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メタデータ	言語: English 出版者: SAGE Publications 公開日: 2022-11-15 キーワード (Ja): 鬼界カルデラ, 火砕流 キーワード (En): holocene, kikai caldera eruption, phytolith analysis, pyroclastic flow, refugia, vegetation 作成者: 林, 尚輝, 井上, 弦, 河野, 樹一郎, 井上, 淳 メールアドレス: 所属: Osaka City University, Nagasaki Institute of Applied science, West Japan Engineering Consultants Inc., Osaka City University
URL	https://ocu-omu.repo.nii.ac.jp/records/2020520

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Naoki Hayashi, Yudzuru Inoue, Tatsuichiro Kawano, Jun Inoue

Citation	The Holocene. 31(5); 709 - 719
Issue Date	2021-05
Type	Journal Article
Textversion	Author
Supplementary Material	Supplementary Material is available at https://doi.org/10.1177/0959683620988057 .
Rights	© The Author(s) 2020. This is the accept manuscript version. This version is free to view and download for private research and study only. Any other use requires prior permission of the Final Published version. Final Published version is available at https://doi.org/10.1177/0959683620988057 .
DOI	10.1177/0959683620988057

Self-Archiving by Author(s)
Placed on: Osaka City University

Vegetation transition from the terminal Pleistocene to early Holocene reconstructed
from phytolith records in the southernmost part of mainland Japan

Naoki Hayashi^a & Jun Inoue^a

^a Department of Geosciences, Osaka Metropolitan University, 3-3-138 Sugimoto,
Sumiyoshi-ku, Osaka 558-8585, Japan

Corresponding author: Naoki Hayashi

E-mail: nhayashi5730@gmail.com

Keywords:

phytolith analysis; last glacial; herbaceous vegetation; terminal Pleistocene; early Holocene; vegetation change

Highlights

- We examined phytolith records in the southernmost part of mainland Japan.
- Andropogoneae species flourished under forests in the late MIS 3.
- Grasslands covered in last glacial maximum (LGM).
- *Sasa* flourished on forest floor between ~18,000 and ~17,000 cal BP.
- Evergreen broad-leaved forests had developed at least until 7,300 cal BP.

Abstract

Phytolith records in paleosols provide valuable information on past vegetation *in situ*, especially for herbaceous plants. Although vegetation transition between the terminal Pleistocene and early Holocene in the southernmost parts of mainland Japan has been examined, detailed information on herbaceous plants during the period is scarce. Therefore, this study examined phytolith records in paleosols in the region to reconstruct the vegetation transition from the terminal Pleistocene to the early Holocene, focusing on herbaceous vegetation. Additionally, the combination of our phytolith and previous palynological records enable us to reconstruct vegetation transition in detail. Before ~30,000 cal BP, Andropogoneae species flourished under forest, comprising temperate pinaceous conifers, deciduous broad-leaved trees, and/or their adjacent area. In the Last Glacial Maximum (LGM), grasslands comprising Panicoideae, Chloridoideae, and Pooideae species were widely distributed under the influence of cool climate conditions and/or Aira caldera eruption. Furthermore, between ~18,000 and ~17,000 cal BP, *Sasa* flourished as a component of grassland or on forest floors, and then was gradually replaced by Andropogoneae species. Evergreen broad-leaved forests had developed at least by 7,300 cal BP in the study region.

1. Introduction

Glacial–interglacial climate dynamics have changed the vegetation distribution on earth. Notably, the last significant climatic changes from the last glacial period to the Holocene caused significant changes in composition and vegetation structures in most regions globally (Nolan et al., 2018). In modern Japan, each subarctic coniferous forest, cool-temperate deciduous broad-leaved forests, temperate coniferous forests, and warm-temperate evergreen broad-leaved forests have covered each region. Also, their distributions have varied significantly since the Last Glacial Maximum (LGM), reconstructed from records of pollen and plant fossils in sediment (e.g., Yasuda and Miyoshi, 1998; Ooi, 2016). However, these records lack detailed information on herbaceous vegetation.

In the southern Kyushu District, the southernmost part of mainland Japan, warm, temperate evergreen broad-leaved forests are locally distributed as natural forests in modern days. In contrast, in the LGM, temperate deciduous broad-leaved forests should have been distributed widely in this region, except for coastal areas where warm, temperate evergreen broad-leaved forests were possibly distributed (Nasu, 1980; Tsukada, 1985). However, few pollen records provide little information on the vegetation transition in this region. For example, in the late Marine Isotope Stage (MIS)

3, a mixed forest comprising temperate pinaceous conifers and temperate deciduous broad-leaved trees was distributed (Hase and Hatanaka, 1984; Iwauchi and Hase, 1995). Additionally, evergreen broad-leaved forests were distributed in the early Holocene (Matsushita, 2002). As mentioned above, the detailed vegetation types and their transition in the region are still poorly understood, especially for the grass component of herbaceous vegetation.

Phytolith records in paleosols provide valuable information on past vegetation *in situ*, especially herbaceous vegetation (e.g., Fredlund and Tieszen, 1997; Blinnikov et al., 2002; Miyabuchi and Sugiyama, 2019). Thus, this study examined phytolith assemblages in paleosols formed from late MIS 3 to early MIS 1 in the southernmost part of Kyushu District, reconstructing past vegetation and focusing on herbaceous vegetation. Further, we comprehensively reconstructed vegetation transition in the region by combining our phytolith records and palynological records in previous studies.

2. Study Region

The study region is the southern part of the Kyushu District, the southernmost part of the Japanese mainland. The Satsuma and Osumi Peninsula are situated in the region (Figure

1). The annual temperature (1991–2020) is 18.3°C and 16.4°C at Ibusuki Climatological Station (31°15'00" N, 130°38'12" E; elevation of 5 m) in the Satsuma Peninsula and Tashiro Climatological Station (31°11'54" N, 130°50'36" E; elevation of 182 m) in the Osumi Peninsula, respectively. The annual precipitation (1991–2020) is 2602.1 mm and 2888.2 mm at Ibusuki Climatological Station in the Satsuma Peninsula and Tashiro Climatological Station in the Osumi Peninsula, respectively (Japan Meteorological Agency, 2021). Therefore, the climate of both peninsulas is assigned to a warm temperate zone. Although plantation forests of *Cryptomeria japonica* and *Chamaecyparis obtusa* or secondary forests cover most regions, natural forests are distributed locally. The natural forest comprises warm temperate evergreen broad-leaf trees, except in mountain areas in the Osumi Peninsula; i.e., in the lowlands, the forest is mainly composed of *Symplocos glauca* and *Castanopsis sieboldii*, and above 400–500 m in altitude, the forest comprises *Distylium racemosum* and *Quercus salicina*. In addition, mixed forests composed of temperate deciduous broad-leaved trees and temperate pinaceous conifers, such as *Abies firma*, are distributed around the summit of the Kimotsuki Mountains in the Osumi Peninsula (Miyawaki, 1981).

