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Spatial changes in the distribution of *Cryptomeria japonica* since the last interstade in Shikoku Island, southwestern Japan

Abstract Spatial changes in the distribution of *Cryptomeria japonica* D. Don since the last interstade were reconstructed based on the pollen records from Shikoku Island, southwestern Japan. During the last interstade, C. *japonica* was dominant throughout the island and then conspicuously declined toward the end of this period, except around the Ikeyama-ike Bog, Muroto Peninsula on the Pacific Ocean side of Shikoku Island. During the pre-full glacial to late glacial periods, *C. japonica* was not abundant on Shikoku Island, except around the Ikeyama-ike Bog and Azono Valley on the Kochi Plain. The occurrence of *Cryptomeria* pollen during this period implies that these areas served as refugia for *C. japonica* during the full-glacial period. During the early part of the post-glacial period, warm-mixed/broad-leaved evergreen forests dominated by *Quercus* subgen. *Cyclobalanopsis* and *Castanopsis* rapidly expanded in the coastal region on the Pacific Ocean side. However, *C. japonica* was not a co-dominant component in these forests throughout this period, except in the areas around several sites such as the Ikeyama-ike Bog, where *C. japonica* rapidly increased in quantity during the late part of this period.
Keywords: *Cryptomeria japonica*, last interstade, pollen analysis, refugium, Shikoku Island

Introduction

Cryptomeria japonica D. Don. is a monotypic, evergreen conifer species that is endemic to Japan. The natural range of *C. japonica* extends from warm temperate to sub-alpine environments in Honshu, Shikoku, and Kyushu Islands. In these regions where *C. japonica* is most widely distributed, annual precipitation is more than 2000 mm (Hayashi, 1960). *Cryptomeria japonica* has been one of the dominant trees throughout the Japanese Quaternary, according to the palynological resultes obtained from long sediment cores (e.g., Tai, 1973; Miyoshi et al., 1999).

Tsukada (1980, 1982, 1986) presented a biostatistical model by combining modern surface pollen data with the present climatic data at pollen sampling sites. By applying this model to fossil pollen records, he was able to interpret the full-glacial refugia and late glacial, and post-glacial migration of *C. japonica*. Tsukada (1986) concluded that full-glacial refugia were distributed along the coastal regions of Honshu between 34° and 36°N, mainly on the Izu Peninula and adjacent areas, Wakasa Bay, and Oki Island. In addition, *C. japonica* expanded to the north and elevetionally higher upslope from the refugial areas immediately following late-glacial climatic amelioration. Actually, at the refugia inferred by Tsukada (1986), *Cryptomeria* pollen occurred nearly consistently at >5% throughout the sediments that were correlated to the full-glacial period (e.g., Takahara & Takeoka, 1992; Takahara et al., 2001; Kanauchi, 2005).

Takahara (1998) summarized previous pollen records published after the mid 1980s and provided a detailed analysis of the spatial changes in the distribution of *C. japonica* since the last interglacial period in Japan. In the regions on the Pacific Ocean side however, there were a limited number of pollen records from the last glacial period. Hence, the history of *C. japonica* from this region could not be elucidated adequately based on present pollen records, even though Kii and Muroto Peninsulas on the Pacific Ocean side are both regarded as probable refugia for *C. japonica* (Tsukada, 1982, 1986).

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Recently, we obtained a number of new pollen records since the last interstade. In this study, the previously published pollen records from the last interstade were combined with the newly acquired data to reconstruct the spatial changes in the distribution of *C. japonica* since the last interstade on Shikoku Island.

Study sites

Shikoku Island is located at the southwestern part of the Japanese Archipelago, ca. 600 km west of Tokyo (Fig. 1). Shikoku Island faces the Seto Inland Sea in the north and the Pacific Ocean in the south. In the center of this island, the Shikoku Mountains extend from the east to the west ends of the island and have an elevation of >1000 m. Mt. Ishizuchi (1982 m a.s.l.) is the highest mountain in southwestern Japan (Fig. 2).

