

Review article

Nobuo Ooi¹: Vegetation history of Japan since the last glacial based on palynological data

大井信夫¹: 花粉分析に基づいた日本における最終氷期以降の植生史

Abstract To clarify the geographical history of Japanese vegetation and flora since the last glacial, the pollen assemblages were compiled into nine periodic groups 40 ka, 20 ka, 14 ka, 12 ka, 9 ka, 7 ka, 5 ka, 2.5 ka, and 0.8 ka named by their median ages that approximately corresponded to Japanese pollen zones. Twenty-five major arboreal pollen types were selected for statistical analyses to map the distribution of pollen types and pollen assemblages. To clarify physiognomical changes in vegetation 25 pollen types were divided into eight physiognomical classes. Chronological succession of the physiognomical classes and pollen types apparently showed vegetation changes since the mid-glacial. During the mid-glacial (period 40 ka), temperate forests of *Cryptomeria* or deciduous broadleaved trees dominated in central to western Japan, and evergreen pinaceous forests did in northern Japan and the mountainous areas of central to western Japan. At the peak of the cold full-glacial (period 20 ka), deciduous coniferous forests of *Larix* prevailed in Hokkaido, and evergreen pinaceous forests did in the other parts of Japan, with a considerable area of deciduous broadleaved forests in the lowland of central to western Japan. During the late-glacial (periods 14 ka, 12 ka), *Betula* forests expanded with evergreen pinaceous forests in the mountainous areas of central to western Japan and in northern Japan, and deciduous forests prevailed in the lower areas of central to western Japan with scattered *Cryptomeria* forests. During period 9 ka of the early post-glacial, deciduous broadleaved forests prevailed except in Hokkaido, where *Betula* and pinaceous forests dominated, and evergreen broadleaved forests appeared in southern Japan. At the hypsithermal (period 7 ka), evergreen broadleaved forests expanded in southwestern Japan, and deciduous broadleaved forests did in northeastern Japan. These trends continued until period 2.5 ka. In the recent (period 0.8 ka), *Pinus* forests expanded around the lowland areas with an increase of human activities except in Hokkaido. The chronological succession of pollen types, however, showed little evidence of plant migration in spite of the above physiognomical changes in vegetation. Horizontal and vertical distribution of *Fagus* and *Cryptomeria* pollen types, for example, changed little chronologically, whereas their frequencies or relative abundance in pollen assemblages changed greatly. Similarly, the chronological succession of other pollen types showed little evidences of migration, but the falls and rises in the dominance of mother species. To clarify changes in plant communities, pollen assemblages were categorized into 20 groups based on the dominance of pollen types with empirical information. The pollen assemblage groups did not have any direct correlation with plant associations, but definitely had a close correlation with vegetation. The distribution of pollen assemblage groups through the nine periods did not simply shift in latitude or altitude, but expanded and shrunk. Thus, vegetation changes since the mid-glacial were not caused by plant migration, but by increases or decreases of existing species.

Keywords: floral change, last glacial, physiognomy, pollen analysis, vegetation history

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日本語要約

はじめに

日本に花粉分析が初めて紹介・導入された1920年代後半以降、数多くの花粉分析が行われ、日本列島の最終氷期以降の植生史が明らかになってきた。しかし、多くの地点で花粉分析が行われているものの、さまざまな分野に適用されているため、分析目的や、データの普及度、その完結性などの違いにより、有効に活用されていないデータも多い。ここでは、日本の最終氷期中期約5万年前以降の花粉記録を総覧し、主要な25樹木花粉型の産出率の分布図を9つの時期ごとに作成し、植物の分布変遷を議論した。なお、本論の付表と付図はCD-ROMに収載されている。

方法

日本における花粉分析を学術論文や、書籍、遺跡発掘報告書、地質調査報告書、環境調査などのあらゆる出版物から蒐集した。花粉分析の行われた地点は基本的に1つのダイアグラムにまとめられたものを1地点とし、国土地理院発行の1/25,000地形図上に落とし、国際的な測地系に準拠したJGD2000の緯度・経度を読み取った。標高は文献記載に従い、記載のないものは地図上の標高を採用した。花粉分析地点の性格を示すため、それぞれの地点を海洋(ocean)、湖沼(lake)、湿原(moor)、機械ボーリング(borehole)、露頭(outcrop)、考古遺跡(archaeological site)、土壌(soil)に区分した。機械ボーリングは部分的に湖沼や、湿原、考古遺跡と重なるものもあるが、長期間にわたるものは機械ボーリングとした。

40 ka, 20 ka, 14 ka, 12 ka, 9 ka, 7 ka, 5 ka, 2.5 ka, 0.8 kaを中心値とする9つの時期を設定し、それぞれの分析地点でこの時期に相当する花粉群がある場合にはもっとも典型的で中心値に近い花粉群を1つ選んで代表させ、主要25樹木花粉型の産出率を図表から求めた。時期を代表する花粉群の層準決定は、地質層序、火山灰層序、放射性炭素年代、考古遺物の年代、隣接する地域の花粉帯や酸素同位体比ステージとの対比に基いて総合的に判断した(図2)。

時期40 kaは最終氷期中期のMIS(酸素同位体比ステージ)3で5~3万年に相当する。この時期は年代の精度が低く、断片的な資料も多いため、他の時期よりも幅を持たせた。時期20 kaは最終氷期最盛期を含む寒冷期で、3~1.5万年前頃となる。この時期のはじめに始良Tn火山灰(AT)が降灰した。時期14 kaは晩氷期の温暖な時期、時期12 kaは晩氷期の寒冷期で、それぞれヨーロッパのアレレード期、ヤンガー・ドリラス期に対応すると考えられる。時期9 kaは後氷期初期で10~8千年前に当たる。時期7 kaは最温暖期(ヒブシサーマル)で8~6千年前の縄文海進期に相当する。この時期には鬼界アカホヤ火山灰(K-

Ah, 7.3 ka)が降下した。時期5 kaは縄文時代中期の約6~4千年前に、時期2.5 kaは縄文時代晩期~弥生時代初期の3~2千年前に、時期0.8 kaは古代から中世の1200~400年前に相当する。時期0.8 kaはマツ属花粉の多産で特徴づけられる花粉帯R-III(塚田, 1967)の時期に相当する。時期5 ka以降は、とくに遺跡発掘に伴う花粉分析で短期間の花粉組成の変化が認められる例が多いため、時間幅を小さくとした。

日本において後期更新世以降の堆積物から記録された化石花粉型のうち樹木花粉は約170型ある(付表1)。分析者によって花粉型の名称が異なったり、同定の精度が異なったりするが、調整を行い主要な25花粉型を選んで統計処理を行った(主要25樹木花粉型とその母植物は付表2参照)。ハンノキ属花粉(*Alnus* type)は多産する樹木花粉ではあるが、しばしば局地的な要素として樹木花粉から除外され、結果として表示されないことも多いため、主要花粉型から除外した。また、コナラ属は常緑コナラ属型と落葉コナラ属型の2つに区分した。寒冷期や北海道においては単にコナラ属と表記されていても、すべて落葉コナラ属とみなした。また、コナラ属の産出率が5%以内の場合で、とくに常緑コナラ属の産出の記載がない場合はすべて落葉コナラ属として扱った。

統計処理は、主要樹木花粉型の計数合計が100を超えるものを対象とし、主要25樹木花粉型総計に対する百分率に換算した。図には計数合計が記載されていないものや一部の花粉型のみ示しているものも多く、とくに記載がない場合は総計200以上計数したとみなして換算した。

結果

約3200地点の花粉分析を検討した結果、1795地点の3791層準の花粉群を統計処理の対象とした(図3~5, 表1, 付表3, 4)。花粉群の数は現在に近い時期ほど多いが、時期40 kaと20 kaは時間幅を広くとったため、晩氷期の時期14 kaや12 kaよりも多くなっている。花粉群の性格によって、時空分布に違いが見られる。湿原と機械ボーリングでは平均して3.0時期以上にわたる長期の植生変遷が捉えられているのに対し、遺跡や露頭では平均1.4時期と短期である。遺跡の花粉分析地点数は時期5 ka以降急速に増加する。これは遺跡数が増加しただけでなく、縄文海進以降の海退で形成された低地で遺跡が数多く発掘されていることによる。このため遺跡は低地に、湿原は山間部に多い(図3~5)。また氷期においては露頭の花粉分析が目立ち、土壌は当然新しい時期に限られる。最終氷期最盛期には海水準が120 m低下して海岸線が拡大したにもかかわらず、氷期の低地のデータは極めて少ない。

時期ごとの主要25樹木花粉型の産出率をQGIS ver.

2.82-Wien を用いて日本列島の平面図および断面図上に示した (付図 2 ~ 26, 表 2)。また、花粉型を主にその母植物の相観と分布する気候帯に基いて以下の 8 つの花粉相観クラスに分類し (ヤマモモ属, クリ属/シイノキ属/マテバシイ属花粉は複数のクラスに入る), それぞれの産出率の水平分布を逆距離加重 (IDW) 法を用いて示した (図 6 ~ 9)。

1. DC-LRX (図 6 左): 落葉針葉樹のカラマツ属花粉のみからなる。現在シベリアを中心に分布する落葉針葉樹で、寒冷乾燥した気候を示す。北海道の氷期と本州中部の山岳地帯に多い。特に北海道東部において氷期の寒冷な時期 20 ka と 12 ka に多産する。後氷期には減少して、時期 9 ka と 7 ka ではわずかしみ見られず、時期 5 ka 以降では中部山岳地帯の限られた地点でのみ産出する。

2. EC-PNC (図 6 右): マツ科常緑針葉樹のトウヒ属と、モミ属、ツガ属花粉がこのクラスを構成する。その母植物は日本の高山帯や北方の針葉樹林の主要な樹種で、温帯域に生育する樹種も含む。氷期に多く、とくに最終氷期最盛期 (時期 20 ka) には、DC-LRX が多い北海道を除いて産出数が最大となる。北海道では時期 40 ka に最大になり、5 ka に最小となりその後再び増加する。他の地域では後氷期に入ると少なくなり、時期 7 ka で最小となる。東北と、中部、四国の山岳地帯では時期 5 ka と 2.5 ka に比較的目的立つ。

3. EC-PIN (図 7 左): マツ属のみからなる。マツ属はマツ科常緑針葉樹であるが、アカマツ由来と考えられる花粉が現在に近い時代に多産するため、EC-PNC と区別した。時期 0.8 ka には北海道以外の低地を中心に、また最終氷期最盛期 (時期 20 ka) にも多産する。前者は主にアカマツ由来、後者は大型植物化石が多産するチョウセンゴヨウや現在森林限界付近に生育するハイマツに由来するものと考えられる。

4. DB-BET (図 7 右): カバノキ属とヤマモモ属 (ヤチヤナギ) 花粉で構成される。カバノキ属とヤチヤナギは落葉広葉樹であるが、次の DB-TDB よりも寒冷な気候を示唆するため別のクラスとした。晩氷期には、産出地点が少ない九州と四国を除いて日本全国で多産する。後氷期初頭 (時期 9 ka) では北海道と日本海側の山岳地域で多産する。北海道と東北、中部の山岳地域では時期 7 ka 以降も産出が見られる。

5. DB-TDB (図 8 左): 温帯性落葉広葉樹のブナ属と、落葉コナラ属、シナノキ属、カエデ属、ハシバミ属、ニレ属/ケヤキ属/ハリゲヤキ属、クルミ属/サワグルミ属、トチノキ属、トネリコ属、クマシデ属/アサダ属、クリ属/シイノキ属/マテバシイ属花粉がこのクラスに属し、もっとも多く花粉型を含んでいる。後氷期に多産し、北海道で

は時期 5 ka に産出数が最大に、西日本では時期 9 ka ~ 7 ka に最大になり時期 5 ka 以降徐々に減少する。

6. EC-CSC (図 8 右): 温帯性針葉樹のスギ属と、コウヤマキ属、ヒノキ科/イチイ科/イヌガヤ科花粉がこのクラスを構成する。最終氷期中期 (時期 40 ka) には西日本の日本海側と伊豆半島で多産し、最終氷期最盛期と晩氷期にはわずかに伊豆半島や、島根、南九州で目立つだけで産出数が最小となる。後氷期に入ると再び増加し、西日本の日本海側と伊豆半島から東海地方で特に目立つ。

7. EB-WDE (図 9 左): 落葉広葉樹のエノキ属/ムクノキ属と、常緑広葉樹の常緑コナラ属、クリ属/シイノキ属/マテバシイ属、アカメガシワ属、ヤマモモ属が含まれる。氷期にはほとんど見られず、点在して多産するのは、時期 12 ka の南九州以外はクリ属/シイノキ属/マテバシイ属とヤマモモ属によると考えられる。後氷期に入ると西日本の海岸地域から時期 2.5 ka まで増加を続け、時期 0.8 ka では全体的に減少する。

8. EC-POD (図 9 右): 南方系針葉樹のマキ属のみが含まれる。産出量は多くないが、後氷期の西日本で特徴的に産出する。最温暖期の時期 7 ka の九州と四国西部でもっとも目立ち、時期 0.8 ka まで連続的に産出する。

相観クラスの分布変遷と、最も優占する相観クラスの分布変遷を見ると、5 万年前以降の日本列島の気候帯および植生帯の変遷が明らかである (図 10 ~ 13)。最終氷期最盛期にはマツ科針葉樹が広範囲で優占していたが、後氷期には落葉広葉樹が優占し、西日本の沿岸部から常緑広葉樹が広がり、最近になってマツ属が優占するようになった。

考 察

1. 花粉型ごとの分布変遷

花粉相観クラスの変遷で明らかなように最終氷期から後氷期にかけて、気候帯が移動するのに合わせて植生は針葉樹から落葉広葉樹、常緑広葉樹へと変化した。しかし、それは植物の移動を示しているわけではない。それぞれの花粉型の分布変遷を見ると、その頻度は時期によって大きく変動するものの、分布域に大きな違いは見られない (付図 2 ~ 26)。最初に、現在の日本の植物相・植生を特徴づける重要な要素であるスギ属とブナ属花粉の変遷を議論する。両者はこれまでに幾度も分布変遷が議論され、最終氷期の逃避地が推定されてきた。

スギ属花粉 (*Cryptomeria* type) (図 14)

スギ属花粉の分布変遷は既存の研究とほぼ一致する。最終氷期最盛期 (時期 20 ka) から晩氷期の時期 14 ka と 12 ka では、スギ属花粉の産出は逃避地と推定されている

隠岐、室戸、伊豆など以外では少なく、後氷期に入ると逃避地周辺などの低地を中心に一見拡大する。しかし、最終氷期最盛期（時期 20 ka）におけるスギ属花粉の地点ごとの産出率を後氷期の時期 2.5 ka のものに、最終氷期中期（時期 40 ka）のものを時期 0.8 ka のものにそれぞれ重ねてみると、産出率に違いはあるがその分布域はほとんど一致する（図 15）。時期 2.5 ka では、現在はスギが分布しない北海道でもスギ属花粉がわずかに産出し、本州のスギ林から飛来したと考えられる。一方、最終氷期最盛期 20 ka では、スギ属花粉は各地でわずかずつ産出しており、推定逃避地以外でも 5% を超えるところがあり、各地にスギが散在して生育していた可能性が示唆される。つまり、スギは長距離移動はしてはおらず、各地点で頻度を変えたのである。

縄文海進期 7 ka 以降、スギ属花粉は西日本の日本海側と東海地方の低地で増加する。とくに日本海側では埋没林が数多く発見され、富山県杉沢にみられるようなスギ湿地林が広く分布していたと考えられる。最終氷期前半の温暖期にはスギ属花粉が東北地方以南で繰り返し多産し、後氷期と同様の湿地林が繰り返し形成されたと考えられる。

ブナ属花粉 (*Fagus* type) (図 16)

ブナ属花粉の最終氷期最盛期 20 ka における分布域は、スギ属花粉と同様に基本的に晩氷期（時期 12 ka）や後氷期（時期 7 ka, 2.5 ka）の分布域に重なる（図 17）。ブナ属花粉がもっとも多産する地域は晩氷期から後氷期にかけて南から北へと移動し、ブナ林の分布域は温暖化にともなって北へ移動したが、ブナが移住したのではない。最終氷期最盛期においてもスギ属と同様に各地にブナ属の林が散在していた可能性が高い。ブナ属花粉は、後氷期ほどではないが、最終氷期中期（時期 40 ka）には本州以南に広く産出しており、時期 20 ka では産出率が低くなるものの関東南部や、四国、九州で比較的多く、半数以上の地点で記録されている。晩氷期（時期 14 ka, 12 ka）には日本海側でブナ属花粉が増加しはじめ、北海道でも 5% を超える産出が記録されている。後氷期に入ると東北地方の日本海側の低地から山地で増加をはじめ、時期 5 ka 以降東北～中部の山地ではブナ属花粉が多産する。北海道では、時期 5 ka 以降ブナ属花粉が多産する地域は次第に北へと移動していく。このブナ属花粉の変遷はブナの移動ではなく、ブナ林の変遷を示していると考えられる。現在のブナ林の分布は積雪と深い関係があり、後氷期のブナ属花粉の増加は日本海に対馬海流が流入し、積雪量が増加したことによると考えられる。しかし、まだ日本海に対馬海流が流入していない晩氷期や東北地方太平洋側でのブナ属花粉の増加など、単純に積雪と結びつけることができない事例も多い。

次に議論するのは寒冷な要素である。

カラマツ属花粉 (*Larix* type) (付図 4)

カラマツ属花粉は最終氷期最盛期（時期 20 ka）に最も頻出し、とくに北海道と東北太平洋側の山地で多産する。晩氷期の時期 14 ka には一旦減少するが、時期 12 ka には北海道で再び増加する。後氷期初頭（時期 9 ka）には減少し、わずかに散在するだけとなる。現在、日本では北海道にカラマツ属は生育せず、本州中部にカラマツがわずかに分布するだけであるが、最終氷期にはグイマツ化石が北海道と本州北部から、カラマツ化石が本州中部から得られていて、北海道と本州北部のカラマツ属花粉はグイマツに、本州中部のカラマツ属花粉はカラマツに由来すると考えられる。グイマツは後氷期に入って日本列島から消滅したが、北方へ移動したとは言えない。

トウヒ属花粉 (*Picea* type) (付図 3), モミ属花粉 (*Abies* type) (付図 6)

トウヒ属とモミ属は北日本から中部山岳地帯の常緑針葉樹林帯の主要な要素であり、本州ではほとんどが固有種である。いずれの花粉型も、最終氷期最盛期（時期 20 ka）には日本全国で多産する（図 18）。後氷期に入ると全体に減少し、北海道では時期 5 ka、本州では時期 7 ka に極小になる。その後、北海道ではともに増加する。本州ではトウヒ属花粉は中部山岳地域でやや増えるのみであるが、モミ属花粉は特に西日本で産出率が高くなり、中部や東北の山地においてもトウヒ属花粉よりも多産する（図 18）。化石花粉が集中して産出する地域は現在の種の分布域に対応している。

ツガ属花粉 (*Tsuga* type) (付図 5)

日本には現在ツガとコメツガの 2 種のツガ属が自生し、ツガは中間温帯と呼ばれる地域に、コメツガはより寒冷な地域に分布する。ツガ属花粉は最終氷期の寒冷期（時期 20 ka と 12 ka）、および後氷期の時期 0.8 ka で最も多く産出し、最温暖期（時期 7 ka）で極小となる。最温暖期以降は、現在のツガとコメツガの分布域に対応するように、四国と中部山岳地域の 2 ヶ所に頻出する地域が分かれる。ツガ属花粉と落葉広葉樹 (DB-TDB クラス) の垂直分布の変遷を見るとツガ属 2 種の変遷が推測できる（図 19）。時期 2.5 ka には 2 つの分布中心がはっきりとしていたが、最終氷期最盛期（時期 20 ka）では連続していた。この時期には、花粉形態による識別から、ツガとコメツガの分布域が近畿地方の低地部では接していたと考えられている。しかし、ツガとコメツガの分布域は後氷期の温暖化に伴ってゆっくりと分かれたのではなく、すでに晩氷期の寒冷な時期 12 ka には中部山岳地帯でツガ属花粉の多産が認めら

れている。つまり、温暖化にともなってコメツガが標高の高いところへ移動したとは考えにくい。最温暖期に極小を示したツガ属花粉はその後増加するが優占することはなく、時期 0.8 ka になると多産する地域の分離は不鮮明となる。この結果をみるとツガとコメツガの分布域はあまり変化していないと考えられるが、実際にツガとコメツガの境界がどのように変化したのかを明らかにするには、現生および化石ツガ属の花粉形態を詳細に調べる必要がある。

カバノキ属花粉 (*Betula* type) (付図 12)

カバノキ属花粉は晩氷期 (時期 14 ka, 12 ka) から後氷期初頭 (時期 9 ka) に多産する。中部山岳地帯上部でみられるカバノキ属花粉の多産はダケカンバに由来すると考えられるが、晩氷期に広がったカバノキ属花粉は、大型植物化石の記録から、ダケカンバは少なくシラカンバに由来し、西日本ではミズメに由来したと考えられる。さらに北海道ではヤチカンバやヒメカンバなどの矮性のカバノキ属植物が広がった可能性も示唆されている。このカバノキ属花粉の多産は、急激な気候変化と、日本海の高気圧変化による降水量の増加が引き起こした攪乱の頻発によってもたらされたと考えられる。類似した環境下で増加したと考えられるカラマツ属やブナ属花粉の分布と比較すると、隣接した地域で優占する花粉型が異なっており、温度環境などによる住み分けを示唆している (図 20)。

温帯性の要素は注目されるものだけを要約する。

コウヤマキ属花粉 (*Sciadopitys* type) (付図 8)、ヒノキ科/イチイ科/イヌガヤ科花粉 (CTC type) (付図 10)

コウヤマキ属花粉とヒノキ科/イチイ科/イヌガヤ科花粉の分布変遷はスギ属花粉とよく似ている。縄文時代晩期～弥生時代初期に相当する時期 2.5 ka におけるコウヤマキ属花粉とヒノキ科/イチイ科/イヌガヤ科花粉の分布を見ると、弥生時代の針葉樹利用との関係が見てとれる (図 22)。

トチノキ属花粉 (*Aesculus* type) (付図 24)

トチノキ属花粉は虫媒花粉のため散布範囲が小さく産出量も少ないため、分布変遷は捉えにくい。最終氷期には稀で、ほとんどは近畿地方から産出し、八甲田からも産出する。晩氷期の時期 12 ka 以降増加し、時期 2.5 ka に最も多くの地点で産出する。多産する地点の多くは遺跡で、人間との関わりが強く示唆されるが、トチノキ属花粉は遺跡以外の地点やそれ以前の時期にも多産する (図 23)。

エノキ属/ムクノキ属花粉 (*Celtis/Aphananthe* type) (付図 22)

この花粉型は後氷期に関東や西日本の海岸部で増加し、

日本海流や対馬海流などの暖流との関係が示唆される。晩氷期の時期 12 ka には鹿児島で多産し、後氷期に入ると優占する地域は時期 9 ka に九州、時期 7 ka で中国地方～近畿地方、時期 5 ka で関東地方と東へと移動する。またその分布域はスギ属花粉の優占地域と接している (図 24)。

常緑コナラ属花粉 (evergreen *Quercus* type) (付図 15)

常緑コナラ属は同定に問題が残るが、氷期においても産出率は低いものの、最終氷期最寒冷期の 20 ka においても 11.4% (33/290) の地点で検出されており、その分布範囲は現在とあまり変わらない (付図 15, 表 2)。後氷期初期の時期 9 ka には太平洋側では関東南部、日本海側では出雲までの沿岸部で普通に産出し、その後は最温暖期以降も増加を続け、時期 2.5 ka まで内陸部と北方へと広がった。後氷期におけるコナラ属の産出率と、落葉と常緑の比率を見ると、常緑コナラ属の優占が始まるのは、九州・四国で時期 7 ka、中国・近畿で時期 5 ka、東海・関東南部で時期 2.5 ka である (図 25)。最温暖期の縄文海進期以降も常緑コナラ属の増加が続くのは、海退によってもたらされた新しい土地に常緑コナラ属が生育したためであろう。このような土地には、時代や地域によって、スギ属や、エノキ属/ムクノキ属、トチノキ属、ハンノキ属などが繁茂することもあった。また、このような土地は人間活動の場でもあり、人間の影響も無視できない。現在の常緑コナラ属の北限にあたる秋田県沖の飛鳥や仙台周辺では遺跡やその周辺で常緑コナラ属花粉が産出している。

2. 花粉群の類型化

より詳細な植生分布を示すために、花粉群を、花粉の生産量や母植物の生態を考慮に入れながら優占する花粉型に基いて 20 の花粉群グループ (pollen assemblage group) に分けた (図 26, 表 4)。花粉群グループの時間的空間的変遷は、植生分布の変遷を考える上で多くの示唆を与えてくれる (図 42～50, 付図 27～30)。

マツ科針葉樹花粉が優占するグループ。LRX (カラマツ属花粉が 5% 以上産出する)、PIC (トウヒ属花粉が最優占する)、TSG (ツガ属花粉が最優占する)、ABS (モミ属花粉が最優占する)、ATW (モミ属、ツガ属花粉に常緑コナラ属花粉が随伴する)、PNC (マツ属を含む様々なマツ科針葉樹花粉からなる)、PIN (マツ属のみが優占する) (図 27, 表 4)

マツ科針葉樹花粉が優占するグループは氷期で高い頻度で現れ、とくに最終氷期最盛期 20 ka には最も多くの地点 (83%, 240/290) に現れる。LRX は北海道の時期 20 ka と 12 ka で多く、カラマツ属花粉が極めて高い頻度を

示すことも多い(図28)。PICは東北地方で、ABSは東北北部太平洋岸で、TSGやPNCは近畿地方を中心に分布する。しかし、後氷期に入ると全般に減少し、LRXは時期9kaを最後に消滅し、PICも北海道では時期2.5kaから0.8kaでやや増える以外は消滅する。それに対して中間温帯林を示すATWが時期2.5kaを中心とする後氷期に目立ち、マツ林を示すPINが時期0.8kaに35.5%(371/1045)の地点に現れる(図29)。それぞれの地域や時代ごとに優占する花粉群グループがあることは、針葉樹林が拡大するのに好適な時期にそれぞれのグループが増大し、移動はあまりしていないことを示している。

カバノキ属が最優占するグループ BET (図30)

BETは晩氷期(時期14ka, 12ka)には20%を超える地点で見られる。最終氷期最盛期には本州の低山でマツ科針葉樹花粉を伴って分布していたBETは、晩氷期には北海道の低地から低山と、本州の低山から高山へと分布を広げた。後氷期に入ると北海道と本州の高山に分布は限定されていき、時期5kaと2.5kaでは2%以下の地点でしか見られなくなる。北海道ではトウヒ属やモミ属花粉を伴い、本州以南の高山ではツガ属や、マツ属、ブナ属花粉を伴った。BETは時期9kaに中部山岳地域にわずかに現れ、その後同じ地域で存在し続け、現在のダケカンバ帯に続いたと考えられる。しかし、すでに述べたように晩氷期に広がったカバノキ林はダケカンバ林だけでなく、シラカンバやミズメなども優占していたと考えられる。西日本では時期9kaにBETはなくなり、東北でも時期7kaには稀となる。

MYR(ヤマモモ属が優占する)グループ

MYRは稀で、ほとんどが湿地に生育するヤチヤナギの多産を反映し、一部が温暖な要素を伴いヤマモモが優占する暖温帯林を示す。

温帯落葉広葉樹花粉が優占するグループ FGS(ブナ属最優占)、D_Q(落葉コナラ属最優占)、TMP(その他の温帯落葉広葉樹花粉優占)(図31, 32)、CAS(温暖要素を伴わないクリ属/シイノキ属/マテバシイ属が優占)(図33, 34)

FGSや、D_Q、TMPは最終氷期最盛期(時期20ka)に産出地点が最も少なくなる(15/290)が、後氷期の時期9ka~5kaには半数以上の地点で見られる(表4)。FGSは主に日本海側の山地で優占し、現在のブナ帯につながる(図31)。温帯落葉広葉樹花粉が優占する花粉群グループを構成するブナ属花粉と、落葉コナラ属花粉、その他の落葉広葉樹の比率の変遷を見ると、この三者の中ではブナ属が現在に向かって増加していく(図32)。FGSやD_Qは

花粉群の数が多いため、随伴する花粉群によってさらにサブグループに細分した(表5, 6)。落葉コナラ属には生態が異なる種が含まれているため、寒冷な要素から温暖な要素まで、幅広い花粉型を随伴していると考えられ、サブグループの分布変遷は種の消長に対応している可能性がある。TMPは様々な花粉型が優占する花粉群をまとめており、その詳細(サブグループ)を主にクリ属が優占していると考えられるグループCASとともに検討すると、いずれも数は少ないが、人間活動との関連性が高いと考えられるものも多いことが分かる(表7, 図33, 34)。

温帯針葉樹花粉が優占するグループ CRY(スギ属優占)、CTC(ヒノキ科/イチイ科優占)、SCI(コウヤマキ属優占)(図35)

SCIは最終氷期中期では寒冷な要素であるマツ科針葉樹を多く伴うが、後氷期の時期2.5kaでは温暖な要素である常緑コナラ属や、クリ属/シイノキ属/マテバシイ属、マキ属を伴い、コウヤマキが幅広い温度条件に適応していることを示している(図36)。CTCは多くの種を含むため解析は難しい(図36)。CRYも最終氷期中期にはマツ科針葉樹を伴うが、ブナ属やコナラ垂属も伴い、後氷期にはSCIと同様の温暖な要素を伴うことが多い(図37)。

温暖な気候を示す花粉群グループ C_A(エノキ属/ムクノキ属優占)、E_Q(常緑コナラ属最優占)、CLW(クリ属/シイノキ属/マテバシイ属が優占し他の温暖な要素を伴う)、POD(マキ属が5%以上産出する)(図38)

日本の常緑広葉樹林(照葉樹林)には花粉が残りにくいクスノキ科や虫媒植物が多いため、詳細な植生復原は難しい。しかし、温暖な気候を示す花粉群の分布変遷は、照葉樹林が後氷期には関東南部を含む西日本沿岸部から増加しはじめ、最温暖期(時期7ka)以降低地に広がり、内陸にも分布拡大したことを示している(図38)。C_Aは時期9kaの九州で目立ち、その後は関東以西で数と割合を減らしながら分布する。E_QとCLWの花粉組成は時間的な変遷だけでなく、地域的な違いも示しており、それぞれの地域で照葉樹林が独自に発達したことを意味している(図39)。PODは四国や九州沿岸部で時期7kaに、出雲で時期2.5ka頃に特徴的にあらわれる。

氷期と後氷期の温暖気候を示す花粉グループにおける温暖な花粉型の産出率とその組成は、まず時期9kaにエノキ属/ムクノキ属とクリ属/シイノキ属/マテバシイ属花粉が増加し、常緑コナラ属は最温暖期(時期7ka)以降に顕著に増加したことを示す(図40, 41)。ヤマモモ属やクリ属/シイノキ属/マテバシイ属花粉はそれぞれヤチヤナギやクリを含むため、氷期でも多産する地点が散在するが、それ

以外にも各地でわずかな産出があり、最終氷期に完全に消滅したとは考えにくい。

3. 日本列島の最終氷期中期以降の植生史

各時期の花粉群グループの分布とその花粉組成をもとに、最終氷期中期以降の植生史をまとめた (図 42 ~ 50)。

最終氷期中期 (時期 40 ka) には北海道ではグイマツにアカエゾマツや、エゾマツ、トドマツが伴う森林が広がっていた (図 42)。東北北部ではトウヒ属とモミ属が優占し、グイマツが伴った。本州中部の山地ではカラマツや、ヒメバラモミ、コメツガに落葉広葉樹が伴った。一方、本州中部低地から西日本では温帯性樹種とマツ科針葉樹が混在していた。スギ林は仙台や、伊豆、近畿、出雲、九州で成立し、コウヤマキやヒノキ科/イチイ科の林も散在したが、最終氷期前半よりも少なかった。最終氷期最盛期 (時期 20 ka) になると、北海道にはグイマツとハイマツが広がり、本州以南はマツ科針葉樹が優占したが、温帯性樹種も低地を中心に少なからず生育していて、関東以南の低地では優占種となるところもあった (図 43)。晩氷期の時期 14 ka にはカバノキ属と温帯広葉樹が増え始めたが、スギはあまり増えなかった (図 44)。再び寒冷化した時期 12 ka には、北海道ではグイマツが増加し、本州中部ではブナ属が増加した (図 45)。この変化は最終氷期前半 MIS5b ~ 4 における植生変遷とよく一致し、晩氷期の北海道と本州で寒冷化の程度が異なるとみても、最終氷期最盛期において日本海の淡水化の影響による寒冷乾燥化が本州でマツ科針葉樹の優占として顕著にあらわれたと見たほうがよい。

後氷期に入ると (時期 9 ka)、マツ科針葉樹とカバノキ属は、北海道と東北北部、中部山岳地域で比較的多かったものの全般に減少し、カラマツ属も減少し、代わってコナラ属が多くなった (図 46)。本州ではブナ属やコナラ属を中心とした温帯性落葉広葉樹が優占した。暖温帯常緑広葉樹は晩氷期にもわずかながら産出したが、後氷期はじめには暖流の影響を受ける日本海側の出雲や太平洋側の関東南部の海岸部でエノキ/ムクノキ林やシイ林が成立した。最温暖期の 7 ka ではマツ科針葉樹はもっとも限定的となり北海道でも落葉広葉樹が増加した (図 47)。本州は山岳地域まですべて温帯性広葉樹がひろがり、ブナが東北地方の山地で増加し、西日本の沿岸部は常緑コナラ属が優占する照葉樹林となり、イヌマキが九州で多産した。

しかし、常緑広葉樹林はこの後も拡大を続けた。これは、最温暖期の縄文海進期の後、海水準の低下によって低地が広がるとともに、それに伴う侵食・剝作用によって台地縁辺部では谷や扇状地ができ、そこに常緑広葉樹林が成立したからである。また、台地縁辺部は人間活動の場でもあり、人間の影響も大きかったと考えられる。時期 5 ka の北海

道では針葉樹は東部に限られ、コナラ属を中心とした落葉広葉樹林が広がった (図 48)。東北地方の山地にはブナ林が広がった。ダケカンパ林はハイマツ林とともに山岳地域に点在した。低地では遺跡の資料が増大し、地域的な違いを示す。仙台平野では落葉コナラ属にニレ科、ときに常緑コナラ属を伴った。関東平野では常緑コナラ属が多く、エノキ属や、シイ類、カヤなども増えた。伊豆ではスギが常緑コナラ属を伴い、東海地方では常緑コナラ属がブナ属やモミ属を、大阪平野では常緑コナラ属がスギやコウヤマキ、ヒノキ科を伴った。北近畿から中国地方東部の海岸沿いではスギが前の時期から引き続いて優占した。高知では常緑コナラ属と中間温帯林のモミとツガが特徴的に現れ、九州ではシイ類やイヌマキを交えた照葉樹林が広がった。

縄文時代晩期から弥生時代初頭の時期 2.5 ka に入ると、北海道や中部山岳地域では針葉樹がやや増加したが、沿岸部では前の時期から引き続いて常緑広葉樹が増加した (図 49)。スギ属は関東地方から東海地方の太平洋側と近畿地方から中国地方の日本海側沿岸部で多産し、スギ林が広がっていた。一方、エノキ/ムクノキの産出は続いたが優占することはなくなった。時期 0.8 ka はマツ属の顕著な増加で特徴付けられる (図 50)。この変化は北海道を除くすべての地域で低地を中心に見られる。

おわりに

最終氷期中期以降の花粉群の変遷は気候変動によく対応している一方で、植物が移動した明らかな証拠はない。ブナ属やスギ属花粉の時空的変遷は、分布域が変化することなく、産出量が大きく変わったことを示している。同定の問題はあるが、暖温帯の要素も同様に海岸部から増加した。一方、氷期に広がっていた寒冷な要素は北上するわけではなく、生育域が限定されたり、あるいは消滅した。

つまり、最終氷期中期以降、植生は大きく変化したものの植物の移動はほとんどなかった。環境変化と植生の変化の間にあまり時間差が見られないのは、環境に適した植物が移動することなく増加したからだろう。植物相の変化を知るにはより古い時代の植物化石の研究が必要である。

このように日本列島には多数の花粉分析資料が蓄積されており、花粉形態や稀産花粉型の再検討によって、さらに深い議論が可能となると予想される。しかし、数多くの花粉分析資料があるにもかかわらず、標本として公開されているものはほとんどない。早急に環境を整備することが求められる。

Introduction

Since the pollen analysis was introduced into Japan in the late 1920s and Jimbo (1932) reported palynological data, many palynological studies have been carried out throughout the Japanese archipelago. Reviews of these studies have revealed the outline of vegetation history in Japan, particularly since 50,000 years ago of the mid-glacial corresponding to the lower limit of the radiocarbon dating (e.g., Nakamura, 1967; Tsukada, 1974; Yasuda & Miyoshi, 1998; Takahara, 2011), and several palaeo-vegetation maps of the last glacial maximum have been proposed (Tsukada, 1974, 1984; Yasuda, 1978; Nasu, 1980; Tsuji, 2007). Thus, we know that, during the last glacial maximum, the major vegetation types in present Japan such as *Fagus crenata* forests, *Cryptomeria japonica* forests, or evergreen broadleaved forests were quite restricted in distribution, and, conversely, now restricted coniferous forests of *Picea* or *Pinus koraiensis* were dominant. Changes in the distribution of these forests have been discussed in relation to glacial refugia and post-glacial expansion from refugia promoted by climatic and geomorphological changes (e.g., Tsukada, 1980, 1982a, b; Hattori et al., 1987; Matsushita, 1987, 1992; Igarashi, 1991, 2008; Takahara, 1998a; Kito & Takimoto, 1999; Kito, 2003, 2008). Although these studies indicated a shift in vegetation, they did not discuss plant migration in those periods.

Presently the whole Japanese archipelago is naturally covered with forest vegetation with evergreen broadleaved, deciduous broadleaved, and evergreen coniferous forests along the latitudinal and altitudinal temperature gradients. The present distribution of forest zones and climatic zones in Japan has been deftly explained by the Warmth Index (WI) proposed by Kira (1945, 1949): WI 180–240 corresponding to the subtropical forests of mangrove plants; WI 85–180 to the warm temperate evergreen broadleaved forests of evergreen *Quercus*, *Castanopsis*, *Lithocarpus*, *Cinnamomum camphora*, *Machilus thunbergii*, *Cleyera*, *Eurya*, and *Camellia*; WI 45–85 to the cool temperate deciduous broadleaved forests of *Fagus crenata* and *Quercus crispula*; and WI 15–45 to the subarctic evergreen coniferous forests of *Abies* and *Picea*. Thus, this index of temperature has sometimes been applied to the reconstruction of past climate and vegetation (e.g., Yasuda & Narita, 1981; Yasuda, 1985; Matsusue et al., 2000). During the last glacial, however, vegetation types differed from modern ones, and a study of historical changes in the distribution of past vegetation types is indispensable to clarify the establishment processes of the modern vegetation.

The flora of Japan is a mixture of remaining cold elements that moved southward during glacial ages, temperate elements of the Sino-Japanese floristic region, and warm elements that moved northward from the south (Murata, 1995). Thus, in the warm temperate forests, we see species growing in the northern extreme of their generic distribution centering in the mountain regions of Southeast Asia, and in the alpine zone, species growing in the southern extreme of their subarctic generic distribution. Recently, distribution changes and migration processes of these species are deduced from the molecular data of modern plants (e.g., Fujii et al., 2009; Seo & Murakami, 2011; Tsumura & Momohara, 2011; Tsumura & Suyama, 2015). To clarify the actual migration history of these plants, we should seek palaeobotanical and palynological evidences.

In Europe and North America vegetation changes and plant migration have been discussed with deglaciation or retreat of ice-sheets. In Europe, Birks (1989) discussed plant migration by showing historical changes in *Fagus* isochrone maps. In North America, Delcourt & Delcourt (1987) illustrated vegetation history by the modern analogue method and plant migration by isopollen maps. The Showtime tool on personal computers (Keltner & Grimm, 1994) gives 15,000-year changes in pollen percentages of major pollen types. In Japan, however, only small glaciers developed in the high mountainous areas even during the full-glacial, and the Japanese archipelago was not connected to the Eurasian continent except Hokkaido during the last glacial. Three large islands of Honshu, Shikoku and Kyushu were connected by the dried up inland sea of Setonai-kai during the last glacial, but they were separated from Hokkaido by the Tsugaru and from Korean peninsula by the Tsushima and Korean straits (Oba, 2006). Thus, chronological pollen maps in Japan are expected to show plant migration since the mid-glacial within the Japanese archipelago excepting Hokkaido.

Recently pollen databases are made worldwide, particularly in North America and Europe, but not in Japan where comparatively large number of pollen analyses have been carried out. Because of the difficulty in standardizing pollen identification, chronological evidences, and taphonomical factors, many reviews have compiled regional palynological (and palaeobotanical) data and presented the regional vegetation history in various areas of Japan, such as Hatanaka (1985) for Kyushu since the last glacial maximum, Nakamura & Yamanaka (1992) and Miyake (2001) for Shikoku, particularly in Kochi Prefecture, Miyoshi (1983) for the Chugoku district since the late Pleistocene, Onishi (1974) for the San-in area (the Japan Sea side of the

Chugoku district) during the middle and late Quaternary, Takahara (1994) for the Kinki and eastern Chugoku districts since the last glacial, Nakabori (1986, 1987) for the mountainous areas of central Honshu since the late-glacial, Yoshikawa (1999) for the Kanto district since 12,000 years ago, Takeuti (2000) for the Tohoku district during the late Cenozoic, Morita (1998, 2000) for the alpine vegetation of Tohoku and Hokkaido, and Igarashi (2008) for Hokkaido and Sakhalin since the mid-glacial. Although these studies clarified vegetation changes and environmental histories in respective regions, comparing their results through the Japanese archipelago was difficult due to differences in assessing pollen data in respective regions. Thus, it seemed indispensable to compare the original pollen data of various studies to discuss wholly the history of vegetation and plant distribution throughout Japan.

Besides the pollen data published in scientific journals, there exist many data not widely circulated in Japan, such as pollen analyses for geology, archaeology, geography, and ecology. In this study, by summarizing the huge number of the palynological data in Japan since the mid-glacial, the horizontal and vertical distribution of pollen types and pollen assemblages in nine periods are compared. The nine periods since the mid-glacial were recognized by considering the proposed pollen zones in Japan. For each period at each pollen site, a single pollen assemblage was selected from the original pollen data to represent the period at that site. The horizontal and vertical distribution of pollen types and pollen assemblage groups during the nine periods were plotted on maps. The maps showed that changes in pollen types and assemblages occurred without migration of species, but with their expansion or contraction. The data compiled here is the most comprehensive database of Japanese palynology so far.

Method of data compilation and analyses

1. Outline of data compilation

Publications in Japan including pollen analytical data have been collected from journals, books, and various other publications such as reports of archaeological excavations, environmental assessments, and active-fault assessments. The publications with available data are listed in the bibliography in the appendix in CD-ROM with appendix figures and tables. Although there should be a number of uncollected reports, the list covers normally available bibliographic information for palynological studies in Japan. I tried to obtain the original or detailed data used in the references, but the cited data were used when the original data were not available. The area of data collection ranged from

Hokkaido to Kyushu of the Japanese archipelago and Ryukyu islands and adjacent seas (Fig. 1, App. Fig. 1).

Nine periods, 40 ka, 20 ka, 14 ka, 12 ka, 9 ka, 7 ka, 5 ka, 2.5 ka, and 0.8 ka, were recognized from chronological events and were named by their median ages. The most typical assemblage for each period was selected from each pollen site for the investigation. The nine periods approximately correspond to the pollen zones representing Japanese vegetation history (Fig. 2). Period 40 ka, that is called the mid-glacial in this paper, is an interstadial stage before the coldest stage of the last glacial, roughly corresponding to MIS (marine isotope stage) 3, and ranges from ca. 50 to 30 ka near the lower limit of the radiocarbon dating. The range of this period is wider than those of the other periods, because the number of data and the dating accuracy decrease in older periods. Period 20 ka, that is called the full-glacial in this paper, includes the last glacial maximum (LGM) estimated at 26.5 ka by ice sheet expansion (Clark et al., 2009). A widespread tephra and an excellent chronological marker of Aira-Tn (AT) from the Aira caldera fell near the lower limit of this period at 26–29 ka (Machida & Arai, 2003) or at 30,009 SG06₂₀₁₂ BP of Lake Suigetsu in Wakasa (Smith et al., 2013). This period ranges from ca. 15 to 30 ka, i.e., from below AT (30 ka) to To-HP (15 ka; Machida & Arai, 2003). Period 14 ka is a warm stage in the late-glacial corresponding to the Allerød in Europe. Period 12 ka is a cold stage in the late-glacial corresponding to the Younger Dryas in Europe. Period 9 ka is the early post-glacial ranging from 10 ka to 8 ka. Period 7 ka is the hypsithermal ranging from 8 ka to 6 ka and includes the Jomon transgression that recorded the highest sea level in Holocene Japan. Period 7 ka includes a widespread tephra of K-Ah, a good chronological marker of 7.3 ka. Period 5 ka ranges from 6 ka to 4 ka of the middle Jomon of the Japanese prehistoric periods, and coastal areas expanded with regression after the hypsithermal. Period 2.5 ka ranges from 3.0 ka to 2.0 ka and corresponds to the cultural transition from the final Jomon to the early Yayoi periods in Japan and includes the Yayoi regression. Period 0.8 ka ranges from 1.2 ka to 0.4 ka and is the ancient and feudal periods in the Japanese history. This period includes several widespread tephra layers of ca. 1000 years ago, such as B-Tm from Mt. Baekdu in northern Korean Peninsula, To-a from Lake Towada in northern Honshu, and As-B from Mt. Asama in central Honshu. This period corresponds to a Japanese pollen zone R-III characterized by an increase of *Pinus* pollen.

For each period at each site, a single horizon close to the median age and having the most typical pollen as-

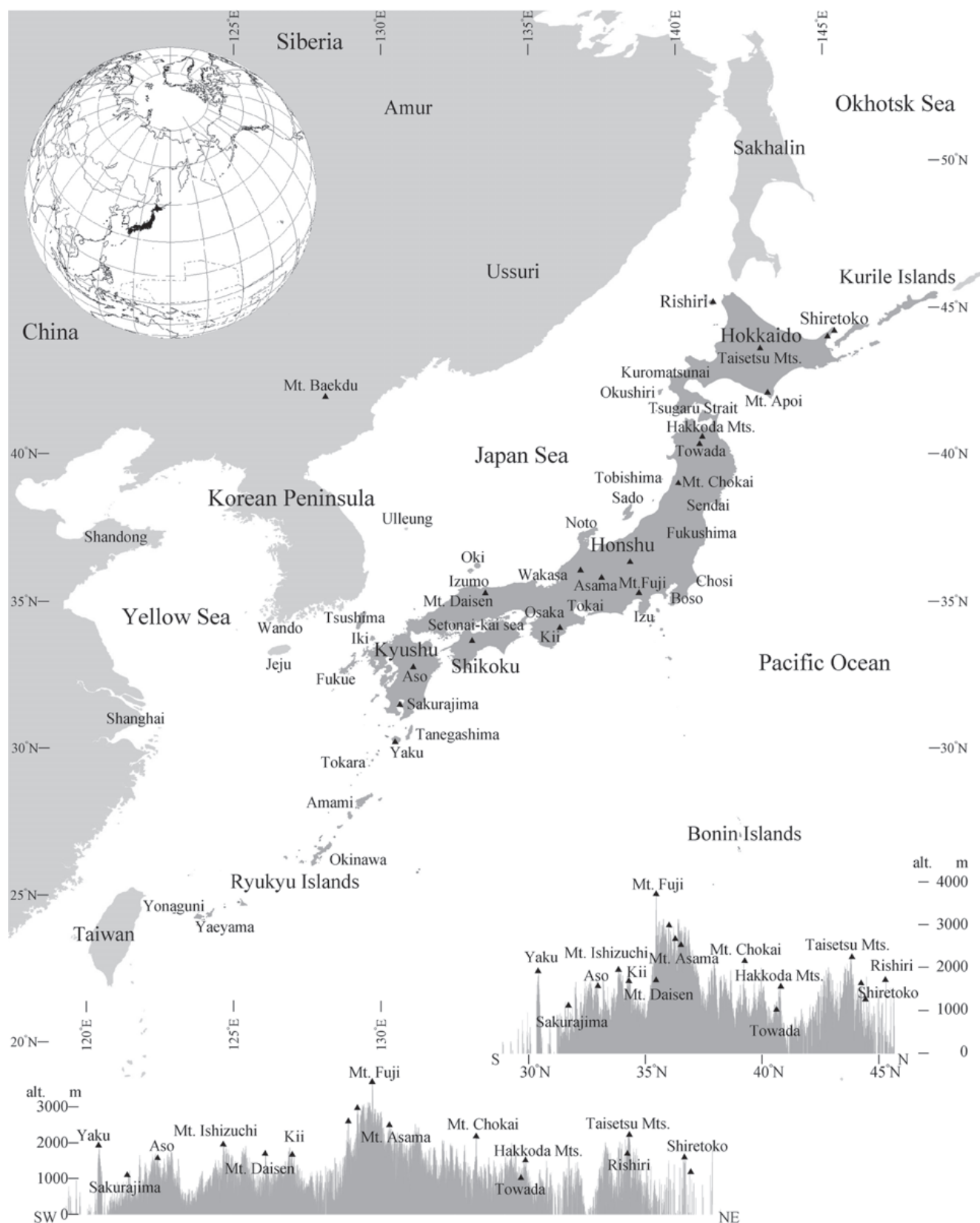


Fig. 1 Location of Japan with vertical profiles from south (S) to north (N) and from southwest (SW) to northeast (NE).

図1 日本の位置と南北および南西-東北断面（正距円筒図法による）。

semblage was selected for the investigation. Only arboreal pollen types were used for the comparison between localities, because many diagrams lack nonarboreal pollen and because forests have been the usual natural vegetation throughout Japan. Although nonarboreal pollen data are important for the glacial periods, in the alpine region, or for areas disturbed by fire and human activities, they were excluded to show the general outline of changes through the periods. From ca. 170 arboreal pollen types recorded since the Pleistocene in Japan (App. Table 1), the following 25 arboreal pollen types were selected and adjusted for statistical treatments: *Podocarpus*, *Larix*, *Picea*, *Abies*, *Tsuga*, *Pinus*, *Sciadopitys*, *Cryptomeria*, Cupressaceae/Taxaceae/Cephalotaxaceae, *Mallotus*, *Betula*, *Carpinus*/*Ostrya*, *Corylus*, evergreen *Quercus*, deciduous *Quercus*, *Fagus*, *Castanea*/*Castanopsis*/*Lithocarpus*, *Juglans*/*Pterocarya*, *Myrica*, *Ulmus*/*Zelkova*/*Hemiptelea*, *Celtis*/*Aphananthe*, *Tilia*, *Aesculus*, *Acer*, and *Fraxinus* types.

Alnus type was omitted from the analysis, because it fluctuates greatly in occurrence affected by local populations near sampling points and is often excluded from arboreal pollen counts.

2. Accuracy of geographical positions and characters of localities

Sampling localities were plotted on 1/25,000 topographical maps published by the Geospatial Information Authority of Japan (GSI), referring to the description of sampling localities and maps in the references. Latitude and longitude were read from the point on GSI maps, considering an update of the Japanese geometry in 2002 from the Tokyo datum to the JGD2000 datum based on ITRF (International Terrestrial Reference Frame). Difference between the two data sets is ca. 15 seconds or 400 m in maximum, and JGD2000 is almost the same as WGS84 widely adopted in GPS. The altitude of each sampling locality was read fundamentally from the description in the references, but was also read from the GSI map when it was obscure or had no description.

Samples in the same pollen diagram were regarded as from the same locality except for composed diagrams. When different researchers have analyzed sediments from the same locality, their data were treated as different data.

Some locality points were difficult to specify, particularly those in old studies, because place-names or addresses have been changed or lost through ages. Moreover, the area of locality points differed with research purposes. In some geological surveys, pollen records were compiled from samples of several out-

crops located more than 1 km apart, whereas, in some archaeological studies, pollen records were obtained from points separated less than 10 m apart.

The accuracy of each locality point is remarked in the Appendix Table 3 as A, B, and C.

A: specified to a second, ca. 20–30 m, that is ca. 1 mm on the 1/25,000 map.

B: specified to 10 seconds, ca. 200–300 m, that is ca. 1 cm on the 1/25,000 map.

