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Range change in Metasequoia: relationship to paleoclimate

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Abstract

Metasequoia was widely distributed across the mid and high latitudes of the Northern Hemisphere in the Cretaceous, and experienced range contraction associated with Tertiary climatic cooling and drying. We compile occurrences of Metasequoia from the literature, museum collections and new localities, and plot them in a plate tectonic framework to document these range changes through time. We note two pulses of range contraction: Eocene-Oligocene associated with cooling at high latitudes, and Late Miocene-Pliocene associated with cooling and drying in mid latitudes. Only the northern limit of the taxon's range changed during these intervals. Because of its apparent climate sensitivity, Metasequoia might be used to reconstruct paleoclimate. To test this hypothesis, we assemble the climatic tolerances of living Metasequoia glyptostroboides under natural and cultivated conditions and compare them to paleoclimatic reconstructions across the genus' former range. Ancient forms appear to have regenerated under warmer conditions, on average, than does living M. glyptostroboides. Therefore, we hypothesize that modern Metasequoia was derived from a cool-tolerant segregate of pre-Pleistocene populations. This result highlights the danger of paleoclimate reconstruction based on taxon-specific modern analogs.

Keywords: Metasequoia, biogeography, Cretaceous, Cenozoic, paleoclimate, Northern Hemisphere

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1. Introduction

A number of genera within the conifer clade Cupressaceae (sensu Brunsfeld et al., 1994) were widely distributed throughout the Northern Hemisphere during the Cretaceous and Paleogene (Florin, 1963). During the Neogene, genera such as Cunninghamia R. Br. in L.C. Rich., Cryptomeria D. Don, Glyptostrobus Endl., Taxodium L.C. Rich., Sequoia Endl., and Sequoiadendron Endl. experienced dramatic range contractions (Florin, 1963), which are commonly linked to global climate change. Metasequoia Miki is probably the best-documented example because its deciduous habit fosters an extensive fossil record. Metasequoia was widely distributed across North America and Asia during the Cretaceous and Paleogene, spanning a range from 20°N to greater than 80°N latitude (Florin, 1963). During the Tertiary, Metasequoia's range contracted, to leave a single relic species Metasequoia glyptostroboides Hu & Cheng, which grows naturally at the boundary of Hupen, Hunan and Szechuan provinces in central China.

In the 40 years since Florin's biogeographic compilation, new collections have added significant temporal and spatial detail to our knowledge of Metasequoia's distribution. This allows a more detailed documentation of both the pattern and timing of range contractions. Today, distribution data can also be plotted in a plate tectonic framework to present more realistic estimates of the genus' paleolatitudinal range. We also place the genus' ancient distribution within the context of independent data and modeling of global climate through time. Thus, we can ask whether range change occurred in pulses or gradually, and explore the specific climatic correlates.

Although Metasequoia displays substantial ecomorphological variation (Li, 1998/1999), its range of morphological variation has remained relatively stable through time (Liu et al., 1999). This, combined with its apparent climatic sensitivity, might make Metasequoia a useful paleoclimatic indicator. To test this hypothesis, we assemble the climatic conditions under which M. glyptostroboides grows today in order to estimate climatic tolerances for both survival of adult plants and regeneration. We refer to these climatic ranges as survival and regeneration tolerances respectively. Regeneration tolerances can then be compared to other lines of paleoclimatic evidence to explore congruences and inconsistencies.

2. Materials and Methods

Metasequoia distribution data were gathered first from the published literature (Appendix), with emphasis on work published since Florin's (1963) compilation and on North American occurrances. We reviewed all literature to verify the identification of Metasequoia fossils. When possible, we reviewed material in museum collections; in other cases, we verified identifications using published illustrations. Material reviewed for identifications is noted in the Appendix. Foliage and cones were identified using the revised classification of Liu and colleagues (1999). In addition, we reviewed all Cretaceous and Cenozoic floras from the University of California Museum of Paleontology's (Berkeley, California, U.S.A.) collection for additional, unpublished occurrences. We also included published and unpublished occurrences in China and Russia reviewed by Liu and colleagues (1999). For unpublished museum collections, we used original locality files for geographic location and the most current age estimates available for each flora.