3. Methods

3.1 Materials

We collected soil samples from outcrops using a plastic cube ($2 \times 2 \times 2$ cm) at three sites for phytolith analysis. Site 1 ($31^{\circ}16'59''\text{N}$, $130^{\circ}34'26''\text{E}$) is located at the Satsuma Peninsula. Sites 2 ($31^{\circ}16'05''\text{N}$, $130^{\circ}52'01''\text{E}$) and 3 ($31^{\circ}18'24''\text{N}$, $130^{\circ}52'46''\text{E}$) are located at the Osumi Peninsula (Figure 1). Figure 2 shows the geological columnar sections at the respective sites, indicating lithofacies, soil colors, and sampling levels. Either Osumi pumice fall (A-Os) or Aira-Tanzawa volcanic ash (AT) layer was found at all sites, which erupted from Aira caldera (Figure 1) at 30,000 cal BP (Kobayashi et al., 1983; Smith et al., 2013). Kikai-Akahoya volcanic ash (K-Ah), which erupted from the Kikai caldera (Figure 1) at 7,300 cal BP (Machida and Arai, 1978; Smith et al., 2013), was found at Site 3. Paleosols lie under and over the A-Os at Site 1, under the A-Os at Site 2, and between the AT and the K-Ah at Site 3. Sakurajima-Satsuma volcanic ash (Sz-S), which erupted from Mt. Sakurajima (Figure 1) at 12,800 cal BP (Okuno et al., 1997), included in the middle part of the paleosols at Site 3.

We dated two paleosol layers at Site 3 using AMS radiocarbon measurement of humin fractions extracted from soils by chemical treatment (Figure 2 and Table 1). Additionally, we calibrated radiocarbon dates to calendar years using Calib Rev 8.1 and

the IntCal20 calibration dataset (Reimer et al., 2020). We constructed the age model of paleosol layers at Site 3 based on the calibrated radiocarbon ages of humin and volcanic ashes (Supplementary Figure 1).

3.2 Phytolith analysis

First, we collected a 1-cm³ subsample from each soil sample. Furthermore, we extracted phytoliths from the subsamples following the method proposed by Kawano et al. (2007) and Okunaka et al. (2012). A known number of glass beads (approximately 200,000 grains) were added to each subsample to estimate the phytolith concentration (Fujiwara, 1976). Organic matter was oxidized with 30% H₂O₂ for 12 h at room temperature and 1 h at 250°C. Calcium carbonate was eliminated using 3 N HCl by heating in a water bath for 1 h. Crays were removed by gravity sedimentation. The extracted phytoliths were dried at 105°C for 24 h. We mounted a portion of the extraction residue on a glass slide using a mounting medium (Eukitt). Then, we observed and counted the phytolith under a transmission-type optical microscope at 400× magnification until we counted 300 glass beads. Finally, we calculated phytolith concentration (grains•cm⁻³) based on the observed number of glass beads and phytoliths on the glass slide.

Phytoliths were identified according to the International Code for Phytolith

Nomenclature 2.0 (ICPN 2.0) (Neumann et al., 2019). Also, some phytolith types were classified into further sub-categories (Figure 4 and Table 2). For example, the BULLIFORM FLABELLATE phytoliths (ICPN 2.0) were further divided into four sub-types: *Sasa*-type, *Pleioblastus*-types, *Bumusoideae*-types, *Andropogoneae*-types, following Sase and Kondo (1974), Sugiyama and Fujiwara (1986), Kondo and Sase (1986), Kawano et al. (2012), Inoue et al. (2016), and Hayashi et al. (2019; 2021). Most of the BLOCKY (ICPN 2.0) was identified as *Panicoideae*-type, following Sugiyama et al. (1988). Additionally, SADDLE was divided into *Bambusoid*-type and *Chloridoid*-type. *Bambusoid*-type corresponds to the collapsed saddle type in Piperno and Pearsall (1998).

The tree-type phytoliths, POLYHEDRAL FACETATE, ELONGATE GENICULATE SINUATE, and ELONGATE BRACHIATE ENTIRE were identified as *Castanopsis*-type, *Litsea*-type, *Distylium*-type, respectively, inferred from Kawano (2008). Furthermore, IRREGULAR SINUATE was identified as jigsaw puzzle-type produced from broad-leaved trees and ferns (*Pteridium*) in Japan (Kawano, 2008; Kondo, 2010).

4. Results

The phytolith analysis results are shown in Figure 4, Figure 5, and Supplementary Table 1. Diagrams were drawn using TILIA 2.1.1 (www.tiliasoft.com). The phytolith assemblages

were divided into five phytolith zones, A, B, C, D, and E, based on percentages of phytoliths.

Zone A is assigned to the phytolith assemblage in the paleosol layer under A-Os layers at Sites 1 and 2. This zone is dominated by *Andropogoneae*-type bulliform cells (Site 1: 27.1%–33.8%; Site 2: 12.4%–25.3%) and ELONGATE (Site 1: 17.2%–22.7%; Site 2: 18.9%–26.7%) phytoliths. Additionally, a percentage of *Sasa*-type bulliform cell phytolith is observed (Site 1: 9.0%–13.8%; Site 2: 3.1%–10.1%). *Bambusoideae*-type bulliform cell phytolith accounts for 1.8%–4.8% at Site 1 and 1.4%–5.7% at Site 2. In short cells, the *Bambusoid*-type is common (Site 1: 5.7%–13.3%; Site 2: 4.3%–26.8%). Few BILOBATE and Chloridoid-type phytoliths occur (BILOBATE: <4.8%; Chloridoid-type: <3.5%); other short cell types are rare (<1.4%). ACUTE BULBOSUS phytolith occurs in small amounts (Site 1: 1.5%–2.5%; Site 2: 1.3%–4.3%), and jigsaw puzzle-type phytoliths occur in some layers (<1%). The phytolith concentrations in this zone are 2.1×10^5 – 4.2×10^5 grains·cm⁻³ at Site 1 and 1.1×10^5 – 40.2×10^5 grains·cm⁻³ at Site 2, respectively. Moreover, the concentration is very high (18.8×10^5 – 40.2×10^5 grains·cm⁻³) under A-Os layer at Site 2.

Zone B is assigned to the phytolith assemblage in the lower part of paleosol layers between K-Ah and A-Os or AT layers at Sites 1 and 3. The abundance of short cells

characterizes this zone. BILOBATE (Site 1: 7.4%–14.1%; Site 3: 10.8%–20.6%) and RONDEL (Site 1: 4.1%–8.4%; Site 3: 5.6%–11.1%) phytoliths have the highest percentages in all zones. Bambusoid-type (Site 1: 9.2%–17.4%; Site 3: 6.9%–18.3%) and Chloridoid-type (Site 1: 5.6%–15.1%; Site 3: 0.0%–3.4%) phytoliths are common. A percentage of CRENATE phytoliths is observed at Site 1 (1.6%–3.0%). However, in bulliform cells, *Sasa*-type phytoliths account for 4.6%–10.7% at Site 1 and 1.8%–10.1% at Site 3. Andropogoneae-type phytoliths are low relative to Zone A (Site 1: 6.3%–11.2%; Site 3: 5.5%–8.9%). However, ELONGATE and ACUTE BULBOSUS phytoliths account for 13.0%–26.4% and 1.7%–3.8%, respectively, and no tree phytoliths is observed in this zone. The phytolith concentrations are 0.7×10^5 – 3.1×10^5 grains · cm⁻³ at Site 1 and 1.2×10^5 – 1.4×10^5 grains · cm⁻³ at Site 3, respectively.

