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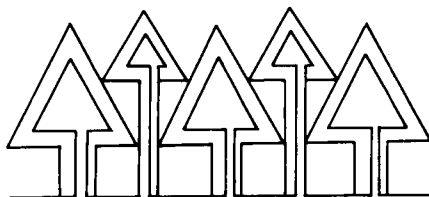
SPECIAL PUBLICATION 2b

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**THE GENUS *Pseudotsuga*:
ANCESTRAL HISTORY AND
PAST DISTRIBUTION**

R. K. HERMANN



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Acknowledgments

The author thanks Dr. Estella B. Leopold of the Department of Botany, University of Washington for thorough manuscript review and valuable counsel. Thanks are also due Dr. Jack A. Wolfe of the U.S. Geological Survey for providing unpublished source material.

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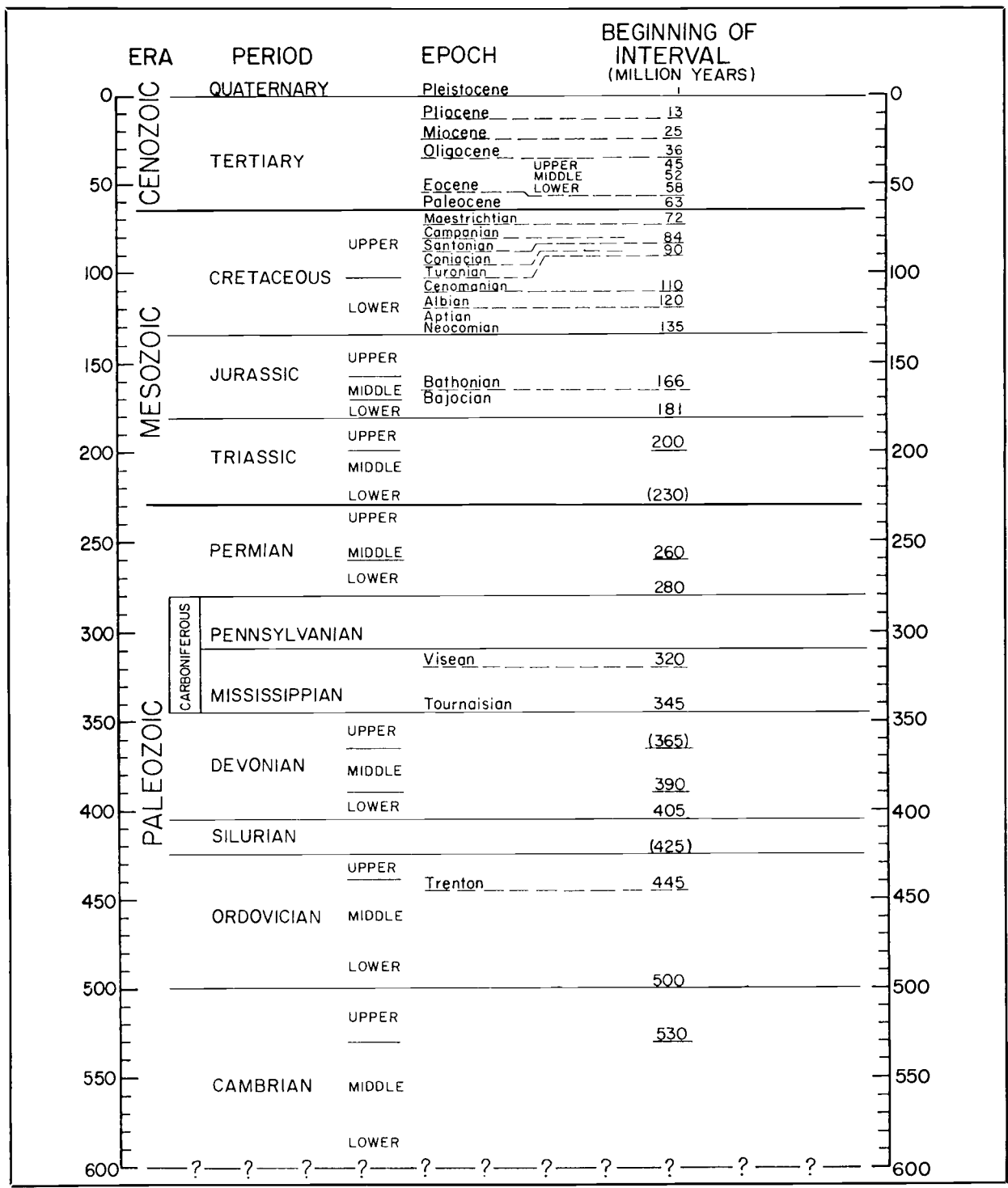


FIGURE 1. Geological time scale. [From Kulp (1961), copyrighted 1961 by the American Association for the Advancement of Science. The figure is used with the permission of the author and the Association.] Changes in the geological time scale since Kulp's article was written now result in the boundary between the Miocene and the Pliocene being placed at 5 million years B.P. (Ryan et al. 1974, Vass and Bagdasarjan 1978). The boundary between the Pliocene and the Pleistocene is now set at 1.8 million years B.P. See also footnote 2 to Table 1 in the present volume.

INTRODUCTION

The present range of the genus Pseudotsuga is strongly discontinuous and is confined to western North America and eastern Asia. Unlike the large and contiguous range of Pseudotsuga in North America, distribution of the genus in Asia is limited to a few isolated mountainous regions in southwestern and eastern China, southern and central Japan, and the island of Taiwan. The fossil record of the genus provides an account, incomplete as it may be, of past changes in the range of the genus up to the present. That record is presented in this, the second in a series of publications attempting to summarize current knowledge of Douglas-fir (referring to Pseudotsuga menziesii unless otherwise noted) and the other species of the genus. For the convenience of the reader, a chart of the geologic eras, periods, and epochs appears as Figure 1.

EVOLUTIONARY HISTORY

Fossil remains of the genus Pseudotsuga in pre-Cenozoic time are not known with one possible exception. Malyavkina (1958) has designated as Pseudotsuga punctata, and as P. punctata var. pseudolimbata, pollen from Lower Cretaceous deposits of the Eastern-Gobi depression in eastern Mongolia. This assignment of pollen to the genus Pseudotsuga, however, is not substantiated by megafossils. By the time Pseudotsuga appears in the Tertiary fossil record, it closely resembles the modern genus. Thus, we lack a record of most of the evolutionary history of the genus Pseudotsuga. All we have are hypotheses based on phylogenetic studies.

Jeffrey (1905) concluded that the Pinaceae (Abietaceae), together with the Taxodiaceae and Cupressaceae, developed as one of two lines from an ancient "pinean" stock. He divided the Pinaceae into an older and more primitive group which included Pinus, Picea, Pseudotsuga, and Larix, and into a younger group composed of Abies, Cedrus, Pseudolarix, and Tsuga. Gaussen (1965) similarly proposed that the members of the Pinaceae evolved from a hypothetical progenitor, Priscopinus.

On the basis of morphological, anatomical, and cytological studies, two principal hypotheses have been advanced concerning the phylogenetic position of Pseudotsuga within the family Pinaceae. One theory holds that Pseudotsuga and Larix branched from a common lineage to Pinus (Boureau 1938; Ferré and Gaussen 1945, 1955). The other hypothesis is that Pseudotsuga descended from Larix, which, in turn, supposedly descended from Pinus (Flous 1936, Campo-Duplan 1950, Gaussen 1966). Even before these theories were proposed, Doyle (1918) called attention to the striking similarities between Pseudotsuga and Larix. They include anatomy of wood, wingless pollen, and structure of the female gametophyte. The close phylogenetic relationship of the two genera is further indicated by the close resemblance of the structure of their nuclei (Vabre-Durrieu 1956). The hypotheses regarding the phylogenetic history of Pseudotsuga, however, are open to question. Staplin et al. (1967) emphasized that pollen of both Larix and Pseudotsuga, which are similar, show profound structural differences from those of other members of the Pinaceae. Some of the morphological characteristics of pollen of the two genera suggest a closer relationship with the Araucariaceae than with the Pinaceae.

THE FOSSIL RECORD

The fossil record of Pseudotsuga-like forms in North America begins in the Early Tertiary about 50 million years ago. Since then, the morphological characteristics of the genus have changed little. Cones, seeds, and needles of the modern Pseudotsuga can scarcely be distinguished from those of its ancestors.

In Japan, the fossil record of the genus is more extensive than seems to be realized generally. However, I was unable to find published accounts of fossil Pseudotsuga in China.

The fossil evidence available does not provide any clues as to whether the genus originated in Asia or North America. A migration route may have existed between Asia and North America in Early Tertiary times by way of the Bering Strait (Florin 1963). MacGinitie (1933) mentioned discovery of Douglas-fir cones by Mason in Tertiary deposits of St. Lawrence Island in the Bering Sea. This report, however, has remained unconfirmed.

Finds of fossil Pseudotsuga (Kräusel 1926, Gothan and Weyland 1954, Walter 1970) have been claimed from several locations in Europe. Florin (1963) has disputed such claims on grounds of insufficient material for identification.

FOSSIL Pseudotsuga IN NORTH AMERICA

Even though the fossil record of Pseudotsuga in western North America is far more extensive than in eastern Asia or Europe, it is still quite fragmentary. Whatever inferences we make as to evolution and past ranges of the genus and its role in ancient forests necessarily involve a considerable element of speculation and may have to be revised as new evidence is uncovered.

LaMotte's (1952) Catalogue of Cenozoic plants of North America through 1950 contains the most recent compilation of megafossil records of Pseudotsuga. One can divide the list into two groups according to plant parts employed for identification.

The first group comprises records based solely on identification of wood specimens. Brought up to date, this group includes:¹

- | | |
|--|------------------|
| <u>Piceoxylon pseudotsugae</u> Gothan, 1905, Abhandl. Preuss. Geol. Landesanstalt n.F., Heft 44:102, California, Tertiary. | (Gothan 1905) |
| <u>Pityoxylon annulatum</u> Platen, 1908, Naturf. Gesellsch. Leipzig, Sitzungsber. 34:20, 109, Petrified Forest, Calistoga, California, Pliocene; Arizona, location unknown, Tertiary. | (Platen 1908) |
| <u>Pseudotsuga annulata</u> (Platen) Torrey, 1923, Boston Soc. Nat. Hist., Mem. 6:67, Cape Blanco, Curry County, Ore., Miocene. | (Torrey 1923) |
| <u>Pseudotsuga douglasii</u> Carrière = <u>Pseudotsuga menziesii</u> (Mirbel) Franco. <u>Pseudotsuga douglasii</u> Carrière, Recent. Penhallow 1904, Roy. Soc. Can. Trans., 2nd ser., vol. 10, sec. 4:62, Mystic Lake, Bozeman, Montana, Pleistocene. | (Penhallow 1904) |
| Penhallow, 1907, Manual N. Amer. Gymnosperms: 272, Mystic Lake, Bozeman, Montana, Pleistocene. | (Penhallow 1907) |
| <u>Pseudotsuga miocena</u> Penhallow, 1902, Roy. Soc. Can. Trans., 2nd ser., vol. 8, sec. 4:68, pls. 15-16, Horsefly R., Brit. Col., Eocene or Oligocene. Penhallow, 1903, Roy. Soc. Can. Trans., 2nd ser., vol. 9, sec. 4:47, fs. 12-13, Cariboo, Brit. Col., Eocene or Oligocene; Great Valley and Porcupine Creek | (Penhallow 1902) |
-

¹ In this and subsequent lists, all entries are cited in standard taxonomic format and are followed (right margin) by the appropriate reference to Literature Cited at the end of this publication.