Shikoku Island has three biomes from the warm-temperate to sub-alpine zones, i.e., warm-mixed/broad-leaved evergreen forest (WAMX), temperate deciduous forest (TEDE), and cool conifer forest (COCO) (Yamanaka, 1978; Kochi Prefecture & Makino Memorial Botanical Foundation, 2009), following the biome classification system and biome codes provided by Prentice et al. (1996). The upper limits of the WAMX and TEDE are 900–1000 m a.s.l. and ca. 1800 m a.s.l., respectively. The WAMX covers the largest area of the island and is dominated mainly by *Castanopsis* spp., evergreen *Quercus* spp., and Lauraceae spp. The TEDE consists mainly of *Fagus crenata*, deciduous *Quercus* spp., *Acer* spp., and *Abies homolepis*. The COCO is composed mainly of *Abies veitchii* and *Tsuga diversifolia*. Temperate conifer forest (TECO), dominated mainly by *Abies firma* and *Tsuga sieboldii*, occurs frequently at the transition zone between the warm-temperate and sub-alpine zones. Presently, *C. japonica* occurs mainly in the TECO (Hayashi, 1960; Yamanaka, 1961) and forms semi-natural, densely populated stands only in the eastern part of this island (around the Tengunomori Bog, site 20) (Hayashi, 1960; Yamanaka, 1961; Miyawaki, 1982).

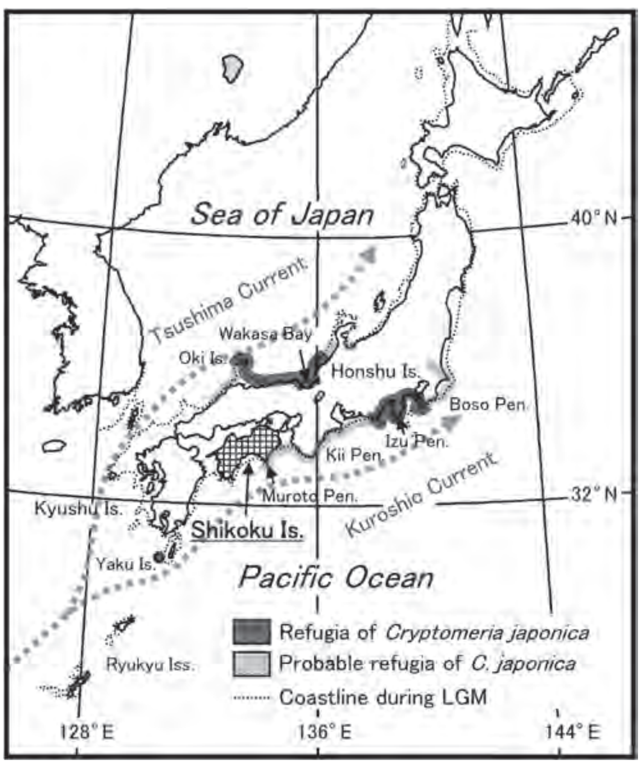

Fig. 1 Maps showing the location of Shikoku Island, refugia and probable refugia of *Cryptomeria japonica* (Tsukada, 1986) during the last glacial maximum. Broken line indicates the coastline during the last glacial maximum (Japan Association of Quaternary Research, 1987).

Methods

On Shikoku Island, 35 fossil pollen records including several from the post-glacial period have been obtained. In addition, 10 rare pollen records from the last glacial period that are correlated with marine isotope stages 5d to 2 (130,000 to 14,000 calendar years, 130–14 ka) were obtained. No records during the early part of this period have been obtained.

In this study, we used raw pollen counts from our records, including unpublished data, and pollen per-

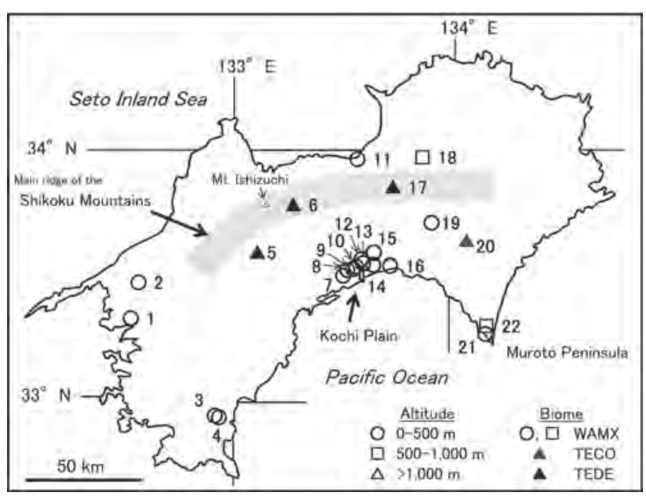

Fig. 2 Map showing the locations of the study sites on Shikoku Island. The site numbers correspond to those in Table 1. Biomes codes are based on Prentice et al. (1996).