Zone C is assigned to phytolith assemblages in the lower middle part of the paleosol layers between K-Ah and A-Os or AT layers at Sites 1 and 3. This zone is characterized by the dominance of *Sasa*-type bulliform cell phytoliths (Site 1: 12.6%–24.4%; Site 3: 26.7%–34.6%). At Site 1, *Sasa*-type phytoliths show an upward increase. Andropogoneae-type bulliform cell phytoliths are common (Site 1: 4.9%–10.1%; Site 3: 4.8%–10.3%). In short cells, Bambusoid-type phytoliths are abundant (Site 1: 15.0%–29.6%; Site 3: 12.2%–28.0%). At Site 1, Chloridoid-type, BILOBATE, and RONDEL short

cell phytoliths show an upward decrease in this zone (Chloridoid-type: 3.9%–8.9%, BILOBATE: 3.4%–8.3%, and RONDEL: 1.5%–4.3%). At Site 3, short cell phytoliths, except for Bambusoid-type, are rare (0.0%–3.7%). ELONGATE and ACUTE BULBOSUS phytoliths account for 11.7%–19.3% at Site 1 and 8.4%–15.3% at Site 3, and 0.8%–2.5% at Site 1 and 2.2%–4.0% at Site 3, respectively. Jigsaw puzzle-type phytoliths occur in some layers (<1%). The phytolith concentrations show a gradual upward increase at both sites (2.5×10^5 – 7.0×10^5 grains·cm⁻³ at Site 1 and 1.7×10^5 – 13.2×10^5 grains·cm⁻³ at Site 3).

Zone D is assigned to the phytolith assemblages in the upper middle part of paleosol layers between K-Ah and A-Os or the AT layers at Site 3. This zone is characterized by the abundance of Bambusoid-type short cell phytoliths (13.9%–34.3%). The percentage of *Sasa*-type bulliform cell phytoliths was lower than zone C (8.7%–20.0%). Also, a percentage of Andropogoneae-type bulliform cell (5.0%–15.7%), BILOBATE (1.8%–10.0%), and RONDEL (1.2%–11.2%) short cell phytoliths were observed. Few Bambusoideae-type bulliform cells (1.2%–4.7%), Chloridoid-type (0.7%–5.2%), and ACUTE BULBOSUS (0.9%–5.2%) phytoliths occurred, and ELONGATE phytoliths accounted for 8.0%–16.8%. The phytolith concentration is 1.8×10^5 – 16.6×10^5 grains·cm⁻³.

Zone E is the phytolith assemblage in the uppermost part of paleosol layers

between K-Ah and A-Os or the AT layers at Site 3. This zone is characterized by phytoliths derived from evergreen broad-leaved tree species. *Castanopsis*- and *Distylium*-type phytoliths are observed in some layers (<1%), and *Litsea*-type phytoliths occur at the upper part of this zone (<1.6%). In bulliform cells, Andropogoneae-type phytoliths are abundant (11.2%–27.5%). A certain percentage of *Sasa*-type bulliform cells (4.3%–13.2%) and Bambusoid-type short cells (5.6%–14.7%) phytoliths were observed. Few Bambusoideae-type bulliform cells (1.6%–4.9%), Chloridoid-type (1.3%–4.2%), BILOBATE (1.4%–8.6%), RONDEL (0.3%–4.4%), and ACUTE BULBOSUS (1.1%–3.3%) phytoliths occurred. ELONGATE phytoliths accounted for 9.9%–16.2%. The phytolith concentration is 1.1×10^5 – 4.4×10^5 grains · cm⁻³.

5. Discussion

5.1 Vegetation history around the study sites reconstructed from phytolith records

Table 2 summarizes plant families and genera that produce phytolith types identified in this study and their habitat and climate zones. *Sasa*, *Miscanthus-Sasa*, and *Miscanthus-Pleioblastus* grasslands are distributed in subarctic, cool-temperate, and warm-temperate zones, respectively (Numata, 1969; 1974). Consequently, *Sasa*, *Pleioblastus*, and *Miscanthus* are distributed in subarctic to cool-temperate, warm-temperate, and cool-

temperate to warm-temperate zones, respectively, as a component of grassland. *Sasa* is also a significant component of deciduous broad-leaved forest understories in cool-temperate zone (Shidei, 1974). Although Chloridoideae and Pooideae are hardly dominant in grassland without grazing pressure in Japan, Chloridoideae is prone to grow in bare land in the temperate zone. In Japan, deciduous broad-leaved forests are distributed in the cool-temperate zone, whereas evergreen forests are distributed in the warm-temperate zone (Numata, 1969). *Castanopsis*, *Distylium*, and *Litsea* are components of the warm-temperate and subtropical evergreen forest. *Pteridium*, a fern, is a component of grassland in cool-temperate to subtropical zone. Therefore, we reconstructed vegetation transitions, and past climate conditions in the region from the phytolith records obtained at the study sites, based on their attributing plants and inhabit the conditions shown in Table 2.

Phytolith assemblages in Zone A are characterized by the dominance of Andropogoneae-type bulliform cell and Bambusoid-type short cell phytoliths with *Sasa*-type bulliform cell phytolith, and jigsaw puzzle-type phytoliths (Figure 4). Andropogoneae-type bulliform cell phytoliths are produced from Andropogoneae (Kondo and Sase, 1986; Sugiyama and Fujiwara, 1986; Kawano et al., 2012), and the Bambusoideae genera are prone to produce Bambusoid-type short cell phytoliths (Kondo

and Ohtaki, 1992; Kondo, 2010). Thus, the dominance of these genera implies that Andropogoneae species flourished with some Bambusoideae species such as *Sasa*. Additionally, the high phytolith concentrations in this zone may imply that the adjacent area of Site 2 was covered densely by the genus. Furthermore, the occurrence of jigsaw puzzle-type phytoliths suggests that broad-leaved tree species or ferns were distributed because jigsaw puzzle-type phytoliths are produced by broad-leaved trees and *Pteridium* species in Japan. (Kawano, 2008; Kondo, 2010).

The phytolith records in Zone B are characterized by the high percentage occurrence in short cell phytoliths, especially BILOBATE and RONDEL (Figures 4 and 5). BILOBATE short cell phytoliths are generally produced from Panicoideae, Chloridoideae, and Arundinoideae, and RONDEL short cell phytoliths are derived from Pooideae and Chloridoideae (ICPN2.0, Neumann et al., 2019). Since Arundinoideae species are prone to produce bulliform cell phytoliths (Chen et al., 2020), the low percentage occurrence in bulliform cell phytoliths implies that no or few Arundinoideae species stood. The percentage of Andropogoneae-type bulliform cell phytoliths in this zone is lower than those in Zone A, suggesting that Andropogoneae genera belonging to Panicoideae decreased after ~30,000 cal BP. Thus, we assume that the grasslands of Panicoideae, Chloridoideae, and Bambusoideae species were distributed.