C: specified to a minute, ca. 1200–1800 m, that is ca. 6 cm on the 1/25,000 map.

Besides plotting locality points, the character of localities has great influence on pollen analytical data. Pollen assemblages are influenced by sedimentary factors. Localities of pollen sites include not only moors or lakes that have relatively stable deposition, but also local and temporal peaty deposits often observed at outcrops. Even in moors or lakes, we can find hiatus in sedimentation caused by such geological events as abrupt changes in water level, floods, or tsunamis. A sedimentological survey of outcrops, on the other hand, sometimes gives good information on pollen taphonomy. To show the differences in the characters of localities, each site was classified into the following seven categories, considering sample sources in modern landscapes or objectives of surveys.

Ocean: Samples taken from ships during ocean surveys. Samples are obtained from the ocean floor, such as continental shelf sediments and sea bottom cores, and from inland seas.

Lake: Samples taken from lakes or ponds, including lakeside. Long cores obtained by machine boring are classified in the borehole.

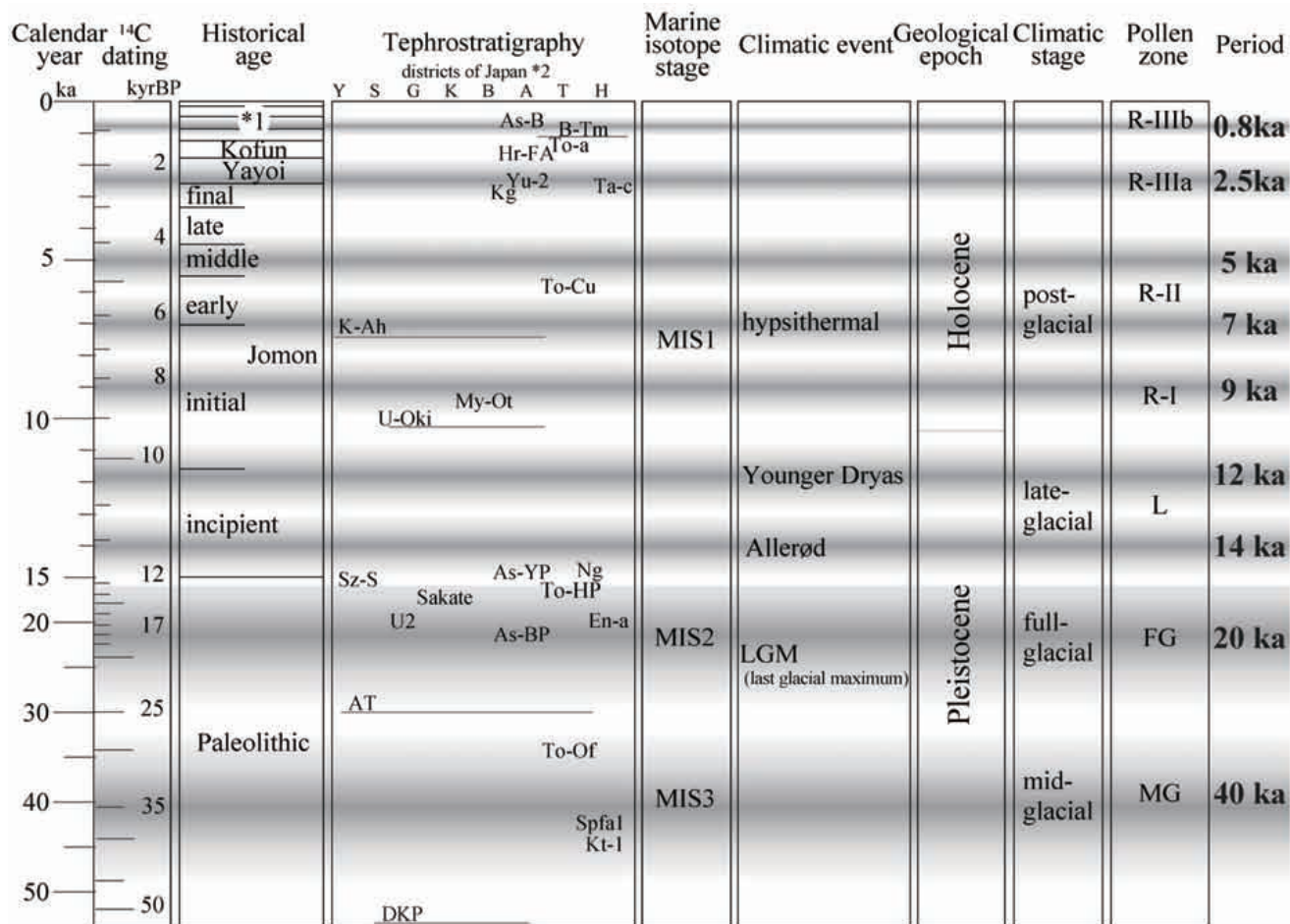
Moor: Samples taken from peaty wetland, such as moors, marshes, or bogs, mostly by hand coring. Works on rice paddy fields are also included in this category.

Borehole: Samples from long cores by machine boring, covering long ages. Pollen analyses of long cores often give continuous pollen spectra for a long time, but long cores covering the whole Pleistocene are often too rough for the age setting of this work.

Outcrop: Samples taken from outcrops with geological surveys. Trenches dug for geological surveys are also included in the outcrop.

Archaeological site: Samples obtained during archaeological excavations, including short coring and trench observations. Machine coring in archaeological excavations are classified in the borehole.

Soil: Samples obtained from soil. Paleosols are categorized in the outcrop, but when sequentially obtained from the modern soil, it is included in this category.



*1 from the bottom, ancient (Asuka, Nara, Heian), feudal (Kamakura, Muromachi), early modern (Adzuchi-momoyama, Edo), modern periods

*2 districts of Japan Y:Kyushu, S:Shikoku, G:Chugoku, K:Kinki, B:Chubu, A:Kanto, T:Tohoku, H:Hokkaido

Fig. 2 Nine periods for the collection of pollen records with evidences for the age estimation.

図2 花粉分析データを集めた9つの時期と年代推定のための根拠。

3. Decision of age

Ages of pollen assemblages were estimated multi-disciplinarily based on geological stratigraphy, tephrochronology, archaeological chronology, radiocarbon dating, and correlation between pollen assemblages in adjacent areas or to climatic events (Fig. 2). Chronologies of older references have been necessarily revised by the recent progress in the whole fields.

Tephrochronology

Tephra layers are valuable time markers in Japan that has ca. 300 active volcanoes now. Several widespread and regional tephra layers are recognized since the mid-glacial (Fig. 2). These tephra layers contributed to the correlation and age determination of pollen data. In this paper the name and ages of tephra layers basically follow Machida & Arai (2003) and Suto et al. (2007) and are updated by Smith et al. (2013).

Radiocarbon dating

Recently radiocarbon dating has been improved with the employment of AMS (Accelerator Mass Spectrometry) instead of the beta-ray metric method. AMS can measure small amounts of samples and not only rare isotopes, but also stable isotopes in shorter measurement time than before. Calibration with dendrochronology and U-Th ages of coral samples now provides a precise chronological scale for the past 50,000 years. In this paper, radiocarbon ages calibrated by IntCal09 (Reimer et al., 2009) are used as the standard time scale. Radiocarbon ages obtained by the old beta-ray method in cited studies were converted with the latest calibration unless otherwise stated.

Archaeological evidences

Archaeological chronology also supplies information on ages with systematic changes in relic types

such as stone tools and earthen pottery. It was updated with the recent progress in radiocarbon dating (e.g., National Museum of Japanese History, 2003; Kudo, 2012) and provides precise correspondence to the adopted periods. Many pollen analyses were conducted with archaeological excavations, and the ages of pollen samples were often estimated from archaeological remains. Although pollen data from archaeological sites tend to be fragmentary or restricted in time and area, pollen analyses in archaeological sites occasionally provide good information on changes in the local vegetation caused by human activities, particularly after 5000 years ago. They also provide a higher chronological resolution supported by rapid cultural changes and denser distribution of archaeological sites of younger ages. Pollen spectra from archaeological sites sometimes show rapid changes that need a more detailed age setting than that in this study. Thus, periods strictly following the archaeological data and data from intermediate periods were excluded. These excluded data are important to discuss the relationship between vegetation and human activities in detail, but data from the other areas often lack data of a similar resolution. To compare as many pollen records in wider areas, the periods were set laxly with a lower resolution. Although a considerable number of uncollected data from Japanese archaeological sites remain, these data come from materials of younger ages and lowland areas and are often not suitable for the present analysis due to insufficient pollen contents.

Oxygen isotope stages or climatic events

Marine isotope stages (MIS) are widely adopted to show the periods of the last glacial corresponding to the global climatic changes such as MIS 3 for the mid-glacial, MIS 2 for the full-glacial, and MIS 1 for the post-glacial. Correlation between pollen assemblages and MIS is commonly discussed with other dating methods such as radiocarbon dating or tephrochronology, or, in high-resolution studies, with regional climatic events such as Older Dryas, Allerød, and Younger Dryas in Europe, Heinrich events in northeast Atlantic (Heinrich, 1988), or the Dansgaard-Oeschger cycle in Greenland (Dansgaard et al., 1993). The correlation with these events should be done carefully in Japan, because these ocean events are detected in areas far from Japan. However, the late-glacial abrupt cooling that seems to correspond to the Younger Dryas in Europe is often detected by pollen analyses in Japan, as in the varved sediments of Lake Suigetsu with a delay of several hundred years from northwest Atlantic (Nakagawa et al., 2003) and in the moor deposits at Kyo-

goku Mire in southwestern Hokkaido (Igarashi, 2000). Although the timing and duration of cooling should be specifically studied, a number of other pollen spectra show obvious and rapid changes by cooling during the late-glacial. Thus, period 14 ka was distinguished from period 12 ka to emphasize this cooling event.

Correlation of pollen assemblages (Pollen zones)

Japanese pollen zones as chronozones were first proposed by Nakamura (1952) to explain the post-glacial vegetation history of Japan and have been sophisticated by Nakamura (1967, 1973), Tsukada (1967, 1974, 1981, 1987), and Yasuda (1981, 1990). Nakamura's (1952) pollen zones of the glacial were MG (mid-glacial) corresponding to period 40 ka, FG (full-glacial) corresponding to period 20 ka, and L (late-glacial; later subdivided by Tsukada (1981) into LI and LII by 12,000 yBP) approximately corresponding to periods 14 ka and 12 ka, respectively. Tsukada (1967) defined pollen zones of the post-glacial into RI (10,000–7000 yBP), RII (7000–4000 yBP, subdivided to RIIa, b), and RIII (since 4000 yBP, subdivided to RIIIa, b). The beginning of RIIIb were characterized by an expansion of *Pinus* at about 1500 years ago (Tsukada, 1981). The ages of these zones are difficult to define unanimously, being determined by a small number of old radiocarbon datings, and resulted in trivial and formal discussions. Tsuji (1988a, b) remarked that the vegetation changes occurred not only with climate changes, but also with sea level changes, and suggested that systematic changes of the natural environment occur with denudation and sedimentation caused by sea level changes and simultaneous changes in vegetation and soil. He proposed four epochs in the environmental change during the post-glacial in Japan, the first one at the bottom of the Holocene, the second one at 8000 yBP with a rapid transgression, the third one at ca. 5000 yBP of the middle Jomon with a regression after the hypsithermal, and the fourth one at ca. 2500 yBP corresponding to the so called Yayoi regression. During the latter two events caused by regression, peaty sediments suitable for palynological studies were deposited in the expanded wetland in the lowland. In 1990s, with the accumulation of pollen data and improvement in dating methods, researchers' interests gradually shifted from pollen stratigraphy based on the correlation of pollen zones to the global climatic oscillation, regional or local differences in pollen assemblages, and the relationship between vegetation and human activities. Because the use of pollen assemblages as age markers is a kind of tautology, the reliability of these pollen zones should be checked with other chronological methods.

Nevertheless, pollen zones are useful to explain the Japanese vegetation history, and the periods in this work succeed the concept of those pollen zones (Fig. 2).

4. Reliability of pollen identification

Pollen types are named after the taxon names, generally genus names, of the mother plants. The names of pollen types and their supposed mother plants sometimes differ between researchers. Arboreal pollen types recorded from the Pleistocene and Holocene of Japan are listed in the taxonomic order of a new classification by Christenhusz et al. (2011) for gymnosperms and of APG III (The Angiosperm Phylogeny Group, 2009) for angiosperms (App. Table 1). About 170 arboreal pollen types are recognized from Japan including synonyms or subdivisions. The mother plants of the arboreal pollen types include not only tree species, but also shrubs or vines. The supposed mother plants of 25 major arboreal pollen types selected for mapping are listed in Appendix Table 2. These mother plants are deduced from the present distribution of plants and the occurrences of macrofossils since the middle Pleistocene. Problems in the naming and identifying of the selected 25 major pollen types are as follows.

Pinus type

Among *Pinus* species, three of subgen. *Diploxylon* and four of subgen. *Haploxylon* grow in Japan. In the *Pinus* type pollen, *Haploxylon* type can be distinguished from *Diploxylon* type by the marginal crests and granules on the inside of leptoma (Ueno, 1958). These features are sometimes difficult to observe due to pollen crumpling or breaking. *Haploxylon* and *Diploxylon* types are usually distinguished in the studies of the glacial period based on the known prevalence of *Haploxylon* type during the last glacial judging from its macrofossil records (Momohara & Okitsu, 1998) and on present growth of dwarf *P. pumila* near the forest limit on Japanese mountains. However, they are often compiled as *Pinus* type in old studies or analyses of the post-glacial. Even when *Haploxylon* type is recognized, it is often recorded with a considerable number of undivided *Pinus* type. Moreover, we have two other *Haploxylon* species, *P. parviflora* and *P. amamiana*, growing in warmer environments at present. Thus, *Pinus* type is used in this study.

Pseudolarix (Tai & Ueno, 1965) and *Cathaya* (Saito et al., 2001) have been recorded in Japan until the early and middle Pleistocene, respectively. Their pollen grains are sometimes difficult to distinguish from *Pinus* type when badly preserved, but *Pseudolarix* and *Cathaya* were extinct from Japan by the mid-glacial.

Picea type

At present six species of *Picea* grow in Japan. *Picea jezoensis* and *P. glehnii* are dominant conifers in Hokkaido accompanied by *Abies sachalinensis*. In other districts *P. koyamae* and *P. maximowiczii* grow in small restricted areas of central Japan, *P. glehnii* relict on Mt. Hayachine in northeast Honshu, and *P. torano*, *P. alcoquiana*, and *P. jezoensis* var. *hondoensis* in recently shrank areas of central Japan (Katsuki et al., 2008). In peaty deposits of the last glacial, *Picea* cones occur frequently and abundantly (Minaki, 1987; Suzuki, 1991). These cones resemble those of *P. koyamae*, *P. maximowiczii*, *P. alcoquiana*, and *P. glehnii*, but are often difficult to identify with modern species. Thus, they have been named as *Picea* cf. *shirasawae* (Minaki, 1987) or as extinct species of *P. tomisawae* and *P. pleistoceaca* (Suzuki, 1991), but are found to be difficult to distinguish (Konishi & Suzuki, 1987; Note et al., 1998). Another extinct species of *Picea koribai* (Miki, 1948) became extinct during the early Pleistocene. The pollen morphology of Japanese *Picea* is similar, except for *P. polita* with relatively small bladders (Nakamura, 1954; Ueno, 1958). Tai (1973) showed stratigraphic changes in the size frequency of fossil *Picea* pollen in the Plio-Pleistocene Osaka Group and accompanying *Picea* macrofossils and concluded that the pollen of extinct *Picea koribai* could be distinguished by its larger size.

Larix type

The mother plants of *Larix* type pollen are *Larix kaempferi* and *Pseudotsuga japonica* native in Japan and *Larix gmelinii* that became extinct from Japan during the post-glacial and now grows widely in Siberia and Sakhalin. Beside them, we have two extinct species of *Pseudotsuga* from the early Pleistocene in Japan (Miki, 1957). The pollen morphology of *Larix* and *Pseudotsuga* is similar, but *Larix* pollen grains have a distinct annular thickening (Ueno, 1958) and can be practically distinguished judging from accompanying pollen types, because *Pseudotsuga japonica* grows in restricted areas of the warm to cool temperate zones, whereas *Larix* mainly grows in subboreal to boreal forests. Actually, only a few probable records of *Pseudotsuga* pollen exist since the last glacial in Japan. The most probable record is from Oono, Kochi Prefecture, where the occurrence of *Pseudotsuga* type was estimated from the modern neighboring vegetation (Nakamura & Katto, 1953a). *Pseudotsuga* pollen occurred frequently in the middle Pleistocene marine clay layers of the Osaka group (Furutani, 1989; Kitani, 2005; Hongo, 2009), corresponding to the odd-numbered, warm oxygen isotope stages from MIS 7 to MIS

17 (Yoshikawa & Mitamura, 1999). Particularly, the pollen assemblage from a marine clay layer of Ma11 (MIS 9 to 11) is named as *Pseudotsuga* zone (Furutani, 1989). Because *Larix* pollen frequently occurred during glacial periods and in northern areas, *Larix* type is conventionally adopted in this study.

Tsuga type

Two endemic species of *Tsuga*, *T. diversifolia* and *T. sieboldii*, grow in Japan. The pollen of these two species is similar, but the marginal ridge of *T. sieboldii* pollen is smaller than that of *T. diversifolia* pollen (Ueno, 1957). This difference is statistically confirmed, but their size ranges overlap (Takahara, 1992). This distinction is important, because *T. diversifolia* grows in a cooler environment than *T. sieboldii*. However, this criterion has not been widely adopted because a sufficient number of *Tsuga* type pollen grains should be studied for a statistical treatment. In Japan, three extinct Pleistocene species of *Tsuga* were recorded (Miki, 1957) and were replaced by the modern ones in the middle Pleistocene. The morphology of their pollen should be different from that of modern species, judging from the size analysis of fossil *Tsuga* pollen by Tai (1973).

Abies type

Four of the five *Abies* species growing in Japan are endemic in the mountainous areas of Honshu and Shikoku. Saito & Tsuchida (1992) described the pollen morphology of Japanese *Abies* and suggested possibility of species distinction among *Abies* pollen grains in Japan. Although their criterion has not been adopted in pollen analyses yet, further studies will probably shed a new light on the species history of Japanese *Abies*.

Picea and *Abies* types are sometimes compiled together in diagrams when they occurred rarely or were badly preserved, because of the similarity of their large bisaccate pollen. In past Japan *Keteleeria* and *Cedrus* also had large bisaccate fossil pollen, but became extinct by the early Pleistocene.

Podocarpus type

Two species of Podocarpaceae, *Podocarpus macrophyllus* and *Nageia nagi* (synonymous to *Podocarpus nagi*), grow in a warm environment in Japan. Because *Nageia nagi* is included in *Podocarpus* in a wide sense, the name *Podocarpus* type is adopted in this study. Podocarpaceae originated in the southern hemisphere. Ueno (1960) studied the pollen morphology of Podocarpaceae for seven genera and 81 species including Japanese ones. Some differences exist in the pollen morphology of *Podocarpus* species, but are not ap-

parent between *Podocarpus macrophyllus* and *P. nagi*. *Podocarpus macrophyllus* and *P. nagi* are often cultivated, and *P. nagi* growing in Honshu is thought to be introduced during the ancient period.

Sciadopitys type

Sciadopitys verticillata is the sole member of the family Sciadopityaceae and the genus *Sciadopitys* and is endemic to Japan. *Sciadopitys* pollen is approximately spheroidal without furrows or papilla (Ueno, 1951), and its surface is covered all over with granules with micro spines (Yamazaki & Takeoka, 1958). *Sciadopitys* pollen apparently differs from the pollen of other Cupressales genera.

Sciadopitys produces good timber and was valued for construction and coffins, particularly during the Kofun period in Japan (Itoh & Shimaji, 1996; Okabayashi et al., 2009). Its natural forests are restricted and difficult to distinguish from ancient plantations. *Sciadopitys* grew more widely throughout the Plio-Pleistocene and in the post-glacial hypsithermal before it was rapidly restricted in geographic distribution since the beginning of intensified human activities in Japan (Tsukada, 1963). Outside Japan, *Sciadopitys* fossils have not been recorded after the early Pleistocene.

Cryptomeria type

The mother plant of *Cryptomeria* type is *Cryptomeria japonica*. *Cryptomeria japonica* is thought to be the sole species of the family Taxodiaceae and is almost endemic to Japan. *Cryptomeria fortunei* grows in coastal mountains of southern China, but is genetically indistinguishable from *Cryptomeria japonica* (Tsumura et al., 1995; Sahashi et al., 1999). Recently, Taxodiaceae was merged into Cupressaceae by a molecular phylogenetic analysis (Gadek et al., 2000). *Cryptomeria japonica* is a temperate conifer preferring moist and wet conditions. Its pollen characterized the early glacial period of Honshu (Takahara, 1998b).

Cryptomeria pollen resembles the pollen of some other Taxodiaceae having papilla, such as *Metasequoia*, *Glyptostrobus*, *Sequoia*, *Sequoiadendron*, and *Taxodium*, all of which were extinct from Japan by the middle Pleistocene. *Cryptomeria* pollen has a characteristic thin wall around the papilla (Yamazaki & Takeoka, 1956; Sohma, 1986; Kvavadze, 1988). In some studies Taxodiaceae was used instead of *Cryptomeria*, but Taxodiaceae can be treated as *Cryptomeria* since the mid-glacial, although *Cryptomeria* pollen is occasionally difficult to distinguish from the following CTC type.

CTC (Cupressaceae/Taxaceae/Cephalotaxaceae) type

This pollen type includes useful timber trees in Japan such as *Chamaecyparis obtusa*, *Chamaecyparis pisifera*, *Thuja standishii*, *Thujopsis dolabrata*, *Taxus cuspidate*, and *Torreya nucifera* and some other species such as *Juniperus communis* and *Cephalotaxus harringtonia*. Their pollen is similar in morphology with an approximately spheroidal shape without apparent papilla or pores and is often compiled in pollen analyses (Miyoshi et al., 2011).

This type is often presented as Cupressaceae or *Chamaecyparis* in pollen analyses without morphological description. *Torreya* is distinguished by the thick costae of its pollen in some studies, but not in others, judging from adjacent pollen data.

A new classification of gymnosperms (Christenhusz et al., 2011) merged Taxodiaceae and Cephalotaxaceae into Cupressaceae and Taxaceae, respectively. However, old taxon names are used for this pollen types here, because *Cryptomeria* type is distinguishable from CTC type and because CTC type cannot represent a single taxon due to its various mother plants.

Mallotus type

Three species of *Mallotus* grow in Japan, *M. japonicus* in the Japanese archipelago and *M. paniculatus* and *M. philippensis* in Ryukyu Islands. Although the pollen morphology of some *Mallotus* species in the tropical area is similar to that of *Macaranga* (*Macaranga tanarius* grows in Ryukyu), *Mallotus japonicus* pollen can be distinguished by the large pollen size, judging from the description in pollen atlases of Japan (Nakamura, 1980), Ryukyu (Fujiki & Ozawa, 2007), and Taiwan (Huang, 1972).

Mallotus species are primarily tropical pioneer plants, and *M. japonicus* grows at the northern limit of the generic distribution with deciduous leaves.

Betula type

Twelve species of *Betula* grow in present Japan, such as *Betula ermanii* in subalpine forests, *B. platyphylla* and *B. maximowicziana* in mountainous areas, several other temperate species in restricted areas of Honshu, and dwarf species in Hokkaido.

In some studies, *Betula ermanii* and *B. maximowicziana* types are distinguished from the other *Betula* type. Nakamura & Tsukada (1960) suggested distinction in Japanese *Betula* pollen and separated *B. ermanii* pollen by its larger size. Nakamura (1968) compared the size of fossil *Betula* pollen in Hokkaido and suggested that small grains of dwarf *Betula* dominated during the last glacial and that large grains of other

Betula occurred abundantly during the post-glacial. However, Morita (2001) suggested difficulties in clearly segregating *Betula* pollen in spite of possible differences. The separation of dwarf *Betula* pollen from that of the others by pollen size and pore depth was suggested for *Betula nana* (*B. exilis*) (Birks, 1968; Blackmore et al., 2003) and *B. glandulosa* Michaux (Clegg et al., 2005), although Mäkelä (1996) showed that simple comparison in size between modern and fossil pollen is not advisable. Dwarf shrubs of *B. apoiensis* and *B. ovalifolia* now grow only in small restricted areas in Hokkaido, and *B. exilis* grows in Sakhalin.

Carpinus/Ostrya type

Five species of *Carpinus* and *Ostrya japonica* are the mother plants of this type. Because *Carpinus tschonoskii* pollen can be distinguished from the others by the pore number and grain size (Yamanaka, 1988), *C. tschonoskii* type was sometimes distinguished in pollen diagrams. On the other hand, *Ostrya* pollen is morphologically quite similar to *Carpinus* pollen excepting *C. tschonoskii*. In this paper, *Carpinus/Ostrya* type is adopted without separating *C. tschonoskii*.

Corylus type

Corylus type includes two species, *C. heterophylla* and *C. sieboldiana*. Their pollen morphology resembles that of *Myrica* type (Edwards, 1981), but they are rarely compiled together in Japan. In some studies, *Corylus* type is confused with *Myrica* type, judging from the environment and macrofossil occurrences. *Corylus* type is sometimes excluded from arboreal pollen when their mother plants are regarded as shrubs.

Deciduous & evergreen Quercus types

About 15 species of *Quercus* grow in Japan, and several varieties or hybrids are distributed in restricted areas. Eight of them belong to subgen. *Cyclobalanopsis*, evergreen oaks, mainly growing in the warm climate, and the rest of them to subgen. *Lepidobalanus*, deciduous oaks except for evergreen *Q. phillyraeoides*, growing in the warm to temperate climate.

Quercus type is usually divided into *Lepidobalanus* and *Cyclobalanopsis* types in Japan by the surface sculpture and size of pollen grains. These two types were sometimes not distinguished when badly preserved or rarely occurring, particularly in old studies. *Lepidobalanus* type was sometimes presented as *Quercus* or deciduous *Quercus* types, and *Cyclobalanopsis* type as evergreen *Quercus* type. Roughly speaking, the pollen of evergreen *Quercus phillyraeoides* of subgen. *Lepidobalanus* resembles *Cyclobalanopsis* type

more than deciduous *Lepidobalanus* type. Names such as deciduous *Quercus* type and evergreen *Quercus* type are used in this work to show the ecological significances of these types.

In the pollen data not distinguishing *Quercus* types, *Quercus* type was regarded as deciduous one, when its occurrence was less than 5% or when the pollen data were from northern Honshu or Hokkaido or when the deposit was of the glacial period with rare occurrence of *Cyclobalanopsis* pollen. *Quercus* type was regarded as evergreen one when pollen types apparently indicating a warm climate such as *Podocarpus* type occurred dominantly together with it.

The pollen of Japanese *Quercus* is morphologically studied by the scanning electron microscope (SEM) (Miyoshi, 1981a; Fujiki & Miyoshi, 1995; Fujiki et al., 1996; Makino et al., 2009) and can be classified into several groups by their micro-sculpture. These results are consistent with the pollen morphology of Chinese *Quercus* (Wang & Pu, 2004). Further studies applying these results to fossil *Quercus* pollen will clarify the distribution history of *Quercus* species.

Fagus type

Pollen of modern *Fagus* species in Japan, *F. crenata* and *F. japonica*, can be distinguished by the size of apocolpium (Miyoshi & Uchiyama, 1987; Uchiyama, 1980) or the polar area index and the mean axis approximating the size of apocolpium (Saito, 1992). These features can be applied to the other *Fagus* species in the world, but their pollen types are not usually recognized (Praglowksi, 1982; Miyoshi et al., 1991; Wang & Pu, 2004). Pollen grains of long petal *Fagus* species such as *F. japonica*, *F. longipetiolata* Seemen, and *F. engleriana* Seemen have a small apocolpium, those of short petal species such as *F. crenata*, *F. hayatae* Palib. ex Hayata, and *F. sylvestris* L. have a large one, and those of *F. grandifolia* Ehrh. distributed in North America have a medium one. However, many studies did not distinguish species in *Fagus* types, and *Fagus* type is adopted in this study.

In Japan, extinct *Fagus microcarpa* Miki (Miki, 1933) that resembles *F. crenata*, but has relatively smaller fruits was recorded until the middle Pleistocene with its affinities named as *Fagus* sp. cf. or aff. *hayatae* or *F. crenata* (Minaki & Okamoto, 1985). Momohara (1996) examined the fruit morphology of *F. crenata*, *F. microcarpa*, and their allies and showed its regional differences. For the pollen morphology, Tai (1973) showed the size frequency of fossil *Fagus* pollen obtained from the Osaka Group and discussed its application to the species distinction. Thus, we need more

data to clarify the dynamic changes of *Fagus* species in Japan.

Species related to Japanese *Fagus* grow in adjacent areas such as *Fagus hayatae* Palib. ex Hayata in Taiwan resembling fossil *Fagus microcarpa*, and *F. multinervis* Nakai in Ulleung Island now merged into *F. engleriana* of China resembling *F. japonica*. Shen (1992) and Denk (2003) distinguished a local species, *F. okamotoi* Shen, from *F. japonica*, but it is not accepted in Japan.

Castanea/Castanopsis/Lithocarpus type

This pollen type is sometimes represented in pollen analyses as separate taxa such as *Castanea*, *Castanopsis* or *Pasania* (synonym of *Castanopsis*), and *Lithocarpus* or *Shiia* (synonym of *Lithocarpus*). *Castanea* is often distinguished from *Castanopsis/Lithocarpus*, but rarely with a morphological description for identification. Pollen of the above genera resembles each other in shape and size (Kataoka & Morita, 1999), but *Castanea* pollen can be distinguished by the relatively smooth surface sculpture that can be observed apparently by SEM (Miyoshi, 1981b; Praglowksi, 1984). This characteristic can also be recognized by the careful observation with the high resolution light microscopy (LM). Miyoshi (1981b) suggested differences between Japanese *Castanopsis* and *Lithocarpus* pollen, but it is problematic considering the morphological similarity in the other species of these genera not growing in Japan (Praglowksi, 1984). *Castanea* is ecologically quite different from the other species of this pollen type and has been used as food or construction timber since prehistoric ages in Japan. *Castanea* seeds and woods were often recovered in archaeological excavations with abundant occurrences of *Castanea* type pollen. However, pollen analyses that distinguished *Castanea* pollen from the others are not many and often lack in reliabilities. In this work, *Castanea* is not distinguished from *Castanopsis/Lithocarpus*, and the name *Castaneal/Castanopsis/Lithocarpus* type is adopted.

Juglans/Pterocarya type

Juglans type is sometimes distinguished from *Pterocarya* type by the pores at the distal side besides the equatorial pores. However, *Juglans* pollen includes isopolar pollen grains without distal side pores, and *Pterocarya* includes heteropolar pollen grains with distal side pores in low frequency (Stones & Broome, 1975). Thus, in this work, they are compiled, and the name *Juglans/Pterocarya* type is adopted.

Myrica type

The pollen morphology of *Myrica gale* and *M. rubra*

differs slightly (Morita & Choi, 1988). Conventionally, however, the subdivision of *Myrica* type was recognized from their ecology, because *M. rubra* is a tree growing in the warm climate, whereas *M. gale* is a dwarf tree growing in peat bogs in the cooler climate, although their present ranges partly overlap. *Myrica* type thought to have derived from *M. gale* is sometimes omitted from arboreal pollen counts and from diagrams because of its conspicuous occurrences.

Ulmus/Zelkova/Hemiptelea type

Hemiptelea pollen can be distinguished by its verrucate surface sculpture from *Ulmus* and *Zelkova* pollen having rugulate surface sculpture (Nirei, 1996). Only one species of *Hemiptelea*, *H. davidii* Planch., grows in China and Korean Peninsula, and a fossil *H. mikii* was described with fruits and woods from Japan (Minaki et al., 1988). *Hemiptelea* pollen was recorded from the end of the mid-glacial in central Japan (Yoshida et al., 2011) with wood fossils (Noshiro, 2004). *Hemiptelea* pollen occurred significantly from Quaternary sediments of the Osaka Group (Hongo, 2007). Morphological studies of Ulmaceae (Zavada, 1983; Takahashi, 1989) showed distinct differences between subfamilies Celtidoideae and Ulmoideae and differences among *Ulmus*, *Zelkova*, and *Hemiptelea*. *Zelkova* pollen has a thicker annulus and coarser surface sculpture and is larger than that of *Ulmus* (e.g., Shimakura, 1973; Nakamura, 1980; Morita et al., 1998). Because many studies did not distinguish these genera, the three genera of Ulmaceae are treated as *Ulmus/Zelkova/Hemiptelea* type here.

Celtis/Aphananthe type

Although sometimes presented as separate genera in pollen analyses, *Celtis* and *Aphananthe* pollen in Japan cannot be distinguished from each other. Four species of Japanese *Celtis* and *Aphananthe aspera* is deciduous, and *Celtis* grows in northern areas than *Aphananthe*. *Celtis* and *Aphananthe* were transferred from Ulmaceae to Cannabaceae by APG III (The Angiosperm Phylogeny Group, 2009), and, consistently, tri-porate pollen of *Celtis* and *Aphananthe* resembles that of Cannabaceae.

Tilia type

Tilia consists of deciduous broadleaved trees with entomophilous flowers. The pollen morphology of Japanese *Tilia* has not been studied critically yet, but its species can be distinguished, judging from the description in pollen atlases (Nakamura, 1980; Miyoshi et al., 2011).

Aesculus type

Aesculus type includes only one species, *Aesculus turbinata*. It is a useful tree as the source of timber, honey, and food, and its fruits were amply used during the Jomon period (Taniguchi & Wada, 2008).

Acer type

About 27 species of *Acer* grow in Japan. Studies on the pollen morphology of *Acer* (Biesboer, 1975; Tian et al., 2001) suggested possibilities of subdividing *Acer* type. However, the morphological variation in fossil pollen has not been studied well, because of its rare occurrences.

Fraxinus type

A preliminary study of the pollen morphology of Japanese *Fraxinus* suggested that the pollen of *F. mandshurica* and *F. platypoda* of sect. *Fraxinaster* can be distinguished from that of sect. *Ornus* by the number of apertures, thinner exine, and colpi status (Nirei & Sakio, 2008). Punt et al. (1991) suggested the same difference between the two sections of European *Fraxinus*. The pollen of sect. *Ornus* can be distinguished into at least three groups, i.e., small pollen of *F. griffithii*, pollen with a coarser reticulum of entomophilous species with petals, and pollen with a fine reticulum of species without petals. Abundant fossil pollen of *Fraxinus* can be attributed to *F. mandshurica*, judging from its habitat in the wetland. *Fraxinus* type pollen can possibly be compiled into Oleaceae type, but Oleaceae type is rarely used or occurs rarely.

5. Statistical treatments and mapping

Occurrences of 25 arboreal pollen types were deduced from tables and/or diagrams in the cited references. Pollen assemblages were excluded from the analysis when the total counts of the 25 arboreal pollen types were less than 100. When the exact total counts were not available in percentage tables or diagrams, they were taken to be ordinary counts of 200 at the least. Thus, if the sum of the 25 arboreal pollen types was less than 50% without information of base counts, the pollen assemblage was excluded from the analysis, because the total counts was regarded as less than 100. In some cases, special statistics were used, such as division of arboreal pollen into trees and shrubs or into local and regional ones. Particularly, *Mallotus*, *Myrica*, *Corylus*, and *Fraxinus* tended to be excluded from arboreal sums, and their occurrences might be obscured in some cases. However, the statistical analysis was basically carried out when the percentages of 25 arboreal pollen types could be calculated and the total arboreal

Table 1 Numbers and percentages (in brackets) of pollen assemblages for each period with site characters**表 1** 各時期における地点の性格ごとの花粉群の数および地点数とその割合

Site character	Period									Total	Number of sites	Assembl. /site
	0.8 ka	2.5 ka	5 ka	7 ka	9 ka	12 ka	14 ka	20 ka	40 ka			
Ocean	5 (0.5)	4 (0.5)	3 (0.5)	2 (0.6)	2 (0.9)	1 (0.5)	1 (0.9)	3 (1.0)	1 (0.5)	22 (0.6)	7 (0.4)	3.1
Lake	44 (4.2)	36 (4.2)	21 (3.7)	13 (4.1)	12 (5.2)	10 (5.3)	5 (4.6)	11 (3.8)	6 (3.2)	158 (4.2)	50 (2.8)	3.2
Moor	342 (32.7)	275 (32.1)	198 (35.3)	107 (33.4)	84 (36.5)	76 (40.0)	47 (43.1)	59 (20.3)	15 (7.9)	1203 (31.7)	377 (21.0)	3.2
Borehole	143 (13.7)	148 (17.3)	164 (29.2)	139 (43.4)	107 (46.5)	68 (35.8)	32 (29.4)	85 (29.3)	75 (39.5)	961 (25.3)	325 (18.1)	3.0
Archaeological site	452 (43.3)	339 (39.6)	127 (22.6)	42 (13.1)	14 (6.1)	13 (6.8)	10 (9.2)	53 (18.3)	23 (12.1)	1073 (28.3)	791 (44.1)	1.4
Outcrop	48 (4.6)	44 (5.1)	42 (7.5)	16 (5.0)	11 (4.8)	22 (11.6)	14 (12.8)	79 (27.2)	70 (36.8)	346 (9.1)	234 (13.0)	1.5
Soil	11 (1.1)	10 (1.2)	6 (1.1)	1 (0.3)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	28 (0.7)	11 (0.6)	2.5
Total	1045	856	561	320	230	190	109	290	190	3791	1795	2.1

pollen counts exceeded 100.

Arboreal pollen types other than the 25 arboreal pollen types sometimes occurred abundantly. Abundant occurrences of shrub pollen that reflect local vegetation, such as *Alnus*, *Salix*, *Ilex*, Ericaceae, etc., are treated together with herbaceous pollen. On the other hand, occurrences of trees such as *Symplocos*, *Trochodendron*, *Phellodendron*, and *Helicia* types over 10% are excluded from the statistical analysis, because they cannot be the main components of vegetation. Pollen diagrams often showed occurrences of selected types only and included hidden occurrences of unselected types. In such cases when the sum of the occurrences of pollen types in diagrams did not reach 90%, the assemblages were excluded from the statistical analysis.

Pollen diagrams sometimes compiled several unimportant types for discussion. When pollen types were compiled, for example, into “other deciduous tree pollen,” “pinaceous pollen,” and “*Abies/Picea*,” these assemblages were included in the statistical analysis only when these types were less than 5%. Similarly, when evergreen and deciduous *Quercus* types were compiled as *Quercus* type, the assemblages was included in the statistical analysis only when *Quercus* type were less than 5%, except when *Quercus* type was apparently synonym to deciduous *Quercus* type as in Hokkaido and during the glacial period of northern areas.

Distribution maps are drawn with Quantum GIS ver.2.82–Wien. Horizontal maps are drawn by the equidistant projection cylindrical, thus with a linear scaling of longitudes and latitudes. Vertical profiles from south to north have the same scales to the latitudes of horizontal maps in the same figures. Altitudes for south to north vertical profiles are ca. 200 times larger than latitudinal distances. The horizontal axis of vertical profiles from southwest to northeast corresponds to the x-axis of the Japan map with an inclination of 45 degrees right (Fig. 1). Thus, in the same

figures, the inclined Japan map and the vertical profile have the same horizontal scales (e.g., Fig. 3–5). The vertical scale of southwest to northeast profile is 2/3 of the south to north profile, ca. 135 to 150 times larger than the horizontal distance that differs with latitude. Horizontal maps of Japan and vertical profiles do not show past coast lines or sea-levels during each period, but show modern ones. Several sites in southern Japan and the ocean area were excluded from mapping, because they could not be shown in the maps.

The 25 major pollen types were categorized into eight physiognomical classes by the physiognomy, distribution, and ecology of their mother plants to clarify physiognomical or climatic changes in vegetation. Pollen percentages for each pollen physiognomical class was calculated, and their distribution during each period were mapped with the IDW (inverse distance weighting) interpolation method. To compare physiognomical changes in forests, the biomization method (Prentice et al., 1996; Prentice & Web III, 1998) is often used, and several studies have applied the biomization to Japanese pollen records (Takahara et al., 2000a; Gotanda et al., 2002). Here, however, the biomization is not adopted, because several of the 25 major pollen types include mother plants growing in various environments. Moreover, the biome used in the biomization is set from the modern vegetation, but fossil pollen assemblages often reflect vegetation rarely occurring at present. Thus, the modern vegetation should be grasped from a historical perspective, not vice versa.

The whole pollen assemblages are divided into 20 pollen assemblage groups, considering dominant pollen types, the pollen production and ecology of the mother plants, or the source vegetation of pollen assemblages. Multivariate analyses such as cluster analysis are difficult to apply, because of various problems on the taphonomy of fossil pollen and difficulties in species level identification. The pollen assemblage groups are

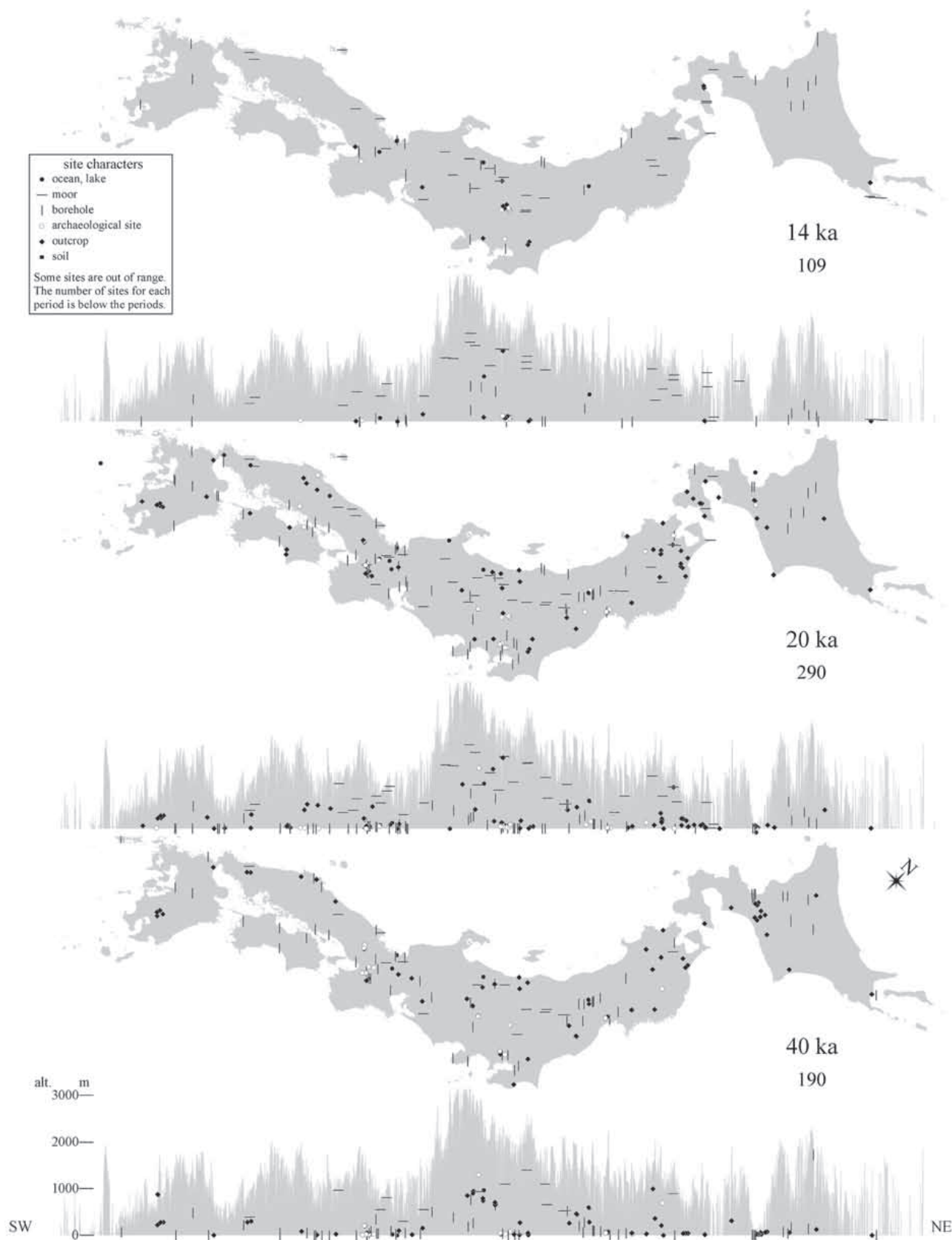


Fig. 3 Horizontal and vertical distribution maps of pollen sites with site characters for periods 14 ka, 20 ka, and 40 ka.

図3 時期 14 ka, 20 ka, 40 ka の花粉分析地点の水平・垂直分布. 花粉分析地点の性格を記号で示す.

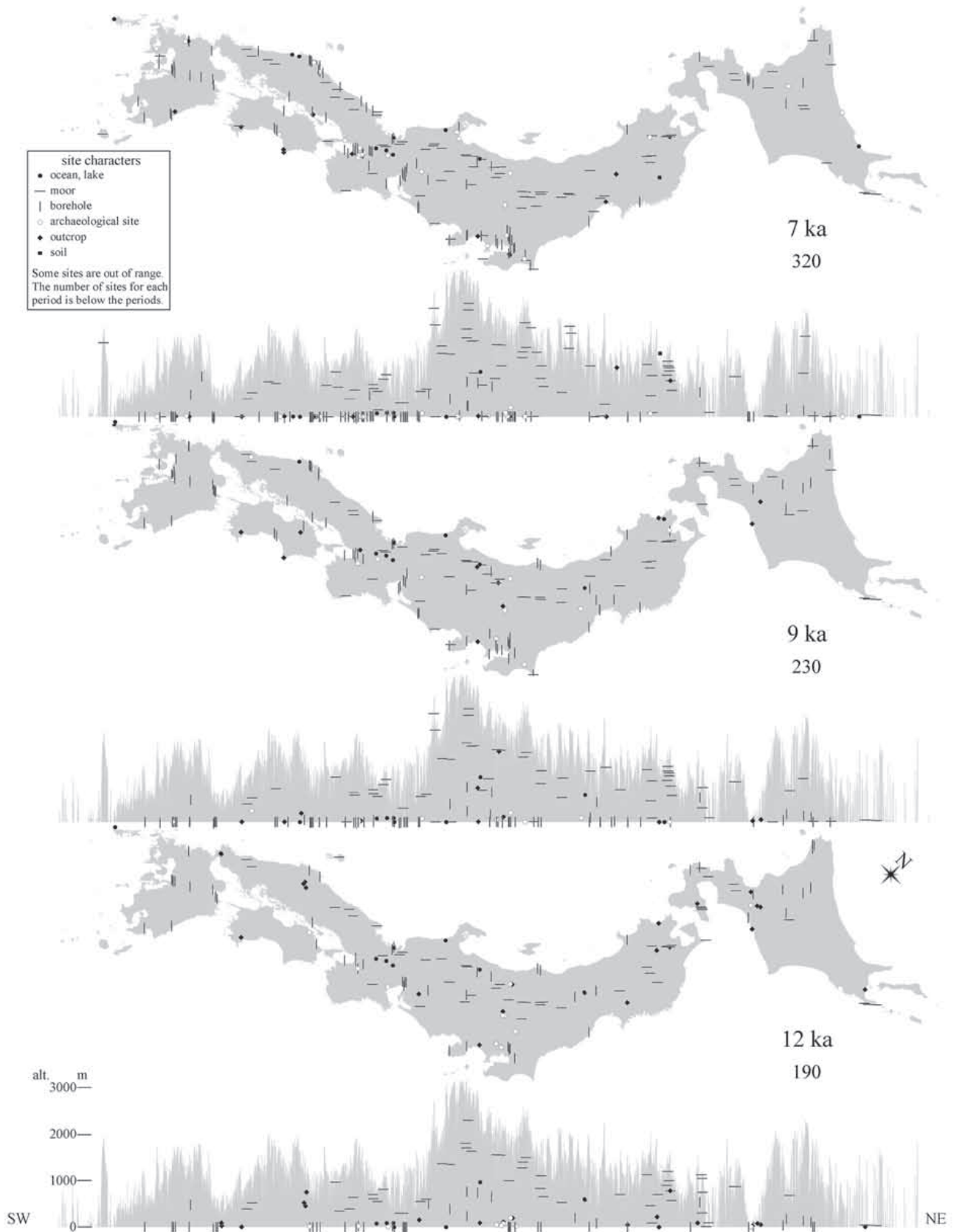


Fig. 4 Horizontal and vertical distribution maps of pollen sites with site characters for periods 7 ka, 9 ka, and 12 ka.

図4 時期7 ka, 9 ka, 12 kaの花粉分析地点の水平・垂直分布. 花粉分析地点の性格を記号で示す.

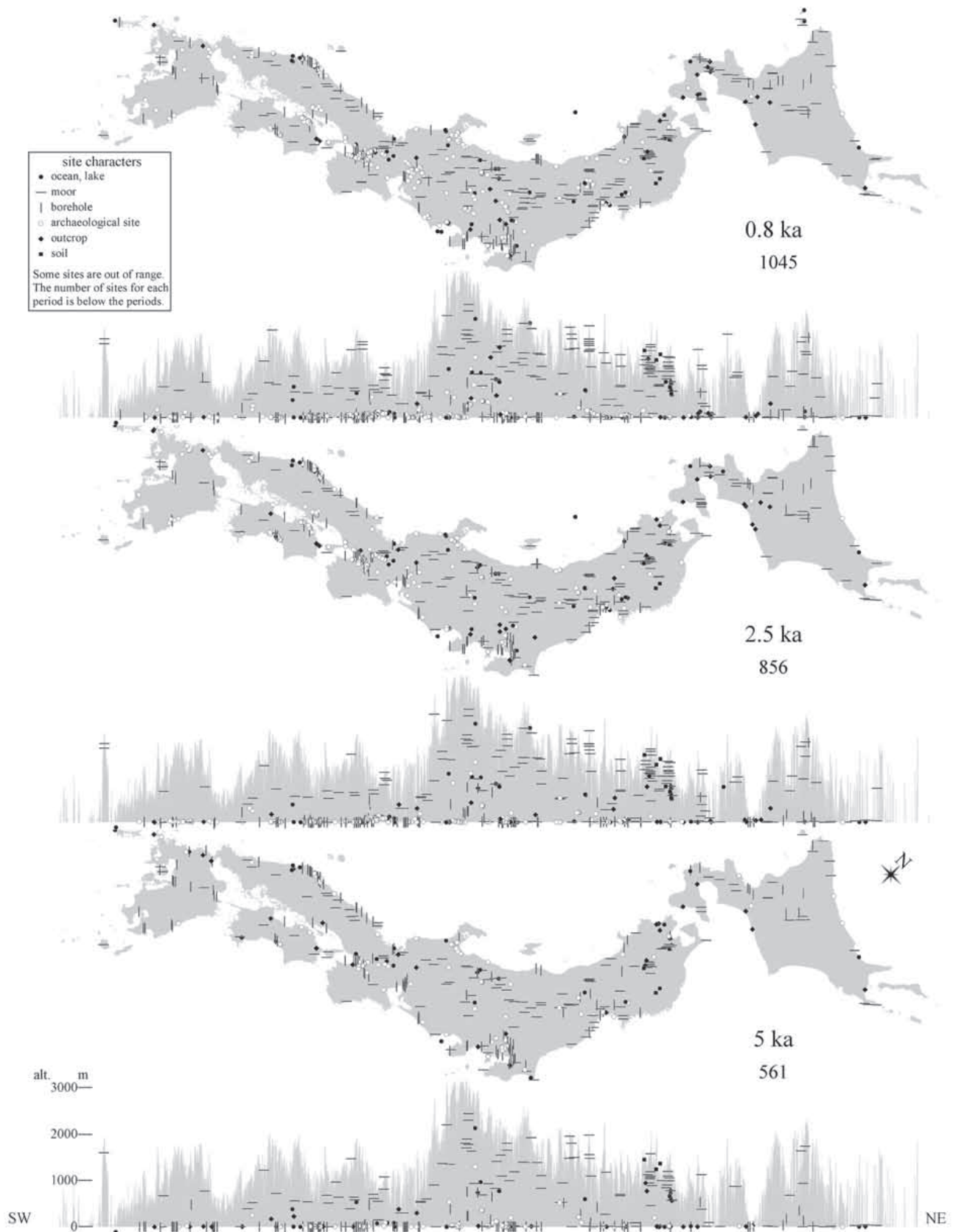


Fig. 5 Horizontal and vertical distribution maps of pollen sites with site characters for periods 0.8 ka, 2.5 ka, and 5 ka.