- Groups, Alberta, Paleocene. Penhallow, 1907, Manual N. Amer. Gymnosperms: 276, Great Valley and Porcupine Groups, Alberta, Paleocene; Cariboo, Brit. Col., Eocene or Oligocene. Penhallow, 1908, Rept., Tertiary Plants Brit. Col.: 80, Horsefly R., Brit. Col., Eocene or Oligocene; Pascapoo, Porcupine Creek, Alberta, Paleocene. (Penhallow 1903)
(Penhallow 1907)
(Penhallow 1908)

Pseudotsuga pseudotsugae (Gothan) Beck, 1945, Northw. Sci. 19:95, fs. 4, 30, Squaw Creek, Ellensburg, Wash., Miocene. (Beck 1945a)

Pseudotsuga sp. Beck, 1945, J. For. 43:336, Russel Forests, Wash., Miocene. (Beck 1945b)

Pseudotsuga sp. Hopkins and Benninghoff, 1953, Geol. Soc. Amer. Bull. 64(12, pt. 2):1436, Kusitrin R., Seward Penins., Alaska, Pleistocene. (Hopkins and Benninghoff 1953)

Pityoxylon is a term coined by the German paleobotanist Kraus in the 1860's to designate woods resembling the pitchy or pine-like conifers. At the turn of the century, Gothan (1905) created the form-genus Piceoxylon to denote spruce-like woods formerly included with the pines. Assignment of a fossil wood, determined from thin sections of often poorly preserved specimens, to the presumed equivalent of a modern genus must be accepted with reservations. Some of the fossil wood described by Gothan (1905) and Platen (1908) very likely represents a forerunner of modern Pseudotsuga. Apparently, the specimens came from fossil-bearing beds in northern California in which occurrence of Douglas-fir has since been confirmed for the Late Tertiary (Dorf 1930). Whether or not Pseudotsuga miocena represents a Douglas-fir is uncertain. Torrey (1923) challenged the validity of Penhallow's identifications. The material of Beck (1945a, 1945b) probably represents Pseudotsuga. He excluded the possibility that the wood was larch (Larix), which is similar to that of Douglas-fir, on the basis of strict 1-seriate cross-field pitting and want of terminal parenchyma.

The second group comprises records based on identification of either leaves, cones, and seeds, or combinations of these. The list, implemented from reports published since LaMotte's compilation, includes:

Pseudotsuga laticarpa Lakhampal, 1958, Carnegie Inst. Wash. Publ. 35(1):21, pl. 1, f. 4, Layng Creek 23 mi. E of Cottage Grove, Ore., Oligocene. (Lakhampal 1958)

Pseudotsuga longifolia Axelrod, 1964, Univ. Calif. Publ. Geol. Sci. 51:109, pl. 6, fs. 33-38, pl. 7, fs. 2-3, Beaverdam: Trapper Creek, Cassia County, Ida., Miocene. (Axelrod 1964)

Pseudotsuga macrocarpa Mayr = Pseudotsuga macrocarpa (Torrey) Mayr = Pseudotsuga macrocarpa (Vasey) Mayr. Pseudotsuga macrocarpa Mayr, Recent. Penhallow, 1904, Roy. Soc. Can. Trans., 2nd ser., vol. 10, sec. 4:70, Orleans, Humboldt County, Calif., Pleistocene. Mason, 1940, Madroño 5:233, f. 1, Carpinteria, Santa Barbara County, Calif., Pleistocene. (Penhallow 1904)
(Mason 1940)

Pseudotsuga macrocarpa (Torrey) Mayr, Recent. Axelrod, 1966, Univ. Calif. Publ. Geol. Sci. 60:62, pl. 5, fs. 16-21, Bautista: Soboba, Riverside County, Calif.; Bautista: Bautista Creek, Calif., Pleistocene. (Axelrod 1966b)

- Pseudotsuga masoni MacGinitie, 1933, Carnegie Inst. Wash. Publ. 416:47, pl. 3, fs. 1-3, Trout Creek, Harney County, Ore., Miocene. Dorf, 1936, Carnegie Inst. Wash. Publ. 476:107, pl. 1, f. 3, Idaho: Weiser, Idaho, Pliocene.² Smith, 1941, Amer. Midl. Nat. 25:492, pl. 2, fs. 4-5, Payette: Thorn Creek, Boise County, Ida., Miocene. Becker, 1961, Geol. Soc. Amer. Mem. 82:49, pl. 7, f. 17-19, Ruby River Basin, T7S, R5W, Mont., Oligocene. (MacGinitie 1933)
(Dorf 1936)
(Smith 1941)
(Becker 1961)
- Pseudotsuga masoni MacGinitie. LaMotte = Cedrela oregoniana (Lesquereux) Brown. (Brown 1937)
- Pseudotsuga masoni MacGinitie. Oliver = Picea sonomensis Axelrod. (Oliver 1934)
- Pseudotsuga masoni MacGinitie. MacGinitie = Pinus knowltoni Chaney. (MacGinitie 1933)
- Pseudotsuga taxifolia (Poiret) Britton = Pseudotsuga menziesii (Mirbel) Franco. Pseudotsuga taxifolia (Poiret) Britton, Recent. Lawson, 1893, Univ. Calif. Dept. Geol. 1(4):145, Merced: Mussel Rock, San Francisco County, Calif., Pliocene. (Lawson 1893)
Hannibal, 1911, Torrey Bot. Club Bull. 38:335, Santa Clara: Calabazas Canyon, Santa Cruz Mts., Calif., Pliocene. Mason, (Hannibal 1911)
1927, Carnegie Inst. Wash. Publ. 346:151, Merced: Mussel Rock, San Francisco County, Calif., Pliocene. Chaney and (Mason 1927)
Mason, 1930, Carnegie Inst. Wash. Publ. 415:8, pls. 3-4, pl. 5, fs. 1-3, Santa Cruz, Willow Creek, Santa Cruz Is., Calif., Pleistocene. Potbury, 1932, Carnegie Inst. Wash. Publ. 415:31, (Chaney and
pl. 1, f. 2, pl. 3, f. 2, San Bruno, San Mateo County, Calif., Mason 1930)
Pleistocene. Chaney and Mason, 1933, Carnegie Inst. Wash. (Potbury 1932)
Publ. 415:57, Carpinteria, Santa Barbara County, Calif., Pleistocene. Chaney and Mason 1933, Carnegie Inst. Wash. (Chaney and
pl. 6, f. 4, pl. 7, fs. 1-2, Tomales: Marin County, Calif., Mason 1933)
Pleistocene. (Mason 1934)
- Pseudotsuga premacrocarpa Axelrod, 1937, Carnegie Inst. Wash. Publ. 476:167, pl. 3, fs. 1-2, Mt. Eden: Beaumont, Riverside County, Calif., Pliocene. (Axelrod 1937)
- Pseudotsuga sonomensis Dorf, 1930, Carnegie Inst. Wash. Publ. 412:72, pl. 6, fs. 2-4, Sonoma: Petrified Forest, Calistoga; Neer's Hill, Santa Rosa; Wildcat: Garberville, Calif.; Merced: Mussel Rock, San Francisco County; Santa Clara: Calabazas Canyon, Saratoga, Calif., Pliocene. Axelrod, 1944, Carnegie Inst. Wash. Publ. 553:191, pl. 36, f. 3, Sonoma: Neer's Hill, (Dorf 1930)
Santa Rosa, Sonoma County; Petrified Forest, Napa County, Calif., Pliocene. Axelrod, 1944, Carnegie Inst. Wash. Publ. (Axelrod 1944b)
553:251, pl. 42, f. 1, Alvord Creek: Alvord, Harney County, Ore., Pliocene. Axelrod, 1956, Univ. Calif. Publ. Geol. Sci. (Axelrod 1944a)
33:277, pl. 4, fs. 21-22, Aldrich Station: Aldrich Hill, Lyon County, Nev., Mio-Pliocene. Chaney and Axelrod, 1959, (Axelrod 1956)
Carnegie Inst. Wash. Publ. 617:143, pl. 13, fs. 13-15, Blue Mts., Grant County, Ore.; Trout Creek: Trout Creek, Harney

² Revision of the geologic time scale (Ryan et al. 1974, Vass and Bagdasarjan 1978) places this fossil, not in the Pliocene, but in the Late Miocene. The same principle applies to other ascriptions to the Pliocene in this and subsequent lists.

- County, Ore.; Payette: Thorn Creek, Boise County, Ida., Miocene. Axelrod, 1962, Univ. Calif. Publ. Geol. Sci. 39(3):228, pl. 42, fs. 10-11, Coal Valley: Chalk Hills, Storey County, Nev., Pliocene. Axelrod, 1964, Univ. Calif. Publ. Geol. Sci. 51:110, pl. 6, fs. 26-30, Beaverdam: Trapper Creek, Cassia County, Ida., Miocene. Axelrod, 1966, Univ. Calif. Publ. Geol. Sci. 59:63, pl. 8, fs. 1-5, Dead Horse tuff: Copper Basin, Elko County, Nev.; Bull Run Basin, Elko County, Nev.; Thunder Mt., N. Centr. Ida., Eocene. (Chaney and Axelrod 1959) (Axelrod 1962) (Axelrod 1964) (Axelrod 1966a)
- Pseudotsuga taxifoliodea Arnold, 1935, Wash. Acad. Sci. J. 25:378, f. 1, Trout Creek, Harney County, Ore., Miocene. (Arnold 1935)
- Pseudotsuga sp. Axelrod, 1934, Amer. Mus. Novitates, No. 729, 2, Eden: Beaumont, Riverside County, Calif., Pliocene. (Axelrod 1934)
- Pseudotsuga sp. Scott, 1927, Torrey Bot. Club Bull. 54:9, Niti-nat Lagoon, Vancouver Is., Brit. Col., Oligocene or Miocene. (Scott 1927)

Pseudotsuga sonomensis appears to be the fossil species most closely related to modern Pseudotsuga menziesii. Chaney and Axelrod (1959) regard Pseudotsuga sonomensis, P. masoni, and P. taxifoliodea as synonymous, because the described specimens do not differ in any fundamental way. Pseudotsuga laticarpa may also represent P. sonomensis. Laxhanpal (1958) emphasized that needles and cones of P. laticarpa were like those of P. sonomensis, but he distinguished a new species because the seeds were like those referred to P. masoni by Smith (1941).

Wood from Mad River of Humboldt County in northern California, assigned by Penhallow (1904) to Pseudotsuga macrocarpa, belongs most likely to P. menziesii (Mason 1940). P. macrocarpa occurs much farther south, and the fossil record does not indicate that the range of this species ever extended into northern California.

Pseudotsuga in the Carpinteria flora probably belongs to P. macrocarpa. Some of the waterworn chips and logs found in the tar pits of Carpinteria were identified as Pseudotsuga menziesii by Chaney and Mason (1933). They assumed that the wood had been carried as marine drift southward along the coast and had been washed up on the beach amidst debris of the local flora. Axelrod (1966b) pointed out that geologic evidence does not favor the hypothesis of Chaney and Mason but rather indicates that the wood was transported to the site by streams draining the Santa Ynez Mountains directly to the north. Axelrod believes that discovery of a waterworn cone of Pseudotsuga macrocarpa in the Carpinteria deposit, radiocarbon-dated as 38,000 years B.P.,³ and supposedly brought down from the mountains to the north (Mason 1940), further supports the assumption that the wood of Pseudotsuga from the Carpinteria pits represents bigcone Douglas-fir.

Of particular interest is Pseudotsuga longifolia from the Miocene Trapper Creek flora of southern Idaho as noted by Axelrod (1964). So far, this is the only record of a fossil Douglas-fir that does not resemble the two modern representatives of the genus in western North America. Axelrod believes that the fossils are most closely related to the east-Asian Pseudotsuga forrestii. Both Pseudotsuga japonica and Pseudotsuga sinensis have shorter needles and shorter winged seeds than Pseudotsuga longifolia. Perhaps P. longifolia should be considered to resemble Pseudotsuga wilsoniana because the taxonomic status of P. forrestii is doubtful (Wilson 1926).

³ A.D. 1950 is now accepted as the standard year of reference for dates B.P. [Before Present] (Editorial statement, Vol. 5, Radiocarbon). Note that, throughout this text, "years B.P." refers to exact radiocarbon dating, whereas "years ago" is an inexact approximation.