The phytolith assemblage in Zone C is characterized by a high percentage of *Sasa*-type bulliform cells and Bambusoid-type short cell phytoliths and a low percentage of other SADDLE, BILOBATE, and RONDEL short cell phytoliths relative to other zones (Figure 5). *Sasa*-type bulliform cell phytoliths are produced from *Sasa* (Sugiyama and Fujiwara, 1986; Kawano et al., 2012). The phytolith assemblage and the increasing trend of phytolith concentrations indicate that *Sasa* replaced Panicoideae and Chloridoideae species at the beginning of the zone and flourished afterward. *Sasa* grows as a component of grassland and deciduous broad-leaved forest understory (Shidei, 1974). Additionally, jigsaw puzzle-type phytoliths produced from broad-leaved trees and/or ferns occur in this zone (Figure 5). Therefore, the area was presumably covered by *Sasa* grassland with ferns or deciduous broad-leaved trees with *Sasa* flourishing on their floor.

In Zone D, the percentage of Andropogoneae-type bulliform cell and BILOBATE short cell phytoliths increased gradually upward, and the percentage of *Sasa*-type gradually decreased upward (Figure 5). These suggest that Andropogoneae species had gradually replaced *Sasa* species in this zone.

Phytolith assemblages in Zone E are characterized by the appearance and increasing upward of evergreen broad-leaved species phytoliths (*Castanopsis*-, *Litsea*-, and *Distylium*-types) (Figure 5). From modern observations of phytolith assemblages, even

in Japanese forest soils, phytoliths derived from arboreal species are less than one-fifth of that of Poaceae-derived phytoliths (Kondo and Sase, 1990). Nevertheless, a certain percentage occurrence and increase in the phytoliths indicate that the evergreen broad-leaved forest had developed in this zone. Furthermore, the higher percentage of Andropogoneae-type bulliform cell phytoliths implies that Andropogoneae species flourished at that time.

Zone A laid under A-Os or AT tephra presumably corresponds to before ~30,000 cal BP based on the date of the Aira caldera eruption. Zone B lies between the A-Os and the soil layers dated at 18,000–19,000 cal BP at Site 3. Thus, the phytolith assemblages potentially represent the vegetation during a certain time between ~30,000 cal BP and ~18,000 cal BP. Although the exact period of Zone B is unclear, it is assumed that the zone includes phytolith assemblages at a period during the LGM of 24–18 ka (Mix et al., 2001). Zone C lies between the soil layers dated at ~18,000 cal BP and ~17,000 cal BP, respectively, suggesting that the phytolith assemblage in this zone represents vegetation during this period. Additionally, Zones D and E lie between Sz-S and K-Ah, indicating phytolith assemblage representing vegetation between ~12,800 cal BP and ~7,300 cal BP corresponding to early Holocene.

Thus, the vegetation change in the study region reconstructed from our phytolith

records is summarized as follows. Before ~30,000 cal BP, Andropogoneae species and *Sasa* were dominant. In the LGM, the grasslands of Panicoideae, Chloridoideae, and Bambuoideae developed. Also, between ~18,000 cal BP and ~17,000 cal BP, *Sasa* flourished as grassland with ferns or deciduous broad-leaved forests floor vegetation. From the terminal Pleistocene (~17,000 cal BP) to the early Holocene, *Sasa* had been gradually replaced by Andropogoneae species. Then, evergreen broad-leaved forests composed of *Litsea* and *Distylium*, and other species had developed until 7,300 cal BP.

5.2 Vegetation transition reconstructed from phytolith and pollen records

We compared phytolith records in this study to pollen records in the study region between terminal Pleistocene and early Holocene (Figure 6). Then, we reconstructed the vegetation from these records and assessed the relationship between vegetation transition and global climate change or regional context.

We presume that at ~30,000 cal BP corresponding to late MIS 3, Andropogoneae species were dominant based on the phytolith records. Also, pollen records reported in previous studies show that mixed forests are mainly composed of temperate pinaceous conifers, such as *Pinus*, *Abies*, *Tsuga*, and temperate deciduous broad-leaved trees, *Carpinus* and *Quercus* subgen. *Lepidobalanus* developed (Hase and Hatanaka, 1984;

Iwauchi and Hase, 1995). Furthermore, wood fossils of Fagaceae and *Pinus* subgen. *Diploxylon* were found in loam under the AT layer in the Satsuma Peninsula (Paleoenvironment Research Co., Ltd, 2013). Considering these findings, mixed forests mainly comprising temperate pinaceous conifers and temperate deciduous broad-leaved trees are developed, and Andropogoneae species likely flourished in the forest and/or its adjacent areas in the late MIS 3. Furthermore, the mixed forest developed at that time indicates that the study region belonged to the intermediate between cool- and warm-temperate zones, based on their distribution in modern Japan (Nozaki, 2005). This is consistent with the dominance of Andropogoneae species, distributed widely in cool-temperate to warm-temperate zones.

Pollen records during the LGM in eastern Asia suggest that deciduous broad-leaved forests likely developed in southern China inlands and Kyushu District Japan (Kawahata and Ohshima, 2004; Yue et al., 2012). However, our phytolith records suggest that the grasslands of Panicoideae, Chloridoideae, and Bambusoideae developed around the study region without forest development in the LGM (Figure 6). The grassland may be partially attributed to the cool and dry conditions in the LGM. In addition to the climatic condition, Nasu (1980) assumed that grassland development in this region was due to the influence of the tephra that erupted from Aira caldera at 30,000 cal BP. Specifically, tephra

deposition devastated the original forests and prevented their regeneration. Additionally, Panicoideae and Chloridoideae species grew on barren land, resulting in the grassland maintenance for a long time. Thus, the eruption and/or the climate conditions presumably contributed to the grassland development during this period. Furthermore, the pollen data imply that some evergreen forests stood in the southernmost part of Kyusyu Island in the LGM (Matsuoka, 1994), similar to southeastern China and Ryukyu Islands (Dai et al., 2021; Kuroda and Ozawa, 1996). However, previous (Sugiyama, 1999; 2002) and present phytolith studies show that evergreen broad-leaved trees were never distributed at any sites in the study region. Therefore, the evergreen broad-leaved trees' distribution was presumably limited to the coastal areas at that time (Figure 1) under the influence of a warm ocean current.

Our phytolith records indicate that *Sasa* replaced Panicoideae and Chloridoideae species and flourished between ~19,000 and ~18,000 cal BP. *Sasa* development might be due to fertile soil formation after the long time elapsed after the Aira caldera eruption. This is because *Sasa* is hardly prone to grow on the sand ground (Shibata, 2015) like volcanic ejecta. The developing *Sasa* communities presumably had prevented Panicoideae and Chloridoideae species from growing because dwarf bamboo, such as *Sasa*, suppresses other species and reduced species diversity (Kudo et al., 2017). The

absence of evergreen broad-leaved tree phytoliths indicates that evergreen broad-leaved trees were never distributed in the area, although the vegetation type is poorly understood.

Our phytolith records show that *Sasa* had been gradually replaced by Andropogoneae species since 17,000 cal BP. Although we have no pollen record in late MIS 2, those in early MIS 1 indicate that temperate deciduous broad-leaved forests of *Carpinus*, *Quercus* subgen. *Lepidobalanus*, and *Ulmus-Zelkova* were distributed in the southernmost part of the Kyushu District (Iwauchi and Hase, 1996; Matsushita, 2002). Thus, the temperate deciduous broad-leaved trees were presumably distributed with Andropogoneae and Bambusoideae species between the terminal Pleistocene and early Holocene. The proportions of the herbaceous plants changed temporally, and the proportion change is possibly related to the climatic warming from MIS 2 to MIS 1.