図5 時期0.8 ka, 2.5 ka, 5 kaの花粉分析地点の水平・垂直分布。花粉分析地点の性格を記号で示す。

Table 2 Numbers and percentages (in brackets) of sites with records of 25 pollen types for each period and their average occurrences through the periods**表 2** 各時期における 25 花粉型の出現地点数とその割合および全時代の合計と平均出現率

Pollen types	Period									Total	Average
	0.8 ka	2.5 ka	5 ka	7 ka	9 ka	12 ka	14 ka	20 ka	40 ka		
<i>Pinus</i>	1021 (97.7)	810 (94.6)	511 (91.1)	288 (90.0)	214 (93.0)	182 (95.8)	103 (94.5)	289 (99.7)	183 (96.3)	3601 (95.0)	15.2
<i>Picea</i>	237 (22.7)	163 (19.0)	144 (25.7)	96 (30.0)	115 (50.0)	158 (83.2)	97 (89.0)	280 (96.6)	170 (89.5)	1460 (38.5)	4.8
<i>Larix</i>	25 (2.4)	15 (1.8)	10 (1.8)	7 (2.2)	23 (10.0)	55 (28.9)	29 (26.6)	100 (34.5)	57 (30.0)	321 (8.5)	0.6
<i>Tsuga</i>	780 (74.6)	652 (76.2)	403 (71.8)	233 (72.8)	182 (79.1)	168 (88.4)	96 (88.1)	282 (97.2)	178 (93.7)	2974 (78.4)	3.6
<i>Abies</i>	634 (60.7)	491 (57.4)	275 (49.0)	186 (58.1)	149 (64.8)	139 (73.2)	87 (79.8)	262 (90.3)	161 (84.7)	2384 (62.9)	5.2
<i>Podocarpus</i>	177 (16.9)	197 (23.0)	75 (13.4)	67 (20.9)	18 (7.8)	5 (2.6)	3 (2.8)	7 (2.4)	6 (3.2)	555 (14.6)	0.3
<i>Sciadopitys</i>	334 (32.0)	306 (35.7)	145 (25.8)	101 (31.6)	58 (25.2)	32 (16.8)	16 (14.7)	48 (16.6)	66 (34.7)	1106 (29.2)	0.8
<i>Cryptomeria</i>	845 (80.9)	660 (77.1)	367 (65.4)	204 (63.8)	131 (57.0)	83 (43.7)	44 (40.4)	123 (42.4)	126 (66.3)	2583 (68.1)	7.1
CTC*	421 (40.3)	350 (40.9)	198 (35.3)	102 (31.9)	62 (27.0)	46 (24.2)	23 (21.1)	58 (20.0)	52 (27.4)	1312 (34.6)	1.5
<i>Mallotus</i>	52 (5.0)	54 (6.3)	43 (7.7)	36 (11.3)	18 (7.8)	4 (2.1)	1 (0.9)	3 (1.0)	2 (1.1)	213 (5.6)	0.1
<i>Betula</i>	771 (73.8)	580 (67.8)	382 (68.1)	223 (69.7)	179 (77.8)	168 (88.4)	106 (97.2)	253 (87.2)	166 (87.4)	2828 (74.6)	6.7
<i>Carpinus/Ostrya</i>	835 (79.9)	691 (80.7)	475 (84.7)	279 (87.2)	190 (82.6)	145 (76.3)	75 (68.8)	176 (60.7)	119 (62.6)	2985 (78.7)	3.9
<i>Corylus</i>	385 (36.8)	304 (35.5)	204 (36.4)	122 (38.1)	95 (41.3)	91 (47.9)	55 (50.5)	141 (48.6)	98 (51.6)	1495 (39.4)	1.1
Evergreen <i>Quercus</i>	676 (64.7)	585 (68.3)	349 (62.2)	215 (67.2)	97 (42.2)	42 (22.1)	15 (13.8)	33 (11.4)	28 (14.7)	2040 (53.8)	8.7
Deciduous <i>Quercus</i>	1022 (97.8)	841 (98.2)	548 (97.7)	313 (97.8)	222 (96.5)	161 (84.7)	98 (89.9)	210 (72.4)	160 (84.2)	3575 (94.3)	16.6
<i>Fagus</i>	824 (78.9)	654 (76.4)	458 (81.6)	271 (84.7)	190 (82.6)	133 (70.0)	70 (64.2)	152 (52.4)	127 (66.8)	2879 (75.9)	8.5
<i>Castanea/Castanopsis/Lithocarpus</i>	640 (61.2)	577 (67.4)	346 (61.7)	198 (61.9)	107 (46.5)	41 (21.6)	17 (15.6)	40 (13.8)	38 (20.0)	2004 (52.9)	4.3
<i>Juglans/Pterocarya</i>	683 (65.4)	609 (71.1)	426 (75.9)	226 (70.6)	175 (76.1)	110 (57.9)	53 (48.6)	84 (29.0)	99 (52.1)	2465 (65.0)	2.3
<i>Myrica</i>	253 (24.2)	184 (21.5)	107 (19.1)	56 (17.5)	37 (16.1)	26 (13.7)	16 (14.7)	54 (18.6)	50 (26.3)	783 (20.7)	0.7
<i>Ulmus/Zelkova/Hemiptelea</i>	850 (81.3)	735 (85.9)	507 (90.4)	293 (91.6)	200 (87.0)	140 (73.7)	89 (81.7)	185 (63.8)	143 (75.3)	3142 (82.9)	4.1
<i>Celtis/Aphananthe</i>	380 (36.4)	393 (45.9)	278 (49.6)	191 (59.7)	101 (43.9)	35 (74.5)	21 (19.3)	20 (6.9)	27 (14.2)	1446 (38.1)	1.7
<i>Tilia</i>	116 (11.1)	97 (11.3)	106 (18.9)	55 (17.2)	77 (33.5)	52 (27.4)	36 (33.0)	70 (24.1)	45 (23.7)	654 (17.3)	0.3
<i>Aesculus</i>	174 (16.7)	292 (34.1)	158 (28.2)	66 (20.6)	39 (17.0)	27 (14.2)	7 (6.4)	10 (3.4)	14 (7.4)	787 (20.8)	0.7
<i>Acer</i>	275 (26.3)	253 (29.6)	208 (37.1)	110 (34.4)	77 (33.5)	55 (28.9)	31 (28.4)	71 (24.5)	55 (28.9)	1135 (29.9)	0.5
<i>Fraxinus</i>	183 (17.5)	213 (24.9)	154 (27.5)	81 (25.3)	60 (26.1)	47 (24.7)	20 (18.3)	34 (11.7)	65 (34.2)	857 (22.6)	0.6
Total sites	1045	856	561	320	230	190	109	290	190	3791	

*CTC: Cupressaceae/Taxaceae/Cephalotaxaceae

practical and discretionary. They did not directly represent vegetation types, but have affinities to vegetation. The vegetation history is discussed with the distribution maps and pollen contents of assemblages.

Results

The total 3791 assemblages from 1795 sites (App. Tables 3, 4) were statistically treated (Figs. 3–5, Table 1). The number of sites increased toward younger periods, although periods 20 ka and 40 ka had more sites than some younger periods. For the full-glacial period 20 ka, the academic interest for the cold maximum vegetation and the existence of an excellent time marker tephra of AT contributed to the increase in the number of sites. Because the cited pollen sites cover a wide area of Japan, forest changes could be discussed without daring extrapolations. The distribution and abundance of pollen sites significantly differed by their site characters. Only several data came from the ocean

and lakes, but included borehole data. Moors, boreholes, and archaeological sites were three major sources of pollen data in Japan. The pollen analysis of moor sediments was the traditional method for palynology even in Japan and allowed to clarify continuous changes in vegetation around moors. Data from boreholes were also continuous when sediments were suitable for the pollen analysis. Moors and boreholes, besides the ocean and lakes, had long time records, as indicated by more than 3.0 assemblages per site in average (Table 1). On the other hand, archaeological sites included 1.4 assemblages per site in average and showed short-term records. Data from archaeological sites increased after period 5 ka, because of the total increase of archaeological sites and changes in the site location. Apparently, archaeological sites were distributed in the lowland, and moors were distributed in mountainous areas (Figs. 3–5). Archaeological sites in the wetland increased with the expansion of the lowland caused by

a sea level regression after the hypsithermal. The modern exploitation of the lowland lead to many archaeological excavations in the lowland suitable for pollen analytical studies to clarify paleoenvironment. Data from outcrops were important for the glacial period, particularly during periods 40 ka and 20 ka, occupying 36.8% and 27.2% of the total samples, respectively. Stratigraphic and geomorphological studies supplied pollen sites of these periods with marker tephra and radiocarbon dates. The sea level around Japan was ca. 120 m lower than the present level during the full-glacial (Yonekura et al., 2001) and 120–130 m lower globally (Yokoyama et al., 2000). Thus, only a few valid data existed for the lowland areas during the full-glacial that are ca. 120 m below the present sea surface. Data from soils were limited to younger periods, because they are continuous from the ground surface.

Occurrences of the 25 major pollen types during each period were mapped throughout the Japanese archipelago (App. Figs. 2–26). *Pinus* type and deciduous *Quercus* type occurred most commonly at more than 90% of sites and most frequently with over 15% in average occurrence (Table 2). These types include several mother plants growing in various climatic ranges. Several pollen types had average occurrences less than 1%: *Larix* type dominant in cold environments, *Podocarpus* and *Mallotus* types occurring in warm environments, entomophyllous types such as *Tilia*, *Aesculus*, and *Acer*, and other types such as *Sciadopitys*, *Myrica*, and *Fraxinus*.

1. Recognition of physiognomical classes

To clarify physiognomical or climatic changes in vegetation, the 25 major pollen types were categorized into the following eight physiognomical classes.

1. DC-LRX: Only *Larix* type belongs to this class. Deciduous conifers grow widely in the cold and dry environment of Siberia at present.

2. EC-PNC: *Picea*, *Abies*, and *Tsuga* types belong to this class. Their mother plants are the main components of present coniferous forests in the alpine and northern regions of Japan, and some species grow in the temperate region.

3. EC-PIN: *Pinus* type is separated from the other evergreen pinaceous conifers, because its mother plants grow in various climatic zones, and is the single member of this class. *Pinus* pollen abundantly occurs in recent sediments, mostly derived from *Pinus densiflora*, a pioneer tree often growing after human disturbances. *Pinus* type also derives from other species growing in various environments, such as *P. koraiensis* with fre-

quent macrofossils in the full-glacial, dwarf *P. pumila* growing near the forest limits, *P. thunbergii* growing in coastal areas, and *P. amamiana* and *P. luchuensis* growing on southern islands.

4. DB-BET: This class consists of *Betula* and *Myrica* types. *Myrica* type also belongs to EB-WDE (evergreen broadleaved tree) class, because its mother plants include a deciduous dwarf wetland shrub of *Myrica gale* and an evergreen warm-temperate tree of *M. rubra*. Some *Betula* species, such as *B. ermanii*, and *Myrica gale* apparently prefer colder environments than those deciduous broadleaved trees whose pollen belong to the following DB-TDB class and often dominate in vegetation.

5. DB-TDB: This class includes pollen types of temperate deciduous broadleaved trees such as *Fagus*, deciduous *Quercus*, *Tilia*, *Acer*, *Corylus*, *Ulmus*/*Zelkova*/*Hemiptelea*, *Juglans*/*Pterocarya*, *Aesculus*, *Fraxinus*, *Carpinus*/*Ostrya*, and *Castanea*/*Castanopsis*/*Lithocarpus* types. This class includes the most pollen types among the eight classes. *Castanea*/*Castanopsis*/*Lithocarpus* type also belongs to EB-WDE, because *Castanopsis* and *Lithocarpus* are evergreen trees, whereas *Castanea* is a deciduous tree. This pollen physiognomical class represents temperate deciduous broadleaved forests.

6. EC-CSC: Pollen types of temperate conifers such as *Cryptomeria*, *Sciadopitys*, and CTC (Cupressaceae/Taxaceae/Cephalotaxaceae) types belong to this class. Their mother plants are evergreen conifers of the temperate to subboreal zones, and only several species of CTC type grow in the alpine or northern regions. Particularly, *Cryptomeria japonica* forest is one of the characteristic temperate forests in Japan.

7. EB-WDE: This class consists of *Celtis*/*Aphananthe*, evergreen *Quercus*, *Castanea*/*Castanopsis*/*Lithocarpus*, *Mallotus*, and *Myrica* types. Their mother plants are mostly evergreen broadleaved trees, but those of *Celtis*/*Aphananthe* and *Mallotus* types are deciduous trees growing in warm evergreen broadleaved forests. As mentioned above, *Myrica* and *Castanea*/*Castanopsis*/*Lithocarpus* types also belong to DB-BET and DB-TDB classes, respectively. This class represents warm temperate evergreen broadleaved forests so called “lucidophyllous” forest.

8. EC-POD: Only *Podocarpus* type belongs to this class and represents southern evergreen coniferous forests under the warm climate. *Podocarpus* forests are fragmentarily distributed in the warm temperate zone in southern Japan at present.

Pollen percentage maps for each pollen physiognomi-

Table 3 Numbers and percentages (in brackets) of the most dominant pollen physiognomical classes for each period

表3 各時期において最優占した花粉相観クラスの数と割合

Pollen physiognomical class	Period									Total
	0.8 ka	2.5 ka	5 ka	7 ka	9 ka	12 ka	14 ka	20 ka	40 ka	
1.DC-LRX	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	4 (2.1)	1 (0.9)	10 (3.4)	0 (0.0)	15 (0.4)
2.EC-PNC	64 (6.1)	28 (3.3)	15 (2.7)	17 (5.3)	14 (6.1)	65 (34.2)	35 (32.1)	173 (59.7)	76 (40.0)	487 (12.8)
3.EC-PIN	361 (34.5)	17 (2.0)	7 (1.2)	1 (0.3)	6 (2.6)	10 (5.3)	11 (10.1)	49 (16.9)	19 (10.0)	481 (12.7)
4.DB-BET	21 (2.0)	13 (1.5)	7 (1.2)	7 (2.2)	23 (10.0)	35 (18.4)	24 (22.0)	23 (7.9)	6 (3.2)	159 (4.2)
5.DB-TDB	344 (32.9)	433 (50.6)	382 (68.1)	220 (68.8)	162 (70.4)	73 (38.4)	37 (33.9)	32 (11.0)	69 (36.3)	1752 (46.2)
6.EC-CSC	207 (19.8)	246 (28.7)	79 (14.1)	33 (10.3)	13 (5.7)	3 (1.6)	1 (0.9)	3 (1.0)	20 (10.5)	605 (16.0)
7.EB-WDE	48 (4.6)	119 (13.9)	71 (12.7)	41 (12.8)	12 (5.2)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	291 (7.7)
8.EC-POD	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.3)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.0)
Total	1045	856	561	320	230	190	109	290	190	3791

cal class by the IDW interpolation method showed vegetation changes since the mid-glacial (Figs. 6–9).

DC-LRX class (Fig. 6 left) was common during the glacial in Hokkaido and the mountainous areas of central Japan. Particularly, it occurred abundantly in eastern Hokkaido during periods 20 ka and 12 ka, representing the glacial maximum and the Younger Dryas cooling, respectively. This class decreased toward the post-glacial and occurred rarely during periods 9 ka and 7 ka, and only at a few sites in the mountainous areas of central Japan from periods 5 ka to 0.8 ka.

EC-PNC class (Fig. 6 right) occurred abundantly during the glacial, particularly during the full-glacial (period 20 ka) except in Hokkaido where DC-LRX class was abundant. In Hokkaido, it occurred most abundantly during period 40 ka and least during period 5 ka and increased toward the recent (period 0.8 ka). Outside Hokkaido, it occurred less during the post-glacial, and least in the hypsithermal (period 7 ka), but frequently in the mountainous areas of northern and central Honshu and in Shikoku during periods 5 ka and 2.5 ka.

EC-PIN class (Fig. 7 left) occurred most abundantly in the lowland areas except for Hokkaido during period 0.8 ka, but showed another peak during the full-glacial (period 20 ka). These two peaks were contributed by *Pinus densiflora* in the former and by *P. koraiensis* and *P. pumila* in the latter. It also occurred abundantly in northern Honshu and northern Kyushu during the mid-glacial (period 40 ka).

DB-BET class (Fig. 7 right) occurred most abundantly during the late-glacial (periods 14 ka, 12 ka) throughout Japan, although data from Kyushu and Shikoku were few or absent. It was not common during the mid-glacial (period 40 ka), but occurred abundantly in the early post-glacial (period 9 ka) in Hokkaido and the mountainous areas of the Japan Sea

side. It continued to occur in the mountainous areas of central to northern Honshu and in Hokkaido after period 7 ka.

DB-TDB class (Fig. 8 left) occurred abundantly during the post-glacial. In Hokkaido, it occurred most abundantly during period 5 ka. In western Japan, it occurred most abundantly during periods 9 ka and 7 ka and gradually decreased after period 5 ka. Occurrences of *Castaneal/Castanopsis/Lithocarpus* type pollen contributed to this class in western Japan after period 7 ka, and the decrease of DB-TDB class toward the recent in western Japan should have been more marked than the trends shown in the maps. DB-TDB class occurred least during period 20 ka, but sporadically in western Japan, particularly in northern Kyushu and southern Kanto. It occurred commonly except in Hokkaido during other glacial periods.

EC-CSC class (Fig. 8 right) occurred abundantly in the Japan Sea side of western Honshu and Izu Peninsula during the mid-glacial (period 40 ka) and least during the full-glacial (period 20 ka) and the late-glacial (periods 14 ka, 12 ka) except for local occurrences in Izu Peninsula, Shimane, and southern Kyushu. It increased in the post-glacial, particularly along the Japan Sea coast of western Honshu and the Pacific coast of central Honshu. It occurred conspicuously at several localities such as Yaku Island, Miyazaki, eastern Kochi, Sado, and Akita during periods 2.5 ka and 0.8 ka, that are present famous sources of *Cryptomeria* timber.

EB-WDE class (Fig. 9 left) occurred least during the glacial period. Except for the abundant occurrences in southern Kyushu during period 12 ka, some local occurrences derived from *Myrica* or *Castaneal/Castanopsis/Lithocarpus* types that are also included in DB-BET or DB-TDB classes, respectively. EB-WDE class increased from the coastal areas of western Japan during the post-glacial until period 2.5 ka and

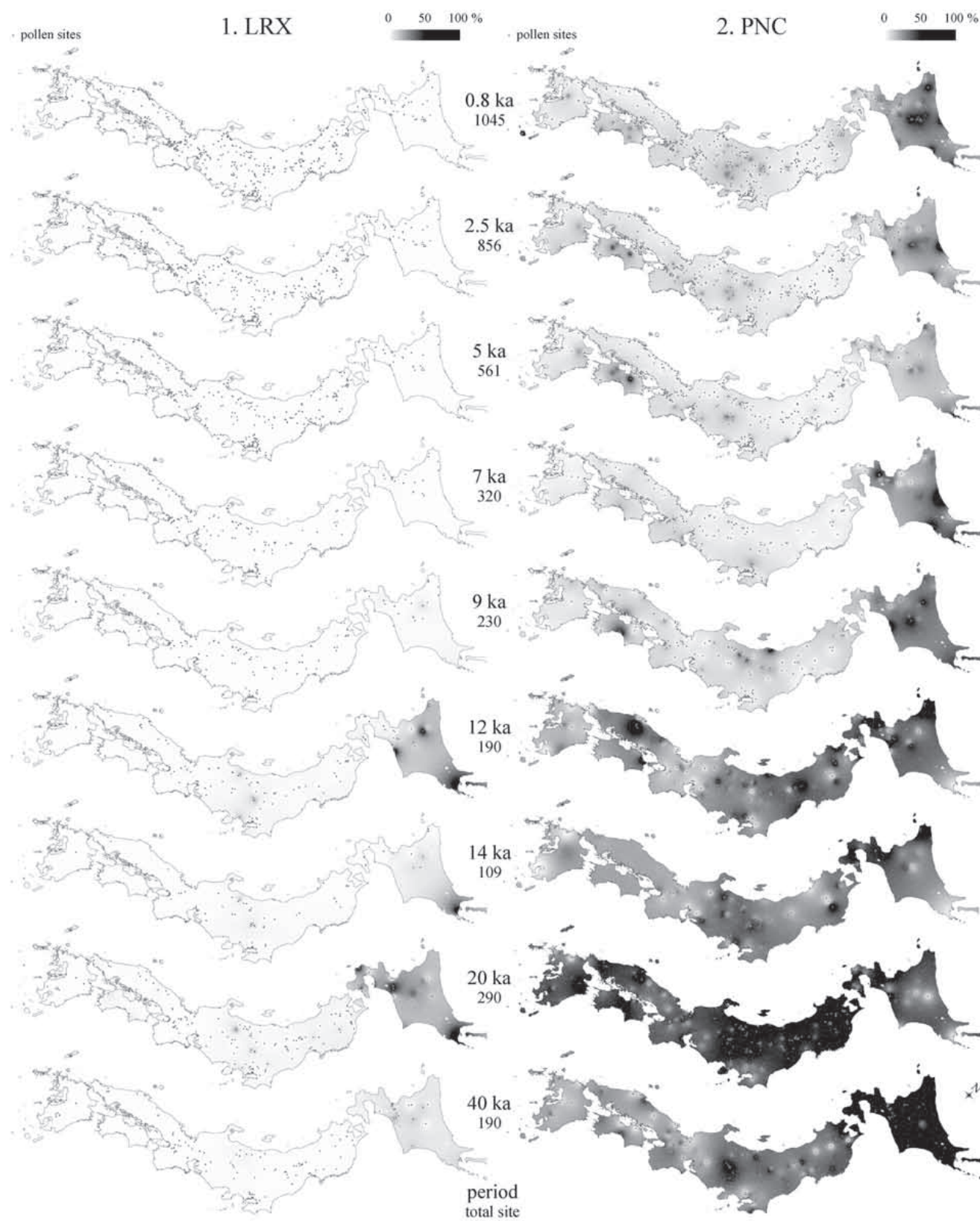


Fig. 6 Chronological succession of the dominance of pollen physiognomical classes DC-LRX and EC-PNC interpolated by the IDW method. Number of sites for each period is shown below periods.

図6 花粉相観クラス DC-LRX, EC-PNC の出現率の水平分布の変遷。IDW 法による推定。

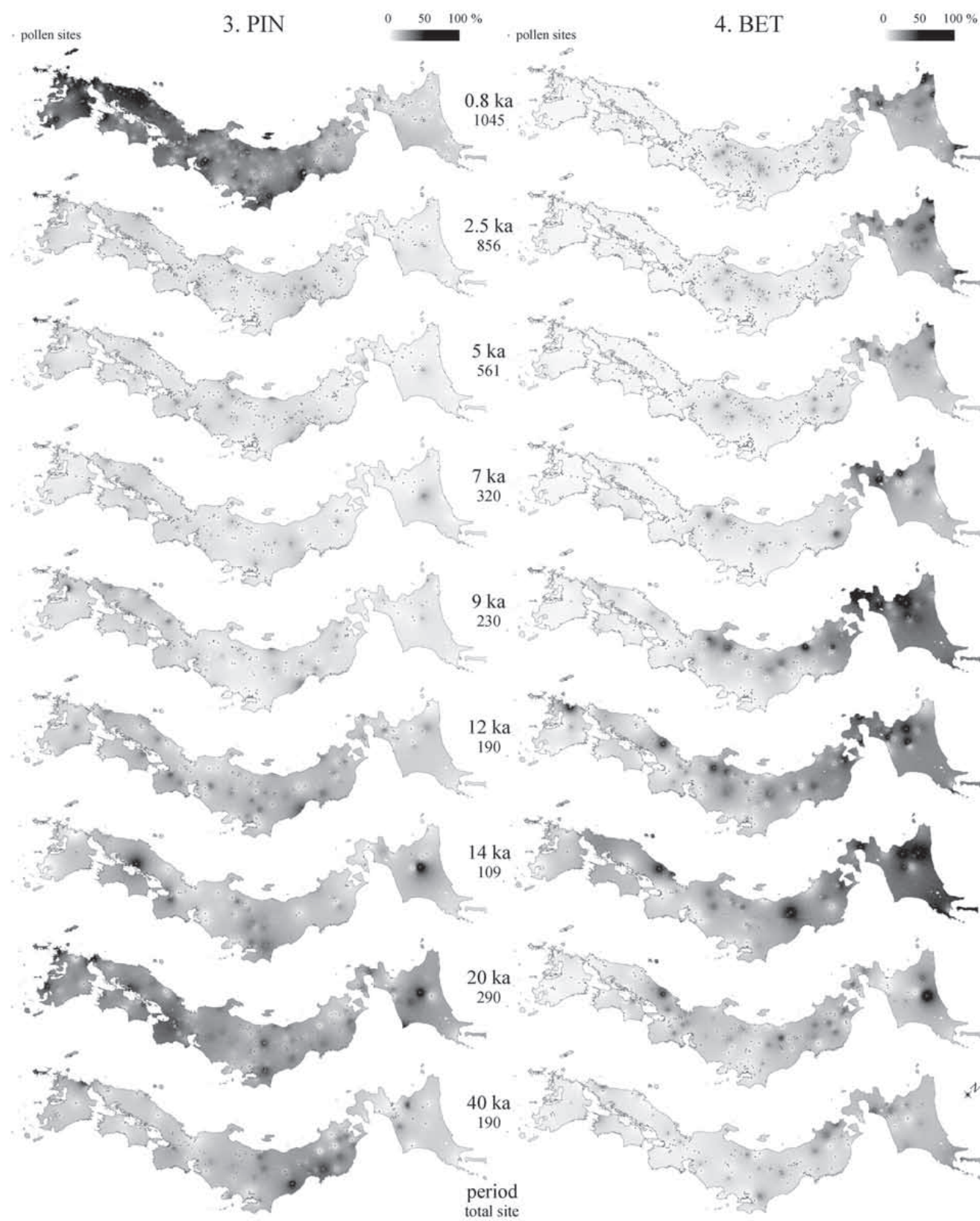


Fig. 7 Chronological succession of the dominance of pollen physiognomical classes EC-PIN and DB-BET interpolated by IDW method. Number of sites for each period is shown below periods.

図7 花粉相観クラス EC-PIN, DB-BET の出現率の水平分布の変遷. IDW 法による推定.



Fig. 8 Chronological succession of the dominance of pollen physiognomical classes DB-TDB and EC-CSC interpolated by IDW method. Number of sites for each period is shown below periods.

図8 花粉相観クラス DB-TDB, EC-CSC の出現率の水平分布の変遷. IDW 法による推定.

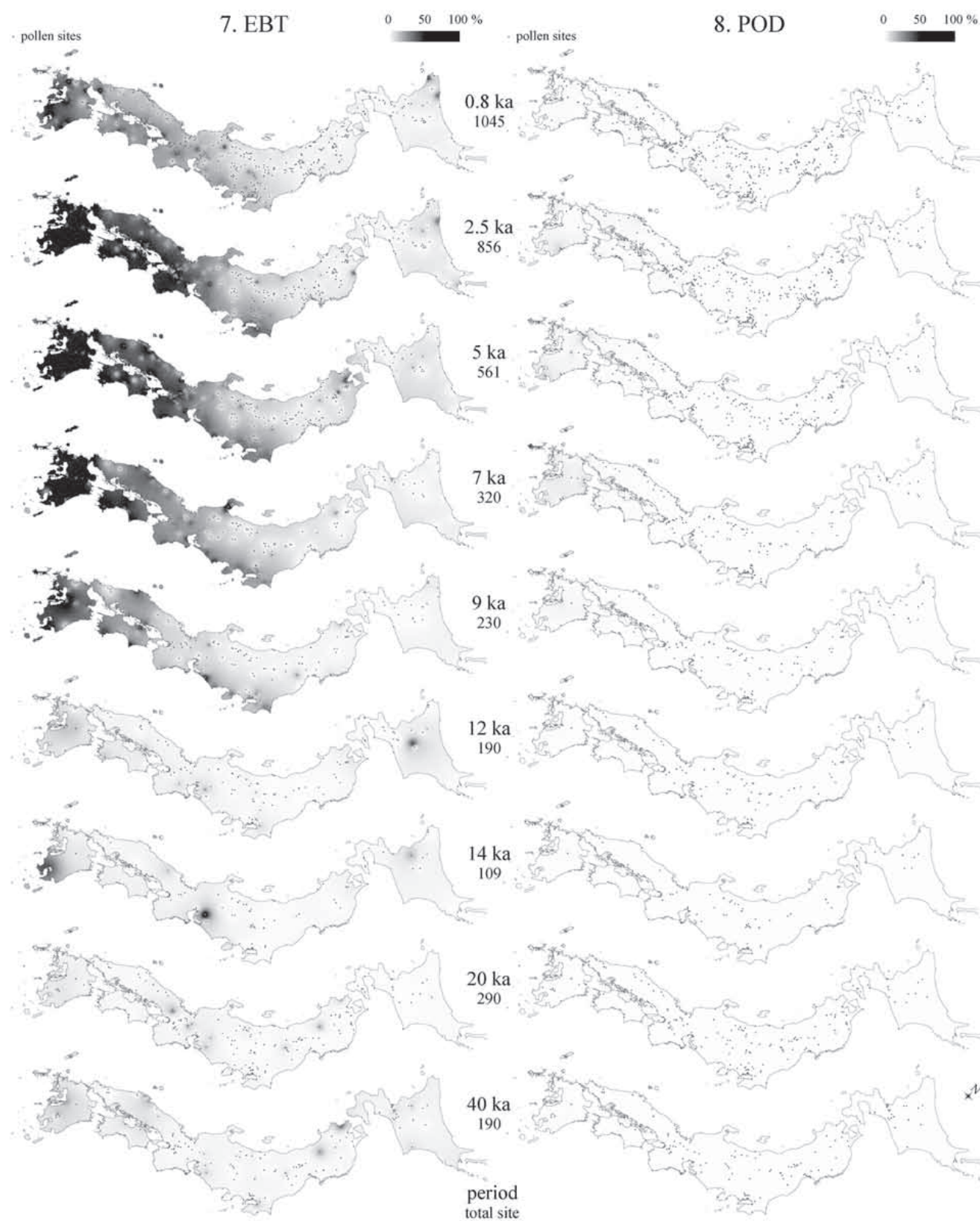


Fig. 9 Chronological succession of the dominance of pollen physiognomical classes EB-WDE and EC-POD interpolated by IDW method. Number of sites for each period is shown below periods.

図9 花粉相観クラス EB-WDE, EC-POD の出現率の水平分布の変遷. IDW 法による推定.

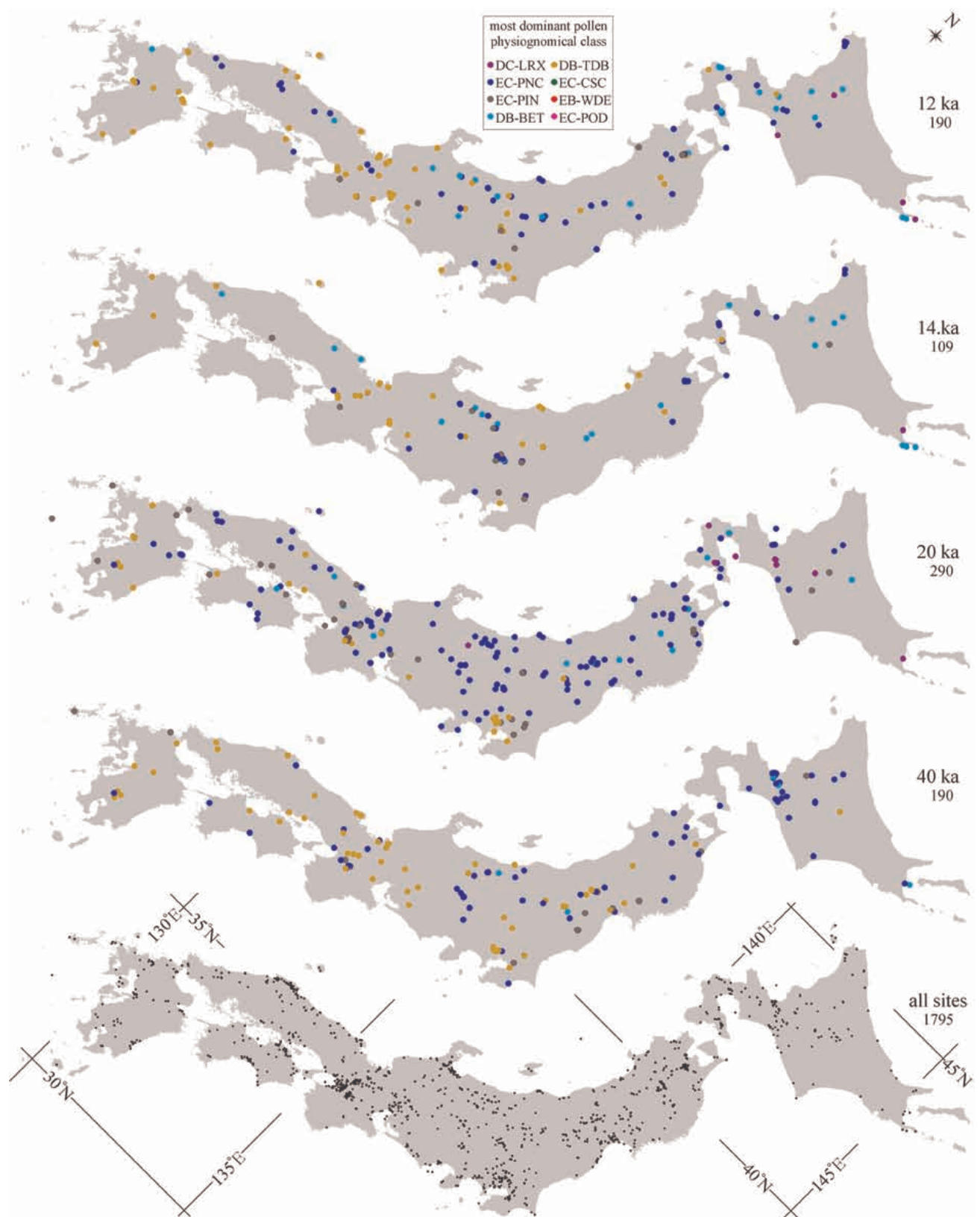


Fig. 10 Horizontal distribution of the most dominant pollen physiognomical classes during the glacial (periods 12 ka to 40 ka) and that of the whole pollen sites on horizontal maps of Japan.

図 10 氷期（時期 12 ～ 40 ka）における各地点で最優占する花粉相観クラスと全地点の水平分布。

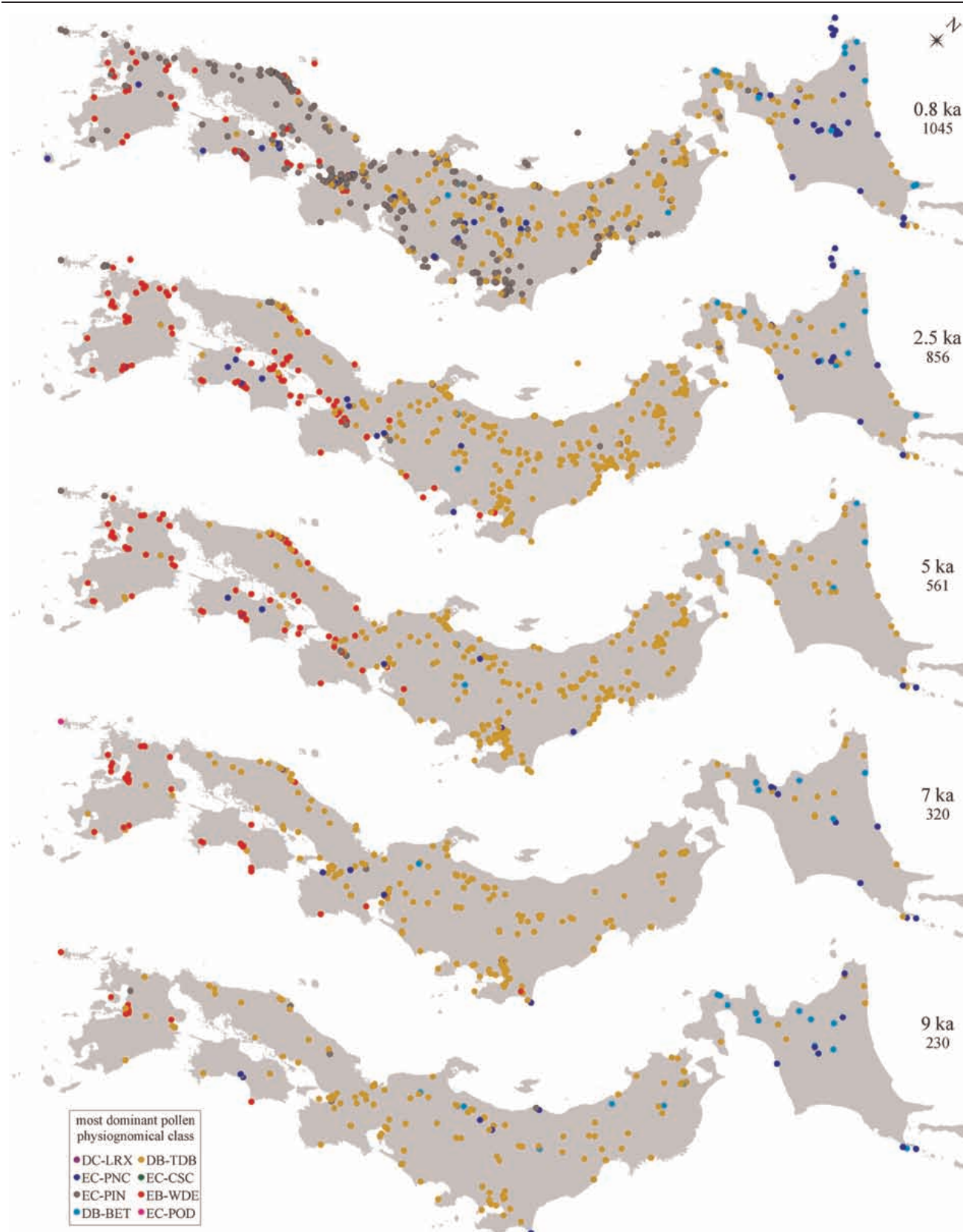


Fig. 11 Horizontal distribution of the most dominant pollen physiognomical classes during the post-glacial (periods 0.8 ka to 9 ka) on horizontal maps of Japan.

図 11 後氷期（時期 0.8 ～ 9 ka）における各地点で最優占する花粉相観クラスの水平分布。

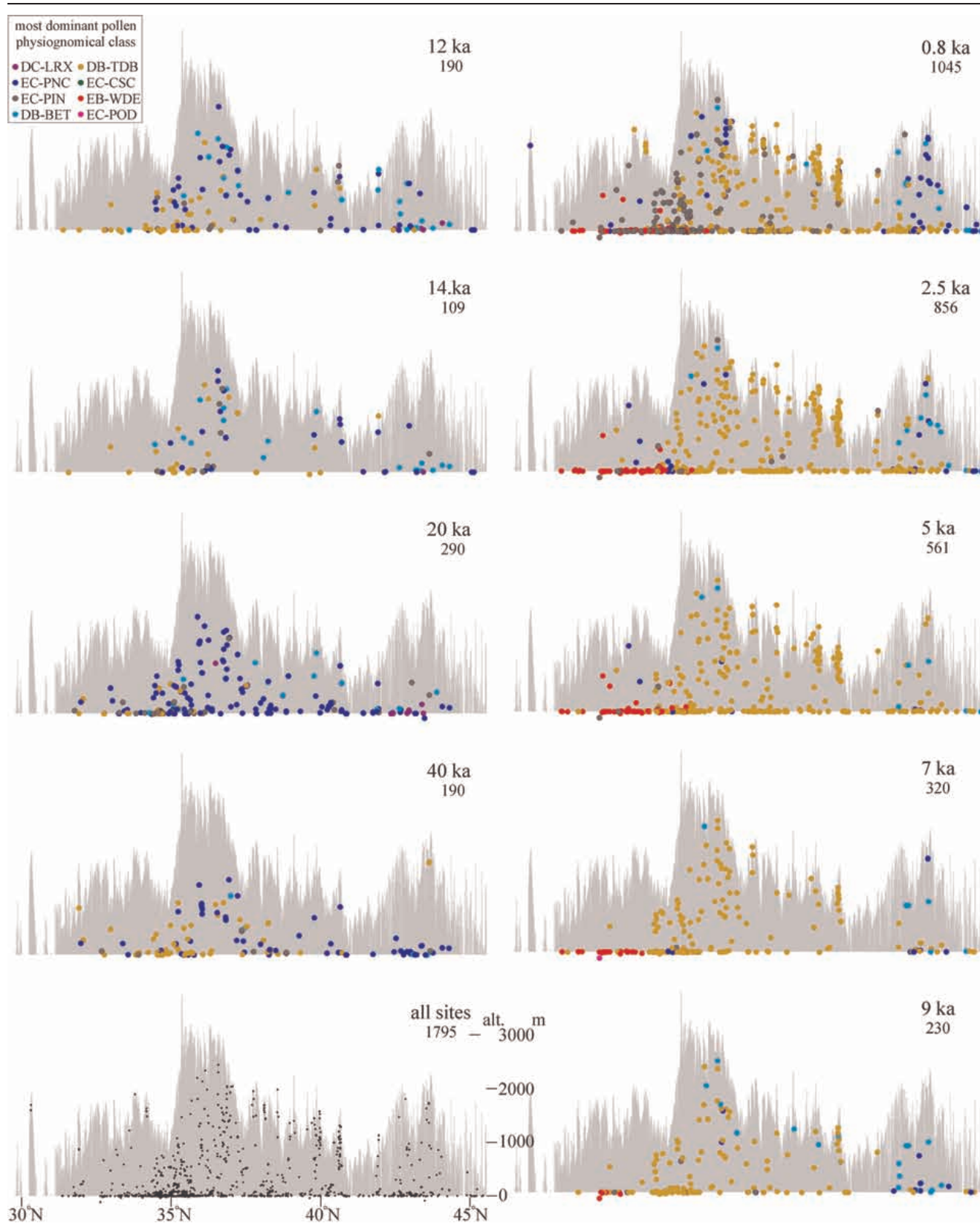


Fig. 12 Vertical distribution of the most dominant pollen physiognomical class during each period and that of the whole pollen sites on vertical profiles of Japan.

図 12 各時期における各地点で最優占する花粉相観クラスの垂直分布および全地点の垂直分布.

decreased totally during period 0.8 ka. Local occurrences during the post-glacial in Hokkaido and northern Honshu also derived from *Myrica* and *Castanea/Lithocarpus* types. The distribution pattern of EB-WDE class nearly corresponds to the modern distribution of evergreen broadleaved forests and does not seem to have shifted from the south to the north, or from the coast to the inland since the glacial period, except for some local spots considered as statistical noises.

EC-POD class (Fig. 9 right) occurred not commonly, but significantly in western Japan during the post-glacial. It occurred most frequently during the hypsithermal (period 7 ka) in Kyushu and western Shikoku and continued to occur in western Japan until the recent (period 0.8 ka).

2. Changes in physiognomical classes

The succession of the most dominant physiognomical classes for respective pollen assemblages through the periods shows physiognomical changes in vegetation since the mid-glacial in Japan (Table 3, Figs. 10–12). If the sums of the two most dominant physiognomical classes were equal, the class consisting of fewer pollen types was selected. These maps roughly show the distribution of past vegetation zones, but their vertical distribution seems not so clear as the horizontal one. Pollen transport by winds and water flows probably affected the vertical distribution more than the horizontal one.

During the mid-glacial (period 40 ka), temperate forests of Cupressales conifers (EC-CSC class) or deciduous broadleaved trees (DB-TDB class) dominated in central to western Japan, and evergreen pinaceous forests (EC-PNC class) did in northern Japan and the mountainous areas of central Japan. Evergreen pinaceous forests also mingled in the temperate forests. Little data for the mountainous areas of western and southern Japan are available in this period. At the peak of the cold full-glacial (period 20 ka), deciduous coniferous forests of *Larix* (DC-LRX class) prevailed in Hokkaido, and evergreen pinaceous forests (EC-PNC) prevailed in the other parts of Japan. Deciduous broadleaved forests prevailed in the lowland with a few Cupressales forests (EC-CSC class) in central to southern Japan, and *Betula* forests (DB-BET class) existed in the mountainous areas throughout Japan during this period. During the late-glacial (periods 14, 12 ka), *Betula* forests (DB-BET) expanded in the mountainous areas of western to central Japan and throughout northern Japan, replacing pinaceous forests, but the range of DB-BET class dominant assemblages did not change

latitudinally or altitudinally. The late-glacial cooling correlated with the Younger Dryas in Europe was not apparent in the maps of the most dominant classes and was only indicated by another increase of *Larix* forests (DC-LRX) in Hokkaido and a revival of evergreen pinaceous forests (EC-PNC) in the mountainous areas of Honshu (Fig. 6). In the lowland of western Japan, deciduous broadleaved forests (DB-TDB) continued to exist through this period. During the early post-glacial (period 9 ka), deciduous broadleaved forests (DB-TDB) prevailed even in the lowland of Hokkaido, where *Betula* and pinaceous forests still dominated. During this period, evergreen broadleaved forests (EB-WDE class) appeared in the coastal areas of Kyushu and Shikoku, and Cupressales forests (EC-CSC) appeared in Izu Peninsula and along the Japan Sea coast of western Japan. During the hypsithermal (period 7 ka), deciduous broadleaved forests increased in Hokkaido, and evergreen broadleaved forests prevailed in Kyushu, Shikoku, and the coastal areas of western Honshu. Assemblages dominated by EC-POD class appeared only during period 7 ka in the Goto archipelago of western Kyushu and in western Shikoku. During period 5 ka, deciduous broadleaved forests prevailed in most areas of Hokkaido, and evergreen broadleaved forests expanded in elevation in western Japan. During this period, Cupressales forests increased, and assemblages dominated by EC-PNC class sporadically appeared in the mountainous areas of western Japan. During period 2.5 ka, *Betula* and evergreen pinaceous forests prevailed in the mountainous areas of Hokkaido and in the high mountainous areas of central Japan. Cupressales forests and pinaceous forests in the mountainous areas of western Japan increased following the trends in the former period. In the recent (period 0.8 ka), *Pinus* forests (EC-PIN class) expanded in and around the plains of southern to central Japan with increased human activities except in Hokkaido. During this period Cupressales forests came to occur in wide areas of southern to central Japan with intensive forestry, and evergreen pinaceous forests increased in Hokkaido and the higher mountainous areas of central Japan.

Succession of dominant physiognomical classes at each pollen site since the mid-glacial showed general changes in the forest vegetation in Japan (Fig. 13). During the post-glacial Pinaceous forests that prevailed during the full-glacial changed to deciduous broadleaved forests, and evergreen broadleaved forests increased from the coastal areas of western Japan. Recently *Pinus* forests increased with increased human activities. These changes superficially seemed to show plant migration from the south to the north, but most-

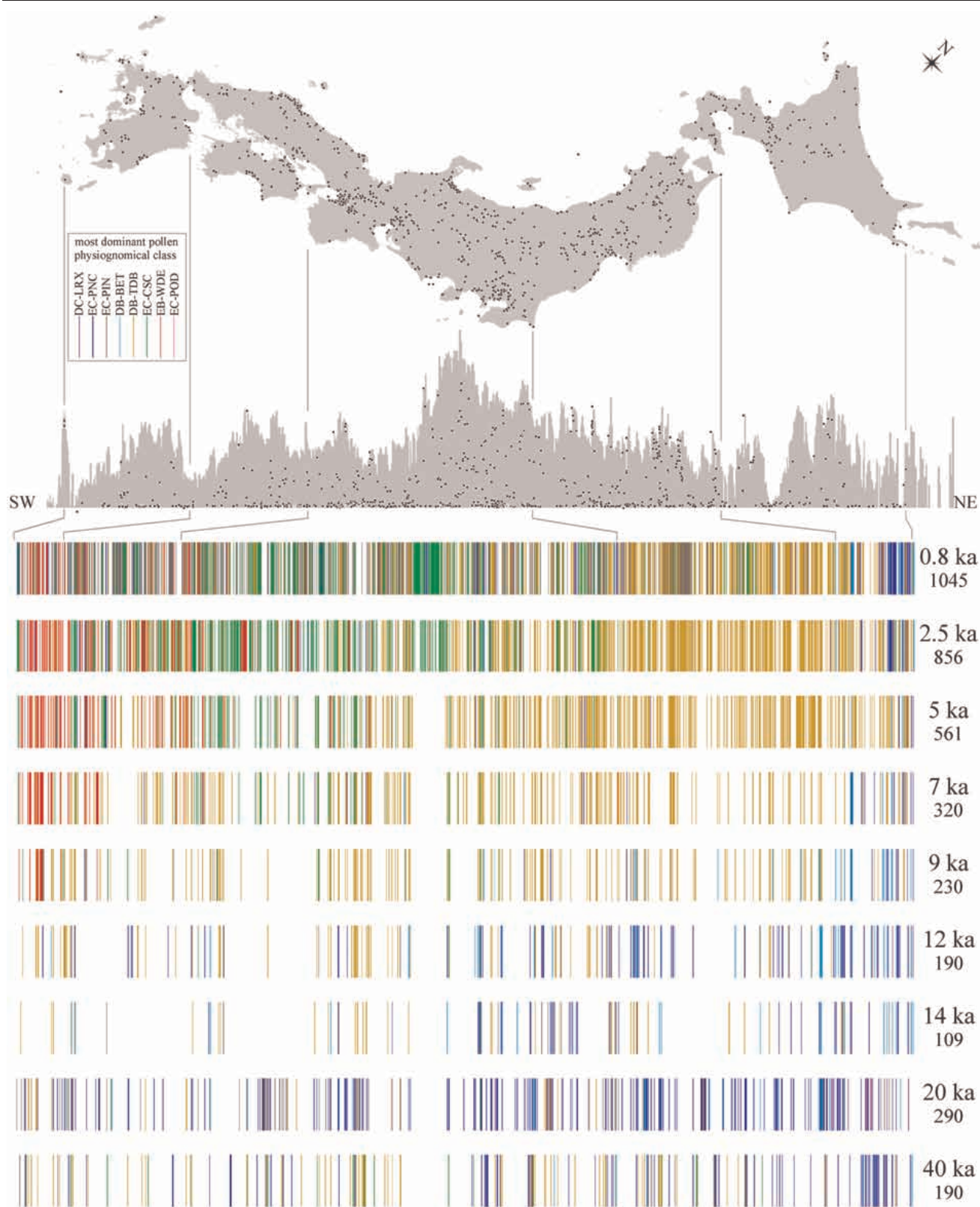


Fig. 13 Correlation between a horizontal map and a vertical profile of Japan and the chronological succession of the most dominant physiognomical classes since the mid-glacial.

図 13 各時期の最優占花粉相観クラスの変遷. 全地点を南西ー北東順に並べ, 各時期における最優占花粉相観クラスを色分けした線で示す. 花粉分析地点の平面図, 断面図との対応関係を細線で示す.

ly, pollen physiognomical classes just changed their frequencies at respective sites.

Discussion

1. Changes in the frequency of pollen types

Vegetation changes clarified by the succession of pollen physiognomical classes showed a shift in vegetation zones with climatic changes, but the shift of vegetation zones does not mean migration of plants. The distribution of pollen types reflected chronological decreases or increases of the mother plants within Japan, but the distribution ranges of pollen types and the mother plants did not change through the periods in spite of great changes in their abundance (App. Figs. 2–26).

Changes in *Cryptomeria* and *Fagus* types will be discussed first, because these two pollen types represent present temperate forest communities in Japan and have often been discussed in relation to the last glacial refugia. Moreover, they allow straightforward discussion on the past distribution of species with pollen types, because they have a limited number of mother plants, one species for *Cryptomeria* type and two for *Fagus* type.

Cryptomeria type

The origin of *Cryptomeria* forests has been one of the hottest research topics since the beginning of Japanese palynology (e.g., Yamazaki, 1943; Takeoka, 1970a, b; Kawamura, 1977). Tsukada (1980, 1982a) compiled palynological data of 34 points covering the Japanese archipelago and discussed changes in the distribution of *Cryptomeria*. He suggested isolation of *Cryptomeria* populations during the last glacial maximum and predicted existence of several refugia in Japan. Tsukada (1987) compiled more data and discussed shifts in the distribution of *Cryptomeria* forests since the last glacial maximum based on the climatic factors governing the modern distribution of *Cryptomeria* pollen. Tsukada's hypotheses for glacial refugia were confirmed by *Cryptomeria* rich pollen assemblages from assumed refugia, such as Oki Island (Takahara et al., 2001), Muroto in Kochi (Miyake et al., 2011), and Izu Peninsula (Kanauchi et al., 1989; Kanauchi, 2005). Takahara (1998b) reviewed the history of *Cryptomeria* by pollen analysis and suggested that the complex vicissitudes of *Cryptomeria* were governed not only by temperature, but also by water condition and snow fall.

