

Relationships Between Rare Plants of the White Mountains and the Late Cenozoic Geology of the Colorado Plateau

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ABSTRACT. A complex geologic history has shaped the distribution of Arizona willow (*Salix arizonica* Dorn) and the Mogollon paintbrush (*Castilleja mogollonica* Pennell). These subalpine plants do not appear to be strict substrate specialists, but they do seem to favor coarse-textured and well-watered soils. Most of their occupied habitats were shaped by Quaternary glaciations, but are ultimately derived from felsic substrates formed before the Pliocene period. Populations of Arizona willow have been identified in the White Mountains of Arizona, the High Plateaus of Utah, and in the Southern Rocky Mountains of New Mexico and Colorado. Species closely related to the Mogollon paintbrush also occur in the Utah plateaus and the Southern Rocky Mountains. Genetic dissimilarity among these populations suggest that these taxa likely share an evolutionary history that extends into the Neogene, when tributaries of the ancestral Colorado River connected young volcanic highlands on the margins of the Colorado Plateau. This history points to the likelihood of additional populations of Arizona willow in the San Juan Mountains, and it suggests that these plants have survived dramatic changes in their environments. These patterns demonstrate the value of analyzing geology at a detailed level when interpreting habitat preferences and distributions of rare species.

INTRODUCTION

A few species are endemic to only the White Mountains of Arizona, but the list has grown shorter in recent years. The Arizona willow (*Salix arizonica* Dorn) was thought to be a member of this select group until Robert Dorn reidentified a specimen in the Rocky Mountain Herbarium that had been collected in 1913 from southern Utah. This realization led to the recognition of Arizona willow populations in southern Utah, northern New Mexico, and southern Colorado (Thompson et al. 2003). The scattered populations in these four states represent the known distribution for the species (Fig. 1).

The Mogollon paintbrush (*Castilleja mogollonica* Pennell) is another rare plant that is endemic to the White Mountains of Arizona, but whose status as a separate species has been questioned. Pennell first described this yellow-bracted paintbrush as a separate species (Pennell 1951). Holmgren (1973) placed it in the Septentrionales group, which includes the yellow-bracted sulphur Indian paintbrush (*C. sulphurea* Rydb.) as well as several endemic species of the Southwest (Fig. 2). National plant databases (the USDA's PLANTS National Database and the University of North Carolina's Biota of North America Program) currently hold that *C. mogollonica* is a synonym for *C. sulphurea*, which is

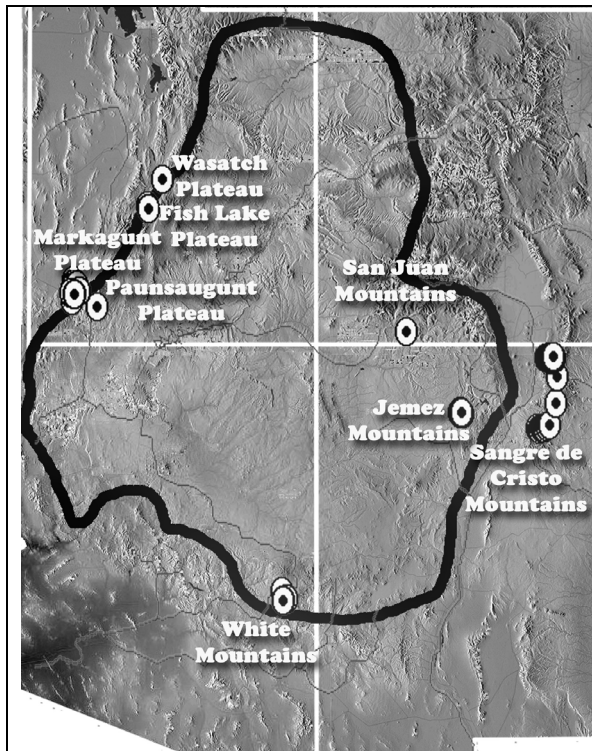


FIGURE 1: Distribution of Arizona willow in the Colorado Plateau region.

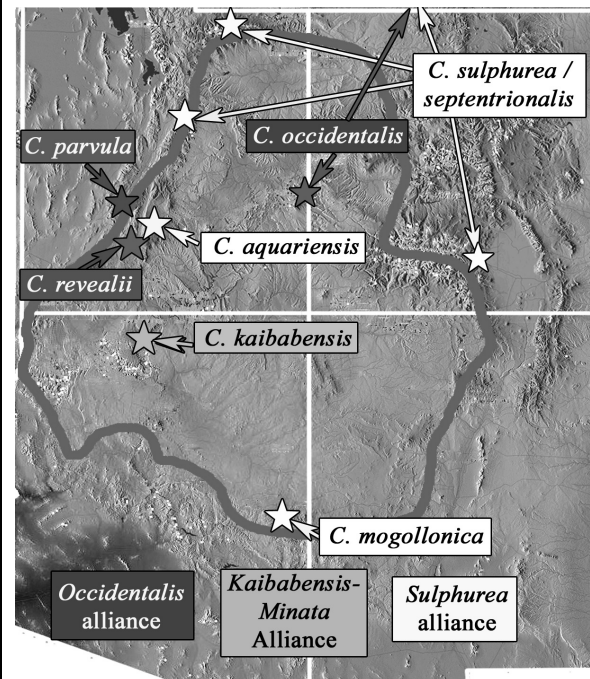


FIGURE 2: Distribution of members of the Septentrionales group of *Castilleja* in the Colorado Plateau region based on Holmgren (1973).

distributed widely in the Rocky Mountains. However, a taxonomist currently working with the genus holds that *C. mogollonica* is a valid species, and instead *C. sulphurea* should be synonymous with *C. septentrionalis* (Lindl.) (Egger 2004).