The presence of evergreen broad-leaved species phytoliths indicates that evergreen broad-leaved trees stood in the early Holocene. Evergreen broad-leaved species phytoliths in paleosol under the K-Ah layer have also been found at other sites in the study region (Hayashi et al., 2021; Sugiyama 1999; 2002). Furthermore, pollen records show that *Castanopsis* and *Q.* subgen. *Cyclobalanopsis* pollens are extremely dominant in the early Holocene sediments (Iwauchi and Hase, 1996; Matsushita, 2002). These findings suggest that evergreen broad-leaved forests were distributed widely in the southernmost part of

the Kyushu District in the early Holocene. The expansion of the forests presumably resulted from the climatic warming at that time.

6. Conclusion

We reconstructed the vegetation transition from late MIS 3 to early MIS 1 by combining phytolith records in this study and palynological records in previous studies in the southernmost part of Kyushu District, southern Japan. Before ~30,000 cal BP, mixed forests composed of temperate pinaceous trees and temperate deciduous broad-leaved trees, and Andropogoneae species flourished in the forest and/or adjacent areas under warm climate conditions in the late MIS 3. In the LGM, grasslands composed of Panicoideae, Chloridoideae, and Pooideae species mostly covered the study region under the influence of cool climate conditions and/or Aira caldera eruption. In the terminal Pleistocene, *Sasa* flourished as a component of grassland or deciduous broad-leaved forest understory between ~18,000 and ~17,000 cal BP, and no evergreen broad-leaved trees likely stood. Since ~17,000 cal BP, *Sasa* had been gradually replaced by Andropogoneae species. Then, evergreen broad-leaved forests were developed and distributed widely in the southernmost part of the Kyushu District, at least by 7,300 cal BP.

Acknowledgments

We would like to thank Dr. Yudzuru Inoue of Nagasaki Institute of Applied Science for his support to our field works. We wish to thank Prof. Muneki Mitamura at Osaka City University for fruitful discussions during the course of this work. We also thank the two anonymous reviewers who provided valuable comments that drastically improved the paper. This work was supported by JST SPRING, Grant Number JPMJSP2139.

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Figure captions

Figure 1. Maps of (A) mainlands Japan showing Kyushu District, (B) the southern Kyushu District showing the location of the volcano related to this study and the previous palynological study sites, and (C) the southernmost part of the Kyushu District showing the sampling sites in this study. The pollen records at site 1, 2, 3, and 4 were reported by Hase and Hatanaka (1984), Iwauchi and Hase (1995), Iwauchi and Hase (1996), Matsushita (2002), respectively. The dotted line in map of the southern Kyushu District (B) indicates the assumed coastline of the Last Glacial Maximum (~20,000 years ago). The base map is the digital map released by the Geospatial Information Authority of Japan (maps.gsi.go.jp/).

Figure 2. Geological columnar sections at the study sites indicating lithofacies, grain size, and sampling level. Abbreviations for the tephra names and their eruption ages are as follows; Kikai-Akahoya volcanic ash (K-Ah: 7,300 cal BP), Sakurajima-Satsuma volcanic ash (Sz-S: 12,800 cal BP) Aira-tanzawa volcanic ash (AT: 30,000 cal BP), and Osumi fall pumice (A-Os: 30,000 cal BP). Both AT and A-Os are erupted from the Aira caldera at the same time.

Figure 3. Microphotographs of the main phytolith morphotypes observed in this study.

a: *Sasa*-type (BULLIFORM FLABELLATE) b: *Pleioblastus*-type (BULLIFORM FLABELLATE) c: Bambusoideae-type (BULLIFORM FLABELLATE) d: Andropogoneae-type (BULLIFORM FLABELLATE) e: Panicoideae-type (BLOCKY) f: Bambusoid-type (SADDLE) g: Chloridoid-type (SADDLE) h: BILOBATE i: RONDEL j: POLYLOBATE k: CROSS l: CRENATE m: ACUTE BULBOSUS n: ELONGATE o: *Castanopsis*-type (POLYHEDRAL FACETATE) p: *Litsea*-type (ELONGATE GENICULATE SINUATE) q: *Distylium*-type (ELONGATE BRACHIATE ENTIRE) r: Jigsaw-puzzle type (IRREGULAR SINUATE)

Scale bar is 20 μm .

Figure 4. Percentage occurrences of phytolith morphotypes at Site 1 and Site 2

Figure 5. Percentage occurrences of phytolith morphotypes at Site 3

Figure 6. Vegetation transition in the southernmost part of Kyushu District inferred from phytolith and pollen records, with representative phytolith and pollen types and

the LR04 marine isotope stack (Lisiecki and Raymo, 2005) between the terminal Pleistocene and the early Holocene. The pollen records were reported by Matsushita (2002), Iwauchi and Hase (1996), Hase and Hatanaka (1984), and Iwauchi and Hase (1995).

Table 1. Radiocarbon ages of humin fractions extracted from the paleosols at Site 3. ^{14}C dates were calibrated to calendar years using the program Calib Rev 8.1 and the IntCal20 calibration dataset (Reimer et al., 2020).

Table 2. Summary of plant families and genera producing phytolith types identified in this study and their habitat and climate zones. The phytolith type produced from the respective plant families, subfamilies, tribes, and genera are based on the following references; ^{*1} Sugiyama and Fujiwara (1986), ^{*2} Kondo and Ohtaki (1992), ^{*3} Kondo and Sase (1986), ^{*4} Sugiyama et al. (1988), ^{*5} Kawano et al. (2012), ^{*6} Sase and Kondo (1974), and ^{*7} Kawano (2008).

Supplementary data

Supplementary Figure 1. Age model of the layers at Site 3. The black dots and bars

indicate the calibrated radiocarbon ages and the ages of volcanic ashes, respectively.

Supplementary Table 1. (a) Raw data for number of each phytolith type observed in this study and phytolith concentrations and (b) Percentage occurrence in each phytolith type calculated from the observed number of the phytolith