The chronological succession of *Cryptomeria* pollen type shows a similar history of *Cryptomeria* forests to that indicated by previous studies (Fig. 14). During the full-glacial and late-glacial, *Cryptomeria* type occurred abundantly in assumed refugia. Areas dominated by

Cryptomeria type enlarged from the supposed refugia and several other spots and covered mainly the low-land areas of Japan except Hokkaido by the recent (0.8 ka). However, this does not mean migration of *Cryptomeria* trees from refugia, but an increase of *Cryptomeria* forests. Traditionally, small amounts of *Cryptomeria* pollen in pollen assemblages were ignored in review works, because *Cryptomeria* yields a large quantity of pollen that disperses long distances (Tsukada, 1974). However, if these rare occurrences of *Cryptomeria* type are included, the distribution of *Cryptomeria* type in period 20 ka overlaps that in period 2.5 ka, and the distribution in period 40 ka overlaps that in period 0.8 ka (Fig. 15). Thus, the distribution range of *Cryptomeria* type during the full-glacial (period 20 ka) is similar to that during the post-glacial (period 2.5 ka), although the abundances are lower during the full-glacial. Such rare occurrences of *Cryptomeria* type may indicate long distance dispersal of exotic pollen and may not show close existence of mother plants. In fact, small amounts of *Cryptomeria* type (below 1%) are observed at several localities in Hokkaido during the post-glacial (period 2.5 ka) and seem to have derived from large populations in Honshu. During the full-glacial (period 20 ka), however, *Cryptomeria* type occurred at 123 sites (42.4% of pollen sites) covering the whole area of Japan except Hokkaido and often significantly, over 5% at 21 sites and over 2% at 51 sites, outside the assumed refugia. Thus, rare occurrences of *Cryptomeria* type did not always derive from exotic pollen. Compared with the post-glacial, few large populations of *Cryptomeria* that can be the source of long dispersal pollen existed during the full-glacial, and *Cryptomeria* populations in the assumed refugia cannot explain the whole occurrences of *Cryptomeria* type during this period. Thus, scattered significant occurrences of *Cryptomeria* type in Honshu during period 20 ka seem to indicate that *Cryptomeria* trees grew widely, but in small patches during this period. Frequent occurrences of *Cryptomeria* type during the mid-glacial (period 40 ka) were probably succeeded by these small patches during the full-glacial and may have lead to the modern distribution of *Cryptomeria*. These facts seem to indicate that *Cryptomeria* did not migrated over long distances through these periods, but only increased or decreased in abundance at respective sites. Because the assumed refugia were probably preferred by *Cryptomeria* trees, they may have supported considerably large populations even during severe periods. Tsukada (1987) and Takahara (1998b) recognized occurrences of populations that were apparently isolated from other population such as that on Yaku Island, but such isolated

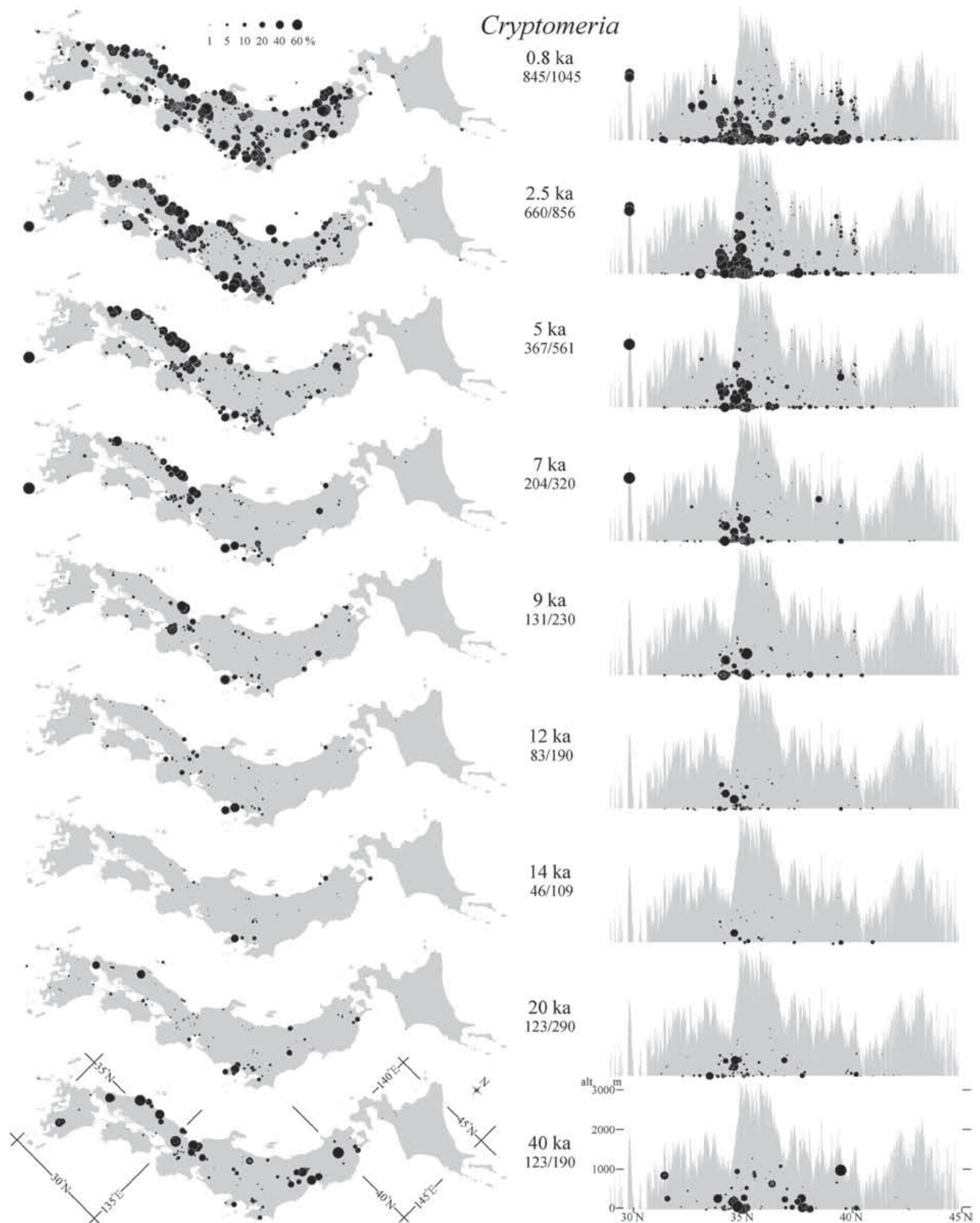


Fig. 14 Chronological succession of the occurrence of *Cryptomeria* pollen type on horizontal maps and vertical profiles of Japan. Numbers of recorded and whole sites for each period are shown below periods.

図 14 スギ属型花粉の出現率の水平・垂直分布（南北断面）の変遷。

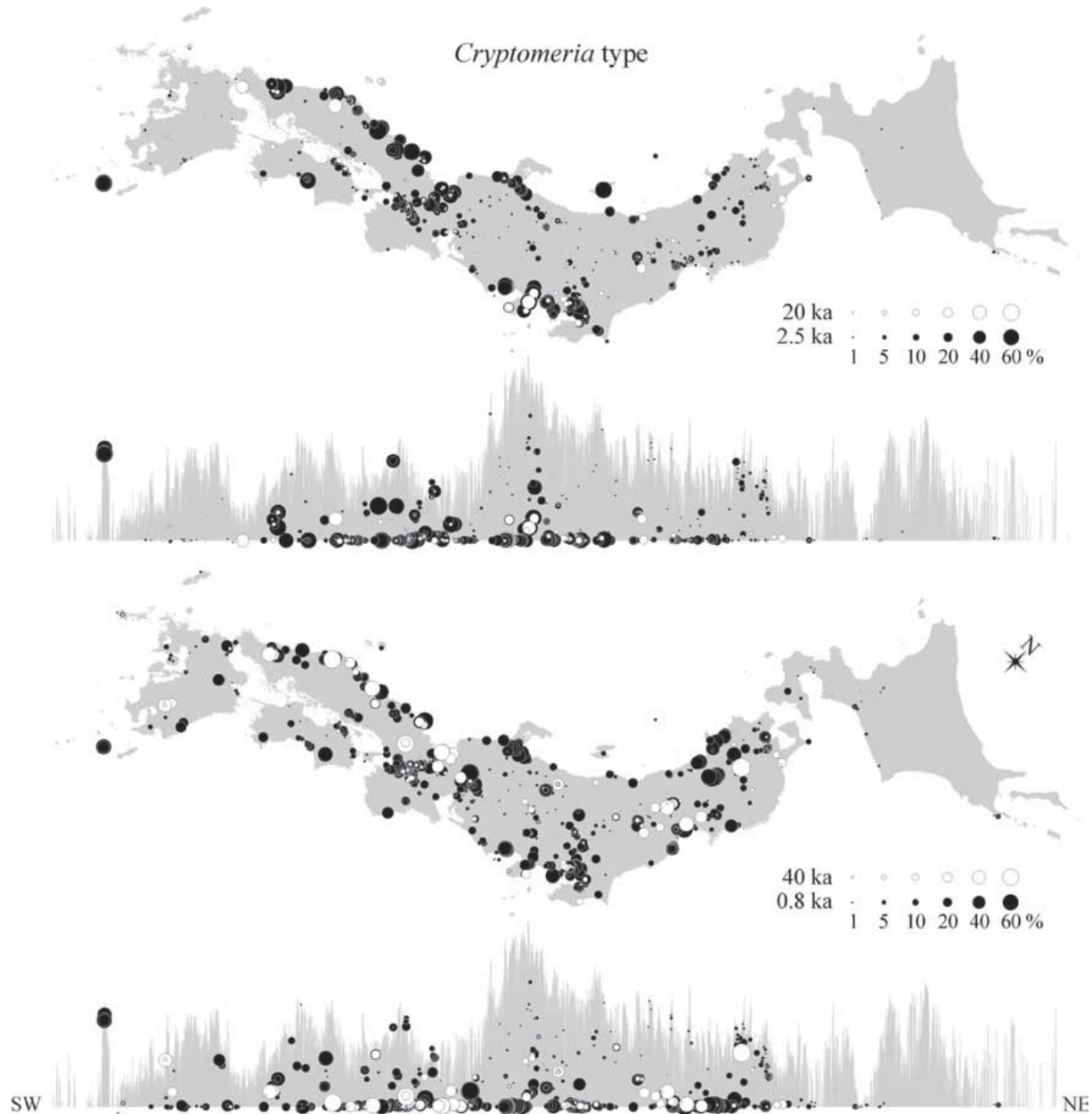


Fig. 15 Occurrences of *Cryptomeria* type during the post-glacial (period 2.5 ka) overlaid with those during the full-glacial (period 20 ka)(upper) and those in recent (period 0.8 ka) overlaid with those during the mid-glacial (period 40 ka)(lower).

図 15 スギ属型花粉出現率の時期 20 ka と 2.5 ka および時期 40 ka と 0.8 ka における分布の比較.

populations were not special or exceptional cases, but seem to have existed commonly. Thus, *Cryptomeria* forests do not seem to have migrated, but changed the areal dominance through these periods, occurring in small patches isolated from the assumed refugia during the full-glacial and expanding in the post-glacial.

Cryptomeria pollen seems to have increased particularly after the hypsithermal (period 7 ka), mainly in the lowland and the Japan Sea side of western to central

Honshu and the Pacific side of central Japan (Fig. 14). In the Japan Sea side, several buried forests of *Cryptomeria* have been recovered under rice paddies or on alluvial fans as at Ubuka (Hatanaka & Miyoshi, 1980), Sanbe (Watanabe et al., 2009), Kurota (Takahara & Takeoka, 1990), Nakaikemi (Ueda & Tsuji, 1992), Uozu (Fuji, 1971, 1996), and Nyuzen (Fujii et al., 1986). At these sites, *Cryptomeria* grew in the wetland with *Alnus* judging from the distribution of stumps,

wide and shallow roots, and pollen assemblages from peaty sediments of stump horizons dominated by *Cryptomeria* and *Alnus* types. These forests rarely exist in present Japan, except for that at Sugisawa at the end of an alluvial fan on the Japan Sea coast of central Japan. Such environment was formed with the formation of fans or back-marshes accompanying a marine regression after the hypsithermal.

During the interstadials of the early glacial in Japan, *Cryptomeria* pollen occurred abundantly in northern Honshu (Morita et al., 2002), the Japan Sea side of central Japan (Palynological Research Group for the Nojiri-ko Excavation, 1984, 1993; Oshima et al., 1997; Iriya et al., 2005), and in the Kinki district (Miyamoto et al., 1996; Takahara et al., 2000b; Ooi et al., 2004; Hayashi et al., 2010). Such dominance of *Cryptomeria* was attributed to the high precipitation contributed by the monsoon and the marine environment of the Japan Sea. Based on the distribution of pollen in a basin, wetland forests of *Cryptomeria* with *Alnus* resembling the post-glacial buried *Cryptomeria* forests stated above were reconstructed at Naka-ikemi (Ooi et al., 2004). Repeated occurrences of *Cryptomeria* forests indicate the recurrent establishment of wet environment ideal for *Cryptomeria* by climatic oscillations.

Fagus type

Tsukada (1982b) discussed the development of *Fagus* forests in Japan by comparing pollen spectra and presented a logistic northward and upward expansion from coastal refugia in the Japan Sea side, south of 38°N, since ca. 12,000 years ago (uncalibrated age). By showing the distribution change of *Fagus* pollen, Tsukada (1987) discussed the history of *Fagus* forests in relation to climatic factors. He recognized rare occurrences of *Fagus* pollen during the glacial period as possible reworks or exotic pollen, or as derived from remaining *Fagus* trees in coniferous forests. Uchiyama (1998) also reviewed the history of *Fagus* and showed the distribution of *Fagus* pollen in northern Honshu during the post-glacial in a higher time resolution.

Here, by mostly covering the pollen records used in these studies with additional records particularly for the glacial and presenting the mid-glacial distribution of *Fagus* type, a number of significant occurrences during the full-glacial and frequent occurrences during the late-glacial have been detected. The resulting distribution maps of *Fagus* type did not support Tsukada's hypothesis (Fig. 16), although the time frame used here may be too rough to detect a logistic expansion. As in *Cryptomeria*, the distribution range of *Fagus* type during period 20 ka is basically not different from those

during the late-glacial (period 12 ka) and the post-glacial (periods 7 ka, 2.5 ka) (Fig. 17). Thus, northward or upward migration of *Fagus* by climatic amelioration could not be detected, but the range of *Fagus* rich pollen assemblages showed a northward shift. So far, changes in the areas with abundant *Fagus* pollen have been considered to reflect migration of plants, and significant occurrences of *Fagus* pollen at several sites during the glacial were emphasized as refugia in spite of the existence of many other sites with records of *Fagus* type. However, the distribution of *Fagus* type shown here does not indicate such migration of plants.

During the mid-glacial (period 40 ka), *Fagus* type frequently occurred in wide areas and even in northern Honshu and Hokkaido (Fig. 16). During the full-glacial (period 20 ka), *Fagus* type occurred least and sporadically at several sites in southern Kanto, Shikoku, and Kyushu, but was recorded at 52.4% (152/290) of pollen sites (Table 2), attaining over 5% at 19 site and over 2% at 60 sites. During the late-glacial (periods 14 ka, 12 ka), *Fagus* type increased in the Japan Sea side of central Japan and in northern Honshu and occurred at several sites even in southern Hokkaido. During the post-glacial, *Fagus* type began to increase in northern Honshu from the lowland to the mountainous areas along the Japan Sea coast. After the hypsithermal, *Fagus* type became abundant after period 5 ka, particularly in the mountainous areas of the Japan Sea side below 2000 m. In Hokkaido, *Fagus* type increased after period 5 ka, and its dominance seems to have expanded northward. The distribution of *Fagus* type, however, did not change latitudinally or altitudinally, and only its dominance at respective sites changed. Because *Fagus* type occurred abundantly since period 5 ka in central to northern Honshu, wind dispersal of exotic pollen may affect its distribution, especially in mountainous areas (Morita, 1984) and in areas with human disturbances (Morita & Hibino, 1994).

The marine environment of the Japan Sea affected the distribution of *Fagus* and other pollen types greatly. According to reviews by Arai et al. (1982), Oba (2006), and Koizumi et al. (2006), during 80,000–30,000 years ago (updated by calibration from the original data), a relatively minor amount of the Pacific seawater flowed into the Japan Sea. A conspicuous decrease in the salinity of the seawater occurred during the glacial stage of 30,000–15,000 years ago, caused by the reduced inflow of seawater from the open sea due to the lowered sea level and the resulting paleogeographic changes at the straits. An inflow of the cold Chishima Current (Oyashio) through the Tsugaru Strait into the Japan Sea began during 15,000–12,000 years ago of the late-

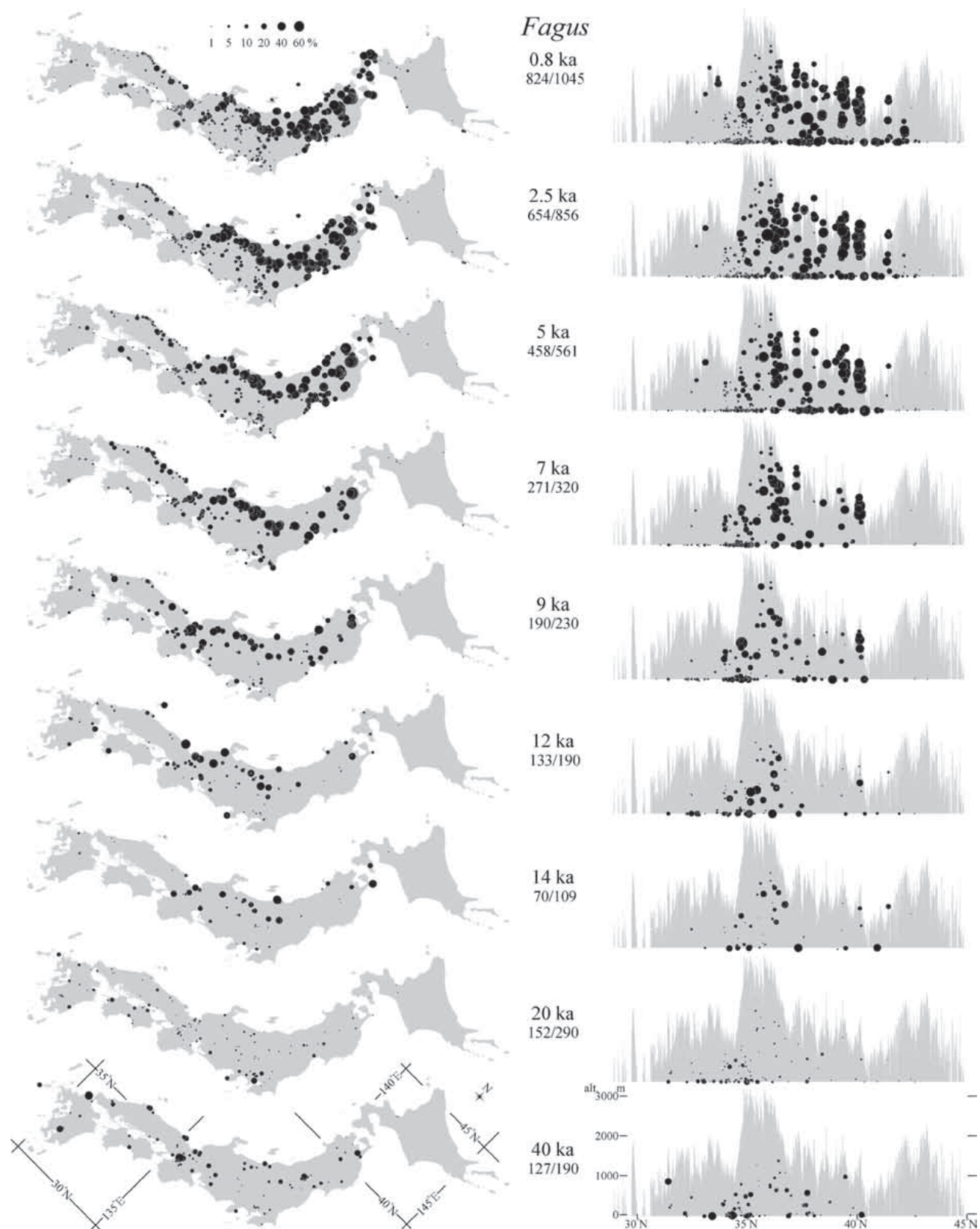


Fig. 16 Chronological succession of *Fagus* type occurrences on horizontal maps and vertical profiles of Japan. Numbers of recorded and whole sites for each period are shown below periods.

図 16 ブナ属型花粉の出現率の水平・垂直分布（南北断面）の変遷。

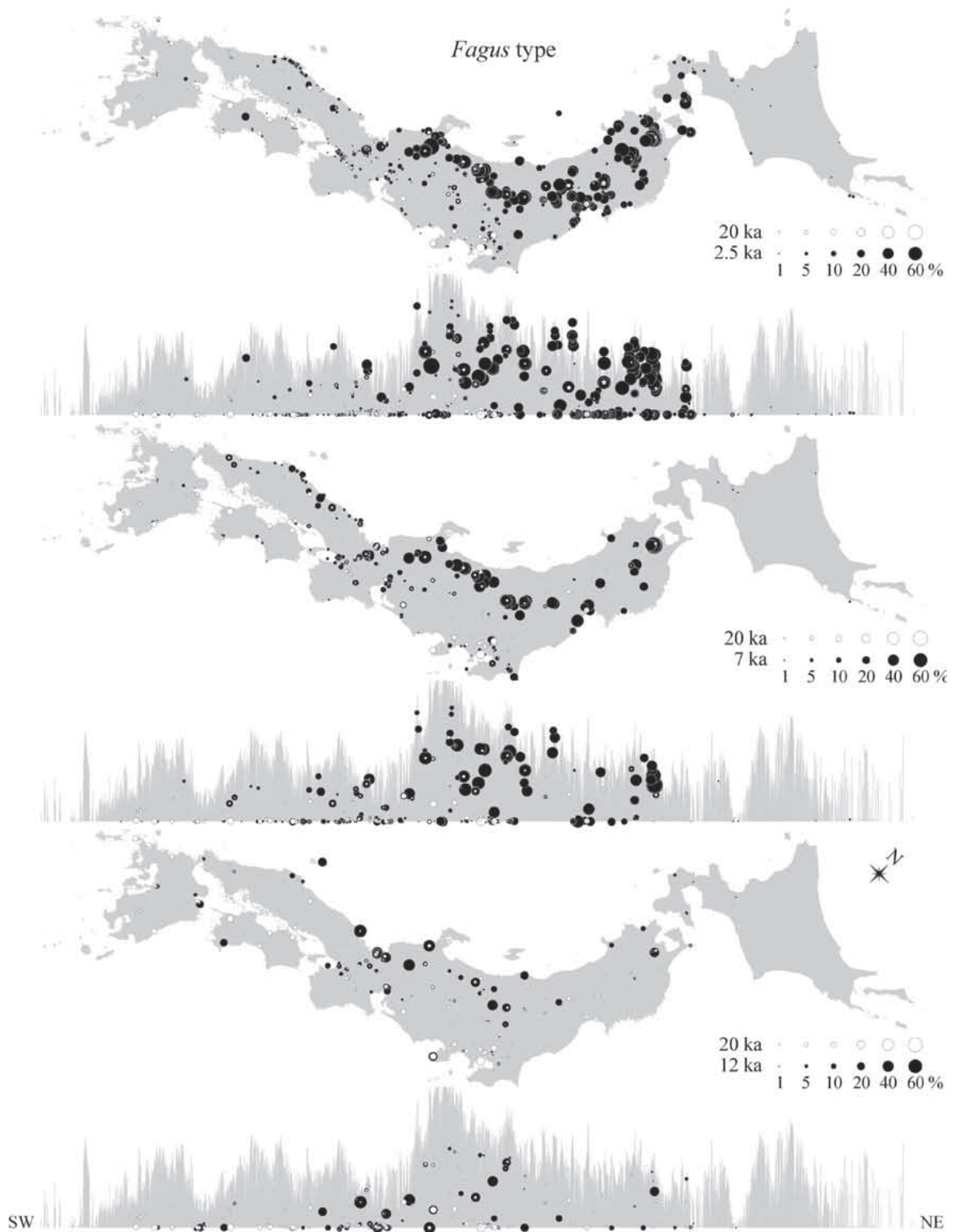


Fig. 17 Occurrences of *Fagus* type during the late-glacial (period 12 ka) and the post-glacial (periods 7 ka and 2.5 ka) overlaid with those during the full-glacial (period 20 ka).

図 17 ブナ属型花粉出現率の最終氷期最盛期（時期 20 ka）と晩氷期（時期 12 ka）、後氷期（時期 7 ka, 2.5 ka）の分布の比較.

glacial. An inflow of the warm Tsushima Current, a branch of the Japan Current (Kuroshio), through the Tsushima Strait started at ca. 10,000 years ago and became vigorous after 9000 years ago, establishing the modern oceanographic regime. The inflow of the Tsushima Current into the Japan Sea induced the warm and wet climatic condition in the Japan Sea side since the hypsithermal.

Although the modern distribution of *Fagus crenata* used to be explained in relation to the snowfall (Honma, 2003), the distribution of *Fagus* type cannot be explained just with snowfall. Changes in the distribution of *Fagus* type since the hypsithermal (period 7 ka) leading to the formation of the modern *Fagus crenata* zone seem to reflect the increase of snowfall caused by the influx of the Tsushima Current. However, other increases of *Fagus* type cannot be explained simply by the increased snowfall. During the late-glacial when the inflow of the warm Tsushima Current had not started and only that of the cold Chishima Current existed, the Japan Sea did not freeze due to the circulation of deep water induced by the increased salinity. This probably established a wet environment along the Japan Sea coast. Frequent occurrences of *Fagus* type around the Tsugaru Strait during this period seem to reflect such environment with snowfall not as heavy as in the post-glacial. *Fagus* type increased since period 9 ka in northern Honshu, not only in the Japan Sea side, but also in the Pacific side, but the increase was larger in the Japan Sea side of central Honshu. This difference in the increase of *Fagus* type probably lead to the modern composition of *Fagus* forests, those mixed with various deciduous broadleaved trees and temperate conifers in the Pacific side of northern Honshu (Hara, 2006a, b) and *Fagus* dominant ones in the Japan Sea side. Occasionally, however, *Fagus* type may include *Fagus japonica* and wind dispersed exotic pollen.

In the Japan Sea side of central Japan, *Fagus* type became abundant during period 12 ka of the Younger Dryas cooling. Hayashi et al. (2010) analyzed a borehole sample since the last interglacial from Lake Biwa and showed that *Fagus* pollen occurred most abundantly during cold phases corresponding to MIS 5d, 5b, and 4. Thus, the full-glacial vegetation differed from those in other cold phases of the glacial period in this area.

In southern Japan *Fagus crenata* has grown only fragmentarily. *Fagus crenata* grows at elevations higher than 700 m in northern Kyushu and higher than 1000 m in southern Kyushu (Matsui et al., 2009), with the southern limit on Mt. Takakuma. In post-glacial Kyushu, over 10% *Fagus* pollen occurred only at Odan-

oiike during period 5 ka (Takeoka, 1986). In Shikoku *Fagus* forests now occupy 1.8% of the forest area, distributed fragmentarily in the mountainous ranges (Kuramoto et al., 2005). In Holocene Shikoku, *Fagus* type occurred over 20% during periods 5 ka and 2.5 ka at Karaike moor (alt. 1223 m), where a relict *Fagus* forest now exists (Yamanaka & Yamanaka, 1977). A *Fagus* forest exists also at Nokanokeyama moor, but the data from this moor with *Fagus* type over 30% since period 7 ka were not sufficient for plotting in the map (Nakamura & Yamanaka, 1951). Similarly, several other data, such as ca. 10–19% occurrences of *Fagus* type at Higashi-akaishi moor (Nakamura, 1952) and Oonogahara (Nakamura et al., 1981), were not plotted. In full-glacial Shikoku and Kyushu, *Fagus* type occurred more frequently than it did during the post-glacial, although only several sites in Shikoku were fit for the analyses. In the UT core from the Uwa lowland of western Shikoku, *Fagus* type occurred continuously at over 50% during the middle Pleistocene cold phase of ca. 240–280 ka corresponding to MIS 8 (Morita et al., 2014). Thus, present *Fagus* forests in Kyushu and Shikoku can be relicts of older ages.

The origin of isolated populations of *Fagus* was often discussed such as those on Sado or Okushiri Islands that had no direct connection with Honshu or Hokkaido during the last glacial. Similarly, *Fagus* in Hokkaido separated from Honshu by the Tsugaru Strait even during the last glacial maximum has been variously discussed. Another much discussed problem is the origin or cause of the northern limit of *Fagus* in the Kuromatsunai lowland in southwestern Hokkaido (e.g., Watanabe, 1994; Kito, 2008). This lowland is not an apparent barrier, and the present climatic conditions allow its growth beyond this lowland, and several explanations exist for its lack in central and eastern Hokkaido (Watanabe, 1994; Kito, 2008). Kito & Takimoto (1999) investigated the population growth and migration rate of *Fagus crenata* during the Holocene based on pollen analyses. The chronological sequence of *Fagus* type distribution, however, suggests that the northern limit of *Fagus* did not shift northward (Fig. 16), but that populations just grew. *Fagus* forests now flourish in southern Hokkaido, probably because of heavy snowfall caused by the inflow of the Tsushima Current into the Japan Sea. According to the compilation of Pleistocene *Fagus* fossils in Hokkaido by Yano (1989), *Fagus* occurred in Oshima Peninsula south of the Kuromatsunai lowland, but was absent from other areas of Hokkaido during the last interglacial, whereas it occurred fragmentarily, but throughout Hokkaido during the previous interglacial.

To clarify the geographical history of *Fagus crenata*, we should consider not only fossil occurrences and climatic events since the last glacial, but also fossil records and geological events since the middle Pleistocene or older periods. In the middle Pleistocene, *F. crenata* and closely related extinct *F. microcarpa* occurred beyond the Kuromatsunai lowland in Hokkaido. According to fossil records, *F. microcarpa* coexisted with *F. crenata* during the middle Pleistocene (Momohara, 1996).

Now the distribution of other pollen types preferring the cold climate will be discussed. These pollen types occurred dominantly during the glacial and decreased during the post-glacial when the number of pollen sites increased.

Larix type

The distribution of *Larix* type is the same as that of DC-LRX class, because DC-LRX class consists only of this pollen type (App. Fig. 4, Fig. 6 left). *Larix* type pollen occurred frequently in the last glacial in northern Japan, but decreased rapidly until period 9 ka of the post-glacial when it occurred sporadically. At present, *Larix* does not grow natively in Hokkaido, and *L. kaempferi* naturally grows only in small areas of central Honshu.

Larix type expanded most extensively during the full-glacial (period 20 ka) and occurred commonly in Hokkaido and at several site in central Japan, especially in the mountainous areas of the Pacific side of northern Honshu. During this period, over 8% of *Larix* type is reported in Shikoku, but this pollen is considered as *Pseudotsuga* from the present existence of *Pseudotsuga* forests near the site (Nakamura & Katto, 1953a). *Larix* type decreased during period 14 ka and increased again during the late-glacial (period 12 ka), but not so prevalently in northern Honshu.

Macrofossils of *Larix gmelinii* are recorded not only from Hokkaido, but also at Sendai of northern Honshu during the latter half of the last glacial (Suzuki & Takeuti, 1989; identified as *Larix kamtschatica* synonymous to *L. gmelinii*). Thus *Larix gmelinii* forests existed in Hokkaido during the full-glacial and probably in the Pacific side of northernmost Honshu. Apparently *L. gmelinii* dominated in Hokkaido during the last glacial, but disappeared from Japan afterward. *Larix kaempferi* expanded during the last glacial in central Japan and still grows in the same area. No apparent evidence for the migration of *Larix* is obtained, and the cause of extinction is not clarified. Warming climate can be one of the reasons for the decline of *Larix*,

but present plantations of *L. gmelinii* grow well in the lowland of Hokkaido. Climatic oscillations occurred repeatedly before the last glacial, and middle Pleistocene fossil cones of *L. gmelinii* are found at Manzidani of the Osaka bay area of central Japan (Miki, 1941). Because *L. kaempferi* endemic in Japan is closely related to *L. gmelinii* (Kisanuki, 2000), evolution of *L. kaempferi* should be considered together with changes in the distribution since the middle Pleistocene.

Picea type

Picea is one of the major components of coniferous forests in northern Japan and the mountainous areas of central Japan. Changes in the distribution of *Picea* type show that it increased from the mid-glacial (period 40 ka) and wholly covered the Japanese archipelago during the full-glacial (period 20 ka) except for Hokkaido (App. Fig. 3). *Picea* in Hokkaido declined during the full-glacial due to the increase of *Larix* type. There is only one species of *Picea*, *P. polita*, growing in Kyushu and Shikoku, but cones of *P. jezoensis* are recorded from glacial sediments in Kyushu (Miki & Kokawa, 1962; Hase & Hatanaka, 1984). *Picea* type pollen decreased during period 14 ka and increased during period 12 ka in northern Japan and became rare during the post-glacial except in Hokkaido. *Picea* type occurred least during the hypsithermal (period 7 ka) and increased again in Hokkaido and in the mountainous areas of Honshu during period 2.5 ka.

Areas with abundant occurrences of *Picea* type seem to have shifted from northern Honshu to Hokkaido, but this does not indicate migration of *Picea*, because the Tsugaru Strait was a barrier between Honshu and Hokkaido even during the last glacial (Oba, 2006). Moreover, *Picea* species of recent Hokkaido probably differed from those of the full-glacial in northern Honshu. In Hokkaido, *Picea* type of the post-glacial (periods 5 ka, 2.5 ka) is thought to derive from *Picea jezoensis* forests now growing on dry mountain slopes or *Picea glehnii* forests occurring in wet or volcanic habitats. *Picea* type of the full-glacial (period 20 ka) in northern Honshu is thought to derive from wetland *Picea* forests, judging from the dominance of *Picea* cones from peaty deposits (Minaki, 1987; Suzuki, 1991). These cones resemble those of extant *P. koyamae*, *P. maximowiczii*, *P. alcoquiana*, and *P. glehnii* distributed in small restricted areas of central Japan (Katsuki et al., 2008), but are often difficult to identify with modern species and are named *Picea* cf. *shirasawae* (Minaki, 1987) or extinct *Picea tomisawae* or *Picea pleistoceaca* (Suzuki, 1991). By studying morphological variation in the cones of modern *P. glehnii*

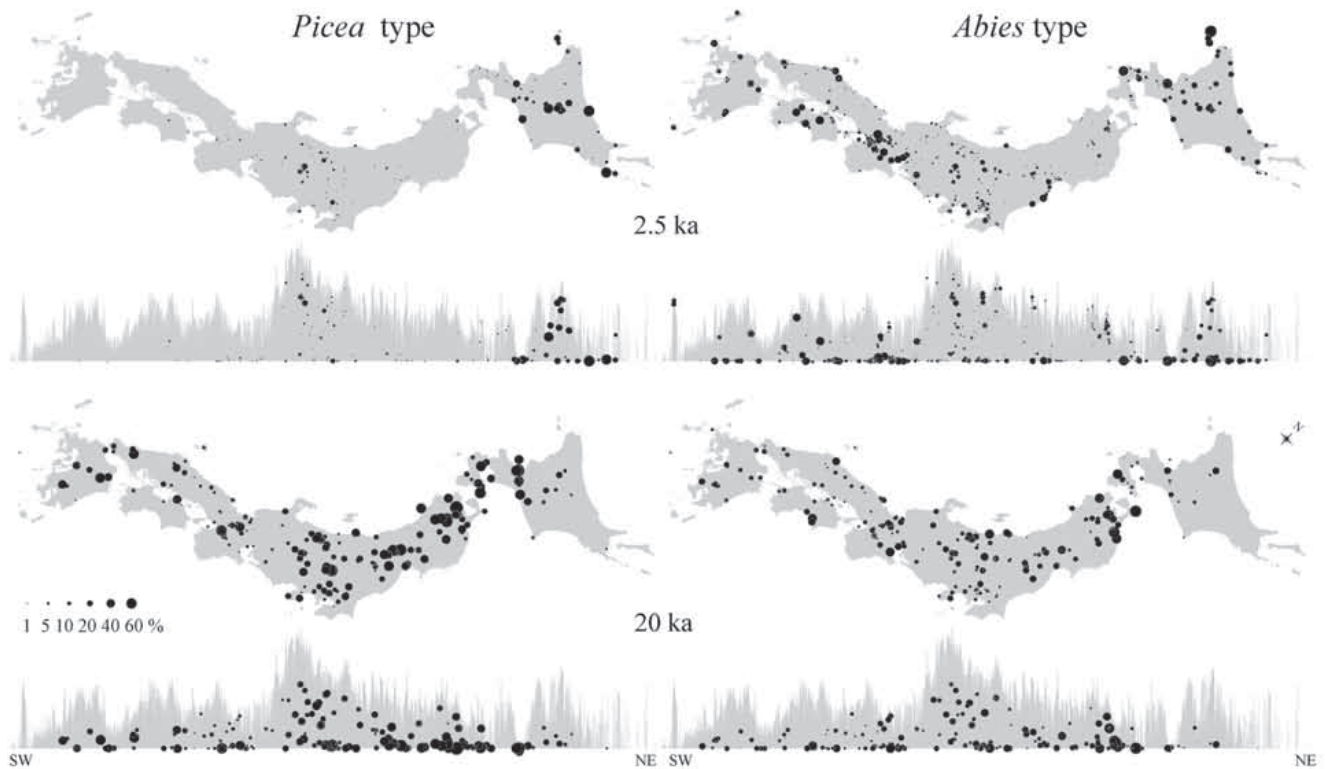


Fig. 18 Occurrences of *Picea* and *Abies* types during the full-glacial (period 20 ka) and the post-glacial (period 2.5 ka).

図 18 トウヒ属型およびモミ属型花粉出現率の最終氷期最盛期 (20 ka) と後氷期 (2.5 ka) における分布。

and *P. koyamae*, Konishi & Suzuki (1997) indicated that cones of these two extant species and fossil *P. cf. shirasawae* or *P. tomisawae* cannot be distinguished. Note et al. (1998) speculated that four species of *Picea*, *P. glehnii*, *P. koyamae*, *P. maximowiczii*, and *P. alcoquiana*, are regional varieties of the same species that grew extensively during the last glacial, because of the similarity in morphology and habitat, and concluded that remnant populations from the last glacial form the present distribution of these species. Macrofossils of *P. jezoensis* including *P. jezoensis* var. *hondoensis* also occur from northern Honshu to Kyushu during the last glacial maximum (Sohma & Tsuji, 1988). *Picea jezoensis* var. *hondoensis* has smaller cones with wider seed scales and wings and narrower bract scales than *P. jezoensis* var. *jezoensis* (Shimizu, 1992). Genetic variation in DNA markers suggested that *P. jezoensis* var. *hondoensis* derived from *P. jezoensis* var. *koreana* in Korean Peninsula (Moriguchi, et al., 2009) and that *P. jezoensis* var. *jezoensis* of Hokkaido derived from that in Sakhalin (Aizawa et al., 2007). Further studies are needed for fossil identification, but probably no relationship exists between *Picea* of Hokkaido during the post-glacial (periods 5 ka, 2.5 ka) and that of

northern Honshu during the full-glacial (period 20 ka). Thus, the distribution range of *Picea* greatly reduced in northern Honshu during the post-glacial.

Abies type

The distribution of *Abies* type is similar to that of *Picea* type in central and northern Japan, but extends relatively southward (App. Fig. 6). During the post-glacial (period 2.5 ka), *Abies* type covered the whole Japanese archipelago, but *Picea* type occurred prevalently only in Hokkaido and in the restricted mountainous areas of central Japan. However, both types occurred widely during the full-glacial (period 20 ka) (Fig. 18).

During the last glacial, *Abies* type occurred prevalently, especially in northern Honshu to southern Hokkaido, but during the post-glacial, decreased to occur sporadically in Hokkaido and western Japan. In Hokkaido, *Abies* type occurred frequently in the lowland and coastal areas in periods 9 ka and 7 ka and increased since period 5 ka also in the mountainous areas. In western Japan where *Picea* was rare since period 14 ka, *Abies* type frequently occurred in the post-glacial. *Abies* pollen generally increased in the mountainous areas of central and northern Honshu

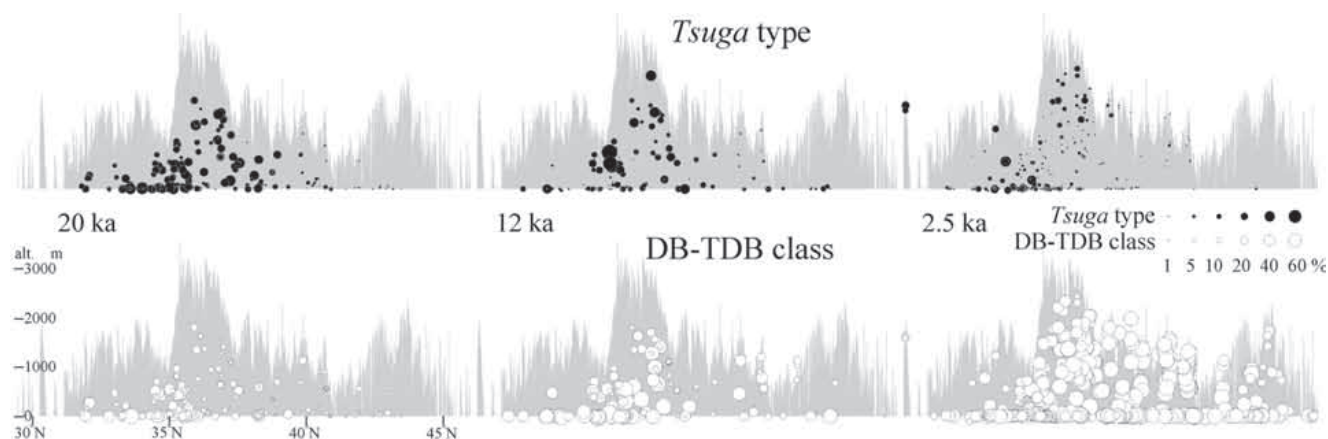


Fig. 19 Occurrences of *Tsuga* type and temperate deciduous broadleaved tree pollen (DB-TDB class) on south to north vertical profile of Japan during the full-glacial (period 20 ka), late-glacial (period 12 ka), and post-glacial (period 2.5 ka).

図 19 ツガ属型花粉と落葉広葉樹花粉 (花粉相観クラス DB-TDB) の出現率の時期 20 ka, 12 ka, 2.5 ka の垂直分布 (南北断面).

since period 5 ka, and its modern distribution seems to be expanding, not shrinking (App. Fig. 6).

In Hokkaido, only *Abies sachalinensis* grows at present, but *Abies* type continuously occurred since period 40 ka and increased after the hypsithermal. This may have resulted in modern *Abies sachalinensis* forests there. Macrofossils of *Abies sachalinensis* occur in deposits of the glacial period in Hokkaido, and those of *Abies veitchii* do in deposits of the middle Pleistocene (Yano, 1987). In northern Honshu, *Abies sachalinensis* grew during the full-glacial with *Larix gmelinii* and *Picea glehnii* (Sohma, 1959).

In Honshu, Shikoku, and Kyushu, areas with frequent occurrence of *Abies* type are disjunct, reflecting the present distribution of species. Four endemic species of *Abies* grow in the mountainous areas of Honshu, *Abies firma* in warmer habitats at 50–1600 m alt., *A. homolepis* in cooler habitats at 1000–1800 m alt., *A. veitchii* at 1400–2600 m alt. with a population in Shikoku occasionally regarded as var. *reflexa*, and *A. mariesii* at 1500–2600 m and 600–1900 m alt. in central and northern Honshu, respectively (Yamazaki, 1995). *Abies mariesii* prefers habitats with heavy winter snowfall and forms subalpine or subarctic forests with *A. veitchii*. The concentration of *Abies* type in the lowland of western Japan corresponds to the distribution of *Abies firma* in western Japan.

Subalpine or subarctic *Abies* dominant forests in Japan have been discussed variously. Murata (1977) suggested that *Abies* dominant forests on the mountains of the Japanese archipelago do not correspond to boreal or subarctic forests, but to cold temperate forests at the top of temperate forests in the Sino-Japanese

floristic region. Tabata (2000) compared the Japanese vegetation zones with the global vegetation zones and suggested correspondence between subalpine and subarctic evergreen coniferous forests in Japan and cold temperate forests in other areas. Because species distinction among *Abies* pollen grains is suggested from pollen morphology (Saito & Tsuchida, 1992), the history of *Abies* dominant forests should be sought from species identification of fossil *Abies* pollen and ecology of fossil *Abies* species.

Tsuga type

The chronological succession of *Tsuga* type (App. Fig. 5) shows that *Tsuga* type occurred most abundantly during the cold phases of the last glacial (periods 20 ka, 12 ka) and in the recent (period 0.8 ka). During the last glacial *Tsuga* type occurred widely even in Hokkaido where *Tsuga* is not growing at present. *Tsuga* type decreased in the post-glacial and became least during the hypsithermal (period 7 ka). After the hypsithermal, *Tsuga* type began to increase in two areas, the lowland of western Japan and the alpine region of central to northern Honshu. These two areas of distribution correspond to those of temperate *Tsuga sieboldii* and subalpine *T. diversifolia*.

The vertical distribution of *Tsuga* type during periods 20 ka, 12 ka, and 2.5 ka contrasts well with that of temperate deciduous broadleaved tree pollen (DB-TDB class) (Fig. 19). The distribution of these two types was continuous during the full-glacial (period 20 ka), but were clearly separated during period 2.5 ka. By making specific distinction from the size of the marginal fringe of *Tsuga* type pollen, Takahara (1998a) indicated that

Tsuga diversifolia expanded in the Kinki district during the full-glacial and grew adjacent to *Tsuga sieboldii* in the lowland with restricted temperate deciduous broadleaved forests in between. The distribution of these two *Tsuga* species was, however, not separated gradually with the upward move of *T. diversifolia* caused by the post-glacial warming. During the late-glacial cool phase (period 12 ka), *Tsuga* type already occurred abundantly also in mountainous areas, and temperate deciduous broadleaved tree pollen (DB-TDB class) increased between the two areas of *Tsuga* type. Thus, the separation of *Tsuga* already started during the late-glacial.

In the subsequent post-glacial, *Tsuga* type decreased wholly and occurred least in the hypsithermal (period 7 ka). *Tsuga* type began to increase in mountainous areas during period 5.0 ka and expanded during younger periods, but never became dominant. Through these ages, the distribution area of *Tsuga* type did not change greatly, and the two areas of its abundant occurrences nearly overlapped with that of deciduous broadleaved tree pollen (DB-TDB class). Increase of deciduous broadleaved tree pollen since the late-glacial made the separation of the two groups of *Tsuga* clearer. These changes seem to indicate changes in the dominance of forest trees, but not their migration. Vegetation changes of this kind induced by climatic changes usually result in a shift in vegetation zones. Tsukada et al. (1989) showed the surface pollen distribution of *Tsuga diversifolia* and *T. sieboldii* types and discussed their clear separation by climatic factors. To clarify what happened in the border area of *T. diversifolia* and *T. sieboldii*, morphological studies of fossil *Tsuga* pollen are indispensable.

In Hokkaido *Tsuga* type occurred rarely, but significantly until period 2.5 ka. *Tsuga* pollen resembling *T. diversifolia* is recorded not only in Hokkaido, but in Sakhalin during the late Holocene (Igarashi et al., 2013). Although *Tsuga* macrofossils are not recorded in Hokkaido, *Tsuga* probably grew in Hokkaido during the late Pleistocene. A simulation from climatic factors controlling the modern *Tsuga* distribution showed that the habitable area for *Tsuga* increased with the global warming in Hokkaido (Tsuyama et al., 2014). This fact is consistent with the occurrence of *Tsuga* type in Hokkaido during the hypsithermal, but *Tsuga* type became extinct afterward, probably quite accidentally.

Betula type

Betula type is another cold element and changed its distribution characteristically in the mountainous areas

in the Japan Sea side of central to northern Honshu and in Hokkaido (App. Fig. 12). The distribution of *Betula* type has not been discussed critically, because *Betula* type often represents local vegetation near pollen sites and is relatively over-represented in pollen diagrams (Tsukada, 1974). However, changes in the distribution of *Betula* type show an interesting history of *Betula*. *Betula* type occurred most abundantly during periods 14 ka to 9 ka, at most sites during period 14 ka, most widely during period 12 ka, and most dominantly in the mountainous areas and the lowland in Hokkaido during period 9 ka.

Frequent occurrences of *Betula* type around the mountaintops of central Japan since the early post-glacial (period 9 ka) are thought to derive from *Betula ermanii* forests above evergreen coniferous forests. Modern *Betula ermanii* forests exist near the forest limit in the mountainous areas of central Japan regulated by the accumulation of snow (Okitsu, 1987, 1991). Thus, *Betula* type continuously occurring in the mountainous areas since period 9 ka probably resulted in modern *B. ermanii* forests.

Betula type occurring widely in lower mountainous areas during the glacial cannot be attributed to *Betula ermanii*, judging from macrofossils of *Betula* recorded in the last glacial maximum. During the last glacial macrofossils of *B. platyphylla* occur abundantly from central to northern Japan, and those of *B. grossa* do mainly from western Japan, but those of *B. ermanii* do rarely (Sohma & Tsuji, 1988). Thus, *Betula* type distributed in lower mountainous areas during the glacial seems to have derived mainly from *B. platyphylla* or *B. grossa* forests. *Betula* type occurred frequently also in the lowland during the last glacial, particularly during period 14 ka in Hokkaido, and may have derived from dwarf species of *Betula* (Nakamura, 1968). Continuous occurrences of *Betula* type in the lowland of eastern Hokkaido since then probably show a continued existence of dwarf *Betula* until the recent.

Ogawa & Okitsu (2010) studied the site environments and maintenance of *Betula* forests of *B. davurica*, *B. platyphylla*, and *B. grossa* in central Japan and showed that these *Betula* forests exist on landslide sites and are maintained by frequent geomorphic disturbances. The abundant occurrences of *Betula* type during the late-glacial to the early post-glacial may reflect similar frequent disturbances caused by abrupt changes in the climate and the marine environment of the Japan Sea. These changes also induced an increase of *Larix* type in Hokkaido and *Fagus* type in the Japan Sea side of central Japan (Fig. 20). *Betula* probably grew adjacent to them, but were separated by other environmen-

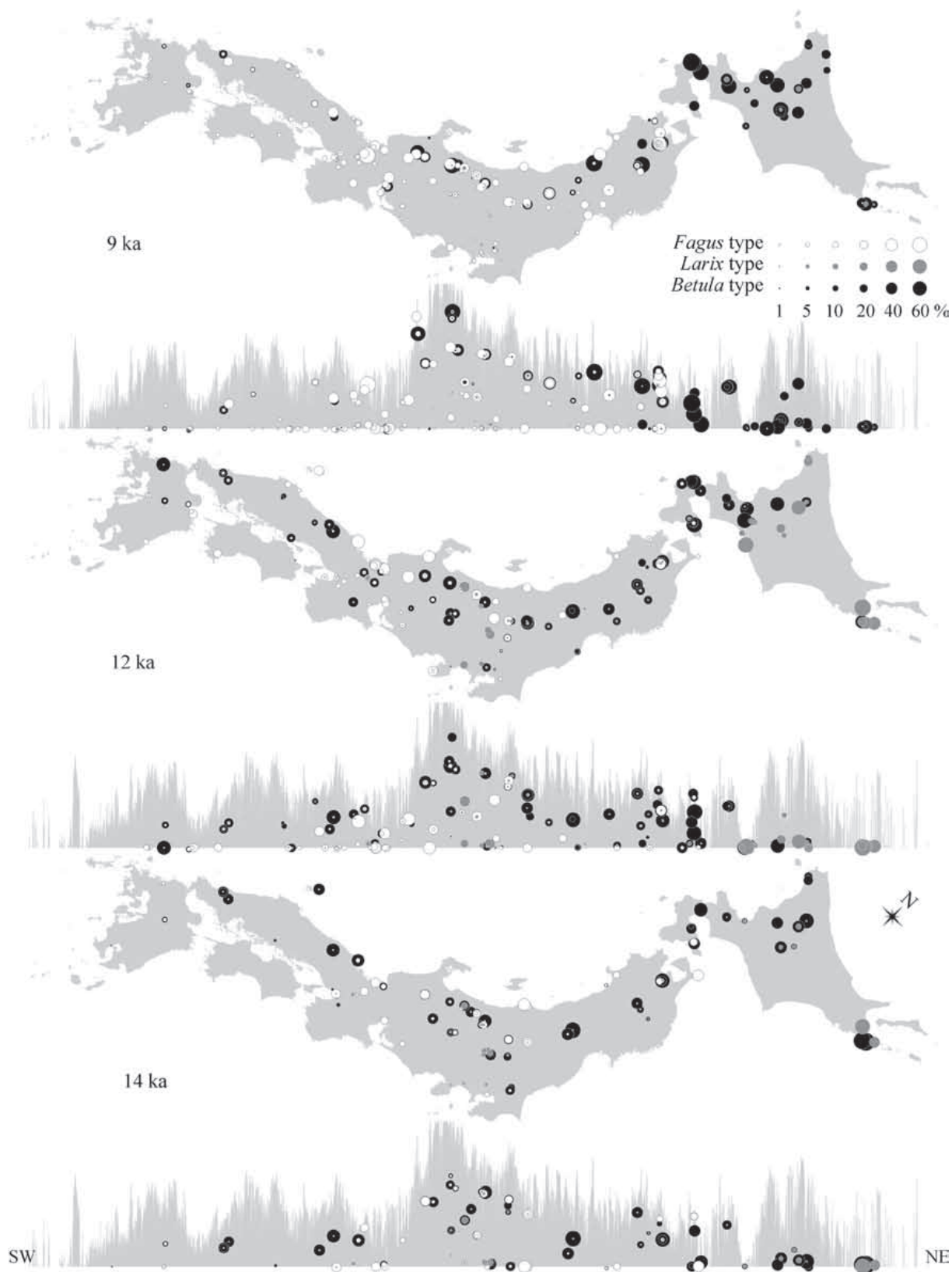


Fig. 20 Occurrences of *Betula* type during the late-glacial (periods 14 ka and 12 ka) and the early post-glacial (period 9 ka) overlaid with those of *Fagus* and *Larix* types.