The microfossil record of Pseudotsuga has also become extensive over the last 30 years. Description of type specimens, however, has begun only recently. Those known to me are:

- Pseudotsuga taxifolia (Poiret) Britton = Pseudotsuga menziesii (Mirbel) Franco. Pseudotsuga taxifolia (Poiret) Britton, Recent; Axelrod and Ting, 1960, Univ. Calif. Publ. Geol. Sci. 39(1):55, pl. 15, f. 1, pl. 20, f. 1, Coso: Haiwee Reserv., ca. 10 mi. SE of Olanda, Calif., SW 1/4 sec. 31, T4S, R31E, Owens Gorge few mi. N of Bishop, Calif.; Crowley Pt., State Hwy. 190, 0.6 mi. SSE of Crowley Pt. Lookout, Calif.; San Joaquin Mt., 10 mi. NW of Mannothe, Calif., Pliocene. Axelrod and Ting, 1961, Univ. Calif. Publ. Geol. Sci. 39(2):151, pl. 35, f. 1, Chagoopa: Sec. 33, T19S, R33E, Beakoven Meadow, 2 mi. N of crest of Monache Mt., Calif.; Sec. 29, T18S, R35E, S fork Kern R., Calif.; Sec. 21, T22S, R36E, Kennedy Meadow, Calif.; Sec. 25, T15S, R36E, Alabama Hills, 1.5 mi. SSW of Lone Pine, Calif., Pleistocene. (Axelrod and Ting 1960)
- (Axelrod and Ting 1961)

Ages of fossil Pseudotsuga in the above lists are those indicated by the authors. The discordance between potassium-argon dates and many paleobotanical age assignments as discussed by Evernden and James (1964) demonstrates the problems associated with age determinations. Some of the dates cited here may require revision.

Tertiary Range

The fossil record of Pseudotsuga provides little information on its range in North America during the Early and Middle Tertiary. Climate at that time was very mild without pronounced regional differentiation and the major mountain systems in the western part of the continent had not yet come into existence. Temperate forests composed of deciduous hardwoods and conifers existed in Alaska and Canada and ranged southward at moderate altitudes in the interior. Representation of Pseudotsuga in floras considered to represent Eocene upland forests is known only from north-central Idaho and northeastern Nevada (Axelrod 1966a). This is also the earliest record of fossil cones, seeds, and leaves of Pseudotsuga. The notable absence of Douglas-fir from Eocene fossil floras in the Rocky Mountains (Leopold and MacGinitie 1972) suggests that Pseudotsuga was a very minor component of forests or had an extremely limited range at that time.

Occurrence of Douglas-fir in Oligocene floras is reported from southwestern Montana (Becker 1961) and from central and western Oregon (Lakhanpal 1958). The fossil flora from western Oregon in which Pseudotsuga occurs is thought to represent a westward extension of an Oligocene hardwood/conifer forest from central Oregon.

Pseudotsuga may have been present in central British Columbia in the Early Oligocene. Among microfossils recovered from Oligocene sediments that outcrop along the Fraser River in the central interior of British Columbia was pollen assigned by Piel (1971) to the genus Pseudotsuga. It came from an assemblage of species, which by inference suggests an indication of a climate with wet summers and dry winters, a type of climate inferred for other localities of Tertiary fossil floras by Chaney (1938, 1959), Axelrod (1956, 1964), and Smiley (1963). The earliest known record of Pseudotsuga pollen in the Rocky Mountains comes from the Florissant fossil beds of Early Oligocene age in Colorado (Estella B. Leopold, personal communication).

Broad-leaved deciduous forests remained dominant in western North America during the Early and Middle Miocene. Upland vegetation in the Northwest contained Pinaceae only as a minor element in contrast to Alaska, where conifers of this family had become dominant in the uplands. The Nuwok pollen assemblage from the Arctic slope of Alaska indicates that,

until at least the Middle or Late Miocene, a rich coniferous forest dominated by Picea, Pinus, and Tsuga, and probably also containing Cupressaceae, Abies, and Larix/Pseudotsuga, grew as far north as latitude 70°N (Wolfe 1972). Miocene megafossils of Pseudotsuga, except for those from Cape Blanco (Torrey 1923) on the southern Oregon coast, are all from floras of distinct upland aspect in the Columbia Plateau region or adjacent to it (LaMotte 1936, Chaney 1959). Pollen spectra, however, show the presence of Douglas-fir in the Pacific Northwest and the Alaskan upland forests from the Late Oligocene to the earliest Pleistocene (Leopold 1969; Wolfe 1962, 1969; Wolfe and Leopold 1967).

The presence of Pseudotsuga pollen in plant-bearing deposits indicates that Douglas-fir grew in south-central British Columbia in the Late Miocene or Early Pliocene (Mathews and Rouse 1963). The most likely climate suggested by the fossil flora to which Pseudotsuga belonged is one that was cool temperate with higher annual precipitation and warmer annual temperature than are found in the same area today. Quesnel, the location of one of the deposits, has today an annual average precipitation of 42 cm and an average temperature of 5°C. Assumed annual temperatures in that locality during the Late Tertiary were 5.5–13°C; precipitation was probably 102 cm annually. Quesnel now lies beyond the northern limit of the range of Douglas-fir. As in the pollen spectra from western Washington and Oregon, frequency of occurrence of Douglas-fir pollen was very low in the spectra from British Columbia. Pollen of Pseudotsuga is definitely present in Late Miocene beds of the Goose Creek area in southern Idaho and in Pliocene rocks of the Snake River Plain, Idaho (Leopold and MacGinitie 1972).

The general trend toward a cooler climate, apparent since the close of the Eocene and only temporarily reversed in the Mid-Miocene, continued in the Late Miocene. Megafossils and pollen data point to major changes in Late Miocene vegetation. Many genera and species became extinct, and the Late Miocene flora assumed a rather modern aspect. On the basis of the vegetational changes reflected by the fossil record and their climatic implications, Wolfe and Leopold (1967) estimated that a drop of about 7°C took place in the mean July temperature within a time span of about 4 million years.

Wolfe (1969) summarized Late Miocene forest cover of northwestern North America as follows:

ALASKA. Conifer forest of Abies grandis, Picea sitchensis, Picea glauca, Pinus monticola, and Tsuga heterophylla, accompanied by Betula papyrifera, that is, a birch-pine forest.

COLUMBIA PLATEAU--CASCADE RANGE. Conifer forest of Abies concolor, Abies magnifica, aff. Cedrus, Keteleeria, Picea breweriana, Picea magna, Pinus monticola, Pinus ponderosa, Tsuga heterophylla, Thuja plicata, and Sequoia sempervirens, accompanied by Betula papyrifera, Quercus chrysolepis, Ulmus spp., and Arbutus idahoensis, that is, a spruce-cedar forest.

NEVADA. Conifer forest of Abies concolor, Picea breweriana, Picea magna, Chamaecyparis nootkatensis, Tsuga heterophylla, accompanied by Quercus chrysolepis, that is, a spruce-cedar-live oak forest.

PUGET-WILLAMETTE LOWLAND. Broad-leaved deciduous forest of Carya bendirei, Fagus, Quercus deflexiloba, Liquidambar, and Arbutus, accompanied by Thuja plicata and Sequoia sempervirens, that is, a hickory-oak-beech forest.

CENTRAL CALIFORNIA. Mixed broad-leaved evergreen and deciduous woodland of Quercus chrysolepis, Castanopsis, Carya, Persea, and Arbutus, accompanied by Pinus (closed cone), that is, a live oak-madrone woodland.

Except for the live oak-madrone woodland, Pseudotsuga was represented in these forest associations, though only as a minor component.

Increasing aridity, greater seasonal amplitudes of temperature, and continuing uplift of the Cordilleran mountain chains in the Pliocene considerably modified vegetation over western North America (Axelrod 1948, 1966c). The fossil record for this period is notably poor, but it indicates that compared to the Miocene, Pliocene forests were less diverse in their composition. Conifer forests, and with them Douglas-fir, apparently retreated toward northern areas and into higher altitudes of mountains. Pollen studies (Wolfe, personal communication) indicate the presence of Douglas-fir during the Pliocene in western Oregon and Washington. The pollen stems from the Early Pliocene Troutdale Formation near Gladstone, Oregon, and from Early Pliocene marine beds near Grays Harbor, Washington. A third spectrum containing Douglas-fir is from marine beds of the Late Pliocene or pre-glacial Pleistocene age, several miles north of Grays Harbor. All three spectra, however, show only small amounts of Douglas-fir.

The Late Pliocene marks the first and only time that Pseudotsuga pre-macrocarpa, the predecessor of modern Pseudotsuga macrocarpa, appears in the Tertiary fossil record (Axelrod 1937, 1950). The character of the accompanying flora was as distinct from that of floras containing Pseudotsuga sonomensis as is the modern forest in which Pseudotsuga macrocarpa lives from the modern forest communities of which Pseudotsuga menziesii is a member. This pattern suggests that bigcone Douglas-fir had already in the Miocene a fairly restricted range.

The Tertiary history of Douglas-fir may be summarized with the statement that ancestral Pseudotsuga was represented through much of its present range but extended considerably farther north than today (Fig. 2, Table 1). However, Douglas-fir does not appear to have been a significant component of Tertiary vegetation. This assumption is based on several considerations. Megafossil remains of the genus are noticeably scarce in Tertiary floras. This alone would not be sufficient to conclude that Pseudotsuga was only a minor component of Tertiary forests because relative representation of megafossils is a doubtful basis for reconstruction of ancient vegetation. The microfossil record, however, suggests also an insignificant role of Pseudotsuga in Tertiary forests because pollen frequency of Pseudotsuga is very low in pre-Pleistocene pollen assemblages known so far. However, it must be remembered that Pseudotsuga is only a moderate pollen producer in its coastal range (Tsukada 1982) and a poor pollen producer in its interior range (Baker 1976). Thus, Douglas-fir may also be underrepresented in pollen profiles of Tertiary age.

Notwithstanding the generally subordinate role of Douglas-fir in Tertiary forests, it may have been prominent locally under particularly favorable conditions. This appears to have been the case in the Miocene Vantage Forest of the Russel Forests complex in the Columbia River basin of central Washington. Beck (1945b) reported that half of the thousands of petrified Vantage logs are Douglas-fir.

Quaternary Range

The Pleistocene set the stage for the development of Douglas-fir forests as a major vegetational unit in medium latitudes and medium altitudes of northwestern North America (Mason 1947). The repeated growth and waning of the huge ice sheets that covered vast areas of temperate North America, and the climatic changes associated with the alternation of glacial and interglacial periods, suggest at once large fluctuations in the range of Douglas-fir at that time.

The extent of glaciation in western North America is today rather accurately known. The main body of the Cordilleran glacier complex lay in Canada between the Coast Ranges and the Rocky Mountains. The ice advanced into western Washington in the Early and Middle Pleistocene during the Salmon Springs Glaciation, which is probably older than the "classical Wisconsin" of the Great Lakes region of central North America, and again in the Late Pleistocene during the Fraser Glaciation to about latitude 47°N (Armstrong et al. 1965, Crandell 1965). Ice also covered the mountains of the Olympic Peninsula, the higher