Table 1 Characteristics of the study sites

No.	Study site	Lat. (N)	Long. (E)	Alt. (m)	Present biome	Record length (ka)	No. of ^{14}C dates	No. of tephra	Pollen samples (ka)							References
									50–40	30	29–14	10	7	4	2	
1	Uwa Basin*	33°23′	132°29′	215	WAMX	0–3, 25?– >44	4	0	○	○	○				○	Shimizu et al. (1980); Miyake et al. (2003)
2	Sugeta*	33°32′	132°35′	9	WAMX	21	1	0			○					Takahashi (1974)
3	Enomura Mire	32°59′	132°52′	8	WAMX	0–8	2	0					○	○	○	Nakajima et al. (2002)
4	Gudo Mire†	32°58′	132°55′	6	WAMX	0–12	2	1				○	○	○	○	Miyake & Ishikawa (2004)
5	Kara-ike Bog*	33°36′	133°05′	1220	TEDE	0–7	2	0					○	○	○	Yamanaka & Yamanaka (1978)
6	Kannarashi-ike Bog*	33°47′	133°13′	1600	TEDE	0–4	2	1						○	○	Miyake, unpublished
7	Ohtani Mire	33°29′	133°30′	10	WAMX	0–9	1	0						○	○	Miyake et al. (2009)
8	Mizukubo Mire*	33°32′	133°30′	10	WAMX	0–5	2	0						○	○	Nakamura (1989)
9	Koda Mire†	33°33′	133°31′	5	WAMX	7–10, 23–27	4	1			○	○				Miyake, unpublished
10	Yoshida*†	33°34′	133°32′	2	WAMX	0–1, 4–5, 7–9	0	1					○	○		Nakamura (1969)
11	Hirata*	33°59′	133°34′	27–28	WAMX	18	1	0			○					Takahashi (1975)
12	Azono Valley	33°35′	133°34′	<10	WAMX	14	1	0			○					Yamanaka, unpublished; Nakamura & Yamanaka (1982)
13	Maruike*†	33°34′	133°34′	0	WAMX	0– >10	0	1					○	○	○	Yamanaka (1984)
14	Itachino Mire	33°31′	133°37′	5	WAMX	0–10, 30–37?, >40	7	0	○	○			○	○	○	Miyake et al. (2005)
15	Oko Mire*†	33°34′	133°37′	4	WAMX	0–9	0	1					○	○	○	Yamanaka et al. (1992)
16	Tamura Site*	33°33′	133°40′	6–8	WAMX	0–3	1	0							○	Yamanaka (1986)
17	Nokano-ike Bog†	33°51′	133°42′	1200	TEDE	0–11	1	1				○	○	○	○	Miyake, unpublished
18	Kurozo Moor	33°59′	133°50′	560	WAMX	0–12, 30–43	6	3	○	○		○	○	○	○	Miyake, unpublished
19	Kami-ike Pond	33°44′	133°53′	430	WAMX	0–7	2	0					○	○	○	Miyake, unpublished
20	Tengunomori Bog*	33°37′	134°04′	1230	TECO	0–3	3	0							○	Nakamura (1978)
21	Murotsu*	33°17′	134°09′	6	WAMX	7–10	2	0				○	○			Matsushita et al. (1988)
22	Ikeyama-ike Bog†	33°21′	134°10′	512	WAMX	0–16, 27–33	4	1		○	○	○	○	○	○	Miyake, unpublished

Site names with asterisks indicate digitized data. Daggers show the dating control estimates are based on the K-Ah tephra (7.3 ka). The biome codes are based on Prentice et al. (1996).

centage values digitized from published records that were radiocarbon (^{14}C) dated and/or tephrochronology (Table 1). The raw pollen counts were obtained from nine sites and digitized pollen percentages were obtained from 12 sites.

