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Taxonomy in Aspen: Ecology and Management in the Western United States

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TAXONOMY

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Quaking aspen, or trembling aspen (*Populus tremuloides*), was named and described by Michaux in 1803. It exhibits marked phenotypic variability throughout its transcontinental range. Numerous authors, especially the early ones, tried to give order to the variability by subdividing it taxonomically. Quaking aspen has been subdivided by various taxonomists at one time or another into 4 species and 13 varieties or forms (Barnes 1969, Beetle 1974). However, Little (1953, 1979) recognized quaking aspen as a single heterogeneous species without subspecific taxa. Barnes (1969) found that much of the total morphological variation within the whole complex can be found in various combinations within single locales. His observation is supported indirectly by numerous observations and investigations of the variation in aspen in the West, notably by Greene (1971).

This report follows Barnes (1969), Little (1979), and current usage in accepting quaking aspen, throughout its North American range, as a single, highly variable species, *Populus tremuloides* Michx.

Paleobotany

Trees similar to quaking aspen appear to have flourished throughout western North America since middle Miocene time, almost 15 million years ago (Axelrod 1941, Chaney 1959, Smiley 1963, Wolfe 1964). In Miocene deposits, quaking aspen-like leaves have usually been designated as *Populus voyana* Chaney and Axelrod (Chaney and Axelrod 1959). Fossil specimens of *P. voyana* display large, apparently thin leaves similar to those produced by living *P. tremuloides* in the wetter portions of its range. Wolfe (1966) gave the name *P. kenaiana* to another Miocene fossil aspen from the Kenai Formation of the Cook Inlet region of Alaska. Although he did not equate his specimen to any living poplar, the leaf used to illustrate the new species seems well within the morphological limits displayed by published silhouettes of leaves from living populations of *P. tremuloides* from Utah, northern Idaho and adjacent Montana, and Vancouver Island (Barnes 1975).

Pliocene fossils referable to quaking aspen have smaller, thicker leaves than those of *P. voyana*. The Pliocene material is commonly assigned to *P. pliotremuloides* Axelrod. These leaves appear to reflect somewhat drier habitats than were common during the Miocene (Chaney and Axelrod 1959). Another fossil poplar, *P. eotremuloides* Knowlton, despite its name, apparently is not related to quaking aspen, but to *P. trichocarpa* (Chaney 1938).

Three other fossil aspen species (*P. booneana* Smith, *P. subwashoensis* Axelrod, and *P. washoensis* Brown) belong to the section *Leuce* of *Populus*. All were widespread in Miocene and Pliocene fossil floras of the western United States (Chaney 1959, Smiley 1963, Wolfe 1964, Wolfe et al. 1966). These fossil species are considered to be closely related to *P. grandidentata*, a living species now confined to eastern North America (Little 1971). Because *P. grandidentata* currently hybridizes with *P. tremuloides* where the two grow together, Barnes (1967, 1975) suggested that the modern leaf morphology of the latter species in western America may have been strongly influenced by episodes of hybridization during the late Cenozoic era, when ancestors of the two species coexisted in the West. He further emphasized that, because modern clones of quaking aspen are large and apparently very old in unglaciated parts of the central and southern Rocky Mountains, only a few sexual generations may separate living aspen from its Pliocene ancestors.

Apparently, the ancestors of both quaking aspen and bigtooth aspen (*P. grandidentata*) differed somewhat in respect to ecological requirements, because the two species rarely occur in the same fossil bed, although they overlap broadly both in time and space (Chaney and Axelrod 1959). Because the two species hybridize now and may have hybridized anciently (Barnes 1967), their continued existence as different species throughout geological times must have been related to somewhat different ecological requirements.

Upland species commonly found associated with quaking aspen-like fossils include many shrubs and trees but almost no herbaceous species. Trees that frequently occur with aspen in the fossil record include species of the following genera: *Abies, Acer, Picea, Pinus, Prunus, Quercus, Sequoia,* and *Tsuga*. Shrub genera regularly occurring with aspen include *Amelanchier, Arctostaphylos, Ceanothus, Mahonia, Rhus, Ribes,* and *Symphoricarpos* (Axelrod 1939, 1950, 1956; Chaney 1959; Smith 1941). Quaking aspen continues to be closely associated with most of these genera, at least somewhere within the modern range of the species.