図 20 カバノキ属型花粉の出現率の時期 14 ka, 12 ka, 9 ka における分布とブナ属型およびカラマツ属型花粉の分布との比較.

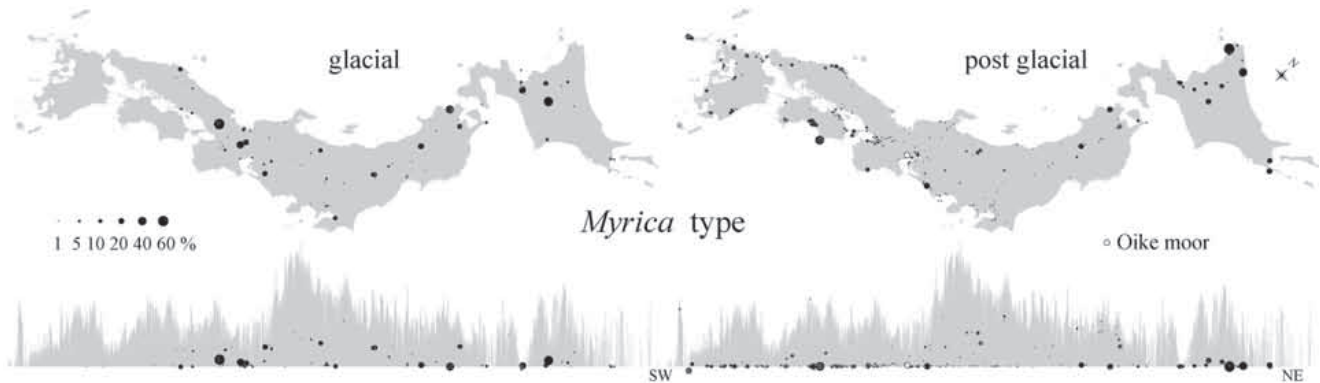


Fig. 21 Occurrences of *Myrica* type during the last glacial (periods 40 ka to 12 ka) and the post-glacial (periods 9 ka to 0.8 ka).

図 21 ヤマモモ属型花粉の出現率の最終氷期（時期 40 ka ～ 12 ka）と後氷期（9 ka ～ 0.8 ka）における分布。

tal factors. Dwarf *Betula* and *Larix gmelinii* grew in the lowland of central to eastern Hokkaido in the late-glacial, and *Larix* declined in the early post-glacial. In Honshu, various species of *Betula*, *Fagus*, and *Larix kaempferi* grew together during the late-glacial, but in the early post-glacial *Betula* type began to dominate in higher areas than those dominated by *Fagus* type in the Japan Sea side, probably showing the origin of the *Betula ermanii* and *Fagus crenata* zones. However, the upward shift of *Betula* abundance may not mean its vertical migration. The specific component of *Betula* type should be clarified by pollen morphology along with the study of its macrofossils.

Myrica type

The distribution maps of *Myrica* type (Fig. 21, App. Fig. 20) reflect the disjunctive distribution of two ecologically distinct species. Abundant occurrences of *Myrica* type in the last glacial and in northern Japan reflect existence of *Myrica gale* growing in moors, and those in southern Japan reflect existence of *Myrica rubra* growing in warm temperate forests. Takeoka (1974) carried out a pollen analysis and recorded the occurrences of *Myrica* pollen during the post-glacial in Oike moor at Yokkaichi of central Japan (Fig. 21 right), situated in the present southern limit of *Myrica gale*. However, this work is not used in the present analysis, because *Quercus* pollen was compiled and occurrences of *Myrica* were not presented in diagrams. This study clearly indicates occurrence of *Myrica gale* during the post-glacial in moors of warm regions and shows difficulties in ecological assumption from pollen analyses. During the full-glacial (period 20 ka), *Myrica* pollen occurred abundantly in central Japan near the present southern limit of *Myrica gale* distribution. Thus, *Myrica gale* in central Japan is definitely a remnant of

the full-glacial.

Thus, pollen types indicating cold environments became limited in distribution during the post-glacial, but did not show apparent migrations. *Larix* and *Tsuga* became extinct from Hokkaido, and *Picea* became extremely restricted in Honshu, but these changes in distribution were not accompanied by plant migration.

Pollen types from the temperate area beside *Cryptomeria* and *Fagus* types also showed similar patterns.

Pinus type

Pinus type has been one of the most prevalent pollen types and occurred almost at all sites, absent only from 5% of pollen sites (Table 2). Judging from the dispersibility of *Pinus* type, it is remarkable that there exist assemblages without *Pinus* type. *Pinus* type attained its peak occurrences during periods 20 ka and 0.8 ka (Fig 7 left, App. Fig. 2). The peak of period 20 ka is contributed mainly by *Pinus koraiensis* now growing in restricted areas of central Honshu and Shikoku, and that of period 0.8 ka is contributed mainly by *P. densiflora* composing present secondary forests. These two species belong to subgen. *Haploxylon* and *Diploxylon*, respectively, whose pollen can be distinguished morphologically. Other species of *Haploxylon* may also have contributed considerably, such as dwarf alpine *P. pumila* and temperate *P. parviflora*, because their macrofossils occur in deposits of the full-glacial (Tsumura & Momohara, 2011). In fact, macrofossils of *Pinus koraiensis* are rare in western Japan in deposits of the glacial period. Nasu (1980) reconstructed the full-glacial vegetation and indicated that *Diploxylon* type pollen occurred distinctly around the Setonai-kai sea that was dried up during the full-glacial. Although most pollen analyses of glacial sediments distinguished

pollen of subgen. *Haploxylon* from that of subgen. *Diploxylon*, these data often included undistinguished *Pinus* type and *Diploxylon* type. Precise identification of *Pinus* pollen is needed to discuss historical changes of *Pinus* type.

Pinus type occupied a wide area of Japan during period 0.8 ka and increased rapidly after period 2.5 ka. This increase of *Pinus* type is widely recognized in Japan except for northern and eastern Hokkaido and is caused by intensive human activities. Even in mountainous areas, this increase of *Pinus* type is detected due to the long distance dispersal of *Pinus* pollen. The cause and timing of the increase of *Pinus* type is estimated in several regions. In the Sendai plain of northern Japan, *Pinus* pollen began to increase before 1000 years ago, but greatly increased since 500 years ago with *Cryptomeria* pollen reflecting the plantation (Morita & Hibino, 1994). In the Kanto area, *Pinus* increased in three steps, during the Yayoi to Ancient periods (2500–1500 years ago), in the 13th century with the formation of secondary forests by forest clearance and expansion of upland farming, and at the beginning of the 18th century with further expansion of secondary forests (Tsuji, 1997). In Kyoto, *Pinus* began to increase around the 7th century with charcoal production and became dominant in the 18th century (Sasaki et al., 2011). The continued collection of firewood resulted in shrubby or bare vegetation on mountains around Kyoto in the 18th century, as reconstructed from old paintings by Ogura (1992, 2012).

Sciadopitys type

The distribution of *Sciadopitys* type is restricted in central Japan and has not changed much (App. Fig. 8). During the mid-glacial (period 40 ka), it occurred at ca. 35% (66/190) of pollen sites and exceeded 10% at 10 sites, the most frequent through the periods. *Sciadopitys* type occurred frequently in many horizons of the early glacial, similar to *Cryptomeria* type, and occurred least during periods 20 ka and 14 ka. In the succeeding post-glacial, however, it increased since period 12 ka and reached its peak occurrence during periods 2.5 ka and 0.8 ka, occurring from Fukushima in the north to Miyazaki in the south, almost corresponding to the present distribution. It frequently occurred in the central Kinki district and Izu Peninsula as shown in the full-glacial map and the Tokai district and the coastal areas of Shikoku. In the Kanto district, *Sciadopitys* type occasionally occurred continuously, although *Sciadopitys* forests do not exist at present. Presently *Sciadopitys verticillata* grows on ridges or flanks of mountains with poor xeric soils, but probably

grew in lowland areas until the recent (period 0.8 ka) and was exhausted due to its excellent timber.

CTC (Cupressaceae/Taxaceae/Cephalotaxaceae) type

The distribution of CTC type (App. Fig. 10) resembles that of *Cryptomeria* (Fig. 14, App. Fig. 9) and *Sciadopitys* types (App. Fig. 8). CTC type occurred least during periods 20 ka and 14 ka, increased since period 12 ka, and reach its peak occurrence during period 2.5 ka. CTC type was common during period 40 ka, similar to *Cryptomeria* and *Sciadopitys* types, and was distributed comparatively northward than *Sciadopitys* type. Contrary to *Cryptomeria* and *Sciadopitys* types with single mother species, CTC type is contributed by many species. Besides, CTC type is occasionally misidentified, and plant migration and distribution changes cannot be discussed with this pollen type. Frequent occurrences of CTC type with evergreen broadleaved trees in the Kanto district during periods 5 ka and 2.5 ka may have derived from *Torreya*, and this type is occasionally identified as *Torreya* type (Tsuji et al., 1986).

The mother plants of CTC type include species useful for timber production. Conifer timber began to be used commonly during the Yayoi period with the renovation of felling tools from stone to iron axes (Suzuki, 2002), although conifers such as *Torreya nucifera*, *Cephalotaxus harringtonia*, and *Cryptomeria japonica* were used already during the Jomon period (Suzuki, 2012). The distribution of CTC and *Sciadopitys* types during period 2.5 ka at the beginning of Yayoi period reflects regional differences in timber resources such as *Thujopsis dolabrata* in northern Honshu, *Torreya nucifera* in the Kanto district, *Chamaecyparis pisifera* in Nagano in central Honshu, *Chamaecyparis obtusa* in Kyoto, and *Sciadopitys verticillata* in Kawachi plain in the Kinki district (Fig. 22). These forests were almost exhausted by the extensive exploitation of later periods except for several restricted areas. The effect of exploitation cannot be discussed clearly until changes in the mother plants of CTC type can be followed with finer identification and a finer time resolution corresponding to the human activities.

Deciduous *Quercus* type

Among the 25 pollen types, deciduous *Quercus* type occurred most abundantly, especially since period 5 ka in the lowland and mountainous areas from Hokkaido to Kyushu (App. Fig. 16). The component species of this type may have changed, but cannot be detected from the distribution pattern. During the full-glacial deciduous *Quercus* type occurred least, but at 72.4%

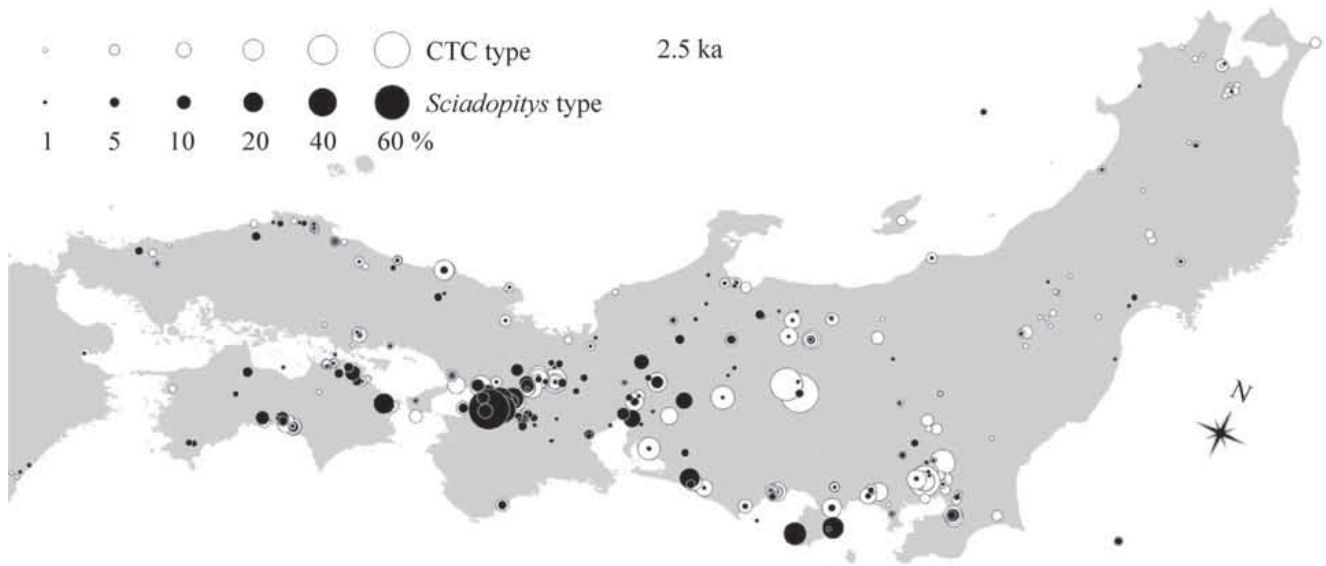


Fig. 22 Occurrences of CTC (Cupressaceae/Taxaceae/Cephalotaxaceae) and *Sciadopitys* types during period 2.5 ka at the beginning of the Yayoi period in Honshu.

図22 ヒノキ科/イチイ科/イヌガヤ科型およびコウヤマキ属型花粉出現率の弥生時代初頭（時期 2.5 ka）の分布。

of sites, and was especially abundant in the lowland along 35°N line.

In Hokkaido Igarashi (1986) showed that *Quercus* pollen increased abruptly at ca. 8000 years ago (calibrated to 8.8 ka), because of the rapid climatic amelioration. Nakamura (1968) suggested existence of *Quercus* even during the last glacial maximum throughout Hokkaido. The distribution of deciduous *Quercus* type in Hokkaido supports existence of *Quercus* during the full-glacial, but did not show the abrupt increase at ca. 8000 years ago. This type occurred infrequently, but continuously during the last glacial in Hokkaido.

No evidence of migration for *Quercus* type is obtained. Deciduous *Quercus* type is contributed by eight species preferring various habitats, which need to be identified.

Tilia type

Entomophilous *Tilia* type occurred rarely, but at more than 30% of sites during periods 14 ka and 9 ka and at ca. 10% of sites during periods 2.5 ka and 0.8 ka (Table 2). *Tilia* type occurred frequently in central Japan during the mid-glacial, in Kyushu during periods 20 ka, 12 ka, and 9 ka, and in Tohoku and Hokkaido since period 5 ka (App. Fig. 23). These occurrences were contributed by different species in respective regions. Five species of *Tilia* grow in present Kyushu with some in restricted areas. *Tilia japonica* and *T.*

maximowicziana grow in Tohoku and Hokkaido, and frequent occurrence of *Tilia* type in these districts since period 5 ka may result in their modern distribution. Morphological studies of fossil and modern *Tilia* pollen may clarify the distribution history of these species.

Acer type

Entomophilous *Acer* type occurred more frequently than entomophilous *Tilia* type (App. Fig. 25). *Acer* type occurred continuously at ca. 30% of pollen sites (Table 2) and was distributed widely, probably because *Acer* type includes many species.

Corylus type

Corylus type occurred continuously from Hokkaido to Kyushu and from the lowland to mountainous areas (App. Fig. 14). *Corylus* type resembles *Myrica* or other Betulaceae pollen, and its identification is difficult. This makes the discussion of the distribution changes of *Corylus* type difficult.

Ulmus/Zelkova/Hemiptelea type

Ulmus/Zelkova/Hemiptelea type occurred at 82.9% of sites, third most frequent after *Pinus* and deciduous *Quercus* types (Table 2). This type occurred abundantly in the lowland, especially in their habitat of alluvial fans, but also occurred considerably in mountainous areas (App. Fig. 21). Areas of frequent occurrences of this type seem to have moved from the west to the

northeast during the post-glacial, but this type occurred throughout Japan through the periods. During the early post-glacial (period 9 ka), *Ulmus/Zelkova/Hemiptelea* type frequently occurred in Kyushu and around Lake Shinji in the Japan Sea side of western Honshu, similar to *Celtis/Aphananthe* type, probably contributed by *Zelkova serrata* in *Celtis* and *Aphananthe* forests. During the hypsithermal (period 7 ka), the area with its frequent occurrences expanded to the central Kinki and Kanto districts together with *Celtis/Aphananthe* type and to the Hokuriku district together with dominant *Fagus* type. During period 5 ka, the area with its frequent occurrences further expanded to the Sendai plain in the Pacific side of northern Honshu and to Hokkaido together with deciduous *Quercus* or *Fagus*, but slightly decreased in western Japan. This type generally decreased a little toward the recent. *Ulmus/Zelkova/Hemiptelea* type occurred rather scarcely during the glacial period except period 40 ka, when its distribution was similar to that of the recent.

This pollen type includes extinct *Hemiptelea*. Macrofossils of *Hemiptelea* from Japan are described as a distinct fossil species, *Hemiptelea mikii* (Minaki et al., 1988), and have been recognized at several sites of the last glacial (Noshiro, 2004; Yoshida et al., 2011). *Hemiptelea* pollen was usually included in *Ulmus/Zelkova*, but could be distinguished from the other types (Nirei, 1996), and was recognized in several studies. Some *Hemiptelea* pollen records from the late-glacial (Masubuchi et al., 2004) need to be re-examined. Hongo (2007) discussed the history of *Hemiptelea* in the Pleistocene Osaka Group and showed that it occurred repeatedly during phases of marine transgression. The cause of its sudden extinction in the late-glacial is difficult to specify, because it survived in Japan for a long period of time through glacial-interglacial climatic oscillations until the last glacial.

Juglans/Pterocarya type

Juglans/Pterocarya type pollen began to increase after period 12 ka in central to northern Japan, but its distribution area changed little since the mid-glacial till the recent (App. Fig. 19). This type occurred most abundantly during period 7 ka in central Hokkaido.

Aesculus type

Aesculus pollen rarely occurred during the last glacial and did most frequently in the Kinki district and also at Hakkoda of northern Honshu (App. Fig. 24). *Aesculus* type increased since period 12 ka and occurred most during period 2.5 ka at 34.1% of sites with conspicuous occurrences at several sites (Table 2).

In Hokkaido *Aesculus* type occurred only at three sites during period 5 ka, at one site during period 2.5 ka, and at four sites during period 0.8 ka. The migration of *Aesculus* type is difficult to discuss, because its entomophilous pollen has low production and a narrow dispersal range. Occasional occurrences of *Aesculus* type in northern Honshu even in the glacial period seem to indicate its distribution, but no evidence of its distribution in Hokkaido have been obtained so far.

Aesculus type occurred frequently in the Kanto district during period 5 ka and in the Tohoku district during period 2.5 ka (Fig. 23). Abundant occurrences of *Aesculus* type is closely correlated with anthropogenic activities, because most records of over 10% *Aesculus* type are derived from archaeological sites (36/49) often with middens of *Aesculus* fruits. Remarkably, *Aesculus* type occurred significantly near archaeological sites during these or previous periods. The increase in *Aesculus* type seems to be caused not only by human activities, but also by environmental changes suitable for the growth of *Aesculus* trees.

Fraxinus type

Fraxinus type occurred widely through the periods, but did not occur commonly, because this type includes anemophilous species. *Fraxinus* type was comparatively more prevalent in the north, but was occasionally omitted from arboreal pollen, because some species grow in the wetland. *Fraxinus* type occurred abundantly at sporadic spots, particularly in Honshu during the mid-glacial (period 40 ka) and in northern Japan since period 7 ka (App. Fig. 26). Abundant occurrences of *Fraxinus* type mainly derive from *Fraxinus mandshurica* in the wetland. The most dominant occurrence of *Fraxinus* type (58.5%) was at Bibai of central Hokkaido together with its fossil woods (Miyaji et al., 2000).

Carpinus/Ostrya type

Carpinus/Ostrya type occurred continuously through the periods, but never became dominant (App. Fig. 13). *Carpinus/Ostrya* type occurred rather rarely in eastern Hokkaido until period 9 ka, in northern Honshu during periods 40 ka and 20 ka, and in Kyushu and westernmost Honshu since period 2.5 ka. This pattern resembles that of DB-TDB class (Fig. 8 left).

The distribution of warm elements was also similar between the last glacial and the post-glacial, but the similarity in distribution was less than that in *Cryptomeria* or *Fagus* types, because of complex contribution of various species.

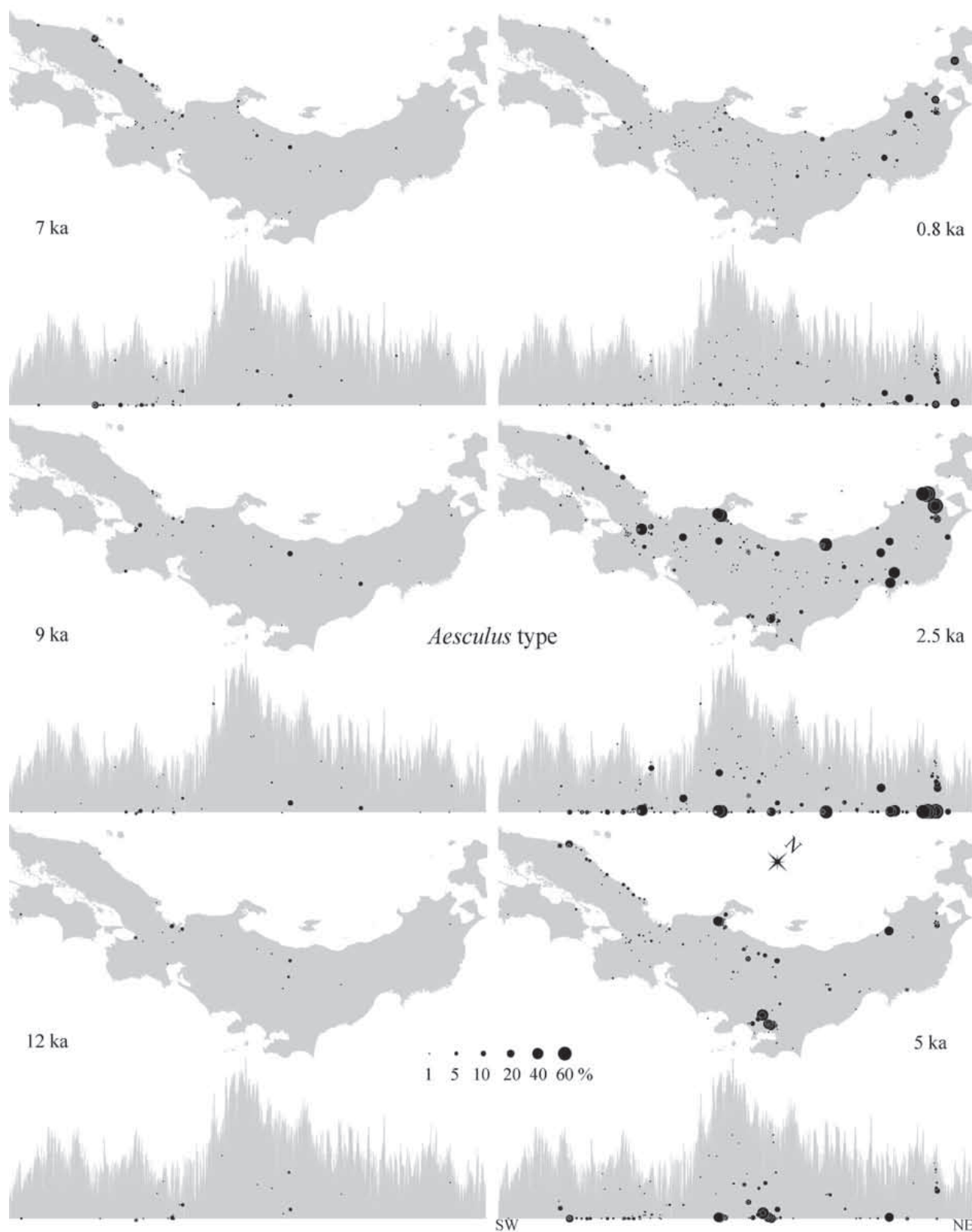


Fig. 23 Occurrences of *Aesculus* type since the late-glacial (periods 12 ka to 0.8 ka) on horizontal maps and vertical profiles of Honshu.

図 23 本州における晩氷期以降（時期 12 ka ～ 0.8 ka）のトチノキ属型花粉出現率の水平・垂直分布の変遷。

Celtis/Aphananthe type

Celtis/Aphananthe type became dominant in the Kanto district and western Japan during the post-glacial (App. Fig. 22). The abundant occurrences of this type seem to be correlated with the northward shift of the warm Kuroshio Current (Japan Current) and the inflow of its branch, Tsushima Current, into the Japan Sea. *Celtis/Aphananthe* type rarely occurred during the last glacial, but began to increase in the coastal areas of western Japan and along the Pacific coast of central Japan during period 12 ka. In southern Kyushu *Celtis/Aphananthe* type occurred abundantly at Kagoshima below Sz-S tephra from Mt. Sakurajima, the center cone of the Aira caldera, dated at ca. 12,800 yr BP (Iwauchi & Hase, 1996). This type increased toward the hypsithermal, and the area of its dominance shifted to the east, in Kyushu during period 9.0 ka, in western Honshu during period 7.0 ka, and in the Kanto district during period 5.0 ka, and decreased toward the recent. In northernmost Honshu, *Celtis/Aphananthe* type occurred abundantly on the coast of Tsugaru Peninsula (Ahn et al., 2008).

The distribution area of *Celtis/Aphananthe* type did not seem to have changed much during the glacial period. *Celtis/Aphananthe* type occurred only at 21 sites during the full-glacial such as Hoshojiri moor in Fukushima Prefecture in northern Honshu (Sohma, 1984). This type also occurred at Kyogoku moor in Hokkaido during period 12 ka (Igarashi, 2000). In Hoshojiri moor *Celtis/Aphananthe* type occurred abundantly during period 40 ka, because Sohma (1984) counted more pollen grains than usual and presented the whole data on the diagrams. Such rare occurrences may reflect derived exotic pollen, but may show records obscured in diagrams with selected pollen types or minimum counts. In this area *Celtis/Aphananthe* type must have existed, because it occurred rarely, but continuously at several adjacent sites.

After period 5.0 ka this type occurred rarely at several sites in northern Japan such as north of Bibai in central Hokkaido. Only *Celtis jessoensis* distributed widely in east Asia is native in present Hokkaido, but it is not known if this species migrated from Honshu.

Celtis and *Aphananthe* forests exist in the coastal areas of western Japan as riparian forests on natural levees and river terraces (Ohno, 1979). These areas correspond to the areas with abundant *Celtis/Aphananthe* type during the post-glacial except for the Kanto district. In these coastal areas, evergreen *Quercus* and *Castanea/Castanopsis/Lithocarpus* types also increased in the post-glacial, and an increase of *Celtis/Aphananthe* type seemed to show an establishment of pioneer veg-

etation prior to that of evergreen broadleaved forests. This type occurred most dominantly during period 9 ka and at the largest number of sites (59.7%, 191/320) during period 7 ka and decreased in the recent. Along the Japan Sea coast of western Honshu, this type occurred abundantly near Lake Shinji, overlapping the distribution of *Ulmus/Zelkova/Hemiptelea* type probably contributed by *Zelkova serrata* in *Celtis* and *Aphananthe* forests. This area is also characterized by the absence of *Cryptomeria* type (Watanabe & Ishiga, 2008). The separate distribution of *Cryptomeria* and *Celtis/Aphananthe* types occurred not only along the Japan Sea coast, but also in the Kinki and Kanto districts during periods 7.0 ka and 5.0 ka (Fig. 24). The difference in habitat preferences between *Cryptomeria* and *Celtis/Aphananthe* types probably caused such differences in distribution.

Evergreen *Quercus* type

During the full-glacial (period 20 ka) evergreen *Quercus* type occurred sporadically and least at 11.4% of pollen sites (App. Fig. 15, Table 2). The area of distribution of this type during the last glacial, however, was almost similar to that during the post-glacial except for northern Honshu. This type is reported to occur at the northernmost highest habitat of Amo moor in central Japan during period 20 ka (Takeoka, 1983), but its identification should be re-examined. In the post-glacial evergreen *Quercus* type occurred commonly during period 9 ka in the coastal areas of western half of Japan, to the southern Kanto district along the Pacific coast and to Izumo along the Japan Sea coast. During period 7 ka this type occurred frequently at more than 60% of pollen sites concentrated in western Japan. Afterward, this type increased in dominance, occurring at more pollen sites, and expanded into the inland and to northern coastal areas. This increase continued to period 2.5 ka, but the occurrence of this type comparatively decreased in period 0.8 ka with the expansion of *Pinus* type by human activities. Thus, evergreen *Quercus* type did not show its peak occurrence at the hypsithermal (period 7 ka), but continued to expand after that. Their habitats must have been restricted until the hypsithermal due to a marine transgression called Jomon transgression. After the hypsithermal, a marine regression produced new open habitats in coastal areas and along the ridges of uplands by erosion and denudation that several evergreen *Quercus* species prefer. Similarly, evergreen *Quercus* type occurred in the upper part of marine clay layers corresponding to the latter half of the interglacial obtained from boreholes covering the middle Pleistocene (Furu-

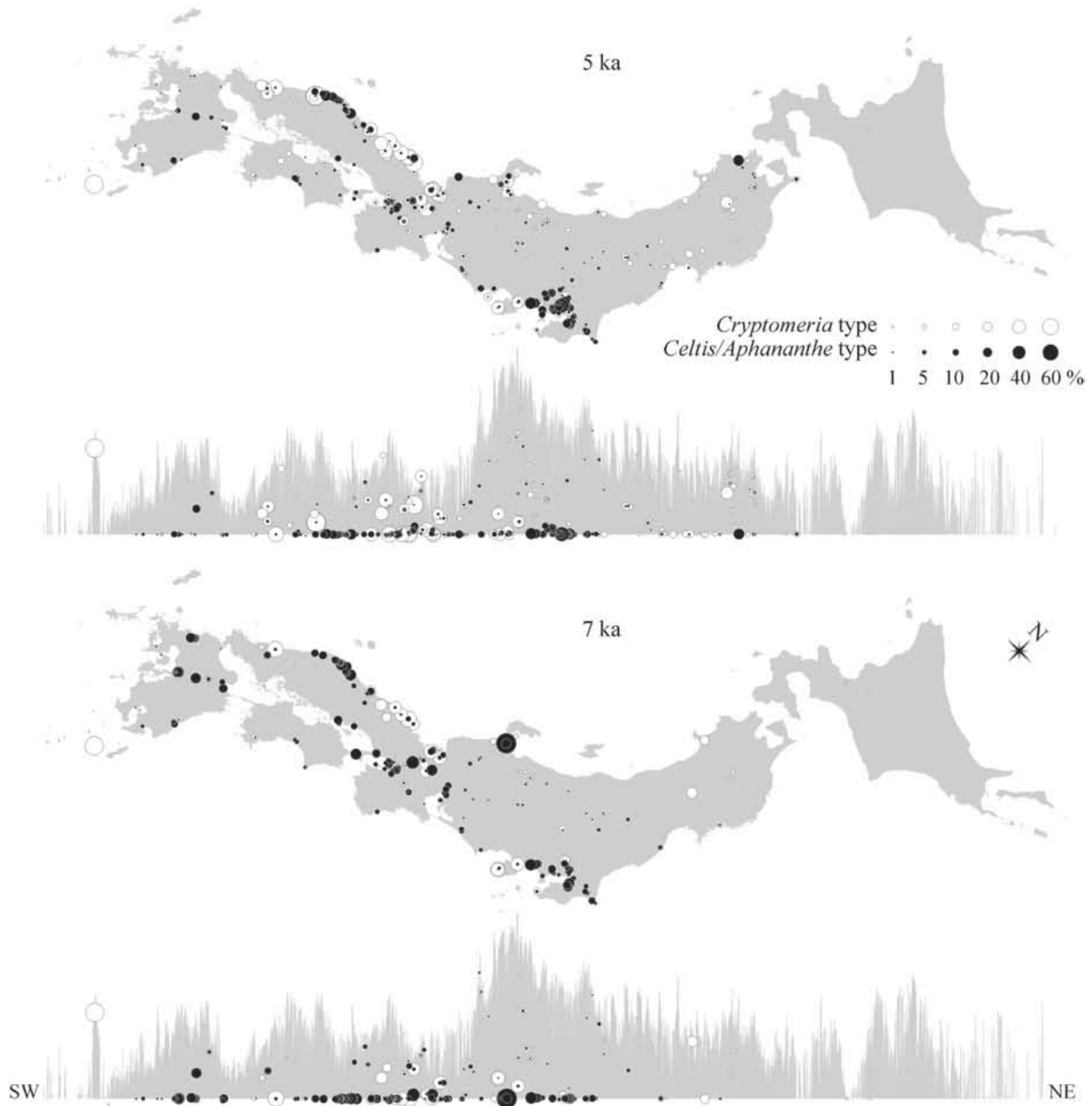


Fig. 24 Occurrences of *Celtis/Aphananthe* and *Cryptomeria* types during the post-glacial (periods 7 ka and 5 ka).

図 24 エノキ属 / ムクノキ属型およびスギ属型花粉の後氷期（時期 7 ka, 5 ka）における分布。

tani, 1989; Kitani, 2005; Hongo, 2009), and expansion of evergreen *Quercus* type with the regression after the hypsithermal was not exceptional.

Occurrences of deciduous and evergreen *Quercus* types since period 9 ka show regional differences in their dominance (Fig. 25). In the Kanto district, Kiyonaga (1994) indicated that evergreen *Quercus* type expanded since period 5 ka, but stopped expanding in

recent historical ages before they became dominant. In the Kinki district, evergreen *Quercus* type expanded since period 7 ka and became dominant during period 5 ka and slightly decreased afterward. In northern Kyushu and southern Shikoku evergreen *Quercus* type were dominant since period 7 ka. In the Kanto district, Tsuji (1985) suggested that human activities and xeric soils caused delay in the expansion of evergreen

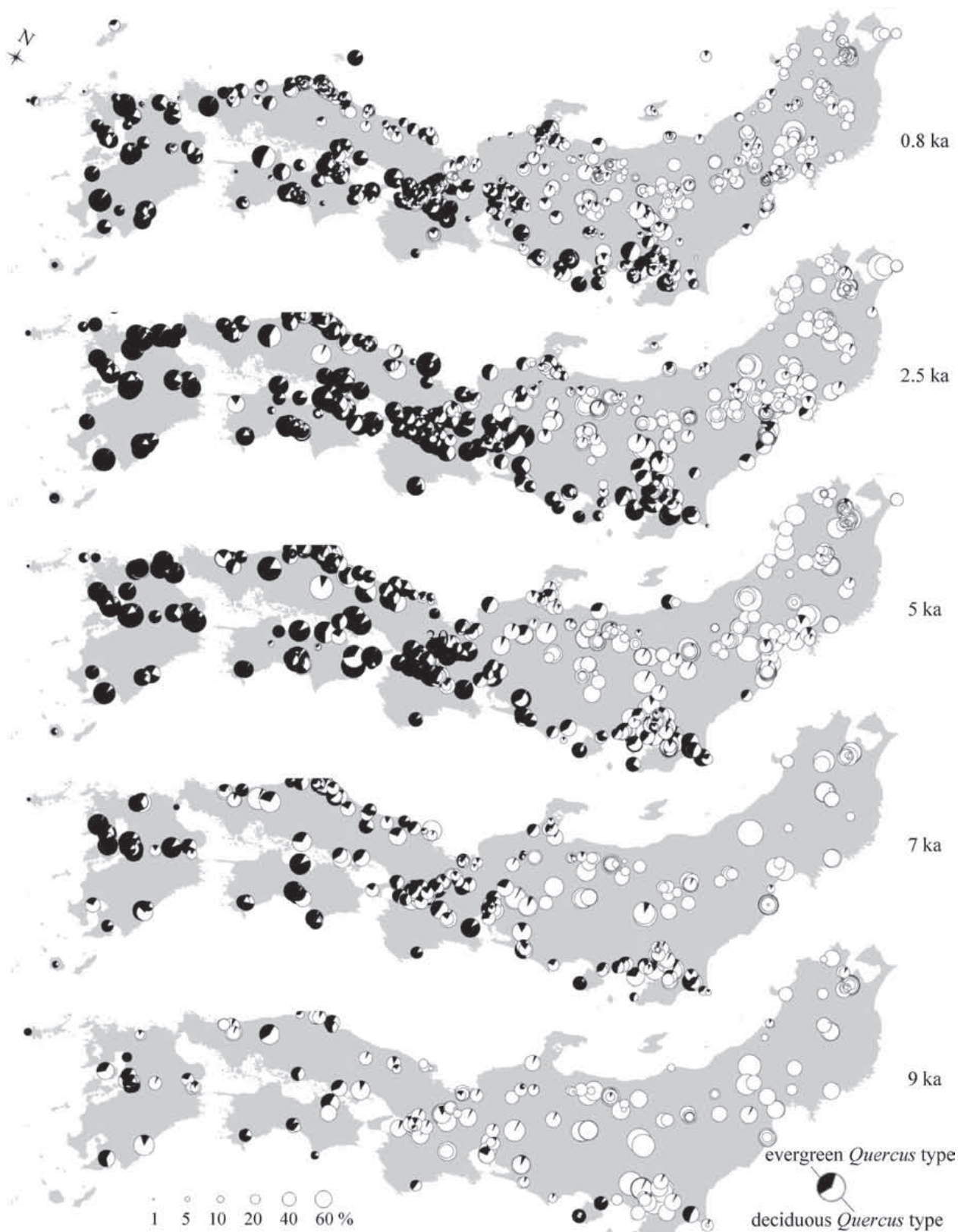


Fig. 25 Composition and occurrences of evergreen and deciduous *Quercus* types during the post-glacial in central to western Japan.

図 25 後氷期における東北地方以南の常緑および落葉コナラ属の出現率と出現比の変遷.

Quercus forests. Habitats opened by the marine regression were suitable for evergreen *Quercus* forests as well as for human beings. Evergreen *Quercus* provided acorns as one of the major food resources and hard timber used variously during the Jomon period. In the Kanto district where Jomon culture flourished, such human activities seem to have hindered the dominance of evergreen *Quercus* even after period 5 ka.

Tsukada (1984) suggested that, during the full-glacial, evergreen broadleaved forests could exist only in submerged Yaku Peninsula in southern Kyushu, in spite of pollen occurrences of species dominant in these forests, such as evergreen *Quercus*, even in central Honshu. Hattori et al. (1987) proposed a migration route of members of evergreen broadleaved forests from glacial refugia in southern Kyushu. The chronological changes in the distribution of evergreen *Quercus* type, however, did not show any long distance migration from southern Kyushu, but increase in abundance from scattered patches in coastal areas, and later invasion into the inland. This invasion into the inland may have occurred with plant migration along with the contribution from glacial remnants, although, we cannot clarify the occurrences of evergreen *Quercus* during the glacial due to problems in the identification of *Quercus* type.

The northern limit of the distribution of evergreen *Quercus* type has historical implications. Distinct occurrences of evergreen *Quercus* type since period 5 ka along the Pacific coast of northern Honshu correspond to the present northern limit of several species of evergreen *Quercus* (Hirabuki, 2005) and evergreen broadleaved forests (Hattori et al., 2008). Because many of these data are from archaeological sites, the distribution of species or forests may be modified by anthropogenic influences. On Tobishima Island in the Japan Sea and around Sendai now situated at the northern limit of evergreen broadleaved forests on the Japan Sea side and on the Pacific side, respectively, archaeological sites of the Jomon period exist near pollen sites with common occurrences of evergreen *Quercus* type. Thus, we have to consider both plant migration and influence of human activities on vegetation.

Species composing evergreen *Quercus* type have respective habit and history. Although all the species of evergreen *Quercus* except *Q. miyagii* distributed in Kyushu share their habitats by elevation and topography (Ito et al., 2007), secondary forests and their component species established after the deforestation of evergreen broadleaved forests differ between regions of Kyushu (Itow, 1971). *Quercus myrsinifolia* remaining characteristically in the Kanto plain as groves surrounding shrines, temples, and residences is thought to

be the main element of the potential natural vegetation of this plain (Miyawaki, 1986). *Quercus gilva* mainly distributed in Kyushu since the early post-glacial appeared in the Kinki district since the middle Jomon period (Noshiro et al., 2014). Unfortunately, pollen data are not sufficient to discuss the distribution or habit of species composing evergreen *Quercus* type.

Castanea/Castanopsis/Lithocarpus type

Castanea/Castanopsis/Lithocarpus type includes cool temperate *Castanea* type that cannot be distinguished easily from warm temperate elements of *Castanopsis/Lithocarpus* type. Changes in the distribution of *Castanea/Castanopsis/Lithocarpus* type is similar to those of evergreen *Quercus* type, but *Castanea/Castanopsis/Lithocarpus* type occurs significantly in Kyushu, Kanto, and northernmost Honshu (App. Fig. 18). Concentrations of abundant occurrences of this type in the Kanto district and northernmost Honshu derive from archaeological sites with *Castanea* fruits and woods, but neighboring sites did not show apparent occurrences of this type as in *Aesculus* type. In the Kanto district, evergreen *Quercus* type frequently accompanied *Castanea/Castanopsis/Lithocarpus* type which derived not only from *Castanea crenata*, but also from evergreen *Castanopsis/Lithocarpus* species.

Matsushita (1987, 1992) suggested that *Castanopsis* forests expanded first in the Pacific regions among evergreen broadleaved forests promoted by the northward shift of the warm Japan Current (Kuroshio). Abundant occurrences of *Castanea/Castanopsis/Lithocarpus* type in several coastal areas in the Pacific side support her scheme and probably resulted in the present coastal forests of *Castanopsis sieboldii* and *Machilus thunbergii*. Since period 7 ka, *Castanea/Castanopsis/Lithocarpus* type occurred more abundantly in Kyushu and in the Pacific coastal areas of central and western Japan.

Podocarpus type

The distribution pattern of *Podocarpus* type is the same as the physiognomical pollen class EC-POD, because EC-POD class consists only of *Podocarpus* type (Fig. 9 right, App. Fig. 7). *Podocarpus* type rarely occurred during the glacial period at less than 3.2% of sites. In the post-glacial, this type still rarely occurred, but in coastal areas eastward to the Kanto district in the Pacific side and to Lake Kahoku-gata in the Japan Sea side. *Podocarpus* type began to occur frequently during the hypsithermal (period 7 ka) in Shikoku and Kyushu. Particularly in Fukue Islands of eastern Kyushu, ca. 50% of arboreal pollen is *Podocarpus* type, representing the most abundant occurrence of this type

since the mid-glacial. Abundant occurrence of *Podocarpus* type is also reported in southwestern Shikoku, but this is not included in the analysis, because of problems in the identification of *Quercus* and obscure age setting (Nakamura & Katto, 1953b). This type widely occurred in Kyushu afterward and profusely at Izumo and Osaka during period 2.5 ka. Onishi et al. (1990) showed characteristic occurrences of *Podocarpus* type around period 2.5 ka in the Izumo area of western Honshu. Watanabe & Ishiga (2008) considered that this increase in *Podocarpus* type reflected an increase in precipitation by comparing the pollen spectra of this area with those of adjacent areas. Environmental factors common to Izumo and Osaka are important, because these areas were habitats of pollen assemblage groups of minor temperate deciduous taxa.

Warm temperate elements seemed to have expanded from coastal areas. During the last glacial, the coastal areas were wider than today, because the sea level was lowered up to ca. 120 m during the last glacial maximum (Yokoyama et al., 2000; Yonekura et al., 2001), and these areas could have provided habitats for warm temperate elements.

Interestingly, not only warm temperate elements, but also temperate pollen types of *Cryptomeria*, *Aesculus*, *Ulmus/Zelkova*, and *Fraxinus* dominated in coastal plains as in Aomori, Sendai, Kanto, Osaka, and Izumo. Besides them, *Alnus* that was excluded from the statistical treatment often occurred abundantly with them. These pollen types include trees preferring sunny wet habitats. Around the coastal plains exist suitable places for these trees, such as flood plains, back marshes, alluvial fans, and river terraces, which are also suitable for human settlement. The dominant pollen types in these habitats changed with frequent disturbances by riverine activities and also human activities. Pollen assemblages in these areas must have changed sometimes too rapidly to be detected with the resolution of time frames used in this study.

2. Grouping of pollen assemblages and their changes

Changes in pollen physiognomical classes showed an outline of vegetation changes, and that in pollen types clarified distribution of component species. Now, by studying components of pollen assemblages, change in component species in plant communities and the history of association can be clarified. Pollen assemblages definitely have a close correlation with vegetation, in spite of such problems as taphonomy and species level identification of fossil pollen.

Many studies tried to clarify the relationship between

pollen assemblages and vegetation. One example is the R-value model (Davis, 1963), in which one taxon's R-value is defined as the ratio between pollen percentages and vegetation percentages. In Japan Tsukada (1958) studied the relationship between surface pollen and vegetation at Shiga-kogen in central Japan. Birks & Gordon (1985) introduced several methods that apply the pollen-vegetation relationship to the reconstruction of past vegetation. These studies confirmed empirical knowledge about pollen representation, i.e., over representation of *Pinus*, *Betula*, and *Cryptomeria* types, and under representation of *Larix* type and entomophilous *Aesculus*, *Acer*, and *Tilia* types among the 25 pollen types. However, these methods are not applied to the collected data here, because of variable sedimentary environment between localities, insufficient surface pollen data, and occurrence of vegetation types not seen in modern vegetation.

Pollen assemblages tend to have more types indicating warmer environments. Pollen assemblages of cold environments consist mainly of pinaceous pollen types and tend to include less pollen types than those of warm environments. Many rare pollen types derived from warm environments included species dominant in modern warm temperate forests in Japan. Lauraceous species of *Cinnamomum camphora* and *Machilus thunbergii* often dominate in modern forests, but are seldom preserved as fossil pollen, because pollen of Lauraceous species contains little sporopollenin in their exines (Traverse, 1988). *Symplocos*, *Helicia*, and *Trochodendron* types occurred significantly at several points, but *Melia*, *Eurya*, and *Camellia* types occurred rarely. *Ilex* type occurred in warm areas, but also often abundantly in moors of cooler environments, deriving from species growing in such moors. These facts complicate the reconstruction of vegetation from pollen assemblages of warm environments.

In the studied pollen assemblages, all the pollen types occurring more than 90% of the most frequent pollen type were regarded as dominant pollen types. About 90% of pollen assemblages were dominated by a single pollen type. Pollen types that often showed single dominance were restricted to the studied 25 pollen types. Coniferous *Picea*, *Abies*, *Tsuga*, *Pinus*, and *Cryptomeria* types, and broadleaved tree pollen types of *Betula*, *Fagus*, deciduous and evergreen *Quercus*, and *Castanea/Castanopsis/Lithocarpus* types showed single dominance in more than 50 assemblages. Dominance of single pollen types in pollen assemblages tends to result in negligence of accompanying pollen types. However, in the case of pollen assemblage groups PNC, ATW, TMP, CLW, and CAS, for example, their contri-

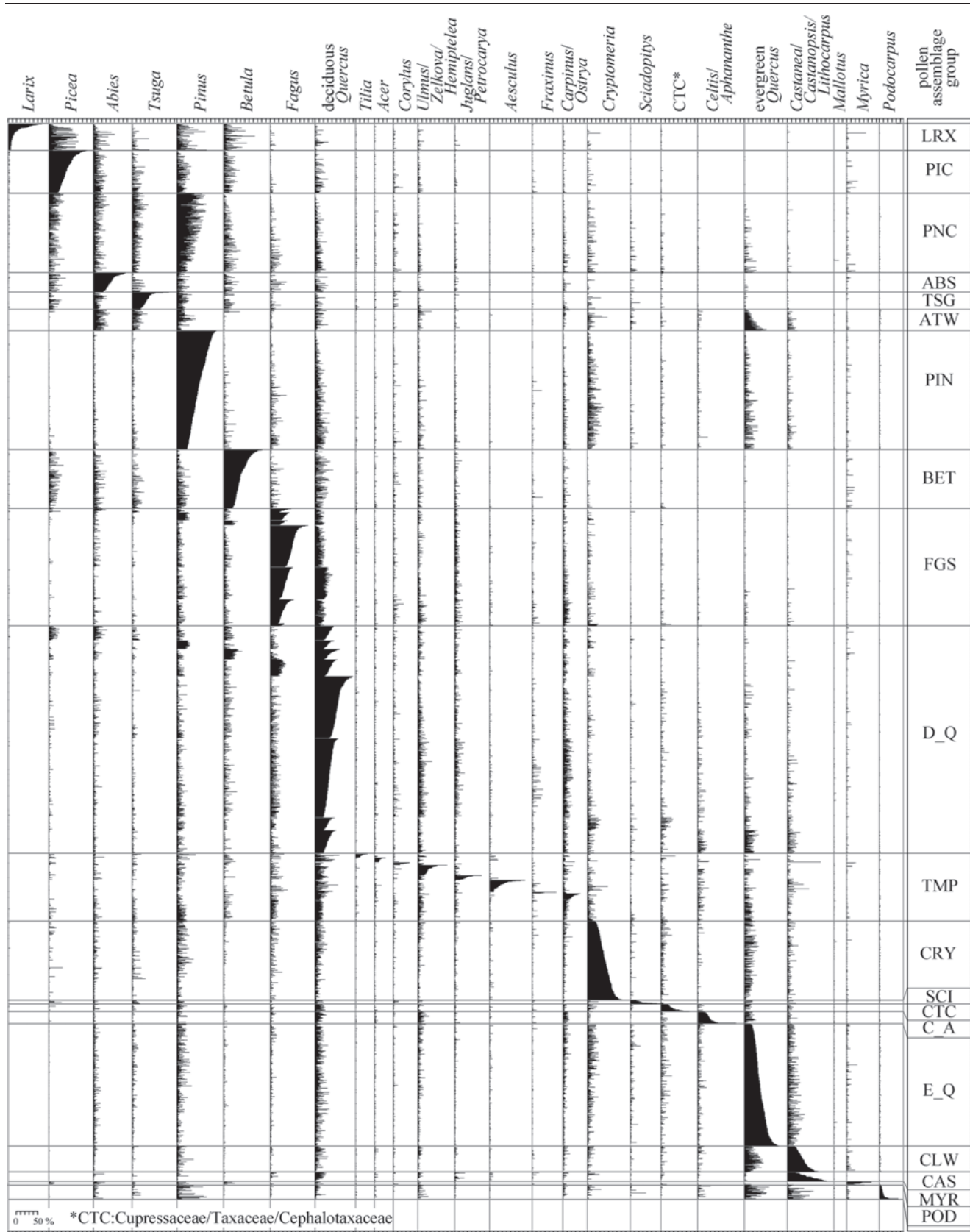


Fig. 26 Occurrences of 25 pollen types in the whole pollen assemblage groups with those indicating colder climate to the top.
図 26 花粉群グループの花粉組成. より寒冷な気候を示唆するグループを上位に示す.

bution is recognized based on the richness of environmental elements, on multiple dominant pollen types, or on characteristic combinations of pollen types.