Florin (1963) reported 82 occurrences of Metasequoia in the fossil record. Our data set (Appendix) includes 179 fossil occurrences, with significantly better coverage in all Epochs surveyed. Greater geographic coverage, particularly in North America, also allows finer-scale resolution of the patterns of range contraction in both space and time. Our extensive review of museum collections and new localities allowed us to better determine whether Metasequoia's absence at a given place and time was a true absence or an artifact of spotty regional collections. For example, we reviewed many Eocene localities from the Rocky Mountain region that lack Metasequoia, suggesting that the genus was absent; in contrast, there are no Cretaceous-age collections from northeastern North America, which precludes interpretation. Our data base is somewhat smaller than that assembled by Yang and Jin (2000) because we were unable to independently verify generic identifications in a number of their fossil occurrences. To be conservative, we did not include these unverified reports. However, or data set includes a more detailed compilation of North American localities.

Age dates for fossil occurrence were placed radiometrically (Ozaki, 1991), biostratigraphically (Tao and Xiong, 1986b; 1986a), or based on lithostratigraphic correlation

(Ozaki, 1991). Latitude, longitude and age data were compiled in the Paleogeographic Mapping System (Earth in Motion Technologies, 1997). This software reconstructs paleogeographic coordinates from Recent data using trigonometric rotation to PaleoMap plate reconstructions (C. Scotese, PaleoMap Project, 1998). We used these coordinate outputs to prepare figures discussed below. We analyzed paleogeographic distribution for the Maastrichtian (70 Ma), Late Paleocene (60 Ma), Middle Eocene (50 Ma), Late Eocene (40 Ma), mid-Oligocene (30 Ma), Early Miocene (20 Ma), Late Miocene (10 Ma), Mio-Pliocene transition (5 Ma), Pleistocene (1 Ma) and Recent (Figs. 1-2).

Data on the climatic tolerances of living Metasequoia glyptostroboides were compiled from North America, China and the United Kingdom. For each of 38 botanical gardens where M. glyptostroboides is cultivated, we recorded altitude (meters above sea level), latitude, mean annual temperature (MAT) (°C), mean cold-month temperature, mean warm-month temperature, and total annual precipitation (mm) (Table 1). Precipitation data should be considered the lower limit available to plants because most of the botanical gardens surveyed use some supplemental irrigation. Actual moisture received by particular trees was not available. In order to assess whether trees were within their climatic tolerance for regeneration, we gathered information on seed production and germination. In the botanical garden setting, many factors may influence a tree's ability to set viable seed. For example, trees may fail to produce viable seeds if they are too young, or if there are too few adults present in the population to permit outcrossing (D.R. Hendricks, Dawes Arboretum, Newark, Ohio, U.S.A., pers. comm., 1998). Therefore, we use only positive data (production of viable seed or natural recruitment in the garden) to set climatic tolerances for regeneration of M. glyptostroboides.

3. Range changes in Metasequoia

During the latest Cretaceous (Maastrichtian 71-65 Ma), Metasequoia was widely distributed across the Northern Hemisphere between 34°N and 82°N latitudes and maintained this distribution through the end of the Eocene (Figs. 1-2). The genus has been reported in the majority of fossil floras from the latest Cretaceous, Paleocene and Eocene, including those in western North America, Greenland, and Asia (Appendix). Metasequoia has not been reported at mid latitudes east of the Cretaceous-age Western Interior Seaway in North America. This may be due, in large part, to a lack of terrestrial rocks of appropriate age from eastern North America. Alternatively, the Seaway may have presented a significant biogeographic barrier. Metasequoia was nearly ubiquitous, although not necessarily common, in most Maastrichtian and Paleocene localities in western North America. By Early Eocene, the genus was extirpated from the Rocky Mountains (Wing, 1987). Metasequoia persisted in most far western localities in the contiguous United States and Canada, Alaska, the high Arctic, and was reported in a single New York State locality (Chaney, 1951). This single report suggests that the genus may have been present in eastern North America during the latest Cretaceous and Paleocene as well. However, lacking additional fossil occurrences, this conclusion remains speculative.