The chronology of the sediments was estimated by simple linear interpolation between the ^{14}C-dated layers. ^{14}C dates were converted to calendar ages using the Fairbanks0107 calibration curve (Fairbanks et al., 2005). Pollen samples are defined as the pollen assemblage data in each layer of sediment. To reconstruct the spatial distribution of *C. japonica* at seven periods (50–40 ka, 30 ka, 29–14 ka, 10 ka, 7 ka, 4 ka, and 2 ka), we extracted the pollen samples from the pollen records whose dates were the nearest to each period and fell within ±0.5 ka of each period. The widely-distributed Kikai-Akahoya (K-Ah) tephra that fell at ca. 7.3 ka (Fukuzawa, 1995)was used as a time marker for the selection of samples. The samples were obtained from the layers immediately below the K-Ah tephra, when it was interbeded in the sediments.

Pollen percentages of *Cryptomeria* in the samples at each period were calculated based on the arboreal pollen sum, excluding *Alnus*, because *Alnus* is a prodigious pollen producer (Saito et al., 1996) and its thickets are often abundant in Japanese bogs (Sakio & Yamamoto, 2002). At the Tengunomori Bog, the percentage value at 2 ka could not be recalculated using the base number mentioned above, because only several tree pollen taxa (excluding *Alnus*) were represented in the diagram.

To explain the composition of the tree taxa including *C. japonica*, pollen assemblages from several samples from unpublished records were assessed. More detailed information about these records will be reviewed in a future paper.

Results and discussion

Based on the pollen samples from each period (Figs. 3a, 3b), the spatial changes in the distribution of *C. japonica* during the last interstade, pre-full glacial to late glacial, and post-glacial periods were reconstructed below.

Last interstade

Pollen samples obtained at 50–40 ka and 30 ka were characterized by the dominance of *Cryptomeria* pollen at 50–40 ka and an abrupt decrease by the end of this period at 30 ka (Fig. 3a). At 40 ka, the percentage of *Cryptomeria* pollen was 14% at the Kurozo Moor (site 18) in the interior mountainous region (Miyake, unpublished). At the Itachino Mire (site 14) and Uwa Basin (site 1) in the coastal area on the Pacific Ocean side, *Cryptomeria* pollen that correlates with the last interstade was also abundant (probably, 50–40 ka) (Shimizu et al., 1980; Miyake et al., 2005). During this period, *C. japonica* is likely to have been abundant around these sites.

At the present time *C. japonica* is distributed mainly in the transition zone between the warm-temperate and cool-temperate zones (Hayashi, 1960; Yamanaka, 1961; Miyawaki, 1982). In the densely populated stands of *C. japonica* in the eastern part of this island, the *Lindera-Cryptomerietum* association (Yamanaka, 1961) and *Rhododendron serpyllifolium-Cryptomeria japonica* community were recognized phytosociologically (Miyawaki, 1982). The former is composed mainly of *Tsuga sieboldii, Abies firma, Chamaecyparis obtusa,* and *C. japonica*, with *Lindera lancea, R. serpyllifolium,* and many evergreen broad-leaved species (e.g., *Quercus salicina, Cleyera japonica*, and *Neolitsea aciculata*). The latter also consists mainly of *T. sieboldii*, *C. japonica,* and *C. obtusa*, with *Rhododendron serpyllifolium*, *Illicium anisatum*, and *Lindera umbellata*.

At the Itachino Mire and Uwa Basin, *Abies*, *Cryptomeria,* and *Tsuga* (probably, *T. sieboldii* type) pollen were abundant, along with that of *Ulmus-Zelkova, Betula,* and *Quercus* subgen. *Quercus* (Shimizu et al., 1980; Miyake et al., 2005). The sample from the Kurozo Moor was dominated by *Tsuga diversifolia* type, Cupressaceae type, *Pinus* subgen. *Haploxylon,* and *Cryptomeria* pollen, with *Sciadopitys, Picea, Quercus* subgen. *Quercus,* and *Carpinus* pollen (Miyake, unpublished). According to the pollen assemblages from the Itachino Mire and Uwa Basin, in the coastal areas, at least on the Pacific Ocean side, *C. japonica* is considered to have been a dominant component of the temperate conifer forests, including deciduous broad-leaved elements. The pollen assemblage from the Kurozo Moor suggests that the site was situated in the upper part of the cool-temperate zone and that *C. japonica* was co-dominant with temperate and cool-zone conifers and deciduous broad-leaved trees.