With the exception of retaining *C. mogollonica*, plant nomenclature used throughout this paper conforms to the PLANTS database (<http://plants.usda.gov>).

Some biologists have even questioned the status of the flagbearer of rare species in the White Mountains, the Apache trout. Some taxonomists contend that this trout should be designated merely as a subspecies (i.e., *Oncorhynchus gilae* ssp. *apache*) (Behnke 2002). These trends reflect in part the vicissitudes of taxonomy. However, they also may reveal a growing recognition that the White Mountains have not been entirely

isolated from other high mountain ranges during the time in which new species have evolved.

SIGNIFICANCE OF GEOLOGY TO PLANT DISTRIBUTIONS

Reconstructing the geologic evolution of landscapes helps to explain the distributions of endemic species. Geology not only explains the past conditions an organism has withstood, but it also regulates present aspects of habitat including climate (through orographic effects), hydrology, and soil chemistry. However, many ecologists studying rare biota in the White Mountains of Arizona have either ignored geologic variation or oversimplified it. For example, in discussing the biogeography of the endemic Mogollon paintbrush, Bainbridge and Warren (1992) described the region as “basaltic.” Similarly, the conservation agreement for the Arizona

willow asserted that all but one population of the plant occur on "basaltic (volcanic) soils" (AWITT 1995). These statements are incorrect, and they mislead readers to assume that the White Mountains are monolithic.

The geologic formations underlying populations of Arizona willow and Mogollon paintbrush in Arizona originated from felsic Tertiary volcanism, which formed several other montane regions in the Southwest. Some researchers have considered the importance of variation among these volcanic landforms as well as the influence of glaciation in evaluating the habitat of rare species in the White Mountains. Ladyman (1996) reported that the endemic Mogollon Clover (*Trifolium neurophyllum* Greene) appeared "to be positively associated with basalt soils and negatively associated with datil soils" [Datil Group volcanics are predominantly felsic pyroclastic rocks containing pumice and ash located east of Mount Baldy in New Mexico (McIntosh and Chamberlin 1994)]. Other researchers have argued that Pleistocene glaciation had been a primary factor controlling the distribution of Arizona willow and other willow species (Price et al. 1996). Rinne (2000) hypothesized that both mineral composition and glacial history could account for reported differences in trout productivity between streams derived from rocks close to the Mount Baldy volcano and those farther away.

GEOLOGIC ASSOCIATIONS OF ARIZONA WILLOW

White Mountains, Arizona

A complex series of volcanic flows created the White Mountains, but the central massif of Mount Baldy was

formed from felsic volcanic flows during the late Miocene period (Merrill 1974). Mudflows and lahars down the young volcano created extensive deposits of colluvium that are known as the Sheep Crossing Formation (Merrill 1974). During the Quaternary, four distinct glacial events sculpted the two highest remnant peaks of the volcano, Mount Baldy and Mount Ord. The earliest glaciation carved out five U-shaped valleys that flowed to the west, north, and east (Merrill 1974). Within the past 3000 years, a very small glacier occurred on Mount Ord, while periglacial activity formed talus deposits in northeastern drainages of the Mount Baldy volcano and also shaped some of its south-facing slopes (Merrill 1974).

Populations of Arizona willow in Arizona are concentrated on landforms derived from the felsic Mount Baldy volcanics (Long and Medina, this proceedings, Geologic Associations of the Arizona Willow in the White Mountains, Arizona). The four populations on glacial deposits are the largest and highest density populations in Arizona, with estimated populations in the hundreds or thousands (AWITT 1995). Nearly half of the subpopulations are located on sites mapped as the Sheep Crossing Formation, which is a sedimentary formation also derived from Mount Baldy volcanics. Most of the remaining populations occur within four kilometers downstream of outcrops of this formation. The Sheep Crossing Formation is texturally indistinguishable from glacial tills in the area, although it was deposited millions of years earlier from debris fans and mudflows from Mount Baldy (Merrill 1974). Comparisons of plant densities to substrates show that alluvium, glacial

deposits, and Sheep Crossing Formation represent the prime habitat for Arizona willow in the White Mountains. Small populations occur on surfaces mapped as basaltic flows, although these deposits may be thin enough that underlying felsic formations yield water and substrates to the inhabited areas.

High Plateaus, Utah

The Utah populations occur in the High Plateaus region (Fig. 1) which is capped by andesitic and dacitic Tertiary volcanics of the Marysvale volcanic field as well as some younger basaltic flows (Stokes 1986; Luedke 1993; Rowley et al. 1994). Thus, the petrology and age of the High Plateaus of Utah are similar to the White Mountains volcanic field of Arizona. The populations of Arizona willow in Utah are scattered across the plateaus, with the greatest concentration on the Markagunt Plateau around Brian Head, a geologic cousin of Mount Baldy. Several drainages on the eastern side of this peak were glaciated. Nearly 100 kilometers to the northeast lie two populations in glacial deposits along Seven Mile Creek on the Fish Lake Plateau, which is also derived from Tertiary volcanics (Mead 1996). Those Tertiary lava flows once connected the Fish Lake and Markagunt Plateaus, although drainages have since cut down between them.