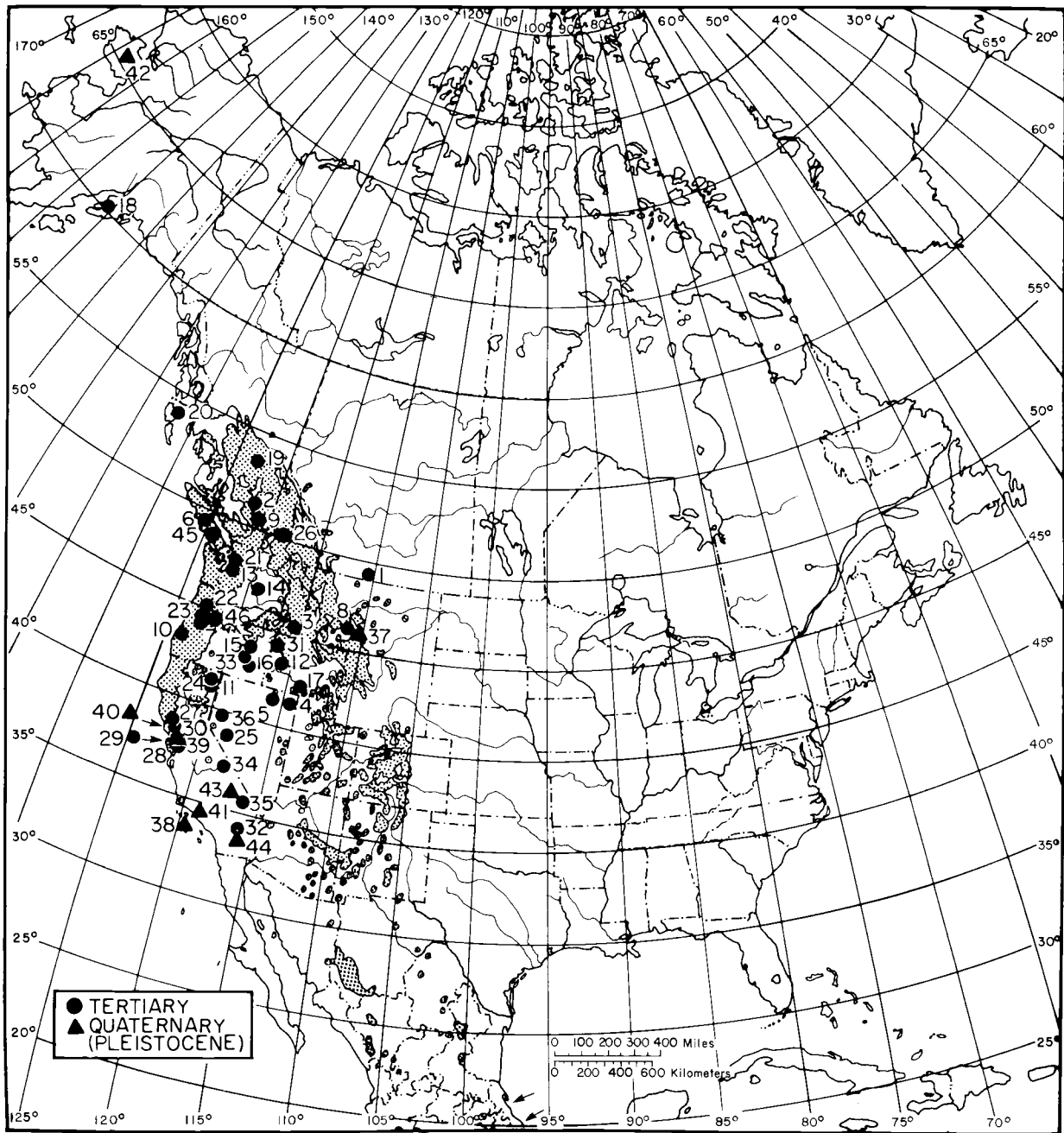


FIGURE 2.

Geographic location of finds of *Pseudotsuga* megafossils from the Tertiary and the Quaternary, and Tertiary microfossils, in North America. Numbers on map refer to those in Table 1. [Modern distribution of Douglas-fir adapted from Little (1971); the map is used with the permission of the U.S. Department of Agriculture, Forest Service.]

TABLE 1.
GEOGRAPHIC LOCATIONS OF FINDS OF FOSSIL PSEUDOTSUGA IN NORTH AMERICA. (NUMBERS REFER TO LOCATIONS INDICATED IN FIGURE 2.)

Years ago ¹ Epoch and location	beginning	Reference
PALEOCENE	63x10 ⁶	
1. Great Valley and Porcupine Groups, Alberta		Penhallow 1907
EOCENE	58x10 ⁶	
2. Horsefly River, Cariboo, British Columbia		Penhallow 1902
3. Thunder Mt., Idaho		Axelrod 1966a
4. Copper Basin, Nevada		Axelrod 1966a
5. Bull Run, Nevada		Axelrod 1966a
OLIGOCENE	36x10 ⁶	
6. Nitinat Lagoon, Vancouver Island, British Columbia		Scott 1927
7. Layng Creek, Oregon		Lakhanpal 1958
8. Ruby River Basin, Montana		Becker 1961
9. Central interior British Columbia		Piel 1971
MIOCENE	25x10 ⁶	
10. Cape Blanco, Oregon		Torrey 1923
11. Cedarville, California		LaMotte 1936
12. Thorn Creek, Idaho		Smith 1941
13. Squaw Creek, Washington		Beck 1945a
14. Russel Forests, Washington		Beck 1945b
15. Blue Mountains, Oregon		Chaney and Axelrod 1959
16. Trout Creek, Oregon		Chaney and Axelrod 1959
17. Trapper Creek, Idaho		Axelrod 1964
18. Type Homerian, Alaska		Wolfe 1969
19. Quesnel, British Columbia		Wolfe 1969
20. Skonum, Queen Charlotte Islands, British Columbia		Wolfe 1969
21. Mashel, Washington		Wolfe 1969
22. Weyerhaeuser, Oregon		Wolfe 1969
23. Hidden Lake, Oregon		Wolfe 1969
24. Pit River, California		Wolfe 1969
MIO-PLIOCENE ²	15-5x10 ⁶	
25. Aldrich Station, Nevada		Axelrod 1956
26. South-central British Columbia		Mathews and Rouse 1963
27. Calistoga, California		Platen 1908
28. Santa Cruz, California		Hannibal 1911
29. Merced, California		Mason 1927
30. Sonoma, California		Dorf 1930
31. Weiser, Idaho		Dorf 1936
32. Mount Eden, California		Axelrod 1937
33. Alvord Creek, Oregon		Axelrod 1944a
34. Owens Gorge, California		Axelrod and Ting 1960
35. Haiwee Reservoir, California		Axelrod and Ting 1960
36. Chalk Hills, Nevada		Axelrod 1962
PLEISTOCENE	1.8x10 ⁶	
37. Mystic Lake, Montana		Penhallow 1904
38. Willow Creek, Santa Cruz Island, California		Chaney and Mason 1930
39. San Bruno, California		Potbury 1932
40. Tomales, California		Mason 1934
41. Carpinteria, California		Chaney and Mason 1933
42. Kusitrin River, Alaska		Hopkins and Benninghoff 1953
43. Chagoopa, California		Axelrod and Ting 1961
44. Soboba, California		Axelrod 1966b
45. Vancouver Island, British Columbia		Alley 1979
46. Lookout Creek, Oregon		Gottesfeld et al. 1981

¹ According to the geological time scale by Kulp (1961).

² Since publication of the papers referred to here as numbers 25 through 36, revision of the geological time scale (Ryan et al. 1974, Vass and Bagdasarjan 1978) has changed the boundary between the Miocene and the Pliocene. Once set at 15+ million years B.P., it now is universally considered to be 5 million years B.P. That change does not merely involve new dates but assignment of a block of "Pliocene" beds to the Late Miocene. Hence, most of the floras at locations listed under numbers 25 through 36, originally designated as Pliocene, now fall in the Miocene. Therefore, fossil remains of Pseudotsuga from these locations are listed here as Mio-Pliocene.

elevations of the Washington and Oregon Cascades, and the Klamath Mountains. In Oregon east of the Cascade Range, glaciation was restricted to mountainous areas above altitudes of 2,400 m. The largest of these is in the Wallowa Mountains.

Four glaciations are recognized in the Pacific Northwest. As listed by Heusser (1977, p. 285), "These are, beginning with the oldest, Orting, Stuck, Salmon Springs [47,000-34,000 years B.P.], and Fraser. Interglaciations are named Alderton (Orting-Stuck), Puyallup (Stuck-Salmon Springs), and Olympia [34,000-28,000 years B.P.] (Salmon Springs-Fraser); a non-glacial interval which separates the Salmon Springs into older and younger stages is unnamed. Fraser Glaciation (after 28,000-10,000 years B.P.) ... consists of the early, alpine Evans Creek Stade and the lowland Vashon Stade, the Everson Interstade (13,500-11,000 years B.P.), and the Sumas Stade (about 11,000 years B.P.). The Vashon Stade represents the last occupation of the Puget Lowland by a major ice lobe." During the Sumas Stade, a lobe of the Cordilleran glacier reoccupied the Fraser River Valley and advanced a short distance into the Fraser Lowland. The Fraser River Valley was free of ice again by about 9,000 years ago (Armstrong et al. 1965). Some of these dates, however, may have to be revised. Alley (1979, p. 235) pointed out that "Numerous radiocarbon dates relating to Middle Wisconsin sediments found in the Fraser Lowland and Georgia Depression and on eastern Vancouver Island demonstrate that the Olympia Interglaciation ranges in age from approximately 29,000 years B.P. to probably more than 58,000 years B.P."

A fairly continuous complex of glaciers formed along the crest of the Sierra Nevada in the Late Pleistocene (Wahrhaftig and Birman 1965). East of the Washington Cascades, the ice reached into northern Washington, Idaho, and Montana, with the farthest advance extending to about 47°30'N latitude (Richmond et al. 1965). In the Rocky Mountains, glaciers of limited extent developed in most of the ranges as far south as 33°22'N latitude during the Pleistocene (Richmond 1965).

In the non-glaciated regions, pluvial cycles alternated during the four major glaciations (Nebraskan, Kansan, Illinoian, Wisconsin) with dry cycles during the interglacial stages (Aftonian, Yarmouthian, Sangamon). Apparently, the dry cycles became increasingly more severe with each subsequent interglacial stage. The effect of dry cycles was further increased by the continuing uplift of the major mountain ranges, which created ever larger rain shadows on their leeward sides.

A cool and moist glacial-pluvial climate prevailed in the Early Pleistocene. The Sierran pine-fir forest, of which Douglas-fir is an associate, extended at that time about 480 km farther south than at present (Axelrod and Ting 1961). Referring to unpublished work, Axelrod (1966b) mentions that Douglas-fir also occurred in the Early Pleistocene in the Kettleman Hills of the Coast Range considerably south of its present limit in this mountain chain. Undoubtedly, the range of Douglas-fir in the Coast Ranges and Sierra Nevada underwent repeated changes in the Middle and Late Pleistocene, but its extent is unknown.

The Santa Clara flora (Hannibal 1911, Dorf 1930) indicates that Douglas-fir was present along the central California coast in the Early Pleistocene. Axelrod and Ting (1960) believe that this coastal forest lived during the first major glacial stage. Pseudotsuga macrocarpa lived in the Early Pleistocene in the same general area where it occurs today, although it may have ranged farther south than at present. Its presence is reported in the Kansan glacial period about 2 million years ago in the hills above the Soboba Basin (Axelrod 1966b). A forest of bigcone Douglas-fir and Coulter pine, with associates Acer, Arbutus, Cupressus, and Quercus, covered the slopes. Pseudotsuga macrocarpa is also represented in the Bautista flora (Axelrod 1966b), which is slightly younger than the nearby Soboba flora.

We have no further record of Douglas-fir on the California coast until the Late Pleistocene. At that time, we find Pseudotsuga at Tomales Bay north of San Francisco (Mason 1934). Pseudotsuga menziesii grew there together with Pinus radiata and Pinus muricata, an association which has no modern counterpart. Radiocarbon dating has set the age of this forest at 29,000 years B.P. (Axelrod 1966b).

Douglas-fir and redwood forests ranged south along the coastal strip into the Santa Barbara area during the Late Pleistocene. The Willow Creek flora (Chaney and Mason 1930) with a radiocarbon date of $14,400 \pm 250$ years B.P. (Fergusson and Libby 1963) shows Douglas-fir as a major constituent of the forest on Santa Cruz Island. Fossil logs of Douglas-fir measure up to 0.9 m in diameter. Chaney and Mason (1930) suggested that the Channel Islands, of which Santa Cruz is the largest, were formerly connected to the mainland as the seaward end of a mountainous peninsula that became occupied by *Pseudotsuga menziesii* when it migrated southward. As the climate became drier and warmer again, Douglas-fir retreated north to more humid and cooler habitats.

The San Bruno flora (Potbury 1932) from the eastern slope of Sawyer Ridge in the San Francisco Bay area indicates that Douglas-fir was a dominant member in the forest there 10,000 years ago and reached considerable dimensions. Today, soft chaparral dominates the area and *Pseudotsuga* is of only minor importance. Douglas-fir may also have been a member of the fossil closed-cone pine forest near Little Sur in Monterey County (Langenheim and Durham 1963), a forest contemporaneous with the San Bruno forest.

Records of Pleistocene communities are rare in the steep, rapidly eroding mountainous terrain of the Cascade Range in Oregon. An assemblage of fossil plant material more than 35,500 radiocarbon years in age, from a streambank along Lookout Creek in H.J. Andrews Experimental Forest, Oregon, yielded two pieces of Douglas-fir wood. The Douglas-fir specimens are fragments of large-diameter stems and are unusual in their minute growth increments--0.14 and 0.10 mm/year. Composition of the assemblage suggests that it represents a subalpine forest community. Whether Douglas-fir was a part of it is uncertain because the material was obviously water-transported before deposition. The Lookout assemblage is probably of Late Pleistocene age and may have formed during the Early Wisconsin or a previous glaciation under conditions significantly drier than those prevailing during the Late Wisconsin Glaciation (Gottesfeld et al. 1981).

