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Paleovegetation and climatic conditions in a refugium of temperate plants in central Japan in the Last Glacial Maximum

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ABSTRACT

Paleovegetation and climatic conditions in the Last Glacial Maximum (LGM; ca. 24.4 and 20.1 ka) were reconstructed based on plant macrofossils and pollen assemblages deposited in a sandy channel outcropped in the Hanamuro River, Ibaraki Prefecture, central Japan. The plant macrofossil assemblages were composed of 31 arboreal and 76 herbaceous taxa. Occurrence of plants with various habitat preferences exhibited distribution patterns of highly diverse vegetation types depending on geomorphology and humidity in and around the drainage of the Hanamuro River. Rich aquatic and wetland flora indicates an expansion of backmarsh mosaic environments along the river channel in the bottom of the valley. Wetland forests composed of *Picea* sect. *Picea* assignable to *Picea koyamae*, and riparian forests dominated by *Alnus inokumae*, are well represented in the macrofossil assemblages. Pinaceous conifers were dominant in mesic or dry places with *Betula* and the other deciduous broadleaved trees. Macrofossils and pollen indicates that *Abies veitchii* was distributed in mesic locations, *Larix kaempferi* and *Picea jezoensis* var. *hondoensis* were on the upper slopes, and *Pinus koraiensis* was dominant on the plateau. Dominant *Selaginella remotifolia* and the other drought-intolerant understory herbs indicate closed canopy of mesic coniferous forests, while many kinds of meadow and/or ruderal plants were indicative of open vegetation along the river and slopes. Annual mean temperature of the fossil site based on occurrence of *Selaginella remotifolia* was 8.1 °C, which is observed in present cool temperate zones where deciduous broad-leaved trees are dominant. This indicates that the distribution limit of subarctic conifers shifted to warmer temperature conditions than at present. The overlapping distribution of temperate and subarctic plants occurred widely in the lowlands in the distribution ranges of temperate trees, south of around 38° N in Japan. In the LGM, with lower precipitation, dryness was an important environmental factor that controlled plant distribution along with temperature. Water stress confined temperate broad-leaved trees to the humid valley bottoms and relieved conifers from competition against broad-leaved trees to promote their expansion to warmer regions. Macrofossils indicate the persistence of temperate plants in humid inland and/or northern refugia during the LGM, locations conducive to Paleolithic human occupation.

1. Introduction

During the Last Glacial Maximum (LGM), a dry and cold winter monsoon climate prevailed in east Asia (Ono and Naruse, 1997; Porter, 2001; Ono et al., 2005; Kim et al., 2015); distributions of modern subalpine pinaceous conifers expanded into the lowlands in central Japan, while those of temperate tree taxa were limited to refugia in the lowlands south of central Japan (Tsukada, 1982, 1983, 1985, 1986; Takahara et al., 2000; Gotanda and Yasuda, 2008). In Japan, temperate plants, including many endemic vicariants, exhibit high diversity (Kato and Ebihara, 2011). The present distributions and/or genetic structures of temperate trees are assumed to have been affected by their distributions during the LGM (Hattori, 1985; Iwasaki et al., 2012). Thus, reconstruction of plant distribution based on fossil assemblages is crucial for understanding the development of modern plant biogeography and local biodiversity (Momohara, 2016). Plant macrofossil assemblages identified to the species level provide detailed information on plant

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distribution and state of the communities during the LGM (Momohara, 2012).

The last glacial sediments distributed along the Hanamuro River, Ibaraki Prefecture, central Japan, have been noted for yielding numerous mammal fossils, such as *Palaeoloxodon naumanni*, *Bison* sp., and *Zalophus japonicus* (Nakashima et al., 2002; Iizumi et al., 2010). In addition to the description of fossil wood flora by Noshiro (2004), the vegetation history between ca. 50 and 17 ka in the area was clarified based mainly on pollen analysis by Yoshida et al. (2011). They reported that vegetation in the LGM was dominated by pinaceous conifers, *Betula*, and *Alnus* with few temperate broad-leaved trees such as *Fagus*, *Quercus*, and *Prunus*. However, plant macrofossil records of the sediments were limited to several large-sized taxa, such as the cones of *Picea* and cupule of *Quercus* collected directly from outcrops.

The drainage of the Hanamuro River includes 14.7 km of upper reaches (Yoshida et al., 2011), with less than 25 m of relative height to the top of the Tsukuba Plateau. Because the limited range of altitude in the drainage excludes macrofossils transported from higher places, the local vegetation and paleotemperature can be reconstructed reliably on the basis of macrofossil assemblage rather than pollen assemblage, including airborne pollen. Investigation of plant macrofossil assemblages obtained by sieving of sediments will clarify the refugium environment of temperate trees that characterize the rich species diversity of present temperate forests in East Asia.

We analyzed both plant macrofossils and pollen from the same sample obtained from a sandy channel deposit dating between ca. 24.5 and 20.1 ka in the LGM, and reconstructed the spatial distribution of vegetation and plants around the research site. We discuss the paleoenvironment during the LGM in central Japan, where temperate plants were mixed with subalpine conifers.