An isolated population has been reported from the Wasatch Plateau, representing the currently known northern limit for the species. Another small population occurs on the East Fork of the Sevier River on the Paunsaugunt Plateau where Tertiary volcanics have been eroded away. This population lies in Quaternary alluvium derived from Wasatch limestone and Kaiparowits Formation (Doelling et al. 1989), and it

appears to be the only one in Utah occurring in a watershed devoid of Tertiary volcanics. However, at least six other populations have diverse substrates in their watersheds, leading Mead (1996) to characterize them as being derived in part from sedimentary formations.

Southern Rocky Mountains, New Mexico and Colorado

In northern New Mexico, the Arizona willow occurs in at least 21 populations in the Sangre de Cristo Mountains and four populations in the Jemez Mountains (Atwood 1996; Atwood 1997; Dorn 1997). The rocks underlying these areas are more varied and much older than those in the White Mountains of Arizona or the High Plateaus of Utah due to the tremendous uplift of the Rocky Mountains. Substrates for Arizona willow habitat appear to become more diverse in these taller mountains. In the Sangre de Cristo Mountains, eight populations in the Pecos drainage are found on areas that have been mapped as Pennsylvanian undifferentiated sedimentary deposits (Miller et al. 1963). Thirteen populations near the northern border of New Mexico coincide with a jumble of upper Oligocene volcanic rocks and glacial deposits (Green and Jones 1997). Populations in the San Pedro Parks of the Jemez Mountains are underlain by lower Proterozoic plutonic rocks (Green and Jones 1997). A recently discovered population in the southern San Juan Mountains of Colorado (Colorado Natural Heritage Program 2001) is located on Oligocene silicic volcanics (Steven 1975) that were sculpted by glaciers during the Quaternary.

GEOLOGIC ASSOCIATIONS OF MOGOLLON
PAINTBRUSH AND RELATED
SEPTENTRIONALES

Stream reaches harboring Mogollon paintbrush were reported by Bainbridge and Warren (1992) and Carl-Eric Granfelt (unpublished data). Approximately 12 populations of Mogollon paintbrush found in the White Mountains occur on surfaces derived from Mount Baldy volcanics and four more are within five kilometers downstream of such outcrops. Four more populations occur on areas mapped as younger basalts in drainages of Snake Creek that do not flow downstream from Tertiary volcanics. However, the basalt layers in this area are thin and contain porous cinder deposits. Consequently, there are likely to be subsurface hydrologic connections to the slopes of Mount Baldy.

Mogollon paintbrush occurs at approximately 15 sites with Arizona willow, with five more sites occurring within three kilometers of Arizona willow populations. This association suggests that habitat for the two species are quite similar, although the paintbrush typically occurs in drier portions of meadows. However, the paintbrush has been observed only in north or northeast-trending drainages in areas that were above tree-line during the last glacial maximum (Merrill 1974).

Although *C. mogollonica* appears to be a distinct species, it has several relatives in the Septentrionales group that occur in the Intermountain and Southern Rocky Mountain regions (Fig. 2). *Castilleja aquariensis* N. Holmgren is a related species that grows in subalpine sagebrush meadows on the Aquarius Plateau. Other paintbrushes isolated in southern Utah include *C. revealii* N. Holmgren on the Paunsaugunt Plateau, *C. kaibabensis* N. Holmgren on the Kaibab Plateau, *C.*

parvula Rydb. on the Tushar Plateau, and *C. occidentalis* Torr. in the La Sal mountains. The closest relative to both *C. aquariensis* and *C. mogollonica* appears to be the yellow-bracted *C. sulphurea*, which grows throughout the Rocky Mountains from Alberta to southern New Mexico (Holmgren 1973). These three species form a group intermediate in morphology between the "occidentalis alliance," which includes *C. revealii* and *C. parvula*, and an alliance of *C. kaibabensis* and *C. miniata* (Dougl. ex Hook.) (Holmgren 1973).

GEOLOGIC FACTORS GOVERNING THE DISTRIBUTION OF ARIZONA WILLOW AND MOGOLLON PAINTBRUSH

Many interrelated factors may constrain habitat for the Arizona willow and Mogollon paintbrush. Factors such as high elevation, cold temperatures, and increased precipitation are associated not only with glaciers, but also with the volcanic formations that cap most of the plateaus and mountain peaks of the Southwest. These correlations and the limited fossil evidence of pre-glacial conditions complicate attempts to infer the role of glaciation in distributing the modern flora. The effects of glaciation appear to have interacted with the composition of underlying formations to produce the habitats presently occupied by these plants.

Glaciation

Glaciation unquestionably had dramatic effects on the habitat currently occupied by Arizona willow in Arizona, since most of that area would have been above treeline during the three major glaciations (Merrill 1974). The cooler and moister climate during the Pliocene-Pleistocene glacial periods would have

created more favorable conditions at low elevations, while proglacial erosion would have deposited favorable substrates far downstream in the three major glaciated river valleys where Arizona willow occurs (Black River, White River, and Little Colorado River).

Periglacial activity also shaped non-glaciated drainages, including Becker Creek, which has prominent talus deposits (Merrill 1974). Becker Creek also has some of the densest populations of Arizona willow and Mogollon paintbrush in Arizona. Price et al. (1996) noted that heavy snows and rock slides help to rejuvenate willow stands. These responses suggest that periglacial activity could stimulate expansion of willow populations.