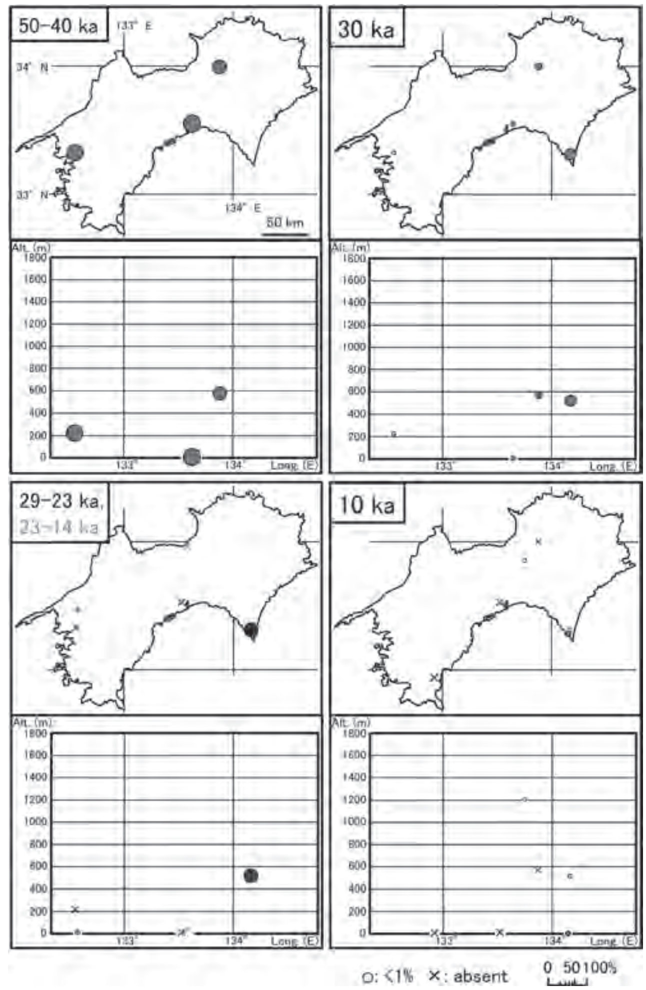

Fig. 3a Horizontal and vertical distributions of *Cryptomeria* pollen percentages at 50–40 ka, 30 ka, 29–14 ka, and 10 ka. The topographic maps are drawn using those issued by the Geographical Survey Institute of Japan. The altitudes of the study sites are based on present land-survey data. The Azono Valley was omitted from this analysis, because of the lack of percentage data.

By the end of this period, *C. japonica* declined conspicuously, because at 30 ka the percent *Cryptomeria* pollen was low at these sites. Chronologically, the decline of *C. japonica* from Shikoku Island almost corresponds with the decline in the area around Lake Biwa, Honshu Island (Hayashi et al., 2010). Moreover, local populations of *C. japonica* probably existed around the Ikeyama-ike Bog, Muroto Peninsula on the Pacific