At the Eocene-Oligocene transition, Metasequoia's northern extent contracted from 63°N to 45°N, which it maintained until approximately 10 Ma (Fig. 2). The genus disappeared from the Arctic during the Oligocene. Throughout the Oligocene and Miocene, Metasequoia's range in North America contracted to lowland and coastal localities west of the Great Basin. The genus is absent from contemporaneous high-elevation localities. In Asia, Metasequoia has been reported in Kazakhstan and southern Russia from the Late Oligocene to Late Miocene, with its distribution centered in China, where it has been reported in most floras from forest localities. Metasequoia was extirpated in North America during the Early Pliocene and was restricted to central China and the Japanese archipelago during the Pleistocene (Fig. 3). The natural occurrence of living Metasequoia in central China represents a relic distribution following the loss of the island and coastal populations during Pleistocene glaciation. Metasequoia's central China refuge parallels those of a variety of other plants, which either have a disjunct distribution of species pairs with eastern North America (e.g., Pachysandra in the Buxaceae) or were previously widely distributed throughout North America but are now restricted (e.g., Glyptostrobus, Platycaria in the

Juglandaceae, and *Cercidophyllum* in the Cercidophyllaceae) (Leopold and MacGinitie, 1972; Hickey, 1977; Wing, 1987).

Figure 4 shows two major contractions in the northerly range of *Metasequoia*, both of which are correlated with Tertiary climatic cooling. The first contraction occurred in response to Late Eocene cooling, but preceded the dramatic Eocene-Oligocene boundary climate event. The second followed Plio-Pleistocene temperature decay. Range contractions reflected only in changes in the northernmost extent of the genus, suggesting a link to cold-month mean temperature or MAT. *Metasequoia*'s southern range changed little through time (Fig. 4). In Asia, the Cretaceous and Paleogene southern limit of *Metasequoia* was controlled by seasonally dry or semidesert conditions that existed at 20°N to 30°N latitude during the Late Cretaceous (Zhao, 1992). In North America, Late Cretaceous leaf floras from the southeastern United States and Gulf Coast suggested subhumid conditions with seasonal drought south of 35°N latitude (Wolfe and Upchurch, 1987). This indicates that the southern limit of *Metasequoia*'s range, in both cases, may have been set by precipitation, rather than temperature. The historical southern limit of *Metasequoia*'s distribution is close to the present latitude of natural populations of *M. glyptostroboides* (30°N latitude). There, mild lowland temperatures in the Yangtze valley allowed *M. glyptostroboides* to persist in this refuge during glacial intervals (Li, 1953). The lower and middle Yangtze valley also have abundant precipitation and warmer winters than surrounding highland regions at similar latitude (Chu and Cooper, 1950). During Pleistocene glacial intervals, the northeasterly trend of the Tsinling Range to the north-northwest of the Szechuan Basin may have pooled warmer air allowing the region to remain ice-free (Hu, 1980). This may have allowed Chinese Pleistocene populations of *M. glyptostroboides* to survive while populations in Japan were extirpated. Southward migration of *Metasequoia* during Plio-Pleistocene climatic collapse was likely restricted by the Tibetan and Yunnan highlands, locking the small population into its current restricted geographic range.

4. Climatic preference of living Metasequoia glyptostroboides

Upon the discovery of extant Metasequoia by Hu and Cheng in 1948, seeds and seedlings were sent to botanical gardens throughout the Northern Hemisphere. Although the horticultural distribution is artificial, data from thriving and reproducing trees may give a more complete picture of the climatic tolerances of living M. glyptostroboides than could be derived from examining only restricted natural populations. Natural stands in Szechuan, central China grow at 750 m to 1500 m elevation under a MAT of 13°C. Average cold month temperatures are > 1°C with a lowest recorded temperature of -8°C. Warm month temperatures average 24°C and the area receives approximately 1500 mm of precipitation annually (Table 1).

In cultivation, adult M. glyptostroboides grow from 22°N to 56°N latitude and at elevations of nearly sea level to 2200 m (at Xiaolongshan Institute of Forestry, Gansu Province, China) in elevation. Adult trees survive in MATs ranging from 8°C to 22°C (Table 1) and will tolerate average cold month temperatures as low as -13°C (Liaoning Province, China). Average warm month temperatures for M. glyptostroboides range from 14°C to 35°C. In botanical gardens where M. glyptostroboides thrives, precipitation ranges from 374 mm to 2800 mm annually. In gardens at the low half of this range, natural precipitation is augmented by irrigation and growth is generally poor in the absence of supplemental watering.

