RELICT TREE POPULATIONS IN THE WHITE MOUNTAINS

Deborah L. Elliott-Fisk

Department of Geography, University of California, Davis

Abstract. The White Mountains contain unusual plant assemblages as a consequence of their tectonic, climatic and, hence, floristic history. The classic montane forest belt of the Sierra Nevada and other mountain ranges of Western North America is absent here, replaced largely by Sagebrush Shrubland. Small populations of four coniferous tree species (Juniperus occidentalis, Pinus jeffreyi, P. murrayana, and P. ponderosa) and two deciduous broadleaf tree species (Betula occidentalis and Populus tremuloides) which may be relicts of a former montane forest occur on unique substrates and in favorable microclimatic settings. These isolated populations have persisted due to favorable water relations and reduced competition.

Introduction

The White Mountains are the westernmost and highest (maximum elevation 4369 m) Great Basin mountain range. Although the range is only 90 km in length, the high lithological diversity, relief (> 3000 m), and topographic dissection provide a wide array of habitats for plants. In such a mountain range, microclimatic settings and unique edaphic sites may harbor unusual plant associations.

This habitat diversity is intensified by the position of the range to the lee of the massive Sierra Nevada. Both elevational and topographic moisture gradients are pronounced. Although the White Mountains are in the rainshadow of the Sierra Nevada, the northern end of the range is immediately east of the Mammoth Gap along the Sierran crest. As a consequence, annual precipitation decreases from the northern to the southern end of the range [Oglesby, 1985]. A moisture gradient is also seen west to east across the range, with (1) a higher probability of summer precipitation along the eastern front of the range with the incursion of maritime tropical airmasses, and (2) increased winter snow catchment in eastern cirques providing abundant water in certain settings during the growing season.

The White Mountains have experienced tectonic activity in the Late Cenozoic, with the most recent major uplift of the range beginning about 3 mya [Huber, 1981; Elliott-Fisk et al., in press]. During the last 3 my, climatic and vegetation changes have also occurred in this region somewhat independent of this tectonic activity [Axelrod, 1958, 1977; Smith et al., 1983]. The gradual cooling trend of the Tertiary was replaced by an almost cyclical series of glacial and interglacial climates, increasing both the frequency and magnitude of climatic change. Also, increasing aridity in the Tertiary led to the replacement of the lush,cool temperate mixed forest of predominately Arcto-Tertiary origin by a less diverse and more open forest of mixed Arcto-Tertiary and Madro-Tertiary components [Raven and Axelrod, 1978]. The moderate, mesic climate with mild winters and high summer precipitation in the mid-Tertiary was replaced by a more continental, xeric climate with cool winters, warm summers and low summer precipitation in the late Tertiary [Axelrod, 1977]. This forced many tree species both coastward and to higher elevations. The topographic dissection and lithologic and microclimatic diversity in this mountainous region when coupled with intense climatic change, rapid tectonic uplift, and episodic but catastropic vulcanism are believed to have triggered rapid vegetation and floristic change.

Unfortunately, little work has been done on the Late Cenozoic environmental history of the White Mountains [Elliott-Fisk, in press]. A major research program on this topic is currently underway by the author (see companion paper in this volume). Previous studies have been done on (1) the general physical geography of the range [Powell, unpublished master's thesis, 1963], (2) Late Pleistocene glaciation [LaMarche, 1965], (3) the dendrochronology and ecology of Bristlecone Pine (Pinus longaeva) [Ferguson, 1969; Fritts, 1969; LaMarche, 1969,1973], and (4) alluvial fan genesis [Beaty, 1963, 1970, 1974]. Maps of the surficial geology of the range [Nelson, 1966; McKee and Nelson, 1967; Krauskopf, 1971; Crowder, Robinson, and Harris, 1972; Crowder and Sheridan, 1972; Robinson and Crowder, 1973] show scattered Quaternary and Pliocene deposits of glacial, fluvial, colluvial and volcanic origin. Information on the glacial and interglacial climates and vegetation of the last 3 my is almost entirely lacking for east-central California (including the Sierra Nevada) and the western Great Basin [Elliott-Fisk and Johnson, 1986; Elliott-Fisk et al., in press]. Inferences on the nature of vegetation change may be made based on information from pollen and plant macrofossils from the central and eastern Great Basin [e.g. Axelrod, 1958; Thompson and Mead, 1982], however.

From this regional information, it is reasonable to hypothesize that the White Mountains contained a mixed montane forest in the recent past, perhaps as long ago as 3 my year or as recent as the last glacial (25,000 -12,000 BP). The aridity of the Xerothermic (8000 - 4000 BP) would have no doubt eliminated a late glacial montane forest from the range, if this was not a consequence of previous interglacials. Isolated populations of tree taxa characteristic of the Sierran mixed montane forest may therefore be relicts that have persisted on favorable sites in the face of environmental change, with the majority of the population eliminated elsewhere in the range. As the primary limiting factor for forest establishment in the range at all but the highest elevations is moisture, competition for moisture is the key variable leading to species restrictions [Elliott-Fisk and Peterson, in press]. The hypothesized relict tree populations should occur in special settings where they can outcompete neighboring species for water.