In Utah, glaciation affected many of the locations harboring Arizona willow. Mead (1996) classified seven sites, including the largest and healthiest stands, as being partially derived from glaciated materials. Two of them, Sidney Valley and Castle Valley, have extensive accumulations of glacial till (Gregory 1950). The Fish Lake and Wasatch plateaus, where isolated populations of Arizona willow occur, were also glaciated (Stokes 1986). The Paunsaugunt Plateau, a third area harboring Arizona willow, was not glaciated, although many slopes show effects of nivation in past and present (Gregory 1950). Moreover, deposits of Quaternary unconsolidated debris are found at the top of the drainage where the Arizona willow occurs (Doelling et al. 1989). Frost action has fractured lava rocks on Brian Head and sandstone blocks on the Markagunt Plateau, forming talus piles at the base of slopes that supply substrates to the alluvial systems (Gregory 1950).

All populations in New Mexico and Colorado are found well above 3000 m in areas that were shaped by glaciers throughout much of the Plio-Pleistocene. Frost action has greatly affected these high altitude areas, since the southern part of the Sangre de Cristo Mountains has the highest incidence of freezing and thawing of any area in North America (Miller et al. 1963).

The retreat of glaciers appears to have created optimal habitat for the Arizona willow; however, many smaller populations of Arizona willow are found in unglaciated areas shaped by periglacial activity such as nivation, frost action and talus formation. Rock slides, exposure of mineral soil, and stream braiding are mechanisms that would have created willow habitat. Glacial and periglacial activity alone do not explain the distribution of Arizona willow, since the plant has not been reported from many other glaciated mountains in the region (e.g., San Francisco Peaks, La Sal Mountains, and Tushar Mountains) and since its distribution is narrow even within areas affected by glacial activity. Therefore, other factors such as mineralogy and hydrologic connections should be considered to explain the biogeography of this species.

Volcanics

Analysis of distributions suggests that the Arizona willow presently has a strong affinity for substrates derived from Tertiary felsic volcanics. The Tertiary volcanics of Mount Baldy in Arizona and the High Plateaus of Utah are dominated by andesitic to dacitic rocks with silica contents ranging from 54 to 70% (Nealey 1989; Luedke 1993). Tertiary volcanics in the Sangre de Cristo Mountains where Arizona willow

occurs include a mixture of rhyolitic-pyroclastic rocks, andesites and basaltic andesites with local felsic flows, and felsic flows and pyroclastic rocks (Green and Jones 1997). The area containing the lone identified population in Southern Colorado appears on a small-scale map (Luedke 1993) to be underlain by Tertiary dacite (62-70% silica). Throughout its range, Arizona willow seems to be rarely associated with basaltic rocks, which have less than 50% silica content.

Many factors that vary between the different mineralogies influence plant distributions, including age of formation, topography, soil texture, hydrology, pH, and nutrient levels. As silica-rich volcanics weather, they form relatively deep, acidic soils with low clay content and low organic matter content (Freeman and Dick-Peddie 1970). Flatter-lying basaltic landforms, on the other hand, tend to form fine-textured soils. At several of the sites in Arizona where Arizona willow does occur on basalt, the rocks are highly fractured (pers. observation). Such fractured substrates may allow greater aeration than is typical of most meadows formed from basalts.

Volcanic-derived Sedimentary Formations

Because felsic volcanics tend to form steep domes (Stokes 1986), erosion of these landscapes may accumulate coarse substrates in alluvial and colluvial valleys. In the White Mountains, these deposits include glacial tills and the Sheep Crossing Formation, which are texturally indistinguishable (Merrill and Péwé 1971). These “gravelly sands” promote hydraulic conductivity and serve as shallow aquifers by conducting flow from Mount Baldy to contact areas

where less permeable basalts force the water to the surface (Merrill 1974). Arizona willow and other willows congregate at these seeps and springs at the base of the mountain.

Non-volcanic-derived Sedimentary Formations

Although Arizona willow appears to favor volcanic substrates in Arizona and in Utah, it does occur in soils derived entirely from sedimentary substrates, including the Claron Formation and Kaiparowits Formation (Mead 1996). However, these substrates appear to share the coarse textures found in the volcanics. Many of the sedimentary formations of southern Utah weather to fairly coarse cobbles and gravels (Doelling et al. 1989). Limestone gravels derived from the Claron Formation resist abrasion and deterioration (Doelling et al. 1989). The Kaiparowits Formation is predominantly sandstone, with occasional conglomeratic beds appearing in the western exposures where Arizona willow occurs (Doelling et al. 1989). Thus, this formation has potential to weather into coarse, silica-rich substrates as well. In New Mexico's Sangre de Cristo Mountains, sedimentary formations bearing Arizona willow include undifferentiated Pennsylvanian formations. The stratigraphy of these formations is complex and hard to discern due to extensive vegetative cover, but they are generally comprised of quartzite-rich sandstones and limestones of widely varying ages (Miller et al. 1963).

Edaphic Characteristics

Many of the geologic formations where Arizona willow grows produce coarse-textured mineral soils. Good hydraulic conductivity and aerobic

conditions provide favorable habitat, particularly for the tallest and most productive willow plants (Long and Medina, this proceedings, Geologic Associations of the Arizona Willow in the White Mountains, Arizona). However, other soil factors, including soil chemistry, may govern the physiologic factors that lead to this association.

No studies have described soil preferences of Mogollon paintbrush, but one should expect correspondence to those of Arizona willow given their close association. Other members of the *Septentrionales* group also inhabit coarse-textured soils. *C. revealii* inhabits "limestone gravelly soil," and *C. aquariensis* grows in "rocky soil" (Holmgren 1973), although neither occurs in wetlands. *C. septentrionalis* inhabits "damp, rocky soil" (Pennell 1935). Given their relatively narrow distributions, some members of the *Septentrionales* group appear to be more edaphically constrained than Arizona willow.