Pollen assemblages from all the periods were classified into 20 pollen assemblage groups with empirical consideration for pollen productivity and dispersibility and affinities to forest associations and climates (Fig. 26, App. Tables 3, 4). Pollen assemblage groups and pollen assemblages are basically arranged from colder to warmer environments (Fig. 26, Table 4).

The following five pollen assemblage groups indicate Pinaceae rich forests under the cold climate, and assemblages are arranged with the dominance of characteristic pollen type.

LRX: *Larix* type occurs more than 5%. This group has priorities to other groups. Occurrence of *Larix* pollen is important, because *Larix* pollen occurs less than the percentage in vegetation due to its productivity and dispersibility (Erdtman, 1969; Igarashi et al., 2003), in spite of its occasional long distance dispersal (Morita, 2004). This group represents *Larix* forests.

PIC: *Picea* type occurs most abundantly and exceeds 20% with the second abundant pollen type less than 90% of *Picea* type. This type indicates *Picea* rich forests.

PNC: The sum of pinaceous pollen exceeds 50%, and pinaceous pollen excluding *Pinus* occupies more than 10%, except pollen assemblage groups LRX, PIC, ABS, TSG, and ATW. This group is rich in Pinaceae, but no single pollen type dominates. *Pinus* in this group often includes *Haploxylon* type. This group indicates forests consisting of several pinaceous species growing in a cold environment.

ABS: *Abies* type occurs most abundantly and exceeds 20% with the second abundant pollen type less than 90% of *Abies* type. This group indicates *Abies* rich forests.

TSG: *Tsuga* type occurs most abundantly and exceeds 20% with the second abundant pollen type less than 90% of *Tsuga* type. This group indicates *Tsuga* dominant forests.

Although rich in pinaceous pollen, the following two pollen assemblage groups represent vegetation of the temperate zone. Assemblages are arranged in the ascending order of the occurrence of warm elements in ATW and with the richness of *Pinus* type in PIN.

ATW: The sum of *Abies* and *Tsuga* types exceeds 20%, and that of warm elements (EB-WDE and EC-POD classes except *Myrica* type) exceeds 10%. This group has priorities to ABS and TSG groups. This as-

semblage group indicates forests consisting of *Abies firma* and/or *Tsuga thunbergii* and evergreen broad-leaved trees.

PIN: *Pinus* type occurs most abundantly and exceeds 25% with the second abundant pollen type less than 90% of *Pinus* type, excluding LRX and PNC groups. This group indicates *Pinus* dominant forests, frequently shown as secondary forests.

BET group represent deciduous broadleaved forests in cold areas. Assemblages of BET are arranged with the abundance of *Betula* type.

BET: *Betula* type occurs most abundantly and exceeds 20% with the second abundant pollen type less than 90% of *Betula* type. This group indicates *Betula* forests.

The following three pollen assemblage groups, FGS, D_Q, and TMP, represent temperate deciduous broad-leaved forests and included many assemblages.

FGS: *Fagus* type occurs most abundantly and exceeds 20% with the second abundant pollen type less than 90% of *Fagus* type. This pollen assemblage group indicates *Fagus* forests.

D_Q: Deciduous *Quercus* type occurs most abundantly and exceeds 20% with the second abundant pollen type less than 90% of deciduous *Quercus* type. This group indicates deciduous *Quercus* forests.

FGS and D_Q groups were divided into eight subgroups by the dominance of accompanying pollen types, considering their ecology.

pnc: Pinaceous pollen types except *Pinus* type dominate.

pin: *Pinus* type dominates.

bet: *Betula* and *Myrica* types (DB-BET class) dominate.

fgs: *Fagus* type occurs more than twice as much as other subgroups in FGS group or *Fagus* type dominates in D_Q group.

d_q: Deciduous *Quercus* type dominates in FGS group or deciduous *Quercus* exceeds 50% in D_Q group.

dbt: Temperate deciduous broadleaved tree types (DB-TDB) excluding *Fagus* type and deciduous *Quercus* type dominate.

csc: Pollen types of EC-CSC class dominate.

wrm: Pollen types of EB-WDE and EC-POD classes dominate.

These subgroups differ with trees mixed in each forests, e.g., FGS-fgs is pure *Fagus* forest, FGS-d_q is *Fagus* dominant forests mixed with deciduous *Quercus*. Pollen assemblages are arranged with the richness of

Table 4 Numbers and percentages (in brackets) of pollen assemblage groups obtained for each period**表 4** 各時期における花粉群グループの数と割合

Pollen assemblage group	Period										Total
	0.8 ka	2.5 ka	5 ka	7 ka	9 ka	12 ka	14 ka	20 ka	40 ka		
LRX	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	3 (1.3)	25 (13.2)	9 (8.3)	44 (15.2)	13 (6.8)	94 (2.5)	
PIC	17 (1.6)	5 (0.6)	6 (1.1)	11 (3.4)	7 (3.0)	8 (4.2)	13 (11.9)	56 (19.3)	29 (15.3)	152 (4.0)	
PNC	74 (7.1)	6 (0.7)	5 (0.9)	4 (1.3)	7 (3.0)	30 (15.8)	18 (16.5)	97 (33.8)	41 (21.6)	282 (7.5)	
ABS	13 (1.2)	9 (1.1)	5 (0.9)	4 (1.3)	3 (1.3)	9 (4.7)	7 (6.4)	15 (5.2)	3 (1.6)	68 (1.8)	
TSG	9 (0.9)	3 (0.4)	1 (0.2)	0 (0.0)	2 (0.9)	8 (4.2)	5 (4.6)	23 (7.9)	9 (4.7)	60 (1.6)	
ATW	20 (1.9)	31 (3.6)	10 (1.8)	5 (1.6)	4 (1.7)	0 (0.0)	0 (0.0)	2 (0.7)	2 (1.1)	74 (2.0)	
PIN	371 (35.5)	19 (2.2)	10 (1.8)	5 (1.6)	3 (1.3)	5 (2.6)	2 (1.8)	3 (1.0)	6 (3.2)	424 (11.2)	
BET	35 (3.3)	16 (1.9)	11 (2.0)	13 (4.1)	31 (13.5)	42 (22.1)	26 (23.9)	27 (9.3)	8 (4.2)	209 (5.5)	
FGS	136 (13.0)	119 (13.9)	82 (14.6)	38 (11.9)	21 (9.1)	10 (5.3)	4 (3.7)	0 (0.0)	4 (2.1)	414 (10.9)	
D_Q	105 (10.0)	210 (24.5)	189 (33.7)	107 (33.4)	96 (41.7)	45 (23.7)	18 (16.5)	8 (2.8)	28 (14.7)	806 (21.3)	
TMP	31 (3.0)	64 (7.4)	46 (8.2)	42 (13.1)	15 (7.0)	6 (3.2)	5 (4.6)	7 (2.4)	15 (7.9)	231 (6.1)	
CRY	106 (10.1)	90 (10.5)	30 (5.3)	17 (5.3)	8 (3.5)	2 (1.1)	1 (0.9)	4 (1.4)	24 (12.6)	282 (7.4)	
SCI	2 (0.2)	5 (0.6)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	5 (2.6)	12 (0.3)	
CTC	7 (0.7)	9 (1.2)	3 (0.5)	3 (0.9)	1 (0.4)	0 (0.0)	0 (0.0)	0 (0.0)	2 (1.1)	25 (0.7)	
C_A	2 (0.2)	3 (0.4)	9 (1.6)	12 (3.8)	15 (6.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	41 (1.1)	
E_Q	94 (9.0)	206 (24.1)	102 (18.2)	29 (9.1)	5 (2.2)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	436 (11.5)	
CLW	11 (1.1)	33 (3.9)	29 (5.2)	13 (4.1)	5 (1.7)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	91 (2.4)	
CAS	4 (0.4)	6 (0.7)	14 (2.5)	5 (1.6)	2 (0.9)	0 (0.0)	1 (0.9)	0 (0.0)	0 (0.0)	32 (0.8)	
MYR	2 (0.2)	2 (0.2)	0 (0.0)	1 (0.3)	0 (0.0)	0 (0.0)	0 (0.0)	4 (1.4)	1 (0.5)	10 (0.2)	
POD	6 (0.6)	20 (2.3)	9 (1.6)	11 (3.4)	2 (0.9)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	48 (1.3)	
Total	1045	856	561	320	230	190	109	290	190	3791	

Fagus pollen and deciduous *Quercus* pollen after subgroups were arranged in the above order.

TMP: Pollen types of temperate deciduous broad-leaved trees (DB-TDB class) excepting *Fagus* and deciduous *Quercus* occur dominantly, but the number of assemblages for each pollen type is too small to be treated as independent groups. TMP group is a complex of assemblages rich in deciduous broadleaved tree pollen other than FGS and D_Q groups and represents temperate deciduous broadleaved forests not dominated by *Fagus* or deciduous *Quercus*. This group was divided into the following nine subgroups based on the dominance of hermophilous pollen types or over 10% occurrence of entomophilous pollen types. If assemblages fit to both criteria, the subgroup of entomophilous pollen types have priorities.

til: *Tilia* type occurs more than 10%.

acr: *Acer* type occurs more than 10%.

cor: *Corylus* type dominates.

uzh: *Ulmus/Zelkova/Hemiptelea* type dominates.

j_p: *Juglans/Pterocarya* type dominates.

aes: *Aesculus* type occurs more than 10%.

frx: *Fraxinus* type dominates.

c_o: *Carpinus/Ostrya* type dominates.

dbt: Temperate deciduous tree pollen occurs most frequently.

TMP groups are arranged in the order of the above subgroups, and assemblages are arranged with the richness of the characteristic pollen types for the subgroups.

The following three pollen assemblage groups, CTC, CRY, and SCI, mainly represent temperate coniferous forests of Cupressales. TCC and SCI are not common. Pollen assemblages are arranged in the ascending order of the occurrences of characteristic pollen types.

CTC: CTC type dominates. This group indicates coniferous forests of Cupressaceae/Taxaceae/Cephalotaxaceae.

CRY: *Cryptomeria* type occurs most frequently and exceeds 20% with the second abundant pollen type less than 90% of *Cryptomeria* type. This group represents *Cryptomeria japonica* forests.

SCI: *Sciadopitys* type dominates. This group indicates *Sciadopitys verticillata* forests.

The remaining six pollen assemblage groups represent warm temperate forests except for CAS representing temperate *Castanea* forests and most MYR representing subgroup bog of *Myrica gale* growing in cold peaty bogs. Assemblages are arranged in the ascending order of the occurrences of characteristic pollen types.

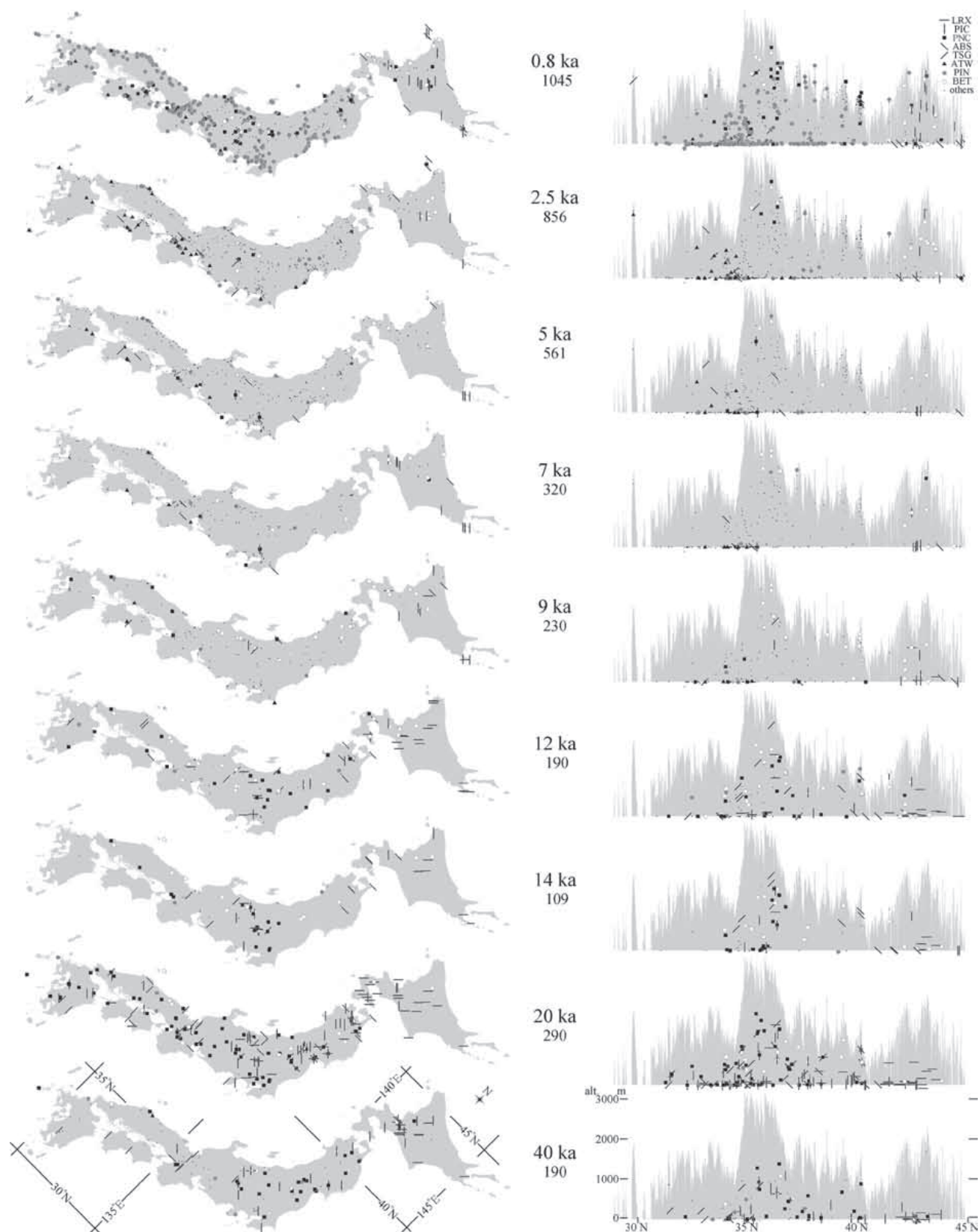


Fig. 27 Chronological distribution of pollen assemblage groups LRX, PIC, ABS, TSG, ABW, PNC, PIN, and BET on horizontal maps and vertical profiles of Japan. Number of sites for each period are shown below periods.

図 27 寒冷な気候を示唆する花粉群グループ (LRX, PIC, ABS, TSG, ABW, PNC, PIN, BET) の水平・垂直分布の変遷.

C_A: *Celtis/Aphananthe* type dominates. This group represent *Celtis/Aphananthe* forests.

E_Q: Evergreen *Quercus* type occurs most abundantly and exceeds 20% with the second abundant pollen type less than 90% of evergreen *Quercus* type. This group represents warm temperate evergreen *Quercus* forests.

CLW: *Castanea/Castanopsis/Lithocarpus* type dominates, excluding the following CAS group. This group represents *Castanopsis/Lithocarpus* forests of the warm temperate zone.

CAS: When *Castanea/Castanopsis/Lithocarpus* type occupies more than 90% of warm elements (*Celtis/Aphananthe*, evergreen *Quercus*, *Castanea/Castanopsis/Lithocarpus*, *Mallotus*, and *Podocarpus* types), it is classified as CAS group separate from CLW group. This pollen assemblage group roughly indicates dominance of *Castanea*, i.e., *Castanea* forests regarded as one of the characteristic forests of the intermediate-temperate zone. Pollen assemblages in this group frequently occur at archaeological sites with remains of *Castanea* fruits and woods, where *Castanea* pollen is often distinguished in *Castanea/Castanopsis/Lithocarpus* type. However, statistical separation of *Castanea* forests and *Castanopsis/Lithocarpus* forests is difficult, because *Castanea* and *Castanopsis* can coexist and because common occurrences of both *Castanea* and *Castanopsis/Lithocarpus* are reported in several pollen assemblages in spite of difficulty in distinguishing these pollen grains.

MYR: *Myrica* type occurs most abundantly. This group is not common and indicates contrasting environments, *Myrica gale* in cold peat bogs or *M. rubra* in warm climate. This group is divided into subgroups bog and wrm with 5% occurrence of EB-WDE class excepting *Myrica*. Subgroups bog and wrm are respectively arranged in the descending or ascending order of *Myrica* type occurrence.

POD: *Podocarpus* type occurs more than 5%. Because differences in warm temperate forests can be distinguished with *Podocarpus* type, this group is recognized in spite of its low pollen occurrences. This group represents warm temperate forests with a southern conifer of *Podocarpus*.

Several pollen assemblages, i.e., ca. 7% of the total assemblages, could not be categorized into any pollen assemblage groups and are classified by the most abundant physiognomical class into corresponding groups. Thus, when assemblages abounded with physiognomical class DC-LRX, EC-PNC, DB-BET, EC-PIN, or EC-POD, they were allotted to LRX, PNC, BET, PIN, or

POD group, respectively. When assemblages abounded with physiognomical class DB-TDB, they were allotted to subgroup dbt of TMP group. When assemblages abounded with physiognomical class EC-CSC or EB-WDE, they were classified with the most dominant pollen type in either class. Thus, when *Cryptomeria* occurred most abundantly in assemblages dominated by physiognomical class EC-CSC, the assemblages were classified into CRY group.

Horizontal and vertical distributions of pollen assemblage groups during each period indicate that vegetation changed with global climatic changes (App. Figs. 27–30, Figs. 44–52). Nevertheless, pollen assemblage groups did not simply shift northward or southward, but tended to expand or contract in each area.

Pinaceous group (LRX, PIC, PNC, TSG, ABS, ATW, PIN)

Assemblage groups rich in Pinaceae occurred most extensively during the full-glacial except ATW and PIN groups (Fig. 27, Table 4). ATW group that indicates intermediate-temperate forests occurred most in the post-glacial, and PIN group dominated by *Pinus* occurred most in the recent (period 0.8 ka).

During the mid-glacial (period 40 ka), Pinaceae rich assemblages occurred sparsely, compared with the even distribution during the full-glacial (period 20 ka), particularly in western Japan. During the mid-glacial ATW group occurred rarely, only at two sites, LRX and PIC groups commonly in Hokkaido, PIC and PNC groups commonly in northern Honshu, and TSG and ATW groups sparsely in western Japan. This regional difference in coniferous forests was succeeded to the pinaceous groups in the full-glacial, which occupied 82.8% (240/290) of the whole pollen sites. During the full-glacial (period 20 ka), LRX group dominated in Hokkaido, PIC group in northeastern Honshu occasionally with ABS group in the northernmost Pacific side, and PNC and TSG groups in the Kinki district. During periods 14 ka and 12 ka of the late-glacial, occurrence of pinaceous groups decreased to 50% (54/109) and 45% (85/190) of the whole pollen sites, respectively. LRX group still dominated in Hokkaido, ABS group in northern Honshu, and LRX, PNC, and TSG groups on the mountainous areas of central Japan. During the post-glacial, pinaceous groups became infrequent except for ATW and PIN groups. LRX group disappeared in the post-glacial, whose last occurrence was at three sites during period 9 ka (Table 4), and PIC group occurred only in Hokkaido during periods 2.5 ka and 0.8 ka. Contrarily, ATW group increased since period 5 ka and showed the peak occurrence during period 2.5

ka in western Japan. PIN group occurred abundantly (371/1045) in period 0.8 ka except in Hokkaido. PNC group also occurred commonly (74/1045) in the mountainous areas of central Japan and in the lowland of western Japan with PIN group.

LRX group in Hokkaido during the glacial period reflected *Larix gmelinii* forests. *Larix* type is under-represented in pollen analyses. Igarashi et al. (2003) compared the surface pollen assemblages of various vegetation types in Siberia and suggested that *Larix* pollen was less represented in the forest tundra and taiga compared with the distribution and stand density of *Larix* trees, affected largely by derived pollen of *Pinus*. Occurrences of *Larix* type, however, sometimes attained more than 50% in LRX group of Hokkaido. In Hokkaido macrofossils of *L. gmelinii* were often accompanied by cones of *Picea glehnii* and seeds of *Mennyanthus trifoliata* that are common in wetland forests of southern Sakhalin (Yano, 1970).

Pollen types composing LRX group can clarify the history of *Larix* forests (Fig. 28). During the mid-glacial (period 40 ka), LRX group occurred mostly (12/13) in Hokkaido with abundant *Picea* or *Abies* pollen. Deciduous broadleaved tree pollen occurred more with *Abies* dominant assemblages. In Honshu, the only one LRX group existed at Lake Nojiri of central Japan accompanied by *Cryptomeria* and *Fagus* types (Mori, 1963; Niigata Pollen Group, 1973). This assemblage at Lake Nojiri must have derived from *Larix kaempferi* forests, because cone and twig fossils were obtained from adjacent sites (Fossil Plant Research Group for Nojiri-ko Excavation, 1984, 2003; reported as *Larix leptolepis* synonymous to *L. kaempferi*). During the full-glacial (period 20 ka), LRX group occurred most prevalently, not only in Hokkaido (25 sites), but in other parts of Japan (19 sites). In Hokkaido, LRX group occurred at over 80% of pollen sites (25/31), with *Larix* pollen dominating at 10 sites and *Pinus* or *Picea* dominating at other sites except for southern Hokkaido where *Abies* dominated. At most pollen sites, a small amount of deciduous broadleaved tree pollen and *Tsuga* were recorded. Thus, during the full-glacial, *Larix* forests covered wide areas of Hokkaido with restricted occurrences of deciduous broadleaved trees and *Tsuga*. In northern Honshu (i.e., the Tohoku district), LRX group occurred only during the full-glacial (period 20 ka), with *Larix* pollen less than 10% accompanied by *Pinus*, *Abies*, and *Picea* types. Judging from records of *Larix gmelinii* macrofossils (Suzuki & Takeuti, 1989; Sohma, 1959), *Larix gmelinii* forests must have existed also in northern Honshu. LRX group in central Honshu (i.e., Kanto and Chubu dis-

tricts) indicated expansion of *Larix kaempferi* forests under the cold dry environment of the full-glacial. The southernmost records of LRX group obtained at Sugeta (Takahashi, 1974) and Oono (Nakamura & Katto, 1953a) in Shikoku probably derive from *Pseudotsuga japonica*. In Hokkaido, LRX group decreased in period 14 ka, increased again in period 12 ka, reduced to three sites in period 9 ka, and disappeared afterward. During period 12 ka, LRX group occurred at 50% of pollen sites (17/33) with *Larix* type dominating at four sites and *Picea* and *Betula* dominating at other sites. Deciduous broadleaved tree types often occurred at sites where *Larix* type dominated. Igarashi et al. (2002) illustrated the history of *Larix* forests in Hokkaido and Sakhalin by 21 pollen spectra, comparing with the surface pollen, and concluded that the climate during the Younger Dryas (period 12 ka) may have been colder and drier than that in the last glacial maximum. Okitsu (1999), however, suggested that expansion of *Larix gmelinii* at period 20 ka was promoted by the dry condition during this period and that expansion at period 12 ka was promoted by a significant increase of disturbance events. Pollen assemblages of these periods seem to support the latter idea in that *Pinus* type probably contributed by *Pinus pumila* occurred more in period 20 ka, whereas deciduous *Quercus* and *Betula* types occurred more during period 12 ka. In Honshu, LRX group disappeared in period 9 ka, but *Larix kaempferi* continues to grow in central Honshu, whereas *Larix gmelinii* disappeared from Japan.

ATW group occurred widely in western Japan in the post-glacial, probably contributed by intermediate-temperate forests of *Abies firma* and *Tsuga sieboldii*, an ecotone between warm temperate and cool temperate forests. ATW group occurred in two assemblages from different analyses at the same site in the mid-glacial (period 40 ka) in the Japan Sea side of the western Japan and two assemblages from Tohoku and Kyushu in the full-glacial (period 20 ka) (Figs. 27, 29). The assemblage of Tohoku accompanied *Betula* and *Castanea/Castanopsis/Lithocarpus* types and differ greatly from other ATW group. ATW group occurred again in the post-glacial and increased to period 2.5 ka, when it occurred most frequently (31/856) and widely from Futaba moor in the Pacific side of Fukushima in the north to the lowland besides hills lower than 800 m in western Japan (Fig. 27). Clusters of this group during period 2.5 ka are clearly recognized in central to eastern Kyushu, Shikoku, and central to eastern Kinki. ATW group is characterized by the coexistence of pinaceous *Abies*, *Tsuga*, and evergreen *Quercus*, besides various temperate deciduous broadleaved trees and

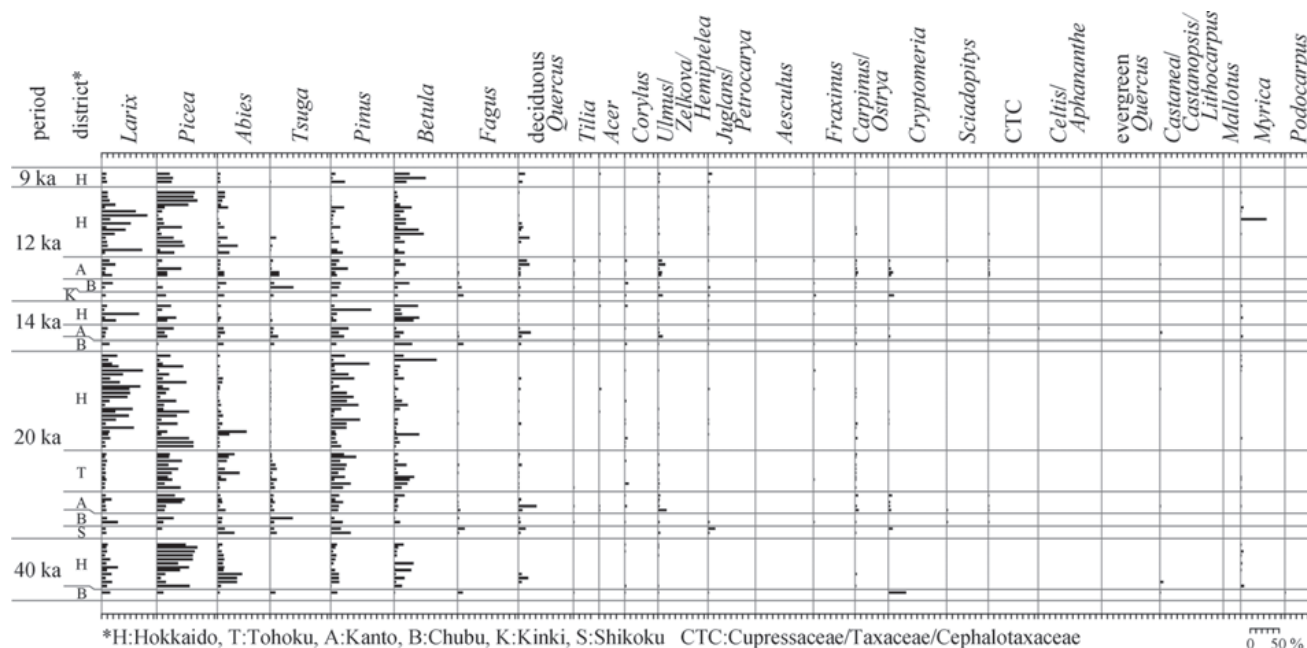


Fig. 28 Pollen diagram of LRX group during each period from north to south in each district.

図 28 花粉群グループ LRX の花粉組成。時期ごとに地方別の北から南の順に示す。

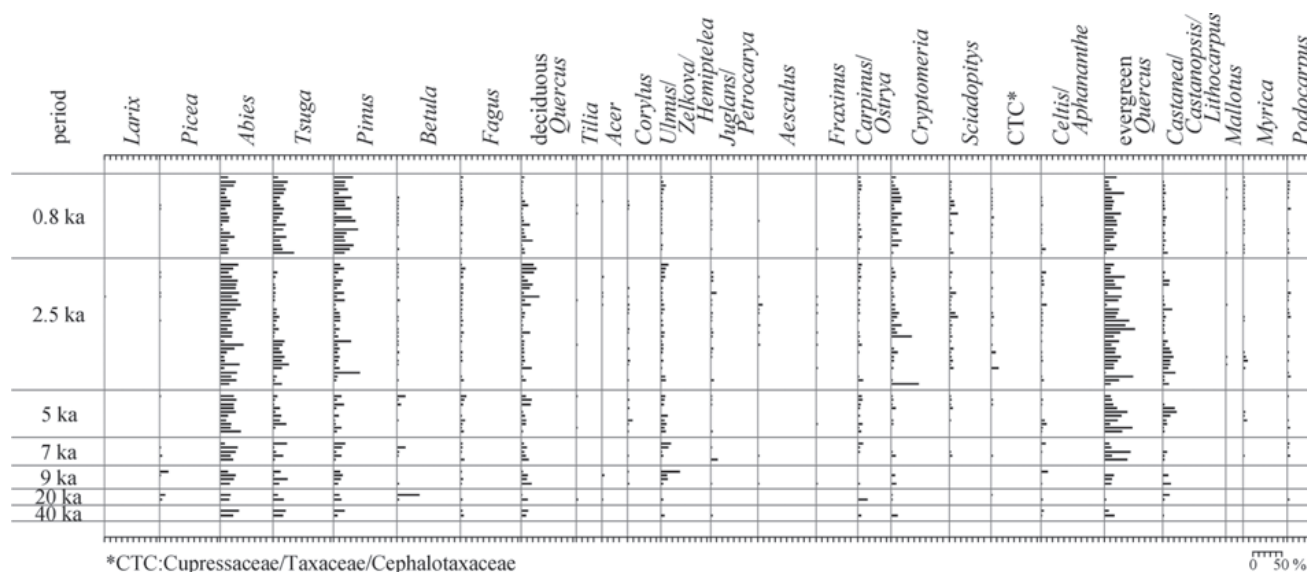


Fig. 29 Pollen diagram of ATW group during each period from north to south.

図 29 花粉群グループ ATW の花粉組成。時期ごとに北から南の順に示す。

conifers and warm elements, and partially resembles subgroup dbt of TMP group (Fig. 33).

PNC group occurred frequently during the last glacial, particularly in the full-glacial (98/290), contributed by *Pinus* subgen. *Haploxylon* with other pinaceous conifers. In the post-glacial PNC group increased to the recent, contributed by coniferous forests without single dominant taxa. On the other hand, PNC group

in the lowland of western Japan during period 0.8 ka was a mixture of ATW and PIN groups. Abundant PIN group in period 0.8 ka except in Hokkaido was contributed by *Pinus densiflora* that increased with human activities.

Pollen assemblage groups that lead to modern mountainous conifer forests in Honshu appeared as PNC group since period 2.5 ka in central Japan and since

period 0.8 ka in northern Honshu. PNC group was distributed only at scattered places in Honshu during periods 9 ka to 5 ka. Thus, modern mountainous forests developed after the hypsithermal, partly contributed by the glacial vegetation.

Generally, the area of coniferous groups did not change, but expanded and contracted. Dominant forests during the full-glacial (period 20 ka) seem to have been *Larix gmelinii* forests in Hokkaido and *Picea glehnii* type forests in Honshu. These forests contracted in the early Holocene, and coniferous forests of Pinaceae excluding *Pinus* and differing from those in the full-glacial expanded since period 5 ka. *Abies* type significantly increased since period 5 ka, contributed by *Abies sachalinensis* and *Picea jezoensis* forests in Hokkaido, by various *Abies* forests in northern Honshu, and by *Abies firma* forests in western Japan. These forests resulted in present coniferous forests. The component species of these forests probably grow in the same areas as in the last glacial. The decline of *Larix* and *Picea* in the post-glacial seems to have been too drastic for their comeback in the next glacial.

BET group

BET group expanded most in the late-glacial, occurring at over 20% of pollen sites during periods 14 ka (26/109) and 12 ka (42/190) (Table 4). This widespread occurrence of BET group during the late-glacial probably reflected unstable environments.

In the mid-glacial BET group occurred sporadically only at several sites (8/190), accompanied by pinaceous types and deciduous broadleaved tree types (Fig. 27). During the full-glacial (period 20 ka), BET group occurred mainly in the lower mountainous areas of Honshu of ca. 500–1000 m in modern elevation with pinaceous groups. During the late-glacial BET group increased its dominance and expanded to the lowland in Hokkaido and to higher elevations in Honshu. In BET group in the lowland of Hokkaido, *Betula* type often dominated, attaining over 50%, probably contributed by dwarf *Betula* species. In Honshu, BET group was accompanied by pinaceous types and deciduous broadleaved tree types as during the mid-glacial (period 40 ka) and included more pinaceous types during cool period 12 ka than during period 14 ka. BET group began to decrease in the post-glacial. In Hokkaido it commonly occurred at less than 10% of pollen sites, with pinaceous groups except period 5 ka. Whereas in Honshu, it was gradually confined to higher mountains in the Japan Sea side without pinaceous groups (Fig. 27), adjacent to temperate broadleaved tree groups of FGS or D_Q (Figs. 46–50, App. Figs. 28, 29). BET group

continued to occur sporadically afterward in spite of the expansion or contraction of pinaceous groups and deciduous broadleaved tree groups.

The contents of BET group reflected changes in adjacent pollen assemblage groups (Fig. 30). BET group was accompanied by more pinaceous pollen during the glacial and also by more deciduous *Quercus* and *Ulmus/Zelkova/Hemiptelea* types during the post-glacial. In southern Hokkaido, *Fagus* accompanied BET group during period 0.8 ka. *Abies*, *Tsuga*, and *Fagus* accompanied BET group in the mountainous areas of Honshu since period 14 ka, reflecting changes in mountainous vegetation, but *Fagus* occurred least in period 12 ka, and *Abies* and *Tsuga* occurred least in the hypsithermal (period 7 ka). BET group became rare in northern Honshu after the hypsithermal (period 7 ka) and disappeared after the early post-glacial (period 9 ka) in western Japan.

Temperate broadleaved tree groups (FGS, D_Q, TMP)

FGS, D_Q, and TMP groups occurred at ca. 20% of pollen sites during period 40 ka (4 FGS, 28 D_Q, 15 TMP), least (5.2%, 15/291) during the full-glacial (period 20 ka), at ca. 30% of sites during the late-glacial (periods 14 ka and 12 ka), and at over 50% of sites during periods 9 ka to 5 ka (Fig. 31, Table 4). FGS occurred mainly in the mountainous areas of the Japan Sea side and continued to dominate there, resulting in the present *Fagus crenata* zone. Although D_Q group continuously occurred except during the full-glacial (period 20 ka) and covered wider areas and altitudes than FGS group, D_Q group occurred most extensively during the early post-glacial (period 9 ka), gradually decreased afterwards, and occurred less than FGS group in the recent (period 0.8 ka). In pollen assemblages *Fagus* pollen is relatively under represented than *Quercus* pollen (Uchiyama, 1998), but FGS and D_Q groups are treated equally in this study, because of the difficulty in precise statistic analysis of *Fagus* dominant forests. Percentages and contents of temperate deciduous broadleaved tree pollen for FGS, D_Q, and TMP groups indicated that *Fagus* type increased its dominance toward the recent (Fig. 32).

Abundant FGS and D_Q groups were subdivided into subgroups (Fig. 26). The numbers of subgroups in FGS and D_Q groups for each period show that D_Q group reflected more varied environments than FGS group, because deciduous *Quercus* includes more species than *Fagus* (Tables 5, 6). Subgroups fgs, d_q, and dbt of FGS group were accompanied by deciduous broadleaved tree type and accounted for more than 80% of FGS group. Subgroups csc (with *Cryptomeria*)

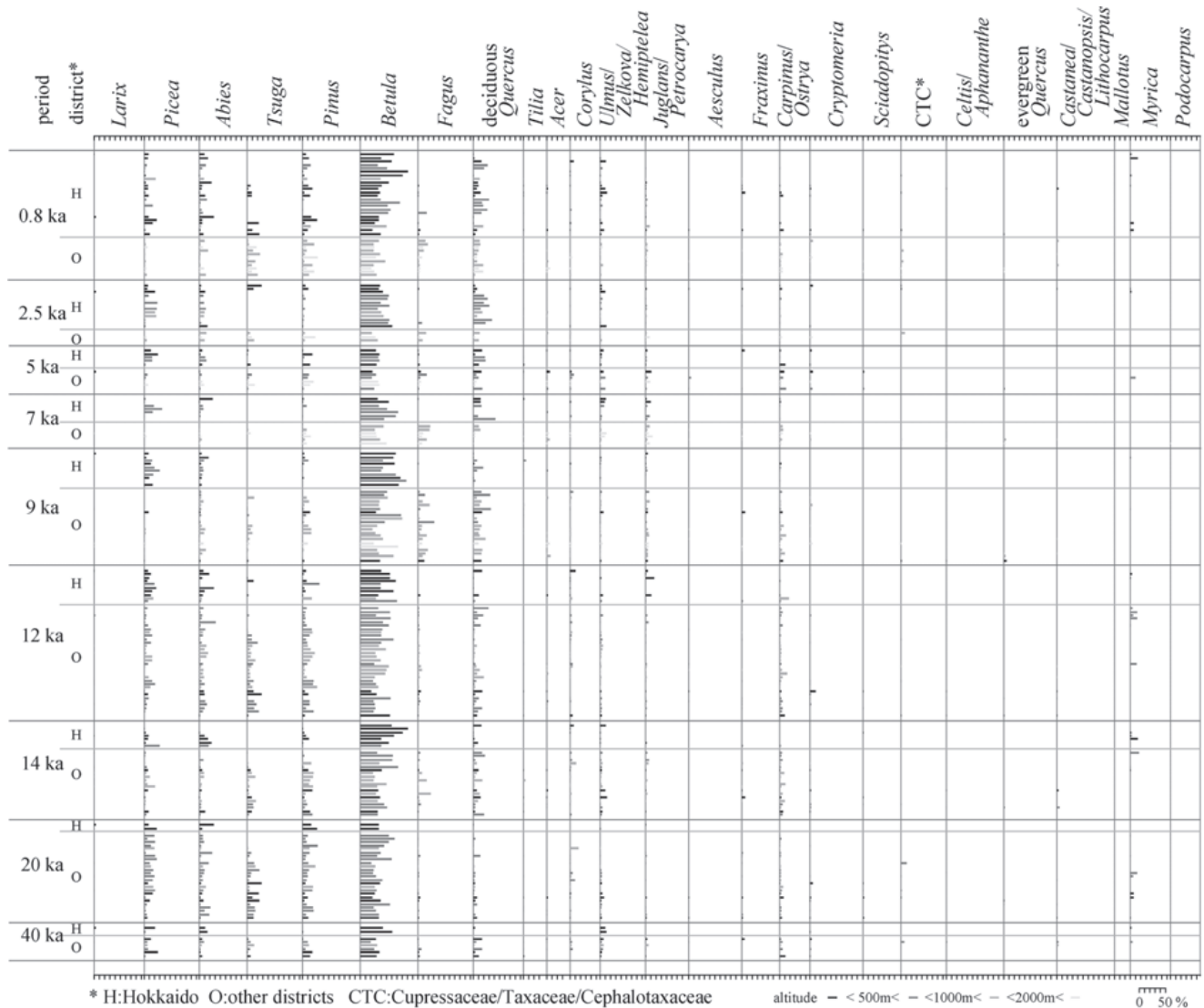


Fig. 30 Pollen diagram of BET group during each period from north to south in Hokkaido and other districts. Lighter colored bars indicate pollen sites at higher altitudes.

図30 花粉群グループBETの花粉組成。時期ごとに北海道と他地方で北から南の順に示し、高い標高のものをより明色で示す。

and pin (with *Pinus*) of FGS group mainly occurred in period 0.8 ka with intense human influences. Subgroup wrm (with warm temperate trees) of D_Q group was probably contributed by warm temperate *Quercus* such as *Q. variabilis* and *Q. acutissima* distributed in western Japan. Subgroups pnc (with pinaceous type) and bet (with *Betula*) of D_Q group mainly occurring in Hokkaido probably reflected *Q. crispula* and *Q. dentata* forests, judging from their modern vegetation.

TMP and CAS groups were not common and occurred only sporadically through the periods at various areas (Figs. 33, 34; Table 7). Pollen types of temperate deciduous broadleaved trees other than *Fagus* and de-

ciduous *Quercus* types occurred conspicuously among DB-TDB class (Fig. 32). Peak periods for the subgroups of TMP group and CAS group were period 7 ka for subgroup j_p, periods 7 ka and 5 ka for subgroup u_z, period 5 ka for subgroup aes, and period 5 ka for CAS group, respectively. Horizontally these groups and subgroups mainly occurred in coastal plains of Aomori, Sendai, Kanto, Osaka, and Izumo, where intensive palynological studies at archaeological sites have been carried out (Fig. 33). Among these groups and subgroups, aes group dominated by *Aesculus* pollen and CAS group dominated by *Castanea* pollen occurred mostly at archaeological sites. During the Jomon peri-

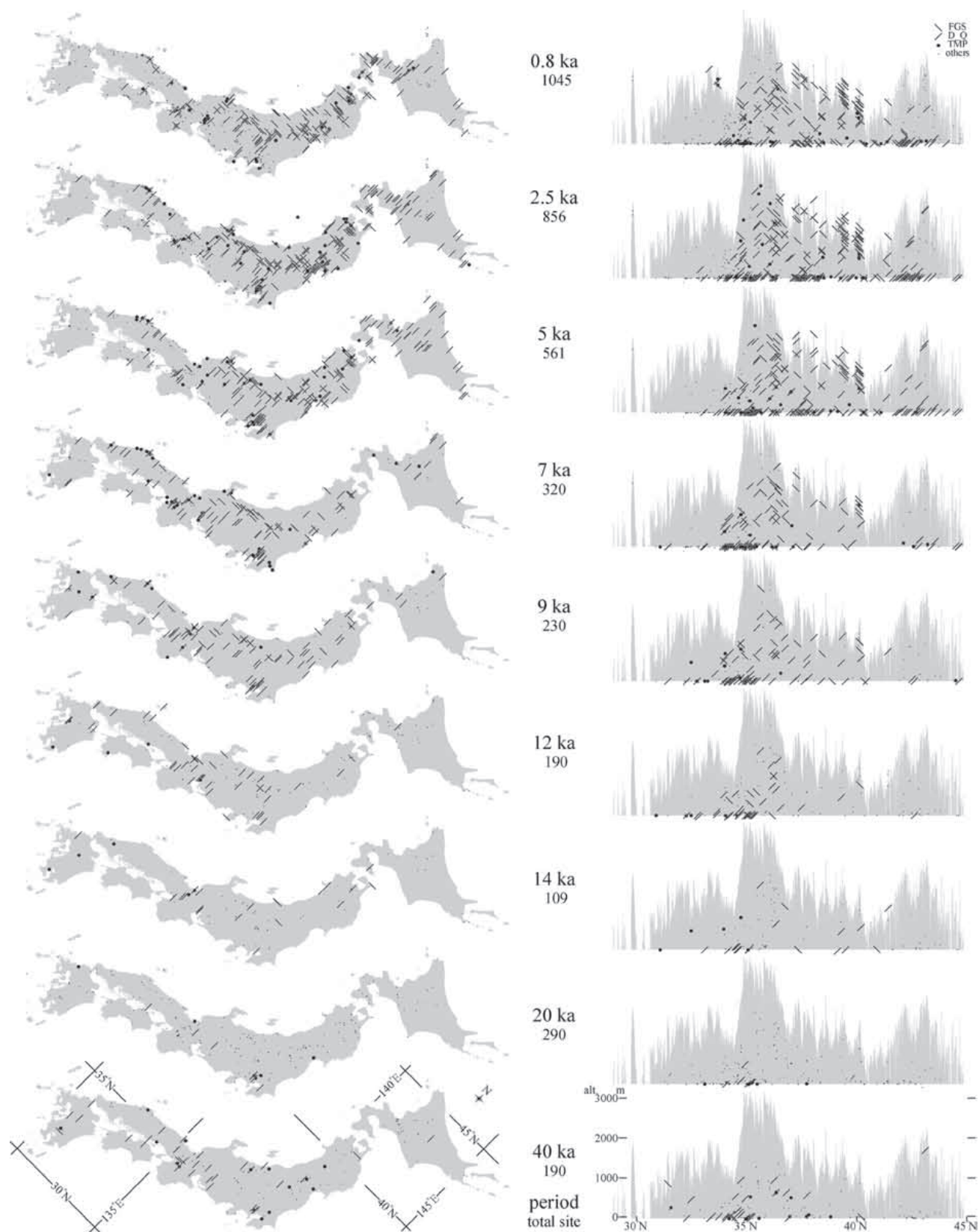


Fig. 31 Chronological distribution of pollen assemblage groups FGS, D_Q, and TMP on horizontal maps and vertical profiles of Japan. Number of sites for each period are shown below periods.

図 31 温帯性落葉広葉樹を主体とする花粉群グループ (FGS, D_Q, TMP) の水平・垂直 (南北断面) 分布の変遷.

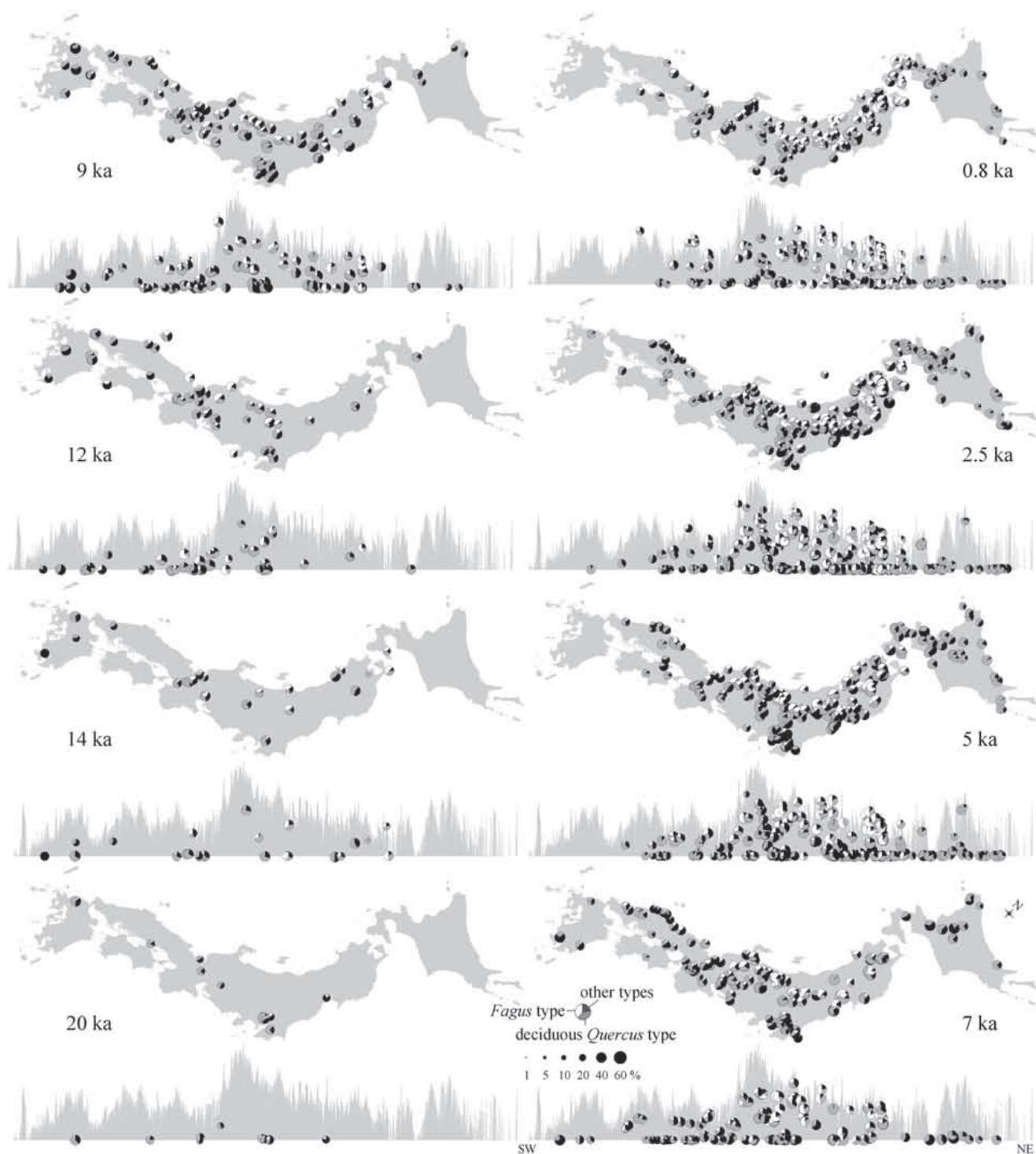


Fig. 32 Composition and occurrences of *Fagus*, deciduous *Quercus*, and other temperate deciduous broadleaved tree types for temperate deciduous broadleaved tree pollen assemblage groups (FGS, D_Q, TMP) since the full-glacial (periods 20 ka to 0.8 ka).