The Pleistocene history of Douglas-fir in Alaska is poorly documented. Douglas-fir seems to have been still present in Alaska in the Early Pleistocene (Hopkins and Benninghoff 1953). Apparently, early Quaternary interglacial intervals in northwestern Alaska were characterized by much greater warmth and humidity than at present. The species was probably eliminated from Alaska in the Middle or Late Pleistocene.

Interglacial Distribution

Stratigraphic palynology has permitted reconstruction of floral associations and climate over the past 50,000 years. Before this time, the record is discontinuous and of uncertain age (Heusser 1965, 1977). But the early studies of interglacial deposits in northwestern Washington (Hansen 1938a; Hansen and Mackin 1940, 1949; Leopold and Crandell 1957; Heusser 1964) demonstrate that Douglas-fir was present in this region during some interglacial periods.

A more recent study (Heusser 1977) utilizing fossil pollen assemblages from various locations in western Washington has provided additional evidence. *Pseudotsuga*, *Alnus*, and *Abies* were the principal components of forests during the Alderton Interglaciation. In this earliest Pleistocene glacial interval, Douglas-fir and alder reached a population peak unequalled in all other pre-Holocene⁴ time, an indication that the Alderton Interglaciation was a period of considerable warmth.

⁴ The Holocene is designated by Heusser (1977) as the period 10,000 to 0 years radiocarbon age B.P. Lemke et al. (1975) and Richmond (1972) have defined the Holocene as beginning at the end of the last abrupt deterioration of Pinedale glaciers.

At the beginning of the Puyallup Interglaciation, forests of Pinus contorta and Pinus monticola dominated the Olympic Peninsula (Heusser 1977). As the climate became warmer, they were first succeeded by arboreal communities consisting mainly of Pinus, Picea, and Abies, and then by forests of Abies, Tsuga heterophylla, Alnus, and Pseudotsuga. A similar succession occurred in the Puget Lowland. Here, Abies and Pseudotsuga succeeded first to Picea and Tsuga mertensiana, and later to a preponderance of Pinus.

The presence of Douglas-fir has not been reported in the forests of the two Salmon Springs non-glacial intervals. Pseudotsuga was present on southern Vancouver Island during the Olympic Interglaciation dated by Alley (1979) as from before 50,000 years B.P. to approximately 29,000 years B.P. Picea is the most important pollen in sediments of the period before 39,000 years B.P. to about 32,000 years B.P. Other coniferous pollens include Pinus with minor amounts of Abies and Tsuga and sporadic occurrence of Pseudotsuga. Pollen spectra encompassing the time between around 32,600 years B.P. to $27,160 \pm 790$ years B.P. resemble modern spectra from the present Douglas-fir zone of Vancouver Island. From this resemblance, Alley (1979) inferred that climatic conditions were similar to those prevailing today along the eastern lowland of Vancouver Island. Additional support for this assumption comes from the presence of a Douglas-fir log from the base of the layer dated $32,600 \pm 550$ years B.P., evidence that the species was growing there during that time. Interglacial beds of unknown age from the Whidbey Formation at Useless Bay, Whidbey Island, contain up to 62 percent Pseudotsuga pollen associated with abundant Alnus and Gramineae pollen. The implication is that mean July temperature reached about 15°C (Heusser and Heusser 1981), which is close to the modern mean.

Post-Glacial Distribution

Palynological studies beginning with the pioneering work of H.P. Hansen (1947a)⁵ have been mainly responsible for providing a comprehensive picture of Douglas-fir in western North America. Radiocarbon dating and advances in tephrochronology have, in many instances, permitted the establishment of remarkably detailed time frames for changes in climate and vegetational types. Contributions toward a better understanding of the processes involved in transport and deposition of Douglas-fir pollen, particularly those made by Tsukada (1982), have allowed more accurate interpretation of pollen diagrams.

The similarity between pollen of Pseudotsuga and Larix has made definite identification difficult, if not impossible, in areas where ranges of both genera overlap or may have overlapped in the past. Under an electron microscope, pollen of Pseudotsuga shows morphological features different from those of Larix. Under an ordinary light microscope, these differences are not recognizable. However, distinguishing features—a triradiate scar⁶ in Pseudotsuga and proximal annular thickening in Larix—become conspicuous after 5 or more minutes of acetolysis or after staining with gentian violet. Through such treatment, fossil pollen of both genera can be positively identified in most cases (Tsukada 1982). Apparently, this technique has not been widely used; thus, identification of pollen may not have been correct in localities in the Pacific Northwest interior where Larix is well represented in the forest communities.

DISTRIBUTION ON THE NORTHERN PACIFIC COAST

The northern limit of the present range of Douglas-fir and the post-glacial pollen record do not favor the assumption that the species persisted in refugia within the region covered by the main body of the Cordilleran ice sheet or in an ice-free corridor between the Cordilleran and Keewatin ice sheets. Tsukada (1982), in his comprehensive discussion of the

⁵ For complete bibliography, refer to Hansen (1967).

⁶ For definition of terms relating to pollen morphology, consult Kremp (1968).

Quaternary history of Pseudotsuga menziesii in the Pacific Northwest, suggested that the Willamette Valley may have been a glacial refugium for this species. The few locations in the region south of the Cordilleran ice sheet for which pollen diagrams exist—Lake Labish 45°02'N, 122°02'W (Hansen 1947a), Silverton Bone Site Bog 45°00'N, 122°46'W (Hansen and Packard 1949), Onion Flat Bog 45°23'N, 122°49'W (Hansen 1942a), Fargher Lake 45°54'N, 122°31'W (Heusser and Heusser 1980), Davis Lake 46°35'N, 122°15'W (Barnosky 1979), Mineral Lake 46°44'N, 122°12'W (Tsukada et al. 1981)—show low but continuous occurrence of Douglas-fir pollen. Tsukada (1982, p. 173) considered this sufficient evidence to conclude that "Pseudotsuga stands were sparsely scattered in the Willamette Valley, and possibly the southern Puget Lowland, during the full- and late-glacial periods." He suggested (p. 159) that "these scattered populations became the source of modern Pseudotsuga forests in the northern Pacific coastal region." Tsukada (1982) speculated that the northern limit of the range of Douglas-fir was then probably somewhere around 46°N latitude because of low sporadic occurrence of Pseudotsuga pollen prior to 12,000 years B.P. at Davis Lake (Barnosky 1979) and complete absence of this species' pollen at Mineral Lake before about 11,250 years B.P. (Tsukada et al. 1981). Beginning about 10,500 years B.P., Pseudotsuga expanded rapidly, as did Alnus. The gradual warming of the climate aided in the expansion of, first, Douglas-fir and, later, of Quercus and Corylus, which reached dominance at the mid-Holocene thermal maximum. Indications of such a period of maximum warmth have been noted for other parts of the world, and the period has been named variously the Xerothermic Period, Altithermal Period, Atlantic Period, Hypsithermal Interval, and Climatic Optimum. For the Pacific Northwest, Hansen (1947a) assigned the time from 8,000 to 4,000 years B.P. to the Xerothermic Period. Heusser (1960) placed the Hypsithermal Interval between 8,500 and 3,000 years B.P. in Washington and southwestern British Columbia.

Climatic changes were not the only factor bringing about all the successional changes reflected by the pollen record. Sharp fluctuations in the amount of Douglas-fir, western hemlock (Tsuga heterophylla), and white fir (Abies concolor) at the lower levels of pollen profiles in the Willamette Valley indicate frequent fires that seem to have prevented western hemlock from assuming dominance when climatic conditions were favorable for it (Hansen 1941d). Fire probably played a significant role in the decline of populations of Douglas-fir in the Puget Lowland about 9,700 years ago (Tsukada 1982). Large increases in the amount of charcoal fragments and pollen of Alnus rubra and spores of Pteridium in deposits from that time support this assumption.

The early stages of recolonization following retreat of the ice from the glaciated portion of the Puget Lowland are marked by the presence of forests containing Pinus contorta, Picea engelmannii, Tsuga mertensiana, and Abies. Open woodlands of Pseudotsuga and Alnus succeeded these late-glacial boreal forests (Hansen 1938b, 1941a; Tsukada et al. 1981). Douglas-fir apparently spread throughout the entire Puget Lowland within a few hundred years. Tsukada (1982) has traced its northward migration in that region. The species was in the Mineral Lake area (46°44'N, 122°12'W) about 11,250 years ago, arrived in the Seattle area (Lake Washington; Leopold et al. 1982) and Hall Lake vicinity (47°49'N, 122°18'W) circa 11,000 years ago, and had reached the Bellingham area (48°47'N, 122°07'W) around 10,700 years ago.

Heusser (1977) found that pollen records from Washington show rising percentages of Pseudotsuga and Alnus to maxima approximately 7,000 to 8,000 years B.P. during the Hypsithermal Interval, followed by an increase of Tsuga heterophylla. He pointed out that an increase in summer temperatures accompanied by lower precipitation would have given Douglas-fir a competitive advantage over western hemlock. To illustrate his point, he used data of modern pollen rain from five sites in Washington and four in Oregon and related these data to average July temperature and precipitation. The results show a sharp decline in Tsuga pollen when average July temperature increases from a range of 16 to 18°C to one of 18 to 20°C and average July precipitation drops from about 18 to 25 mm to 8 to 12 mm.

That an increase of 1 to 2°C in average July temperature would bring about dominance of Pseudotsuga is a conservative estimate based on these data. According to Heusser, temperatures in this range prevailed during the Hypsithermal Interval for at least two millenia.

The Pseudotsuga peak in the early post-glacial period, marked at every site in the Puget Lowland, may not necessarily reflect a much drier climate than that prevailing subsequently when Douglas-fir became less abundant (Tsukada 1982). The rapid expansion of Pseudotsuga may simply signify absence of serious competitors during that period (Sugita and Tsukada 1982).

The proportion of western hemlock and of western redcedar (Thuja plicata) increased significantly in the closed forests that succeeded the open woodlands dominated by Pseudotsuga and Alnus. Douglas-fir, however, remained a major element in the cool-temperate evergreen forests that have been in the Pacific Northwest for about five millenia (Tsukada et al. 1981). Recurring fires have probably prevented western hemlock and western redcedar from assuming dominance in the forests of this region (Hansen 1947b).

The successional pattern for forests on the Olympic Peninsula in post-glacial time is similar to that in the Puget Lowland, although Douglas-fir was less prominent in the pollen record (Hansen 1941b). Heusser's data (1973, 1974) provide evidence for the northward migration of Douglas-fir along the west side of the Olympic Peninsula. The species reached the Hoh Valley (47°48'N, 124°11'W) somewhat earlier than 9,000 years B.P., the Soleduk Bog (47°57'N, 124°29'W) area about 9,000 years B.P., Wentworth Lake (48°01'N, 124°32'W) circa 8,500 years B.P., and the Wessler Bog (48°09'N, 124°32'W) area around 8,000 years B.P. The migration route to the Hoh Valley area is still uncertain. Populations either moved northward along the Oregon and Washington coasts, were present in post-glacial time along both coasts (Hansen 1941c, 1943b, 1944a), or progressed westward from the Olympia and Shelton areas (Tsukada 1982). In the Peninsula, Pseudotsuga disappeared completely from the pollen record about 4,500 years B.P. and appeared again about 1,200 years B.P. This disappearance probably indicates that Douglas-fir lost most of its ground to such competitors as western hemlock and western redcedar. However, small residual populations of the species must have remained to reappear at a later stage in the pollen record (Tsukada 1982).