While Arizona willow and members of the *Septentrionales* group do not appear to be strict substrate specialists, they both show affinity for coarse-textured soils. The sands and gravels may be derived from a variety of parent materials, including extrusive volcanic and sedimentary deposits from the Precambrian, Paleozoic, and Cenozoic eras. However, populations are small or absent from fine-textured soils derived from Pliocene or Pleistocene basalts. The La Sal, Henry, and Abajo Mountains represent a very different landscape type because they are relatively steep, laccolithic mountains composed of igneous rocks penetrating

up through shales and sandstones (Stokes 1986; Betancourt 1990).

Ecologists have reported many examples of glacial-pluvial flora whose distributions are governed by differences in substrates. Several willow species may reach their southern limits in the igneous White Mountains of New Mexico because the coarse-textured geology maintains adequate soil water (Freeman and Dick-Peddie 1970). Several conifer species extend their lower elevation limits in sandstone-derived soils (Betancourt 1990). On the other hand, shale and limestone substrates may impose higher elevation limits, where only specially-adapted species may survive (Betancourt 1990). Bristlecone pine (*Pinus longaeva* D.K. Bailey) enjoys a competitive advantage on dolomite in the Sierra Nevada due to its tolerance for low water and nutrient conditions (Wright and Mooney 1965). These examples reveal the importance of geology in determining suitable refugia for subalpine plants in the Southwest.

EVOLUTIONARY HISTORY OF THE ARIZONA WILLOW AND MOGOLLON PAINTBRUSH

The distributions of the Arizona willow and the Mogollon paintbrush could yield insights into the broader landscape evolution of the Colorado Plateau. If the presence of these plants were tightly linked to the Pleistocene glaciations, then continued warming might portend rapid doom for these species. On the other hand, if the plants had dispersed across the Colorado Plateau far earlier, then they would have demonstrated resilience to the dramatic climatic swings of the Pleistocene.

Opportunities for a Quaternary Dispersal

During the Pleistocene, the range of Arizona willow may have been larger and more contiguous (Price et al. 1996). A cooler and moister climate during the Pleistocene would have created more favorable conditions at low elevations. Increased rainfall, glacial and periglacial processes would have accelerated erosion, invigorating populations of the willow and exposing new areas for colonization on gravel-rich fan deposits. Frost action and erosion may have broken up thin basalt deposits at the edges of the volcanic outcrops, exposing new microsites. Headwater stream captures also may have provided yet another avenue for dispersal into unoccupied habitats.

Biogeographers have contended that the mountains of Central Arizona and the High Plateaus of Utah were ecologically connected to the Southern Rocky Mountains of Colorado and New Mexico during the last glacial maximum (Moore 1965; Betancourt 1984). Bailey (1970) posited that *Pinus aristata* (Engelm.) descended the Sangre de Cristo Mountains, crossed the Rio Grande, traveled the high mountains of west-central New Mexico to the White Mountains of Arizona, and then spread across the Mogollon Rim to Flagstaff during the Pleistocene. This hypothesis is supported by pollen samples from Hay Lake in the White Mountains that reveal the presence of bristlecone pine during the Middle Wisconsin (Jacobs 1985). A nearly continuous range of mountains leads from the White Mountains of Arizona to the Sangre de Cristo Mountains of New Mexico, and these are dominated by Oligocene andesitic to basaltic-andesitic volcanics that might have provided suitable habitat for the Arizona willow. Endemic plants of the

White Mountains, including the Mogollon clover, the Goodding onion (*Allium gooddingii* Ownbey), and the Gila groundsel (*Packera quaerens* (Greene) W.A. Weber & A. Löve), extend into the Mogollon Mountains of New Mexico. However, because those plants occur in lower elevation, drier microsites on mafic soils, they are less likely to share the evolutionary history of the Arizona willow and Mogollon paintbrush.

Populations of Arizona willow in Utah remain hydrologically connected through the drainages of the Sevier River, which flow into Sevier Lake, a vestigial Pleistocene pluvial lake. This distribution suggests that Arizona willow may have been more widely distributed throughout the Sevier watershed, perhaps extending to the shores of the Pleistocene Lake Bonneville along with other subalpine flora (Betancourt 1990). A colder and wetter Pleistocene climate would have promoted contiguity among the populations in Utah.

Arguments for a Tertiary Dispersal

An earlier dispersal of the species may be favored by the fact that populations of Arizona willow in Arizona and Utah are separated by vast expanses of basalt flows and sedimentary deposits across the Colorado Plateau, in addition to the chasm of the Grand Canyon. This separation has allowed bristlecone pine populations in the two states to form separate species, perhaps indicating isolation since the mid-Tertiary (Bailey 1970). Many theories concerning the origin of willows and other Arcto-Tertiary flora propose that diversification occurred during the Neogene (Wolfe 1997). Holmgren