図 32 最終氷期最盛期以降（時期 20 ka ～ 0.8 ka）における花粉群グループ（FGS, D_Q, TMP）の温帯性落葉広葉樹の産出率とその花粉組成（ブナ属型，落葉コナラ属型，その他の温帯性落葉広葉樹）。

Table 5 Numbers and percentages (in brackets) of subgroups in pollen assemblage group FGS for each period

表 5 各時期における花粉群グループ FGS のサブグループの数と割合

Subgroup of FGS	Period									Total
	0.8 ka	2.5 ka	5 ka	7 ka	9 ka	12 ka	14 ka	20 ka	40 ka	
pnc	5 (3.7)	0 (0.0)	0 (0.0)	0 (0.0)	6 (28.6)	0 (0.0)	0 (0.0)	0 (0.0)	1 (25.0)	12 (2.9)
pin	19 (14.0)	5 (4.2)	2 (2.4)	1 (2.6)	0 (0.0)	1 (10.0)	0 (0.0)	0 (0.0)	0 (0.0)	28 (6.8)
bet	7 (5.1)	3 (2.5)	4 (4.9)	0 (0.0)	2 (9.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	16 (3.9)
fgs	50 (36.8)	46 (38.7)	37 (45.1)	12 (31.6)	2 (9.5)	2 (20.0)	1 (25.0)	0 (0.0)	0 (0.0)	150 (36.2)
d_q	26 (19.1)	42 (35.3)	21 (25.6)	16 (42.1)	6 (28.6)	2 (20.0)	2 (50.0)	0 (0.0)	0 (0.0)	115 (27.8)
dbt	24 (17.6)	21 (17.6)	18 (22.0)	8 (21.1)	5 (23.8)	5 (50.0)	1 (25.0)	0 (0.0)	3 (75.0)	85 (20.5)
csc	5 (3.7)	2 (1.7)	0 (0.0)	1 (2.6)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	8 (1.9)
wrm	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Total	136 (13.0)	119 (13.9)	82 (14.6)	38 (11.9)	21 (9.1)	10 (5.3)	4 (3.7)	0 (0.0)	4 (2.1)	414 (10.9)
Total sites	1045	856	561	320	230	190	109	290	190	3791

Table 6 Numbers and percentages (in brackets) of subgroups in pollen assemblage group D_Q for each period

表 6 各時期における花粉群グループ D_Q のサブグループの数と割合

subgroup of D_Q	Period									Total
	0.8 ka	2.5 ka	5 ka	7 ka	9 ka	12 ka	14 ka	20 ka	40 ka	
pnc	11 (10.5)	9 (4.3)	8 (4.2)	3 (2.8)	2 (2.1)	4 (8.9)	3 (16.7)	2 (25.0)	8 (28.6)	50 (6.2)
pin	9 (8.6)	3 (1.4)	6 (3.2)	4 (3.7)	1 (1.0)	2 (4.4)	0 (0.0)	1 (12.5)	2 (7.1)	28 (3.5)
bet	8 (7.6)	11 (5.2)	9 (4.8)	0 (0.0)	3 (3.1)	4 (8.9)	1 (5.6)	0 (0.0)	0 (0.0)	36 (4.5)
fgs	10 (9.5)	26 (12.4)	11 (5.8)	3 (2.8)	6 (6.3)	3 (6.7)	0 (0.0)	0 (0.0)	0 (0.0)	59 (7.3)
d_q	20 (19.0)	56 (26.7)	56 (29.6)	32 (29.9)	32 (33.3)	17 (37.8)	3 (16.7)	3 (37.5)	2 (7.1)	221 (27.4)
dbt	19 (18.1)	78 (37.1)	69 (36.5)	36 (33.6)	43 (44.8)	15 (33.3)	10 (55.6)	2 (25.0)	13 (46.4)	285 (35.4)
csc	20 (19.0)	10 (4.8)	5 (2.6)	3 (2.8)	2 (2.1)	0 (0.0)	1 (5.6)	0 (0.0)	3 (10.7)	44 (5.5)
wrm	8 (7.6)	17 (8.1)	25 (13.2)	26 (24.3)	7 (7.3)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	83 (10.3)
Total	105 (10.0)	210 (24.5)	189 (33.7)	107 (33.4)	96 (41.7)	45 (23.7)	18 (16.5)	8 (2.8)	28 (14.7)	806 (21.3)
Total sites	1045	856	561	320	230	190	109	290	190	3791

Table 7 Numbers and percentages (in brackets) of subgroups in pollen assemblage group TMP with those of group CAS for each period

表 7 各時期における花粉群グループ TMP のサブグループおよび花粉群グループ CAS の数と割合

subgroup of TMP	Period									Total
	0.8 ka	2.5 ka	5 ka	7 ka	9 ka	12 ka	14 ka	20 ka	40 ka	
til	2 (6.5)	2 (3.1)	1 (2.2)	1 (2.4)	1 (6.7)	1 (16.7)	0 (0.0)	1 (12.5)	3 (20.0)	12 (5.2)
acr	2 (6.5)	6 (9.4)	5 (10.9)	1 (2.4)	0 (0.0)	0 (0.0)	1 (20.0)	0 (0.0)	1 (6.7)	16 (6.9)
cor	0 (0.0)	0 (0.0)	2 (4.3)	0 (0.0)	0 (0.0)	1 (16.7)	1 (20.0)	3 (37.5)	2 (13.3)	9 (3.9)
uzh	2 (6.5)	7 (10.9)	9 (19.6)	11 (26.2)	3 (20.0)	0 (0.0)	0 (0.0)	0 (0.0)	4 (26.7)	36 (15.6)
j_p	3 (9.7)	4 (6.3)	4 (8.7)	5 (11.9)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	16 (6.9)
aes	5 (16.1)	23 (35.9)	12 (26.1)	1 (2.4)	1 (6.7)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	42 (18.1)
frx	0 (0.0)	2 (3.1)	1 (2.2)	1 (2.4)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	4 (1.7)
c_o	2 (6.5)	5 (7.8)	1 (2.2)	5 (11.9)	4 (26.7)	2 (33.3)	1 (20.0)	0 (0.0)	1 (6.7)	21 (9.1)
dbt	15 (48.4)	15 (23.4)	11 (23.9)	17 (40.5)	6 (40.0)	2 (33.3)	2 (40.0)	3 (42.9)	4 (26.7)	75 (32.5)
Total TMP	31 (3.0)	64 (7.5)	46 (8.2)	42 (13.1)	15 (6.5)	6 (3.2)	5 (4.6)	7 (2.4)	15 (7.9)	232 (6.1)
CAS	4 (0.4)	6 (0.7)	14 (2.5)	5 (1.6)	2 (0.9)	0 (0.0)	1 (0.9)	0 (0.0)	0 (0.0)	32 (0.8)
Total sites	1045	856	561	320	230	190	109	290	190	3791

od, plenty of *Aesculus turbinata* and *Castanea crenata* fruits were collected and stored as food, and *Castanea crenata* timber was often used for construction with *Aesculus turbinata* timber for utensils. Mother plants of dominant pollen types in other temperate deciduous broadleaved tree groups prefer sunny places along rivers

such as flood plains, alluvial fans, river terraces, and hill slopes. These places were affected by riverine conditions that changed with the sea level. Anthropogenic disturbances and cultivation of plants also affected occurrence of these pollen assemblage groups. Furthermore, intermediate-temperate forests in northern

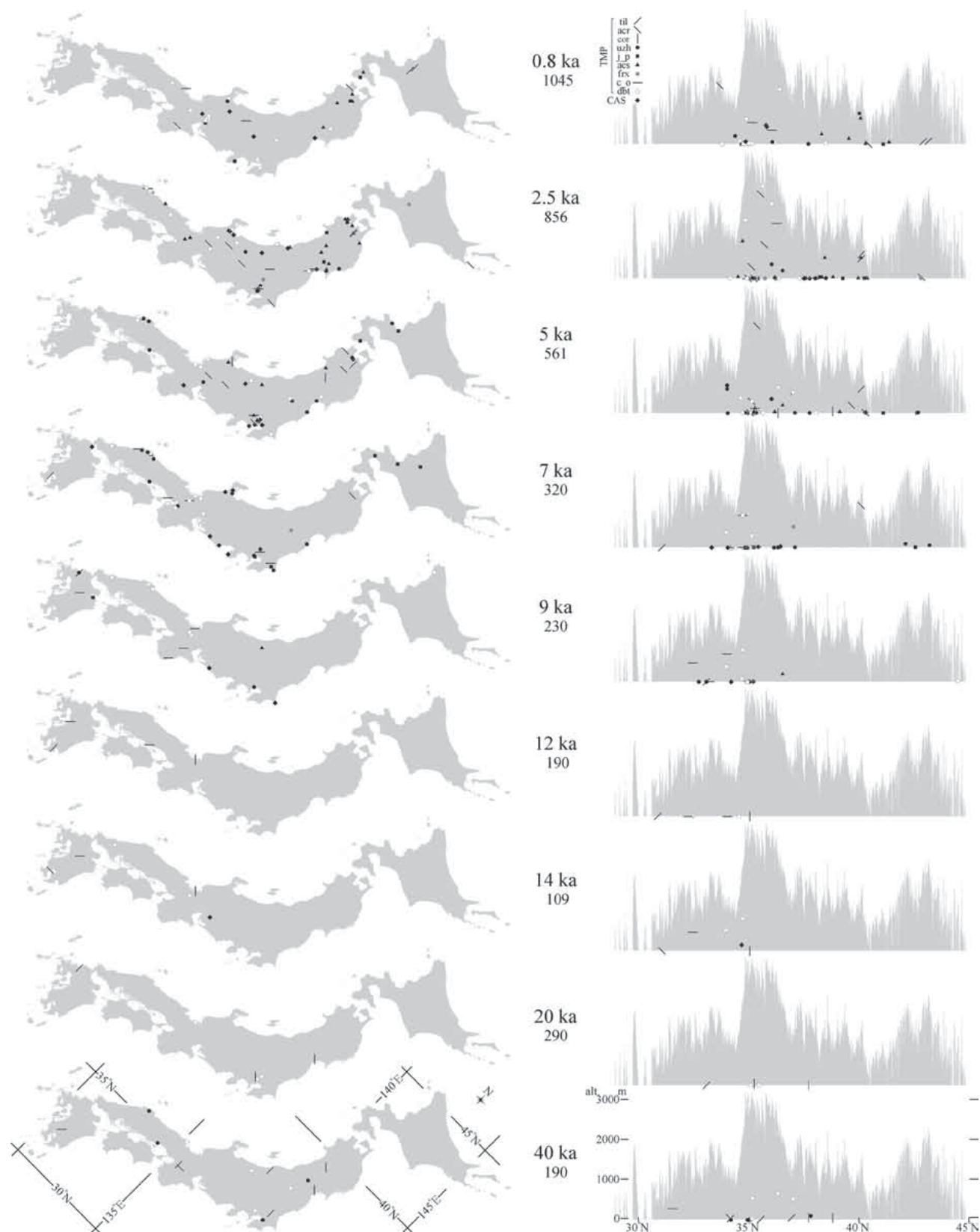


Fig. 33 Chronological distribution of subgroups of pollen assemblage group TMP (til, acr, cor, uzh, j_p, aes, frx, c_o, dbt) and that of CAS group on horizontal maps and vertical profiles of Japan. Number of sites for each period is shown below periods.

図 33 花粉群グループ TMP のサブグループ (til, acr, cor, uzh, j_p, aes, frx, c_o, dbt) と CAS の水平・垂直分布の変遷.

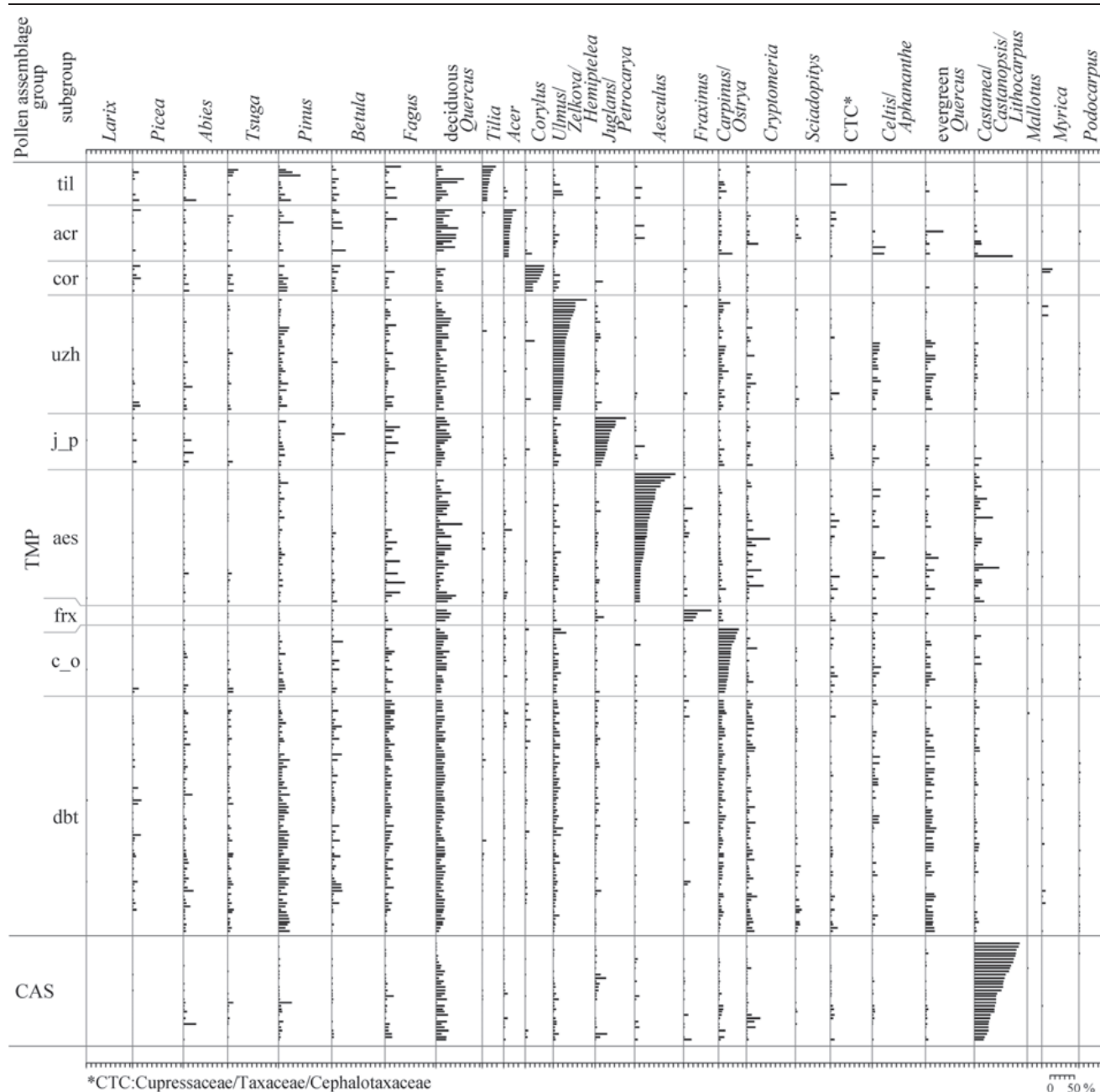


Fig. 34 Pollen diagram of subgroups of TMP group and that of CAS group enlarged from Fig. 25.

図34 花粉群グループTMPのサブグループおよびCASの花粉組成。Fig. 25の部分拡大。

Japan consist of *Castanea crenata* and other deciduous broadleaved trees in TMP group. Thus, many factors should affect the complex TMP group.

Temperate conifer groups (CRY, SCI, CTC)

SCI and CTC groups occurred rarely, the former group mostly in the mid-glacial (period 40 ka) and the latter mostly in period 2.5 ka (Table 4, Fig. 35). The pollen contents of these two groups indicated their

wide adaptability to temperature fluctuations (Fig. 36). These two groups were accompanied by pinaceous type during period 40 ka and evergreen broadleaved tree type during the post-glacial. SCI group occurred with pinaceous types including *Larix* type during the mid-glacial, but also with *Mallotus* and *Podocarpus* types during the post-glacial. *Sciadopitys* type, however, kept its distribution range since the mid-glacial (App. Fig. 8). Thus, the wide adaptation to temperature fluctuations

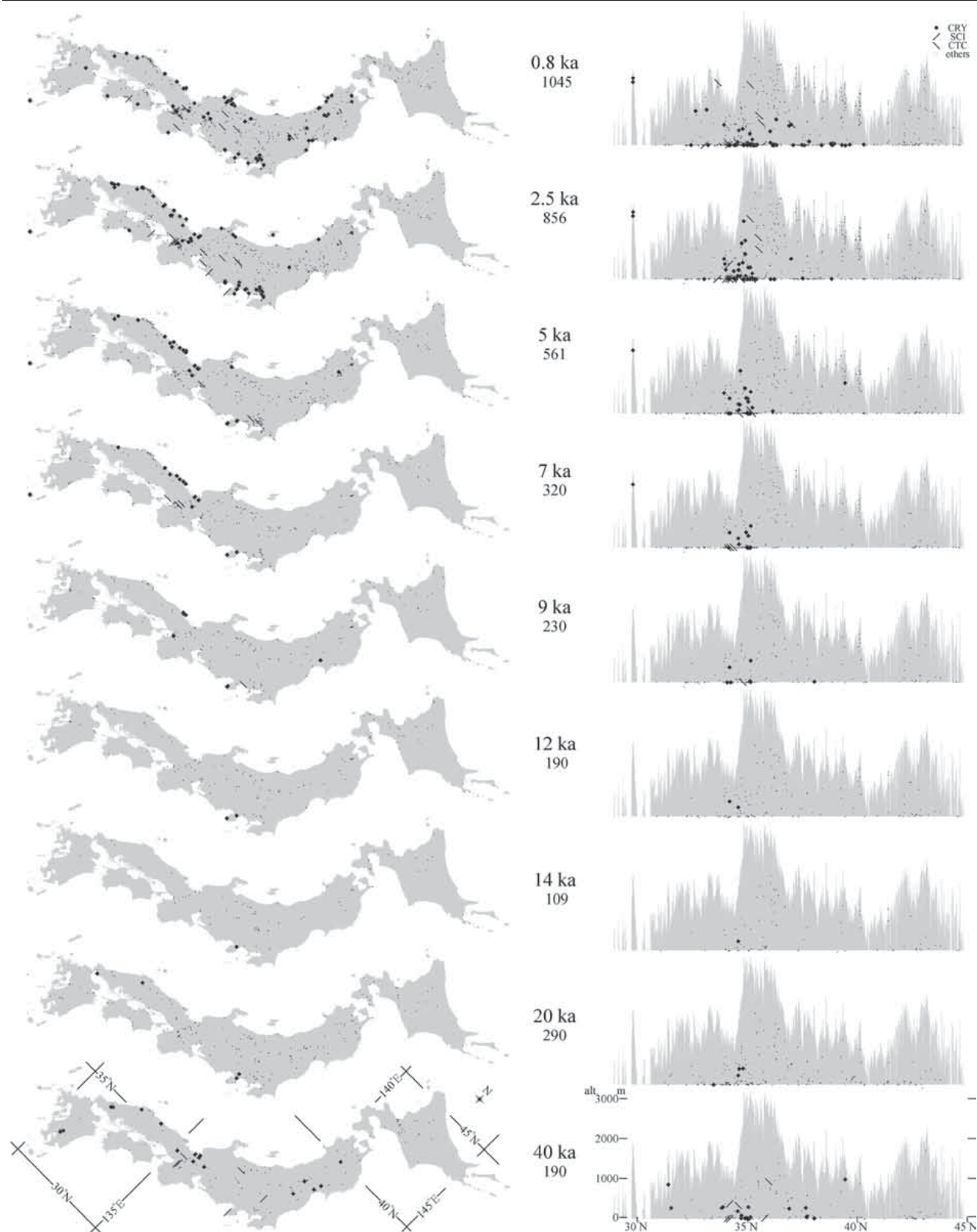


Fig. 35 Chronological distribution of pollen assemblage groups CRY, SCI, and CTC on horizontal maps and vertical profiles of Japan. Site number for each period are shown below periods.

図 35 花粉群グループ (CRY, SCI, CTC) の水平・垂直 (南北断面) 分布の変遷.

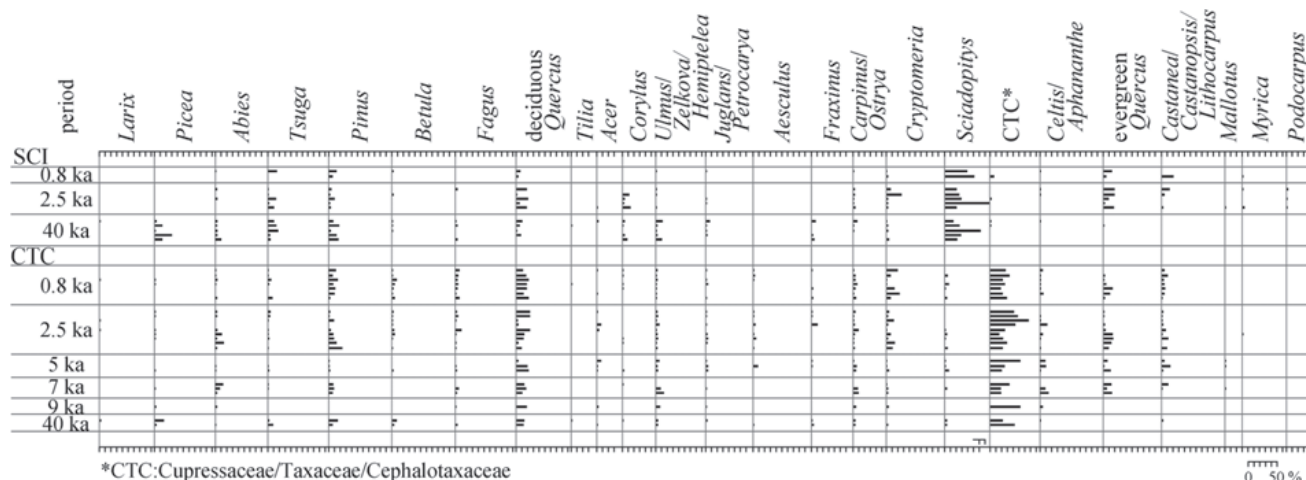


Fig. 36 Pollen diagram of SCI and CTC groups during each period from north to south.

図 36 花粉群グループ SCI, CTC の花粉組成. 時期ごとに北から南の順に示す.

in SCI group seemed to have derived from the flexible adaptability of *Sciadopitys*.

CRY group occurred frequently during the mid-glacial (period 40 ka) and two most recent periods (periods 2.5 ka, 0.8 ka) (Table 4) and showed a disjunctive distribution mainly in coastal areas (Fig. 35). Similar to CTC and SCI groups, this group was accompanied by pinaceous and deciduous broadleaved tree types during the mid-glacial (period 40 ka) and by evergreen broadleaved tree types during the post-glacial (Fig. 37). *Cryptomeria* type derives only from *Cryptomeria japonica* having a wide adaptability to temperature fluctuations. CRY and SCI groups differ in that CRY group was accompanied by more deciduous broadleaved tree types, particularly *Fagus* type, during period 40 ka and had several assemblages rich in *Fagus* type, but poor in evergreen broadleaved tree types during the post-glacial in the Tohoku and Chubu districts. These differences suggest that, compared with *Sciadopitys*, *Cryptomeria* preferred habitats with more precipitation or winter snow similar to *Fagus*.

Evergreen broadleaved tree pollen rich assemblage groups (C_A, E_Q, CLW, POD, MYR)

Evergreen broadleaved forests called lucidophyllous forests are the main forest type of the warm temperate zone in Japan (Imanishi & Kira, 1953). The pollen of Lauraceae species composing these forests, such as *Cinnamomum camphora* and *Machilus thunbergii*, has little sporopollenin in their exines and is seldom preserved as fossils (Traverse, 1988). Besides, pollen of many entomophilous plants growing in these evergreen broadleaved forests are usually not recorded signifi-

cantly. Thus, the actual vegetation cannot be reconstructed just from pollen data, but pollen assemblages from these groups reflect differences in vegetation.

Assemblage groups C_A, E_Q, CLW, and POD began to occur along the coastal areas of western Japan during period 9 ka and became more prevalent toward younger ages except period 0.8 ka (Fig. 38, Table 4). C_A group appeared markedly during period 9 ka in Kyushu as the forerunner of warm groups and in the Japan Sea side of western Japan. During periods 5 ka and 2.5 ka warm groups almost covered the coastal areas of western Japan with CLW group frequently in the Pacific side. E_Q group occurred abundantly and widely among warm groups and occurred most during period 2.5 ka. On lower mountains of western Japan E_Q group occurred since period 7 ka with D_Q and CRY groups. POD group occurred mainly in the coastal areas of Kyushu and Shikoku and showed its peak occurrence in period 7 ka and at Izumo along the Japan Sea coast of western Japan in period 2.5 ka.

C_A group attained its peak occurrence during period 9 ka and decreased afterwards with occasional occurrences (Fig. 39, Table 4). C_A group indicating *Celtis/Aphananthe* forests characteristically occurred in the coastal areas of western Japan during the early post-glacial. *Celtis/Aphananthe* type, the main component of this group, occurred most abundantly during period 9 ka of Kyushu and accompanied evergreen *Quercus* and *Castanea/Castanopsis/Lithocarpus* types in the southern part. CTC type characteristically occurring during periods 7 ka and 5 ka in the Kanto district was probably contributed by *Torreya*.

E_Q group occurred increasingly from periods 9 ka

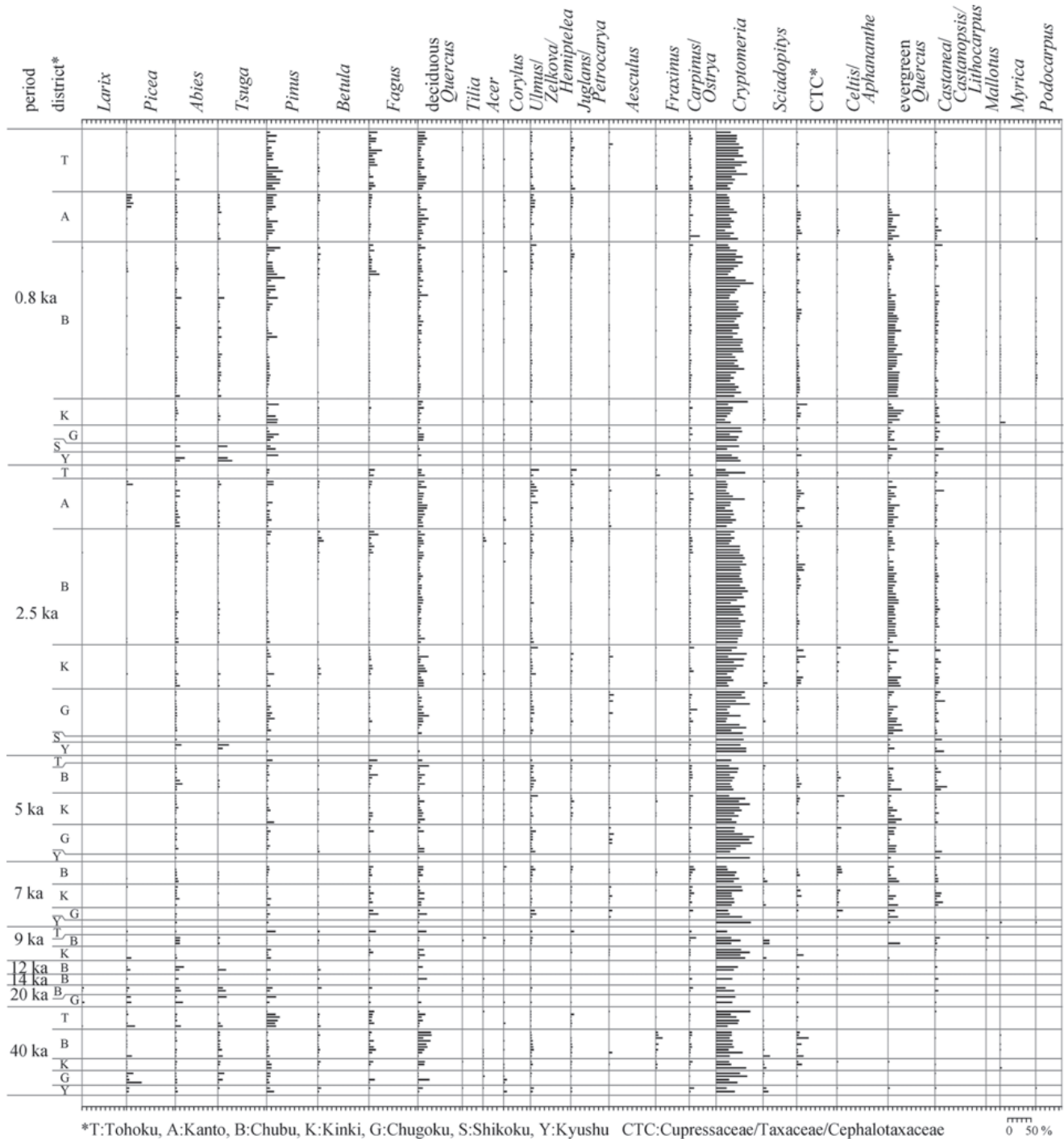


Fig. 37 Pollen diagram of CRY group during each period in each district from north to south.

図 37 花粉群グループ CRY の花粉組成。時期ごとに地方別に北から南の順に示す。

to 2.5 ka at an increasing number of pollen sites due to an expansion of lucidophyllous forests and declined with an expansion of *Pinus* type in period 0.8 ka (Table 4). CLW group consisting of *Castanopsis/Lithocarpus* began to occur in period 9 ka along the Pacific coast

and in western Kyushu (Fig. 38). CLW group continuously occurred mainly in Kyushu and sporadically along the Pacific coast to the Kanto district and at Izumo in the Japan Sea side of western Honshu.

The pollen composition of E_Q and CLW groups

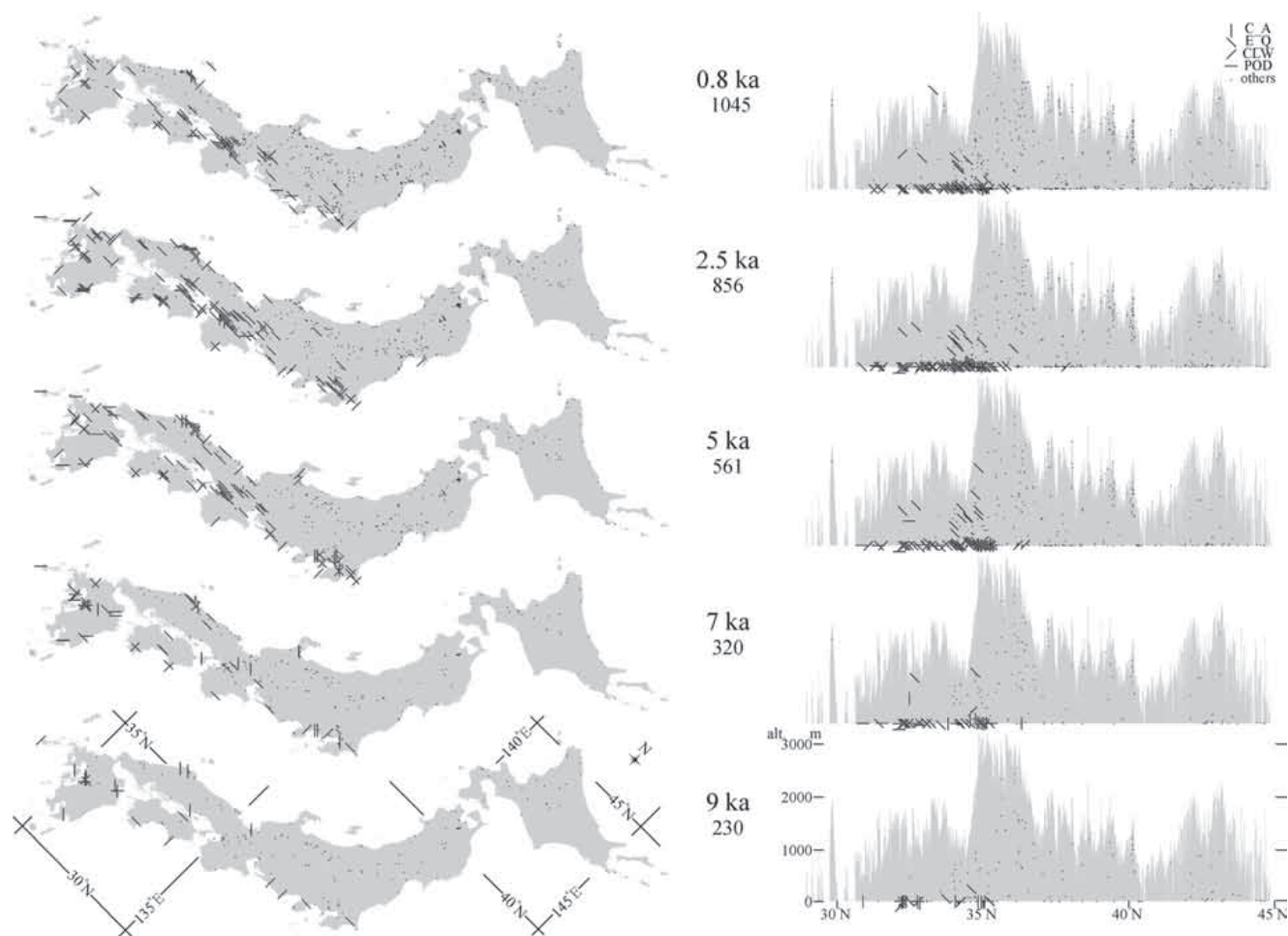


Fig. 38 Chronological distribution of pollen assemblage groups C_A, E_Q, CLW, and POD on horizontal maps and vertical profiles of Japan. Site numbers for each period are shown below periods. There are no records for the glacial period.

図 38 温暖な気候を示唆する花粉群グループ (C_A, E_Q, CLW, POD) の水平・垂直 (南北断面) 分布の変遷。氷期は記録無し。

showed not only chronological changes, but also regional differences in lucidophyllous forests (Fig. 39). These groups were accompanied by various pollen types except *Larix* type. In the Kanto district, they were frequently accompanied by *Ulmus/Zelkova/Hemiptelea*, CTC, and *Celtis/Aphananthe* types. *Castanea/Castanopsis/Lithocarpus* type of E_Q and CLW groups in the Kanto district must have derived from both *Castanea* and *Castanopsis/Lithocarpus* types, because CAS group occurred adjacent to these groups. E_Q and CLW groups were accompanied by *Betula* and *Fagus* types in the Chubu district, especially analog the Pacific coast (Tokai area), by temperate conifer types of *Cryptomeria*, *Sciadopitys*, and CTC in the Kinki district, and rather frequently by *Celtis/Aphananthe*, *Ulmus/Zelkova/Hemiptelea*, and *Aesculus* types in the Chugoku district, mainly in the coastal areas of

the Japan Sea side. In Shikoku, mainly in the Pacific side, E_Q and CLW groups were accompanied characteristically by *Tsuga* and *Myrica* types and rarely by deciduous broadleaved tree types excepting deciduous *Quercus* type. In Kyushu, E_Q and CLW groups were commonly accompanied by *Castanea/Castanopsis/Lithocarpus* type and rarely by temperate conifer types of *Cryptomeria*, *Sciadopitys*, and CTC. These regional differences in component pollen types implied an independent development of lucidophyllous forests in respective areas.

POD group occurred occasionally similar to C_A group and occurred most abundantly during the hypsithermal (period 7 ka), mainly in Kyushu. During the periods 2.5 ka, it characteristically occurred in Izumo on the Japan Sea coast of western Japan besides Kyushu, as discussed for *Podocarpus* type. POD group is

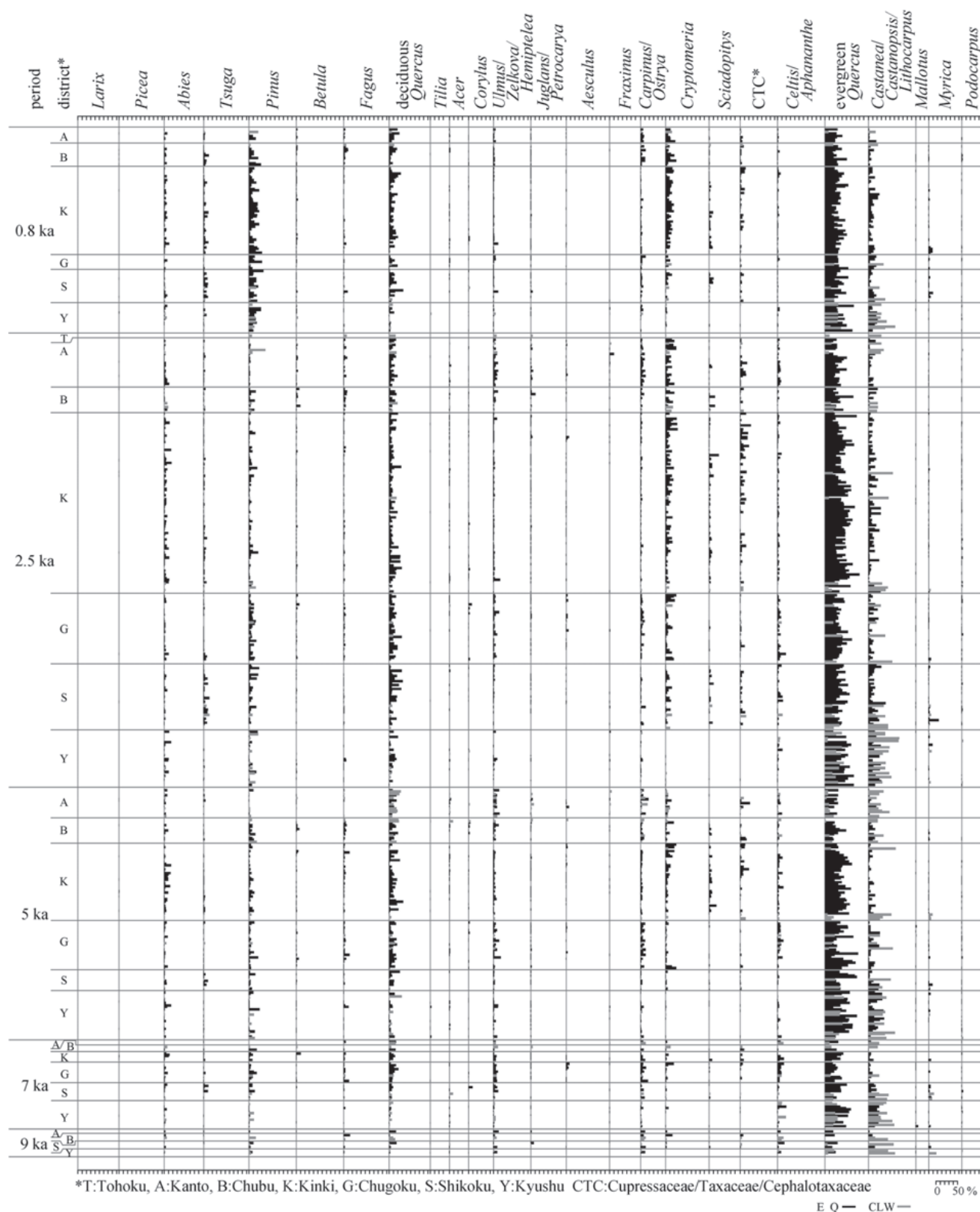


Fig. 39 Pollen diagram of E_Q and CLW (grey bars) groups during each period from north to south in each district.

図 39 花粉群グループ E_Q と CLW (灰色) の花粉組成。時期ごとに地方別の北から南の順に示す。

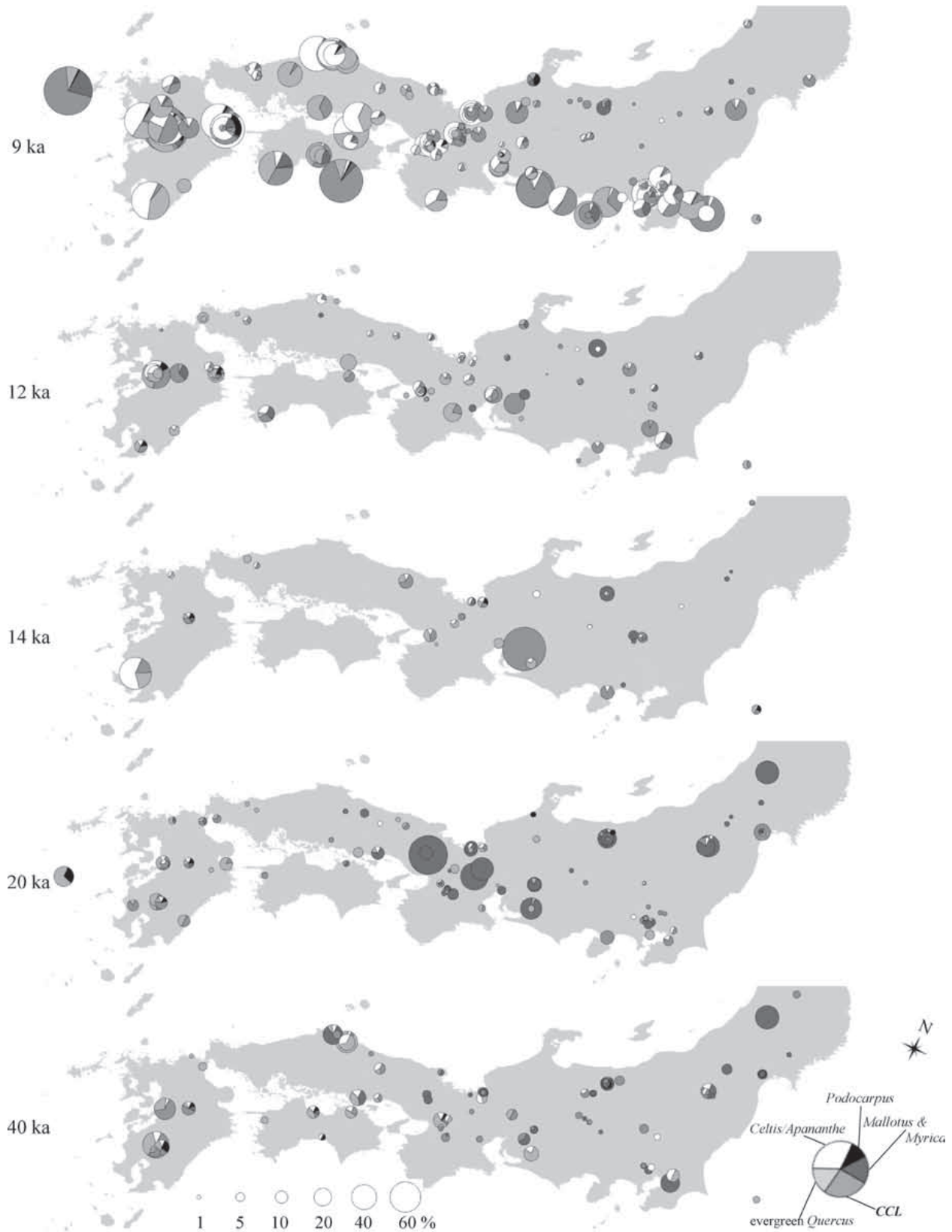


Fig. 40 Composition and occurrences of *Celtis/Aphananthe*, evergreen *Quercus*, CCL (*Castanea/Castanopsis/Lithocarpus*), *Mallotus*, *Myrica*, and *Podocarpus* types during the glacial and early post-glacial (periods 40 ka to 9 ka).

図 40 最終氷期と後氷期初頭における温暖な気候を示す花粉の産出率とその組成

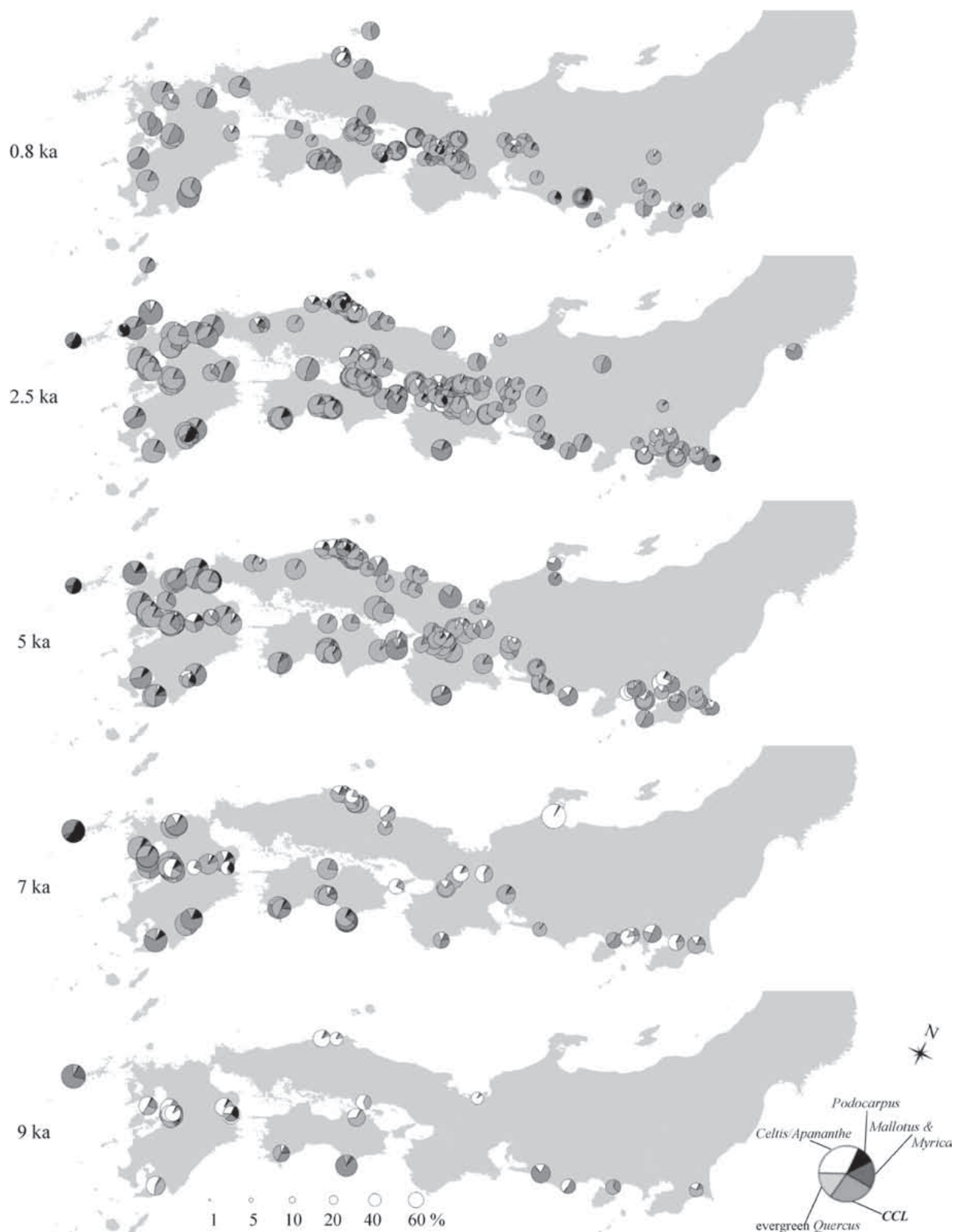


Fig. 41 Composition and occurrences of *Celtis/Aphananthe*, *evergreen Quercus*, *CCL*, *Mallotus*, *Myrica*, and *Podocarpus* types for warm pollen assemblage groups during the post-glacial (9 ka to 0.8 ka). Scales half of those in Fig. 40.

図 41 後氷期における温暖な花粉群グループの分布と温暖な気候を示す花粉の産出率と組成。産出スケールは Fig. 40 の 1/2。

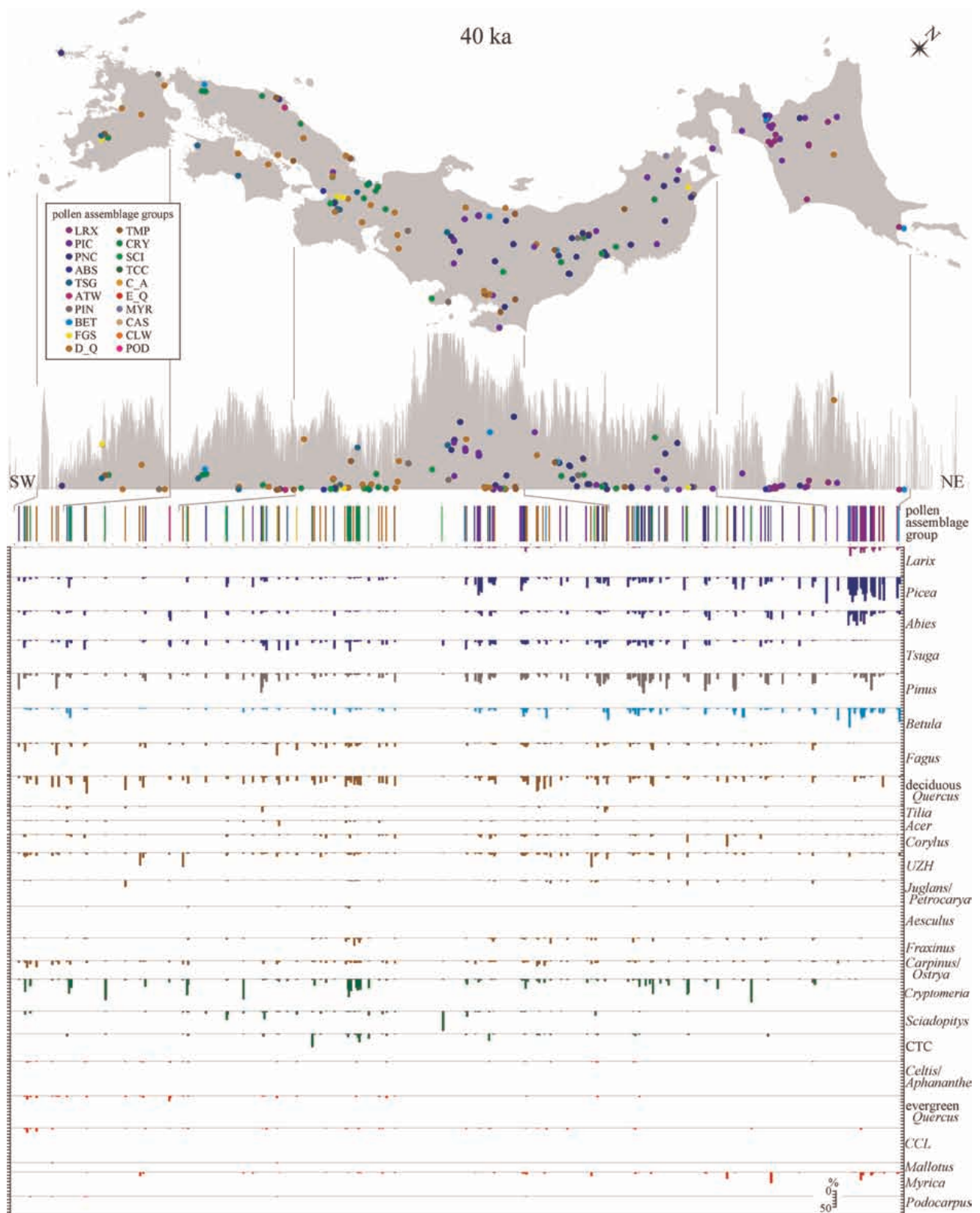


Fig. 42 Horizontal and vertical distribution of pollen assemblage groups with pollen diagram showing southwest to northeast locality series during the mid-glacial (period 40 ka). Colors in site maps and locality series show pollen assemblage groups, and percentage bars in the diagram show pollen physionomical classes (CCL and *Myrica* types colored as EB-WDE class). UZH: *Ulmus/Zelkova/Hemiptelea*, CTC: Cupressaceae/Taxaceae/Cephalotaxaceae, CCL: *Castanea/Castanopsis/Lithocarpus*.

the only group that showed its peak occurrence during the hypsithermal.

MYR group rarely occurred and included subgroups bog and wrm reflecting *Myrica gale* and *Myrica rubra*, respectively. The history of MYR group was already discussed in the chronological changes of *Myrica* type.

Migration of lucidophyllous forests has been frequently argued in Japan. Tsukada (1984) considered that lucidophyllous forests remained only in southern Kyushu, whereas Matsushita (1987, 1992) argued that they remained in coastal areas along the Pacific coast based on the early post-glacial increase of lucidophyllous pollen. Chronological changes in the occurrences of warm temperate types during the glacial (Fig. 40) and warm temperate pollen assemblage groups and their contents during the post-glacial (Fig. 41) show the history of the lucidophyllous trees and forests. During the glacial, warm temperate types occurred sparsely but widely, although *Myrica* and *Castanea/Castanopsis/Lithocarpus* types may include abundant *Myrica gale* and *Castanea crenata* pollen. Warm temperate types abruptly increased in the subsequent early post-glacial (period 9 ka) in the coastal areas of western Japan and the Pacific side of central Japan. This seems to deny migration of lucidophyllous forests, that was repeatedly proposed. *Celtis/Aphananthe* first occurred in most areas except the coastal areas in the Pacific side, and *Castanea/Castanopsis/Lithocarpus*, *Myrica*, and *Podocarpus* types occurred abundantly during periods 9 ka and 7 ka. *Myrica* and *Podocarpus* types stayed in the coastal areas and occurred frequently in some areas afterward, but did not expand beyond the distribution ranges during the hypsithermal (period 7 ka). *Castanea/Castanopsis/Lithocarpus* type probably including *Castanea* even in Kyushu showed a similar distribution to *Myrica* and *Podocarpus* types in western Japan and occurred in such areas as the Japan Sea side of northern Kyushu, Izumo of western Honshu, the Pacific coast of southern Kyushu, Shikoku, Kii Peninsula, Tokai area, and southern Kanto district. These areas provided warm wet habitats, supported by the warm Tsushima Current flowing into the Japan Sea since ca. 8000 years ago and the Japan Current (Kuroshio) flowing along the Pacific coast continuously. Although the expansion of evergreen *Quercus* type was delayed, changes in the distribution of warm temperate assemblage groups (Fig. 38) and regional differences in pollen contents of E_Q and CLW groups (Fig. 39) show

that lucidophyllous forests originated in respective areas. The distribution of warm temperate types during the glacial suggested existence of multiple refugia for the component species of these types.

Importantly, the first assemblages rich in warm temperate types in period 9 ka were dominated by *Celtis/Aphananthe* and *Castanea/Castanopsis/Lithocarpus* types (Figs. 40, 41). The contents of pollen assemblages showed that E_Q group was accompanied more by temperate conifer and deciduous broadleaved tree types than CLW group (Fig. 26). Although evergreen *Quercus* tolerates cooler environments than *Castanopsis* at present judging from the present distribution, *Castanea/Castanopsis/Lithocarpus* type appeared prior to evergreen *Quercus* type in the late-glacial and showed its peak occurrence in the hypsithermal, similar to such warm elements as *Myrica* and *Podocarpus* types. This delay in the expansion of evergreen *Quercus* type was probably due to the restriction of habitats by the post-glacial transgression in spite of favorable climatic environments for lucidophyllous forests. Thus, *Castanea/Castanopsis/Lithocarpus*, *Myrica*, and *Podocarpus* types occurred abundantly in coastal areas by the hypsithermal, and evergreen *Quercus* occupied new open habitats produced by the regression. In later periods, human disturbances affected vegetation variously, resulting in complex vegetation types, and promoted vegetation changes.

3. Vegetation history

Vegetation history of the Japanese archipelago for respective periods since the mid-glacial will be summarized based on changes in pollen assemblage groups and their composition (Figs. 42–50).

Period 40 ka (Fig. 42)

The mid-glacial, MIS 3, was an interstadial after the cooling of MIS 4, following the early glacial climatic oscillations of MIS 5d to 5a. Several pollen spectra showed these oscillations by cyclic changes of pollen assemblages (e.g., Ooi et al., 1997, 2004; Hayashi et al., 2010).