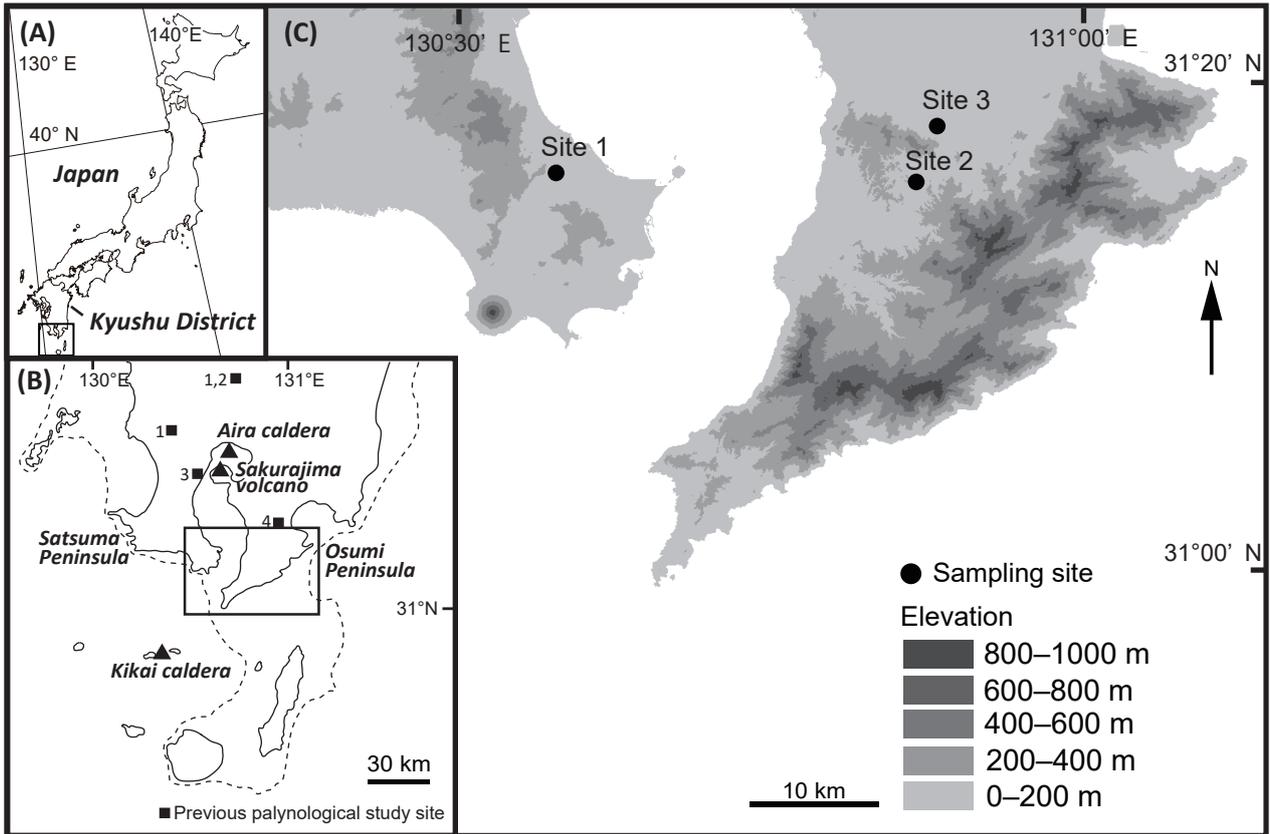


Figure 1

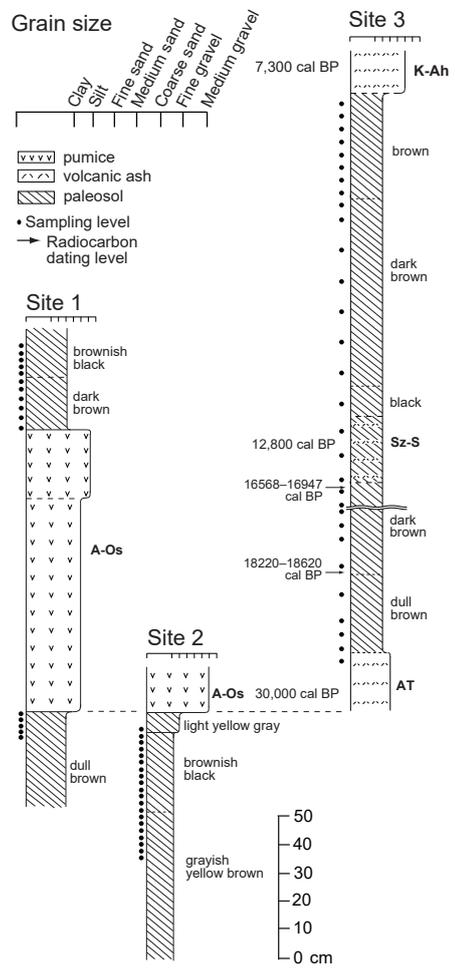


Figure 2

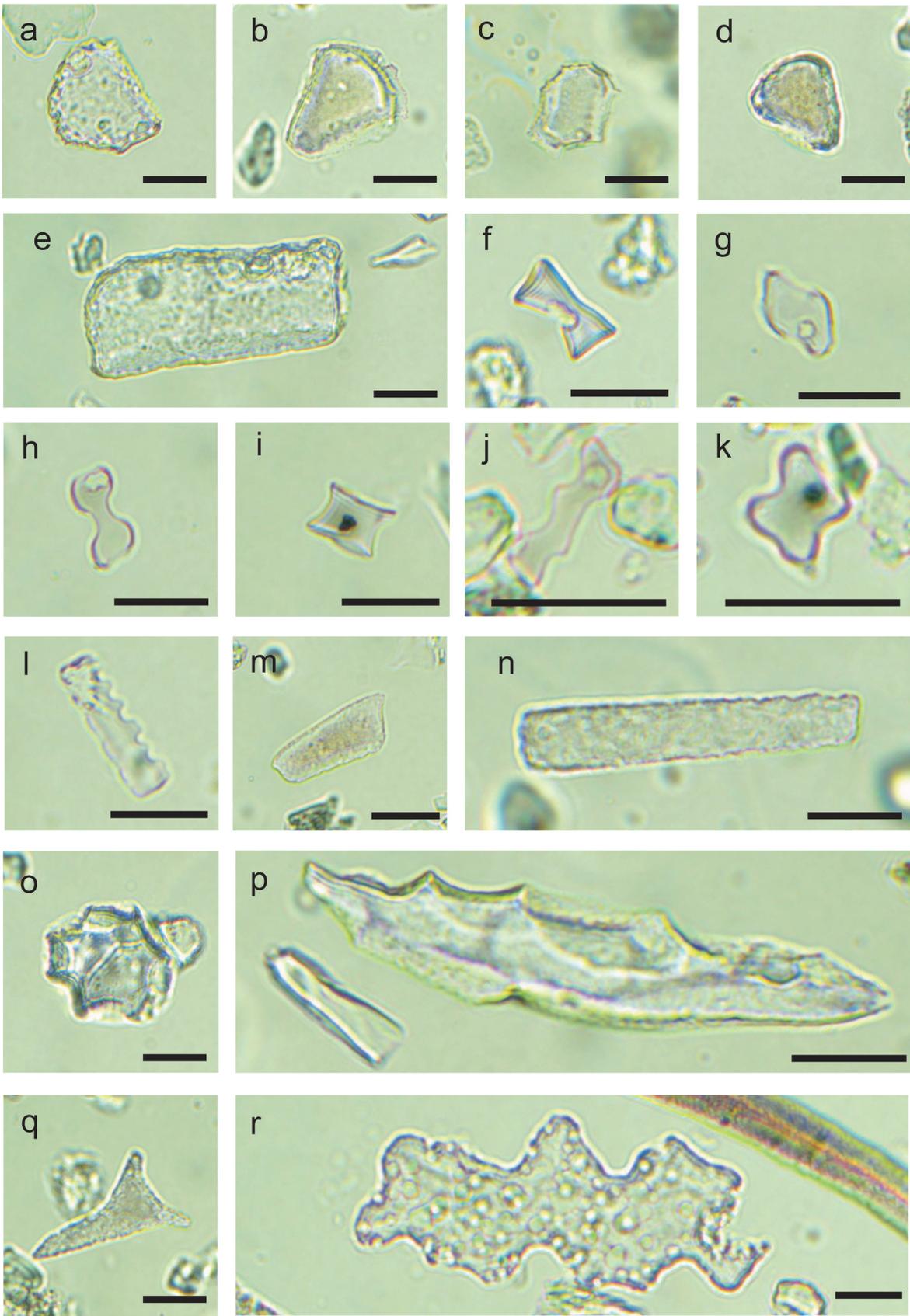


Figure 3

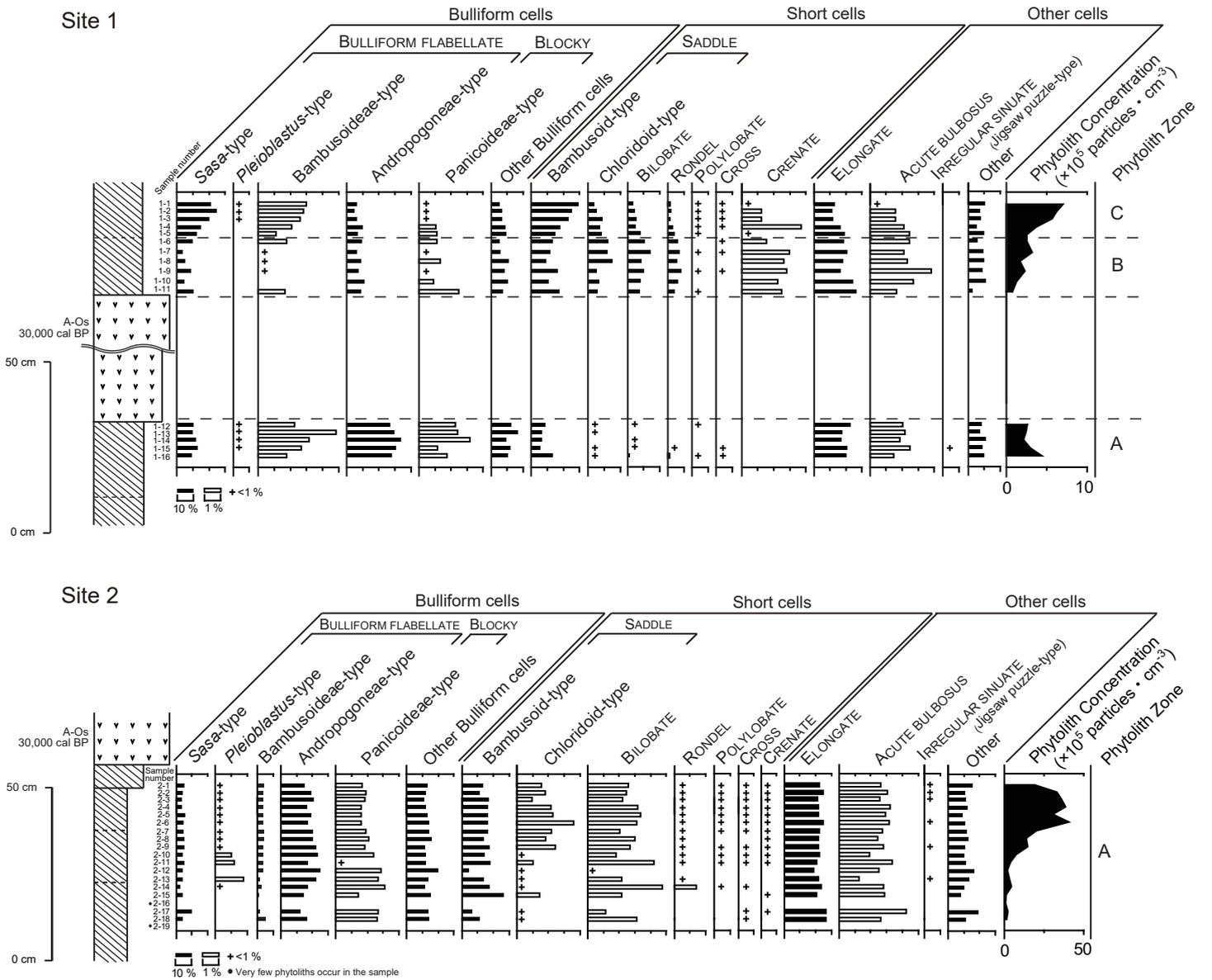


Figure 4

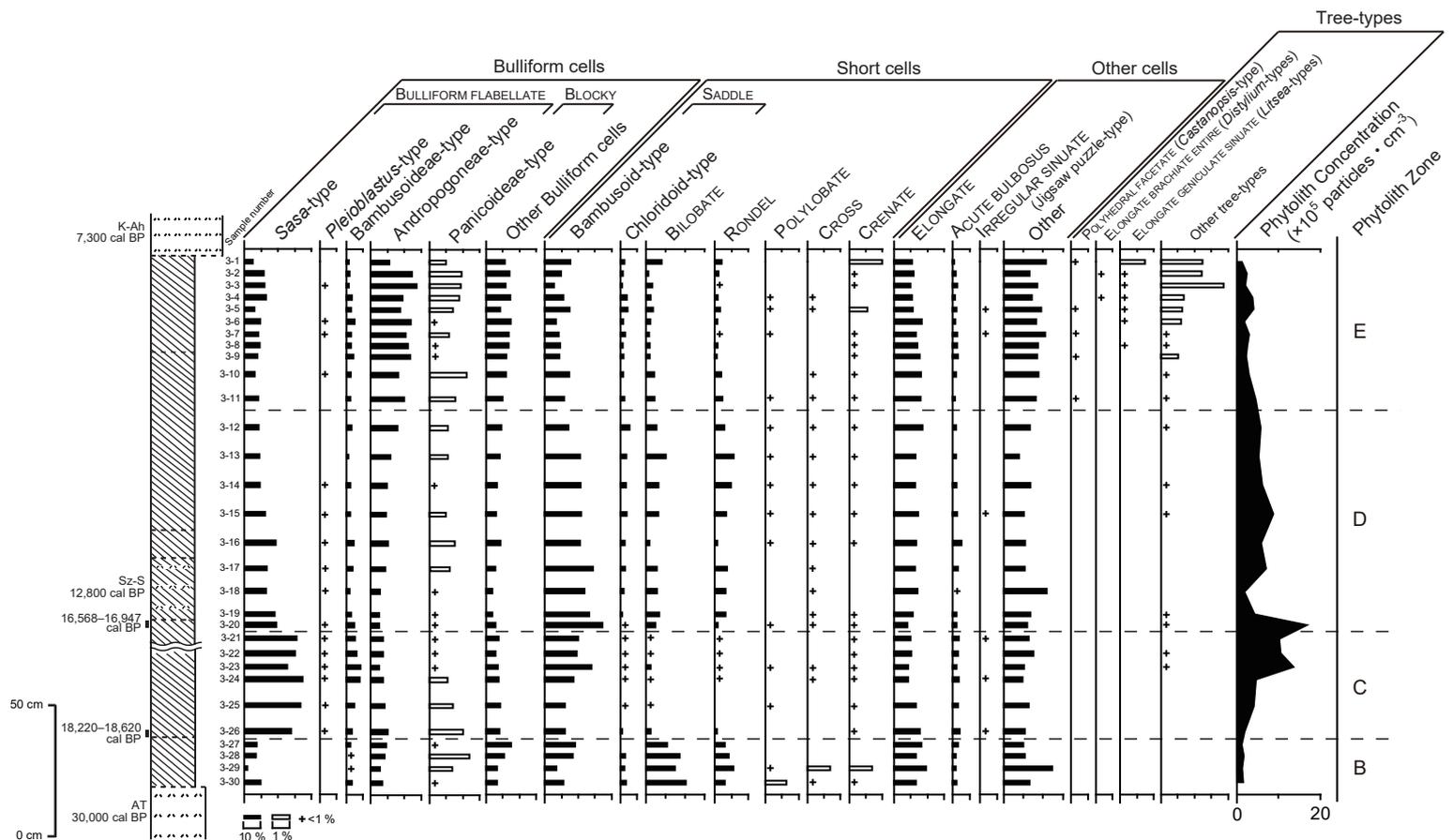


Figure 5

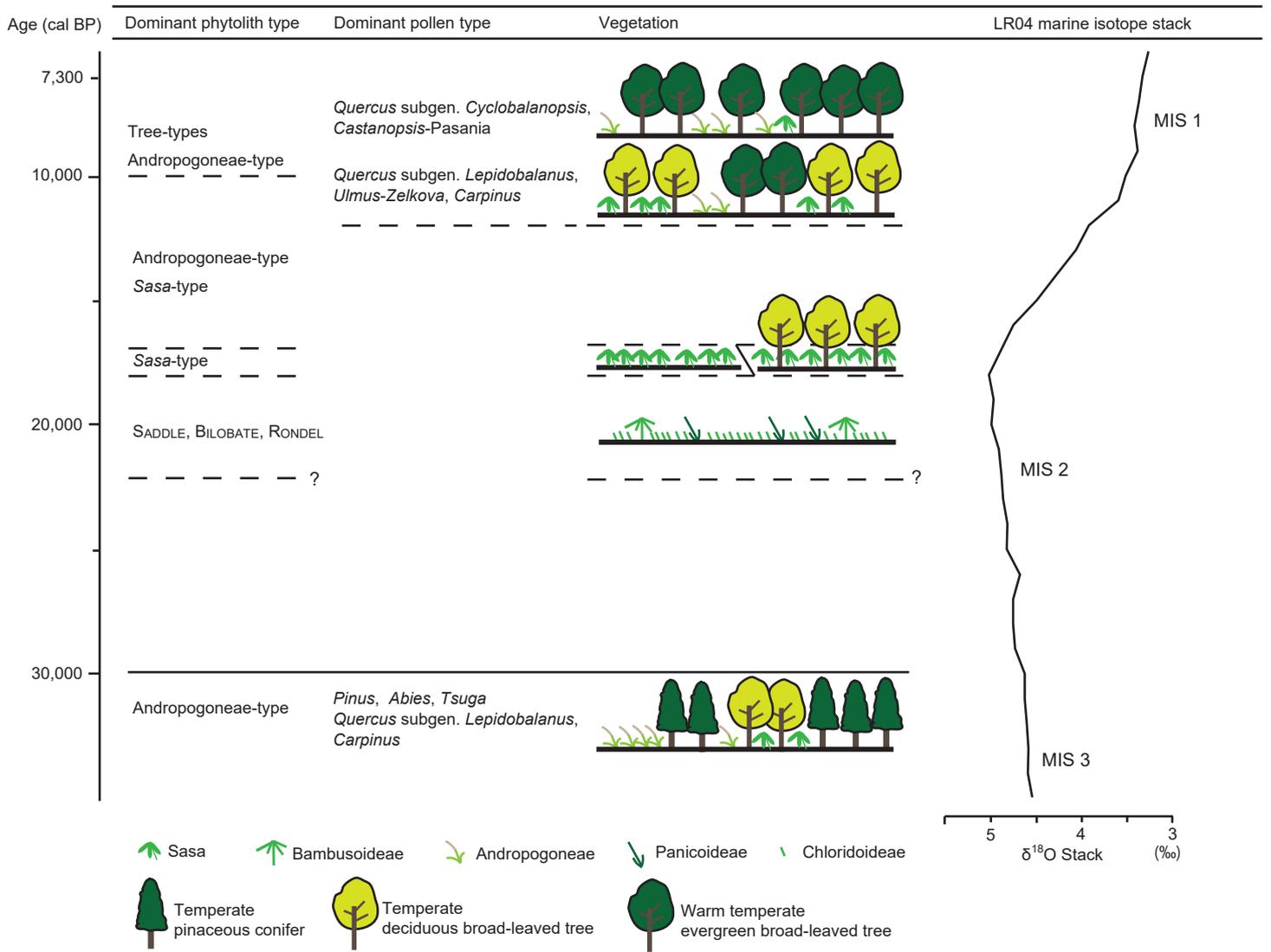


Figure 6

Table 1

Sample site	Sampe number	¹⁴ C date BP ±1σ	Cal BP with 2σ error	δ ¹³ C(‰)	Material	Code
3	3-20	13800 ± 40	16568–16947	–20.53	Humin fractions	Beta- 597151
3	3-26	15040 ± 40	18220–18620	–20.91	Humin fractions	Beta- 597150

Table 2

Family, Subfamily, or Tribe	Genus	Carbon fixation type	Main habitat	Climate zone	Produced phytolith-type
Herbs					
Bambusoideae					