The range of conditions under which M. glyptostroboides produced viable seed or where seeds germinated naturally in botanical gardens was more restricted. In our survey, germination was reported from 27°N to 43°N latitude and under a MAT range of 9°C to 16°C. Average cold month temperatures ranged from -5°C to 4°C; average warm month temperatures ranged from 18°C to 28°C. Mean annual precipitation (MAP) under which seeds germinated without human cultivation ranged from 953 mm to 2039 mm, although the low-precipitation plantings were supplemented by significant irrigation. Since natural populations must regenerate in order to persist, these ranges represent the best approximation of the climate requirements for the species, although adult plants may survive colder or warmer extremes or occasional drought encountered during the lifetime of the tree. The regeneration tolerance defined here is also consistent with the conditions experienced by natural populations.

5. Correlations of Metasequoia glyptrostroboides climatic tolerance with paleoclimate

Using a modern analog approach, the range of temperature (MAT 9°C – 16°C) and precipitation (MAP 953-2039 mm) discussed above for regeneration of living Metasequoia glyptostroboides might be used to reconstruct paleoclimate throughout the genus' former range. This assumes that significant no change in climatic preference occurred through time (Mosbregger, 1999). How does this interpretation compare to other lines of paleoclimatic evidence?

Using dicotyledon leaf margin analysis (Wolfe, 1995; Wilf, 1997; Wolfe and Spicer, 1999), Wolfe and Upchurch (1987) reconstructed a mean annual temperature (MAT) of 22°C to 26°C, with small annual range of temperature, for 30°N latitude in western North America during most of the Late Cretaceous. Metasequoia was not present in the floras they studied and has not been reported south of 35°N to 40°N during this interval. Within the Late Cretaceous latitudinal range of Metasequoia, Johnson and Hickey (1990) reported mean annual temperatures between 10°C and 16°C at 46°N latitude in North Dakota. The floras used to develop these reconstructions also contained Metasquoia. Megathermal (MAT 20-30°C) climate prevailed at 50°N and mesothermal (MAT 13-20°C) temperatures at 65°N during the Maastrichtian (Wolfe, 1980; Spicer and Parrish, 1986). Near-polar floras (80°N-85°N) on the North Slope of Alaska, which also contained Metasequoia, yielded MAT reconstructions of 2°C to 8°C (Parrish and Spicer, 1988). This suggests that the range of temperatures under which M. glyptostroboides reproduces today is restricted to the cool end of fossil M. occidentalis' broad regeneration tolerance.

Wolfe and Upchurch (1987) noted continued warm temperatures in the early Paleocene (MAT 24-26°C at 30°N latitude), with a decline to early Maastrichtian MAT in the latter half of the epoch. This warming is consistent with Metasequoia's restriction to latitudes north of 35°N to 40°N during the Paleocene and Early Eocene. Johnson and Hickey (1990) reported cooling (MAT

11°C at 46°N latitude) in the earliest Paleocene of North Dakota. The 11°C MAT in North Dakota is also consistent with abundant Metasequoia fossils recovered from these and other Paleocene localities in Montana and Wyoming.

Using the size and shape of fossil leaves (Wolfe, 1995; Wilf et al., 1998; Wolfe and Spicer, 1999), Wolfe and Upchurch (1987) estimated Late Cretaceous precipitation in the mid latitudes of the Northern Hemisphere to have been approximately 1100 mm. This pattern shifted significantly in the early Paleocene, with MAP exceeding 1500 mm. However, using a non-quantitative approach, Johnson and Hickey (1990) reported drying in the earliest Paleocene of North Dakota. Given general trends toward larger leaves, indicating wetter climates, across the western interior of North America during the early Paleocene, the North Dakota drying trend, if robust, was likely regional.

Wolfe and Upchurch (1987) reported that post-Cretaceous humid climate continued into the early Eocene warming that characterized most of the Northern Hemisphere (Miller et al., 1987; Wolfe and Upchurch, 1987). However, with the early Eocene came generally drier climates and more rainfall seasonality throughout central North America (Peterson and Abbott, 1979; Wing, 1987; Wolfe and Upchurch, 1987; Frederiksen, 1991). Regional drying coincided with extirpation of Metasequoia and associated plants in the Rocky Mountain regions (Wing, 1987), while the genus persisted in humid portions of eastern North America (Chaney, 1951) and the far west (Fig. 1). Despite the extirpation of Metasequoia from many regional localities in response to Early Eocene drying, the major range contraction in both North America and Eurasia (Figs. 1-2) was more closely correlated with the Late Eocene cooling recorded by both marine isotopes (Shackleton and Kennett, 1975; Miller et al., 1987) and terrestrial leaf physiognomy (Wolfe, 1995).