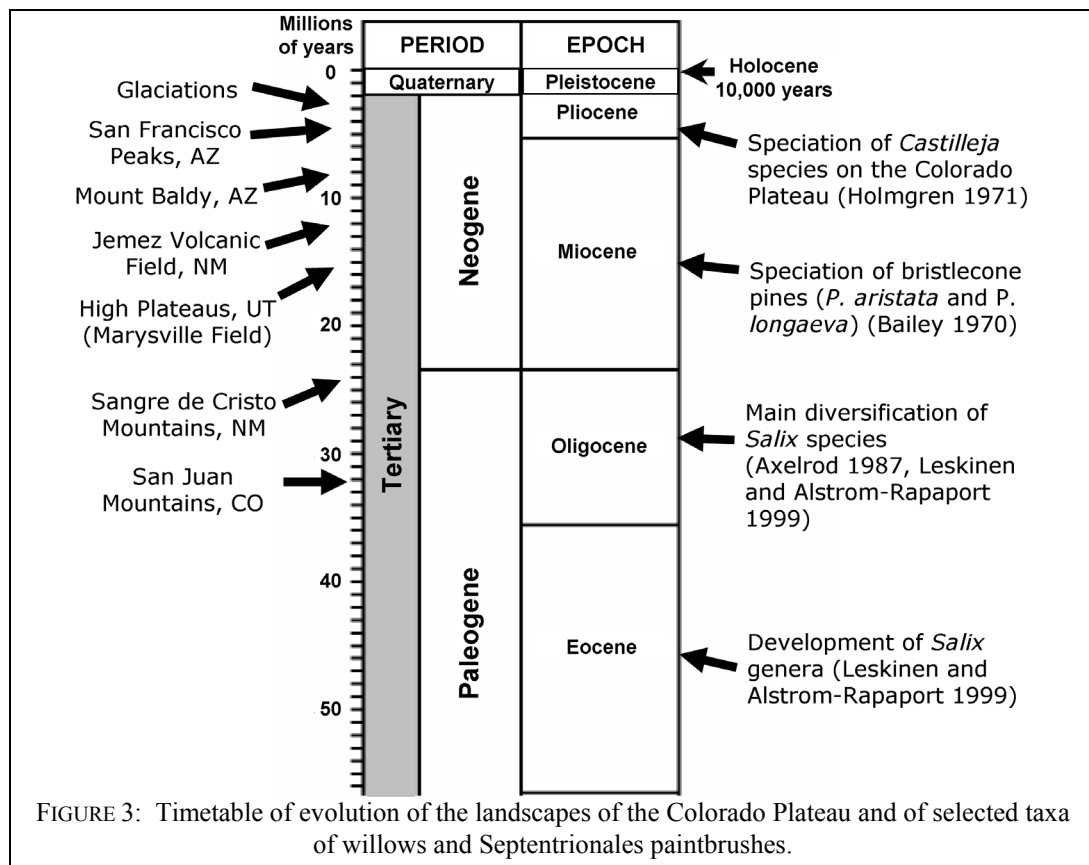
(1971) suggested that various endemic species of *Castilleja* in the Southwest became isolated during the Pliocene.

The volcanism that formed Mount Baldy and Brian Head had ended by the start of the Pliocene (Fig. 3). Extensive erosion occurred as the Plateaus were elevated (Stokes 1986), and as Mount Baldy was reduced by 600 m from its peak elevation (Merrill 1974). Massive debris slides in the valleys below these mountains could have yielded ideal substrates for the willow to colonize. Similar geomorphic evolution transpired in New Mexico and Colorado at an earlier date. Extensive volcanism formed the San Juan mountains during the Oligocene (24-38 M yr) (Fig. 3). During the Miocene period, 14-15 M yr, the region appeared to have a mild winter climate (Axelrod and Bailey 1976), but

Hydrologic Connections

the climate then cooled (Wolfe 1997). The climate of the Southern Rocky Mountains then became more favorable to dispersal of subalpine plants. Formation of volcanic peaks and regional uplift promoted cooling and increased precipitation at high elevations. Even without changes in climate, peaks such as the White Mountains of Arizona would have been cooler than at present due to their higher elevation (Merrill 1974). The ancestral Rio Grande dates to the upper Pliocene, following rapid uplift and block-faulting of the Sangre de Cristo Range (Axelrod and Bailey 1976). Subalpine plants could have spread overland or along shifting rivers in the Rockies to occupy the uplifting Sangre de Cristo mountains.

Hydrologic connections between



Arizona's White Mountains and Utah's High Plateaus apparently existed during the mid-late Neogene (Fig. 4). In Arizona, the ancestral Little Colorado River from Mount Baldy toward the Colorado River. Along the way, the system was dammed in places to form the lacustrine/playa deposits of the Bidahochi Formation, or Hopi Lake, in northeastern Arizona (Fig. 4) (Scarborough 1989; Gross et al. 2001). The source drainages of this formation remain uncertain, but they included the ancestral Little Colorado River and may have at times included tributaries of the ancestral Colorado River from the Rocky Mountains (Dallegge et al. 2003). Fossil records of beaver and an ancestral pikeminnow (*Ptychocheilus*) in the formation indicate abundant wetland habitat, although the climate may have been relatively warm on average (Repenning and Irwin 1954; Scarborough 1989). Geologic evidence suggests that an arrangement of mountains and drainages similar to the present-day was in place within the region by the Mid-Miocene, except that the ancestral Colorado River had not yet breached the Kaibab Plateau (Gross et al. 2001). Instead, the river may have flowed north along the present-day course of Kanab Creek (Lucchita 1990). This course leads directly to the plateaus of Utah, coinciding with drainages of the Sevier River where Arizona willow occurs (Fig. 4). Consequently, during the Neogene, this drainage system may have linked the Rockies to the volcanic peaks of Mount Baldy and southern Utah.