2. Geographical and geological settings

The research site is situated in a valley bottom of the Hanamuro River (36°03′44″ N, 140°09′50″ E; 5 m above sea level) that has a main stream ca. 14.7 km in length (Yoshida et al., 2011) originating from sources in Tsukuba City, south Ibaraki Prefecture (Fig. 1). The river dissects the Tsukuba Plateau on a flat upland plain at an altitude of 25–30 m and flows southeast into Lake Kasumigaura. Annual mean temperature (AMT) of the site is 13.8 °C, coldest month mean temperature (CMMT) is 2.9 °C, warmest month mean temperature (WMMT) is 25.4 °C, and annual precipitation is 1180 mm (JMA, 2011). The potential vegetation of the lowlands and hilly zone below ca. 750 m is warm temperate evergreen broad-leaved forests dominated by *Quercus* subgen. *Cyclobalanopsis* and *Castanopsis sieboldii* (Ito, 1966). Cool temperate deciduous broad-leaved forest dominated by *Fagus crenata* is distributed in the mountain zone above 750 m around the top (877 m) of Mt. Tsukuba, 18 km north-northeast of the site.

In the valley bottom of the Hanamuro River, the last glacial sediments are composed of gently sloping surfaces exposed in the southern and/or southeastern face of the valley, along the border with the Tsukuba Plateau (Fig. 1; Unozawa et al., 1988). The last glacial sediments are covered by Holocene fluvial deposits in and around the center of the valley and outcropped along the riverbed of the Hanamuro River (Nakashima et al., 2002).

At the outcrop (HS1) of the study site (Fig. 1), last glacial sediments lie unconformably over the middle Pleistocene Kami-Iwahashi Formation, which is composed mainly of unconsolidated marine silt. The last glacial sediments are ca. 2 m in thickness and are composed mainly of sandy fluvial channel deposits and backmarsh deposits of silty peat and/or silt (Fig. 2). The sandy channel deposits exhibit trough cross-stratification that accretes laterally from west to east, indicative of a point bar in a meandering river channel. The sandy sediments include granules in the basal ca. 30 cm and fine upward to alternating sand and silt that occasionally includes wood logs and organic layers composed mainly of conifer leaves and shoots. The plant fossil assemblages analyzed in this study were obtained from seven organic silty sand layers deposited in the order of HS1-A to HS1-G (Fig. 2), accompanied with lateral accretion of the point bar. The sandy sediments are covered by massive silt–silty peat, indicative of backmarsh sediments. Both sandy sediments and massive silty sediments include several tephra layers. The uppermost part of the last glacial sediments were covered by loamy deposits, including the As-YP tephra dated to 17–15.5 ka (Yoshida et al., 2011).

The AMS ages of wood, fruits, and seeds in the last glacial deposits outcropping along the riverbed are concentrated between ca. 50 and 43 ka in the lower part and between 38 and 21 ka in the upper part (Yoshida et al., 2011). The AMS ages of *Picea* needles from four plant macrofossil assemblages (HS1-A, HS1-C, HS1-E, and HS1-G) were dated by Paleo Labo Co., Ltd. after extraction of graphite in the National Museum of Japanese History. The carbon ages were calibrated by OxCal version 4.2 (Ramsey, 2009) based on IntCal13 (Reimer et al., 2013) (Table 1). The oldest 2σ calibrated age, 24,440–23,900 cal. BP, was obtained from the lowermost HS1-A. Age of the upper HS1-C was slightly younger, 23,985–23,385 cal. BP. The upper assemblage HS1-E was dated to 21,315–20,520 cal. BP, about 2 ka younger than HS1-C. Two of the youngest ranges of 2σ calibrated ages were obtained from the uppermost HS1-G: 20,930–20,730 (9.2%) and 20,550–20,145 (86.2%). Thus, the point bar accretion observable at the outcrop succeeded at least during ca. 4 ka between 24.4 ka and 20.1 ka, a later stage of the LGM (Hughes and Gibbard, 2015).

Table 1
AMS ages of plant macrofossils from the Hanamuro River site, Ibaraki, central Japan.

Assemblages	Laboratory number	Materials	$\delta^{13}C$ (‰)	^{14}C age (yrBP ± 1σ)	Calibrated age (cal BP) (2σ)
HS-A	PLD-19188	Picea needles	−29.88 ± 0.13	20,260 ± 60	24,440–23,900 (95.4%)
HS-C	PLD-19189	Picea needles	−29.78 ± 0.16	19,870 ± 60	23,985–23,385 (95.4%)
HS-E	PLD-19190	Picea needles	−29.65 ± 0.15	17,580 ± 50	21,315–20520 (95.4%)
HS-G	PLD-19191	Picea needles	−29.58 ± 0.18	17,185 ± 50	20,930–20,730 (9.2%) 20,550–20145 (86.2%)

3. Materials and methods

Sediment blocks for the plant macrofossil analysis were collected from seven organic rich layers (HS1-A to HS1-G in Fig. 2) at the outcrop. For sieving the plant macrofossil samples, we prepared sediment blocks of 100 cm^3 and additional volumes of samples. To macerate sediments and remove inorganic materials from plant fragments, alternate processes of freezing at −40 °C for one day and melting were repeated three times. We washed the