A second pulse of Metasequoia range contraction occurred in the Early to Middle Miocene (Fig. 2). Extirpation of Metasequoia in high Northern Hemisphere latitudes was well-correlated with the increase in marine oxygen isotopic values (interpreted as cooling and/or ice accumulation) observed between 20 Ma and 15 Ma (Shackleton and Kennett, 1975; Miller et al., 1987). A shift in the northern range of the genus was coupled, in North America, with contraction of range to near sea level localities in California, Oregon and Washington state. These localities maintained humid conditions during this interval (Wolfe, 1985). The observed Metasequoia range contraction was consistent with the expansion of North American grasslands and savanna woodlands in the mid to late Miocene, in response to lower and seasonal rainfall in the central portion of the continent (Wolfe, 1985; Cerling et al., 1993). Continued cooling and drying resulted in the extirpation of Metasequoia in North America by the earliest Pliocene, and its continued range contraction to coastal and wet in Asia with the onset of Pleistocene glaciation. In Asia, moist climates persisted over the mid latitudes until the end of the Miocene (Chen, 1992), allowing Metasequoia to retain a relatively broad, if patchy, distribution across China and central Asia (Figs. 2-3). However, Metasequoia was no longer a ubiquitous part of Miocene floras in Asia. Coastal refuges for Metasequoia in Japan north of 30°N were lost with the onset of major Plio-Pleistocene glaciation about 1 Ma (Cao, 1992). The single surviving form persisted in its central China refuge due to the moderate temperatures and abundant rainfall that persisted in this region through glacial intervals (Cao, 1992). Intolerance of low temperatuer may therefore explain the Pliocene extirpation of Metasequoia at higher latitudes, with cool-tolerant survivors remaining as population isolates and giving rise to the living populations. In contrast, ancient M. occidentalis and natural populations of living M. glyptostroboides appear to have shared a requirement of 1000 mm to 2000 mm of precipitation annually.

Comparing Metasequoia's climatic tolerances, past distribution, and other lines of paleoclimatic evidence suggests that the regeneration temperature tolerances of M. glyptostroboides may be more restricted than those of ancient forms, such as M. occidentalis. Since M. occidentalis and M. glyptostroboides are indistinguishable in the fossil record, the shift in climatic preferences has occurred without correlative morphological change. Therefore, using modern Metasequoia's climatic tolerance to reconstruct paleoclimate might lead to cooler MAT and cold month temperatures than inferred from a variety of other methods. This highlights the danger of using modern analog species to develop paleoclimatic reconstructions, even for Pleistocene and Holocene forms that vary little from their living counterparts.

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Figure Legends

Fig. 1. Distribution of Metasequoia fossils plotted on paleogeographic reconstructions for the Maastrichtian (70 Ma), Late Paleocene (60 Ma), and Middle Eocene (50 Ma).

Fig. 2. Distribution of Metasequoia fossils plotted on paleogeographic reconstructions for the Late Eocene (40 Ma), mid-Oligocene (30 Ma), and Early Miocene (20 Ma).

Fig. 3. Distribution of Metasequoia fossils plotted on paleogeographic reconstructions for the Late Miocene (10 Ma), Mio-Pliocene transition (5 Ma), and the present.

Fig. 4. Northern Hemisphere latitudinal distribution of Metasequoia from the latest Cretaceous to the present. Points represent individual fossil occurrences in our database of 179 localities. Black lines chart maximum northern and southern distributions through time. Heavy gray line tracks trends in Northern Hemisphere temperature change based on marine oxygen isotope data (Miller et al., 1987). Major Tertiary climatic events including the Paleocene-Eocene Temperature Maximum (PETM), Eocene-Oligocene boundary cooling event and Plio-Pleistocene climatic decline are noted. Two major contractions of Metasequoia's northerly range are observed: in the late Eocene and late Pliocene; the genus' southern range remains relatively stable through the Tertiary.