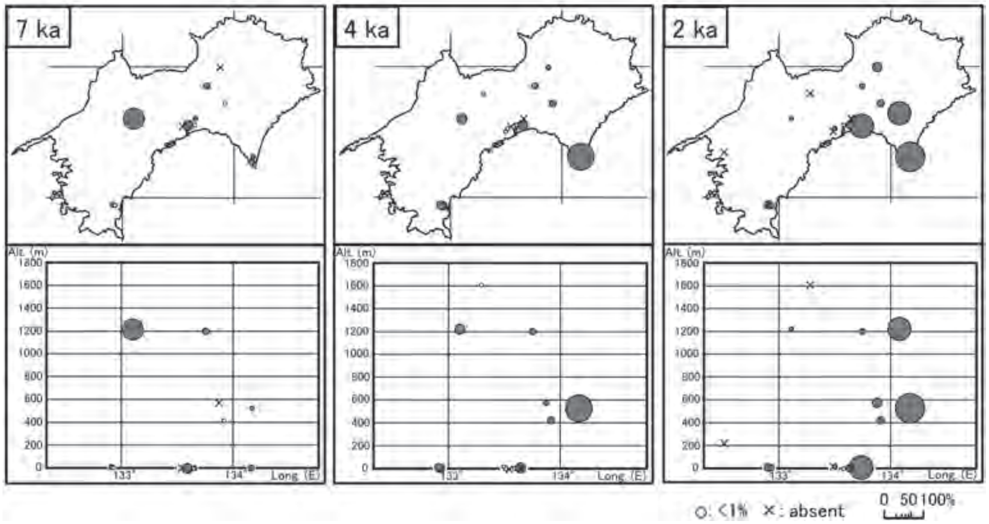

Fig. 3b Horizontal and vertical distributions of *Cryptomeria* pollen percentages at 7 ka, 4 ka, and 2 ka. The topographic maps are based on those issued by the Geographical Survey Institute of Japan. The altitudes of the study sites are also based on present land survey data.

Ocean side, since *Cryptomeria* pollen showed a relatively high percentage of 8% at 30 ka.

Pre-full glacial to late glacial periods

Pollen samples obtained at 29–14 ka show percentages of *Cryptomeria* pollen, except at several sites (Fig. 3a). Between 29 ka and 14 ka, the percent *Cryptomeria* pollen ranged between 6 and 15% (11% in average) at the Ikeyama-ike Bog, although the sedimentary record was slightly discontinuous (Miyake, unpublished). In the sample from the Ikeyama-ike Bog, *Cryptomeria* pollen was abundant along with *T. sieboldii* type, *Abies, Fagus crenata* type, *Carpinus*, *Quercus* subgen. *Quercus,* and *Betula* pollen. This area is considered to be a refugium for *C. japonica* during the full-glacial period, and this species was probably co-dominant with temperate conifers and deciduous broad-leaved trees. The inference of the refugium of *C. japonica* in the Muroto Peninsula (Tsukada, 1982, 1986) was confirmed by the palynological evidence from this study.

At the Koda Mire (site 9) in the Kochi Plain, the centeral part of the coastal area on the Pacific Ocean side, *Cryptomeria* pollen did not appear at 29–14 ka and 10 ka (Miyake, unpublished). At the Azono Valley near the Koda Mire, the pollen assemblage dates back to ca. 1.4 ka and was predominated by *Cryptomeria* and *Alnus*, with *Abies*, *Fagus, Pinus, Tsuga*, and *Pterocarya*, although the percentage data are unknown (Yamanaka, unpublished; referred by Nakamura & Yamanaka, 1982). Additionally, at 7 ka, *Cryptomeria* pollen also reached a high value of 28% at the Kara-ike Bog (1220 m a.s.l., site 5), which is more than 100 km northwest of the Muroto Peninsula (Yamanaka & Yamanaka, 1978). The ecological study of a buried forest during the late part of the postglacial period (Takahara & Takeoka, 1990) shows that *C. japonica* can establish and regenerate forests in wetlands. Thus, in addition to the Muroto Peninsula, very small, isolated populations of *C. japonica* probably existed in wetlands, river marshes, and alluvial fans of the Kochi Plain.

At the other sites, *Tsuga* (or *T. sieboldii* type), *Abies, Pinus* (or *Pinus* subgen. *Haploxylon*), *Quercus* subgen. *Quercus*, *Carpinus*, *Fagus* (or *F. crenata* type), and *Betula* pollen were co-dominant (Shimizu et al., 1980; Takahashi, 1974, 1975; Miyake et al., 2003). Percentages of *Cryptomeria* pollen were low, ranging between 0 and 2.8%. These data imply that during this period the mixed forests composed of temperate conifers and deciduous broad-leaved trees were widely distributed in the coastal area, and *C. japonica* was not a major component.

