora and were transported long distances from the plant communities growing on the upper delta

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plains (Gastaldo et al., 1987). The possibility of plant transportation from a higher altitude is presumed from the composition of Cenozoic fossil floras with a mixture of subtropical evergreen trees (e.g., *Cyclobalanopsis*, *Actinodaphne*, *Cinnamomum*) and cool temperate and/or subarctic trees (e.g., *Abies*, *Picea*, and *Betula*), which inhabit different climate conditions (e.g. Huzioka, 1963). The altitudinal transportation might be estimated from the temperature difference between the distribution limits of the most thermophilous and the most cold-loving elements in assemblage components (e.g., Momohara et al., 2017). However, the altitudinal limit of plant distribution is decided by plural temperature parameters, along with the other environmental factors, such as precipitation, wind, snow depth, and geology (Cantón et al., 2004; Ozaki, 1969; Takahashi, 1962; Wolfe, 1993; Woodward and Williams, 1987). Therefore, proxy changing at a constant rate along altitude is necessary to estimate the altitudinal transportation of plant organs.

To clarify the altitudinal transportation of a leaf, we considered the stomatal frequency variation of leaves of one species as a possible proxy of the CO<sub>2</sub> partial pressure (*p*CO<sub>2</sub>) decreasing with altitude. The stomatal frequency of fossil leaves has been used as a proxy of paleo-CO<sub>2</sub> for a long time (e.g. Bai et al., 2015; Hu et al., 2015; Wang et al., 2015; Royer, 2003; Beerling and Royer, 2002; Rundgren and Beerling, 1999; Kürschner, 1997), while many reports suggest the potential of altimetry by using stomatal frequency that is sensitive to the *p*CO<sub>2</sub> change with altitude (Kouwenberg et al., 2007; McElwain, 2004). If one species of fossil leaves in an assemblage demonstrates a variation of stomatal

frequency larger than that observed in its modern population at the same altitude, we can estimate the altitudinal transportation range of leaves based on the predictable decrease in *p*CO<sub>2</sub> with altitude.

In this research, we studied the altitudinal change of stomatal frequency in modern *Fagus crenata* leaves to clarify the altitudinal transportation of leaves from a Lower Pleistocene Sayama Formation fossil assemblage. The detected altitudinal transportation can be used to explain the co-existence of elements that have different climatic requirements in the fossil assemblage (Ito et al., 2017).

## 2. Materials

### 2.1. Modern materials

*Fagus crenata* is a dominant element of the cool temperature forest in Japan and is distributed in a wide altitudinal range between ca. 600 and 2000 m a.s.l. in central Japan (Takahashi, 1962). For the present study, the extant, mature leaves of *Fagus crenata* were collected from 120 individuals at different elevations ranging from 250 to 1980 m a.s.l. in eight localities. In most of the localities, five individuals were collected at an altitudinal interval of 100 m (Fig. 1; Supplementary data Table S1). As sun and shade leaves have different stomatal frequencies (Kouwenberg et al., 2007; Kürschner et al., 1996; McElwain, 2004; Royer et al., 2001), we collected sun and shade leaves from different portions of the trees. Sun leaves were collected from the surface in the top or southern side of the canopy, while shade leaves were collected

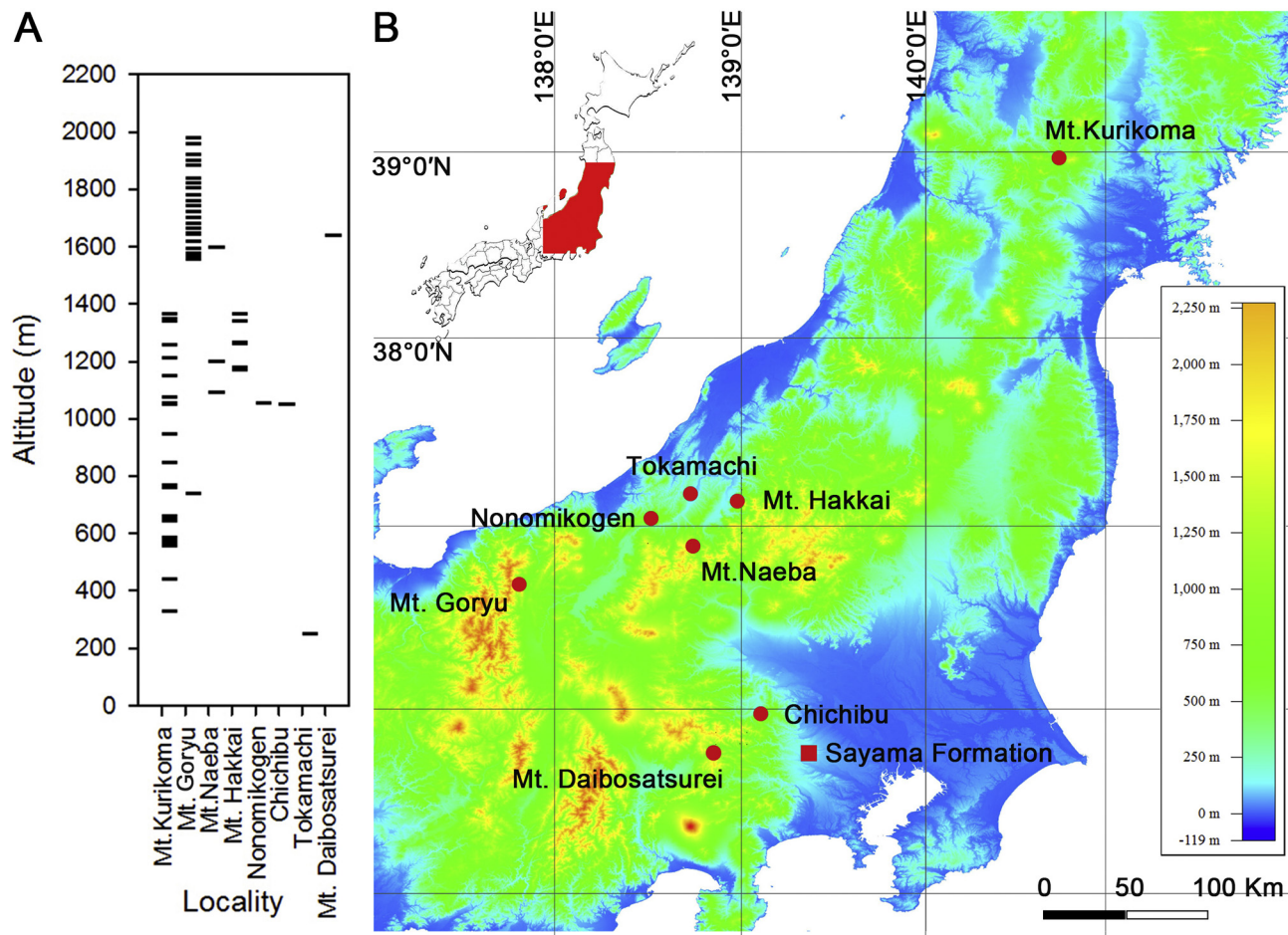


Fig. 1. Map showing the sampling sites for extant and fossil leaves of *Fagus crenata*.

(A) Altitude information of modern sampling sites from eight localities. (B) Eight localities where extant leaves of *Fagus crenata* were collected (circles) and one fossil site of the Lower Pleistocene Sayama Formation in Sayama Hill where fossil leaves of *Fagus crenata* were collected (square). The original map was downloaded from Consortium for Spatial Information (CGIAR-CSI; <http://www.cgiar-csi.org/>).

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