Recolonization of the Fraser Lowland after the retreat of the Vashon ice began about 13,000 years ago. Hansen (1940a) concluded from a study of two bogs in the Fraser River delta that the pioneer post-glacial forests consisted largely of Pinus contorta and that this period was cool and damp. These forests were followed by a spruce-pine forest in which spruce predominated, an indication that this second period was characterized by increased moisture and temperature. A third period--in which moisture and temperature decreased--was marked by the increase and dominance of western hemlock and Douglas-fir, a dominance that has persisted to the present. Sediment cores from two lakes in the University of British Columbia Research Forest 50 km east of Vancouver, B.C., indicate also that lodgepole pine dominated early post-glacial vegetation (Mathewes 1973). The arrival of Douglas-fir at this location is indicated by sudden abundance of its pollen about 10,500 years B.P. Until about 6,000 years B.P., a seral type of vegetation prevailed, characterized by Douglas-fir, alder (Alnus), and bracken fern (Pteridium aquilinum). After that time Tsuga heterophylla, Thuja plicata, and Chamaecyparis gained dominance. Mathewes' (1973) study revealed trends of post-glacial succession similar to those described by Hansen (1940a) and Heusser (1960) in the Fraser Valley. Mathewes, however, emphasized that the palynological evidence does not support occurrence of a Hypsithermal Interval in the western Fraser Lowland.

Pollen profiles from Pinecrest Lake on the eastern slope of the Coast Mountains and Squeah Lake in the western Cascade Mountains, both of which border the Fraser River between Hope and Yale in southwestern British Columbia, reveal the sudden appearance of abundant Pseudotsuga/Larix-type pollen about 10,400 years B.P. (Mathewes and Rouse 1975). Although Mathewes and Rouse could not determine with absolute certainty that the fossil pollen was Douglas-fir, they felt justified in so designating it because of the abundance of Douglas-fir in southwestern British Columbia and the more easterly distribution of Larix

species. The increase in the percentage of Douglas-fir pollen was accompanied by a decrease in Pinus pollen, a pattern that suggests the natural replacement of the pine by the more shade-tolerant Douglas-fir. Frequencies of Betula and Alnus pollen increased consistently after 6,600 years B.P. Mathewes and Heusser (1981) utilized transfer functions for converting pollen frequencies to estimates of July mean temperature and annual precipitation; they applied these functions to fossil pollen data from Marion Lake, British Columbia. The highest temperatures were indicated by this method for the period 10,000 to 7,000 years B.P., coinciding with the xerothermic interval postulated by Mathewes (1973) for the Yale area east of Marion Lake. The successional pattern observed in the Yale area corresponds with that observed in the University of British Columbia Research Forest near Haney (Mathewes 1973). Climatic amelioration may not have been solely responsible for the important vegetational changes marked by the sudden increase in Douglas-fir pollen. That increase may simply mark the time when Douglas-fir reached the region in the course of its northward migration from unglaciated areas to the south (Mathewes and Rouse 1975). Because both birch and Douglas-fir are generally more abundant in the Interior Douglas-fir Zone in the coastal zones, Mathewes and Rouse concluded, on the basis of palynological patterns, that the presently transitional biogeoclimatic conditions between the Coastal Western Hemlock Zone and the drier Interior Douglas-fir Zone in the Yale area have persisted for much of post-glacial time.

Douglas-fir probably did reappear on Vancouver Island around 10,000 years B.P. (Tsukada 1982). Pollen diagrams from locations along the east coast of Vancouver Island (Hansen 1950a, Heusser 1960) indicate that Douglas-fir apparently never attained abundance there as it did on the mainland. It was more common on the southern end of Vancouver Island, probably because the rain shadow of the Olympic Mountains gave that end a drier climate and an absence of competition from western hemlock. The pollen profiles do not indicate climatic fluctuations during this period. Hansen concluded that recorded changes in forest composition represent normal forest succession in response to general amelioration of the climate and modification of sterile mineral substrates left in the wake of glaciation.

In locations such as the San Juan Islands, western hemlock never assumed dominance. This failure resulted because of insufficient precipitation and unfavorable edaphic conditions. Pollen diagrams from bogs on Orcas Island (Hansen 1943a) indicate very simple patterns of succession. Either lodgepole pine (Pinus contorta) continued to remain dominant or it was replaced by Douglas-fir, which retained dominance until the present.

Some evidence exists that Douglas-fir migrated north of its present range in the coastal region of the Pacific Northwest late in the post-glacial period. Heusser (1960) mentions occurrence of very small amounts of Douglas-fir pollen in profiles at the northern end of Vancouver Island at Port Hardy (50°44'N, 127°25'W) and on nearby Hope Island (50°56'N, 127°55'W). Farther north on the mainland, at Cape Caution (51°13'N, 127°35'W), Fitzhugh Sound (51°42'N, 127°52'W), and Susan Island (52°29'N, 128°17'W), Heusser (1960) found Douglas-fir only in the upper level of pollen profiles. He interpreted this as evidence of recent migration of the species and speculated that fire may have favored its advance. The northernmost locations on the Pacific coast from which Heusser (1960) described post-glacial pollen profiles containing Douglas-fir are in the vicinity of Prince Rupert, B.C. (54°15'N, 130°02'W). On the basis of the abundance of Douglas-fir pollen at several levels in the profile, Heusser concluded that the species advanced and retreated several times in the Prince Rupert region. Pseudotsuga appears to have been an important, if temporary, link in early post-glacial forest succession in that coastal area. At present, the nearest known occurrence of Douglas-fir to Prince Rupert is about 100 km to the southeast in the vicinity of Kemano, B.C. Schmidt (1957, p. 21) emphasized that "In the natural forests of coastal British Columbia, Douglas-fir has been dependent almost entirely upon past fires to create environmental conditions necessary for its re-establishment. Consequently, the existing range of Douglas-fir is related to climatic conditions which permit high fire danger to build up, and as far north as Kemano there is a good correlation between the distribution of Douglas-fir and a high fire risk during the summer. Although areas of warm, dry summers exist north of Kemano, Douglas-fir has been unable to migrate farther north, presumably

because an intervening area of high summer rainfall (250–375 mm) separates Kemano from the nearest rain shadow area to the north."

The pollen record does not indicate that Douglas-fir was present in the Queen Charlotte Islands at any time during the post-glacial periods (Heusser 1960), although it may have lived there in the Late Miocene (Martin and Rouse 1966, Wolfe 1969).

DISTRIBUTION IN THE OREGON MOUNTAIN RANGES

Records of the post-glacial history of Douglas-fir in the Oregon Cascades are scant. Pollen profiles from the northern Oregon Cascades (Hansen 1946) indicate that both Douglas-fir and ponderosa pine (*Pinus ponderosa*) were present before the Xerothermic Period and competed with mountain hemlock (*Tsuga mertensiana*), western hemlock, and lodgepole pine. During the Xerothermic Period, Douglas-fir increased together with ponderosa pine in the northern Cascades while Douglas-fir probably lost considerable ground during this period in the southern Oregon Cascades, the Klamath and Siskiyou Mountains, and the southern Oregon and northern California Coast Ranges. Axelrod (1966b) pointed out that the yellow pine forest, which is composed mainly of *Abies concolor*, *Libocedrus decurrens*, *Pinus lambertiana*, *Pinus ponderosa*, and *Pseudotsuga menziesii*, expanded greatly during the Xerothermic Period and that part of this expansion occurred in a northerly direction. The return to a moister and cooler climate after the Xerothermic Period favored the expansion of western hemlock in the northern parts of the Cascades (Hansen 1946) and enabled Douglas-fir to regain ground on the west side of the southern Oregon Cascades and the mountains to the west. Detling's (1953) studies of relict islands of xeric plant communities in Oregon west of the Cascades and the present distribution of the yellow pine forest lend support to Axelrod's belief in its remarkable advance to the north in the Xerothermic period. The yellow pine forest occupies the east flank of the Cascades and extends westward across the mountains from Klamath Falls to Ashland. It is common in the Rogue River Valley but disappears rapidly to the north and west. Axelrod lists notable relict patches of yellow pine forest in the western Oregon Cascades in the following areas: Middle Fork Willamette River, upper North Umpqua drainage, and headwaters area of South Umpqua River.

Since eruption of ancient Mt. Mazama about 6,700 years B.P., forest succession on the east slope of the central Oregon Cascades has been influenced largely by the thick mantle of pumice deposited at that time (Hansen 1942b). Lodgepole pine has remained dominant in the pumice region that extends north and east of Crater Lake, which formed after the collapse of Mt. Mazama. In the Willamette Pass area, however, pollen profiles indicate a gradual increase of Douglas-fir, western hemlock, and Engelmann spruce (*Picea engelmannii*), an increase apparently reflecting higher precipitation and, consequently, more rapid weathering of the pumice mantle.

Hansen's (1939a, 1939b, 1940b, 1941e, 1944b) early studies demonstrated that Douglas-fir was not abundant in post-glacial time east of the Cascades in central Oregon and central Washington. In north-central Washington (Hansen 1942c), it played an important role in post-glacial forests, but not to the extent as in western Washington and southern British Columbia.

DISTRIBUTION IN THE PACIFIC NORTHWEST INTERIOR

Tsukada (1982), in his description of the post-glacial history of *Pseudotsuga menziesii* var. *glauca* in the northern Pacific Northwest interior, postulated that this variety originated from glacial refugia somewhere in the southern Rocky Mountains and moved north along the

foothills of the mountains with the advent of a milder climate about 11,000 years ago. Tsukada's estimate that Douglas-fir reached northern Montana and Idaho approximately 10,000 years ago is based on Hansen's (1948) work at Johns Lake (48°38'N, 113°52'W) as well as Hansen's (1947a) study at Bonners Ferry (48°33'N, 116°24'W). Pollen diagrams from the Kootenai River Valley in northwestern Montana (Mack et al. 1983) indicate that Douglas-fir may have been there as early as 11,000 years B.P. Farther west, at Hager Pond, 5 km west of Priest Lake in northwestern Idaho, pollen of Douglas-fir appeared first between 8,300 and 7,600 years B.P. (Mack et al. 1978a), and at Big Meadow (49°43'N, 117°34'W) (Mack et al. 1978c) in northeastern Washington, pollen of Pseudotsuga/Larix type appeared for the first time 9,700 years B.P. During the following period, 7,000 to 3,300 years B.P., Diploxylon pine became prominent while Pseudotsuga/Larix remained a minor component. From 3,300 to 2,400 years B.P., Pseudotsuga/Larix pollen occurred with high constancy. The pollen record at the Big Meadow site is at variance with the basic three-stage post-glacial vegetation sequence in northeastern Washington and northwestern Idaho as outlined by Hansen (1939b, 1939c, 1943c).

Pollen diagrams from three sites close to the limits of the present range of Douglas-fir in northeastern Washington-- Waits Lake (48°11'N, 117°47'W), Simpsons Flats (48°19'N, 118°44'W), and Bonaparte Meadows (48°47'N, 119°04'W)--and from one--Mud Lake (48°36'N, 119°38'W)--already outside the species' present range show low and sporadic occurrence of Pseudotsuga/Larix-type pollen. Because Pseudotsuga and Larix pollen were not identified separately and because Pseudotsuga/Larix-type pollen occurred intermittently in early post-glacial time, the pollen diagrams from Waits Lake (Mack et al. 1978d), Simpsons Flats (Mack et al. 1978b), and Mud Lake (Mack et al. 1979) are not reliable indicators of the time Douglas-fir arrived at these sites.

In contrast, the pollen diagram from Bonaparte Meadows (Mack et al. 1979) provides more evidence for establishing the time of arrival of Douglas-fir in the area. The tree appeared around 6,900 years B.P. and became more prominent probably about 4,800 years B.P. After 2,500 years B.P., Douglas-fir pollen deposits nearly doubled in amount, an indication that the modern forest community that includes Douglas-fir has a history of only 2,500 years.

Tsukada (1982) pointed out that refugia for the interior variety of Douglas-fir cannot presently be identified. It is fairly certain, however, that Douglas-fir began to expand in the northeastern Pacific Northwest approximately 10,000 years ago. Tsukada suggested southern Canada as the center of the migrational route and concluded, although concrete evidence is lacking, that initial contact between the coastal and interior varieties was not earlier than 7,000 years ago.