In Hokkaido *Larix gmelinii* forests with *Picea jezoensis* and *P. glehnii* were dominant, accompanied by *Abies sachalinensis* in the western part. Temperate deciduous trees occurred rarely, but widely with pinaceous conifers. Giant eruptions of Shikotsu and Kuttara volcanoes in southwestern Hokkaido occurred

←
図 42 最終氷期中期 (時期 40 ka) における花粉群グループの分布とその組成。上部に水平・垂直分布を示し、その下に全地点を南西-北東順に並べ、細線で結んで各地点の花粉群グループとその花粉組成を示す。花粉型の産出率は花粉相観クラス別に色分けしたバーで示す (2つのクラスに属するクリ属/シイノキ属/マテバシイ属型とヤマモモ属型は EB-WDE クラスの色)。

during the mid-glacial. Forests buried by the ash falls were found at several places and consisted of *Picea jezoensis* at Bibi of central Hokkaido (Katsui, 1958) and of *Larix gmelinii*, *P. jezoensis*, *P. glehnii*, and *Abies sachalinensis* at Noboribetsu in southwestern Hokkaido (Iburi Collaborative Research Group, 1984, 1987).

In northern Honshu, evergreen conifers of *Picea*, *Abies*, *Tsuga* and *Pinus* dominated with some *Larix gmelinii* forests in mountainous areas. *Cryptomeria* occurred around Sendai in the Pacific side. In central Honshu, conifers differing from those in Hokkaido such as *Larix kaempferi*, *Picea maximowiczii*, and *Tsuga sieboldii* dominated in mountainous areas with deciduous broadleaved trees, judging from macrofossils from Lake Nojiri (Fossil Plant Research Group for Nojiri-ko Excavation, 1984, 2003). In the lowland of northern Honshu, CRY group and pinaceous groups such as PNC, PIC, and PIN occurred, probably reflecting patches of *Cryptomeria* and pinaceous forests or vegetation changes in the long mid-glacial.

In the lowland of central to western Japan, temperate trees dominated with pinaceous trees. *Cryptomeria* dominated sporadically in such areas as Sendai, Izu, Kinki, and southern Japan, and *Sciadopitys* and Cupressaceae occurred sporadically. These trees occurred less than during the cooling phase of the early glacial. *Fagus* and warm temperate trees did not dominate in vegetation. Actually *Fagus* existed, but did not dominate, occurring less than deciduous *Quercus* at most sites except Natsuihama (Hatanaka, 1985) in northern Kyushu. Warm elements such as *Celtis/Aphananthe* and evergreen *Quercus* types accounted for less than 5% of the total pollen types at most pollen sites, but occurred at ca. 15% of sites (27/190 for the former and 28/190 for the latter), particularly in western Japan and north to Hoshojiri in Fukushima (Sohma, 1984) and Lake Nojiri in central Japan (Palynological Research Group for Nojiri-ko Excavation, 2012).

Period 20 ka (Fig. 43)

During the full-glacial (20 ka), *Larix* expanded in Hokkaido, accompanied by *Pinus*. This *Pinus* was probably *Pinus pumila* that often grows with *Larix gmelinii* in the present forest tundra. Probably, dwarf species of *Betula* expanded in eastern Hokkaido, and *Picea* was abundant in southwestern Hokkaido. During the full-glacial the permafrost is thought to have prevailed, particularly in eastern Hokkaido, and is shown as the tundra environment in eastern Hokkaido in several vegetation maps. Deciduous broadleaved trees, however, seem to have survived in restricted areas without permafrost, because their pollen occurred

rarely, but distinctly at most sites in the full-glacial Hokkaido. *Tsuga*, now extinct from Hokkaido, also survived with them. *Larix gmelinii* forests also grew in northernmost Honshu, judging from its fossil records (Suzuki & Takeuti, 1989; Sohma, 1959).

Evergreen pinaceous forests prevailed in the other parts of Japan. *Betula* forests occurred in lower mountainous areas. Deciduous broadleaved trees and temperate conifers decreased, but occurred significantly at many sites. *Fagus* occurred quite rarely, but deciduous *Quercus* occurred abundantly at several sites. Assemblages dominated by temperate trees occurred in the lowland of central to western Japan. *Cryptomeria* commonly occurred only at Tanna in Izu Peninsula (Yamazaki, 1988), Oki Island off Izumo (Takahara et al., 2001), Fukuhara of Izumo (Onishi, 1989), and Onoda in the western coast of the Setonai-kai sea (Yasuda, 1983). Even in this period warm elements occurred in the same range as in the mid-glacial such as *Celtis/Aphananthe* at Hoshojiri in Fukushima (Sohma, 1984) and evergreen *Quercus* at Amo Moor in Gifu (Takeoka, 1983), but at the least number of pollen sites (6.9% for the former and 11.4% for the latter).

Period 14 ka (Fig. 44)

Climatic amelioration after the full-glacial occurred during this period. *Betula* and temperate deciduous broadleaved forests expanded at many sites, but *Cryptomeria* did not recover from the cold phase in period 20 ka.

In Hokkaido *Larix* occurred abundantly only in the easternmost part and grew with *Picea* and *Betula* in the central part. *Larix* and *Pinus* decreased, and *Betula* increased from period 20 ka. This *Betula* in eastern Hokkaido probably was dwarf species. In northernmost Honshu and southern Hokkaido, coniferous forests of *Abies* and *Picea* prevailed, but *Fagus* and deciduous *Quercus* forests were already established at some sites. In central Honshu, pinaceous forests of *Larix*, *Pinus*, *Picea*, *Abies*, and *Tsuga* occurred from the mountainous areas to the lowland. *Betula* forests expanded widely on the lower mountainous areas in the Japan Sea side. This *Betula* must be *B. platyphylla*, *B. grossa*, and/or *B. ermanii*, not dwarf ones in eastern Hokkaido. Temperate deciduous broadleaved forests began to increase not only in the lowland, but in the mountainous areas of Honshu and Kyushu. *Cryptomeria* dominant forests occurred only at Tanna in Izu Peninsula, as in previous periods (Yamazaki, 1988).

Period 12 ka (Fig. 45)

Period 12 ka is a cold phase of the late-glacial, cor-

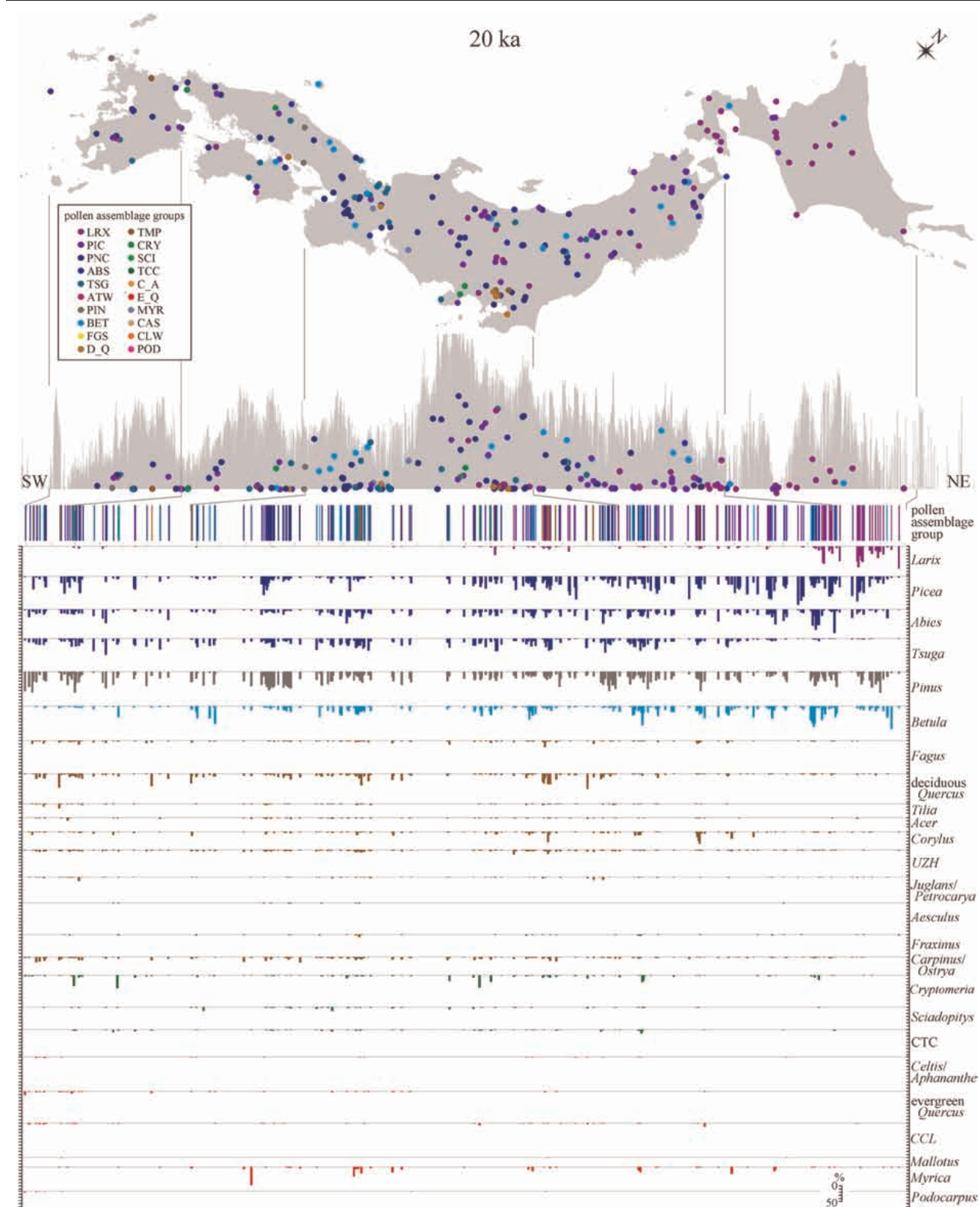


Fig. 43 Horizontal and vertical distribution of pollen assemblage groups with pollen diagram showing southwest to northeast locality series during the full-glacial (period 20 ka). See Fig. 42 for additional explanation.

図 43 最終氷期最盛期（時期 20 ka）における花粉群グループの分布とその組成。上部に水平・垂直分布を示し、その下に全地点を南西－北東順に並べ、各地点の花粉群グループとその花粉組成を示す。詳細は図 42 参照。

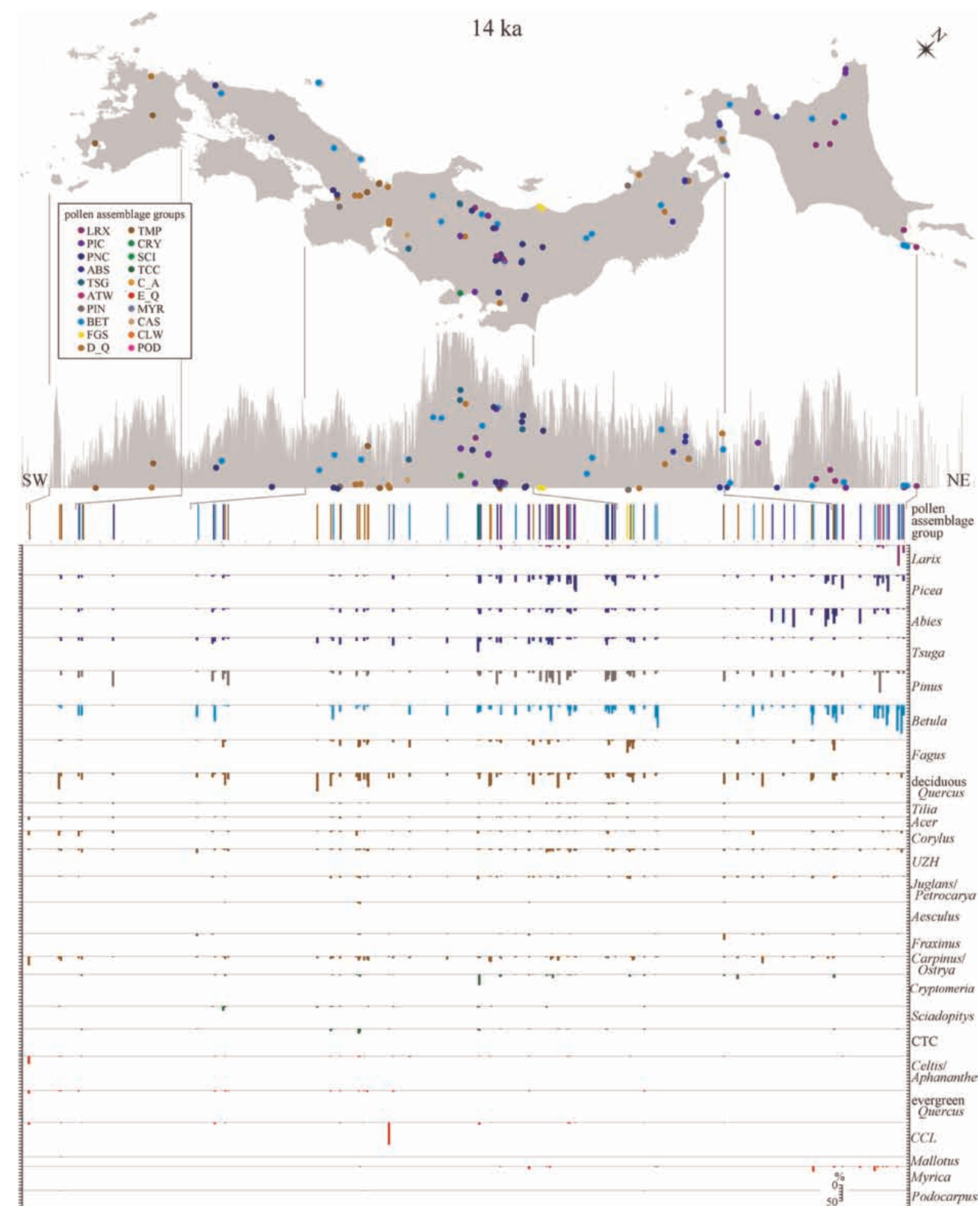


Fig. 44 Horizontal and vertical distribution of pollen assemblage groups with pollen diagram showing southwest to northeast locality series during the late-glacial (period 14 ka). See Fig. 42 for additional explanation.

図 44 晩氷期（時期 14 ka）における花粉群グループの分布とその組成。上部に水平・垂直分布を示し、その下に全地点を南西-北東順に並べ、各地点の花粉群グループとその花粉組成を示す。詳細は図 42 参照。

responding to the Younger Dryas. This climatic change was indicated by a revival of *Larix* in Hokkaido and an increase of *Fagus* in Honshu. Occurrence of pinaceous trees did not increase apparently, but warm elements began to occur significantly in southern Kyushu.

In Hokkaido, *Larix* occurred abundantly, more than in the previous period 14 ka, accompanied by *Picea* and *Betula*. The distribution of *Larix* in other areas is similar to that in period 14 ka. In northernmost Honshu and southern Hokkaido, coniferous forests of *Abies* and *Picea* prevailed with sporadic occurrences of *Fagus* and deciduous *Quercus*. In central Honshu, pinaceous forests of *Larix*, *Pinus*, *Picea*, *Abies*, and *Tsuga* occurred from the mountainous areas to the lowland. *Betula* forests occurred widely on the lower mountainous areas in the Japan Sea side. *Fagus* forests began to occur frequently in mountainous areas in Japan Sea side of central Japan, and deciduous *Quercus* increased in the same areas as in period 14 ka. *Cryptomeria* dominant forests occurred only in Izu on the Pacific coast of central Japan.

The cooling during this period was milder and shorter than that during the full-glacial and is considered severer in Hokkaido than in central Japan, because of the abundant occurrences of deciduous broadleaved trees in central Japan. The full-glacial cooling was severer than the other cold phases in the last glacial, because the closure and resulting decline in salinity of the Japan Sea promoted the cold and dry environment. In Honshu, conifers prevailed most in the full-glacial and formed quite different assemblages from those in the other cold phases. In Hokkaido, *Larix* showed its peak occurrences in cold phases, but *Pinus* was abundant in the full-glacial, whereas *Betula* and deciduous *Quercus* were common in period 12 ka. Besides, studies on vegetation changes since the last interglacial showed that forests in period 12 ka were similar to those of the cold phase in the early glacial in Hokkaido and Honshu (e.g., Ooi et al., 1997; Iriya et al., 2005; Hayashi et al., 2010). Thus, environmental differences between the cold phases of the glacial were clearly reflected in pollen assemblage groups.

Period 9 ka (Fig. 46)

During the early post-glacial (period 9 ka), pinaceous forests decreased except in Hokkaido, and deciduous broadleaved forests prevailed in Honshu. Evergreen broadleaved forests already grew in the coastal areas of Kyushu, Shikoku, and even southern Kanto.

In Hokkaido, *Larix* decreased, and *Betula* forests and evergreen coniferous forests of *Picea* and *Abies* prevailed with deciduous broadleaved trees. *Betula* for-

ests particularly developed in western Hokkaido.

In Honshu, deciduous *Quercus* occurred most abundantly, and other temperate deciduous trees increased. *Fagus* increased in the mountainous areas in the Japan Sea side of central to northern Honshu, where *Betula* forests spread in the previous period. *Fagus* was not dominant as it is today and formed forest patches with deciduous *Quercus* and remnant *Betula*. *Cryptomeria* sporadically occurred as a dominant element as in Izu Peninsula on the Pacific coast of central Honshu and in Wakasa on the Japan Sea coast of western Honshu. *Cryptomeria* significantly occurred even in the full-glacial in both areas.

Along the coasts of western Japan, evergreen broadleaved trees increased. *Celtis/Aphananthe* abundantly occurred together with *Ulmus/Zelkova/Hemiptelea* in Kyushu and at Izumo in the Japan Sea side of western Japan, probably deriving from *Celtis/Aphananthe* forests. A similar increase occurred around Setonai-kai sea, in southern Kanto, and at Wakasa, corresponding to the increased inflow of warm currents. Evergreen *Quercus* also increased in the similar areas, and *Castanea/Castanopsis/Lithocarpus* occurred sporadically as an abundant element along the Pacific coast of western Japan, east to Choshi in the Kanto district. In Kyushu *Podocarpus* occurred significantly in this period.

Period 7 ka (Fig. 47)

During the hypsithermal (7 ka), pinaceous conifers become restricted. Temperate forests increased even in Hokkaido, and *Fagus* became dominant in the mountainous areas of central to northern Honshu. Evergreen broadleaved trees occurred abundantly in the coastal areas of western Japan with evergreen *Quercus* as the dominant element.

In Hokkaido, deciduous broadleaved forests increased in the lowland, and evergreen coniferous forests and *Betula* forests prevailed as in previous periods, restricted in the eastern tip and mountainous areas. *Larix* still occurred at several sites.

In Honshu, deciduous broadleaved forests almost covered the mountainous areas. *Fagus* prevailed in the Japan Sea side, whereas deciduous *Quercus* occurred abundantly in the Pacific side and western Japan. *Betula* came to be restricted at higher elevations. Other deciduous broadleaved trees also increased generally and occurred sporadically at several sites in the lowland. *Cryptomeria* forests increased in Izu and the Japan Sea coast of central Japan, as in the previous period.

Evergreen broadleaved trees increased in the coastal areas of western Japan as in the previous period with regional differences reflecting regional vegetation. In

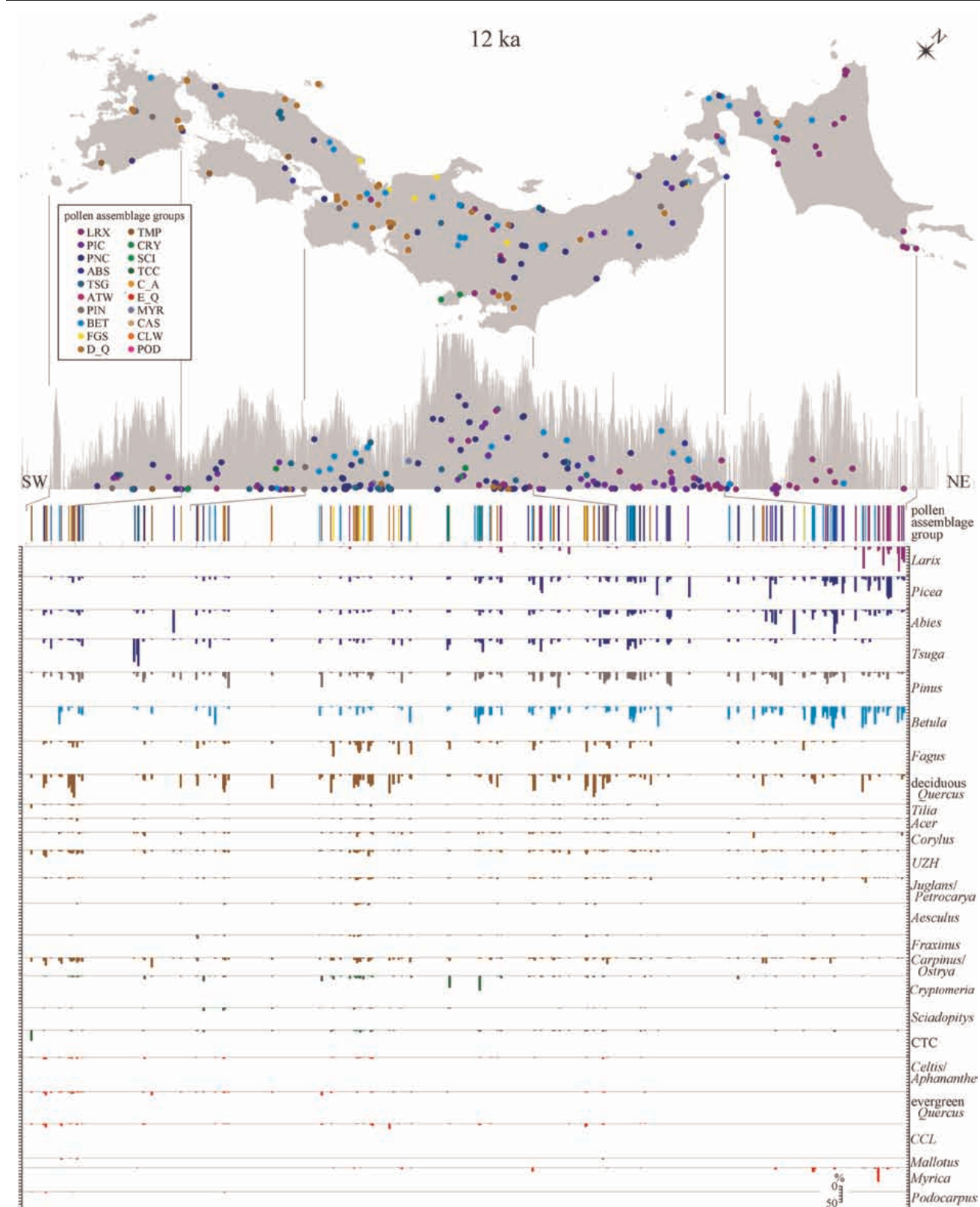


Fig. 45 Horizontal and vertical distribution of pollen assemblage groups with pollen diagram showing southwest to northeast locality series during the late-glacial (period 12 ka). See Fig. 42 for additional explanation.

図 45 晩氷期（時期 12 ka）における花粉群グループの分布とその組成。上部に水平・垂直分布を示し、その下に全地点を南西―北東順に並べ、各地点の花粉群グループとその花粉組成を示す。詳細は図 42 参照。

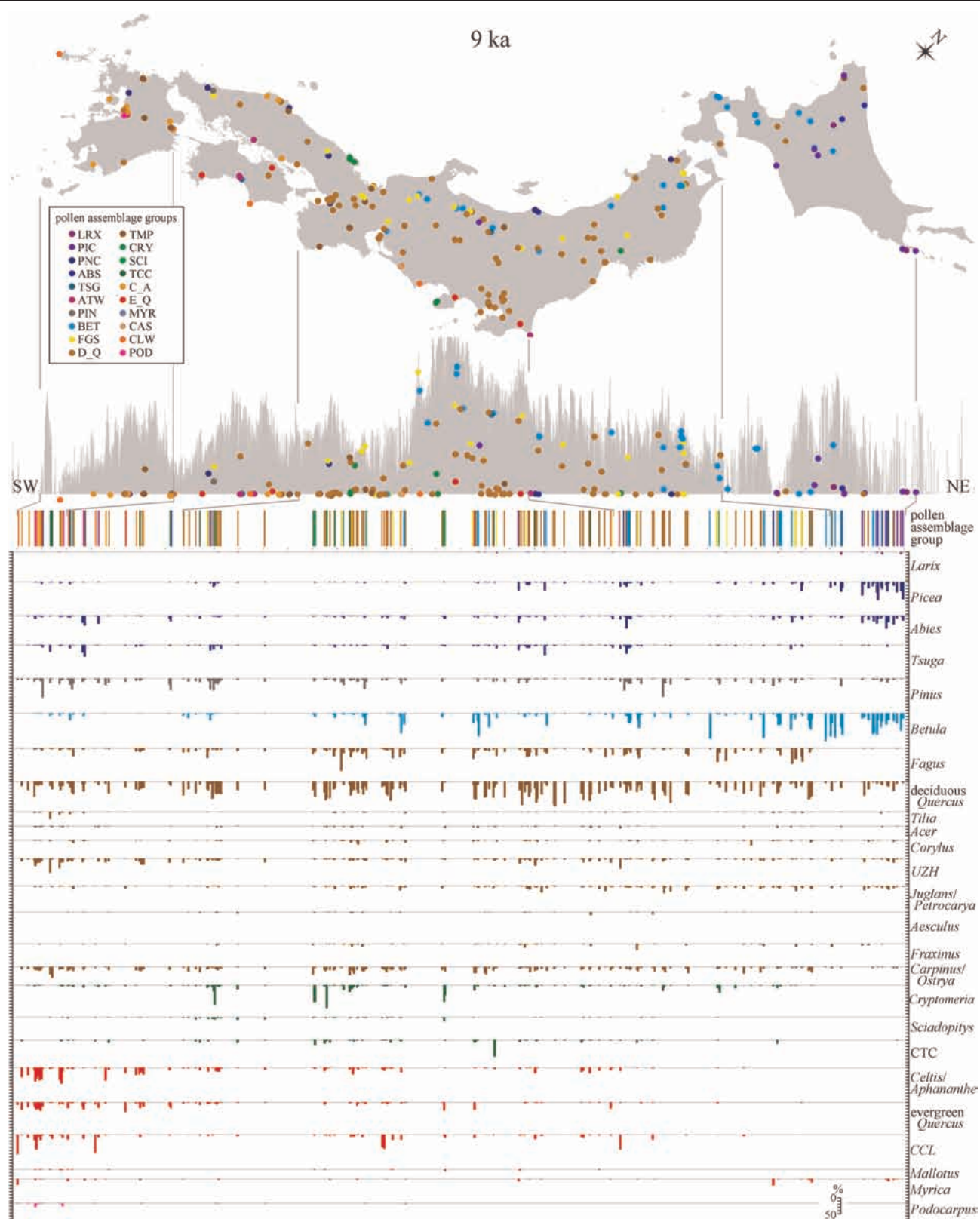


Fig. 46 Horizontal and vertical distribution of pollen assemblage groups with pollen diagram showing southwest to northeast locality series during the post-glacial (period 9 ka). See Fig. 42 for additional explanation.

図 46 後氷期初頭（時期 9 ka）における花粉群グループの分布とその組成。上部に水平・垂直分布を示し、その下に全地点を南西―北東順に並べ、各地点の花粉群グループとその花粉組成を示す。詳細は図 42 参照。

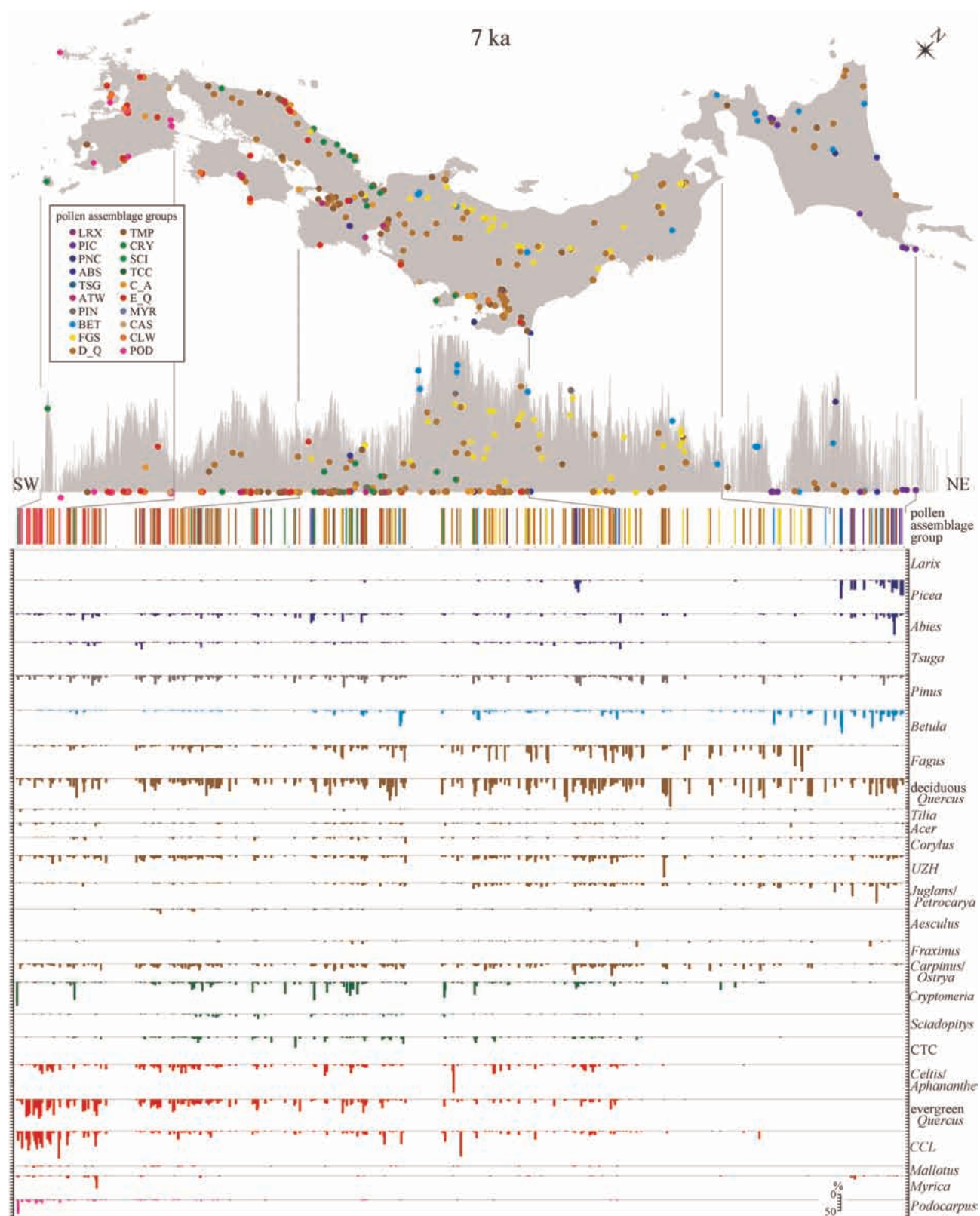


Fig. 47 Horizontal and vertical distribution of pollen assemblage groups with pollen diagram showing southwest to northeast locality series during the hypsithermal (period 7 ka). See Fig. 42 for additional explanation.

図 47 最温暖期（時期 7 ka）における花粉群グループの分布とその組成。上部に水平・垂直分布を示し、その下に全地点を南西―北東順に並べ、各地点の花粉群グループとその花粉組成を示す。詳細は図 42 参照。

Kyushu and southwestern Shikoku, replacing previously dominant *Celtis/Aphananthe*, evergreen *Quercus* and *Castanea/Castanopsis/Lithocarpus* occurred abundantly, accompanied by abundant *Podocarpus* and *Myrica* at a few sites. In other coastal areas of western Japan, evergreen broadleaved trees also increased, but did not dominate, accompanied by temperate pollen types such as deciduous *Quercus* and *Ulmus/Zelkova/Hemiptelea* preferring warm environments.

This period corresponds to the hypsithermal, but the vegetation did not seem to reflect warm environments apparently. In this period evergreen broadleaved forests were in the process of increasing except for *Podocarpus* and *Myrica* that showed maximum occurrences at several sites. Pinaceous forests occurred in restricted areas, which were almost the same as in the previous and next periods. Evergreen forests expanded from the coastal areas, but their habitats in the coastal areas came to be restricted toward the hypsithermal, because of the marine transgression. After the hypsithermal, the regression provided open habitats not only in the coastal areas, but also along ridges in the upland by erosion and denudation.

Period 5 ka (Fig. 48)

During period 5 ka, the marine regression promoted the increase of evergreen broadleaved forests in coastal areas. As in the previous period, *Fagus* and deciduous *Quercus* dominated in the mountainous areas of central to northern Japan, the former in the Japan Sea side and the latter in other regions including Hokkaido. In the lowland of central to northern Japan, other temperate deciduous trees sporadically occurred with deciduous *Quercus*. *Cryptomeria* increased not only in the lowland, but also in the mountainous areas of western Honshu, forming forest patches with pinaceous forests, temperate deciduous forests, *Cryptomeria* forests, and evergreen broadleaved forests.

In Hokkaido, deciduous *Quercus* prevailed extensively except for the eastern tip with pinaceous forests. *Betula* dominant forests became rare, but *Betula* occurred commonly with deciduous *Quercus*, accompanied by other deciduous trees such as *Ulmus/Zelkova/Hemiptelea* and *Juglans/Pterocarya*. Only two records of *Larix* have been obtained for this period in Hokkaido among the selected 55 horizons in this study.

In northern Honshu, *Fagus* forests occurred widely in the mountainous areas. Around the mountain tops of central Honshu, *Betula* forests remained, and *Pinus* rich assemblages occurred above them, corresponding to the present tree limit of *Betula ermanii* forests below *Pinus pumila* scrubs.

In the lowland, data from archaeological sites abruptly increased, and their data concentrated around large cities clearly showed regional differences. In northernmost Honshu, *Castanea* dominant assemblages concentrated around the San-nai Maruyama sites, a large Jomon site with abundant remains of *Castanea* fruits and timber. In the Sendai plain, deciduous *Quercus* occurred with *Ulmus/Zelkova/Hemiptelea* and occasionally with evergreen *Quercus*. In the Kanto district, evergreen *Quercus* occurred frequently, but never became dominant, accompanied by such warm elements as *Celtis/Aphananthe*, *Castanea/Castanopsis/Lithocarpus*, CTC (*Torreya*), and deciduous broadleaved trees that were particularly frequent in the inland. In Izu Peninsula, *Cryptomeria* dominated with evergreen *Quercus*. In Tokai, evergreen *Quercus* occurred with *Fagus*, and *Abies* or deciduous *Quercus* dominated at some sites. In central Kinki, evergreen *Quercus* occurred with temperate conifers of *Cryptomeria*, *Sciadopitys*, and CTC type. In northern Kinki to Chugoku districts along the Japan Sea coast except Izumo, *Cryptomeria* dominated, succeeding the trends in the previous period. In Izumo evergreen *Quercus* and *Celtis/Aphananthe* occurred with *Ulmus/Zelkova/Hemiptelea* (*Zelkova*). In Kochi in the Pacific side of Shikoku, evergreen *Quercus* occurred with temperate pinaceous conifers of *Tsuga* and *Abies*. In Kyushu, lucidophyllous forests dominated with *Podocarpus*, *Abies*, or deciduous broadleaved trees, but rarely with temperate conifers such as *Cryptomeria*, *Sciadopitys*, and CTC type.

Period 2.5 ka (Fig. 49)

During period 2.5 ka, pinaceous conifers slightly increased in Hokkaido and the mountainous areas of central Honshu, and evergreen broadleaved forests increased in the coastal areas of central and western Japan, *Fagus* and deciduous *Quercus* dominated in the mountainous areas of central to northern Japan as in previous periods, and *Cryptomeria* increased in the lowland of central and western Japan.

Abies and *Picea* increased with *Betula* in central and northern Hokkaido, but *Picea* dominant assemblages were replaced by deciduous *Quercus* dominant assemblages in eastern Hokkaido, and *Fagus* increased in southern Hokkaido.

In the mountainous areas of central and northern Honshu, *Fagus* continuously occurred in the same area as in the previous age and slightly increased its dominance. Pinaceous forests increased in the higher mountainous areas of central Japan, accompanied by *Betula* and deciduous *Quercus*. In the mountainous

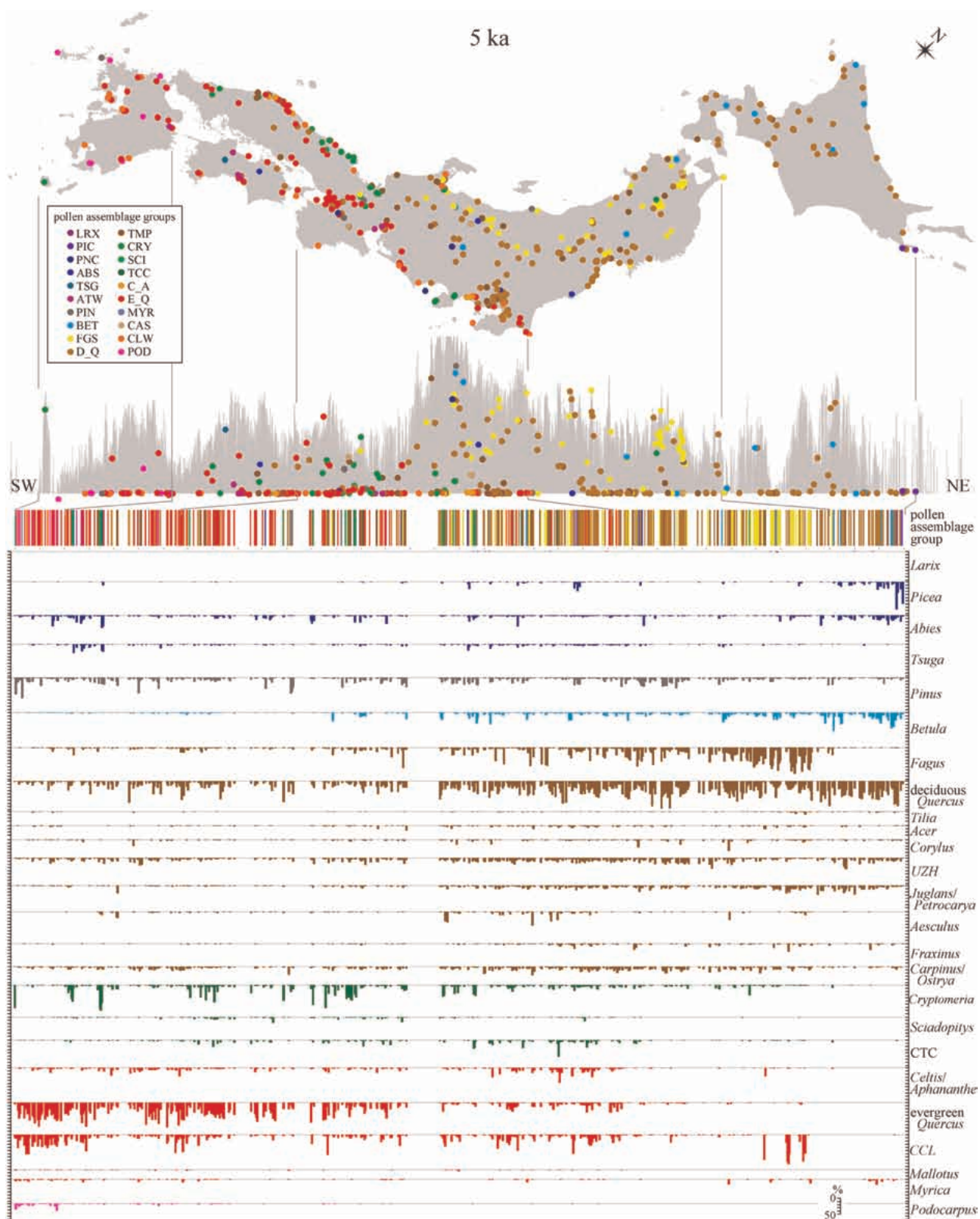


Fig. 48 Horizontal and vertical distribution of pollen assemblage groups with pollen diagram showing southwest to northeast locality series during the post-glacial (period 5 ka). See Fig. 42 for additional explanation.

図 48 後氷期（時期 5 ka）における花粉群グループの分布とその組成。上部に水平・垂直分布を示し、その下に全地点を南西-北東順に並べ、各地点の花粉群グループとその花粉組成を示す。詳細は図 42 参照。

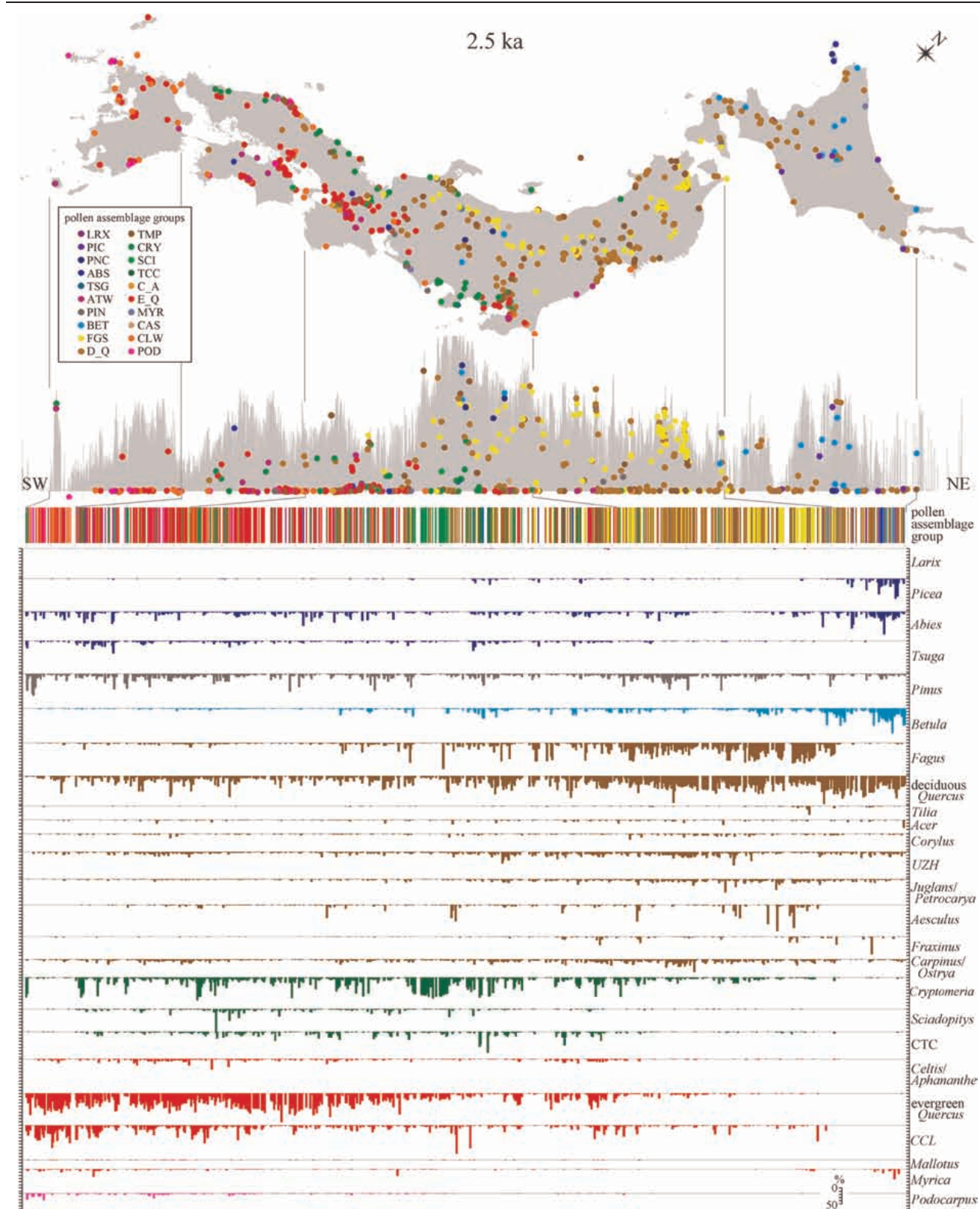


Fig. 49 Horizontal and vertical distribution of pollen assemblage groups with pollen diagram showing southwest to northeast locality series during the post-glacial (period 2.5 ka). See Fig. 42 for additional explanation.

図 49 後氷期（時期 2.5 ka）における花粉群グループの分布とその組成。上部に水平・垂直分布を示し、その下に全地点を南西―北東順に並べ、各地点の花粉群グループとその花粉組成を示す。詳細は図 42 参照。

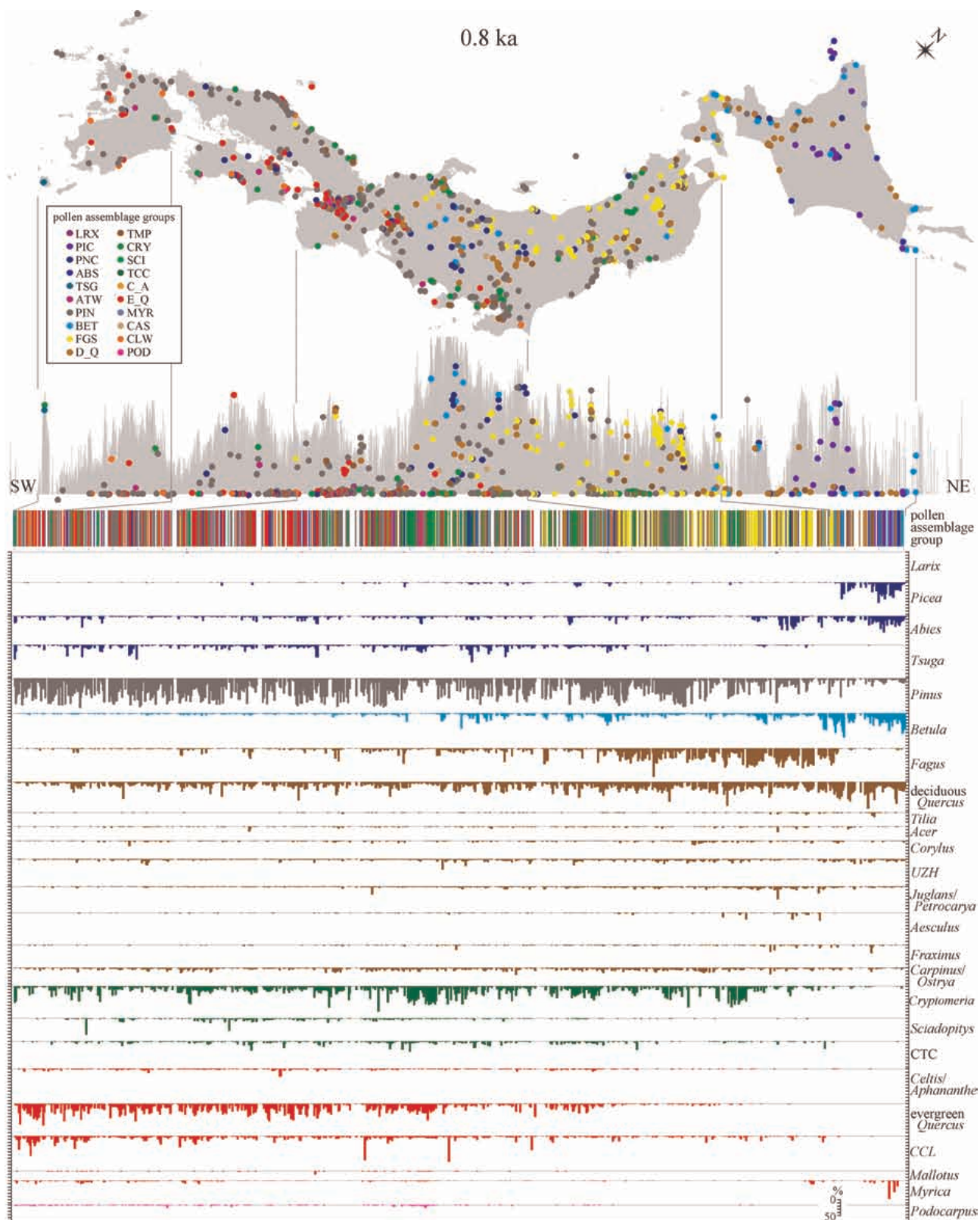


Fig. 50 Horizontal and vertical distribution of pollen assemblage groups with pollen diagram showing southwest to northeast locality series during the post-glacial (period 0.8 ka). See Fig. 42 for additional explanation.

図 50 後氷期（時期 0.8 ka）における花粉群グループの分布とその組成。上部に水平・垂直分布を示し、その下に全地点を南西ー北東順に並べ、各地点の花粉群グループとその花粉組成を示す。詳細は図 42 参照。

areas of western Japan no changes were detected, and forest patches of pinaceous forests, temperate deciduous forests, *Cryptomeria* forests, and evergreen forests continued to occur.

In the lowland, lucidophyllous elements and *Cryptomeria* apparently increased, but regional differences as in the previous age continued to exist. Evergreen *Quercus* increased in almost all the areas except those areas with abundant *Cryptomeria* such as Izu, the Japan Sea coast of western Japan, and Kyushu with an increase of *Castanea/Castanopsis/Lithocarpus*. *Podocarpus* increased in the coastal areas of southern Kyushu and Izumo of western Japan. *Celtis/Aphananthe* decreased totally and only occurred sporadically.

Period 0.8 ka (Fig. 50)

In the recent (period 0.8 ka), *Pinus* dominated, particularly in the lowland except Hokkaido, and other elements decreased totally even in the lower mountainous areas. The timing of increases of *Pinus* differed within and between areas.

Throughout Hokkaido *Picea* and *Abies* increased except for the southwestern part, where *Fagus* increased in the present range of its distribution. In the mountainous areas outside Hokkaido, *Fagus* barely dominated in the previous range of its distribution, but deciduous *Quercus* growing at lower elevations than *Fagus* was hardly affected. On the higher mountainous areas in central Japan, Pinaceous forests continued to exist with *Betula*, enlarging its distribution from that in the previous age. Pinaceous forests also occurred in the lower mountainous areas around Mt. Fuji, where few post-glacial data exist.

In the lowland, the expansion of *Pinus* greatly affected occurrences of other groups, but regional differences seem to have been preserved from previous ages. In this period, *Cryptomeria* continued to occur in the Japan Sea side of northern Honshu and the inland Kanto district, and pinaceous forests sporadically occurred around the Setonai-kai sea with a decline of evergreen broadleaved forests.

Conclusion

Changes in pollen assemblages corresponded to climatic changes since the mid-glacial. With the climatic warming after the last glacial, dominant taxa in pollen assemblages changed from Pinaceae, through temperate deciduous broadleaved trees, to evergreen broadleaved trees in western Japan. This change in dominant taxa was induced not by migration of plants, but by succession of vegetation caused by the climatic change. Autochthonous species fit to the changing

environment quickly became dominant. Chronological occurrence maps of *Fagus* and *Cryptomeria* types apparently showed that not their ranges, but their abundances changed. Percentages of these types at each site were quite low during the last glacial maximum, but frequently high during the post-glacial. Although less clear due to problems in identification, warm temperate elements also showed the same trends and increased from the coastal areas that were wider due to regression during the glacial period. In the post-glacial, species that flourished under the cold dry climate of the last glacial decreased rapidly. However, they did not move northward, but became restricted in distribution. For example, *Picea* and *Pinus koraiensis* that occurred abundantly during the full-glacial now grow fragmentarily in restricted areas of central Japan. *Larix gmelinii* that grew widely in Hokkaido during the last glacial disappeared from Japan in the post-glacial.

Thus, no evidence is obtained for the migration of plants, but vegetation changed with environmental changes since the mid-glacial. Quick response of vegetation to the environment changes is caused by the growth of populations among existing species that are fit to the new environment.

Murata (1995) suggested that the flora of Japan is a mixture of cold elements that are remnants of the northern flora coming down from the north during glacial ages, temperate elements of the Sino-Japanese region, and warm elements coming up from the south. Tsukada (1984) drew a paleo-vegetation map of the Japanese archipelago and estimated a fall of 8°C in average annual temperature and an accompanying shift of vegetation zones. However, as shown in this study, most dominant trees did not seem to have migrated since the mid-glacial. Study of fossils of older ages is necessary to clarify the floral history of longer periods in this archipelago.

Further discussion will be facilitated by re-examining pollen assemblages with finer morphological observation and attention to rare pollen types, along with studies of other plant fossils such as woods, leaves, fruits, or seeds. Unfortunately, voucher specimens for pollen analyses such as sediments, residues, and single-mounts are rarely preserved in public facilities, but personally, and storage and utilization of vouchers as well as the original pollen data in public facilities are urgently needed.

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