					Bambusoideae-type (BULLIFORM FLABELLATE) ^{*1} , Bambusoid-type (SADDLE) ^{*2}
	<i>Sasa</i>	C ₃	Grassland Understory of deciduous forest	Subarctic–Cool-temperate zone	<i>Sasa</i> -type (BULLIFORM FLABELLATE) ^{*1+3}
	<i>Pleioblastus</i>	C ₃	Grassland	Warm-temperate zone	<i>Pleioblastus</i> -type (BULLIFORM FLABELLATE) ^{*1+3}
Panicoideae					
					Panicoideae-type (BULLIFORM FLABELLATE) ^{*4+5} BILOBATE, POLYLOBATE, RONDEL, CROSS
	Andropogoneae (<i>Miscanthus</i>)	C ₄	Grassland, Bare land	Cool-temperate–Warm-temperate zone	Andropogoneae-type (BULLIFORM FLABELLATE) ^{*5+6}
Chloridoideae					
		C ₃ & C ₄	Grassland (especially pasture) Bare land	Cool-temperate–Warm-temperate zone	Chloridoid-type (SADDLE) ^{*2} , RONDEL
Pooideae					
		C ₃	Grassland (especially pasture)	Subarctic–Cool-temperate zone	CRENATE
Trees					
Deciduous broad-leaved tree					
Quercoidaeae					
	<i>Castanopsis</i>	C ₃	Forest	Warm-temperate–Subtropical zone	<i>Castanopsis</i> -type ^{*7} (POLYHEDRAL FACETATE)
Hamameloideae					
	<i>Distylium</i>	C ₃	Forest	Warm-temperate–Subtropical zone	<i>Distylium</i> -type ^{*7} (ELONGATE GENICULATE SINUATE)
Lauraceae					
	<i>Litsea</i>	C ₃	Forest	Warm-temperate–Subtropical zone	<i>Litsea</i> -type ^{*7} (ELONGATE BRACHIATE ENTIRE)
Ferns					
Dennstaedtiaceae					
	<i>Pteridium</i>	C ₃	Grassland	Cool-temperate–Subtropical zone	Jigsaw puzzle-type (IRREGULAR SINUATE) ^{*7+8}