A pollen diagram from Kelowna Bog (49°56'N, 119°23'W), 175 km northwest from Simpsons Flats in the Okanagan Valley of southern central British Columbia, indicates that Pseudotsuga became a significant component of vegetation in that area for the first time at about 6,600 years B.P. (Alley 1976). Although distinguishing between pollen of Pseudotsuga and Larix presented problems, Alley designated pollen grains with an exine thickness of 4 to 5 μm as Pseudotsuga and those with an exine thickness of about 2 μm as Larix. He attributed the appearance of Douglas-fir to the change from a climate too arid for growth of the tree to one cooler and more moist. Subsequent climatic fluctuations are indicated by a decline of Douglas-fir about 3,600 years B.P. and a renewed increase of the species about 3,200 years B.P. Farther north in south-central and central British Columbia, Hansen (1955) noted the most consistent record of Douglas-fir in the Vernon-Kamloops region. With progressing distance to the north, pollen of Douglas-fir became consistently less in profiles. The northernmost occurrence of Douglas-fir pollen reported by Hansen was about 100 km north of Prince George. He concluded that in the grassland sector of British Columbia, the climate apparently was never sufficiently moist to encourage the expansion of Douglas-fir.

DISTRIBUTION IN THE CANADIAN ROCKY MOUNTAINS

The Canadian Rocky Mountains were glaciated less extensively than the ranges farther west. Nevertheless, glaciers from the Canadian Rocky Mountains formed piedmont tongues over the eastern foothills and the adjacent plains; these tongues reached to the border attained by the Laurentide ice that had moved westward from central Canada. Pollen studies of Heusser (1956) in Jasper National Park show a general sequence of pine-spruce-fir succeeding to pine-spruce-Douglas-fir, thence to pine-spruce-fir, and finally to pine-spruce-western hemlock. The presence of Douglas-fir suggests a period of warming and some drying. Thus, under an environment where moisture was not limiting, a rise of temperature may explain the apparent expansion of Douglas-fir in an area where today its occurrence is sporadic. Heusser (1956) believes that at an earlier time Douglas-fir was a relatively more important component of the forest in the Canadian Rocky Mountains. Today, it is largely confined to the montane zone at elevations below 1,068 m on the west side of the Continental Divide. In this zone Douglas-fir is an associate together with Abies lasiocarpa and Tsuga heterophylla in a forest dominated by Thuja plicata and Picea engelmannii.

Evidence is lacking that Douglas-fir ever advanced into the plains to the east of the Canadian Rocky Mountains. Hansen's (1949a, 1949b, 1950b) pollen profiles in Alberta revealed only traces of Douglas-fir, which probably represented pollen that had originated in the Rocky Mountains and drifted over a long distance.

Cores from a bog near Lost Trail Pass (elevation 2,152 m) on the crest of the Bitterroot Range near its junction with the Continental Divide indicate a change from climatic conditions cooler than those prevailing today to a warmer and perhaps drier climate about 7,000 years ago (Mehringer et al. 1977). At that time Douglas-fir and lodgepole pine replaced the then existing whitebark pine (Pinus albicaulis) forest. With the return to cooler climates, about 4,000 years B.P., Douglas-fir was no longer common in the pine forest. Today, Pseudotsuga menziesii is near its upper elevational limit in the vicinity of Lost Trail Pass Bog and is largely restricted to steep south- and west-facing slopes. Pollen diagrams from the east side of Yellowstone Park in northwestern Wyoming (Waddington and Wright 1974, Baker 1976) indicate climatic and successional sequences that are strikingly similar to those of Lost Trail Pass. However, pollen of Douglas-fir occurs sporadically in profiles from Yellowstone Park after 11,600 years B.P.

DISTRIBUTION IN THE CENTRAL AND SOUTHERN ROCKY MOUNTAINS

The history of Douglas-fir is least known for the central and southern Rocky Mountains and the Sierra Madre Occidental and Oriental of northern Mexico. The Tertiary fossil record of these regions is meager and so far has failed to provide information on Douglas-fir. As of now, the fossil record of Pseudotsuga in these regions is limited to the Quaternary.

Archaeological excavations at the Cowboy Caves (38°19'N, 110°13'W, elevation 1,710 m) in southeastern Utah yielded needles of Douglas-fir and Engelmann spruce within a 50-cm-thick layer of herbivore dung (Spaulding and Van Devender 1977). A radiocarbon date of dung from the entire 50 cm was 11,810 ± years B.P. The nearest occurrence of Douglas-fir today consists of relict stands in canyons within 10 km of the Cowboy Caves at elevations of 1,980 m. Montane forest apparently extended to lower elevations during the last glacio-pluvial period, and some of the disjunct montane forests in south-central Utah were perhaps connected during that period.

Maher's studies (1961) in the San Juan Mountains of southwestern Colorado indicate that, during the last 13,000 years, the montane forest of which Douglas-fir is locally a member migrated upward by about 600 m.

Middens, compacted refuse heaps of plant food debris and fecal pellets, yield plant megafossils from within 30 to 50 m of sampling locality. Analysis of packrat (*Neotoma*) middens in northeastern Arizona and northwestern New Mexico also indicate that altitudinal limits of montane forests in the early Holocene were lower than today (Betancourt and Davis 1984). Fossil needles of Douglas-fir, radiocarbon-dated $11,900 \pm 300$ years B.P. from middens in Canyon del Muerte ($36^{\circ}08'N$, $109^{\circ}25'W$) in Canyon de Chelly National Monument, Arizona, show that the species extended at least down to an elevation of 1,770 m. Large quantities of fossil needles and buds were recovered from middens at Atlatl Cave ($36^{\circ}02'N$, $107^{\circ}54'W$, elevation 1,910 m) in Chaco Canyon National, New Mexico. The assemblages, dated 10,600 to 9,460 years B.P., are dominated by Douglas-fir, *Juniperus scopulorum*, and limber pine (*Pinus flexilis*).

A packrat midden sequence from the Sacramento Mountains in south-central New Mexico provides an 18,000-year record of vegetation for the northern Chihuahua Desert (Van Devender et al. 1984). Megafossils from the middens indicate the presence of a mesic woodland in which Douglas-fir was represented between 18,000 and 16,000 years B.P. As the climate became gradually more and more xeric, desert grasslands replaced arboreal communities about 8,000 years B.P.; these communities in turn gave way to Chihuahuan desert scrub that has been present since about 4,000 years B.P. The present mixed-conifer forest containing Douglas-fir begins at 2,500 m elevation.

On the basis of plant megafossils radiocarbon-dated $14,920 \pm 360$ years B.P., evidence of *Pseudotsuga* was also detected in a Late Pleistocene mixed-conifer forest at an elevation of 1,705 m in the San Andres Mountains of New Mexico (Van Devender et al. 1984). Plant megafossils recovered from cave fill and fossil packrat middens of the Upper Sloth Caves (elevation 2,000 m) in Guadalupe Mountains National Park in western Texas record a transition from a mesic, subalpine forest dominated by spruce and limber pine to a relatively more xeric forest with *Pseudotsuga menziesii*, *Pinus edulis*, and *Quercus gambelii* (Van Devender et al. 1977). The transition occurred between 13,000 and approximately 11,500 years B.P. The time of transition from the xeric forest community to the present desert scrub community has not been established but may have been as early as 10,000 years ago.

Martin and Mehringer (1965) pointed out that the extraordinary occurrence of a lungless salamander (*Aneides hardyi*) in the Sacramento Mountains of New Mexico (Lowe 1950) has been interpreted as the result of Late Tertiary expansion of its favored habitat--mixed conifer forest with Douglas-fir--spreading southward through the Rocky Mountains from the Pacific Northwest where relatives of this salamander live now. A connection between disjunct populations of Douglas-fir in the southern Rocky Mountains probably did exist at those times in the Pleistocene when pluvial-glacial climate prevailed and may even have lasted into early post-glacial time.

EVOLUTIONARY HISTORY

In contrast to the Tertiary, *Pseudotsuga* is often abundantly represented in Quaternary mega- and microfossil assemblages. This would indicate that Douglas-fir assumed its important role in the forests of northwestern America in the Quaternary. Wolfe (1969) emphasized that Early Pleistocene assemblages still have low amounts of Douglas-fir pollen, whereas interglacial deposits begin to show large quantities of pollen of this genus. Therefore, he concluded that dominance of *Pseudotsuga* in the present conifer forest of the Northwest was attained during the Middle or Late Pleistocene.

The appearance of Pseudotsuga in pure stands may suggest development of a new species. The Pleistocene may very well have been the time when the modern Pseudotsuga menziesii with a chromosome complement of $n = 13$ evolved. The haploid number of chromosomes for the Asian Douglas-firs and for bigcone Douglas-fir (Pseudotsuga macrocarpa) is 12; thus, the Asian Douglas-firs and bigcone Douglas-fir appear to be the more ancient forms because it seems unlikely that several species with a chromosome complement of $n = 12$ evolved from a single species with a complement of $n = 13$. The cyclic climatic changes during the Pleistocene and the ensuing migrations must have resulted in considerable selection pressure favoring evolution of new species. Axelrod (1966b, p. 60) very aptly remarked that "During the Quaternary almost everything that can happen at the level of speciation has happened."

The differentiation of common Douglas-fir into coastal and interior forms is an event in its evolutionary history whose time of occurrence has remained uncertain. Galoux (1956) proposed that both forms descended from a common ancestor in the Mid-Pliocene. According to him, the interior form (P. menziesii var. glauca) originated as the result of eastward migration across the Great Basin and subsequent adaptation to the environment of the Rocky Mountains. Galoux based his theory on the observation that the Pacific floral elements most closely related to woody species in the Rocky Mountains occur in the southern Cascades and in the Sierra Nevada. The presence of Pseudotsuga in the mountains of northeastern Nevada 40 million years ago (Axelrod 1966a) does not tend to support Galoux's thesis. One might just as well argue that evolution of the interior form began when connections of the southern Rocky Mountains to the northwestward were severed by the development of the deserts of southern Wyoming. According to Weber (1965), relict stands of northwestern species will provide traces of the old connection. The best argument against placing the time of evolution of the interior and coastal forms in the Mid-Pliocene comes from the evidence of extensive plant migrations in the Great Basin and the Southwest during the Late Quaternary (Martin and Mehringer 1965). Several species of the family Pinaceae—Abies concolor, Pinus contorta, Pinus ponderosa—are differentiated into well-defined geographic races on opposite sides of the Great Basin. Critchfield and Allenbaugh (1969) consider it improbable that the Great Basin acted as a barrier between Pacific and Cordilleran segments of these conifers through all of the Pleistocene. However, they believe that these races could not have evolved as recently as the last Pluvial about 20,000 years ago. Both the long generation interval of these trees and the geographic extent of their races argue against such a possibility.

Post-glacial forest succession was not under the exclusive control of climate. Fire, volcanic eruptions, insect calamities, and fungal diseases were often instrumental in changing the course of succession. For instance, Schmidt (1957) recounted that within the last 1,100 to 1,200 years 12 major forest fires occurred on Vancouver Island. The most recent fire of gigantic proportions occurred about 300 years ago when approximately 800,000 ha of forest were consumed on Vancouver Island. Disastrous fires in the first half of this century, such as the Lochsa Burn in Idaho, Yacolt Burn in the southern Washington Cascades, and the Tillamook Burn in the Oregon Coast Range, are recent and impressive demonstrations of the role of fire in forest succession within the natural range of Douglas-fir.

Changes in the range of Douglas-fir continue, although they are so slow as to be little noticed. The northern limit of the species appears to be in the process of being gradually shifted southward. Relict stands of Douglas-fir occur in the interior of British Columbia north of its common range, and there is evidence that the species has been replaced by white spruce (Picea glauca) in some localities of north-central British Columbia (Brink and Farstad 1949). North of latitude $54^{\circ}30'N$, white spruce grows much faster than Douglas-fir. Spruce is generally 4.6 to 6.1 m taller than Douglas-fir on the same site at age 100 years (Revel 1966). In the Interior Subalpine Section (SA. 2 of Rowe 1972) north of latitude $54^{\circ}N$, isolated groups of overmature Douglas-fir on ridge tops and decaying stumps and snags of this species on southern exposures testify to its former presence.

Douglas-fir has both suffered and profited from the activities of man in historic times. Settlement of the Douglas-fir region and clearing of land for agricultural and other purposes

has reduced the total forest area. Lumbering in the forest of the Northwest, however, has frequently interrupted succession from Douglas-fir to western hemlock and western red-cedar and created conditions that tend to perpetuate the Douglas-fir forest (Franklin and Hemstrom 1981).