Fossil pollen studies have made very little contribution to knowledge of aspen distribution. *Populus* pollen has a delicate exine and is, therefore, generally poorly preserved (Axelrod and Ting 1960, Sangster and Dale 1961). Also, recognition of *Populus* species by pollen alone is very difficult, as is the case with numerous other woody genera. In contrast, fossil pollen has been useful in indicating the herbaceous angiosperms that may have been associated with aspen in late Cenozoic time. It has been generally concluded that the flowering herbs did not make a significant contribution to the vegetative

cover of the earth until Miocene time. During Miocene, there was a pronounced increase in percentage and taxonomic diversity of probable herbaceous pollen types, although macrofossils of herbs remained uncommon (Wolfe 1962). Wolfe (1962) concluded, on the basis of fossil pollen, that the following taxa probably were represented by herbs in a Miocene upland forest of the Oregon Cascades: *Chenopodiaceae, Compositae* (including *Chichoreae* and *Astereae*), Galium, *Graminae, Malvaceae, Onagraceae*, and Valeriana. The woody flora of the beds considered included a fossil quaking aspen (Chaney 1959). Aspen may have occurred in the same community as the herbaceous taxa listed previously.

Relationships

The genus *Populus* has been subdivided into several sections. Aspen belongs to the section *Leuce*, subsection *Tripidae*. In Alberta, Canada, Brayshaw (1965) found what seemed to be evidence that aspen hybridizes in nature with poplars belonging in other sections. However, Ronald et al. (1973) could find no evidence of such crosses in Manitoba, despite widespread association of quaking aspen with species of other sections. In the United States, there are no known natural hybrids of aspen and poplars belonging to other sections.

In some parts of North America, quaking aspen hybridizes naturally with *P. alba* of the subsection *Albidae*, introduced widely from Europe (Barnes 1961, Einspahr and Winton 1977, Spies 1978). However, there are no reports of natural hybrids with *P. alba* in the West.

The only species of subsection *Albidae* native to North America is *Populus monticola* (Sargent 1891), found in southern Baja California, Mexico between 2,100 and 5,100 feet (650 m and 1,550 m) elevation (Standley 1920). Aspen does not grow in that part of Mexico. Bailey (1930) suggested that *P. monticola* is not native at all, but actually *P. alba* var. *subintegerrima* introduced by early Spanish settlers and subsequently naturalized.

The subsection *Tripidae* includes, besides quaking aspen, bigtooth aspen (*P. grandidentata* Michx.) of eastern North America, the Eurasian *P. tremula* Linnaeus, and several Asian taxa. All of the species in subsection *Tripidae* are easily crossed (Einspahr and Winton 1977). Natural hybrids of quaking aspen and bigtooth aspen are fairly common in some eastern locales (Andrejak and Barnes 1969, Barnes 1961, Pauley 1956). Although the occurrence of backcrossing and introgression has been suggested (Barnes 1961, Pauley 1956), they have not been compellingly demonstrated.

Hybrids between quaking aspen and *P. tremula* may survive and grow either well or poorly (Einspahr and Benson 1964; Pauley et al. 1963c, 1963d). However, the same is true of quaking aspen seedlings planted outside their own provenance.

Middle-latitude sources of European aspen, *P. tremula*, survived and grew about as well in Massachusetts as did aspen of local and Lake States sources, while *P. tremula* from Scandinavia performed there about as poorly as western aspen (Pauley 1963, Pauley et al. 1963a, 1963b).

Before 1803, when Michaux described *P. tremuloides*, quaking aspen seems to have been regarded by some simply as an American occurrence of *P. tremula* (Marshall 1785, cited by Sudworth 1934). Pauley[1] wrote that when the full range of variability within each species is considered, there seemed to be no sharp morphological or physiological discontinuities between quaking aspen and *P. tremula*. He wrote further that, physiologically at least, *P. tremuloides* from the Lake States is probably more similar to *P. tremula* of southern Sweden than to *P. tremuloides* of Arizona or the Yukon Territory. Barnes (1975) noted that some Utah clones more closely resembled the Asian aspens *P. rotundifolia* and *P. bonati* than they do quaking aspen clones in the northern Rocky Mountains and adjacent Canada, or those typical of eastern North America.

Considering the broad variability within *P. tremuloides* and the Eurasian and Tertiary aspens, the apparent lack of traits that clearly differentiate them, and the interfertility of modern forms, a case could be made for considering most of the subsection of *Tripidae* a single circumboreal superspecies. But *P. tremuloides* itself, with the broad variability discussed more fully in the GENETICS AND VARIATION chapter, already stretches the concept of a species.

[1] *Personal communication from Scott S. Pauley, February 10, 1964.*