Population and Site Characteristics

Isolated populations of four coniferous tree species (Juniperus occidentalis, Pinus jeffreyi, P. murrayana, and P. ponderosa) and two deciduous broadleaf tree species (Betula occidentalis and Populus tremuloides) characteristic of the Sierran montane forest occur in the range. Although most of these are at elevations between 2800 - 3100 m (Table 1), a zone largely occupied by Sagebrush Shrubland

TABLE 1. Elevational Range of Species

Tree Species	Min. Elev. (m)	Max. Elev. (m)
Betula occidentalis	1675	2600
Pinus jeffreyi	2065	2350
Pinus ponderosa	2085	2300
Juniperus occidentalis	2760	3220
Populus tremuloides	2750	3300
Pinus murrayana	3030	3080
Mean	2394	2808

TABLE 2. Population Characteristics of Stands

Species	Stand	~# of Individuals	Stand Area (ha^{-1})	Max. Tree Age (y^{-1})	Seedlings
Betula occidentalis	S. Fork of Perry Aiken Ck.*	600	17	150	yes
Juniperus occidentalis	Cottonwood Ck. (E)	300	385	500	yes
Pinus jeffreyi	Jeffrey Mine Ck.	500	125	700	yes
Pinus murrayana	Cabin Ck.	2500	285	500	yes
Pinus ponderosa	Lone Tree Ck.	120	35	700	no
Populus tremuloides	Crooked Creek*	1000	50	200	yes
Mean		620	150	458	-

* As stands of this species are found in several locations, representative sites are shown.

above the Pinyon or Pinyon-Juniper Woodland and below the Subalpine Bristlecone Pine-Limber Pine Woodland [Mooney, 1973], species occassionally are found at unusual sites within these two woodland belts. Mean minimum and maximum elevations are largely within the upper Pinyon-Juniper Woodland, a reflection of some of the species extending to lower elevations in riparian habitats [Elliott-Fisk and Peterson, in press].

The size of the populations and area of the stands is variable (Table 2). All conifer stands are properly considered woodlands. It is interesting to note that the conifer populations (all individuals of one species) are largely restricted to one site, with only a few scattered individuals occurring outside this primary stand [Elliott-Fisk and Peterson, in press]. This may be largely a function of edaphic restriction, with the population occurring on the only suitable site for its existence. Small stand areas lend further creedence to this hypothesis. In some instances, what appear to be similar microclimatic sites occur elsewhere in the range and are not inhabited by similar conifer stands.

Dendrochronological studies (D.L. Elliott-Fisk, in preparation) show largely stable populations with continual regeneration and the presence of juveniles. All of the conifers have sensitive ring series and relatively old adults in the population. This is a different age structure than has been proposed for some marginal relict conifer stands [Elliott-Fisk, 1983], but not unexpected with edaphic restriction.

The sites inhabited by the hypothesized relict populations are characterized in Table 3. As the two deciduous species occur in several localities, representative sites are listed. For a full listing of the distribution of these species see Elliott-Fisk and Peterson [in press] and Peterson [1986].

As stated previously, the mountain range consists of a variety of rock types that range in age from Precambrian to Holocene. These relict stands of trees are largely absent on sedimentary formations, which are so favored by the Pinyon-Juniper and Bristlecone Pine-Limber Pine Woodlands [Wright and Mooney, 1965]. Stands are best developed on soils formed from unconsolidated deposits and not on bedrock, a reflection of both surface age or stability and the water-holding capacity of the soil. However, Sierra Juniper (Juniperus occidentalis) is commonly found rooted in joints in quartz monzonite in the Cottonwood Creek drainage basin, much as it is in the Sierra Nevada.

Soils in the White Mountains are generally weakly developed (Tables 3 and 4), due to surface instability, climate change, and arid but fluctuating conditions [Elliott-Fisk, in press]. Soil development is best under what appear to be stable stands on old geomorphic surfaces, as the alfisols at Cabin Creek and Crooked Creek associated with Lodgepole Pine (Pinus murrayana) and Aspen (Populus tremuloides) attest to. Shallow soils on steep, slopes are poorly colonized, but have proven suitable for Ponderosa Pine (Pinus ponderosa) in Lone Tree Creek canyon.

Soil nutrient status is generally good, as most parent materials release adequate amonts of essential elements upon weathering. Soil pH values near or slightly above neutral are typical. The elemental composition of both the soils and the trees (reflecting nutrient uptake) was determined using proton-induced X-ray emission (PIXE) analysis [Cahill, 1975; Elliott-Fisk, 1985]. Aeolian input (both dust and tephra) has increased cation availability at most sites [Marchand, 1970; King, 1985].