FOSSIL *Pseudotsuga* IN JAPAN

Three species of fossil *Pseudotsuga* have been distinguished in Japan. They are:

Pseudotsuga gondylocarpa Miki, 1957, Osaka Univ. Inst. Polytech. J. 8:256, pl. 9, F-G, f. 9, D, f. 10, Bc, Pliocene. (Miki 1957)

Pseudotsuga japonica (Shirasawa) Beissner, Recent; Miki, 1948, Minn. & Geol. 2:111, f. 4, A-B (exc. Ab), Pliocene. Miki, 1957, Osaka Univ. Inst. Polytech. J. 8:257, pl. 9, H-J, f. 9, B, f. 10, Ba, Pleistocene. (Miki 1948)
(Miki 1957)

Pseudotsuga subrotunda Miki, 1948, Minn. & Geol. 2:132, pl. 2, G, Ia, f. 4, b, Pliocene. Miki, 1957, Osaka Univ. Inst. Polytech. J. 8:257, pl. 9, A-E, f. 9, c, f. 10, Bb, Pliocene. (Miki 1948)
(Miki 1957)

Pseudotsuga gondylocarpa has been found in the northeastern part of Shikoku in Kagawa Prefecture and in two locations on Honshu (Fig. 3). The fossil remains are cones 2 cm long

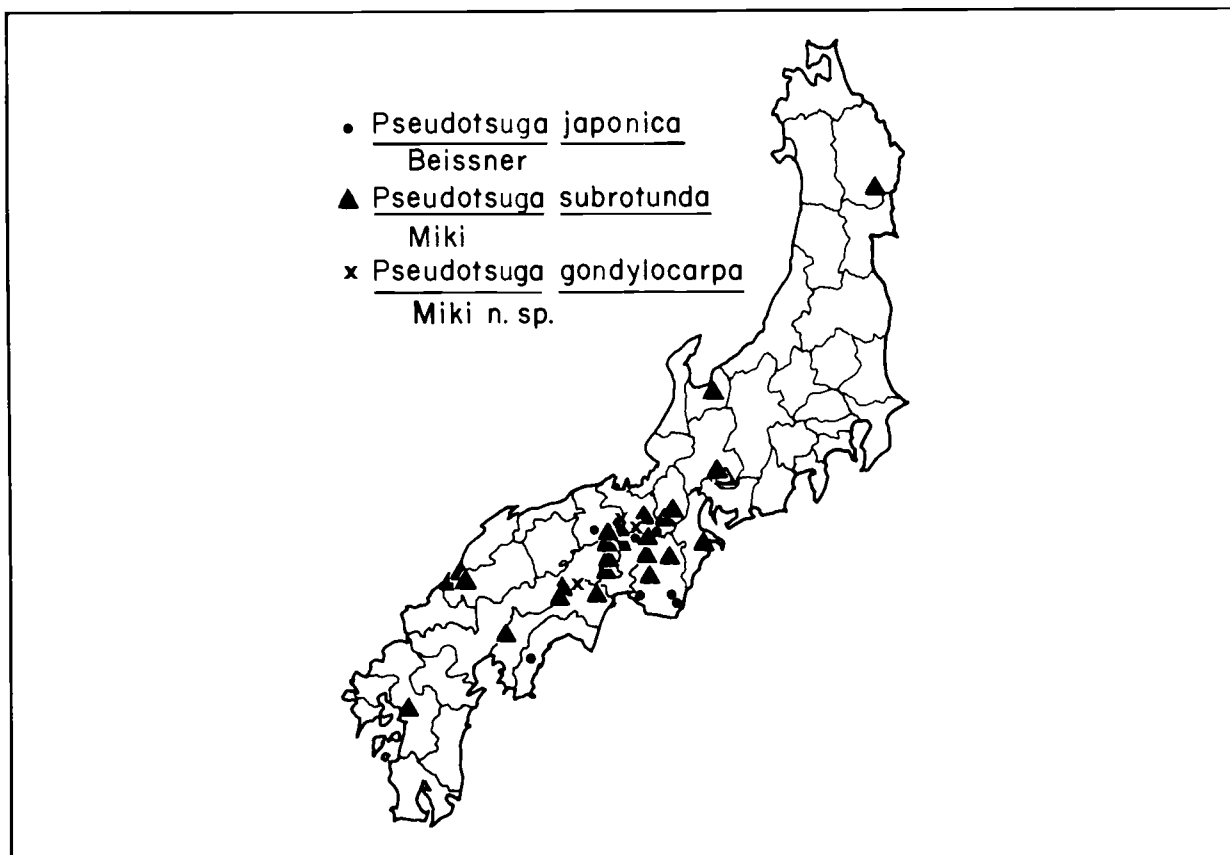


FIGURE 3.

Locations of fossil Douglas-fir in Japan. [Revised from Miki (1957); the map is used with the permission of Osaka City University.]

and 1 to 2 cm wide. Representative genera associated with *P. gondylocarpa* were *Cunninghamia*, *Glyptostrobus*, *Metasequoia*, *Cephalotaxus*, *Pinus*, and *Thuja*. The species has become extinct, perhaps in the Early Pleistocene.

Fossil *Pseudotsuga japonica* is known from one deposit of Pliocene age and six floras assigned to a Pleistocene interglacial. Fossil remains include cones and leaves almost indistinguishable from the modern Japanese Douglas-fir. Principal associates of *Pseudotsuga* in the fossil forests were *Cryptomeria*, *Abies*, *Picea*, *Tsuga*, *Thuja*, *Torreya*, *Cunninghamia*, and *Metasequoia*. The range of fossil *P. japonica* appears to have extended only slightly to the north and east beyond the distribution of its modern counterpart.

The most frequent of the fossil species is *Pseudotsuga subrotunda*. Fossil remains are known from 27 locations throughout Japan (Fig. 3) with the exception of Hokkaido in the north. The fossils include cones, leaves, and seeds. The cones of *P. subrotunda* are larger than those of *P. japonica*, and their bracts are not constricted in the center part as in *P. japonica*. Miki (1957) remarked that the cone of *Pseudotsuga subrotunda* at first glance looks like that of *Pseudotsuga menziesii*, but that closer inspection will show a different arrangement of cone scales in each species. Other members of the forests in which *P. subrotunda* once grew belonged to the genera *Sequoia*, *Metasequoia*, *Pseudolarix*, *Cephalotaxus*, *Glyptostrobus*, *Abies*, *Picea*, *Pinus*, *Tsuga*, *Keteleeria*, *Cunninghamia*, *Stewartia*, *Styrax*, and *Liquidambar*. *Pseudotsuga subrotunda*, like *Pseudotsuga gondylocarpa*, has become extinct.

FOSSIL *Pseudotsuga* IN EUROPE

The fossil record of *Pseudotsuga* in Europe is scant and has been a matter of controversy. Fossil species of *Pseudotsuga* are most commonly described in terms of the remains of wood. They include *Piceoxylon pseudotsugae* Gothan from Eocene beds in the Paris Basin of France (Fritel and Viguié 1911) and Miocene strata of Konin, Poland (Grabowska 1956); *Pseudotsuga silesiaca* Kubart from Miocene beds near Gliwice (Gleiwitz), Poland; *Pseudotsuga stiriaca* from Unter-Weissenbach, Austria (Kubart 1924); and *Piceoxylon macrocarpum* (Prill) Kräusel of Miocene age from two locations in Upper Silesia, Poland (Kräusel 1919, Reyman 1956). Why the identification of some of the purported fossil remains of Douglas-fir is questionable is apparent from the following translated quotation by Fritel and Viguié (1911, p. 68): "In any case we must consider our wood (specimen) as belonging to the Pinaceae, and probably to one of these three genera, namely, *Picea*, *Larix*, or *Pseudotsuga*."

There are several reports of the occurrence of microfossils of *Pseudotsuga* in Europe. What is believed to be fossil pollen of this genus has been described from Upper Oligocene deposits at Rott in the Siebengebirge Mountains, West Germany (Thiergart 1958), Upper Oligocene beds at Guerzenich 4 km southwest of Dueren, West Germany (von der Brelie and Wolters 1958), the Upper Pliocene formation of Willershausen in the Harz Mountains of Germany (Strauss 1952), Lower Miocene beds near Gliwice, Poland (Macko 1957, Szafer 1961), and from Miocene deposits at Hauterive and Mollon in the Rhone Basin of France (Pons 1964, cited by Gaussen 1966, p. 556). Neuy-Stolz (1958) described fossil pollen presumably belonging to the genus *Pseudotsuga* from Miocene softcoal beds in the Lower Rhine Basin. She wrote (p. 509, author's translation): "Inaperturate pollen forms, 50-100 μ in size, which regularly are present in the Lower Rhenanian softcoal, belong probably to the genus *Pseudotsuga*, not *Larix*. Designation of this fossil pollen form is *Inaperturopollenitis magnus* (R. Pot.) Th. & Pf." Lona (1950) identified, as *Pseudotsuga*, pollen of spectra from the Pleistocene Leffe Formation near Bergamo, Italy. Gams (1954) interpreted Lona's spectra as an indication that *Pseudotsuga* remained in Europe until a warm period between the two Mindel Glaciations.

Zalewska (1961) has reported the only megafossil assemblage that contained cones and needles of Pseudotsuga. It was discovered in Lower Miocene beds near Turow, Poland. Incidentally, Zalewska claimed that Engelhardt and Kinkelin (1908) found cones of Pseudotsuga in Upper Pliocene deposits in the lower Main Valley of Germany but erroneously identified them as belonging to the genus Keteleeria. However, the cones designated by Zalewska (1961) as Pseudotsuga lack the bracts characteristic of that genus. She assigned detached bracts to Pseudotsuga. Whether these are indeed bracts of Pseudotsuga is difficult to ascertain on the basis of a photograph (Plate X, No. 5) reproduced in Zalewska's (1961) paper.

Fossil wood is normally identified from thin sections of often poorly preserved specimens. Assignment of such wood to the presumed equivalent of a modern genus must be accepted with reservations. Identification of fossil pollen also poses problems and should be corroborated by megafossil evidence. Although Zalewska's report appears to furnish such evidence, it too is open to question.

Florin (1963) is certainly justified in his assertion that the one-time presence of Pseudotsuga in Europe is poorly documented. The fossil floras of Europe, however, contain many genera, now extinct in that continent, that are known associates of Pseudotsuga in fossil and present forests of eastern Asia and western North America (Stuedt 1926). This may be regarded as another argument in favor of the thesis that Pseudotsuga was once represented in Europe. Fossil remains of Pseudotsuga in Europe, however, cannot be matched with any of the modern representatives of the genus (Gaussen 1966). Thus, distinct European species of the genus Pseudotsuga may have existed that now have completely disappeared.

SUMMARY

The fossil record of Pseudotsuga in North America goes back to the Early Tertiary. The earliest known occurrence of fossil cones, seeds, and leaves of Pseudotsuga in North America is from the Eocene Copper Basin flora of northeastern Nevada. Although the fossil record of Pseudotsuga provides little information on its range during the Early and Middle Tertiary, it appears to indicate a rather restricted range of the genus. During the Late Tertiary, the range of Pseudotsuga had expanded considerably; it extended into Alaska until at least the Middle or Late Miocene. Both the megafossil and microfossil records indicate that Pseudotsuga was a minor component of forests throughout the Tertiary.

The Pleistocene set the stage for the development of Douglas-fir forests as major vegetational units in medium latitudes and medium altitudes of northwestern North America. The frequency of fossil pollen of Pseudotsuga in Quaternary deposits shows that Douglas-fir became an important part of northwestern forests during the interglacial intervals.

A general amelioration of the post-glacial climate saw the emergence of Douglas-fir as a dominant element in the coniferous forests of western North America. Beginning about 10,000 years B.P., Pseudotsuga began to migrate from glacial refugia into the range it occupies at present.

The fossil record of the genus Pseudotsuga in eastern Asia is limited to Japan. Three fossil species, probably dating from the Late Miocene, have been described. Two of these do not have modern counterparts.

The genus Pseudotsuga may have been present in Europe until the Mid-Pleistocene. However, reports of fossil Pseudotsuga in Europe are based primarily on fossil pollen and are in need of critical reevaluation.

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