Around 5 to 6 million years ago, the Colorado River changed its course to follow its present path to the Gulf of California, forming the Grand Canyon (Scarborough 1989). The Canyon cut

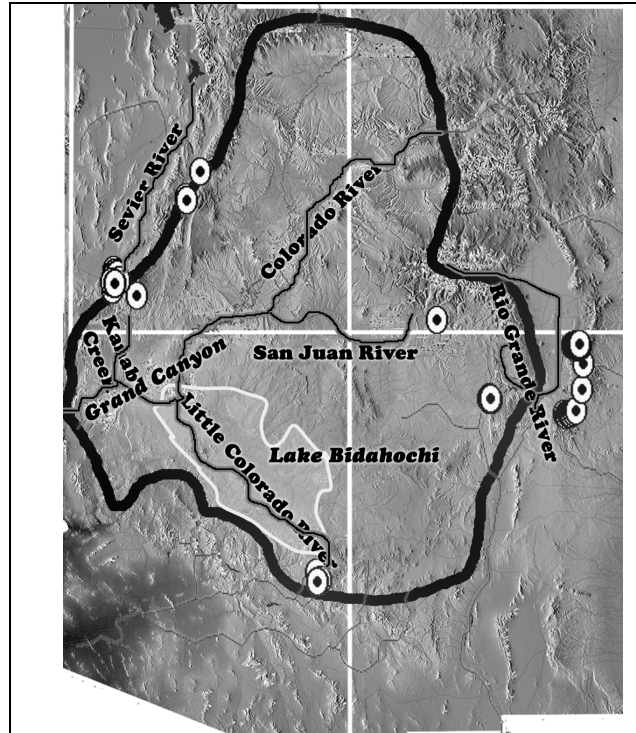


FIGURE 4: Hydrologic connections among features of the Colorado Plateau and Southern Rocky Mountains during the Neogene.

deeper as the area uplifted; simultaneously, the plateaus of southern Utah also rose (Doelling et al. 1989). The orogeny coincided with a change to a drier climate that may have been similar to the present (Scarborough 1989). During the late Pliocene and Pleistocene, the Springerville volcanic field reached its peak activity (Condit and Connor 1996). These relatively flat basalt flows overlaid parts of the Bidahochi formation and may have disrupted stream flow along the Little Colorado River from Mount Baldy. These formations may have restricted the Arizona willow to the areas close to the older and steeper slopes of Mount Baldy.

Arizona willow is well-distributed throughout the glacial tills and exposed Sheep Crossing Formation except on the western slopes of Mount Baldy and

Mount Ord. This asymmetrical distribution suggests that hydrologic connections played an important control on its dispersal. The imposing massif of Mount Ord and the deeply incised canyon of Big Bonito Creek appear to have blocked its spread to westerly-flowing drainages. The concentration of subpopulations along the Little Colorado River strongly suggests that this drainage first brought the plant to the White Mountains of Arizona. Headwater stream transfers and low drainage divides could have permitted extension to the White and Black River watersheds. Behnke (1979) presumed that headwater transfers during the Quaternary glaciations were important mechanisms in distributing fish species in the White Mountains.

In Utah, most populations of Arizona willow occur on tributaries of the Sevier River, which lies in the transition between the Great Basin and Colorado Plateau. Populations on the Fish Lake and Wasatch plateaus flow into tributaries of the Colorado, although these populations are located close to the divide with the Sevier watershed. The population on the East Fork of the Sevier River on the Paunsaugunt Plateau is found less than three kilometers from the drainage divide with Kanab Creek, indicating potential dispersal from the Colorado drainage.

Populations of Arizona willow in New Mexico extend across several major watersheds and occur on all aspects. This distribution supports the idea that the species might have dispersed through the southern Rockies via a shifting network of high-elevation drainages. Straddling the basins of the Colorado and Rio Grande, the San Juan Mountains were hydrologically

connected during the Pliocene to all the areas where Arizona willow occurs in New Mexico, Utah and Arizona (Fig. 4).

The San Francisco Peaks and Mount Taylor are prominent peaks in the Southwest within the range of Arizona willow. The composition of these volcanoes range from basalt to dacite. However, the species has not been reported from those peaks. This absence could be explained by the fact that these volcanoes formed during the Pliocene and Pleistocene, possibly after Arizona willow had dispersed.

The Mogollon Mountains of New Mexico are older volcanoes of intermediate to felsic composition that include Sierra Blanca, which was the southernmost glaciated peak in North America during the Pleistocene. Arizona willow and Mogollon paintbrush have not been reported from those mountains, although it is unlikely that systematic surveys have been made of the region. A predominantly water-based journey from this region to the other Arizona willow populations would require a rather long path through either the relatively low, warm valley of the Rio Grande to the Sangre de Cristo Mountains or across mostly mafic plateaus via the San Francisco River.

Genetic Evidence

The time frame for the dispersal of Arizona willow and its closest relatives across the Southwest is a subject for debate. Arizona willow is similar in appearance and in genetics to Booth's willow (*Salix boothii* Dorn) (Thompson et al. 2003). Mead (1996) claimed that Argus, a taxonomic expert on willows, thought that Arizona willow may have diverged from *S. boothii* during Pleistocene glaciations. However, Argus

has said that there is not sufficient evidence to draw conclusions about the timing or direction of evolution of these species (Argus 1999). Dorn (1976) asserted that nearly all American species originated “before or during glaciation.” Glaciation influenced the regional distribution of some willow species, as Dorn (1975) suggested that *S. boothii* and *S. myrtillifolia* Anderss. may have been separated during the Wisconsin glaciation and then converged in the Northern Rocky Mountains of the United States. Because *S. arizonica* overlaps with *S. boothii* over such a large area, it seems unlikely that it could have evolved as a separate species in such a relatively short time. Based on flavonoid analyses (which are admittedly more primitive than DNA testing), Arizona willow appears chemically “very different” from *S. boothii* and instead appears more similar to the low-growing blueberry willow, *S. myrtillifolia* (Dorn 1975). Both *S. boothii* and *S. myrtillifolia* are identified as synonyms for *S. pseudomyrsinites* (Dorn 1975), the name originally applied to the 1913 collection of Arizona willow from Utah (AWITT 1995). These three species may share a complex evolutionary history, but DNA comparisons of Arizona willow populations (Thompson et al. 2003) did not include any *S. myrtillifolia*.