The Jeffrey Pine (Pinus jeffreyi) stand at Jeffrey Mine Creek is on a nutrient-poor, acidic entisol derived from highly weathered pyrophyllite. This geomorphic surface is an old slump deposit at the inactive, uplifted apex of the alluvial fan. Although andalusite was mined at this site and the stand was thus disturbed, many old trees are still present. The presence of Ponderosa and Jeffrey pines on chemically altered igneous rocks has been previously noted by Billings [1950] for areas of the western Great Basin north of the White Mountains.

Microclimate appears to play a secondary, but at times important, role in stand existence. The moisture regimes of the stands are variable (Table 3), reflecting both the soil, elevation, site aspect and topographic position. Although these hypothesized relict stands are usually in more mesic positions on north to east-facing slopes, Sierra Juniper along Cottonwood Creek and Jeffrey Pine in Jeffrey Mine Creek canyon have more xeric south and west-facing aspects, respectively. Here, soil parent material plays an especially important role in stand existence.

Discussion

The relict montane forest tree populations are restricted to unusual substrates and favorable microclimatic sites. Adequate soil water-holding capacity, decreased evaporative stress, and decreased competition (due to the chemical imbalance of some soils) allow these populations to persist at these sites. The pines in particular are vigorous competitors requiring high light levels for establishment. Their deep tap root system allows them to utilize a broad section of the edaphic environment for water and nutrients. Both the junipers and pines are capable of anchoring themselves on steep slopes. The more shallowly rooted conifers present in the Sierra Nevada (such as Abies, Calocedrus and Tsuga spp.) have not been found here.

Populations of these six tree species are largely limited to the Sierra Nevada, floristically affiliated with Pacific Coast forests, and rarely occur in the Great Basin. Aspen is by far the most widespread in its distribution, found in several Great Basin ranges, but it is also the most widely distributed tree in North America. Similar species and other varieties of some of the taxa occur in the Rocky Mountains, but these have been isolated from the Sierran populations for tens of thousands of years.

It is thus inferred that the White Mountain populations are affiliated with the montane forest of the Sierra Nevada, and that this forest was once more widespread in central-eastern California before the major uplift of the Sierra Nevada and the warm interglacials of the Late Cenozoic. Our paleoecological work to date shows that a woodland dominated by Utah Juniper (Juniperus osteosperma) was present in Owens Valley at an elevation of 1341 m on the Bishop Tuff Volcanic Tableland as recent as 9830+280 BP [Jennings, 1986]. In situ stumps of Lodgepole Pine (as yet undated) have been

TABLE 3. Site Characteristics

Species	Site	Lithology	Type of Deposit	Soil Type	Aspect	Moisture
Betula occidentalis	S. Fork of Perry Aiken Ck.*	granite/quartz monzonite	alluvium/till	entisol	E	high
Juniperus occidentalis	Cottonwood Ck. (E)	quartz monzonite	bedrock/colluvium	inceptisol	S	moderate
Pinus jeffreyi	Jeffrey Mine Ck.	felsic metavolcanics	slump/alluvial fan apex	entisol	W	low
Pinus murrayana	Cabin Ck.	metavolcanics/granite	older outwash/till	alfisol	N-NE	moderate
Pinus ponderosa	Lone Tree Ck.	felsic metavolcanics	bedrock/colluvium	entisol	N-NW	low
Populus tremuloides	Crooked Creek*	sandstone/quartz monzonite	colluvium	alfisol	N	moderate

* As stands of this species are found in several locations, representative sites are shown.

TABLE 4. Soils at Select Sites

Species	Site	Age of Deposit	Profile	Depth (cm)	pH (A-C)	Soil Chemistry High	Soil Chemistry Low
Juniperus occidentalis	Cottonwood Ck. (E)	recent	O/A/C	45	na	na	na
Pinus jeffreyi	Jeffrey Mine Ck.	1-2 my(?)	O/A/C1/C2/C3	60	4.2/4.5/3.5/<3	Mn,K,Ti,Fe	P, Mg,S,Cl
Pinus murrayana	Cabin Ck.	2.5 my	O/A1/A2/B/C	55	7.2/7/6/6/6	K,Ca, Fe	Mg,P, S,Cl
Pinus ponderosa	Lone Tree Ck.	recent	O/CA	10	7.7	Al,Ca,Ti,Fe,K	Mg,P,Cl,Mn

found above and outside the contemporary stand at Cabin Creek. We hope that our continuing study of fossil materials sheds light on the history of these tree species and their communities.

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D.L. Elliott-Fisk, Department of Geography, University of California, Davis, CA 95616.