Post-glacial period

Pollen samples obtained from 10 to 2 ka were characterized by the dominance of evergreen broad-leaved trees. *Cryptomeria* pollen did not become dominant throughout this period, except at several sites (Figs. 3a, 3b). At 10 ka, *Cryptomeria* pollen showed very low percentages, ranging between 0 and 1.5% at all sites, even at the Ikeyama-ike Bog. At 7 and 4 ka, *Cryptome-*

ria pollen was identified over a wide geographic area, but the percentage values were small at many sites except for the Kara-ike and Ikeyama-ike Bogs. At 2 ka, *Cryptomeria* pollen showed high percent values at the Tamura site (site 16), Tengunomori Bog, and Ikeyama-ike Bog. Thus, from 7 to 4 ka, *C. japonica* expanded its distribution, especially in the interior, mountainous area, but it was not a major forest component throughout Shikoku Island.

At the Gudo Mire (site 4), Itachino Mire, and Murotsu (site 21), *Quercus* subgen. *Cyclobalanopsis* and *Castanopsis* pollen became dominant by 8 ka (e.g., Matsushita et al., 1988; Miyake & Ishikawa, 2004; Miyake et al., 2005). At the Nokano-ike Bog (1200 m a.s.l., site 17), *Quercus* subgen. *Cyclobalanopsis* pollen occurred frequently at percentages of greater than 5% after ca. 7 ka (Miyake, unpublished). These data suggest that during the early part of this period, the warm-mixed/broad-leaved evergreen forests expanded, especially in the coastal area on the Pacific Ocean side, and then reached the present upper limit of this biome in the mountains until ca. 7 ka. Despite the change of the preferred climate for *C. japonica* from the late glacial to postglacial periods, this species was probably out-competed by evergreen broad-leaved trees, because this species is shade-intolerant, long-lived, and depends strongly on gap formation during regeneration (Suzuki, 1997). On the other hand, the occurrence of *Cryptomeria* pollen from 7 to 2 ka from the Kochi Plain indicate that there were local populations of *C. japonica* in the wetlands on this plain throughout this period, even though they did not persist in the area.

At the Kara-ike Bog and Ikeyama-ike Bog, *Cryptomeria* pollen showed temporal changes in percentage. At the Kara-ike Bog, *Cryptomeria* pollen had a high value at 7 ka (Yamanaka & Yamanaka, 1978). Probably, during the early part of this period, *C. japonica* dominated the forests locally around the bog and then declined conspicuously by 4 ka. It is assumed that the establishment and rapid decline of *C. japonica* were caused by local changes in the soil environment around the bog from the early to middle parts of this period (Yamanaka & Yamanaka, 1978). At the Ikeyama-ike Bog, *Cryptomeria* pollen was abundant, 36% at 4 ka and 59% at 2 ka, respectively, whereas *Quercus* subgen. *Cyclobalanopsis* pollen percentage values decreased conspicuously (Miyake, unpublished). Presently, there are no natural populations of *C. japonica* around the bog, but the data suggest that they disappeared from this locality recently. *Cryptomeria japonica* seems to have outcompeted the evergreen broad-leaved trees only around this bog (site 22). The rapid increase of *C. japonica* pollen during the late part of this period suggests an environmental change that was suitable for the regeneration of this species, but we cannot explain why this species dominated in the forests only around the bog at this time. As mentioned below, around the Tengunomori Bog and Tamura Site, *C. japonica* forests seem to have been well developed before 2 ka. Terrestrial climate change and habitat instablility in and around this island during this period should be made evident by high-resolution environmental proxy records comparable with the pollen records to clarify the changes that occurred at this time.

At the Tengunomori Bog and Tamura Site, *Cryptomeria* pollen reached 34% and 26% at 2 ka, respectively (Nakamura, 1978; Yamanaka, 1986). Presently, there are semi-natural, densely populated stands of *C. japonica* around the Tengunomori Bog. Prior to at least 2 ka, *C. japonica* is considered to have been abundant around the bog. Unfortunately, the establishment and development of these stands is unclear, even though the origin can be regarded as the glacial refugium of the Muroto Peninsula, because the Tengunomori Bog is horizontally and altitudinally close to the Ikeyama-ike Bog in the Muroto Peninsula and linked by the same mountain ridge. In river marshes around the Tamura Site, *C. japonica* populations were distributed abundantly at 2 ka (Yamanaka, 1986), although this species is not naturally distributed at the present time in lowlands around the site.

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