Those DNA tests did reveal that the populations of Arizona willow in Utah and Arizona were highly divergent (Thompson et al. 2003). Based on this finding, Thompson et al. (2003) hypothesized that the species was panmictic only as late as the Eocene (ca 50 M yr), when vast lakes connected the White Mountains of Arizona to the High Plateaus of Utah. The fact that the

Saliceae family in general has a slow evolutionary rate (Leskinen and Alstrom-Rapaport 1999) lends some support to the hypothesis that the diaspora of Arizona willow may indeed be ancient. Yet, despite being one of the oldest genera of angiosperms, *Salix* itself dates only to the Eocene (55-65 M yr, Fig. 3) (Leskinen and Alstrom-Rapaport 1999). Furthermore, researchers believe that diversification of most species occurred after the Oligocene (post 38 M yr, Fig. 3) (Axelrod 1987; Leskinen and Alstrom-Rapaport 1999). The limited genetic evidence does not seem to support either a very recent dispersal of Arizona willow or a far more ancient one.

Palynological Evidence

Unfortunately, pollen samples provide little insight into the timing of the radiation of Arizona willow. Willow pollen is rarely identified to the species level, and it is not even reported from the handful of pollen records from the White Mountains of Arizona (e.g., P.S. Martin and R. Hevly unpublished data in (Whiteside 1965), (Merrill and Péwé 1977)). *Salix* pollen is also absent in reports from Hay Lake (Jacobs 1985) and from Dead Man Lake in the Chuska Mountains (Wright et al. 1973). This absence may be the result of low pollen production, insufficient identification, absence of willow in the sampled depressions, or the tendency of willow pollen to clump (Faegri and Iversen 1964). Regardless of these problems, the short time frame of most pollen records could not resolve whether the plant was present in the White Mountains of Arizona before the last glacial period.

Mechanisms of Dispersal

Arizona willow and various paintbrush species may have distributed along paths different from those of upland species such as bristlecone pine. Members of the *Saliceae* have the potential to disperse long distances due to their light seeds with long tails that catch the wind (Wells 1983). Moreover, suitable climatic conditions may have been lowered by 1000 meters or more in canyon bottoms on the Colorado Plateau during the last glacial maximum (Betancourt 1990). However, willow seeds are short-lived and usually must land in a sustained moist environment within days to germinate (Densmore and Zasada 1983). Thompson et al. (2003) argued that prevailing winds do not support seed flow between populations in Utah and Arizona. A Pleistocene dispersal across unfavorable habitat between Arizona and Utah appears less likely than a Pliocene voyage along favorable drainages. However, connections across the Arizona-New Mexico Mountains may have permitted dispersal into Arizona from the southern Rocky Mountains. Without a more detailed fossil record or DNA studies, the timing of the arrival of Arizona willow to the White Mountains will remain speculative.

Implications for Environmental Tolerance

Understanding how long Arizona willow has lived in its present regions may help resolve its environmental tolerances. Regardless of whether the species existed in Arizona and Utah before the last glacial maximum or after, it would have withstood the dramatic climatic change of the Altithermal warming period (about 8000-4000 year ago) as well as grazing by the large-bodied mammals that dominated the

Pleistocene landscape. However, the unusually warm and dry climate experienced in the White Mountains in recent years (Lynch 2004) combined with increased ungulate abundance and more continuous grazing may have created novel habitat conditions. Herbivory by ungulates, particularly elk, has been linked to reduce plant vigor of Arizona willow (Maschinski 2001) and has been a contributing factor in the loss of individual plants (Granfelt 2004). Aided by construction of watering tanks, reduction of predator populations, and introductions of both domestic livestock and the Rocky Mountain subspecies of elk (*Cervus elaphus* ssp. *nelsoni*), ungulate behavior has changed in seasonality and extent from the conditions under which subalpine flora have evolved (Axelrod 1987; Burkhardt 1996).

IMPLICATIONS FOR CONSERVATION AND FUTURE RESEARCH

This interpretation of the biogeography of Arizona willow has several implications. Conservation of the species should recognize that the glacial and Tertiary volcanic formations yield substrates that promote the highest densities of these plants and serve as natural refugia. Populations on basalt and other fine-textured formations may experience greater stress associated with warming and drying. Although different species may have dispersed at different times, similarities among the subalpine flora of the White Mountains of Arizona, High Plateaus of Utah, Southern Rocky Mountains of New Mexico, and San Juan Mountains of Southern Colorado point to parallel geologic origins and past linkages during both the Neogene and Pleistocene. Surveys in the San Juan

Mountains are likely to reveal additional populations of Arizona willow.

Future research may help to resolve questions concerning the evolution of these rare plants. Genetic comparisons of willow populations in New Mexico and Colorado with those in Utah and Arizona could help to resolve the sequence by which existing populations separated. For example, if the populations in Arizona are more similar to those in New Mexico, then a Quaternary dispersal to the White Mountains, like that of bristlecone pine, would seem plausible. However, if the Arizona, Utah, and Rocky Mountains populations are equally dissimilar, then an earlier Neogene dispersal would seem more likely.

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